

# **Selection, Maternal Effects and Inbreeding in Reindeer Husbandry**

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## Abstract

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In extensive grazing systems where several owners' flocks are allowed to mix, selection strategies will also interact, due to gene flow between flocks. The aim of the thesis was to analyse breeding schemes in terms of genetic gain and rate of inbreeding ( $\Delta F$ ), given the complexity of ownership and interaction of selection strategies within a mixing reindeer population. The data, collected between 1986 and 1997 in the reindeer herding district of Ruvhten Sijte, Sweden, comprised 12,500 records of autumn calf weights.

The mean phenotypic difference in calf weights between selected and non-selected flocks was 0.67 kg after 11 years of selection in Ruvhten Sijte. The genetic difference was 0.35 kg and the realized heritability was 0.2. Based on the realized heritability, it was shown that if all owners had applied selection, the genetic response would have been 2 kg (corresponding to an annual genetic gain of 0.4% of the phenotypic mean, including the initial lag due to age structure).

The relationships between life-time patterns of female weight, calving incidence and offspring weight were examined. A female rearing a calf was shown to weigh 3.1 kg less in winter than one not rearing a calf. The regression coefficient of calf autumn weight on female weight the previous winter was 0.26. Detailed life-history patterns were obtained for females aged 1 – 15 years.

The expected long-term genetic contribution method to predict genetic gain and  $\Delta F$  in selected populations was developed to include maternal effects. It was shown that variation in inherited maternal effects influences  $\Delta F$  more than does variation in non-inherited maternal effects. Furthermore, population structures affect  $\Delta F$  much more when there are maternal effects, than direct genetic effects alone, especially in populations with large family size.

This method was used to evaluate different selection schemes in reindeer husbandry, with different proportions of a population included in each scheme. It was shown that for reindeer population sizes greater than 2,000 there is no risk of inbreeding effects.

*Keywords:* breeding programme, communal grazing, randombred populations, *Rangifer tarandus tarandus*, semidomestic reindeer

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*For Birgit*

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# Appendix

## Publications I – V

The present thesis is based on the following five publications, which will be referred to by their Roman numerals.

### I.

Rönnegård, L. & Danell, Ö. 2001. Gene flow and potential selection response in age-structured subpopulations having a common male pool. *Animal Science* 72: 427-440.

### II.

Rönnegård, L. Forslund, P. & Danell, Ö. 2002. Lifetime patterns in adult female mass, reproduction and offspring mass in semidomesticated reindeer (*Rangifer tarandus tarandus*). *Canadian Journal of Zoology* 80:2047-2055.

### III.

Rönnegård, L. & Danell, Ö. 2003. Genetic response to selection on reindeer calf weights. *Rangifer* (in press).

### IV.

Rönnegård, L. & Woolliams, J.A. 2003. Predicted rates of inbreeding with additive maternal effects. *Genetical Research* (Submitted for publ.).

### V.

Rönnegård, L., Woolliams, J.A. & Danell, Ö. 2003. Breeding schemes in reindeer husbandry (Submitted for publ.).

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## Introduction

Communal grazing is practised worldwide, especially in developing countries (Dixon *et al.*, 2001). Furthermore, animals on common grazing grounds usually mix and uncontrolled mating frequently occurs between animals having different owners (*e.g.* Ayalew *et al.*, 2002b; Kretov *et al.*, 2002; Roderick *et al.*, 2000). Hence, if these owners apply different selection strategies, there will be a collision of strategies due to the gene flow between flocks, and consequently the possibility of developing efficient breeding schemes may be constrained. Such animal production systems, including reindeer husbandry in Nordic countries, are also generally extensive, have a low resource input and have low production, compared with systems based on improved livestock.

A main goal in extensive grazing systems is to utilize the pasture efficiently. This is achieved primarily by having optimal stocking rates (Baars, 2002; Campbell *et al.*, 2000; Illius & O'Connor, 1999). But it is also important to have animals that efficiently convert pasture resources to production values (*e.g.* meat or milk). In this conversion, the maternal ability of females is an important factor. For instance, development of the offspring depends heavily on the mother's ability to efficiently convert pasture into milk and energy. Maternal effects may be especially important in reindeer husbandry, as reindeer live in an extreme environment and the close mother-offspring relationship lasts for a long time.

Animals in a herd need to be adaptable to unforeseen changes in their environment. It is therefore important to develop breeding programmes that maintain the animals' adaptive fitness by controlling the rate of inbreeding (Bijma *et al.*, 2002). When the rate of inbreeding is lower, detrimental changes caused by genetic drift are slower, allowing more time for natural selection or greater opportunity for husbandry measures to counteract such changes. Furthermore, preserved genetic variation will also help a population adapt to changed environmental conditions.

It has been suggested that nucleus breeding schemes (*i.e.* where a part of the population is selected and contributes genetic material to the remainder) may be suitable in low input systems in developing countries, by virtue of their low costs (Bondoc *et al.*, 1989). Nucleus breeding schemes have been modelled thoroughly in earlier investigations to achieve maximized prediction of genetic gain (Hopkins, 1978; Hopkins & James, 1978; James, 1977). However, it was assumed in these investigations that the sires were known and that the gene flow from the nucleus to the remainder of the population could be controlled.

In the case of reindeer husbandry, breeding programmes have been evaluated retrospectively. These investigations have analysed effects of herd structure (sex ratio, age structure and weight distribution of adult females) on meat production without taking into account inherited effects (Lenvik, 1988a; 1990). Also, rough estimates of heritabilities in experimental herds have been made (Varo, 1972), and the affect that calf selection has on weights at older ages has been examined

(Petersson & Danell, 1993b). Furthermore, in a recently published paper, when weights of slaughtered calves were compared between owners, it was found that calf weights were probably associated with different selection strategies (Weladji *et al.*, 2002a).

## **Objectives of the thesis**

The main objective of the thesis is to evaluate different breeding schemes, in terms of genetic gain and rate of inbreeding, in a mixing population where selection strategies interact. The focus is on reindeer husbandry, but the system analysed is general for communal grazing where flocks mix and have different owners.

The main objective can be subdivided as follows:

- (1) to develop methodology for analysing an ongoing selection scheme in reindeer husbandry in terms of genetic response to selection
- (2) to develop methodology to predict rates of inbreeding in populations undergoing selection, when maternal effects influence the trait under selection
- (3) to analyse possible future selection schemes in reindeer husbandry (in terms of genetic gain and rate of inbreeding), when selection strategies interact within a mixing population
- (4) to estimate life-time patterns of female weight, reproduction and calf weight in reindeer, thereby obtaining parameter estimates for the analyses of selection schemes.

## **Background**

### **Characteristics of reindeer husbandry**

#### *Ownership and rights of communal grazing in reindeer husbandry*

The Sami are an indigenous people of northern Europe, of whom around 15,000 live in Sweden (Ruong, 1982). Sami reindeer husbandry access approximately 40% of the land in Sweden, based on immemorial rights. Use of this land for reindeer grazing requires Sami-origin and membership in a herding community (according to the Reindeer Husbandry Act). About 20% of the Sami in Sweden are members of a herding community.

Each of these 51 different herding communities in Sweden uses common grazing. The grazing grounds used by a herding community is called the herding district. The reindeer are privately owned by community members. In Sweden there are on average 18 enterprises within a community (Statistics Sweden, 1998). Management decisions, such as participating in a breeding programme, is made by each individual enterprise.

## Definitions

Throughout this thesis the reindeer population within a herding district is referred to as a *herd*, and the animals owned by each owner are referred to as a *flock*.

### *Development of reindeer husbandry during the 20th century*

In the early 20th century, the basis of the economy consisted of flocks that the herding families tended year-round, and their subsistence economy was primarily tied to a variety of reindeer products. In the early and mid-1900s reindeer husbandry underwent a transition to monoculture meat production based on less intensive herding.

As herding became less intensive, new ways of controlling the herds became necessary (Riseth, 2000), made possible by snowmobiles and other technological developments such as modern fencing and corrals. This in turn increased the need for income and reindeer husbandry became more market oriented, especially in the period 1960–1980. Snow mobiles eliminated the dependency on draft animals, which were castrated male reindeer. The reduced need of adult males allowed meat production to increase by retention of mainly female reindeer. A possible solution to the increased need of income was, therefore, to increase herd productivity by improving herd structure (*i.e.* sex ratio, age structure and mean weight of dams).

Contemporary reindeer husbandry is a market oriented transhumance pastoral system, where different ecological systems are used seasonally. It is a low input system with extensive utilization of resources, and the reindeer are only occasionally given supplementary feed, when forage is inaccessible due to severe winter conditions.

### *Development of contemporary breeding programmes*

The development of increasing the productivity by improving herd structure was initiated by the herders of Riast/Hylling reindeer herding district in southern Norway (Riseth, 2000). A development programme was applied in the 1970s by the herders in collaboration with the consultant from the reindeer administration (Lenvik, 1988b). The condition of the reindeer was determined by weighing them, and individual female reindeer productivity was recorded and analysed. This development required several technical solutions such as individual plastic ear-tags, an effective corral system where the identities of mother and calf could easily be coupled, and a recording system with real-time data access (Pettersson *et al.*, 1990). The system spread to neighbouring herding communities, and meat production per reindeer increased from 10 to 14 kg in the herding districts of southern Norway between 1976 and 1994 (Riseth, 2000).

Ruvhten Sijte (formerly Tännäs Sameby), the neighbouring herding community to Riast/Hylling on the Swedish side of the border, adopted the Riast/Hylling-system in the early 1980s. It is one of the very few communities in Sweden where the Riast/Hylling-system has been applied.

## Material

The data analysed in **II** and **III** (Table 1) were collected and recorded between 1986 and 1997 in Ruvhten Sijte. Parts of the data, collected between 1986 and 1989, were described and analysed earlier by Petersson & Danell (1993a).

The herders in Ruvhten Sijte apply the practice of reindeer herding common in Sweden, where all animals mix within a herding district on common grazing grounds during the summer season (*i.e.* between calving and calf slaughter, see Figure 1). At this time of year the reindeer are mainly in mountainous regions above the tree line. At the annual calf markings in July, the reindeer in the whole herding district are gathered. The ownership of a calf is determined by identifying the owner of the mother rearing the calf, and the calf is ear-marked with the owner's personal calfmarking. The sires are not known, nor are the birth dates of calves as they are born on calving grounds with little or no control by the herders. The rut commences in late September and all animals mate without any intervention from the herders. During the winter season, the owners keep their reindeer separated on their winter grazing grounds.

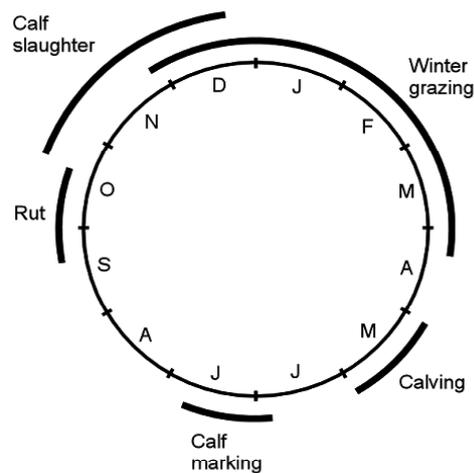


Figure 1. The production year in the herding community of Ruvhten Sijte.

Table 1. Description of data recorded in Ruvhten Sijte between 1986 and 1997

	Calf autumn weight, sex and culling status <sup>a</sup>	Calf autumn weight, sex, and dam age	Female weight	Calf autumn weight, sex, and dam's weight previous winter
No. of obs.	12 484	8056	3449	1571
No. of dams	-	3035	1877 <sup>b</sup>	1117
Years	1986-1997	1986-1997	1987-1991, 1994, 1996	1988-1992, 1995, 1997
Female ages	-	1-15	1-10	2-12

<sup>a</sup> Recorded as culled or retained    <sup>b</sup> No. individual females

Ruvhten Sijte is one of the southernmost herding districts in Sweden (63° N, 12° E; Härjedalen), and the area available for summer grazing is relatively small (926 km<sup>2</sup>) compared with the winter grazing area (2 936 km<sup>2</sup>). Herd size after slaughter has varied between 4,500 and 8,000 reindeer over the period 1986–1997. Winter pasture is good and differences between the areas where different owners kept their reindeer during the winter were small. The animals were given supplementary feed on occasions when there was no access to lichens because of severe weather conditions (*e.g.* ice crust). None of the herders in Ruvhten Sijte gave supplementary feed prior to the calving period.

The data were collected by three owners who apply selection based on calf weight. They owned about half of all reindeer in Ruvhten Sijte. It was they who introduced a recording system in the early 1980s (Petersson & Danell, 1993a; Petersson *et al.*, 1990) which has been used since then. Use of individual ear-tags started in 1980 and calves have been weighed since 1986. The calves were coupled with their dams at the calf markings and were ear-tagged with individual codes. They were also weighed on the same occasion, but these data were not analysed in the present thesis. Late autumn calf weights were recorded (October–December), and adult female weights were also recorded in several winters (November–January) between 1986 to 1997. At the autumn slaughter, the reindeer were gathered in groups of approximately 500 to 1,500 animals, and their owners used the recorded weights to select the heavier calves (*i.e.* not all calves were gathered on one occasion for evaluation). Selection has been based mainly on individual calf weights and to a lesser extent upon earlier production of the dam (*i.e.* calves from dams with many and heavy calves were selected), but no formally defined selection index has been applied. A selection decision was made for each individual calf as they were gathered and weighed.

The other owners in Ruvhten Sijte did not use individual ear-tags, nor did they weigh their reindeer, and therefore did not select on calf weight. Calves from the non-selected flocks were weighed during 4 days in November 1996 and 6 days in November 1997. A total of 1,125 calf weights were recorded, together with sex and date of recording. The ages of the calves' mothers were not known as the owners did not use individual ear-tags on their reindeer. The animals were weighed before slaughter, and no difference in recording was made between culled and retained animals.

## Methods

### Hill's gene flow method and Expected long-term genetic contribution theory

The term 'gene flow' is used to describe the exchange of genes between populations (Wright, 1931) and also the inheritance of genes from parents in different age classes within a population (Hill, 1974). Although these are two different processes, the modelling is similar and the terminology is therefore the same. The purpose of these models is to predict changes in gene frequencies, genetic gain and rate of inbreeding.

Hill's (1974) gene flow method is a deterministic model to predict genetic gain from selection in age-structured populations. The method of 'expected long-term genetic contributions' (Woolliams *et al.*, 1999) is also a deterministic method but the derivations are distinctly based on a stochastic model. The long-term genetic contribution is the gene flow from an individual to a cohort in the distant future. An important property of the method of expected long-term genetic contributions is that both genetic gain and rate of inbreeding can be predicted simultaneously (Woolliams & Bijma, 2000).

Bijma & Woolliams (2000) showed that asymptotic genetic gains predicted with both methods are accurate, even though the long-term gene flow predicted by Hill's method is less accurate in cases of intensive selection. The expected contribution method takes into account inherited selective advantages, where selective advantages are effects that influence the probability of selection of descendants. In Hill's method the predicted gene flow does not take into account further selection in offspring and descendants in later generations, and therefore does not adequately predict the long-term gene flow.

Another important difference between the two methods is that Hill's method does not take into account changes in genetic (co)variances due to selection (Bulmer, 1971), whereas the expected contribution method calculates equilibrium genetic (co)variances and the genetic gain is predicted after that equilibrium has been attained. Thus, Hill's method assumes that every cohort before and after selection has the same distribution of breeding values as the base population, except that the mean of the distribution has changed.

### Concepts of gene flow and selection response used in the thesis

Response to selection and the effects of gene flow between the selected and the non-selected parts of a randomly bred population were studied in **I**, **III** and **V**.

Two cases are explored. The first of these is the situation when the selected and non-selected parts mix and there is no isolation of gene flow between the two parts

(i.e. the case of an open nucleus in Figure 2). This is the present situation in Ruvhten Sijte. The response to selection in the selected flocks is reduced by the gene flow from the non-selected flocks. Furthermore, the non-selected flocks gain from selection thanks to the gene flow from the selected flocks. With a constant and continuous selection intensity the two parts of the herd will evolve asymptotically at the same rate ( $\Delta G$ ) with a constant difference in response between them ( $\Delta R$ ).

In the second case (closed nucleus in Figure 2) it was explored what would happen if there was no gene flow from the non-selected to the selected flocks. The response that would be achieved in the selected part of the herd, after  $t$  years of selection, is defined as the potential response,  $R_p$  (Rönnegård & Danell, 2001).

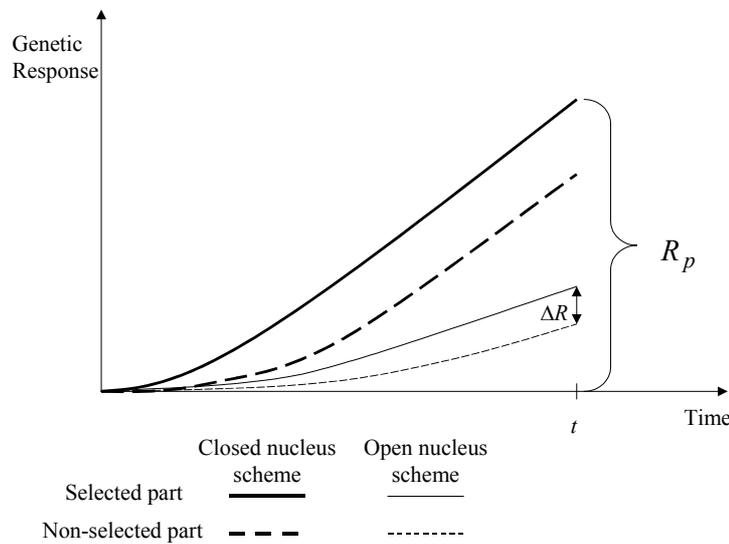


Figure 2. Development of selection response for a one-way (closed nucleus scheme) and two-way gene flow (open nucleus scheme) between a selected and a non-selected subpopulation. The response in the closed selected subpopulation represents the potential response ( $R_p$ ). The upper of the two lines, in the case of an open selection scheme, is the predicted development in Sel and the lower line corresponds to Cont.  $\Delta R$  is the difference in genetic response between the selected and non-selected parts in year  $t$ . The predicted curves of the selected and non-selected parts are asymptotically parallel, but the asymptotic slope is shallower in the open scheme than in the closed scheme.

### Rate of inbreeding and effective population size

In a given year  $t$  the level of inbreeding ( $F_t$ ) is defined as the probability that two alleles in a locus are identical by descent from an ancestor in a base generation  $t$  years ago. The annual rate of inbreeding, defined as  $\Delta F = (F_t - F_{t-1}) / (1 - F_{t-1})$ , can be easily calculated from pedigree information. In the planning stage of a breeding programme, predictions of  $\Delta F$  are necessary in order to evaluate the benefits of different possible selection schemes. Furthermore, selection is expected to affect

$\Delta F$ , because families superior with respect to the selected trait will contribute more offspring to the next generation than inferior families (Robertson, 1961).

$\Delta F$  is assumed to apply to alleles in loci that are unlinked to the genes controlling the trait (*i.e.* neutral loci). However, if the infinitesimal genetic model is assumed (*i.e.* the selected trait is assumed to be controlled by many unlinked loci, each with small additive effect), then the rate of inbreeding at selected loci is expected to be the same as at a neutral locus.

The effective population size ( $N_e$ ) is inversely proportional to  $\Delta F$ ,  $N_e = 1/(2 \Delta F)$ . This concept, developed by Wright (1931), gives a good intuitive understanding of the risks of selection (see V).

### Maternal effects

A mother's ability to take care of and nourish her calf affects the calf's weight. This is a maternal effect, defined as: the mother's ability to contribute to the development of the offspring's phenotype, other than by her genotype for the offspring trait, associated with one or several dam traits or the environment that she experiences (*e.g.* Mousseau & Fox, 1998). Furthermore, a maternal effect is a maternal genetic effect if the ability of the mother is a trait with genetic inheritance (Figure 3).

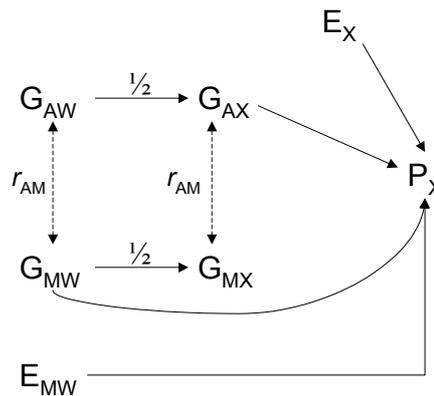


Figure 3. Path coefficient diagram showing Willham's model of maternal effects on an offspring's phenotype  $P_X$  (After Willham, 1972). The phenotypic value is composed of the offspring's direct breeding value ( $G_{AX}$ ), the non-maternal environment of the offspring ( $E_X$ ), the mother's breeding value of maternal effects ( $G_{MW}$ ) and the environmental component of the maternal effect ( $E_{MW}$ ). Subscripts X and W indicate offspring and mother, respectively.  $r_{AM}$  is the correlation between direct and maternal breeding values.

There are several different models of maternal effects (reviewed by Kirkpatrick & Lande, 1989). One of the main differentiating factors among these models is whether the trait measured in the offspring is regarded as the same as that describing the mother's ability to contribute to the offspring's development (Falconer, 1965), or not (Willham, 1963; 1972). Intermediate models have also been developed where the environmental component of the mother's ability is

correlated with the non-maternal environmental component of the phenotype measured in the offspring (Mueller & James, 1985; Riska *et al.*, 1985). In this thesis, Willham's (1963) model was investigated, because it is simple and the one most widely used to estimate genetic (co)variances. An important feature of Willham's model is that the traits related to the mother's ability need not be specifically identified and the mother's ability is treated as an unspecified combination of traits.

In an attempt to study an individual trait in its complete setting, maternal effects were incorporated in all five investigations of this thesis. In **II**, maternal effects on reindeer calf weight related to the mother's age, weight and previous reproduction were investigated in a broad perspective without specifically investigating the inheritance of the maternal effects. Further, the studies reviewed by Kirkpatrick & Lande (1989) focused upon the selection response in populations. For instance, in Willham's model the predicted response is proportional to the selection differential applied with a proportional constant  $h_W^2$ . In the thesis,  $h_W^2$  is referred to as the Willham heritability, and is expressed as a function of the direct heritability ( $h_A^2$ ), the maternal heritability ( $h_M^2$ ) and direct-maternal genetic correlation ( $r_{AM}$ ):  $h_W^2 = h_A^2 + 1.5r_{AM}h_Ah_M + 0.5h_M^2$

In earlier investigations the influence of maternal effects on  $\Delta F$  had not been examined, which is a novelty of the thesis (**IV**).

## Outline of Investigations

The thesis can be divided into two main parts; in the first, the selection programme applied in Ruvhten Sijte was investigated. The method developed in **I**, together with the parameters estimated in **II**, was used in **III** to investigate retrospectively the short-term effects of selection. In the second part of the thesis, the long-term effects of different possible future selection programmes on genetic gain and rate of inbreeding were investigated. These analyses were performed in **V**, using the method of expected contributions with maternal effects, developed in **IV**. The estimates of female reproduction and calf weights obtained in **II** were also used in **V**.

### Investigation I

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

A method was developed to estimate the potential response ( $R_p$ ) from the observed difference ( $\Delta R$ ) in calf weights between a selected and non-selected part of a herd where animals are randomly bred. Based on Hill's (1974) gene flow method, it was shown that the difference between the two parts of the herd is independent of the proportion of the whole herd that is included in the selection programme, and that  $R_p$  could be estimated from  $\Delta R$  without prior knowledge of the direct heritability. The objective of the paper was to test the method for the sensitivity of

input parameters ( $h_M^2$ , age structure of sires) and model assumptions (equal dam age structure in both parts of the herd, disregarding effects of selective advantages of sires). The method was found to be sensitive to maternal genetic effects and that some prior knowledge of  $h_M^2$  and  $r_{AM}$  is required in order to apply the method. Furthermore, adult males in the selected part of the herd will be more likely to have offspring selected, than sires from the non-selected part, because the selected ones have a selective advantage. This effect is not taken into account in Hill's (1974) gene flow method, but it was found that the selective advantage of sires does not have a great influence on the estimate of  $R_p$ .

An important and appealing feature of the model is that the difficulty of accounting for annual non-genetic variations in calf weight is taken care of by comparing calf weights in the selected and non-selected flocks simultaneously, where all flocks have been exposed to similar environmental conditions.

The method was applied on empirical data in **III**.

## **Investigation II**

### *Lifetime patterns in adult female mass, reproduction and offspring mass in semidomesticated reindeer (Rangifer tarandus tarandus)*

The data recorded by the herders in Ruvhten Sijte were used to examine relationships between life-time patterns of female weight, calving incidence and offspring weight, thereby testing the hypothetical relationships in Figure 4. Earlier studies have investigated the relationships separately (see references in **II**). The objective of this paper was to obtain a comprehensive picture of the phenotypic relationships between mother and calf. Genetic components of the maternal effects were not estimated and the results were mainly aimed at being applied in population dynamic models (required in **III**).

The average calving percentage for adult females was 73%. A female rearing a calf was shown to weigh 3.1 kg (S.E. 0.3) less in winter than a female not rearing a calf (Figure 5a). There was little difference in calving incidence between females rearing a calf in the previous year and those that did not, but old females tended to have a decreased calving incidence if they had reared a calf in the previous year (Figure 5b). Calf weights were affected by both the mother's weight and by her age. The regression coefficient of calf's autumn weight on female weight the previous winter was 0.26 (S.E. 0.02). Mothers aged 2 to 4 years had calves that weighed less than calves of older mothers. The average difference in autumn weight between male and female calves was 2.9 kg (S.E. 0.2), but the difference was less for calves with mothers aged 2 to 4 years.

These results corresponded well to earlier investigations in reindeer and caribou (Eloranta & Nieminen, 1986; Gerhart *et al.*, 1997; Lenvik, 1988a; Weladji *et al.*, 2002b), but the estimates in **II** had lower standard errors and were modelled in greater detail over the lifespan of a female reindeer (see Figures 2 to 5 in **II**).

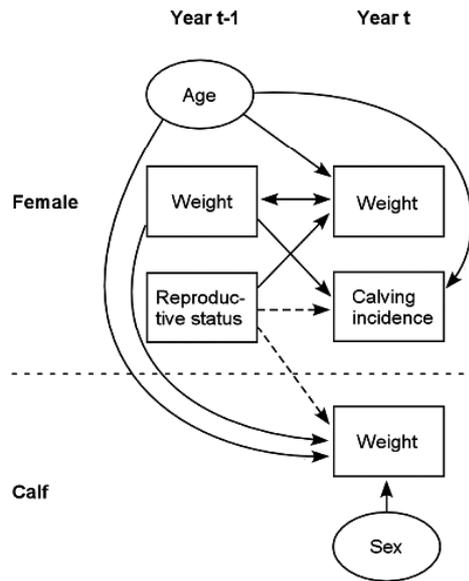


Figure 4. Hypothetical relationships between a female's age, winter weight and calving incidence in two consecutive years  $t-1$  and  $t$ , together with the relationships to offspring weight in autumn. A production year starts in May at calving. Arrows go from independent to dependent variables. Previously uninvestigated relationships are shown as dashed arrows and a repeated expression of a trait (weight) is connected by a double-headed arrow.

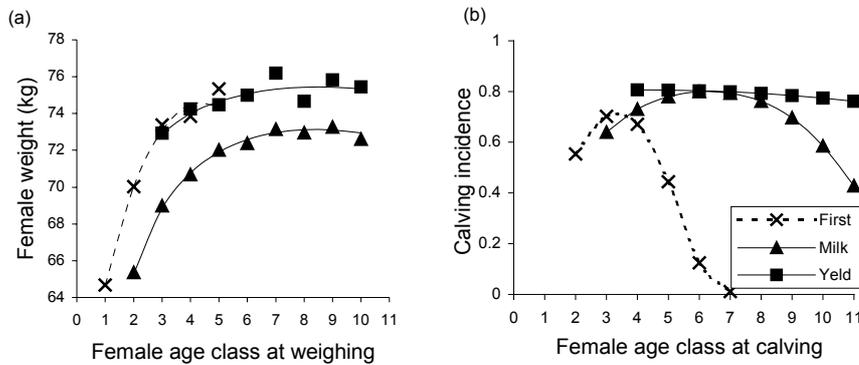


Figure 5. Female weight (Figure 5a) and calving incidence (Figure 5b) in relation to female age and reproductive status. "First" are females that have not previously reproduced. "Milk" are those that reared a calf the previous year. "Yeld" are those that have reproduced but did not rear a calf the previous year. Note that females in age class 1 are  $1\frac{1}{2}$  years old at weighing. Furthermore, a mother in age class  $t$  at calving is in age class  $t-1$  when weighed the previous winter.

### **Investigation III**

#### *Genetic response to selection on reindeer calf weights*

The method in **I** was applied by comparing autumn live weights of calves between flocks. The main novelty of the paper is that different selection strategies in reindeer husbandry were compared in a common environment. 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, 1988a; 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, 1993b). These earlier investigations did not include comparisons of alternative breeding strategies.

For simplicity of notation the selected flocks were called Sel (for selected) and the non-selected flocks, Cont (for control). After 11 years of repeated selection, the difference in mean calf weight between Sel and Cont, in 1996 and 1997, was 0.67 kg. Using the results from **II**, it was shown that the non-genetic effect due to different dam age structures in Sel and Cont was 0.32 kg. Therefore, accounting for this effect, the estimated difference in genetic level ( $\Delta R$ ) was 0.35 kg, which was the value used to predict  $R_p = 2.0$  kg. Hence, the expected genetic gain from 1986 to 1997 would have been 2 kg in the selected flocks, if the selected part of the herd had been isolated from gene flow.

### **Investigation IV**

#### *Predicted rates of inbreeding with additive maternal effects*

The influence of maternal effects on genetic gain has been extensively investigated (see Kirkpatrick & Lande, 1989) but earlier methods have not predicted rate of inbreeding ( $\Delta F$ ) in selected populations with maternal effects. The aim of the paper was to extend the theory of expected long-term genetic contributions to include Willham's model of maternal effects (Figure 3) and, thereby, investigate the influence of maternal effects on predicted  $\Delta F$  for populations under mass selection. Furthermore, the accuracy of these predictions was tested by comparison with stochastic simulations.

The model and the simulations showed that a variation in inherited maternal effects (measured as  $h_M^2$ ) influences  $\Delta F$  more than does a variation in non-inherited maternal effects ( $c^2$ ).  $h_M^2$  had substantial impact on  $\Delta F$  (Figure 6), and the impact was even greater when the annual genetic gain,  $\Delta G$ , was held constant. Furthermore, population structures (offspring per dam, dams per sire, and age structure) affect  $\Delta F$  much more when there are maternal effects, rather than just direct genetic effects, and especially in populations with a large number of offspring per dam.

The predictions of  $\Delta F$  were good with prediction errors (mostly less than 8%) generally less than those of  $\Delta G$ , which were equal to those from conventional predictions.

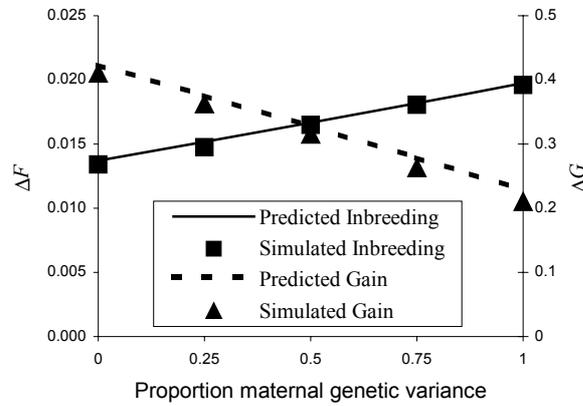


Figure 6. Rates of inbreeding ( $\Delta F$ ) and annual genetic gain ( $\Delta G$ ) for fixed sum of direct and maternal genetic variance equal to 0.4 (i.e.  $h_A^2 + h_M^2 = 0.4$ ,  $r_{AM} = 0$ ). The proportion maternal genetic variance equals  $h_M^2/(h_A^2 + h_M^2)$ . The simulated population with discrete generations consisted of 25 males and 25 females, and 8 offspring per female.

## Investigation V

### *Breeding schemes in reindeer husbandry*

The objective of this investigation was to explore possible future developments of selection schemes that do not require all owners within a herding district to take part in the selection programme. One such approach is to develop a closed nucleus (Figure 2). The design of a closed nucleus, in a reindeer husbandry context, 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. Isolation of gene flow is likely to increase  $\Delta F$ , however.

The method developed in **IV** was used and further developed to apply specifically to reindeer husbandry with calf selection and mixing subpopulations. The method was used to investigate  $\Delta G$ , and the influence of selection on  $N_e$  in open and closed breeding schemes.

A herding district with population size of 5,000 reindeer was simulated with a mating ratio of 14 adult females per male. In conservation biology  $N_e > 500$  has been advocated as a general rule that gives the minimum population size to maintain a viable population with sustainable genetic variation (Franklin, 1980; Lande, 1988; Mace & Lande, 1991), and this limit was used to examine where the risk of selection becomes too great. The minimum limit was not reached for the

open and closed breeding schemes investigated, and will not be reached in populations exceeding 2,000 animals (Figure 7). In the case of a closed nucleus and for proportions of the population included in the selection programme of less than 0.33, male calves were partly recruited from the non-selected part of the herd to maximize  $\Delta G$ .

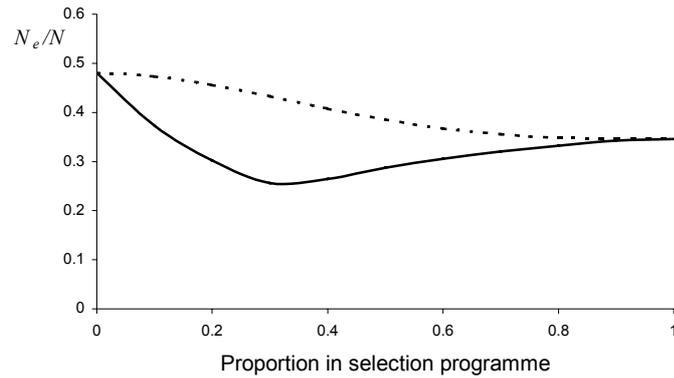


Figure 7. Effective population size ( $N_e$ ) related to the proportion of the population included in the selection programme (---- open nucleus, — closed nucleus), given as proportion of the total population size ( $N$ ).

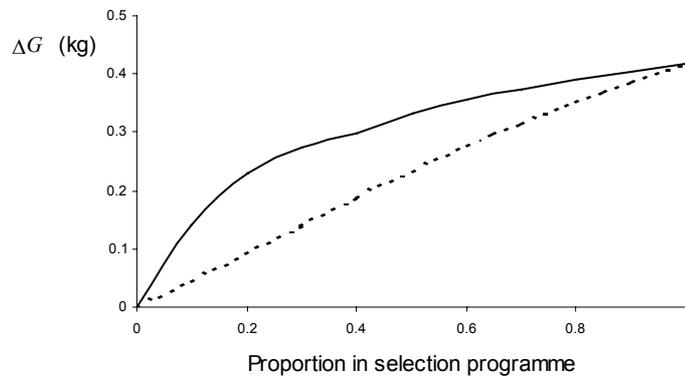


Figure 8. Annual genetic gain ( $\Delta G$ ) related to the proportion of the population included in the selection programme (---- open nucleus, — closed nucleus).

$\Delta G$  increased from 0 to 0.4 kg as the proportion of the population included in the selection programme increased, for both the open and closed selection schemes (Figure 8). As expected,  $\Delta G$  was the same in both the selected part and the non-selected part of the herd, and the difference in genetic level between the selected

and the non-selected parts in a given year (*i.e.*  $\Delta R$ ) was within the range of 0.31–0.36 units of phenotypic standard deviations (approx. 1 kg). This corresponds closely to the prediction of  $\Delta R = h_w^2 i_f$  in **I** (equation 4), equal to 0.34 units of phenotypic standard deviations for the simulated population structure ( $h_w^2 = 0.42$ , 50% of the female calves selected in the selected flocks, *i.e.* selection intensity  $i_f = 0.8$ ).

When the proportion of the herd included in the selection programme was 0.33, the difference in  $\Delta G$  between a closed and an open nucleus scheme was 0.13 kg and  $N_e$  reached a minimum of 1,300.

## General Discussion

### The rôle of breeding programmes in reindeer husbandry

In this thesis I have proposed that a co-operative selection scheme can be used as an efficient tool with which to develop profitable reindeer husbandry by increasing the meat production. However, the essential question: why should meat production be increased (*i.e.* the breeding objective), has not been examined.

Reindeer husbandry is a marginal producer of meat in Sweden, yielding between 1,000 and 3,000 tons annually (Statistics Sweden, 1998), which is less than 1% of Sweden's total meat production. However, it is an important producer of non-marketable values for the Sami culture and society, for Sami within as well as outside reindeer husbandry because there is a common interest of Sami to participate in reindeer husbandry. Furthermore, the reindeer is symbolically important in Sami tradition and culture.

The non-marketable values are distinguishable in the well developed Sami organizations, education, language and handicraft, but reindeer owners receive no direct economic compensation for this 'production'. There is therefore a need to develop a profitable reindeer husbandry by increasing meat production and at the same time maintaining the production of non-marketable values.

Viable reindeer husbandry is also essential for the Sami to maintain their rights of land use, according to current legislative practice in Sweden. If a landowner questions in court the right of a herding community to use the land for grazing, the community has been requested to present evidence of continuous land use over the previous 90 years (Hahn, 2000). These immemorial rights include not only use for reindeer grazing, but also hunting and fishing rights, the right to extract materials for building the cabins and corrals used in reindeer herding and also for use in handicrafts.

The regional economy in the northern parts of Sweden depends to a fairly large extent indirectly on the reindeer husbandry. For example, in the municipality of Jokkmokk (approx. 7,000 residents), reindeer husbandry is estimated to support

indirectly about twice as many as are directly employed, *i.e.* approximately 15% of the total occupancy in Jokkmokk (Danell, 2000). Reindeer husbandry is also important for Swedish society as a whole, by fulfilling the objective of biodiversity and in fulfilling parliamentary obligations to maintain and develop the Sami cultural heritage in the Swedish mountain regions (prop. 1997/98:145).

Breeding programmes in reindeer husbandry, and in other extensive farming systems in developing countries, should consider these non-marketable production values as well as the primary production (Ayalew *et al.*, 2002a). In order to define a broad and appropriate breeding objective, however, these secondary production values need to be clearly defined and valued. Reindeer husbandry should be developed according to these values, and the values outlined above imply that the production based on natural grazing should be sustained.

### **Developed methodology**

Methods were developed in the thesis to analyse breeding schemes in populations with mixing flocks and interacting selection strategies. The genetic response to selection was examined in the early stages of the selection programme in Ruvhten Sijte, using Hill's gene flow method (**III**), whereas the expected contribution method was used to predict  $\Delta G$  and  $\Delta F$  in future selection schemes (**V**). In both cases the methodology was developed within a general framework including a wide range of important effects, such as age structure and maternal effects. Thus, other selection schemes in communal grazing systems with mixing flocks can be evaluated using a similar approach. However, as the methods assume mass selection based on a single trait, they will have to be extended for selection programmes where the selection decisions are based on more detailed information from relatives and involving several traits. As mentioned in **IV**, however, the extension to a combined index and multiple-trait selection is straightforward.

The advantages of choosing Hill's gene flow method rather than an expected contribution method in **III** were twofold. First, Hill's method is much simpler and a method based on expected contributions would have required more input parameters, such as direct heritability and proportion of the total number of adult males included in the selection programme. Second, the method was designed to estimate the potential response after a few generations in the initial stages of a selection programme under fairly weak selection, which is the case in reindeer husbandry compared to *e.g.* production systems where artificial insemination is used.

### **Co-operative selection schemes in a mixing herd**

The results of the thesis have shown the extent to which both selected and non-selected flocks gain from selection in the selected flocks (**I**, **III** & **V**). However, with an open selection scheme, the genetic gain is reduced by the non-selected flocks. The best solution among those investigated, in terms of maximized  $\Delta G$  and

reasonable  $\Delta F$ , is to include all owners in the selection programme (V). This may be difficult to accomplish, especially in situations where there are many owners with few animals. A possible solution would then be to include as many owners as possible in the selection scheme and to let all other owners retain females only. At least in reindeer husbandry, however, there are practical aspects that have to be solved for such a system to be applied.

Reindeer flocks need to be manageable, especially during the autumn and spring migration between winter and summer pastures. According to some reindeer herders a flock is more difficult to manage without adult males (*e.g.* Holand *et al.*, 2001). If this is a major problem then it is not desirable to cull all males in a flock. On the other hand, if an owner decides not to take part in a selection programme but agrees to cull all male reindeer in the flock, the production in this flock will be improved in two ways. First, the production will increase because the proportion of females in the flock can be increased and also because more male calves, which are heavier than female calves, will be available for slaughter. Second, the production will also be improved in the long term because the non-selected flocks will gain from the selection applied in the selected flocks.

### **Specific aspects of developing reindeer breeding programmes**

From the perspective of the reindeer herders, a breeding programme should aim to increase the meat yield without substantially increasing the herd's grazing pressure. Danell (1998) defined three steps towards optimum herd productivity. The first is to have a herd size that is economically optimized for the available grazing resources. A second step is to maximize the proportion of highly productive females in the herd (Lenvik, 1988b), *i.e.* females aged 6 to 10 years, which have a high calving incidence and high calf weights (II). Thirdly, the productivity of the herd can be increased in the long term by increasing the genetic capacity of individual reindeer by selection. In this thesis the main focus has been on this final step.

In Ruvhten Sijte, selection has been based primarily on calf weight (III). A possible improvement, acknowledged by the reindeer owners, is to select calves from dams that repeatedly produce heavy calves year after year. This should give a better measure of the long-term genetic capacity of productivity, but there are difficulties in comparing calves based on this information. A dam's production depends on the factors shown in Figure 4 that may be difficult to evaluate separately (II). Furthermore, its future production is not known at the time of selection of a calf, and the calves from older dams will have more information than calves from younger dams. Consequently, there will be a trade-off between selecting calves from older dams with high accuracy and selecting calves from younger dams to decrease the generation interval (Hopkins & James, 1977). Under such circumstances, objective selection decisions will be impossible without using a predefined index that combines these different factors into a single value. In addition to selection accuracy and generation interval it also needs to take into account the calf's future survival and reproduction. However, this might be

simplified if the development at young ages is a good predictor of life-time productivity, as is the case in *e.g.* red deer (Albon *et al.*, 1987; Kruuk *et al.*, 1999; Loison & Langvatn, 1998; Post *et al.*, 1997; Rose *et al.*, 1998). Nevertheless, it will require an appropriately designed recording system. A computerized recording system is currently in use in Ruvhten Sijte where correction factors for fixed effects of dam age are incorporated, and is being developed so as to combine multiple sources of information into a single selection index. The results in **II** will be incorporated into the recording system, giving correction factors both for the dam's age and previous reproduction.

A computerized recording system is not only necessary, to be able to analyse the complex information that the selection is to be based on, but is also needed so that possible undesirable side effects due to selection, or environmental changes, can be quickly identified and eliminated.

## **Future Research**

### **Reindeer husbandry**

During the course of this thesis work, three main tasks have appeared important to be solved by future research if the benefits from breeding programmes are to be appropriately utilized in reindeer husbandry.

First of all the non-marketable values have to be clearly defined and valued to be able to define a breeding goal that develops animals to suit the rôle they have in the reindeer husbandry – Sami society system. Furthermore, if these values are not clearly define, the economic and social motivation of reindeer husbandry will deteriorate (Danell, 2000).

The second task is to develop methods of making optimal use of existing resources. In fluctuating and highly variable systems such as reindeer husbandry this has to be done by applying adaptive management approaches (*e.g.* Walters, 1986). In adaptive management the herd size is controlled by retrospectively analysing trends in resources and the condition of the animals, where a trend showing a decline leads to an appropriate decrease in herd size. Such systems based on monitoring resources and the physical condition of animals have been proposed and are undergoing scientific development (Dahle *et al.*, 1999; Danell, 2002). Only when adaptation to available resources is appropriate can breeding become an efficient tool for the development of reindeer husbandry.

The third task for future research is to gain a better understanding of natural selection in reindeer husbandry. How will artificial selection affect the overall productivity (or fitness) of the population? Further, in extensive grazing systems the purpose of selection is to retain animals with a good genetic ability to make efficient and sustainable use of the pasture. It is therefore essential to find an accurate measure of this genetic capacity. In such an endeavour of future research

it will be necessary to take into account the likely interaction between artificial and natural selection, which was not included in the analyses in this thesis.

Knowledge of how reindeer production can be improved by selection is also closely linked to an understanding of natural selection and life-history evolution. A reindeer owner wishes to retain female calves that will produce many and heavy calves throughout its lifetime. However, a constraint in resources leads to a trade-off between current and future reproduction. This trade-off together with natural selection favours a certain life-history strategy (Roff, 1992). In reindeer these optimal life-histories need to be understood if a comprehensive insight into female productivity is to be obtained. The results in **II**, showing how previous reproduction influences female weight and how female weight influences future reproduction, is a step towards a better understanding of life-history strategies in female reindeer.

## Maternal effects

Maternal effects in both natural and domestic populations need further development by modelling and empirical investigation. The main task is to find ways to distinguish maternal effects that are inherited environmentally (or socially) from those that are inherited genetically. In animal breeding, Willham's model (see Figure 3) is generally assumed, which ignores the non-genetic inheritance of maternal effects (see Discussion in **IV** for further details). Other models of maternal effects have been thoroughly developed (Kirkpatrick & Lande, 1989), but only a few investigations have attempted to establish which model best explains the influence of maternal effects (but see *e.g.* Koerhuis & Thompson, 1997; Schluter & Gustafsson, 1993). Thus, different models of maternal effects should generally be examined in greater detail in empirical investigations of breeding programmes, which will require specific knowledge of the biological mechanisms of maternal effects. Furthermore, an improved understanding of maternal effects will indirectly improve our understanding of natural selection and microevolution, since maternal effects have been suggested to be an important factor of masking microevolution in natural populations (Merilä *et al.*, 2001).

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# Svensk sammanfattning

## Urval, maternella effekter och inavel i renskötseln

Hur kan man förbättra renhjordens produktion genom urval? För en renskötare är målet med urvalsarbete att spara kalvar som kan tänkas leda till en produktiv renhjord i kommande generationer. Ur detta perspektiv har jag studerat hur urvalsarbetet förbättrar de enskilda renarnas genetiska kapacitet. Dessutom har jag undersökt hur man kan samarbeta inom en sameby för att dra största möjliga nytta av urvalsarbetet.

Avhandlingen är främst inriktad på urvalsprogram inom renskötseln, men frågeställningen är av allmän art för extensiva produktionssystem där djur som tillhör olika ägare blandas och parar sig. Sådana produktionssystem är vanliga särskilt i utvecklingsländer.

Materialet i mina undersökningar insamlades av ägare i Ruvhten Sijte (tidigare Tännäs Sameby) åren 1986 – 1997. De som har bedrivit urval baserat på registrerade kalvvikter ägde ca 50% av renarna i samebyn. Materialet bestod av 12500 kalvvikter registrerade vid höstskiljningarna, och dessa kalvar hade drygt 8000 registrerade mödrar med känd ålder. Övriga renägare i Ruvhten Sijte har inte bedrivit urval med hjälp av registrerade vikter men kan tänkas ha baserat sitt val av livdjur på andra kriterier.

Om inte alla renägare inom en sameby bedriver urval kommer det genetiska framsteget att påverkas för dem som bedriver urval. Det beror på att man inte kan styra vilka sarvar som betäcker olika renägars vajor. Den som bedriver urval får en del av sina vajor betäckta med sarvar som inte valts ut på registrerade vikter, medan de som inte bedriver urval påverkas av andras urval genom att utvalda sarvar betäcker deras vajor.

En viktig frågeställning i avhandlingen har därför varit: Hur påverkas det genetiska framsteget när inte alla bedriver avel? Jag har studerat den frågan genom att simulera hur gener blandar sig hos renarna inom en sameby och hur detta påverkar det genetiska framsteget och inavelsgraden.

Åren 1996 och 1997 vägdes också kalvar tillhörande renägare som inte bedriver urval i Ruvhten Sijte. En jämförelse visade att skillnaden i medelkalvvikt mellan de som bedriver urval och de som inte bedriver urval var 0,67 kg. Utifrån denna skillnad beräknades att det genetiska framsteget i kalvvikt skulle ha varit 2 kg om alla hade bedrivit urval 1986 - 1997. Detta motsvarar en genomsnittlig ökning av kalvvikten med 0,4% per år. Denna förväntade årliga ökning är dock mindre de första åren då urvalet bedrivs, eftersom det tar tid innan de utvalda kalvarna i sin tur får kalv.

Jag undersökte vidare hur kroppsvikt, reproduktion och kalvvikt förändrades under vajans livstid, samt också vilka samband som fanns mellan dessa variabler.

En viktig anledning till att denna studie genomfördes var att få underlag till beräkningarna av det genetiska framsteget, men den ger även en ökad förståelse för hur vajornas åldersstruktur och medelvikt påverkar en renhjords produktivitet. De flesta av dessa beroenden mellan egenskaper har studerats tidigare av andra men med mindre datamaterial och oftast har endast ett enskilt samband åt gången undersökts. En vaja med kalv vägde i genomsnitt 3,1 kg mindre än en vaja utan kalv. Regressionskoefficienten mellan kalvens vikt och vajans vikt var 0,26, dvs en ökning av en vajas höstvikt med 1 kg beräknas öka vikten på dess kalv med 0,26 kg året därpå. Skillnaden i vikt mellan han- och honkalvar var i genomsnitt 2,86 kg, men skillnaden var något mindre för kalvar med unga mödrar (2 till 4 år). Kalvprocenten vid märkning för vajor i åldrarna 4 till 10 år var 73%. Beräkningarna visade tydliga mönster över hur vajans vikt, kalvprocent och kalvvikter utvecklas med vajans ålder. Vajorna i åldrarna 4 till 10 år är tyngst, och får flest och tyngst kalvar.

Nästa steg i avhandlingen var att undersöka: Hur bör ett urvalsprogram inom en sameby utformas på bästa sätt, utan att alla renägare behöver delta i urvalsprogrammet? Hur stor är fördelen om alla bestämmer sig för att delta i urvalsprogrammet?

När man utvecklar urvalsprogram vill man få så stort genetiskt framsteg som möjligt, men samtidigt är det viktigt att beakta riskerna för inavelseffekter. Vidare påverkar en moders förmåga att ta hand om kalven (dvs den maternella effekten) sannolikheten för att kalven sparas vid urval. I tidigare metoder för att förutsäga riskerna för inavelseffekter i urvalsprogram hos husdjur har maternella effekter inte beaktats. I avhandlingen utvecklades en ny metod för att simulera förändringen av inavelsgraden då maternella effekter påverkar urvalet.

Denna metod användes för att analysera olika möjliga urvalsprogram inom renskötseln. Det genetiska framsteget av urval ökade linjärt med den andel av samebyns renhjord som ingick i urvalsprogrammet. Maximalt kan kalvvikterna öka med ca 0,4 kg per år om alla bedriver urval. Hur gör man då om inte alla har möjlighet att bedriva urval?

En möjlighet är att de som inte bedriver urval inte heller sparar några sarvar. Den som bedriver urval får då inte sina vajor betäckta med sarvar som inte valts ut. Därmed bromsas inte urvalsvinsten. Samtidigt får de som inte bedriver urval sina vajor betäckta endast av utvalda sarvar och får därmed full tillgång till urvalsvinsten på handjurssidan. Däremot måste de som bedriver urval spara fler hankalvar för att inte problem med betäckningarna ska uppstå. Urvalet blir därmed inte lika stort. Denna lösning är inte lika effektiv som då alla renägare bedriver urval, men betydligt bättre än om de som inte bedriver urval också skulle rekrytera sarvar. Risken för inavelseffekter trots begränsat sarvantal är inte något problem för samebyar med fler än 2 000 djur i vinterhjorden.

I avhandlingen diskuteras även möjligheterna att öka det långsiktiga genetiska framsteget i renhjorden genom att spara kalvar från vajor som genomgående får tunga kalvar. Detta skulle eventuellt kunna resultera i att renhjorden i större

utsträckning kommer att bestå av djur som effektivare omvandlar betesresurserna till kött. En annan viktig fråga som diskuteras är hur det naturliga urvalet kan tänkas påverka det långsiktiga genetiska framsteget. Har extremt tunga kalvar lägre överlevnad? Blir urvalet mindre påverkbart av det naturliga urvalet om man sparar kalvar främst från vajor som genomgående får tunga kalvar? Dessutom diskuteras ”produktion”, utöver köttproduktionen, som bör beaktas då avelsprogram utvecklas inom renskötseln. Icke-marknadsvärderad produktion från renskötseln är troligen av större samhällligt intresse än själva köttproduktionen. I dessa ”produkter” ingår t.ex. välutvecklade samiska organisationer, utbildning och slöjd som inte skulle existera utan renskötseln. Vidare är renskötseln viktig för det svenska samhället för att upprätta de nationella miljömål som riksdagen har beslutat om. Renägarna kompenseras inte ekonomiskt för denna icke-marknadsvärderade produktion. Det är därför viktigt att utveckla en ekonomiskt bärkraftig renskötsel. I detta sammanhang kan urvalsprogram ha en viktig roll.

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