Population density and inbreeding effect on moose Alces alces reproduction

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ORIGINAL ARTICLES

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Wallin, K., Bergström, R. & Vikberg, M. 1995: Population density and inbreeding effect on moose *Alces alces* reproduction. - Wild. Biol. 1: 225-231.

The relationship between reproduction, age-structure, inbreeding and population density was analysed in an enclosed moose *Alces alces* population in Sweden. There was a strong negative relationship between the yearly average number of calves produced per cow and population density. Other variables, such as the average age of the cows and inbreeding also covaried with density. Taking these variables into account, a relationship remained between density and reproductive rate. An inbreeding index of three-year-old cows was negatively related to their calf production. Inbred, old (≥ 4 years) cows had a significantly lower calf production than old, outbred cows. Taking density into account, the effect of inbreeding remained. Even though inbreeding had a measurable effect at the individual level, the impact at population level was small and insignificant. During the early growth phase of the founder population, inbreeding remained low and had no negative effect on early population dynamics. The reason for this is that the first inbred individuals did not appear until the third generation. Therefore, a founder population can grow for a fairly long time and reach high population numbers before the effect of inbreeding appears. This means that the negative effects of inbreeding may increase in importance beyond our 12 years of study.

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Reproduction is one of the main components determining population dynamics (e.g. Caswell 1989). In order to understand how population numbers vary over time and geographical areas, we need to know how different factors affect reproduction. Such knowledge is also essential when forecasting fluctuations in population size, and thus also for our ability to manage a population in accordance with specific objectives.

In many mammal species, reproductive rate decreases when population density increases (e.g. Fowler 1987). On the other hand, when population density becomes low other factors such as inbreeding and Allee effects may de-

plete reproduction (e.g. Lande 1988, Ralls & Ballou 1986, Charlesworth & Charlesworth 1987). In recent years, the management of small populations has received special attention (e.g. Frankel & Soulé 1981, Soulé et al. 1986, Caughly 1994) and the importance of both demographic and genetic factors for the development of such populations has been discussed (e.g. Lande 1988, Wallin 1992).

We present results based on a twelve-year study of an enclosed moose *Alces alces* population in central Sweden. Our aim was to study how reproduction is affected by inbreeding and population densities. For this purpose, a small founder population was allowed to grow freely for several years, reaching a density beyond that normally observed in the moose. After this phase of "free" population growth, the population was reduced.

Material and methods
Study area

The present study was carried out in the Sunnäs Moose Pen, east-central Sweden (61°06'N, 17°05'E), covering 6.2 km². The forest has been managed according to ordinary Swedish standards with clear-cutting and planting, mainly of Scots pine *Pinus sylvestris* but also of Norway spruce *Picea abies*.

When the population was founded in 1978, about 30% of the area was covered with eight-year-old forest plantations. Another 30% was covered with 16 to 40-year-old trees and roughly 20% was covered with trees older than 40 years; this altogether made the tree age composition within the pen considerably younger than in the surrounding area. The remaining area, almost 18%, was covered by mires, some of which were drained and fertilised. Towards the end of the study period, some stands had been cleaned. Otherwise, no forestry took place in the pen during the study period.

Intermixed with the coniferous tree species were two birch species *Betula puberscens* and *B. pendula*, aspen *Populus tremula* and mountain ash *Sorbus aucuparia*. Together with pine, the birches dominate the shrub layer and the field layer was mostly dominated by dwarf-shrubs, mainly bilberry *Vaccinium myrtillus*, cowberry *V. vitis-idaea* and heather *Calluna vulgaris*.

The ground is mainly covered by snow for five months, from mid-November to mid-April. Mean snow depth in February, based on records covering 30 years, was 0.3 m and mean temperatures were -4°C in January (the coldest month) and 16°C in July (the warmest month).

Population
Population management
During late summer 1978, five moose (four cows and one bull), were enclosed in the pen. At that time, the cows

were 4, 4, 4 and 7 years old, respectively. The cows were confined when the fence was erected while the bull was immobilised outside the pen and moved into the pen. For five years, this founder population was allowed to grow freely. The maximum number of moose individuals within the pen reached 37 in 1984. In autumn 1983 the first animals were shot and thereafter the population was controlled by selective hunting in accordance with defined objectives.

Marking of animals
Each animal was immobilised by darting from helicopter and marked with ear-tags and collars. The markings took place each winter in order to mark the calves and to re-mark the moose who had lost their tags. For immobilisation, a mixture of anaglesium and tranquillizer was used (Ethorphine and Xylazine, or Fentanyl and Azaperone; Sandegren et al. 1987).

Estimation of population density and composition
Density, sex ratio and age distribution were determined from ground observations during the entire year and from aerial surveys during winter. On two occasions, i.e. in 1983 and 1986 (both during the rut), a mature bull from outside the pen broke through the 2.5-m wire fence and might have mated with cows inside the pen. Both intruding bulls managed to stay inside the pen for two rutting periods, and they were both killed in fights. The fence was checked regularly in order to discover possible breakthroughs.

Measurement of reproduction
After each calving period in May-June, special efforts were taken to find each cow and record the number of calves. As no radio-transmitters were used, the number of calves sometimes could not be determined until late summer. In spite of the intense field work in the enclosure, only two calves and three of the founder cows were found dead during the twelve years of study. These facts indicate a low natural mortality.

Average age of the cow population
As moose reproduction is known to be age dependent (e.g. Markgren 1969, Blood 1974, Sæther & Haagenrud 1983), we wanted to take into account the change in the mean age of the females over the years. As most moose were born during the study, the exact age of most individuals was known. In the case of the founder animals the age was determined by counting *cementum annuli* (Sergeant & Pimlott 1959).

Inbreeding
We assumed that the individuals of the founder population were unrelated, but their true relatedness was not

known. The cows were caught inside the fence after the age of natal dispersal, and three out of four were of the same age which might indicate low relatedness among the founder individuals. As the experiment started with four cows and one bull the effective population size was 3.2 (Crow & Kimura 1970). As stated previously, two bulls living outside the pen managed to break in during the rut. Even though these bulls did not manage to stay for long, they may have mated with some cows. Consequently, they have to be taken into account when making the inbreeding analyses among animals born after their intrusion. Bulls born inside the pen were included in the analyses as potential reproducers at the age of roughly 2.5 years.

From each individual's pedigree, we estimated an inbreeding index which is similar to the ordinary inbreeding coefficient (e.g. Falconer 1981). We used this index, because the exact inbreeding coefficient could not always be determined for each individual, as the true father was not always known. Consequently, for some individuals, there are more than one possible path of relatedness. In these cases, we estimated the expected inbreeding index from all possible paths of relatedness, which is the best achievable estimate, assuming random mating (see example in Fig. 1). This measurement is labelled inbreeding index, instead of the traditional inbreeding coefficient. Even if this inbreeding index is not the same as the traditional coefficient, it will lead to the same estimate under the random mating assumption. It is also important to keep in mind that an estimate of an ordinary inbreeding coefficient is a probability measurement of gene sharing too, and consequently not an absolute measurement of the true inbreeding. The inbreeding index applied here is a probability measurement as well but weaker than the ordinary one as it also includes the possibility of alternative mating patterns. Consequently, the application of this index will have less power to detect inbreeding effects. Thus, the use of the inbreeding index should have a conservative effect on any analysis. The assumption of random mating is of course critical for the inbreeding index. Unfortunately, we do not know whether this assumption is correct. We do know, however, that related individuals mate with each other as we have some exact pedigrees on this.

Results
Population development

From the start in 1978, the population was allowed to grow freely until 1983, whereafter it was limited by hunting (Fig. 2). In 1988, population size was reduced in order to break the positive correlation between population size and year. This was done in order to increase the reliability of the estimated relationship between reproduction and population density. Still, a significant correlation exists between population density and year ($r_s = 0.67$, N = 12, P = 0.017).

The average age of the cow population changed parallel to the change in population size (Fig. 3). At first, average age tended to decline, but after the introduction of population control, average age increased. As a result there is a weak correlation between the increase in average age of the cow population and year ($r_s = 0.54$, N = 13, P = 0.056). It is more important, however, that the correlation between the average age of the cow population and population density was efficiently broken ($r_s = -0.065$, N = 12, P = 0.84).

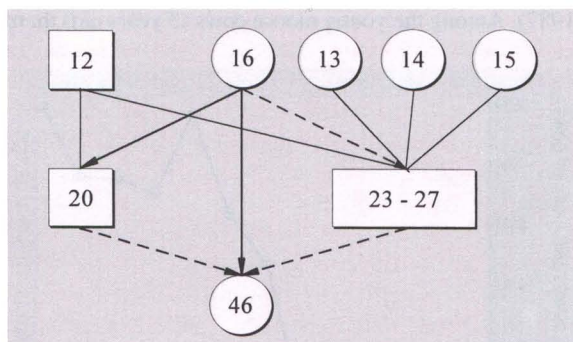The average calf production shows a negative, but in-

Figure 1. Example of a path diagram showing the pedigree used to analyse the inbreeding index for individual moose. Circles represent cows and squares represent bulls. Broken lines connect possible parents and offspring. Unbroken lines connect true parents and offspring. Bold lines with arrows indicate possible paths resulting in inbreeding. This path example is used to estimate the inbreeding index of cow *46*. There are six circular paths that give rise to inbreeding [*46*-20-16-*46* and *46*-16-(23,24,25,26 or 27)-*46*], all of which have an inbreeding index of $\frac{1}{2}^2 = \frac{1}{4}$. There are 15 open paths resulting in a zero inbreeding index [16-*46*-(23-27)-(13-15)]. Thus, although there are 21 possible paths which result in an estimated inbreeding index of F = $6/21 \times \frac{1}{4} + 15/21 \times 0 \approx 0.0714$.
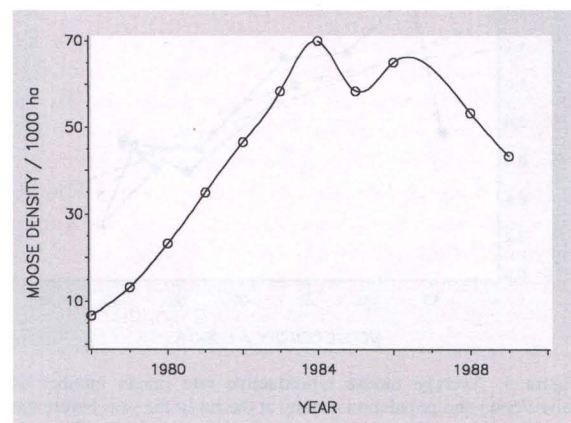

Figure 2. Temporal development of the moose population studied. Density is measured as number of animals per 1,000 hectares during the rut (4 October).
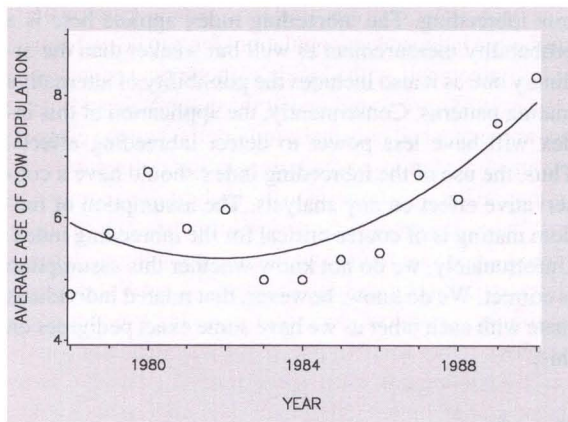
Figure 3. Development in the average age of mature cows over the years of study, measured as the deviation from an assumed average age of four years for the founder population in 1979.

significant trend over the years (r_s = -0.47, N = 12, P = 0.12)

Reproduction and population density

At different times before and during pregnancy, population density may have different effects on a cow's ability to produce calves. We therefore estimated the relationship between density and calf production at four different times: summer density in the year before the calves were born (1 June), during the rut (4 October), during the winter (just after the hunt, on average 22 November), and during the summer when the calves were born. There are significant (P < 0.05), negative effects of population density on the number of calves produced per cow prior to the summer when the calves were born, but not for the sum-

mer when calves were born. The correlation between density and reproduction tends to decrease depending on how long after the rut the analyses were made.

The relationship between rut density and calf production seems to be linear or negatively accelerating in the interval studied (linear model: calf production = 1.35 - 0.0133 (rut density), R^2 = 0.49, F = 11.7, N = 12, P = 0.0065; non-linear model: calf production = 1.26 (1 - $e^{(-0.0387(72.6-\text{rut density}))}$); Fig. 4). It is not possible to discriminate between these relationships.

Reproduction and population demography

Of course, other factors than density could have caused the observed decrease in reproduction. Moose cows are known to improve reproduction at older ages (e.g. Sæther & Haagenrud 1983). If the average age in the population drops, so will reproduction. This would also be the case if the average age grew very high. There is a positive, but insignificant tendency between calf production and the average age of the cow population (r_s = 0.41, N = 12, P = 0.19). Having age as a background variable, the relationship between rut density and calf production remains significant (r_s = -0.66, N = 12, P = 0.026).

Inbreeding and reproduction

In a population originating from a small founder population, inbreeding will increase over time. Accordingly, the population's average inbreeding index increased with time (r_s = 0.92, N = 12, P < 0.0001; Fig. 5). Inbreeding may reduce the reproductive capacity among females (e.g. Ralls & Ballou 1986, Charlesworth & Charlesworth 1987). Among the young moose cows (3 years old) there
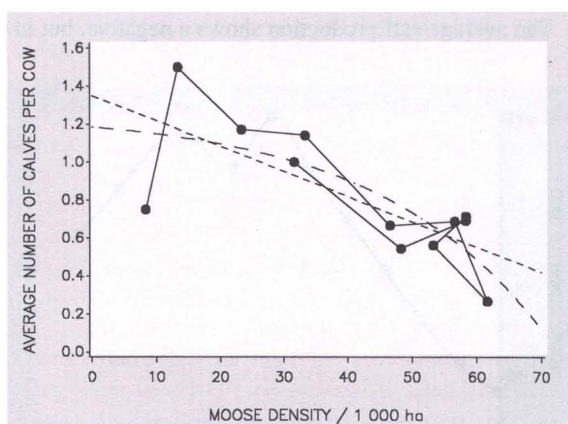

Figure 4. Average moose reproductive rate (mean number of calves/cow) and population density at the rut in the year before the calves were born. The trajectories (broken lines) represent the models described in Results. The dots represent yearly averages and the lines in-between the dots indicate the time schedule starting at the lowest density.
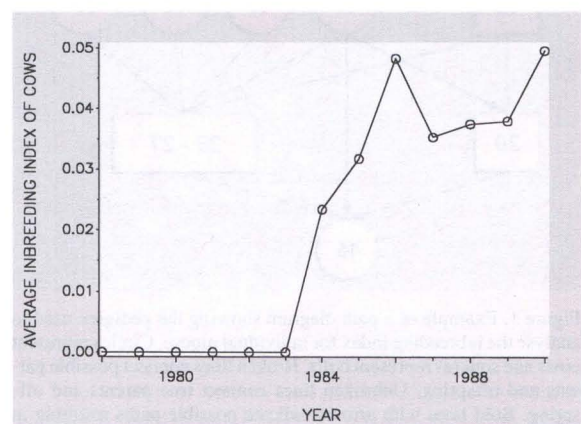

Figure 5. Temporal development of the average inbreeding index of the cow population since it was founded in 1978. Note that inbreeding does not appear until six years after the population was founded and that it seems to continue to increase after end of the study period.

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is a significant negative correlation between number of calves produced and the estimated inbreeding index of the cows (r_s = -0.81, N = 16, P = 0.0001). This result remains significant when population density at rut is taken into account ($r_{s(partial)}$ = -0.53, N = 16, P = 0.042). Among older females (≥ 4 years), the sample size is too small for analyses on separate age categories, and consequently we made a combined analysis. In order to control for the effect of variation in population density between years the analysis was done as follows: the number of calves of each female was measured as the deviation from the yearly average calf production. From this standardised measure of reproduction, we estimated the average calf production of each individual over their lifetime or until the end of this study. This was done over the years 1986-1990, as the first inbred females of the age of four years appeared in 1986. Females were then divided into two groups, inbred (inbreeding index > 0) and outbred (inbreeding index = 0). This gives a sample of five inbred cows and 10 outbred cows (out of these 15 cows, 12 had an "exact" estimated inbreeding coefficient). On average, inbred females produced significantly fewer calves than outbred individuals (inbred: = -0.423, s^2 = 0.0868, N = 5; outbred: = +0.214, s^2 = 0.128, N = 10; t = 3.67, df = 13, P < 0.005). The variances of the two samples did not differ significantly (F = 1.47; df = 4,9). In each of the five years studied, inbred cows produced fewer calves, on average, than outbred cows (one-tailed sign-test, P = 0.031).

At population level we observed a negative, but insignificant, tendency between the yearly average inbreeding index in the population and calf production (r_s = -0.46, N = 12, P = 0.13). Thus, even if inbreeding seems to have a significant negative effect on the reproductive capacity of individual cows, both among younger and older females, the effect at population level seems to be small.

Discussion

There are many pitfalls when analysing inbreeding effects on phenotypic characters (e.g. Lynch 1988). In addition to fundamental theoretical difficulties, there might even be difficulties in achieving basic information on inbreeding as for instance is the case in large mammals. In our analyses on the effects of inbreeding we have tried to overcome these difficulties by carrying out analyses along several different routes (e.g. at population and individual level). In most experiments with inbreeding, character estimates change monotonically over time and the variance decreases (Lynch 1988). In this study, calf production did not change monotonically as did the index of inbreeding, nor did the variance in calf production differ significantly between inbred and control individuals. Still, our study is just one case where inbreeding seems to have a negative effect on reproduction. Before we can

conclude, however, that this is a general pattern more studies on independent populations have to be performed.

In agreement with Lande's theoretical conclusion (1987, 1988), we found that at the end of the study period inbreeding had only had a minor effect on the progress of our studied moose population, in spite of reduced calf production among cows with the highest inbreeding indices. Instead, we noticed a larger influence of density on reproduction due to the fact that the population, during a short period, reached high densities. A similar development may, of course, occur in free-living founder populations: a rather small impact of the genetic factors on the early development, even if the reproductive rate is reduced among inbred individuals. It is important to notice that inbreeding did not increase in the population until six years after it was founded (Fig. 5). This is an effect that is or may be typical for long-lived species, where the reproductive debut occurs somewhat late in life, as is the case for the moose (e.g. Markgren 1969, Blood 1974, Sæther & Haagenrud 1983). Thus, for several years the founder individuals, which were not inbred, provided the population with new individuals and thereby efficiently increased population size. There are two important consequences of this: 1) the effect of inbreeding is postponed until later in the population's development. For our study population, an observed effect of inbreeding might occur at a later stage, after the end of this study. This will occur when the founder individuals and their offspring, which are not inbred, have disappeared. Until now they have produced the vast majority of the animals born into the study population. 2) Inbreeding depression occurs when genes with rare, deleterious alleles appear in homozygote form (Charlesworth & Charlesworth 1987). However, if a population can grow large before inbreeding occurs, the number of individuals expressing deleterious traits due to inbreeding might only be a fraction of all individuals. If the remaining fraction, i.e. individuals that are inbred but show no sign of inbreeding depression, can carry the population through the phase of early development, the population might "get rid of" the deleterious allele combinations via natural selection (Lande 1988, but see Frankel & Soulé 1981 for another view). If this occurs, we expect the negative relationship between degree of inbreeding and calf production to vanish. As a consequence, the effect of inbreeding might only be temporary. Therefore, in species having a long life span, such as the moose, the acute effect of inbreeding might not be as troublesome as previously believed. However, a larger negative effect due to inbreeding might occur at some time later on when the average inbreeding in the population has reached a higher level. This might be the reason why populations founded by a few individuals suddenly crash, after having reached high densities.

In the discussion above we have focused on a factor

usually supposed to be important for the dynamics of populations at low numbers. At the other end of the density scale, there are factors which are important when numbers grow large. The highest summer or rut densities in this study exceed the corresponding densities observed among free-living moose populations. In Sweden, the highest moose densities during summer or rut are about half of that observed at maximum during our experiment. However, winter moose densities among free-living moose may reach even higher levels than the maximum densities reported in this study. The result might therefore seem somewhat artificial, but, when predicting the kind of dynamics possessed by a population as well as the carrying capacity of the population, knowledge of the shape of the relationship between reproduction and population density is crucial. To be able to make good predictions, we must not attempt to guess this shape outside the "normal" range through extrapolations. A more efficient approach, but often a very difficult one, is to experimentally manipulate the density to obtain these results.

In our study it seems clear that density had a strong effect on the reproductive rate of individual moose cows. Unfortunately, we were unable to show whether this relationship had a negative linear shape or a negatively accelerating shape. The effect on the population dynamics will be large depending on which of these shapes are prevalent (e.g. May 1986, Grenfell et al. 1992). In the Finnish moose, Nygren (1983) indicated that reproduction is increasingly reduced at higher densities. Surprisingly, however, reproduction was also increasingly reduced at densities below four moose/1000 ha. If this is caused by an Allee effect, it will be important in the moose, as most populations have densities below this level. Thus, in many moose populations the reproductive rate should increase as population density increases.

Although we have no detailed information about the mechanisms by which population density affects reproduction, our results indicate that population density prior to and during the rut is the time when reproduction is mostly affected by population density.

It seems reasonable to believe that the decreased reproduction at higher densities is due to increased competition for available food. Interestingly, it seems as if the moose does not make long-lasting depletion of its food resources. After the peak density had been reached and population density had decreased, calf production returned along the same route as it came (see Fig. 4). If the moose depleted its food resource more permanently, the recovery of reproduction should follow a lower trajectory when population density decreases than that observed in Figure 4. This suggests that moose reproduction is mainly affected by the food resources renewed each summer (e.g. Sæther & Heim 1993).

There are, of course, factors other than density that may

influence the relationship observed in our experiment. As discussed above, inbreeding has been shown to have only a small impact on the moose population studied. Another factor that may be potentially important is that of the age structure. As moose usually show an increased reproductive rate at older ages, the negative effect of population density on reproduction could in fact be due to a reduced average age of the population. This is typical of increasing populations (e.g. Hoogentyk & Estarbrook 1984). However, there was no correlation between population density and the average age of the cow population. From other studies, adults are known to be less sensitive to density than subadults (Fowler 1987). Thus, in a population with a stable age structure the effect of density on reproduction might be even more dramatic than that observed in our study.

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