

Effective size of harvested ungulate populations

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Abstract

The harvest of ungulate populations is often directed against certain sex or age classes to maximize the yield in terms of biomass, number of shot animals or number of trophies. Here we examine how such directional harvest affects the effective size of the population. We parameterize an age-specific model assumed to describe the dynamics of Fennoscandian moose. Based on expressions for the demographic variance σ_{dg}^2 for a small subpopulation of heterozygotes Aa bearing a rare neutral allele a , we use this model to calculate how different harvest strategies influence the effective size of the population, given that the population remains stable after harvest. We show that the annual genetic drift, determined by σ_{dg}^2 , increases with decreasing harvest rate of calves and increasing sex bias in the harvest towards bulls 1 year or older. The effective population size per generation decreased with reduced harvest of calves and increased harvest of bulls 1 year or older. The magnitude of these effects depends on the age-specific pattern of variation in reproductive success, which influences the demographic variance. This shows that the choice of harvest strategy strongly affects the genetic dynamics of harvested ungulate populations.

Introduction

It has long been recognized that directing harvesting towards certain age or sex categories can increase the yield in terms of biomass or number of harvested animals (MacArthur, 1960; Beddington & Taylor, 1973; Slobodkin, 1973; Law, 1977). In general, the number which can be removed from an age class should be inversely related to their expected number of future offspring or the reproductive value of Fisher (1930). Theoretical analyses of deterministic age-structured models often show that the greatest yield is obtained by harvest of only two age classes with small reproductive value (Beddington & Taylor, 1973; Beddington, 1974; Law, 1977). Similarly, simple theoretical analyses also showed that male-biased harvest will increase the yield dramatically (Caughley, 1977), provided that a sufficient number of males remain in the population to fertilize all sexually mature females.

Many populations of ungulates across the world are subject to harvest either for consumptive use (e.g. meat or trophies) or for reducing the damage to agriculture or forestry (Hudson, Drew & Baskin, 1989). Such harvest often involves large changes in the social structure and the age and sex composition of the populations (Ginsberg & Milner-Gulland, 1994; Milner-Gulland *et al.*, 2003), often with large demographic consequences (Coulson *et al.*, 2004) that will influence the genetic dynamics (Allendorf *et al.*, 2008) as

well as evolutionary responses to changes in the environment (Kuparinen & Merilä, 2007; Proaktor, Coulson & Milner-Gulland, 2007; Fenberg & Roy, 2008). Fennoscandian moose represents one of the most extreme examples of such harvest-induced structural changes of populations because the harvest has been directed towards young animals and bulls over large areas for several decades (Solberg *et al.*, 2002, 2006; Lavsund, Nygren & Solberg, 2003). Because annual variation in offtake is closely related to changes in quotas (Solberg *et al.*, 1999), this has resulted in strongly skewed sex and age distributions of moose populations in many parts of Fennoscandia (Solberg *et al.*, 2002, 2005, 2006).

Although the strong directional harvest has contributed to the large increase in yield over the past decades (Lavsund *et al.*, 2003; Solberg *et al.*, 2005), the changes in social structure and age composition affect the genetic dynamics in the populations (Ryman *et al.*, 1981). The concept of effective population size is crucial for understanding changes in gene frequencies in finite populations because it determines the rate of random genetic drift and interacts with natural selection to influence the probability of fixation of deleterious and advantageous mutations. Wright (1931) defined the effective size of a diploid population n_e as that which produces the same rate of random genetic drift as an ideal population of constant size, n , reproducing by random sampling of gametes with non-overlapping generations and

an approximately Poisson distribution of family size. In real populations, the ratio $p = n_e/n$ is often considerably smaller than 1 (Caballero & Hill, 1992; Grant & Grant, 1992; Nunney, 1993; Nunney & Elam, 1994; Frankham, 1995; Creel, 1998; Engen *et al.*, 2007) because of uneven sex ratios, large individual variation in reproductive success and temporal fluctuations in population size.

Overlapping generations and age structure considerably complicate the calculation of effective population sizes (Nunney, 1991). Formulas for effective population with overlapping generations have been derived by several authors [e.g. Felsenstein (1971), Hill (1972, 1979) and Pollak (2000)]; however, they all assume constant age structure and often constant population size, which do not make them applicable to study long-lived harvested species in which harvest-induced fluctuations in age composition can be large (Sæther, 1987; Solberg *et al.*, 1999).

Here we use the derivation of Engen, Lande & Sæther (2005a) for the effective size of an age-structured population with two sexes in a fluctuating environment. We apply this modelling framework on a stage-structured population model that includes stochastic variation in demographic traits for the dynamics of a moose population well below the carrying capacity (see Sæther, Engen & Solberg, 2001). Our aim is to examine how changes in the structural composition, assuming a stable population after harvest, will affect the rate of random genetic drift and the effective size. This will provide a generalization of previous approaches (Ryman *et al.*, 1981; Allendorf *et al.*, 2008) because we can examine the effects of changes in the structural composition of the population while keeping a constant population size. This allows us to examine how changes in age structure caused by choice of harvest strategy will interact with other parameters affecting the effective size.

Effective size of age-structured populations

Engen *et al.* (2005a) derived an expression for the demographic variance σ_{dg}^2 of a small subpopulation of heterozygotes Aa bearing a rare allele a under the assumption of neutrality and no density regulation. This derivation was based on the concept of demographic variance of an age-structured population as defined by Engen *et al.* (2005b). In the two sex model the population vector $\mathbf{N} = (F_0, F_1, \dots, F_k; M_0, M_1, \dots, M_k)^T$ is a column vector, where F_i and M_i are the number of females and males in the i th age class. The dynamics are given by the matrix multiplication $\mathbf{A}\mathbf{N}$ defining the population vector the next year. The non-zero elements of \mathbf{A} are fecundities defining females and males produced by females and males, as well as the probabilities of survival for males and females. The effective population size is then

$$n_e = n/(\sigma_{\text{dg}}^2 T) \quad (1)$$

where n is the population size and T is the generation time, that is, the mean age of mothers and fathers of newborns.

The population growth rate λ is the real dominant eigenvalue of the expected projection matrix $\mathbf{a} = E\mathbf{A}$. The right and left eigenvectors defined by $\mathbf{au} = \lambda\mathbf{u}$ and $\mathbf{va} = \lambda\mathbf{v}$ are the stable sex-age distribution and the vector of reproductive values of the sex-age classes, respectively, provided that they are scaled by $\sum u_i = 1$ and $\sum v_i u_i = 1$. The non-zero elements of \mathbf{A} are the mean fecundities and survivals for the different sex-age classes over all individuals in the age class in a given year, which are stochastic variables for a finite population size. For a description of how to calculate σ_{dg}^2 and T from the mean and variances of the individual vital rates we refer to Engen *et al.* (2005a).

Population model

In the absence of large predators, moose populations may have mean multiplicative growth rates λ up to 1.3 (Sæther *et al.*, 2007). Here we consider constant harvest strategy subject to the constraint that the value of λ resulting from harvesting equals 1, corresponding to an approximately stable population size. By this approach harvesting leads to a dynamics with no density regulation so that the theory of Engen *et al.* (2005a) applies.

The focus for our analyses is a Norwegian moose population living well below the carrying capacity under favourable environmental conditions, assuming no density regulation. Although we have no particular population in mind, most parameters are chosen as typical for the population at the island of Vega in northern Norway, for which a large number of population parameters has been estimated using individually radio-collared animals (Stubsjøen *et al.*, 2000; Sæther, Solberg & Heim, 2003; Sæther *et al.*, 2007; Solberg *et al.*, 2007, 2008). For parameter values, see Table 1.

In general, we define a harvesting strategy by factors $(1-h)$ that are different for each sex-age class, reducing the survival for the class from s to $s(1-h)$. If $h = 0$ for a given class, then no individuals in this class are harvested, whereas $h = 1$ means that all individuals in the actual class are harvested. In the two sex model with $k+1$ age classes, a harvesting strategy then requires specification of $2k+2$ parameters h . In order to obtain a stable population size we may for example specify the values of h up to an unknown constant factor and finally compute this factor numerically to obtain $\lambda = 1$.

Here we focus on the two options that are usually considered by moose managers, varying the proportion of calves shot and changing the proportion of adult males in the population by sex-biased harvesting.

Varying the proportion of calves harvested

In order to study the effect of varying the proportion of calves harvested, we may first choose the values of h up to an unknown constant for all adult age classes. Then we subsequently choose increasing values of h for the calves and compute the unspecified constant to obtain $\lambda = 1$. The adult age classes of both sexes are accordingly harvested with the

Table 1 The parameters used in the population model

Parameters	Estimate
Survival	
P_{10}	0.75
P_{11}	0.85
P_{12}	0.94
P_{13}	0.90
P_{14}	0.90
P_{15}	0.88
P_{16}	0.88
P_{20}	0.75
P_{21}	0.85
P_{22}	0.97
P_{23}	0.97
P_{24}	0.97
P_{25}	0.97
P_{26}	0.97
Fecundity rate	
F_0	0
F_1	0
F_2	1.0
F_3	1.0
F_4	1.0
F_5	1.1
F_6	1.1
Carcass mass (kg)	
W_{10}	75
W_{11}	150
W_{12}	185
W_{13}	195
W_{14}	210
W_{15}	230
W_{16}	270
W_{20}	75
W_{21}	140
W_{22}	170
W_{23}	180
W_{24}	180
W_{25}	180
W_{26}	180

P_{ij} is the survival of sex category i ($i=1, 2$), where $i=1$ and $i=2$ represents male and female, respectively, in age class j ($j=0$ (calf), 1 (yearling), 2, 3, 4, 5 and ≥ 6 -year-old individuals). f_j is the fecundity of females (mean number of calves produced per female) in age class j . W_j is the mean carcass weight in sex class i of individuals in age class j .

prescribed relative intensity, whereas the proportion of calves harvested is increased while similarly reducing the overall harvest of adults. In this way, we keep λ constant but are still able to vary the proportion of calves in the harvest.

Changing the adult sex ratio

In order to analyse the effect of varying the sex ratio by harvesting, we first choose the parameters h up to an unknown constant for males, and up to another unknown constant for females. Then, we may choose increasing values of the constant for males and for each such choice compute

the constant for the females required to obtain $\lambda = 1$. Then, the age classes of females as well as males are separately harvested with a relative intensity according to the prescribed initial values, whereas the relative intensity for males compared with females are changed, which then alters the sex ratio of the population.

Variation in male mating success

The number of matings in a population is determined by the females, and the total number of male matings must be equal to the number obtained by the females. This constrains the fecundity of the males, so that only the relative number of matings among males at different ages is allowed to vary in the model. This is done by choosing some preference value for each age class of males. For instance, if one age class has the double value of another age class, the expected number of matings of a male in that age class is the double of those males in the other age class. The absolute values of these preferences are finally scaled so that the sum of preferences of all males in the population is the total expected number of offspring produced by females. These scaled male preferences are then the fecundities of males in the different age classes.

Results

The random genetic drift determined by σ_{dg}^2 decreased with increasing proportion of the calves that were harvested (Fig. 1). A harvest strategy that involves avoiding shooting calves, which was practiced over large areas in the middle of previous century, will result in high loss of neutral alleles. Similarly, increasing the offtake of adult males, which results in a biased sex ratio in the population, also causes increased random genetic drift. A particular dramatic increase in σ_{dg}^2 occurs when the sex ratio becomes very skewed (Fig. 1).

The effects on σ_{dg}^2 of changes in the proportion of calves shot were dependent on the assumed mating system (Fig. 1). If there are large differences among males in mating success, this will increase the random genetic drift, especially when few calves are harvested.

The effective population size n_e relative to the actual population size n (p) was also influenced by the choice of harvest strategy (Fig. 2). If older males were more preferred among the females than younger males, p increased with increasing harvest of calves. This relationship was not present if we assumed age-independent variation in mating success. This difference was due to an influence of both σ_{dg}^2 and generation time T on p (equation 1). The generation time increased with increasing proportional harvest of calves, whereas σ_{dg}^2 decreased (Fig. 1). For larger variation in male mating success σ_{dg}^2 is the major component of p , whereas for age-independent mating success σ_{dg}^2 is less and p more influenced by variation in T .

If the adult sex ratio was changed by selective hunting of males, this strongly affected p (Fig. 2). In particular,

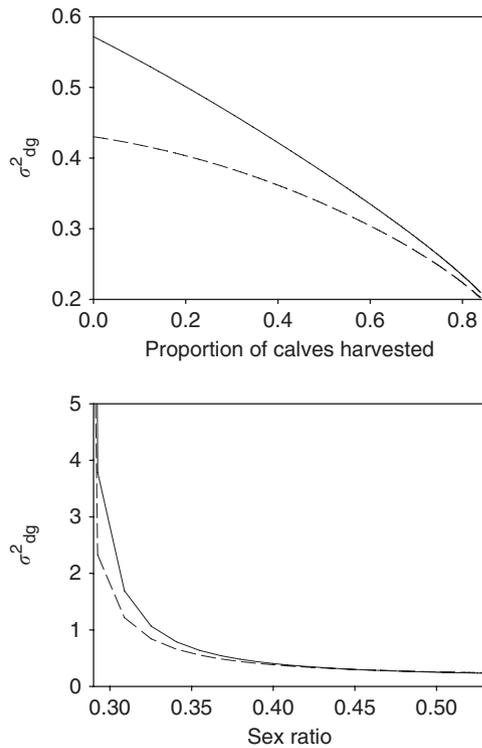


Figure 1 Rate of random genetic drift σ_{dg}^2 for different proportions of calves harvested (top) and the sex ratio, that is, the proportion of adult (≥ 1 year old) males in the population (bottom). The population is harvested to keep a stable population size (population growth rate $\lambda=1$) after harvest. The sex ratio (bottom) is skewed by selective harvest of adult (≥ 1 year old) males, where the different age classes are harvested proportional to their relative proportion of the adult male segment. The proportional harvest of the calf segment was equal to 0.30, and independent of the sex of the calf. The solid lines indicate large age-specific variation in male mating success ($m_0=m_1=0$, $m_2=1$, $m_3=1.5$, $m_4=2$, $m_5=4$ and $m_6=6$), whereas the dotted lines are for more similar mating among adult males ($m_0=m_1=0$, $m_2=1$ and $m_3=m_4=m_5=m_6=1.5$). For other parameter values, see Table 1.

reducing the adult sex ratio below 30% reduced the effective size and hence increased the drift per generation dramatically.

Discussion

In this study, we show that choice of harvest strategy strongly affects the rates of random genetic drift in harvested ungulate populations (Figs 1 and 2). We show that selective harvest of males as well as small harvest rates of calves will reduce the effective size. These effects occur even after keeping the population growth rate constant and assuming no consistent individual differences in male quality.

Our results show that increasing the proportion of calves that are harvested decreases σ_{dg}^2 (Fig. 1). The major reason for this is that a high proportion of calves in the harvest reduces the variation among females in recruitment success

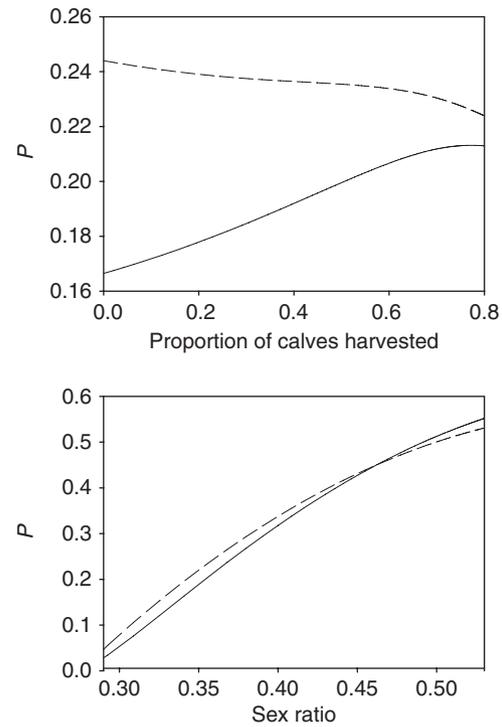


Figure 2 Variation in p , the relative size of the effective size n_e to the actual population size n , for different proportions of calves harvested (top) and the sex ratio, that is, the proportion of adult (≥ 1 year old) males in the population (bottom). The population is harvested to keep a stable population size (population growth rate $\lambda=1$) after harvest. The sex ratio (bottom) is skewed by selective harvest of adult (≥ 1 year old) males, where different age classes are harvested proportional to their relative proportion of the adult male segment. The proportional harvest of the calf segment was equal to 0.30, and independent of the sex of the calf. The solid lines indicate large age-specific variation in male mating success ($m_0=m_1=0$, $m_2=1$, $m_3=1.5$, $m_4=2$, $m_5=4$ and $m_6=6$), whereas the dotted lines are for more similar mating among adult males ($m_0=m_1=0$, $m_2=1$ and $m_3=m_4=m_5=m_6=1.5$). For other parameter values, see Table 1.

because fewer females will provide a recruit to next generation. In addition, more females will also survive from one year to another, which reduces the survival component of the demographic variance (Engen *et al.*, 2005b). This decreases the demographic variance in the female segment of the population. In our model population (Table 1), the demographic variance for the females σ_{df}^2 was reduced from 0.27 to 0.13 when the proportion of harvested calves was increased from 0 to 0.82. This illustrates that long-term evolutionary consequences of harvesting may depend on how the harvest affect the stochastic components of the population dynamics.

In many areas of Fennoscandia, hunters have been reluctant to shoot calves. As a consequence, in these areas yearlings make up a large proportion of the harvest of younger (< 2 years old) animals. The choice of such a harvest strategy with selective harvesting of mainly yearlings and the minimum proportion of calves results in increased

genetic drift, compared with more intensive harvest of calves (Fig. 1). For instance, for our set of parameter values (Table 1) harvesting the minimum proportion of calves (0.05) to keep $\lambda = 1$ gives $\sigma_{\text{dg}}^2 = 0.27$, which is 28.5% larger than σ_{dg}^2 for the maximum proportion of calves in the harvest (Fig. 1). This is associated with larger demographic variance σ_{dr}^2 for a harvest strategy directed against yearlings than for a harvest strategy based on intensive calf shooting. This occurs because increased harvest of yearlings decreases the probability of survival of yearling females, which increases the component of demographic variance (Engen *et al.*, 2005b) due to among-individual variation in survival. In contrast, a high proportion of calves in the harvest reduces the variation in reproductive success among adult females. Although the major reduction in the effective size occurs when harvest rates of calves are relatively high (Figs 1 and 2), the average proportion of calves in the harvest are in most regions of Fennoscandia between 30 and 45% (Lavsund *et al.*, 2003; Solberg *et al.*, 2006).

In correspondence with the results from analyses of models of harvest strategies our model shows that changing the adult sex ratio by selective harvest of males is an important tool to increase the yield in terms of number of animals or total biomass (Caughley, 1977; Sæther *et al.*, 2001), provided that all sexually matured females still become mated. For instance, changing the proportion of adult males from 50 to 28.8% in our model resulted in a 84.5% increase of the yield in biomass, using mean age- and sex-specific values of biomass of Norwegian moose (Sæther *et al.*, 2001; Solberg *et al.*, 2006). However, such a sex-specific strategy will increase the random genetic drift dramatically (Figs 1 and 2). Thus, managers face a conflict in choice of optimization criteria. If they decide to maximize the yield in terms of number of animals or biomass by altering the adult sex ratio, the effective population size will be smaller, resulting in increased random genetic drift, than for a harvest strategy that keeps an approximate equal proportion adult males and females.

Our modelling is based on the assumption that changes of the adult sex ratio do not affect the demographic traits of the female segment of the populations. Several lines of evidence suggest that this may not necessarily be true for populations of ungulates (Myrsterud, Coulson & Stenseth, 2002). For instance, reduction in the proportion of adult males in Norwegian moose populations are associated with increased proportion of female calves shot during the autumn (Sæther *et al.*, 2004a; Bjørneraas *et al.*, 2009), probably reflecting a change in the neonatal sex ratio composition of the populations (Moe *et al.*, 2009). Other empirical evidence also support such a response in the calf sex ratio to structural changes in the adult segment of the population (Røed *et al.*, 2002, 2007; Sæther *et al.*, 2004a). If the recruitment of new recruits into the populations becomes more female biased as a response to increased harvest of adult males, this will increase the rate of genetic drift and reduce the effective population size even more than in our model, as depicted in Figs 1 and 2.

According to Engen *et al.* (2005a), the rate of random genetic drift and the effective size are simply σ_{dg}^2 and the inverse of the product $\sigma_{\text{dg}}^2 T$, respectively. An important feature of this theory is that it allows a description of the genetic dynamics from demographic variables without making biologically unrealistic assumptions such as constant population size or stable age structures. This is especially important when evaluating the genetic consequences of the choice of harvest strategies because the harvest rapidly changes the age composition of the population (Sæther *et al.*, 2001). In the present model, changes in the proportion of calves harvested changed the generation time, which in turn affected the rate of genetic drift (Fig. 1). This supports previous simulation results by Ryman *et al.* (1981).

Although the theory of Engen *et al.* (2005a) gives some simple results for the genetic drift, calculation of these expressions often becomes extremely complicated because it involves estimation of a large number of parameters even when some simplifying assumptions about the model structure is made (e.g. Engen *et al.*, 2007). In the present case, individual variation in male reproductive success is especially important. Different assumptions about the age-specific variation in male mating success strongly affected how choice of harvest strategies affected the rate of random genetic drift (Fig. 1). Theoretical analyses have shown that inter-individual differences in mating preferences strongly affect the variance in male mating success (Lee, Engen & Sæther, 2008) and hence the component of σ_{dg}^2 due to the demographic variance of males. Several studies have shown that variation in male mating success strongly affects the effective population size (Caballero & Hill, 1992; Nunney, 1993). Thus, a proper understanding of how harvest affects the genetic dynamics of populations requires that the changes in social systems can be reliably predicted as a function of changes in age or sex composition. In ungulates, these effects on social structure of variation in male mating success can be large because of changes in the intensity of male–male competition or in female mating preferences (Myrsterud *et al.*, 2002; Holand *et al.*, 2003, 2006; Røed *et al.*, 2005, 2007).

Our modelling of the population dynamics is based on three important simplifying assumptions. First, we assume no density dependence. In Norwegian moose populations, this assumption is probably only partly fulfilled, but still seems to hold for populations in central and northern Norway (Sæther *et al.*, 1996; Solberg *et al.*, 2006). Second, we assume no environmental stochasticity, which is known to influence the population dynamics of ungulates in general (Sæther, 1997) including moose (Solberg *et al.*, 1999; Herfindal *et al.*, 2006). Fluctuations in population size caused by density dependence or environmental stochasticity will not affect the rate of genetic drift at a given time, but it will influence the effective population size per generation (Wright, 1931, 1969; Waples, 2002). Over longer time periods n_e will, in addition to σ_{dg}^2 , be influenced by the environmental variance σ_e^2 and the deterministic specific population growth rate $r = \ln \lambda$ (equation 15 in Engen *et al.*, 2005b). In general this will reduce p even further than

in Figs 1 and 2 because we have assumed no environmental stochasticity or density dependence. Third, we assume no consistent differences among the individuals that are independent of age. Several evidence now indicate that hunters may selectively remove high-quality individuals for example with large antlers or large body sizes (Coltman *et al.*, 2003; Festa-Bianchet, 2003; Garel *et al.*, 2007), which will affect the estimates σ_{dg}^2 through an influence on the inter-male variation in mating success.

A lot of evidences are now available indicating that harvest induce evolutionary responses in important quantitative traits (Law, 2000, 2007; Stokes & Law, 2000; Olsen *et al.*, 2004; Kuparinen & Merilä, 2007). In ungulates, sport hunting of bighorn *Ovis canadensis* trophy rams resulted in declining breeding values for weight and horn size (Coltman *et al.*, 2003). Similarly, the increasing proportion of tuskless elephants *Loxodonta africana* in many African populations have been suggested to be an evolutionary response to selective ivory poaching (Jachmann, Berry & Imae, 1995). Furthermore, many harvested populations are strongly influenced by changes in the environment for example due to climate change (Sæther, 1997; Sæther, Sutherland & Engen, 2004b), which may select for evolutionary responses in fitness-related characters. Our analyses show that the choice of harvest strategy will influence the rate of these adaptive responses because the probability of fixation of beneficial mutations are closely related to the effective population size (Haldane, 1927). Thus, maintenance of viable populations of harvested species requires that consequences of the harvest strategy for the genetical dynamics within the population are carefully considered.

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