

Estimating the growth of a newly established moose population using reproductive value

Bernt-Erik Sæther, Steinar Engen, Erling J. Solberg and Morten Heim

B.-E. Sæther (Bernt-Erik.Sather@bio.ntnu.no), Dept of Biology, Norwegian Univ. of Science and Technology, NO-7491 Trondheim, Norway. – S. Engen, Dept of Mathematical Sciences, Norwegian Univ. of Science and Technology, NO-7491 Trondheim, Norway. – E. J. Solberg and M. Heim, Norwegian Inst. for Nature Research, Tungasletta 2, NO-7485 Trondheim, Norway.

Estimating the population growth rate and environmental stochasticity of long-lived species is difficult because annual variation in population size is influenced by temporal autocorrelations caused by fluctuations in the age-structure. Here we use the dynamics of the reproductive value to estimate the long-term growth rate s and the environmental variance σ_e^2 of a moose population that recently colonized the island of Vega in northern Norway. We show that the population growth rate was high ($s = 0.26$). The major stochastic influences on the population dynamics were due to demographic stochasticity, whereas the environmental variance was not significantly different from 0. This supports the suggestion that population growth rates of polytocous ungulates are high, and that demographic stochasticity must be assessed when estimating the growth of small ungulate populations.

The specific growth rate of populations at small densities is a key population parameter that determines many important characteristics of population dynamics. Unfortunately, this parameter is difficult to estimate in natural populations. Firstly, growth rates at smaller population sizes are strongly influenced by demographic and environmental stochasticity that tend to reduce the long-term growth rate. Thus, estimating the population growth rate requires that these effects of stochastic variation are accounted for. Secondly, for larger populations interpolation of fluctuations over a large range of population sizes is often required to estimate the growth at small population sizes. Such interpolation may even lead to biased estimates of the population growth rate (S. Aanes et al. 2002). Thirdly, in larger populations the current population growth rate may be influenced by the population size due to direct and indirect density-dependent effects. Fourthly, fluctuations in age structure can induce changes in population size that may affect estimation of the population growth rate. And, finally, estimation error in population estimates will strongly affect estimates of population growth rate even in the case of no density

dependence (Clark and Bjørnstad 2004, Freckleton et al. 2006). Thus, an ideal data set for estimating population growth rates should contain individual-based demographic data as well as time series of exact population counts especially at small population sizes.

Of course, such data sets are only rarely accessible, especially for larger long-lived mammals that often is difficult to census because of a concealed way of living (Gaillard et al. 2003). Reintroduction of individuals into areas previously occupied by the species does not only represent an important management tool (Griffith et al. 1989), but may also give rarely accessible information about important ecological processes (Sarrazin and Barbault 1996). For instance, studies of reintroduced ungulate populations has provided knowledge about population growth rates at small population sizes (Komers and Curman 2000, Gaillard et al. 2000, Sæther et al. 2002, Asbjørnsen et al. 2005) as well as the mechanisms of density-dependence (Sæther et al. 2002) and effects of environmental stochasticity (R. Aanes et al. 2002, Asbjørnsen et al. 2005).

A problem with many studies of the dynamics of reintroduced ungulate population is that they ignore

the effects of age-structure. In general, the ungulates have high adult survival rates (Gaillard et al. 2000), resulting in long generation times. Analyses of stochastic age-structured population models (Lande et al. 2002, 2006, Engen et al. 2007) have shown that fluctuations in age composition causes temporal auto-correlations in population fluctuations that must be accounted for when estimating parameters such as the environmental variance and strength of density dependence. However, Engen et al. (2007) showed that estimates of the long-term growth rate and environmental stochasticity for a density-independent population in a random environment that account for the effects of fluctuations in age-structure can be obtained from temporal variation of the total reproductive value.

A unique opportunity to obtain unbiased estimates of the population growth rate at small densities that involved no human translocation appeared at the island of Vega. This island was colonized by 3 moose *Alces alces* that swam across from the nearby mainland to the island in 1985. From 1992 and onwards almost all adult individuals on the island has been individually followed by the use of radio-collars (Sæther et al. 2003, 2004a). These data enabled us to estimate the demographic variance of the female segment of the population using the method of Engen et al. (2005). We then estimated the population growth rate and the environmental variance from the dynamics of the reproductive value (Engen et al. 2007).

Methods

The island of Vega (65°40'N, 11°55'E) is ca 119 km² and located off the coast of Helgeland in northern Norway (Sæther et al. 2003). Two yearling females and 1 yearling male arrived at the island in 1985 (Sæther et al. 2001). Later 8 yearling males (4 in 1993, 3 in 1994, and 1 in 1999) and 2 females (1 yearling female in 1999 and 1 adult female in 1993) arrived at the island during the study period from 1992 to 2000. In contrast, 2 yearling females (1997), 2 yearling males (1 in 1998, 1 in 1999) and 1 adult male (1996) left the island.

During the winter of 1992, we immobilized and radio-collared 18 of the 24 animals present on the island using a helicopter and a remote drug-delivery system (Dan-Inject, Børkop, Denmark). Two of the remaining unmarked animals were later immobilized from the ground and radio-collared the following spring and summer. The last 2 unmarked animals remaining from the previous winter, as well as all new calves, were radio-collared using a helicopter during the winter of 1993. Each of the following winters, we continued radiocollaring all calves and immigrants, and changed radiocollars on animals with malfunctioning

transmitters. After the end of the rutting season in the autumn 1994, the male age-structure was changed by removing all adult (≥ 1.5 -yr-old) males in the population (Sæther et al. 2004a). Furthermore, after the 1996 rutting season the adult sex ratio in the population was altered to ca 25% males, corresponding to a sex ratio recorded in several intensively managed Scandinavian moose populations (Sæther 1987, Solberg et al. 1997, 2002, 2006). Finally, in the latter part of the study period some regular harvest occurred.

In most cases, we determined the age of individuals by the time elapsed since they were radiocollared as calves. Older animals, killed or found dead of natural causes, were age-determined from the pattern of tooth replacement (yearlings) or, in the laboratory, by counting the number of layers in the secondary dentine of the incisors (Haagenrud 1978).

The number of calves was determined by approaching adult females on foot during the calving season (May–July) at 3–5 d intervals until the presence of a calf was verified (Sæther and Heim 1993). We also assumed that this method gave precise estimates of fecundity rates (the maximum number of calves recorded per female), as parturition was verified for a large proportion of all adult females present.

Model and estimation procedures

We estimated the demographic variance σ_d^2 from data on individual variation in the number of female recruits and in survival of females that were not killed by hunting. The estimating procedure of σ_d^2 follows Engen et al. (2005). The method is based on first estimating the within-year variance in number of offspring, $\sigma_{B_i}^2$, for each age class i by sum of squares as shown in Engen et al. (2005). Similar types of estimates are also found for variances in survival, $\sigma_{S_i}^2$, and the correlation between number of offspring and the indicator variable for survival, $\sigma_{\tau_i}^2$. The demographic variance is finally computed from the relation $\sigma_d^2 = \lambda^{-2} \sum_i (v_0^2 \sigma_{B_i}^2 + v_{i+1} \sigma_{S_i}^2 + 2v_0 v_{i+1} \tau_i)$, where u is the stable age-distribution and v is the reproductive value (see Engen et al. 2005, pp. 213–215 for further details).

We estimate the vital rates in the expected Leslie matrix L (Caswell 2001) as mean values across the study period of observed survivals and fecundities for all age-classes. The stable age distribution is then the left eigenvector u associated with the dominant eigenvalue λ defined by $Lu = \lambda u$ and scaled so that the sum of the elements equals 1. The vector of reproductive values is the right eigenvector (Caswell 2001) defined by $vL = \lambda v$ and scaled by $\sum_i v_i = 1$ (Lande et al. 2006, Engen et al. 2007). Writing N_i for the number of individuals in age class i the total reproductive value of the population is $V = \sum_i v_i N_i$. Then, Engen et al.

(2005) has shown that $\Delta \ln V_t = \ln V_{t+1} - \ln V_t$, where t denotes time, are independent variables to the first order with mean $s = r - \sigma_e^2/2 - \sigma_d^2/(2N_t) = s - \sigma_d^2/(2N_t)$ and variance $\sigma_e^2 + \sigma_d^2/N_t$. This can be used to estimate s and σ_e^2 from observed values of $\Delta \ln V_t$. Because the population is harvested we use the yearly change in log reproductive values in the absence of harvesting by measuring the change in number of females from just after harvest (posthunt period) to the number of individuals present just before harvest the following year (prehunt period). We assume that all calves shot the previous year would have survived and are thus included as yearlings in the latter figure. Following Engen et al. (2007) we then use the estimator based on n differences of $\Delta \ln V_t$

$$\hat{s} = \frac{1}{n} \sum \Delta \ln V_t + \hat{\sigma}_d^2 / \tilde{N} \quad (1a)$$

and

$$\hat{\sigma}_e^2 = \frac{1}{n-1} \sum [\Delta \ln V_t - \hat{s} - \hat{\sigma}_d^2 / (2N_t)]^2 - \hat{\sigma}_d^2 / \tilde{N}, \quad (1b)$$

where $\hat{\sigma}_d^2$ is the estimate of the demographic variance σ_d^2 and \tilde{N} is the harmonic mean of the population sizes recorded at the beginning of each interval, that is, just after harvesting.

Results

Highest reproductive values were found among 5–6 yr old females (Fig. 1). However, small variation was found in reproductive value among females that were between 3 and 11 yr of age. The reproductive value of 1 yr old females was 54.3% of the reproductive value of 6 yr old females.

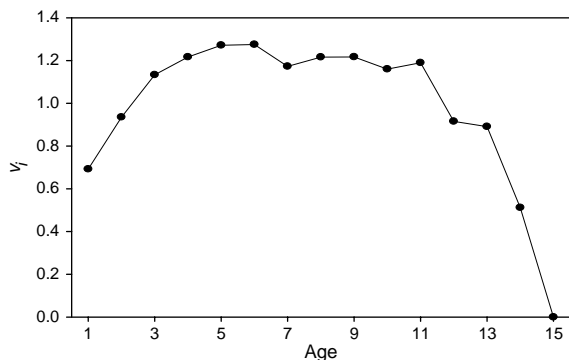


Fig. 1. The age-specific variation in the reproductive value v_i for the female part of the moose population at the island of Vega, calculated from mean values across the study period of observed survivals and fecundities for all age-classes.

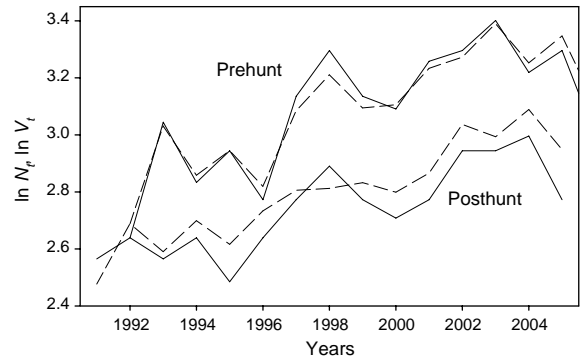


Fig. 2. Annual variation in the (log-) population size of females ($\log N_t$) (solid line) and (log-) total reproductive value ($\log V_t$) for the female segment of the moose population at the island of Vega just before the onset (Prehunt) and just after (Posthunt) the hunting season.

The annual fluctuations in the total reproductive value V_t were similar to the fluctuations in the total female population size both for the posthunt- and the prehunt-period (Fig. 2), showing that the reproductive value gives an accurate estimate of the variation in the size of this population.

Demographic stochasticity was the major stochastic factor affecting the population growth ($\hat{\sigma}_d^2 = 0.15$). In fact, the environmental variance ($\hat{\sigma}_e^2 = 0.0012$) was not significantly larger than 0 (standard deviation of $\hat{\sigma}_e^2 = 0.30$).

The long-term growth rate of the moose population at Vega was high ($\hat{s} = 0.26 \pm 0.02$ (SD)).

Discussion

The rapid growth of the moose population at Vega (Fig. 1) was expected from the high fecundity rates (Sæther et al. 2003, 2004a), high survival rates (Stubsjøen et al. 2000) and large body mass (Sæther et al. 2003) of moose at this island. This indicates that Vega represents a very favourable area for the moose and suggests that our estimate of s is likely to be located in the upper range of growth rates for moose populations (Van Ballenberghe 1983). Accordingly, our estimates of s is ca 3 times higher than obtained by approximating the population variations with fluctuations in the reproductive value for a population of bighorn sheep *Ovis canadensis* in Canada (Engen et al. 2007), estimated for the period before significant density dependent effects started to operate on this population.

An important source for information about density independent growth rates is provided by the growth of ungulate populations that have been re-introduced into new areas. Our estimate of the growth of the moose

population at Vega was higher than recorded for most re-introduced ungulate populations (Komers and Curman 2000, Loison et al. 2002, Sæther et al. 2002, Asbjørnsen et al. 2005). Similar high growth rates have only been estimated in some populations of mouflon *Ovis musimon* (Komers and Curman 2000), for the isard *Rupicapra pyrenaica* (Loison et al. 2002) and some ibex *Capra ibex* populations (Loison et al. 2002, Sæther et al. 2007). This provide some support for the suggestion by Gaillard et al. (2000) that most rapid population growth is likely to occur in polytocous ungulates such as moose.

No significant environmental stochasticity was present in the population dynamics of moose at the island of Vega. Small environmental variance has also been found after accounting for the effects of demographic stochasticity in other rapidly growing small ungulate populations (Engen et al. 2007, Sæther et al. 2007) as well as in density regulated ungulate populations (Lande et al. 2006, Sæther et al. 2007). Our estimate of the demographic variance is typical for species with long generation times (Sæther et al. 2004b) and is very similar to the estimate of demographic variance for the red deer *Cervus elaphus* at Rhum (Lande et al. 2006). The demographic stochasticity is the major stochastic component in the population dynamics. The effect of demographic stochasticity per generation time T $\sigma_{d,T}^2 = \sigma_d^2 T$ (Sæther et al. 2005a) will be even larger because of the high adult survival rate of the moose at Vega (Stubsjøen et al. 2000). This implies that the environmental variance will be extremely difficult to estimate using time series of population fluctuations when the mean population size is small. In such cases, direct partitioning of the variance in individual contributions to future generations based on demographic data (Engen et al. 1998) may be a more useful approach (Sæther et al. 2005b).

Several methods have been used to estimate the growth rate of ungulate populations from time series of population counts. It is important to realize that these different approaches do not give directly comparable estimates. Most commonly, the growth rate is estimated, according to Dennis et al. (1991), by the differences between the logarithmic of the final and initial population size divided by the period between the first and last population estimate (Komers and Curman 2000). This yields the stochastic growth rate. To obtain the deterministic growth rate r , information about σ_d^2 and σ_e^2 is necessary because $r = s + \frac{1}{2} \sigma_e^2 + \frac{1}{2N} \sigma_d^2$ (Lande et al. 2003). In contrast, the mean of the relative change in population size at an absolute scale yields an estimate of the deterministic growth rate $\lambda = e^r$. Both these approaches ignore the effects of

fluctuations in age-structure. In long-lived species such as ungulates (Gaillard et al. 2000) age structure may induce autocorrelations in the population fluctuations that will bias the estimates of specific growth rates and environmental variance (Lande et al. 2002). Such age-structure effects may be especially important in harvested populations (Solberg et al. 1999). Our approach by using total reproductive value gives a white noise process that describes the fluctuations in $\ln N_t$ quite accurately (Fig. 2). Thus, we can by this method account for the effects of harvesting and obtain reliable estimates of basic population parameters. However, this is based on the assumption that all calves shot otherwise would have recruited into the population. Accordingly, on Vega almost all calves alive after the hunting season survived to the age of yearling (Stubsjøen et al. 2000).

The reproductive value v_i was highest among the high-reproductive age-classes (Fig. 1). Large values of v_i was reached at earlier age-classes and remained high for a larger proportion of the female's lifespan at Vega than reported for a moose population in northern Sweden (Ericsson et al. 2001). A more rapid decrease of v_i with age was also found in a population of domestic sheep *Ovis aries* (Caughley 1967). The slower age-specific decrease in v_i in our study (Fig. 1) may be related to the favourable habitat-characteristics for moose at Vega, with high food availability and usually little snow during winter (Sæther et al. 2003, 2004a). Under such conditions it is likely that the rate of senescence in fitness-related characters such as survival and fecundity will be slower than in less favourable environments. Alternatively, the age-specific variation in reproductive value (Fig. 1) may also be affected by deviations from the stable age-distribution that are known to influence the demographic variation of ungulate populations (Festa-Bianchet et al. 2003, Crampe et al. 2006).

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