Predicting the growth of a small introduced muskox population using population prediction intervals

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Summary

1. A key issue in ecology is the prediction of future population fluctuations. Such population predictions are fundamental for population-viability analysis and are essential for assessing the implications of various management actions. Development of reliable population predictions is however, difficult because it requires estimation and modelling of the separate effects of the deterministic components of the population dynamics as well as the stochastic influences on the population fluctuations. Here we model the stochastic dynamics of an introduced population of muskox *Ovibos moschatus* in the Dovrefjell mountains of central Norway, using a simple model without density regulation. Our aim is to examine quantitatively factors affecting the accuracy of the population projections by applying the concept of Population Prediction Interval (PPI).

2. The long-term growth rate was $\hat{s} = 0.0511$, assuming no density dependence. The environmental variance was relatively large ($\hat{\sigma}_e^2 = 0.0159$). This gives a deterministic growth rate of $\hat{r} = 0.0591$. However, accounting for losses due to various kinds of human activities resulted in a nearly doubling of s ($\hat{s} = 0.0980$).

3. Autumn temperature and late winter snow depth were each able to explain a significant proportion of the annual variation in population growth rates.

4. The impact of environmental stochasticity made the PPI wide after only a few years. Uncertainties in the estimates of the population parameters were quite small and had a minor impact on the PPI.

5. A sensitivity analysis showed that ignoring demographic stochasticity led to an overestimate of the environmental variance σ_e^2, but that the impact on the width of the PPI was small.

6. This study shows that reliable projections of future population growth, even based on simple population models without density regulation, are dependent on assessment of the accuracy in the population predictions that must be based on estimating and modelling the stochastic influences on the population dynamics.

Key-words: environmental stochasticity, muskoxen, *Ovibos moschatus*, Population Prediction Interval, population viability analysis.

Introduction

An important challenge for ecologists in the years to come will be to develop predictions of future fluctuations in population size, especially for species of manage-ment concern. Reliable population projections will require information about expected changes of the population, determined by the specific growth rate, carrying capacity and form of the density regulation. In addition, we need to estimate and to model the stochastic influences on the population dynamics. Demographic stochasticity is caused by random differences between individuals in their ability to reproduce or survive (Engen, Bakke & Islam 1998), with

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strongest effects on the population growth rate at small population sizes (Leigh 1981; Lande 1993, 1998). Environmental stochasticity refers to stochastic variation that affects all individuals in a certain group similarly and is important both in small and large populations (May 1973; Leigh 1981; Lande 1993). Unfortunately, separating the relative contribution of demographic and environmental stochasticity requires a combination of individual-based data on fitness-variation and accurate long-term time-series on population fluctuations (Sæther & Engen 2002), which are rarely available. Finally, reliable population projections are also dependent on assessment of how uncertainties in the estimates of the parameters affect the accuracy of the population predictions (Ludwig 1996; Sæther *et al.* 2000; Ellner *et al.* 2002).

Following the introduction of the concept of the population prediction interval (PPI) into population viability analysis (Dennis, Munholland & Scott 1991), it became possible to examine quantitatively how stochasticity and parameter uncertainties affect future population predictions. Following Sæther *et al.* (2000), Engen & Sæther (2000) and Sæther *et al.* (2002a), a PPI is defined as the stochastic interval that includes the population size with probability $(1 - \beta)$, where β is the probability that the variable we want to predict is not contained in the stochastic interval. This means that the confidence of the PPI decreases with increasing β. When large stochastic effects are present, or population estimates are uncertain, the PPI soon becomes wide (Sæther *et al.* 2000, 2002a; Engen, Sæther & Møller 2001). Furthermore, the PPI will increase as the time elapsed since the last observation increases.

The specific growth rate at small population sizes r is an important parameter influencing the expected dynamics of the population. Unfortunately, this parameter is extremely difficult to estimate (Taylor 1995; Sæther *et al.* 2000), because in populations fluctuating around the carrying capacity interpolation over a large range of population sizes is often necessary (Aanes *et al.* 2002). Translocation of individuals (IUCN 1987) can provide here an important source of information for obtaining estimates of this parameter because usually a limited number of individuals are introduced into a pristine environment. In general, the success of such translocations increases with habitat quality, the release of wild-caught instead of captive animals and increasing numbers of released animals (Griffith *et al.* 1989; Wolf *et al.* 1996; Wolf, Griffith & Garland 1998; Komers & Curman 2000). Also, a strict regulation of human caused mortality is often required (Spalton, Lawrence & Brend 1999). In addition to their use as a tool for preventing species extinction, translocations often provide the possibility to study general ecological processes (Sarrazin & Barbault 1996; Komers & Curman 2000). Here we will use translocation of muskox *Ovibos moschatus* from eastern Greenland to the mountain range Dovre in Central Norway to parameterize a simple population model without density regulation

that can be used to improve our ability to predict future fluctuations of small populations.

Population dynamics of ungulates are affected strongly by climate (see review in Sæther 1997). Different studies of ungulates have shown an effect from summer climate affecting juvenile as well as adult mortality, and furthermore, variation in summer climate has been reported to influence body weight, inducing variation in fecundity among cohorts (Albon, Clutton-Brock & Guinness 1987; Gaillard *et al.* 1997; Solberg *et al.* 1999). The reason for this variation is often linked to the effect summer climate has on the forage quality. Effects from winter climate are often associated with high mortality during harsh winters (Tener 1965; Smith 1984; Sæther 1997; Aanes, Sæther & Øritsland 2000; Solberg *et al.* 2001). However, the influence of variation in climate-induced stochasticity on the population growth rate of ungulates has been quantitatively examined in only a few cases (Coulson *et al.* 2001; Sæther *et al.* 2002b). The magnitude of such effects is important because they generally reduce the long-term growth rate of the population (Lande, Engen & Sæther 2003) and hence increase the vulnerability of small populations.

As a result of intensive hunting, the global distribution of the muskox *Ovibos moschatus* was restricted to certain areas in northern Canada and eastern Greenland at the beginning of the 20th century (Boertmann *et al.* 1992; Ferguson & Gauthier 1992; Lent 1998). In efforts to decrease the risk of extinction many reintroductions and introductions were made, and the species is now increasing globally. After an unsuccessful attempt prior to the Second World War, in the period 1947–53 muskoxen were taken from eastern Greenland and introduced into a mountain range in central Norway (Myrberget 1987).

In this study, we analyse the dynamics of this muskox population. An important focus is to use the theoretical framework presented in Lande *et al.* (2003) to estimate essential population parameters. We use these estimates to predict future population sizes, illustrating the application of the concept of PPI (Sæther *et al.* 2000). Finally, we relate annual variation in population growth rates to local climate, in order to quantify the effects of this environmental stochasticity on the long-term growth rate of the population.

Study area

The study was conducted in the Dovre Mountains (DM), located in central Norway at 62°2′N, 9°3′E (see Asbjørnsen 2002 for map). The mountain range is a typical alpine tundra environment, having considerable variation in terrain structure. Altitudes vary from 600 m above sea level in valley bottoms to > 2000 m on peaks. This includes open plateaus, U-shaped valleys and rugged terrain. Alpine tundra vegetation dominates, which ranges from snow-bed vegetation to lichen heath and grass heath communities and barren rock. The area is among the driest in Norway, with average precipitation levels less than 500 mm per year. Normally,

the area is snow-covered from late October to late May. The area is bisected by a major two-lane highway and an intercity railway that both remain open year-round. Most of the range of muskoxen is within a national park and a military training area. During winter, the population feeds on steep slopes and windblown ridges, owing to their preference for low snow cover and low plasticity to snow-rich environments (Alendal 1973; Thing 1984; Klein 1992; Nellemann 1997, 1998).

In the period 1947–53, 27 calves and yearlings were introduced in DM. Most of these individuals died, and by the end of August 1953 probably only 10 individuals were left alive (Alendal 1973). Today's population descends from these individuals.

Methods

POPULATION CENSUSES AND REGISTERED MORTALITY

Summer censuses were performed from late July until early September. Numbers of muskoxen in DM until 1983 were based on censuses performed and presented by E. Alendal (see Alendal 1973 for presentation of parts of these censuses). After 1983, local rangers performed the summer censuses presented in this study. The method for these censuses involved walking through areas that traditionally contained muskoxen and then counting the animals. Normally around 10 people participated in these censuses (T. Bretten pers. comm.). Given the open landscape, the high visibility and sedentary nature of the species, and the familiarity that the rangers have with muskoxen in the area, it is likely that these minimum counts came close to representing total counts. Recorded age- and place-specific mortality of the muskoxen in DM was collected from rangers, local newspapers and game departments. In total, 265 animals were lost to the population during the study period. Human-caused mortalities dominated (74 were shot, 63 were killed by the train, six died in research immobilization attempts and five were accidentally poisoned), but natural mortalities also occurred (12 died in lightning strikes and 11 died in avalanches or falls). Many animals also dispersed. In total 64 were found more than 10 km from the population's distribution. Most of these animals died or were shot (included in the above numbers) but a small propagule established another population in Sweden (Laikre *et al.* 1997).

POPULATION MODEL

No evidence for density regulation was found because the change in population size from one year to another was not related to population size, either on an absolute scale (correlation coefficient = 0·06, $n = 30$, $P > 0·1$) or on a logarithmic scale (correlation coefficient = –0·28, $n = 30$, $P > 0·1$, see also Asbjørnsen 2002). We therefore adopted a population model without density regulation writing N_t for the population size at time t so that:

$$E(N_{t+1} \mid N_t) = rN_t \qquad \text{eqn 1a}$$

and

$$\text{var}(N_{t+1} \mid N_t) = \sigma_d^2 N_t + \sigma_e^2 N_t^2. \qquad \text{eqn 1b}$$

Here r is the specific population growth rate, σ_d^2 is the demographic variance and σ_e^2 is the environmental variance. The first order approximation of the mean and variance in $X_{t+1} = \ln N_{t+1}$ is then:

$$E(X_{t+1} \mid X_t) = r - \frac{1}{2}\sigma_e^2 - \frac{1}{2}e^{-X_t}\sigma_d^2 \qquad \text{eqn 2a}$$

and

$$\text{var}(X_{t+1} \mid X_t) = \sigma_d^2 e^{-X_t} + \sigma_e^2. \qquad \text{eqn 2b}$$

Climate effects

The model described by eqns 2a and b can be rewritten as

$$X_{t+1} = E(X_{t+1} \mid X_t) + U_d \sigma_d / \sqrt{N_t} + U_e \sigma_e \qquad \text{eqn 3}$$

where U_d and U_e are independent variables with zero mean and unit variance. We can use eqn 3 to examine how different climate variables affect fluctuations in population size. We introduce the climate variables $y_{i,t}$ as random effects, writing:

$$U_e \sigma_e = \sum a_i y_{i,t} + U\sigma, \qquad \text{eqn 4}$$

where U is another normalized variable and Σ is the component of the environmental variance that cannot be explained by fluctuations in the covariates. This leads to the relation:

$$\sigma_e^2 = \text{var}(\sum a_i y_{i,t}) + \sigma^2, \qquad \text{eqn 5}$$

so that the covariates together explain a fraction:

$$p = \text{var}(\sum a_i y_{i,t}) / [\text{var}(\sum a_i y_{i,t}) + \sigma^2], \qquad \text{eqn 6}$$

of the total environmental variance.

Estimating population parameters

A problem in estimating the population parameters is that individuals were killed by humans. We therefore made two analyses. In the first analysis we used the total population counts (excluding individuals that had emigrated out of the area). In the second analysis we removed the individuals that had been killed by various kinds of human activities.

Our estimation procedures are based on the assumption that X_{t+1} given X_t is normally distributed. Writing x_t for the observed logarithm of abundance in year t, the log likelihood function takes the form

$$\ln L(s, \sigma_e^2, \sigma_d^2) = \sum \left[1/2 \ln(\sigma_e^2 + \sigma_d^2 e^{-x_t}) - \frac{(x_{t+1} - s - 1/2\sigma_d^2 e^{-x_t})^2}{2(\sigma_e^2 + \sigma_d^2 e^{-x_t})} \right], \quad \text{eqn 7}$$

where $s = r - 1/2\sigma_e^2$ is the stochastic growth rate. The sum is taken over values of t for which x_{t+1} as well as x_t are recorded.

Equation 7 is maximized numerically with respect to the unknown parameters s and σ_e^2. The uncertainties were found by parametric bootstrapping, simulating the process a large number of times using the estimated population parameters (Sæther *et al.* 2000).

We then repeated the analyses, subtracting the number of animals killed by humans from the mean of EN_t (eqn 1). Similarly, $-\ln(1 - k_t)$ must be subtracted in the expression for EX_t (eqn 2), where k_t is the proportion of animals killed.

Computation of PPI

We compute the PPI following the simulation approach by Engen *et al.* (2001). We first estimate the parameters (see eqn 7). Secondly, the process with these parameters is simulated in such a way that it ends up with the same population size as the one recorded at the last year of observation. The same process is then simulated further until it first reaches extinction or a predefined upper time, t_{max}. From each simulation we estimate the population parameters as for the real data and perform parametric bootstrapping. We then simulate the process for each bootstrap replicate to extinction or t_{max} and check whether extinction occurs before the simulated 'real' extinction time, using the last parameter estimates, or have smaller population size at t_{max} if extinction is not reached. Writing Q for the proportion of simulations giving smaller values, the simulations would give prediction intervals with exact coverage if Q was distributed uniformly between 0 and 1. We perform this procedure a large number of times and fit a beta-distribution to the simulated Q-values and use this fitted distribution to obtain a prediction method with improved coverage. For further details, see Engen *et al.* (2001).

Climatic data

Climatic data were collected from Fokstua Meteorological Station, situated a few kilometres south of the muskox distribution area for the period January 1957–May 2001. These data consist of daily precipitation, mean daily temperature and daily snow depth. Climatic observations were aggregated at monthly, bimonthly and 3-monthly intervals.

The significance testing of the covariates was performed by simulating 1000 times under the null hypothesis.
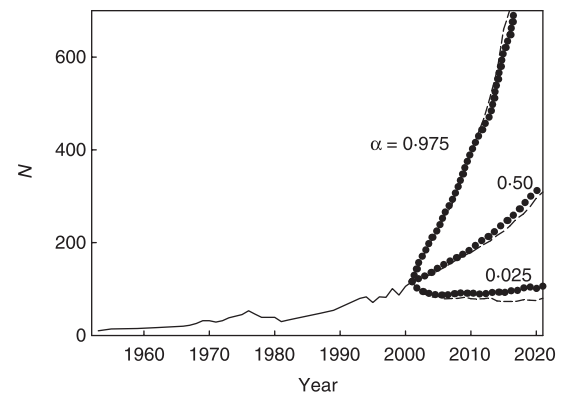
Fig. 1. The actual population fluctuations in the size of the muskox population in the Dovre Mountains (solid lines) and population prediction interval (PPI) of future population sizes with (stippled line) and without (dotted lines) uncertainties in the parameter estimates. The values of alpha are quantiles in the distribution representing predicted population sizes. Accordingly, the interval between $\alpha = 0.025$ and $\alpha = 0.975$ represents the 95% PPI.

Results

The population increased from 10 individuals in 1953 to 116 animals in 2001 (Fig. 1). The stochastic growth rate in this population was $\hat{s} = 0.0511 \pm 0.0177$ (SD) with environmental variance $\hat{\sigma}_e^2 = 0.0159 \pm 0.004$. According to eqn 2a, the deterministic growth rate was then $\hat{r} = 0.0591$.

Annual variations in the population growth rates were significantly related to autumn climate and winter climate between year t and $t + 1$. High growth rates were found in years with mild weather during the period September–November ($b = 0.039$, $P = 0.001$) and with little snow depth in May ($b = -0.005$, $P = 0.008$). The proportion of explained variance in σ_e^2 was 9.7% and 1.1% for autumn temperature and May snow depth, respectively.

Based on the 50% of the PPI we predicted the population to grow from 116 individuals in the last year of study (2001) to 147 individuals after 5 years in 2006 (Fig. 1). However, the uncertainty in the predictions was large because after 5 years the estimated 95% PPI (the interval between the 2.5% and 97.5% quantiles) already ranged from 79 to 259 individuals. The small effects on the position of the quantiles of assuming precise parameter estimates (Fig. 1) showed that the width of the PPI was influenced more strongly by the environmental stochasticity than uncertainties in the parameter estimates.

So far, we have assumed that the demographic variance was small enough to be ignored. To evaluate the sensitivity of the PPI to variation in σ_d^2 we used the method of Engen *et al.* (2005) for estimating the demographic variance in age-structured populations of species with only one offspring. Assuming a similar demography as in the Arctic Wildlife Refuge population in north-eastern Alaska (Reynolds 1998), we assume that 59 calves were produced per 100 females

> 2 years old with 83% of the calves surviving their first year of life, which for an equal sex ratio gives 0·245 female recruits per adult female. To obtain a maximum estimate of the demographic variance (Sæther *et al.* 2004), adult survival rate was assumed equal to the average yearling survival rate (70%), giving $\hat{\sigma}_d^2 = 0.240$. Inclusion of demographic variance reduced the width of the PPI. After 10 years the width of the PPI was 19·2% smaller with σ_d^2 included than without any demographic stochasticity.

Discussion

This study demonstrates large uncertainties in predicting the future growth of an introduced small population of muskox in Central Norway, owing mainly to the effects of environmental stochasticity (Fig. 1). A significant proportion of this variability was explained by climate during autumn and late spring. This illustrates the importance of including assessments of uncertainties in the population projections when making predictions about future growth of small populations (Fieberg & Ellner 2000; Ellner *et al.* 2002).

The population growth rates estimated in this study were smaller than those recorded in some other introduced populations of this species. After an introduction in Nunivak Island, Alaska, the stochastic growth rate $\hat{s} = 0.0980 \pm 0.0207$ (estimated from a time-series presented in Spencer & Lensink 1970; assuming no census error and demographic stochasticity) was 91·7% higher than on DM. Similarly, the censuses from muskox introductions in Angujaartorfiup Nunaa, West Greenland (Pedersen & Aastrup 2000) indicated $\hat{s} = 0.21 \pm 0.10$ during the expansion phase 1986–90. Similar high growth rates have also been indicated in several North American muskox populations (Gunn *et al.* 1991; Reynolds 1998). One reason for the lower population growth rate of the population in DM is that muskoxen in this area are killed frequently by various kinds of human activities. This happens mainly because a railroad that passes through important habitat kills up to several animals per year, and because animals that end up in populated areas are often shot. If the number of animals that are known to be killed by humans are subtracted from the mean of EN_t (eqn 1), we obtain almost a doubling of s ($\hat{s} = 0.0980 \pm 0.0186$) in DM. In contrast, the effects on $\hat{\sigma}_e^2$ was negligible ($\hat{\sigma}_e^2 = 0.0163 \pm 0.0042$). Thus, a major reason for the reduced growth rate of the muskox population in DM compared to other introduced muskox populations (see Hénaff & Crête 1989; Gunn *et al.* 1991; Reynolds 1998) was the killing of animals by humans. However, the growth rate of the DM population was still smaller than the estimates for many introduced ungulate populations (Komers & Curman 2000; Sæther *et al.* 2002b). Several events of emigration from DM to other areas (Asbjørnsen 2002) may have contributed to a reduction of the overall growth rate.

A significant proportion of the environmental stochasticity was explained by variation in climate during autumn and late winter. These climate effects remained even after accounting for the effects of known killings by humans. In correspondence with our results, survival of muskox calves in the Arctic Wildlife Refuge in north-eastern Alaska was related negatively to the snow depth in May and June (Reynolds 1998). Thus, the long-term growth rates of muskox populations are affected by stochastic climate effects operating during the nonbreeding season, as has been found for many other ungulate populations (Sæther 1997; Coulson, Milner-Gulland & Clutton-Brock 2000).

The PPI predicted a high probability of future growth of the population (Fig. 1). Several studies have indicated that uncertainties in parameter estimates may strongly influence the accuracy of the predictions (Sæther *et al.* 2000; Sæther & Engen 2002). This was not the case in the present case where neglecting uncertainties in the parameter estimates had only a small effect on the width of the PPI (Fig. 1). This illustrates one of the advantages of population studies of introduced populations, because simple models without density dependence and population estimates over a wide range of population sizes make it possible to obtain unbiased estimates of population growth rates at low densities. This is a crucial parameter, for instance in population viability analysis (Lande *et al.* 2003), that is often extremely difficult to estimate (Taylor 1995). In ungulates, long-term population growth rates at small population sizes between 0·05 and 0·20 seem typical for re-introduced ungulates (Komers & Curman 2000; Sæther *et al.* 2002b).

In most of the analyses, we assumed that the demographic variance was small enough to be ignored. However, Komers & Curman (2000) found a strong non-linear effect of propagule size on subsequent population growth that suggests that demographic stochasticity may be important. Our sensitivity analyses showed that neglecting the demographic variance led to an overestimate of σ_e^2, as has been noted previously by Engen *et al.* (2001). Because the contribution of the demographic variance to the variance in the change in population size decreases with population size (eqns 1b, b), this results in an increase in the width of PPI owing to too large estimates of σ_e^2. However, the effect was small, suggesting that demographic stochasticity is of minor importance for predicting the long-term growth of ungulate populations that have not gone extinct during the first period after introduction. This is probably related to the high adult survival rate and small litter size of larger ungulates, life-history traits that are often correlated with small demographic stochasticity (Fox & Kendall 2002; Sæther *et al.* 2004).

Nature Management and the Office for Environmental Affairs of Sør-Trøndelag county.

References

Aanes, S., Engen, S., Sæther, B.-E., Willebrand, T. & Marcström, V. (2002) Sustainable harvesting strategies of willow grouse in a fluctuating environment. *Ecological Applications*, **12**, 281–290.

Aanes, R., Sæther, B.-E. & Øritsland, N.A. (2000) Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. *Ecography*, **23**, 437–443.

Albon, S.D., Clutton-Brock, T.H. & Guinness, F.E. (1987) Early development and population dynamics in red deer. II. Density independent and cohort variation. *Journal of Animal Ecology*, **56**, 69–81.

Alendal, E. (1973) *Muskox at Dovrefjell: population dynamics, social interactions and nutritional ecology*. MSc Thesis, University of Bergen, Bergen, Norway.

Asbjørnsen, E.J. (2002) *Dynamics of an introduced muskox population in Norway*. MSc Thesis, Department of Zoology, Norwegian University of Science and Technology, Norway.

Boertmann, D., Forchhammer, M., Olesen, C.R., Aastrup, P. & Thing, H. (1992) The Greenland muskox population status 1990. *Rangifer*, **12**, 5–12.

Coulson, T., Milner-Gulland, E.J. & Clutton-Brock, T. (2000) The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. *Proceedings of the Royal Society London Series B*, **267**, 1771–1779.

Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.D., Clutton-Brock, T.H., Crawley, M.J. & Grenfell, B. (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, **292**, 1528–1531.

Dennis, B., Munholland, P.L. & Scott, J.M. (1991) Estimation of growth and extinction parameters for endangered species. *Ecological Monographs*, **61**, 115–123.

Ellner, S.P., Fieberg, J., Ludwig, D. & Wilcox, C. (2002) Precision of population viability analysis. *Conservation Biology*, **16**, 258–261.

Engen, S., Bakke, Ø. & Islam, A. (1998) Demographic and environmental stochasticity – concepts and definitions. *Biometrics*, **54**, 830–836.

Engen, S., Lande, R., Sæther, B.E. & Weimerskirch, H. (2005) Extinction in relation to demographic and environmental stochasticity in age-structured models. *Mathematical Biosciences*, **195**, 210–227.

Engen, S. & Sæther, B.-E. (2000) Predicting the time to quasi-extinction for populations far below their carrying capacity. *Journal of Theoretical Biology*, **205**, 649–658.

Engen, S., Sæther, B.-E. & Møller, A.P. (2001) Stochastic population dynamics and time to extinction of a declining population of barn swallows. *Journal of Animal Ecology*, **70**, 789–797.

Ferguson, M.A.D. & Gauthier, L. (1992) Status and trends of *Rangifer tarandus* and *Ovibos moschatus* populations in Canada. *Rangifer*, **12**, 127–141.

Fieberg, J. & Ellner, S.R. (2000) When is it meaningful to estimate an extinction probability? *Ecology*, **81**, 2040–2047.

Fox, G.A. & Kendall, B.E. (2002) Demographic stochasticity and the variance reduction effect. *Ecology*, **83**, 1928–1934.

Gaillard, J.M., Boitin, J.M., Delorme, D., Van Laere, G., Duncan, P. & Lebreton, J.D. (1997) Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia*, **112**, 502–513.

Griffith, B., Scott, J.M., Carpenter, J.W. & Reed, C. (1989) Translocation as a species conservation tool: status and strategy. *Science*, **245**, 477–480.

Gunn, A., Shank, C. & McLean, B. (1991) The history, status and management of muskoxen on Banks Island. *Arctic*, **44**, 188–195.

Hénaff, D.L. & Crête, M. (1989) Introduction of muskoxen in northern Quebec: the demographic explosion of a colonizing herbivore. *Canadian Journal of Zoology*, **67**, 1102–1105.

IUCN (1987) Position Statement on the Translocation of Living Organisms: Introductions, Re-Introductions, and Re-Stocking. IUCN Council, Gland, Switzerland.

Klein, D.R. (1992) Comparative ecological and behavioral adaptions of *Ovibos moschatus* and *Rangifer tarandus*. *Rangifer*, **12**, 47–55.

Komers, P.E. & Curman, G.P. (2000) The effect of demographic characteristics on the success of ungulate re-introductions. *Biological Conservation*, **93**, 187–193.

Laikre, L., Ryman, N. & Lundh, N.G. (1997) Estimated inbreeding in a small, wild muskox *Ovibos moschatus* population and its possible effects on population reproduction. *Biological Conservation*, **79**, 197–204.

Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity, and random catastrophes. *American Naturalist*, **142**, 911–927.

Lande, R. (1998) Demographic stochasticity and Allee effect on a scale with isotropic noise. *Oikos*, **83**, 353–358.

Lande, R., Engen, S. & Sæther, B.-E. (2003) *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford.

Leigh, E.G. (1981) The average lifetime of a population in a varying environment. *Journal of Theoretical Biology*, **90**, 213–239.

Lent, P.C. (1998) Alaska's indigenous muskoxen: a history. *Rangifer*, **18**, 133–144.

Ludwig, D. (1996a) Uncertainty and the assessment of extinction probabilities. *Ecological. Applications*, **6**, 1067–1076.

May, R.M. (1973) Stability in randomly fluctuating versus deterministic environments. *American Naturalist*, **107**, 621–650.

Myrberget, S. (1987) Introduction of mammals and birds in Norway including Svalbard. *Meddelelser fra Norsk Viltforskning*, **3**, 1–26.

Nellemann, C. (1997) Grazing strategies of muskoxen (*Ovibos moschatus*) during winter in Angujaartorfiup Nunaa in western Greenland. *Canadian Journal of Zoology*, **75**, 1129–1134.

Nellemann, C. (1998) Habitat use by muskoxen (*Ovibos moschatus*) in winter in an alpine environment. *Canadian Journal of Zoology*, **76**, 110–116.

Pedersen, C.B. & Aastrup, P. (2000) Muskoxen in Angujaartorfiup Nunaat, West Greenland. Monitoring, spatial distribution, population growth, and sustainable harvest. *Arctic*, **53**, 18–26.

Reynolds, P. (1998) Dynamics and range expansion of a re-established muskox population. *Journal of Wildlife Management*, **62**, 734–744.

Sæther, B.-E. (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology and Evolution*, **12**, 143–149.

Sæther, B.-E., Engen, S., Lande, R., Arcese, P. & Schmidt, J.N.M. (2000) Estimating time to extinction in an island population of song sparrows. *Proceedings of the Royal Society London Series B*, **267**, 621–626.

Sæther, B.-E. & Engen, S. (2002) Including uncertainties in population viability analysis using population prediction intervals. *Population Viability Analysis* (eds S.R. Beissinger & D.R. McCullough), pp. 191–212. University of Chicago Press, Chicago.

Sæther, B.-E., Engen, S., Filli, F., Aanes, R., Schröder, W. & Andersen, R. (2002b) Stochastic population dynamics of an introduced Swiss population of the ibex. *Ecology*, **83**, 3457–3465.

Sæther, B.E., Engen, S., Moeller, A.P., Weimerskirch, H., Visser, M.E. *et al.* (2004) Life history variation predicts the effects of demographic stochasticity on avian population dynamics. *American Naturalist*, **164**, 793–802.

Sæther, B.-E., Lande, R., Engen, S., Both, C. & Visser, M. (2002a) Density-dependence and stochastic variation in the dynamics of a newly established small songbird population. *Oikos*, **99**, 331–337.

Sarrazin, F. & Barbault, R. (1996) Reintroduction: challenges and lessons for basic ecology. *Trends in Ecology and Evolution*, **11**, 474–478.

Smith, T.E. (1984) Population status and management of muskoxen on Nunivak Island, Alaska. *Proceedings of the 1st International Muskox Symposium. Biological Papers University of Alaska, Special Report*, **4**, 52–56.

Solberg, E.J., Jordhøy, P., Strand, O., Aanes, R., Loison, A., Sæther, B.-E. & Linnell, J.D.C. (2001) Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. *Ecography*, **24**, 441–451.

Solberg, E.J., Sæther, B.-E., Strand, O. & Loison, A. (1999) Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology*, **68**, 186–204.

Spalton, J.A., Lawrence, M.W. & Brend, S.A. (1999) Arabian oryx reintroduction in Oman: successes and setbacks. *Oryx*, **33**, 168–175.

Spencer, D.L. & Lensink, C.J. (1970) The muskox of Nunivak Island, Alaska. *Journal of Wildlife Management*, **34**, 1–15.

Taylor, B.L. (1995) The reliability of using population viability analysis for risk classification of species. *Conservation Biology*, **9**, 551–558.

Tener, J.S. (1965) *Muskoxen in Canada: a Biology and Taxonomic Review*. Canadian Wildlife Service.

Thing, H. (1984) Food and habitat selection by muskoxen in Jameson Land, northeast Greenland: a preliminary report. *Proceedings of the 1st International Muskox Symposium. Biological Papers University of Alaska, Special Report*, **4**, 69–74.

Wolf, C.M., Garland, T. & Griffith, B. (1998) Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. *Biological Conservation*, **86**, 243–255.

Wolf, C.M., Griffith, B., Reed, C. & Temple, S.A. (1996) Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Conservation Biology*, **10**, 1142–1154.