



## Sustainable harvest strategies for age-structured Eurasian lynx populations: The use of reproductive value

Bernt-Erik Sæther<sup>a,\*</sup>, Steinar Engen<sup>b</sup>, John Odden<sup>c</sup>, John D.C. Linnell<sup>c</sup>, Vidar Grøtan<sup>a</sup>, Henrik Andrén<sup>d</sup>

<sup>a</sup> Centre for Conservation Biology, Department of Biology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway

<sup>b</sup> Centre for Conservation Biology, Department of Mathematical Sciences, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway

<sup>c</sup> Centre for Conservation Biology, Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

<sup>d</sup> Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, SE-730 91 Riddarhytta, Sweden

### ARTICLE INFO

#### Article history:

Received 28 October 2009

Received in revised form 19 April 2010

Accepted 26 April 2010

#### Keywords:

Demographic stochasticity

Lynx

Population extinction

Reproductive value

Stochastic population dynamics

Sustainable harvest strategies

### ABSTRACT

Eurasian lynx in Scandinavia are subject to regular harvest and lethal control to reduce depredation on domestic livestock and semi-domestic reindeer. Here we introduce the use of total reproductive value to model the effects of current harvest on population dynamics and to propose sustainable harvest strategies for lynx. Demographic stochasticity strongly influences lynx population dynamics. Analyses of the number of lynx shot in relation to the number of family groups registered in annual censuses showed proportional harvest in large parts of Norway because the quotas were higher at larger population sizes. In other areas of Norway the number of lynx shot was independent of population size. The analyses of the model showed that a pure proportional harvest strategy may lead to rapid extinction of lynx populations. In contrast, applying a threshold or proportional threshold harvest strategy in which no harvest occurs below a given threshold can result in the maintenance of viable populations. Thus, this study shows that harvest without any lower threshold for stopping harvest will result in rapid extinction of lynx populations. Accordingly, lynx harvest is not likely to be sustainable if the illegal killing of animals is not controlled because poaching can result in a de facto proportional harvest even at very small population sizes. Under the influence of the large demographic stochasticity in lynx populations this harvest would result in short expected times to extinction. This gives an empirical demonstration that a correct choice of harvest strategy is essential for maintenance of viable populations of harvested species. Our analyses illustrate that parameters determining the viability of small populations can be estimated from individual-based demographic data from a sample of individuals without using time series of fluctuations in population size, which facilitates quantitative analyses of how harvest or removal of individuals, e.g. for captive breeding or translocations, affect the expected lifetime of populations.

© 2010 Elsevier Ltd. All rights reserved.

### 1. Introduction

Many populations of large carnivores are subject to human exploitation. In Scandinavia, Eurasian lynx *Lynx lynx*, brown bears *Ursus arctos*, wolves *Canis lupus* and wolverines *Gulo gulo* are all subject to regular harvest by hunters or lethal control exercises to reduce the conflict level associated with depredation on free-ranging livestock (e.g. domestic sheep *Ovis aries* and semi-domestic reindeer *Rangifer tarandus*). In addition, all these species are subject to substantial rates of illegal killings (Andrén et al., 2006; Wabakken et al., 2001; Persson et al., 2009). To evaluate the conse-

quences for the viability of populations of large carnivores we need tools that can be used to predict the consequences for the population dynamics of these human induced demographic changes.

Many aspects of the life histories of large carnivores make it difficult to predict the impact that demographic changes will have on their population dynamics. A general characteristic of the life history of large carnivores is that they are, in the absence of human persecution, long lived once they have reached sexual maturity. For instance, the natural annual survival rate of adult female lynx in Fennoscandia was 92.3% (Andrén et al., 2006). In populations of such long-lived species changes in age-structures (e.g. caused by harvest) will easily result in time lags in the population dynamics (Caswell, 2001; Haridas and Tuljapurkar, 2007; Lande et al., 2003), which can erroneously be interpreted as environmental stochasticity and result in biased predictions of future population fluctuations.

\* Corresponding author. Address: Centre for Conservation Biology, Department of Biology, Realfagsbygget, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway. Tel.: +47 73590584; fax: +47 73596100.

E-mail address: [Bernt-Erik.Sather@bio.ntnu.no](mailto:Bernt-Erik.Sather@bio.ntnu.no) (B.-E. Sæther).

Another complication in the population dynamics of large carnivores is that the population dynamics are strongly influenced by stochastic effects. Studies of wolverine (Sæther et al., 2005) and brown bears (Sæther et al., 1998) have shown that demographic stochasticity, i.e. random individual variation in fitness (Lande et al., 2003), strongly influences population fluctuations, especially at smaller population sizes. Failure to account for demographic stochasticity will therefore strongly bias important features such as the risk of extinction and the critical lower threshold for the onset of harvest (Tufto et al., 1999). Furthermore, environmental stochasticity, i.e. chance events that affect the whole or part of the population simultaneously (Lande et al., 2003), are important, especially at larger population sizes (Cohen, 1977, 1979; Tuljapurkar 1990).

Thus, estimating the population growth rate and environmental stochasticity of large carnivores is difficult because annual variation in population size is influenced by temporal autocorrelations caused by fluctuations in the age-structure. These effects of age-structure, in addition to the influence of demographic stochasticity, make it often difficult to estimate population dynamical parameters such as population growth rate and environmental stochasticity from time series of population counts alone (Caswell, 2001; Lande, 1998; Lande and Orzack, 1988), even at so small population sizes that density dependence can be ignored. This occurs because changes in the age-distribution may induce fluctuations in the population size that must be accounted for. An alternative approach is to make inferences about future population fluctuations from individual-based demographic data (Caswell, 2001). However, this requires precise estimation of a large number of parameters (Fieberg and Ellner, 2001; Gross et al., 2006), no autocorrelation in the environment (Tuljapurkar and Haridas, 2006) and that fluctuations in age-structure do not induce changes in population size that may affect estimation of the population growth rate (Caswell, 2001; Haridas and Tuljapurkar, 2007; Holmes, 2001). Engen et al. (2009) showed, motivated by a suggestion by Fisher (1930), 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 based on time series of individual-based demographic data from only a sample of individuals. Thus, no population counts are necessary. An advantage with this approach is that it reduces the number of parameters necessary for characterizing the dynamics, provided that there is no density dependence in the population dynamics and no autocorrelation in the environment.

We have proposed elsewhere (Engen et al., 2001; Sæther et al., 2007a) that the concept of Population Prediction Interval may be useful in developing reliable population projections. A PPI is defined as the stochastic interval that includes the population size with a fixed probability  $(1 - \alpha)$ , where  $\alpha$  is a small number, typically of order 0.01–0.10. The advantage of this approach is that changes in expected population size, population variation due to demographic and environmental stochasticity, and uncertainties in parameter estimates all affect the width of the PPI. Large uncertainties in parameter estimates as well as strong stochastic influences on the population dynamics will typically result in a wide PPI. Furthermore, the width of the PPI will also increase through time until some stationary distribution is reached (see examples in Sæther et al. (2007a)). Another advantage of this approach is that PPI relates directly to the IUCN's ([www.iucnredlist.org/info/categories\\_criteria](http://www.iucnredlist.org/info/categories_criteria)) criteria E for quantitative classification of population extinction risk. For instance, a population is defined as vulnerable, i.e. it has a 10% probability of extinction within 100 years, if the lower 10% quantile of PPI decreases below one before 100 years. The PPI is found by parametric bootstrapping from the

sampling distributions of the parameter estimates, which is now commonly used in population viability analyses (Holmes, 2004; Holmes et al., 2007). This method has previously been used to explore management strategies for wolverines and brown bears in Scandinavia (Sæther et al., 1998, 2005; Tufto et al., 1999).

In this paper we will use temporal variation in the reproductive value of a sample of individuals to estimate the population growth rate as well as the influence of demographic and environmental stochasticity on the population dynamics of Eurasian lynx in Norway (Hedmark county) in which long-term demographic data are available (Andrén et al., 2002, 2006), using the approach of Engen et al. (2009). We also include a similar analysis of the Sarek population in Sweden, which, we believe, has demographic characteristics also representative for lynx in northern Norway. In Norway, lynx are actively managed and harvested in many parts of the country to limit the predation on free-ranging domestic sheep and semi-domestic reindeer (Herfindal et al., 2005). We will apply the estimates of the demographic traits to evaluate, by using the PPI-approach, the current management regimes of lynx in different management regions of Norway and suggest sustainable harvest strategies to secure viable lynx populations in Norway.

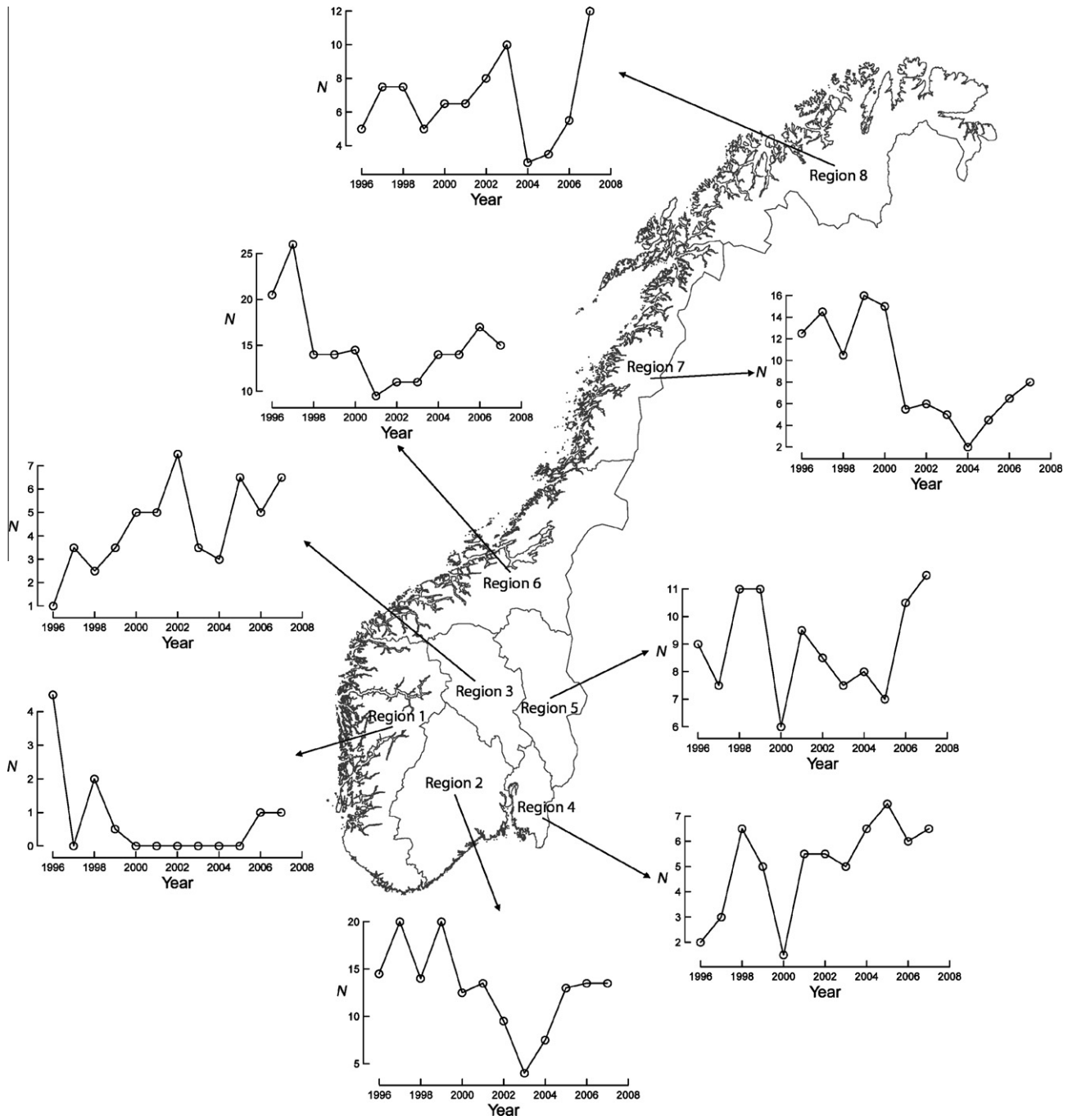
## 2. Management practices of lynx in Norway

Lynx in Norway have recovered during the last 20 years from mid 20th century lows when they were confined to two small relict populations (Linnell et al., 2010). Today they have expanded to cover most of the country, with the exception of the extreme southwest. The Norwegian population is currently around 500 animals, and has broad connectivity to the larger Swedish population, resulting in a total population size of around 1800–2000 lynx. Only limited exchange has been documented with the adjacent Finnish population. In response to widespread depredation on free-ranging sheep and semi-domestic reindeer (Odden et al., 2002; Pedersen et al., 1999), as well as concern among hunters about the impact of lynx on roe deer populations (Melis et al., 2010), the size of the population is regulated through quota regulated harvest (season is February and March). The last parliamentary white paper (2003) delegated responsibility for lynx harvest management to politically appointed committees in each of eight management regions (Fig. 1). Each management region has an own population target for the number of reproductive lynx (family groups) that are meant to be present each year. This target is technically both a minimum and a maximum. The total population is censused each year using a combination of methods, but is mainly based around obtaining counts of the number of family groups through track surveys on snow (Linnell et al., 2007a,b). However, the timing of monitoring activities is such that the results of that winters census activity (reflecting the previous summers reproduction) are not available when quotas are set (around January), forcing managers to use results from the previous year (Linnell et al., 2010).

## 3. Model

### 3.1. Population model

We consider a model in which census occurs just prior to reproduction. Then the first age-class will be one-year-old individuals and fecundity is equal to the number of new recruits (i.e. 1 year old individuals) entering the population. For simplicity let us consider a model with only two categories of animals, where  $N_0$  and  $N_1$  denote the number of individuals of each age-category. The next years population ( $N'_0, N'_1$ ) in terms of the present population ( $N_0, N_1$ ) is then



**Fig. 1.** The location of different lynx management regions in Norway. The panels show the annual fluctuations in the number of family groups  $N$ . Region 1 constitutes the counties of Vest-Agder, Rogaland, Hordaland and Sogn & Fjordane, region 2 the counties of Vestfold, Buskerud, Telemark and Aust-Agder, region 3 the county of Oppland, region 4 the counties of Østfold, and Oslo & Akershus, region 5 the county of Hedmark, region 6 the counties of Møre & Romsdal, Sør-Trøndelag and Nord-Trøndelag, region 7 the county of Nordland and region 8 the counties of Troms and Finnmark.

$$N'_0 = L_{00}N_0 + L_{01}N_1$$

$$N'_1 = L_{10}N_0 + L_{11}N_1,$$

where  $L_{ij}$  is a projection matrix (Caswell, 2001),  $L_{00}$  and  $L_{01}$  are the fecundities and  $L_{10}$  and  $L_{11}$  are the survivals. If individuals in category 1 survive, they stay in this category representing the adult population. Here we apply the theory of Engen et al. (2009) to estimate the mean matrix as well as the demographic and environmental variance components of each age-class.

Writing  $B_i$  and  $J_i$  for the number of offspring and the indicator of survival for an individual in age-class  $i$ , the stochasticity in the model can be expressed by the environmental fecundity components  $f_{eij} = \text{cov}[E(B_i|Z), E(B_j|Z)]$ , where  $Z$  is a vector with temporal fluctuations representing the state of the environment in a given year and  $E$  denotes the expectation with respect to  $Z$ . Similarly, the environmental survival components are  $s_{eij} = \text{cov}[E(J_i|Z), E(J_j|Z)]$ . An important component of the dynamics is also the covariation between fecundity and survival (Sæther and Bakke, 2000; van Tienderen, 1995), which is  $c_{eij} = \text{cov}[E(J_i|Z), E(B_j|Z)]$ .

Similarly, the dynamics of an age-structured population are also influenced by different age-specific components of the demographic stochasticity as well as the interaction among them in a given year (Engen et al., 2005). There are three different types of age-specific demographic variance components  $f_{di} = \text{Evar}(B_i|Z)$ ,  $s_{di} = \text{Evar}(J_i|Z)$  and  $c_{di} = \text{Ecov}(J_i, B_i|Z)$ . These components are estimated using the reproductive value by the method developed by Engen et al. (2009).

The expected change in the population size during one year is found by replacing the  $L_{ij}$  by the estimated mean matrix. The stochasticity in terms of variances and covariances is given by the relations (Engen et al., 2009).

$$\text{var}(N'_0|N_0, N_1) = \sum_{ij} N_i N_j f_{eij} + \sum_i N_i f_{di},$$

$$\text{var}(N'_1|N_0, N_1) = \sum_{ij} N_i N_j s_{eij} + \sum_i N_i s_{di},$$

$$\text{cov}(N'_0, N'_1|N_0, N_1) = \sum_{ij} N_i N_j c_{eij} + \sum_i N_i s_{ci}.$$

These expressions can be used to simulate the two-dimensional stochastic process with environmental and demographic stochasticity using the normal approximation for the distribution of  $(N'_0, N'_1)$  conditioned on the population the previous year.

To perform predictions of future population sizes and extinctions under different harvesting strategies we need estimates for the environmental and demographic variance of the total population (Engen et al., 2007, 2009). The stochastic individual vital rates  $B_i$  and  $J_i$  will in general have a complex structure of dependence generated by a fluctuating environment as well as dependence between survival and reproduction of a single individual. This is a difficulty when it comes to analyzing how these vital rates contribute to the environmental and demographic variance of the population and to the uncertainty in future population sizes. Here we use the approach of Engen et al. (2009) for estimating these variances and their components based on the concept of individual reproductive value, defined as each single individual's stochastic contribution to the total reproductive value of the population the next year.

### 3.2. Harvest strategies

Here we analyse the effects of adopting three different harvest strategies: (1) proportional harvesting (Lande et al., 1997), (2) threshold harvesting (Lande et al., 1997) and (3) proportional threshold harvesting (Engen et al., 1997; Tufto et al., 1999). For all three harvest strategies the harvested females are assumed to be chosen at random since the hunters typically are unable to visually differentiate between the age and sex of lynx in a hunting situation. Proportional harvesting implies that a certain fraction  $p$  of the females is harvested each year. Under threshold harvesting the population  $N_0 + N_1$  is harvested down to a threshold  $c$  if  $N_0 + N_1 > c$ , otherwise no hunting occurs. Proportional threshold harvesting has in particular been shown to be a good strategy when the population estimates  $\hat{N}_0$  and  $\hat{N}_1$  are uncertain (Engen et al., 1997), in which case the harvest is  $(\hat{N}_0 + \hat{N}_1)a$  when  $\hat{N}_0 + \hat{N}_1 > c$ , and otherwise there is no harvest.

## 4. Methods

### 4.1. Individual-based demographic studies

This study is based on individual data obtained from radio-collared lynx from the county of Hedmark in Norway (Fig. 1) and Sarek in northern Sweden. The northernmost area Sarek is partly

located within the Sarek National Park around Kvikkjokk in the county of Norrbotten (67°N 17°40'E) and consists of a mixture of coniferous forests, mountain birch *Betula* sp forests and alpine tundra. The Norwegian area is situated in the county of Hedmark (61°15' N 11°30'E) in southeastern Norway. The topography of this county is dominated by several parallel river valleys running from north to south. About 72% of the area consists of coniferous forests with the rest being bogs and agricultural land. For further descriptions of the study areas, see Andrén et al. (2002, 2006) and Linnell et al. (2001).

A total of 45 lynx in Hedmark (1995–2000) and 89 lynx in Sarek (1993–2007) were captured and fitted with radio-collars. In both areas lynx were captured using several methods, including darting from helicopters, box-traps, foot-snares placed at fresh kills and by using dogs to chase lynx into trees. The captured lynx were immobilized and equipped with a radio-collar or an implanted radio-transmitter, usually with a mortality function. The lynx were radio-tracked at least 2–4 times per month, but normally more often. In June the reproductive status of all female lynx was checked by localisation of the female on foot and counting the kittens in the natal lair. The mortality of kittens within a family group during the first year of life was assessed either by the confirmed death of radio-implanted kittens or by the loss of kittens between birth and snow-tracking in February (Arnemo et al., 1999). The handling protocol for lynx has been examined by both the Swedish Experimental Animal Ethics Committee and the Norwegian Experimental Animal Ethics Committee and fulfils their ethical requirements for research on wild animals.

In the analyses we included data on all lynx that were not killed through regular legal harvest or control. Illegal killings and traffic collisions constitute important components of the mortality of the lynx (Andrén et al., 2006) and are important for assessing the consequences of choice of harvest strategy. In total, reproduction and survival of adult (>2 years old) lynx females was followed for 45 lynx-years and 100 lynx-years in Hedmark and Sarek, respectively.

### 4.2. Population censuses

In most of Norway, lynx are censused by counts of reproductive units, termed family groups. This method is based on the fact that kittens stay with their mothers until they are 10 months old. Adult female lynx are strictly territorial (Breitenmoser et al., 1993). In such a solitary species tracks in the snow from two or more individuals travelling together are likely to represent a family group. Such counts are done during the period December–February 2–3 days after a snowfall. This method gives reliable estimates of the number of reproducing females in an area (Linnell et al., 2007a,b). An analysis of the structure of the population and losses of kittens based on radio-collared females indicated that an average of 54% of the adult females had offspring in February (Andrén et al., 2002).

### 4.3. Estimation of population parameters

Following Engen et al. (2009) our method is based on observations of individual reproductive value for each individual, defined as

$$W_{ij} = J_{ij} v_{i+1} + B_{ij} v_i,$$

where  $t$  is time,  $i$  is age-class,  $j$  is the numbering of individuals for a given time and age, and  $v_i$  is the reproductive value of an individual in age-class  $i$  calculated from the mean projection matrix (Caswell, 2001). In the present model  $v_3 = v_2$  by definition. The age-specific components  $\sigma_{di}^2$  of the total demographic variance  $\sigma_d^2$  are defined

as the temporal mean of the within year variance of individual reproductive value of individuals in age-class  $i$ . The total demographic variance is then  $\sigma_{di}^2 = \sum u_i \sigma_{di}^2$ , where  $u_i$  is the mean proportion of individuals in age-class  $i$ ,  $i = 1, 2$ , which is the stable age distribution calculated from the mean projection matrix (Caswell, 2001; Lande et al., 2003). For a set of observations of female offspring  $B_{tij}$  and the indicators  $J_{tij}$  of survival, an unbiased estimator for the demographic component a given year  $t$  with environment  $Z$  defined as  $\sigma_{di}^2(Z) = \text{Evar}(W_{tij}|Z)$  is the simple sum of squares

$$\hat{\sigma}_{di}^2(Z) = \frac{1}{n_{ti} - 1} \sum_{j=1}^{n_{ti}} (W_{tij} - \bar{W}_{ti})^2,$$

where  $n_{ti}$  is the number of individuals in age-class  $i$  recorded in year  $t$  and  $\bar{W}_{ti} = n_{ti}^{-1} \sum_{j=1}^{n_{ti}} W_{tij}$ . Estimates  $\hat{\sigma}_{di}^2$  of each  $\sigma_{di}^2$  are computed as the mean value of the above estimates over years with at least two recordings from individuals in the actual age-class, weighted by  $n_{ti} - 1$ , and the estimate of the total demographic variances is  $\hat{\sigma}_d^2 = \sum u_i \hat{\sigma}_{di}^2$  (Engen et al., 2009). The estimator  $\hat{\sigma}_{di}^2(Z)$  can further be decomposed into three components, writing

$$(W_{tij} - \bar{W}_{ti})^2 = (J_{tij} - \bar{J}_{ti})^2 v_{i+1}^2 + (B_{tij} - \bar{B}_{ti}) v_1^2 + 2(J_{tij} - \bar{J}_{ti})(B_{tij} - \bar{B}_{ti}) v_{i+1} v_1$$

so that the corresponding sums are estimates of the components of demographic variance due to stochastic survival, stochastic fecundity, and the covariation among these.

Environmental covariance components  $\sigma_{eij}^2$  are defined as the temporal covariance of the yearly mean of individual reproductive values for age-classes  $i$  and  $j$ . The total environmental variance is then  $\sum u_i u_j \sigma_{eij}^2$ . In order to estimate the environmental components Engen et al. (2009) proposed considering the two bivariate observations  $(W_{tij}, W_{ujm})$  and  $(W_{til}, W_{ujm'})$  at times  $t \neq u$ , where  $i$  and  $j$  may refer to any age-classes. If  $i = j$  it is required that  $l \neq l'$  and  $m \neq m'$ . Otherwise these are any pair of individuals in the actual class. Then,  $\frac{1}{2}(W_{til} - W_{ujm})(W'_{til} - W_{ujm'})$  is an unbiased estimator for  $\sigma_{eij}^2$ . Hence, an efficient unbiased estimator for this parameter is the mean value of the above cross-product over all combinations of  $t, u, l, l', m, m'$ , which is straightforward to compute although the number of terms may be quite large.

Estimation of the age-specific environmental components due to survival and fecundity and the covariation between them can be done in a similar way using the recordings of  $J_{tij}$  and  $B_{tij}$ . The survival and fecundity components  $f_{eij}$  and  $s_{eij}$  of the demographic variance components are estimated by sum of squares as above with  $W$  replaced by  $J$  and  $B$ , respectively. The covariance terms are estimated by the corresponding mean value of the cross-products  $\frac{1}{2}(J_{tij} - \bar{J}_{tim})(B_{tijl'} - B_{ujm'})$ , which has expected value  $c_{eij}$ .

When the mean proportion of females  $Q$  among newborns is known and the female's total numbers  $X_{tij}$  of offspring are recorded, a more efficient estimator is obtained by replacing the sum of squares by the expected value of this statistic given the data, that is, replacing each term by their expected value given the data. From the theorem of double expectations the estimators obtained in this way are still unbiased. Omitting indices we then have to consider properties of  $W$  given the recordings of  $X$ , where  $B$  conditioned on  $X$  is binomially distributed with parameters  $(X, Q)$ . Consequently,  $E(B|X) = QX$ ,  $\text{var}(B|X) = XQ(1 - Q)$  and  $E(B^2|X) = Q^2X^2 + XQ(1 - Q)$ . The three components of the estimator of demographic variance should now be replaced by their expected value given the data  $X_{tij}$ . The first (survival) component should then be kept unchanged, and in the third  $B$  should be replaced by  $QX$ . The second must also be replaced by its expectation given the data.

$$E \sum (B_j - \bar{B})^2 = E \sum B_j^2 - nEB^2,$$

where the indices  $ti$  have been omitted. Using the above expressions for the conditional means and variances given the  $X_j$  we find

$$E \sum (B_j - \bar{B})^2 = \sum (QX_j)^2 - \frac{1}{n} \left( \sum QX_j \right)^2 + \frac{n-1}{n} X_j Q(1 - Q).$$

For the components of environmental stochasticity all products of factors  $B$  that are independent when conditioned on the data. Hence, we simply need to replace  $B$  by its expectation  $QX$  everywhere.

## 5. Results

### 5.1. Demographic parameters

The population growth rate omitting individuals which were killed during regular (legal) hunter harvest, was significantly larger than one for the population in Sarek (Table 1), whereas the bootstrap distribution  $\lambda$  contained a large proportion of small values of  $\lambda$  in Hedmark.

The population dynamics of the lynx were influenced by stochastic effects. In both areas the demographic variance was significantly larger than one, irrespective of whether fecundity was estimated from numbers of kittens born or kittens recruited (Table 1). There was no significant environmental stochasticity present in either of the two study areas (Table 1), although the environmental variance was considerably larger in Sarek.

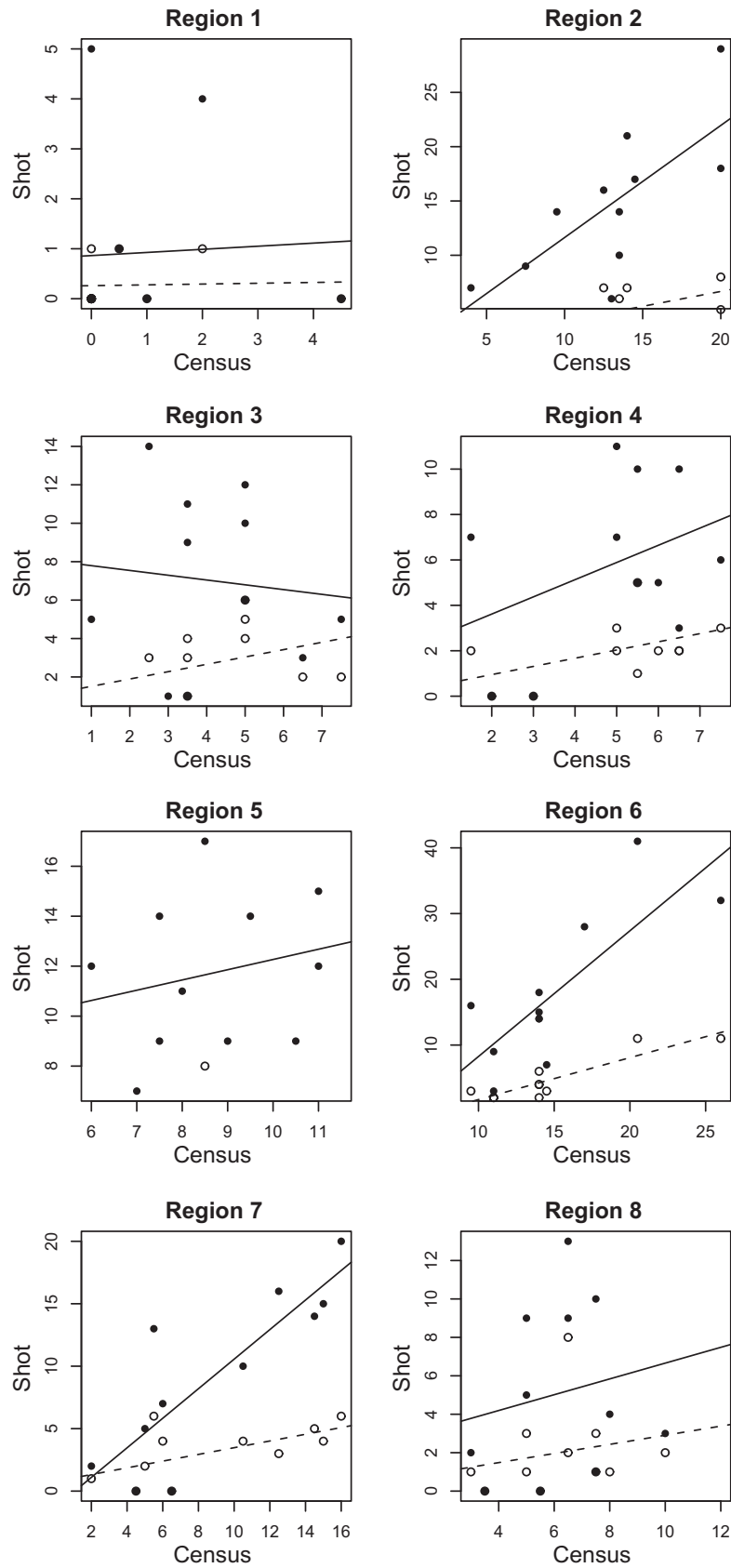
### 5.2. Harvest dynamics

In all Norwegian management regions the change in the number of family groups from year  $t$  to year  $t + 1$  was negatively related to population size in year  $t$  (the slope was significantly less than 0 in 6 out of 8 management regions), which could suggest the presence of density dependence in the lynx population dynamics. However, fluctuations in the size of the Norwegian lynx population were strongly influenced by annual variation in the number of animals killed by humans. In management regions 2–8 in Norway (Fig. 1) lynx are subject to regular harvest regulated by quotas (Linnell et al., in press). This quota-system can induce a relationship between the number of lynx harvested and variation in population size and thus cause a confounding effect with the density dependent feed-back mechanisms in the population dynamics (Fryxell et al., 1988). This can occur in two different ways. If the harvest

**Table 1**

Estimates of demographic parameters for lynx populations in Hedmark and Sarek based on the dynamics of reproductive values;  $\lambda$  is the population growth rate,  $\sigma_d^2$  is the demographic variance with components due to random variation in survival  $\sigma_{ds}^2$  and reproduction  $\sigma_{df}^2$ , and  $\sigma_e^2$  is the environmental variance. The values in brackets denote 95% confidence intervals, obtained by bootstrapping. The census was assumed prior to reproduction and the model contains two age-classes (1 year old and 2 year old or older females) with fecundity measured as the number of females recruited to the population.

Parameter	Population	
	Sarek	Hedmark
$\lambda$	1.09 (1.00–1.17)	1.06 (0.93–1.19)
$\sigma_d^2$	0.312 (0.240–0.420)	0.309 (0.170–0.490)
$\sigma_{ds}^2$	0.125 (0.079–0.170)	0.197 (0.076–0.330)
$\sigma_{df}^2$	0.158 (0.128–0.217)	0.115 (0.090–0.172)
$\sigma_e^2$	0.019 (–0.006–0.054)	0.000 (–0.027–0.026)



**Fig. 2.** The relationship between the number lynx shot and the recorded number of family groups registered the previous year in different management regions of Norway (see Fig. 1 for their location). Solid line and filled circles denote total number of legally shot lynx, whereas open circles and dashed lines denote number of shot  $\geq 1$  year old females.

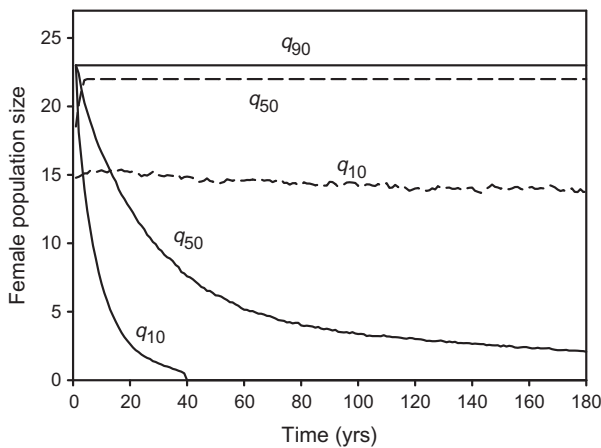
success is determined by the number of lynx present, we should expect a relationship between the number of lynx shot and the population size during the harvest period. A significant relationship was found between the total number of shot and population size in region 6 (slope  $b = 2.03$ ,  $P = 0.002$ ) and in region 7 ( $b = 0.83$ ,  $P = 0.0455$ ). In region 6 the number of shot adult females was also positively related to population size ( $b = 0.60$ ,  $P = 0.010$ ). The other way fluctuations in population size can affect the harvest is if the size of the quota determines the number of lynx that are shot. In this case we would expect a positive relationship between the population size and the size of the quota and hence the number of animals shot the following year. The size of the quota was significantly related to the number of family groups recorded the previous year in region 6 ( $b = 2.59$ ,  $P < 0.001$ ) and in region 7 ( $b = 1.62$ ,  $P < 0.001$ ). Furthermore, a significant relationship was found between the total number of lynx as well as the number of adult females that were shot and the population size the previous year in these two regions (Fig. 2). Such a relationship was also present in region 2. Thus, over large parts of Norway (Fig. 1) the number of lynx killed legally is determined by the size of the quotas.

These analyses show that the population fluctuations of the lynx are strongly influenced by a density dependent effect of changes in the size of the quotas. To examine whether this human-induced variation also can explain the density dependent variation in annual changes in population size, we regressed the change in total population size from year  $t + 1$  to year  $t$  also including the number of shot animals in year  $t$  on the population size in year  $t$  (Sæther et al., 2007b). In all regions this relationship was insignificant ( $P > 0.2$ ), both when using the total number individuals shot and the number of shot adult females as estimates for the harvest effort. These analyses strongly indicate that the density dependence in population dynamics of the Norwegian lynx is strongly affected by management decisions related changes in

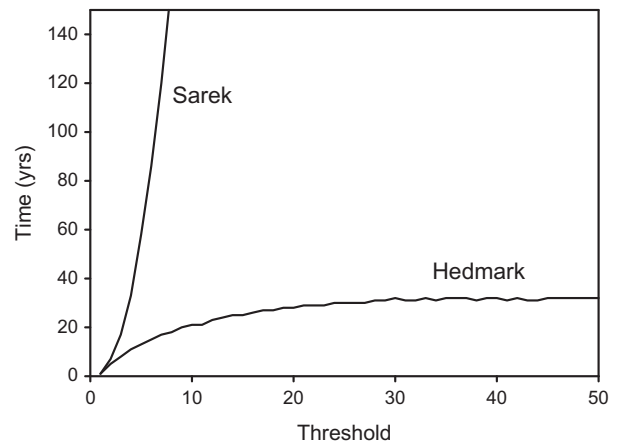
the quotas and not by density dependence in demographic feedback mechanisms.

### 5.3. Sustainable harvest strategies

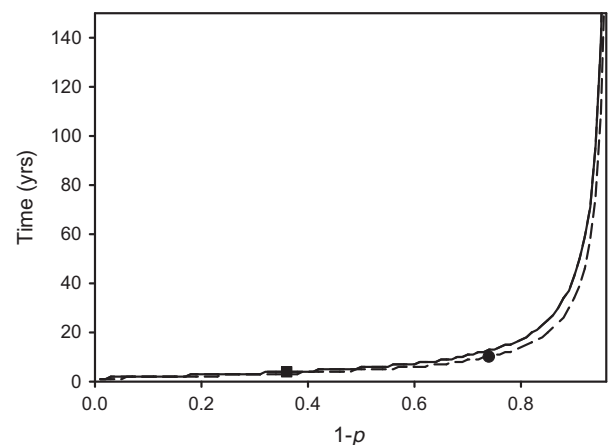
We explored the sustainability of the current harvest strategies by simulating the future population fluctuations based on bootstrap replicates of the demographic parameters estimated for the Hedmark population. In this county the minimum (politically determined) threshold for the population size is 10 family groups. Based on the proportion of adult females that have kittens (Andrén et al., 2002), this represents an adult population size of 19 adult ( $\geq 2$  years old) females. Assuming a stationary age-distribution eight one-year-old females are also assumed to be present. As ex-



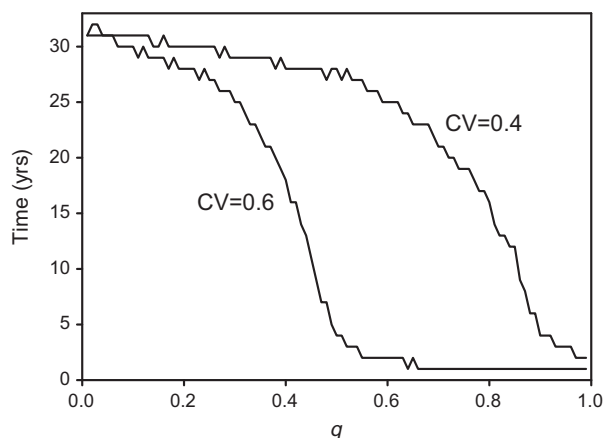
**Fig. 3.** Prediction of population fluctuations of lynx in the county of Hedmark (region 5 in Fig. 1) (solid lines) and in the county of Nordland (region 7 in Fig. 1) (dashed lines) under threshold harvesting.  $q_{10}$ ,  $q_{50}$  and  $q_{90}$  denote the 10%, 50% and 90% quantiles of the population prediction interval (PPI). For the northern population demographic characteristics were assumed to be similar to those estimated from the Sarek population in northern Sweden (Table 1). In both areas the threshold is set at 10 reproductive females (i.e. females recorded during winter with kittens). We assume that this represents 54% of the adult ( $\geq 2$  years old) females actually present in the population (Andrén et al., 2002). Furthermore, we assume that based on the structure of the stable age-distribution that 1 year old females constitute 28% and 23% of the female segment of the population in the county of Hedmark and the counties of Nordland and Troms, respectively. This gives a threshold of 27 and 25 one year or older female lynx in Hedmark and Sarek, respectively. The simulations were done using the population counts in 2007 as initial population size and that harvest occurred according to the proportion of each age-class in the population.



**Fig. 4.** The time it takes for the lower 10% quantile of the population prediction interval  $q_{10}$  to reach 1 female in relation to the harvest threshold of females ( $\geq$  one-year-old)  $c$  for the populations in Hedmark and Sarek. We assume the same initial sizes of the populations (eight 1 year old and 19 adult ( $\geq 2$  years old) females). No harvest occurs below the harvest threshold and all females above the threshold are immediately harvested ( $p = 1.0$ ).



**Fig. 5.** The time it takes for the lower 10% quantile of the population prediction interval  $q_{10}$  to reach 1 female in relation to the proportion remaining  $(1 - p)$  after proportional harvest with proportion  $p$  of females ( $\geq 1$  year old) for the populations in Trøndelag (region 6 in Fig. 1) (stripped line) and in the county of Nordland (region 7 in Fig. 1) (solid line). We assume the initial size of 11 one-year-old and 28 adult ( $\geq 2$  years old) females and 6 one-year-old and 28 adult females in regions 6 and 7, respectively, which was assumed to represent the structure of the winter population in 2007. For region 6 we used the demographic data estimated in Hedmark as input, whereas the demography in Sarek was assumed to be typical for region 7. The square and circles represent the estimated harvest rates in regions 6 and 7, respectively (see Fig. 2).



**Fig. 6.** The time it takes for the lower 10% quantile of the population prediction interval  $q_{10}$  to reach 1 female in relation to the proportion of the animals above the threshold  $c=23$  that is removed in Hedmark for different uncertainties in the population estimates (CV). We assume an initial size of the populations of 8 one-year-old and 19 adult ( $\geq 2$  years old) females. No harvest occurs below the threshold.

pected from the large uncertainties in the parameter estimates and the large demographic stochasticity (Table 1), the prediction intervals soon become wide (Fig. 3). However, the simulations show that if the minimum number of 10 reproductive adult females is used as a threshold and if the population size is harvested down to this threshold, the lower 10% quantile is below 1 already after 34 years. Similarly, the population will have a 50% probability of extinction after 273 years.

Assuming that the demographic characteristics of the lynx population in Nordland county (region 7 in Fig. 1) are similar to that of the Sarek population, a threshold harvest strategies with no harvest when less than 10 family groups are recorded, will result in stationary fluctuations between 15 and 23 one year or older females (Fig. 3). In general, a threshold harvest strategy for populations with demographic characteristics similar to the Sarek population will ensure viable populations even for relatively low values of the threshold (Fig. 4). In contrast, the population in Hedmark is likely to go extinct even if a large threshold is chosen. However, assuming a proportional harvesting strategy, extinction is likely irrespective of the demographic characteristics of the population (Fig. 5). For instance, the rate of proportional harvest estimated in regions 6 and 7 over the past years (Fig. 2) will give short times to extinction (Fig. 5).

Uncertainties in population estimates provide another complication. Large observation errors in population estimates require more careful harvesting and Engen et al. (1997) proposed that proportional threshold harvesting should be applied if the population estimates are uncertain. For the lynx in Hedmark, uncertainties in the population estimates strongly affected the time to extinction (Fig. 6). For a coefficient of variation in the population estimate of 40%, removal of more than 60% of the population above the threshold of 27 female lynx will lead to a rapid increase in the risk of extinction. For more uncertain population estimates this increase in extinction risk will occur even if the proportion of the population removed above the threshold  $a$  is smaller.

## 6. Discussion

In this paper we have used annual fluctuations in the reproductive value from a sample of individuals to estimate the demographic characteristics of two lynx populations. We utilized the simple dynamic properties of Fisher's total reproductive value

(Fisher, 1930) as outlined by Engen et al. (2007, 2009). In an age-structured population the total population size will show transient fluctuation due to stochastic fluctuations in the age-structure (Caswell, 2001). The reproductive value serves as a filter removing these fluctuations, the difference between the total reproductive value and the total population size being a process fluctuating around zero with a return time to zero at the order of one generation. This suggests that this method can be useful in estimating crucial population parameters for management of small populations of endangered species such as many large carnivores using individual-based data from only a sample of individuals in the population. However, obtaining reliable estimates of especially the components of the environmental stochasticity require quite large samples of individuals over several years and that there is no autocorrelation in the environment.

The importance of such an approach that accounts for age-structure effects in viability analyses of small populations of large carnivores is illustrated by the estimated large values of demographic variance for the lynx populations (Table 1). Similar large effects of demographic stochasticity on the population dynamics have also been estimated for other large carnivore species (Sæther et al., 1998, 2005), implying that the stochastic fluctuations in age-structure may be considerable. Also, since adult survival is high (Andrén et al., 2006), the generation time and return time to equilibrium is likely to be large. Therefore, working with population size and not reproductive value would lead to considerable errors in the estimates of parameters describing the stochasticity and hence also lead to erroneous predictions of time to extinction under different harvesting strategies.

The approach of Engen et al. (2009) used in this study estimating population parameters from fluctuations in the total reproductive value of the population assumes no density dependence in the population dynamics. If the demographic traits are related to fluctuations in population size, this can easily lead to complex dynamical patterns in age-structured populations (Lande et al., 2006). Our analyses show that a large population size is followed by a decrease in population size the following year in most of the management regions in Norway (Fig. 1), but that this relationship is caused by an increase in human-induced killings at larger population sizes (Fig. 2). Furthermore, our individual-based data were also collected in two populations (Sarek and Hedmark) in which legal harvest and illegal killings of females were frequent (Andrén et al., 2006), suggesting that these populations were kept far below the carrying capacity (Andrén and Liberg, 2008). Accordingly, the estimated population growth rate based on individual-based demographic data was positive (Table 1) and the estimates of the stochastic components were well within the range for species with similar kinds of life histories (Lande et al., 2003; Sæther et al., 1998, 2004, 2005). This indicates that our parameter estimates were not biased by density dependent effects.

Our analyses also assume that the management regions (Fig. 1) represent separate biological units with no interchange of individuals among the populations. This is obviously not the case because radio-collared lynx frequently move over longer distances. Natal dispersal distances of up to 400 km have been documented (Andersen et al., 2005). Thus, the predictions of time to extinction (Figs. 3–6) will be strongly influenced by immigration of lynx from surrounding areas. However, including spatial dynamics into harvest models requires several specific assumptions about the pattern of interchange of individuals among sub-populations and the spatial distribution of critical resources affecting the population growth rate (Jonzén et al., 2001; Robinson et al., 2008). For instance, dynamics in space are strongly influenced by the patterns of density dependence in the dispersal rate (Sæther et al., 1999). Such data are not yet available for any Eurasian lynx population, or in fact for any felid.



In general, the uncertainties in the parameter estimates were large (Table 1). One reason for this was that it was possible to obtain data for only a few one-year-old individuals and that the study period was relatively short, especially in Hedmark. However, some patterns were still evident. First, the population growth rate  $\lambda$  was significantly larger than one in the Sarek population but not so in the Hedmark population (Table 1). However, both estimates were quite similar to the estimates obtained by Andrén et al. (2006) when females that were poached and killed by traffic were included. Second, demographic stochasticity had a considerably influence on the population dynamics of the lynx. The estimates of the demographic variance in both populations were of similar magnitude, but somewhat higher than previously recorded for vertebrates with similar generation times (Lande et al., 2003, 2006; Sæther et al., 2004, 2005, 2007b) with relatively equal contributions from fecundity and survival. Third, there were some indications of larger environmental stochasticity in Sarek than in Hedmark (Table 1). This is probably due to fact that lynx are resident, whereas the main prey, the semi-domesticated reindeer, migrate between summer- and winter-ranges (Danell et al., 2006). This migratory behaviour makes the number of reindeer remaining in the study area during winter vary substantially from year to year (Pedersen et al., 1999). Thus, the approach using reproductive value seems useful for comparing the variance components of the dynamics of the different populations.

The differences in demography were related to differences in the predicted outcome of a chosen harvest strategy. If we assume the demography of the Hedmark population, the lower 10% quantile of the prediction interval will soon reach the extinction barrier (Fig. 3). Even when a large harvest threshold is chosen, this time will be short (Fig. 4). One reason for this effect is that the large uncertainties in the estimates of  $\lambda$  will result in many bootstrap replicates with  $\lambda < 1$  (Table 1). This illustrates the importance of including uncertainties in the parameter estimates when projecting future growth of populations. In contrast, because  $\lambda$  was larger than one in most of the bootstrap replicates (Table 1), the Sarek population was much more resilient to harvest (Figs. 3 and 4). This was mainly due to higher survival of one-year-old radio-collared females included in our data in Sarek than in Hedmark.

In three of the Norwegian management regions we found evidence for proportional harvest with a 1 year delay in the response to changes in population size (Fig. 2). Our simulations showed that such a harvest strategy will decrease the viability of lynx populations dramatically, irrespective of demographic characteristics (Fig. 5). This supports previous theoretical analyses (Sæther et al., 1996; Lande et al., 1997), which showed that proportional harvest gives shorter times to extinction than threshold harvesting. This assumes that the population sizes are exactly known. This is obviously not the case for the lynx (Andrén et al., 2002; Linnell et al., 2007b). If the census-errors are large, only a proportion of the individuals above the harvest threshold should be removed (Fig. 6). Thus, we recommend that lynx populations, if harvested, should be managed according to a threshold harvest strategy or a proportional threshold harvest strategy (Engen et al., 1997).

The choice of a threshold harvest strategy implies that no harvest occurs if the population decreases under a certain threshold. This requires no poaching, which reduces survival considerably in many areas of Scandinavia (Andrén et al., 2006). Accordingly, several of the females included in the present study were illegally shot. Thus, this offtake reduced the estimates of  $\lambda$  and should lead to a more cautious harvest strategy than under conditions with no poaching. If a threshold harvest strategy is implemented with no control of the illegal hunting this may result in a de facto proportional harvest, which will drive the population rapidly to extinction (Fig. 5). This occurs because killing of only a few individuals will constitute a large proportion of the population at small population

sizes. Furthermore, demographic stochasticity influences the dynamics of lynx (Table 1). Illegal harvest will also affect the estimates of the demographic variance. If poaching increases the variation among females in important fitness components such as recruitment or survival, illegal harvest will increase the stochastic components of the dynamics. This will in turn reduce the time to extinction (Lande, 1998). Thus, illegal harvest will affect the deterministic and stochastic component of the population dynamics that should be accounted for when choosing harvest strategies, and no sustainable harvest of lynx can occur if the illegal offtake of animals is not stopped or dramatically reduced.

The goal for managing lynx in the different regions is the number of family groups, i.e. the number of females that are recorded with kittens during winter. In our analyses of the harvest strategies we have assumed that this represents about half of the actual adult females present in an area. This proportion will be influenced by the losses of kitten during their first period of life as well as the proportion of adult females that reproduce. As this proportion varies, it will affect the threshold which is necessary for obtaining viable lynx populations (Fig. 5). Furthermore, the presence of observation error will influence the choice of harvest strategy (Engen et al., 1997; Sæther et al., 2005; Tufto et al., 1999) and should lead to a more cautious harvest strategy (Fig. 6). It is therefore important to complement the extensive census programmes with demographic studies of individually known lynx females which can improve our knowledge of basic demographic variables as well as the precision of the winter censuses.

To summarize, these analyses of the lynx illustrate that parameters determining the viability of small populations can be estimated from individual-based demographic data from a sample of individuals without using time series of fluctuations in population size. This represents an important advantage in population viability analyses because this allows quantitative analyses of the effects on the expected lifetime of populations in which continuous time series of population counts are not available because of harvest or removal of individuals, e.g. for captive breeding or translocations. Furthermore, because relatively few parameters are involved, it is relatively easy to perform sensitivity analyses of the robustness of predictions for population growth to uncertainty in the parameter estimates or to violation of critical assumptions.

## Acknowledgements

The Norwegian field study was funded by the Directorate for Nature Management, the Research Council of Norway and the Offices of Environmental Affairs in the counties of Oslo & Akershus, Østfold, Hedmark, Oppland, Buskerud and Telemark. The Swedish field study was funded by the Swedish Environmental Protection Agency, the World Wide Fund for Nature (Sweden) and the local government of Norrbotten County.

## References

- Andersen, R., Odden, J., Linnell, J.D.C., Odden, M., Herfindal, I., Panzacchi, M., Høgseth, Ø., Gangås, L., Brøseth, H., Solberg, E.J., Hjeljord, O., 2005. Lynx and roe deer in Southeastern Norway: activity 1995–2004. NINA Rapport 29, 1–41.
- Andrén, H., Liberg, O., 2008. Den svenska lodjurstammen 2004–2008. Rapport Grimsö forskningsstation/Viltskadecenter SLU 1, 24.
- Andrén, H., Linnell, J.D.C., Liberg, O., Ahlqvist, P., Andersen, R., Danell, A., Franzén, R., Kvam, T., Odden, J., Segerström, P., 2002. Estimating total lynx *Lynx lynx* population size from censuses of family groups. *Wildlife Biology* 8, 299–306.
- Andrén, H., Linnell, J.D.C., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P.F., Ahlqvist, P., Kvam, T., Franzén, R., Segerström, P., 2006. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. *Biological Conservation* 131, 23–32.
- Arnemo, J.M., Linnell, J.D.C., Wedul, S.J., Ranheim, B., Odden, J., Andersen, R., 1999. Use of intraperitoneal radio-transmitters in lynx *Lynx lynx* kittens: anaesthesia, surgery and behaviour. *Wildlife Biology* 5, 245–250.
- Breitenmoser, U., Kavczeny, P., Dotterer, M., Breitenmoserwursten, C., Capt. S., Bernhart, F., Liberek, M., 1993. Spatial organization and recruitment of lynx

- (Lynx lynx) in a re-introduced population in the Swiss Jura Mountains. *Journal of Zoology* 231, 449–464.
- Caswell, H., 2001. *Matrix Population Models*, second ed. Sinauer, Sunderland, Massachusetts.
- Cohen, J., 1977. Ergodicity of age structure in populations with Markovian vital rates, III: finite-state moments and growth rate: an illustration. *Advances in Applied Probability* 9, 462–475.
- Cohen, J.E., 1979. Ergodic theorems in demography. *Bulletin of the American Mathematical Society* 1, 275–295.
- Danell, A.C., Andrén, H., Segerström, P., Franzén, R., 2006. Space use by Eurasian lynx in relation to reindeer migration. *Canadian Journal of Zoology* 84, 546–555.
- Engen, S., Lande, R., Sæther, B.-E., 1997. Harvesting strategies for fluctuating populations based on uncertain population estimates. *Journal of Theoretical Biology* 186, 201–212.
- 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.
- 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., Lande, R., Sæther, B.-E., Festa-Bianchet, M., 2007. Using reproductive value to estimate key parameters in density-independent age-structured populations. *Journal of Theoretical Biology* 244, 208–317.
- Engen, S., Lande, R., Sæther, B.-E., Dobson, F.S., 2009. Reproductive value and the stochastic demography of age-structured populations. *American Naturalist* 174, 795–804.
- Fieberg, J., Ellner, S.P., 2001. Stochastic matrix models for conservation and management: a comparative review of methods. *Ecology Letters* 4, 244–266.
- Fisher, R.A., 1930. *The Genetical Theory of Natural Selection*. Oxford at the Clarendon Press, Oxford.
- Fryxell, J.M., Mercer, W.E., Gellately, R.B., 1988. Population dynamics of Newfoundland moose using cohort analysis. *Journal of Wildlife Management* 52, 14–21.
- Gross, K., Morris, W.F., Wolosin, M.S., Doak, D.F., 2006. Modeling vital rates improves estimation of population projection matrices. *Population Ecology* 48, 79–89.
- Haridas, C.V., Tuljapurkar, S., 2007. Time, transients and elasticity. *Ecology Letters* 10, 1143–1153.
- Herfindal, I., Linnell, J.D.C., Moa, P.F., Odden, J., Austmo, L.B., Andersen, R., 2005. Does recreational hunting of lynx reduce depredation losses of domestic sheep. *Journal of Wildlife Management* 69, 1034–1042.
- Holmes, E.E., 2001. Estimating risks in declining populations with poor data. *PNAS* 98, 5072–5077.
- Holmes, E.E., 2004. Beyond theory to application and evaluation: diffusion approximations for population viability analysis. *Ecological Applications* 14, 1272–1293.
- Holmes, E.E., Sabo, J.L., Viscido, S.V., Fagan, W.F., 2007. A statistical approach to quasi-extinction forecasting. *Ecology Letters* 10, 1182–1198.
- Jonzén, N., Lundberg, P., Gårdmark, A., 2001. Harvesting spatially distributed populations. *Wildlife Biology* 7, 197–203.
- Lande, R., 1998. Demographic stochasticity and Allee effect on a scale with isotropic noise. *Oikos* 83, 353–358.
- Lande, R., Orzack, S.H., 1988. Extinction dynamics of age-structured populations in a fluctuating environment. *PNAS* 85, 7418–7421.
- Lande, R., Sæther, B.-E., Engen, S., 1997. Threshold harvesting for sustainability of fluctuating resources. *Ecology* 78, 1341–1350.
- Lande, R., Engen, S., Sæther, B.-E., 2003. *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford.
- Lande, R., Engen, S., Sæther, B.-E., Coulson, T., 2006. Estimating density dependence from time series of population age structure. *American Naturalist* 168, 76–87.
- Linnell, J.D.C., Andrén, R., Kvam, T., Andren, H., Liberg, O., Odden, J., Moa, P.F., 2001. Home range size and choice of management strategy for lynx in Scandinavia. *Environmental Management* 27, 869–879.
- Linnell, J.D.C., Fiske, P., Herfindal, I., Odden, J., Brøseth, H., Andersen, R., 2007a. An evaluation of structured snow-track surveys to monitor Eurasian lynx *Lynx lynx* populations. *Wildlife Biology* 13, 456–466.
- Linnell, J.D.C., Odden, J., Andrén, H., Liberg, O., Andersen, R., Moa, P., Kvam, T., Brøseth, H., Segerström, P., Ahlqvist, P., Schmidt, K., Jedrzejewski, W., Okarma, H., 2007b. Distance rules for minimum counts of Eurasian lynx *Lynx lynx* family groups under different ecological conditions. *Wildlife Biology* 13, 447–455.
- Linnell, J.D.C., Brøseth, H., Odden, J., Nilsen, E.B., 2010. Sustainably harvesting a large carnivore? Development of Eurasian lynx populations in Norway during 160 years of shifting policy. *Environmental Management*. doi:10.1007/s00267-010-9455-9.
- Melis, C., Basille, M., Herfindal, I., Linnell, J.D.C., Odden, J., Gaillard, J.M., Andersen, R., Høgda, K.A., 2010. Roe deer population growth and lynx predation along a gradient of environmental productivity and climate in Norway. *Ecoscience* 17.
- Odden, J., Linnell, J.D.C., Moa, P.F., Herfindal, I., Kvam, T., Andersen, R., 2002. Lynx depredation on domestic sheep in Norway. *Journal of Wildlife Management* 66, 98–105.
- Pedersen, V., Linnell, J.D.C., Andersen, R., Andrén, H., Segerström, P., Lindén, M., 1999. Winter lynx predation on semi-domestic reindeer in northern Sweden. *Wildlife Biology* 5, 203–212.
- Persson, J., Ericsson, G., Segerström, P., 2009. Human caused mortality in the endangered Scandinavian wolverine population. *Biological Conservation* 142, 325–331.
- Robinson, H.S., Wielgus, R.B., Cooley, H.S., Cooley, S.W., 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. *Ecological Applications* 18, 1028–1037.
- Sæther, B.-E., Bakke, Ø., 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81, 642–653.
- Sæther, B.-E., Engen, S., Lande, R., 1996. Density-dependence and optimal harvesting of fluctuating populations. *Oikos* 76, 40–46.
- Sæther, B.-E., Engen, S., Swenson, J.E., Bakke, Ø., Sandegren, F., 1998. Assessing the viability of Scandinavian brown bear, *Ursus arctos*, populations: the effects of uncertain parameter estimates. *Oikos* 83, 403–416.
- Sæther, B.-E., Engen, S., Lande, R., 1999. Finite metapopulation models with density dependent migration and stochastic local dynamics. *Proceedings of the Royal Society London B* 266, 113–118.
- Sæther, B.-E., Engen, S., Møller, A.P., Weimerskirch, H., Visser, M.E., Fiedler, W., Matthysen, E., Lambrechts, M.M., Badyaev, A., Becker, P.H., Brommer, J.E., Bukacinski, D., Bukacinska, M., Christensen, H., Dickinson, J., du Feu, C., Gehlbach, F., Heg, D., Hötker, H., Merilä, J., Nielsen, J.T., Rendell, W., Robertson, R.J., Thomson, D.L., Török, J., Van Hecke, P., 2004. Life-history variation predicts the effects of demographic stochasticity on avian population dynamics. *American Naturalist* 164, 793–802.
- Sæther, B.-E., Engen, S., Persson, J., Brøseth, H., Landa, A., Willebrand, T., 2005. Management strategies for the wolverine in Scandinavia. *Journal of Wildlife Management* 69, 1001–1014.
- Sæther, B.-E., Lillegård, M., Grøtan, V., Filli, F., Engen, S., 2007a. Predicting fluctuations of re-introduced ibex populations: the importance of density-dependence, environmental stochasticity and uncertain population estimates. *Journal of Animal Ecology* 76, 326–336.
- Sæther, B.-E., Engen, S., Solberg, E.J., Heim, M., 2007b. Estimating the growth of a newly established moose population using reproductive value. *Ecography* 30, 417–421.
- Tufto, J., Sæther, B.-E., Engen, S., Swenson, J.E., Sandegren, F., 1999. Harvesting strategies for conserving minimum viable populations based on World Conservation Union criteria: brown bears in Norway. *Proceedings of the Royal Society London B, Biological Sciences* 266, 961–967.
- Tuljapurkar, S., Haridas, C.V., 2006. Temporal autocorrelation and stochastic population growth. *Ecology Letters* 9, 324–334.
- van Tienderen, P.H., 1995. Life cycle trade-offs in matrix population models. *Ecology* 76, 2482–2489.
- Wabakken, P., Sand, H., Liberg, O., Bjørvall, A., 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978–1998. *Canadian Journal of Zoology* 79, 710–725.