Nordic Society Oikos

Assessing the viability of Scandinavian brown bear, *Ursus arctos*, populations: the effects of uncertain parameter estimates

Bernt-Erik Sæther, Steinar Engen, Jon E. Swenson, Øyvind Bakke and Finn Sandegren

Based on data from radio-collared individuals, we present an analysis of the viability of two small populations of the Scandinavian brown bear, *Ursus arctos*. The northern and southern populations had different demographic characteristics, even though the population growth rate r and the demographic variance s_d^2 were high in both populations ($r = 0.13$ and $s_d^2 = 0.180$ in the north, and $r = 0.15$ and $s_d^2 = 0.155$ in the south). In the northern population the environmental variance s_e^2 was not significantly different from 0, whereas in the south $s_e^2 = 0.003$. In the south, this was related to high environmental stochasticity in the survival rate of the youngest animals, which resulted in an increase in survival with age in this population. In contrast, in the north, the probability of survival showed a slight decrease with age. Uncertainties were obtained from the joint distribution of bootstrap replications of r, s_d^2 and s_e^2. Although the uncertainty in these estimates is quite large, it is unlikely that even relatively small populations (> 10 females ≥ 1 year old) will decline to size less than 1 after 100 years. Analysis of the distribution of the critical population size (i.e. the population size where the population's logarithmic growth rate is zero) shows that these brown bear populations must be larger than 3–4 females 1 year or older to secure a positive growth rate. Similarly, if we define a viable population as the population size where the chance of survival is greater than 90% during a period of 100 years, 8 females ≥ 1 year old must be present in the north and 6 females in the south. This high viability of even small brown bear populations is due to high reproductive and survival rates. A relatively small increase in the mortality rate will strongly reduce the viability of even relatively large brown bear populations.

B.-E. Sæther, Dept of Zoology, Norwegian Univ. of Science and Technology, N-7034 Trondheim, Norway and Norwegian Inst. for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway (bernt-erik.sather@chembio.ntnu.no). – S. Engen and Ø. Bakke, Dept of Mathematical Sciences, Norwegian Univ. of Science and Technolgy, N-7034 Trondheim, Norway. – J. E. Swenson, Norwegian Inst. for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway. – F. Sandegren, Research Div., Swedish Hunters' Association, Bäcklösavägen 8, SE-75651 Uppsala, Sweden.

Many large mammalian carnivore populations have decreased dramatically in size during the last century, mainly due to human persecution and habitat degradation (Servheen 1990). For instance, the Scandinavian brown bear (*Ursus arctos*) population was driven almost to extinction by 1920–1930 through overhunting (Swenson et al. 1995). The number of bears has steadily increased during the past 60 years or so (Swenson et al.

1994, 1995). Because the brown bear is a very controversial species in Norway due to its predation on untended sheep (Sagør et al. 1997), an important question has been to determine the minimum size of a viable brown bear population.

Viability analyses have now been conducted for a large number of species (Boyce 1992, Burgman et al. 1993). For instance, it has been actively used for at least

a decade in the management of the Yellowstone grizzly bear (*Ursus arctos horribilis*) population (Shaffer 1983, Boyce 1995). One of the great advantages of population viability analysis is that it introduces a quantitative element into the risk assessment. However, as forcefully argued by Caughley (1994), many of these analyses involve parameters with great uncertainties, which may give unreliable predictions. This problem is clearly illustrated by Mills et al. (1996), who showed that small differences in the procedures for estimating the population growth rate and the form of the density dependence among four viability analysis computer programs lead to very different viability predictions, even for the same data set from a hypothetical, increasing and decreasing grizzly bear population.

The purpose of the present paper is to perform a viability analysis of the Scandinavian brown bear population, using data on reproduction and survival of individually recognizable individuals. A central focus will be to estimate the amount of uncertainty in the parameters, and to evaluate how this uncertainty affects the viability estimates.

The Scandinavian brown bear

The authorities encouraged efforts to exterminate the brown bear in Scandinavia during several centuries. This effort was successful in Norway, but a few remnant populations were saved in Sweden after authorities began efforts to save the species around the turn of this century (Swenson et al. 1995). The total number of bears in the four geographically distinct remnant populations that survived to the present may have been as low as 130 around 1930, but the population has increased slowly since then and hunting has been allowed in Sweden since 1943 (Swenson et al. 1994, 1995). Bears show sex-biased dispersal, with males dispersing far and females remaining near their place of birth, often establishing a home range within their mother's home range (Rogers 1987, Reynolds 1993). Based on this, and the dispersal distances we have observed in radio-marked bears (unpubl.), we expect that the four remnant populations, where females are concentrated, have no interchange of females but that interchange of males does occur. An analysis of genetic structure, based on mitochondrial DNA, supported this conclusion (Taberlet et al. 1995). Our two study populations, separated by approximately 600 km and located in two different remnant populations, were therefore probably demographically distinct. The northern population was centred in the vicinity of Kvikkjokk, southern Norrbotten county, whereas the southern population was centred in the vicinity of Noppikoski and Älvdalen, northern Kopparberg county in Sweden.

Both study areas were dominated by boreal forest, with Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) as the most common tree species. The southern area was rolling, but the northern area also included mountains, with alpine areas, and a birch (*Betula* spp.) dominated subalpine zone.

In studies of demography, it is important that the selection of individuals is as representative as possible. Almost all bears in this study were first captured in one of three ways: (1) by location of tracks on spring snow and following them, and capturing by darting from a helicopter, (2) by locating unmarked bears in company with radio-marked bears during the breeding season and capture from a helicopter, and (3) capture of yearlings with radio-marked females, also from a helicopter. Our study included no bears that were captured because they had been in conflict with humans. After the first capture, we were able to continue to follow most females until they died or to the end of 1995, because we recaptured them using helicopters to change the radio-transmitters before the batteries became exhausted. However, in a few cases, radio failure caused us to lose contact with females.

Another important aspect of demographic studies is that the animals in the study area are similar enough to the others that the results can be extrapolated. In this case, there were differences between our study animals and bears generally in Sweden. The mountainous portions of the northern study area were dominated by national parks, where bear hunting is forbidden and, in the southern study area, the landowners have traditionally been restrictive regarding bear hunting. The result is that bears in the study areas were less exposed to legal hunting than 'average' brown bears in Sweden (Swenson et al. 1994). Another difference is more difficult to document, but it is our definite impression that bears are more often killed illegally outside the study areas than inside them. This difference appears to be most pronounced in the north, where illegal killing generally seems to be more widespread than in the south. Finally, the high survival of cubs-of-the-year in the northern study area might not have been representative. No adult males were killed legally in the northern study area during the study period. Using a retrospective experiment and using data from both areas, we have shown that cub mortality increased dramatically following the killing of adult males, presumably due to infanticide perpetrated by immigrating males (Swenson et al. 1997). All of these factors tend to give our study populations a somewhat higher population growth rate than the bears outside our study areas.

Our data on survival are based on 50 cubs-of-the-year in the north and 74 in the south. These were not marked, but were in the company of marked mothers. Cubs following marked females were counted when they left the den with their mother in the spring and at least before they entered a den with their mother in the autumn. If they disappeared during their first year of life, they were assumed to have died. We know that

these young can survive if they are separated from their mother in summer or autumn (Swenson et al. in press); however most young were lost before summer (Swenson et al. 1997). Any young that had died in the den or at the den site were not considered, because we were only able to visit dens in the south. All other data were based on radio-marked bears. We captured bears only during the spring, so we used the Kaplan–Meier technique to estimate survival (Kaplan and Meier 1958). In the north, we followed 19 yearling females, 10 two-year-olds, 8 three-year-olds, 8 four-year-olds, and 15 individual adults for a total of 54 years. In the south, we followed 22 yearling females, 13 two-year-olds, 11 three-year-olds, 10 four-year-olds, and 18 individual adults for a total of 62 years. The bears were located every week, so it was relatively easy to determine the time and cause of death. In addition, many bears bore transmitters with mortality sensors. Sometimes a transmitter would suddenly quit working when it had not shown any signs of malfunction earlier. If this occurred during the autumn hunting season or in the spring when it was still possible to drive a snowmobile on the snow, this was considered to be an illegal killing. This may have inflated the mortality levels somewhat, but bears that have been classified as 'probably killed illegally' have not been recaptured subsequently, and only one has been killed subsequently during a hunting season.

The reproductive data are based on 20 litters born to 13 females in the north and 31 litters born to 12 females in the south. We followed 13 females ≥ 5 years old during 52 reproductive seasons in the north and 18 females ≥ 4 years old during 70 reproductive seasons in the south. The earliest age of reproduction was 5 years in the north and 4 in the south.

Prediction of fluctuations in brown bear populations

Definitions

The probability of extinction of a population of size N is determined by the long-term population growth rate r_0. When $r_0 < 0$, the population will certainly go extinct. Even when $\bar{\lambda} = e^{r_0} > 1$ the population may not persist. The probability of extinction will depend on the demographic variance (i.e. variance in the individual fitness per year) and environmental variance, arising from fluctuations in the environment affecting all individuals equally (May 1974, Leigh 1981, Goodman 1987, Lande 1993).

First, assume a population with no age structure (we later relax this assumption). The contribution R_i of one female i to the next season is the number of surviving female offspring plus 1 if the female survives herself. Then, assuming no intraspecific competition, the demo-

graphic variance (Engen et al. 1998, Sæther et al. 1998) is defined as

$$\sigma_d^2(N) = \text{var}(R_i) - \text{cov}(R_i, R_j) = \tfrac{1}{2}\text{var}(R_i - R_j) \qquad (1)$$

for $i \neq j$. This parameter describes the variation among the individuals within the same season, and can generally depend on population size N.

The mean value of R_i may vary across seasons due to annual variation, e.g. in the food supply, climate or predation rate. This environmental variance can be defined as

$$\sigma_e^2(N) = \text{cov}(R_i, R_j) \qquad (2)$$

for $i \neq j$, where R_i and R_j are contributions within the same year (Engen et al. 1998, Appendix 1).

Let ΔN be the change in population size from one season to the next. From eqs (1) and (2), the variance in the population size will, according to Engen et al. (1998), be

$$\text{var}(\Delta N) = \sigma_d^2(N)N + \sigma_e^2(N)N^2. \qquad (3)$$

Now consider an age-structured population with no density dependence. Let t be a discrete time interval and assume $E(\Delta N) = \rho N$ and $\text{var}(\Delta N) = \sigma_d^2 N + \sigma_e^2 N$, where ΔN is the change in population size during interval t. This process can be approximated by a diffusion process with infinitesimal mean and variance $\mu(N) = rN$ and $v(N) = s_d^2 N + s_e^2 N^2$, provided that the stochastic fluctuations are not too large. We achieve a diffusion process with exactly the same expectation and variance in ΔN as in the discrete process (Engen et al. unpubl.) by choosing r, s_e^2, and s_d^2 as appropriate functions of ρ, σ_e^2 and σ_d^2, as shown in Appendix 1.

The diffusion approximation in age-structured populations with demographic and environmental stochasticity

We now consider an age-structured population as a Markov process without density dependence. Let $\mathbf{N}_t = (N_{0,t}, N_{1,t}, \ldots, N_{k,t})$ represent the population vector at time t, where k is the maximum age. Thus, $N_{i,t}$ is the number of individuals in age class i at time t. Let $\boldsymbol{\theta}_t$ be a vector that describes the environment at time t (Engen et al. unpubl.), and assume that $\boldsymbol{\theta}_0, \boldsymbol{\theta}_1, \ldots$ is a sequence of independent stochastic vectors. According to Goodman (1967), we obtain a general class of age-structured population models by assuming that the contribution of an individual to the next season, conditional on $\boldsymbol{\theta}_t$, is a random variable dependent on the age of the individual and $\boldsymbol{\theta}_t$. This class of models can be approximated by a diffusion process with infinitesimal mean in the form rN and constant, but positive, demo-

Table 1. The estimated age-specific survival of female brown bears ($p(x, t)$) in the northern and southern population. The stochasticity in $p(x, t)$ is modelled by assuming that the logit-value is normally distributed, i.e. logit $[p(x, t)] = \phi(x) + \psi(x)U_t$, where $\phi(x)$ and $\psi(x)$ are functions of age x, and U_t is a sequence of independent normally distributed variables. $\phi(x)$ and $\psi(x)$ then are the expectation and standard deviation of logit $[p(x, t)]$. $\beta(x) = e^{\phi(x)}/(1 + e^{\phi(x)})$, which is the survival when $\psi(x)$ (or U_t) is set to 0, i.e. when the environmental stochasticity is excluded. $\psi(x)$ shows the age-specificity in the environmental stochasticity.

Age	Population	$\beta(x)$	$\psi(x)$	$p(x, t)$
0	North	0.9601	0.0000	0.9601
	South	0.8320	1.3136	0.7720
1	North	0.9517	0.0000	0.9517
	South	0.8867	0.6732	0.8697
2	North	0.9416	0.0001	0.9416
	South	0.9252	0.3450	0.9217
3	North	0.9296	0.0001	0.9296
	South	0.9513	0.1768	0.9507
4+	North	0.9153	0.0004	0.9153
	South	0.9687	0.0906	0.9685

graphic and environmental variances (Engen et al. unpubl.). The total population size N_t at time t will, in general, be a process with autocorrelations generated by changes in the age structure. Engen et al. (unpubl.) have shown that for life histories similar to the brown bear, the effects of these autocorrelations in many cases will disappear after 3–10 years.

Stochastic variation in θ_t will generate environmental variance, whereas the stochastic variation remaining when conditioning on θ_t, typically will generate demographic variance. Unfortunately, analytic methods for computing relevant values of demographic and environmental variances in stochastic generalisations of Leslie models are not yet available. However, Engen et al. (unpubl.) pointed out that the parameters in the diffusion approximation can be estimated by means of stochastic simulations (see Appendix 1).

Estimation of demographic parameters

No significant difference with age was found in either reproduction or survival among females that were 4 years or older in either of the populations ($P > 0.1$). In all of the following calculations, these individuals are pooled into one age class. Furthermore, we assume no annual variation in the distribution of the number of offspring, so that it is sufficient to model only the demographic stochasticity in reproduction. In contrast, variation among years in environmental conditions may generate stochastic variation in the probability of survival. The modelling of the stochasticity in $p(x, t)$, the probability that a female of age x survives to age $x + 1$, is shown in Appendix 2.

In both populations, the age-specific survival rates were high, being larger than 0.77 in all age classes

(Table 1). More than 90% of the females 2 years or older survived. The age-specific pattern of variation in the survival rate was different in the two populations however. In the north the probability of survival decreased with age, whereas in the southern population it increased. In the north, there was no reduction in the probability of survival due to an age-dependent effect of the environment. However, in the south, there was a larger environmental variation in the survival rate among the younger than among the older females (Table 1).

In both populations the estimate of the population growth rate $\hat{r}$ was large ($\hat{r} = 0.13$ and $\hat{r} = 0.15$ in the north and south, respectively). The distribution of the bootstrap replicates showed, however, that these estimates are relatively uncertain (Fig. 1a). Nevertheless, the probability that a bootstrap replicate of $\hat{r}$ is larger than 0 is very high in both populations.

The demographic variance s_d^2 was significantly larger than 0 in both populations (Fig. 1b). A somewhat larger demographic variance was found in the north ($\hat{s}_d^2 = 0.180$) than in the south ($\hat{s}_d^2 = 0.155$). The probability is high that the bootstrap replicates for $\hat{s}_d^2$ are greater than 0.1 in both populations.

A difference was found between the populations in the environmental variance s_e^2. In the south, the estimate was $\hat{s}_e^2 = 0.003$, which is significantly larger than 0 (Fig. 1c). In contrast, in the north, $\hat{s}_e^2$ was not significantly different from 0.

Population simulations

We assumed that the fluctuations in population size can be approximated by a diffusion process. We obtained the parameters in the process from the joint distribution of bootstrap replications of r, s_d^2 and s_e^2 and then examined how uncertainties in the parameter estimates affected the population fluctuations. The high population growth rate in both populations made it unlikely that even small populations would go extinct (Figs 2, 3). Even when we started with as few as 5 females 1 year or older, none of the simulated populations with parameters generated by the bootstrap distribution went extinct during a period of 100 years.

In order to examine the accuracy of the predicted population growth based on the diffusion approximation, we also constructed an individual-based simulation model. In this model we simulated the development of an initial population consisting of individuals of known age and sex, where the number of years since last birth and the number of offspring still alive were known for each female. The mortality of the offspring during their first year of life was divided into two groups. First, the probability p_k that the whole litter will die was modelled. This probability was dependent on the age of the mother, and whether she was

alive or not. Then, we entered into the model the probability p_i that a single offspring will die, which was assumed to be dependent on the mother's age. Thus, the probability that an offspring survives becomes $P = (1 - p_k)(1 - p_i)$. For parameters used in the simulations, see Sæther et al. (1997).

The age-specific probability of onset of maturation was determined by the age when young radio-collared females gave birth for the first time (Swenson et al. unpubl.). Then, the probability of the next birth depended on the time since the last birth (1–4 years), and whether the whole litter was lost. The probability that a litter should contain 1, 2, 3 or 4 offspring was assumed to be age-independent (see Table 4.2 in Sæther et al. 1997).
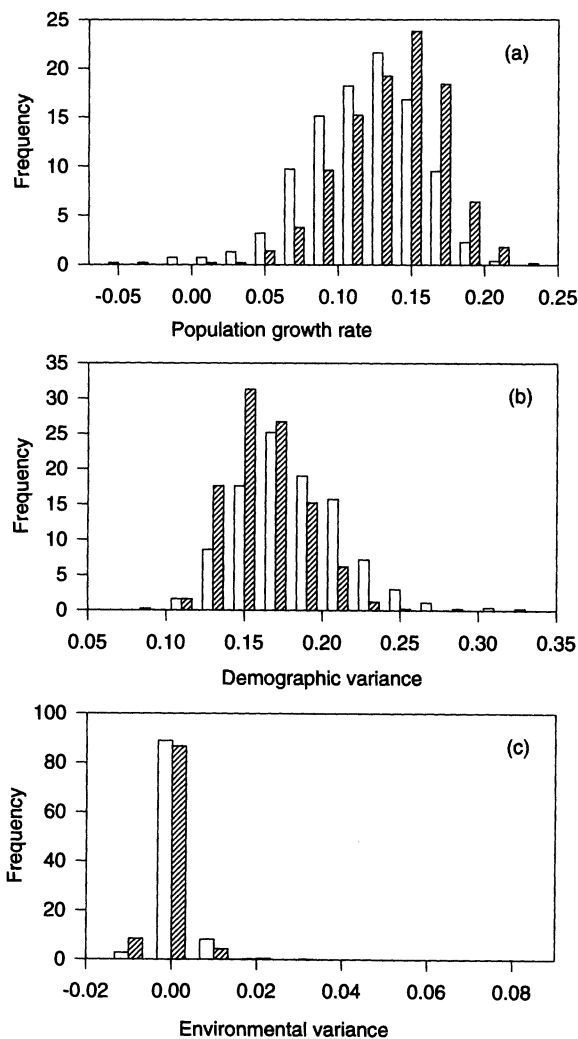

Fig. 1. The bootstrap distribution of the population growth rate (a), the demographic variance (b) and the environmental variance (c) in the southern (cross-hatched columns) and northern (open columns) population of the Scandinavian brown bear.

Ten simulations were made in each population for initial populations of different size (3, 5 or 10 adult females). These populations were formed by randomly drawing individuals from a larger initial population of approximately 100 individuals that was allowed to develop for 20 years.

The growth rate of the population simulated by the individual-based model (Fig. 4) was very similar to the growth rate estimated by means of the diffusion approximation (Fig. 2) in both the northern ($\hat{r} = 0.129$) and southern ($\hat{r} = 0.166$) population. However, the variation among simulations in predicted population size was less than in the diffusion models. This was due to the fact that the individual-based model did not take the bootstrap variation into account. As in the diffusion models, a large increase in the risk of extinction occurred in small populations when the growth rate was reduced (Fig. 4), e.g. due to increased harvest.

Our ability to correctly predict the development of the Scandinavian brown bear population in the future was quite low, however (Fig. 5). This was due to both the high uncertainty in the parameter estimates (Fig. 1) and the demographic and environmental variance in the process. Nevertheless, the lower end of the 99% prediction interval for the size of the southern population after 100 years was larger than 0 if we started with 20 females. If we choose a 95% interval, this would also occur with a similar-sized initial population in the north (Fig. 5b).

Population viability analysis

Definitions

We assumed that a population of a sexual species such as the brown bear goes extinct when the population size is 1. Such a population of size N, assuming that s_d^2 and s_e^2 are independent of N, will either grow to infinity or go extinct in the absence of density-regulation. The population will go extinct with probability 1 if

$$r_0 = r - \tfrac{1}{2} s_e^2 < 0. \tag{4}$$

If $r_0 > 0$, the probability of extinction is

$$\left(\frac{\alpha + N}{\alpha + 1} \right)^{-\beta}, \tag{5}$$

where $\alpha = s_d^2 / s_e^2$ and $\beta = 2r_0 / s_e^2$, and the variances s_d^2 and s_e^2 are defined by eqs (A8) and (A9). The expected time to extinction, given $r_0 < 0$, can be found by integrating the Green function (Karlin and Taylor 1981) for the process from 1 to infinity (see Appendix 2).

The diffusion approximation for $\ln(N)$ has the expectation

$$\mu_0(N) = r - \tfrac{1}{2} s_e^2 - \tfrac{1}{2} s_d^2 / N = r_0 - \tfrac{1}{2} s_d^2 / N \tag{6}$$
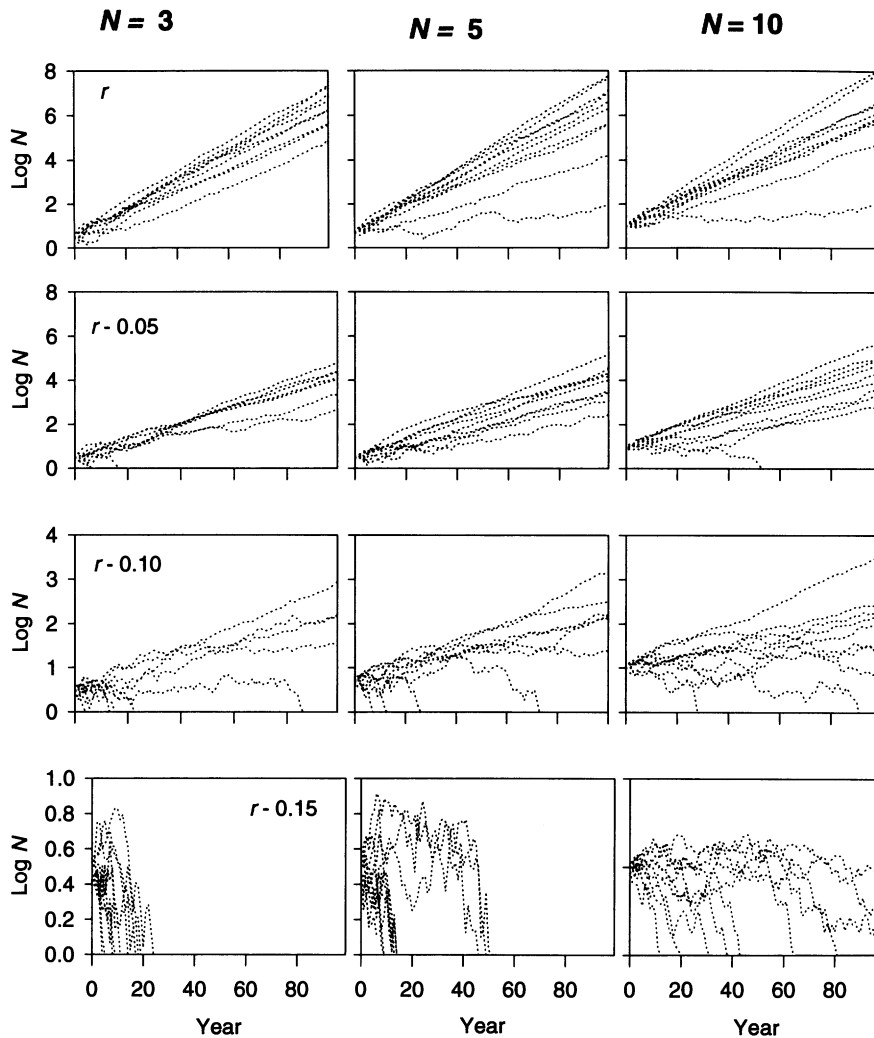
Fig. 2. Simulation of the growth of the northern population of the Scandinavian brown bear in relation to initial population size and different population growth rates. We assume that the population fluctuations can be approximated by a diffusion process.

and variance

$$v_0(N) = s_e^2 + s_d^2/N \qquad (7)$$

(Karlin and Taylor 1981). From eq. (6) it is evident that $\mu_0(N)$ (i.e. the specific growth rate of the population in the deterministic case) is always small for small values of N if the demographic variance is positive. If $r_0 > 0$, a critical population size N_c exists so that $\mu_0(N_c) = 0$. If the population size is less than this critical size, the deterministic population growth rate will be negative. This critical population size is

$$N_c = \frac{s_d^2}{2r - s_e^2} = \frac{s_d^2}{2r_0} \qquad (8)$$

for $r_0 = r - \frac{1}{2}s_e^2 > 0$. If $r_0 < 0$, $N_c = \infty$, because the growth rate of $\ln(N)$ will be negative for all N.

Critical population sizes also can be defined according to the probability that the population will go ex-

tinct. If we require that this probability, given by eq. (5), should be less than p, this requires that N should be greater than N_p, given by

$$N_p = \frac{p^{s_e^2/2r_0}(s_d^2 + s_e^2) - s_d^2}{s_e^2.} \qquad (9)$$

Results

As expected from other theoretical studies (Goodman 1987, Lande 1993), the probability that the population will go extinct decreased with increasing population size (Fig. 6). In addition, the probability of extinction also increased with the length of the time period that is considered. In both populations the risk of extinction reaches a threshold after some years when a further increase in the length of time only has a very slight influence on the probability of extinction. In the southern population, this threshold was reached after about 30 years, whereas in the northern population it oc-

408

Fig. 3. Simulation of the growth of the southern population of the Scandinavian brown bear in relation to initial population size and different population growth rates. We assume that the population fluctuations can be approximated by a diffusion process.
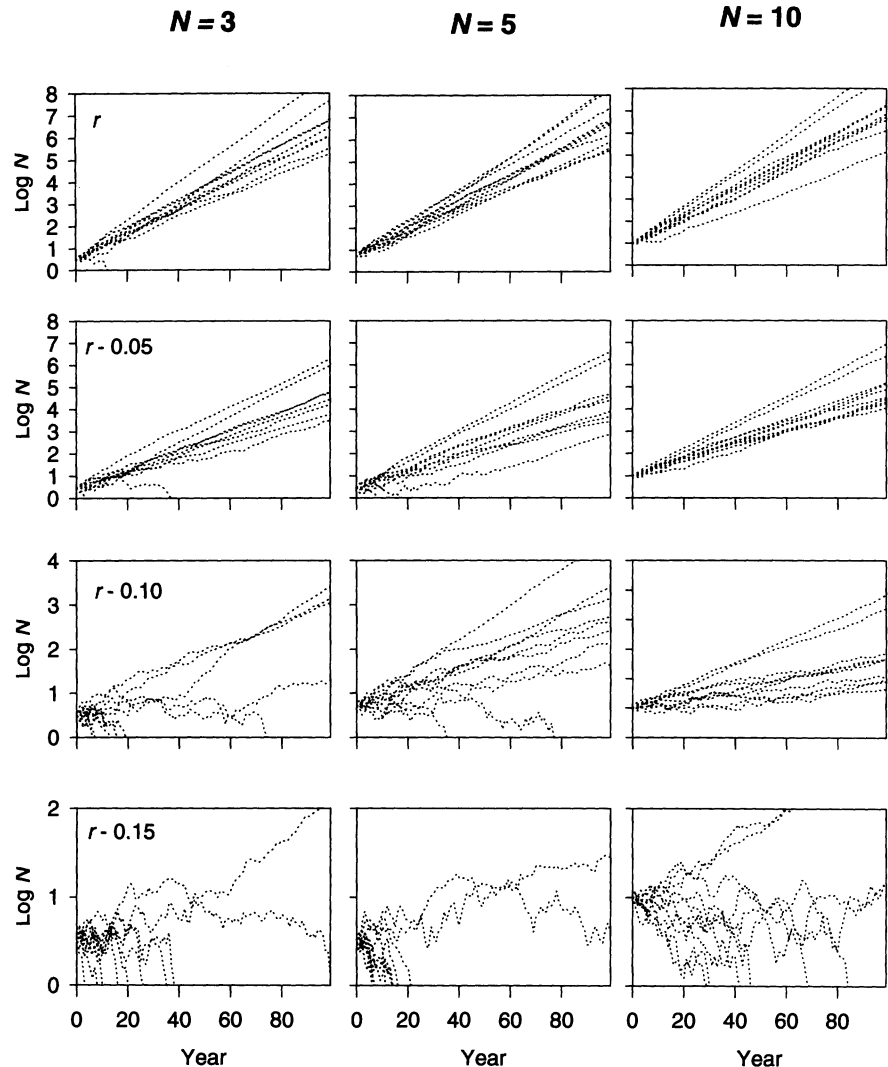
curred after about 60 years. Thus, the risk for this brown bear population going extinct (assuming no density dependence) will be relatively independent of whether a time period of 50 or 100 years is considered.

The large standard deviations in the bootstrap replications of r, s_d^2 and s_e^2 also introduce uncertainties to the predictions of the risk of extinction of a brown bear population. A necessary condition for a viable population is that the population growth rate is positive. The sampling distribution of the critical population size C (Fig. 6) shows that a brown bear population must be larger than 3–4 females 1 year or older in order to have positive growth rate.

Mace and Lande (1991) proposed that a viable population must have a risk of extinction less than 10% during a 100-year period in order to be considered viable. This was later adopted by IUCN (IUCN 1994). In the present case, the choice of time period had little effect on the evaluation of viability because the risk of

extinction only showed a small increase between 50 and 100 years (Fig. 5). The bootstrap distribution of the population size where the chance of survival was greater than 90% ($N_{0.90}$) showed that a minimum of 8 females ≥ 1 year old in the northern and 6 females in the southern population must be present at the start of the period to secure viable populations according to IUCN's criteria (Fig. 6). If the probability of survival should be higher than 95%, as suggested by Sæther and Engen (1997), the critical population size $N_{0.95}$ should be larger than 9 and 7 females in the northern and southern populations, respectively.

A reduction in the population growth rate, for instance due to an increased harvest, had a great effect on the critical population sizes necessary for securing viable brown bear populations (Fig. 6). If the total mortality from the population were increased 10 percentage points above the rate suffered by radio-collared females during the study period, $N_{0.90}$ would
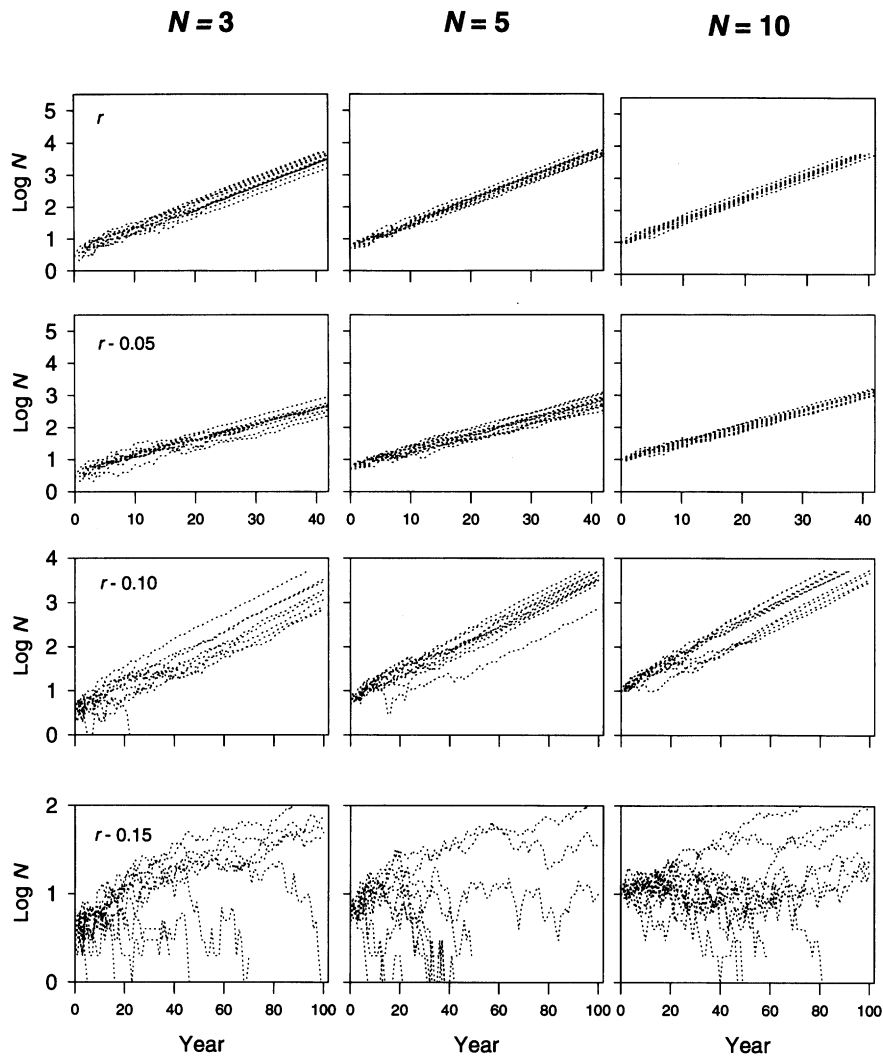
Fig. 4. Simulation by the individual-based model (see text) of the population growth of the southern population of the Scandinavian brown bear in relation to initial population sizes and population growth rates.

have to be larger than 25 females to fulfil IUCN's criteria. Similarly, the consequences of a reduction of 15% will be that even very large populations cannot be considered viable. This can be illustrated by the fact that most estimates, especially in the north, of C, $N_{0.90}$ and $N_{0.95}$ will be larger than 25 females if the population growth rate is reduced by 15% (Table 2).

Discussion

Demographic characteristics of the Scandinavian brown bear

A high growth population growth rate ($r > 0.13$, that is $\lambda > 1.14$) was found both in the northern and southern populations (Fig. 1a). These are higher growth rates

than recorded in North American grizzly bear populations (Servheen et al. 1994, Hovey and McLellan 1996). For instance, in the grizzly bear population in Yellowstone National Park, Eberhardt et al. (1994) calculated $\lambda = 1.046 \pm 0.023$ (SD) by the Euler–Lotka equation. The highest previously reported growth rate for the brown bear is $\lambda = 1.09$ from Flathead Valley, British Columbia, Canada (Hovey and McLellan 1996).

The high population growth rate of Scandinavian brown bear populations is related to a combination of both high survival and fecundity rates. Reproduction in the Scandinavian populations was higher than those reported for 16 North American populations, as summarized by McLellan (1994). The survival rate in the first part of life was higher than is generally found among bears in North America (Bunnell and Tait 1985). The difference in survival rate is less among the oldest age classes, where the survival rate also in North
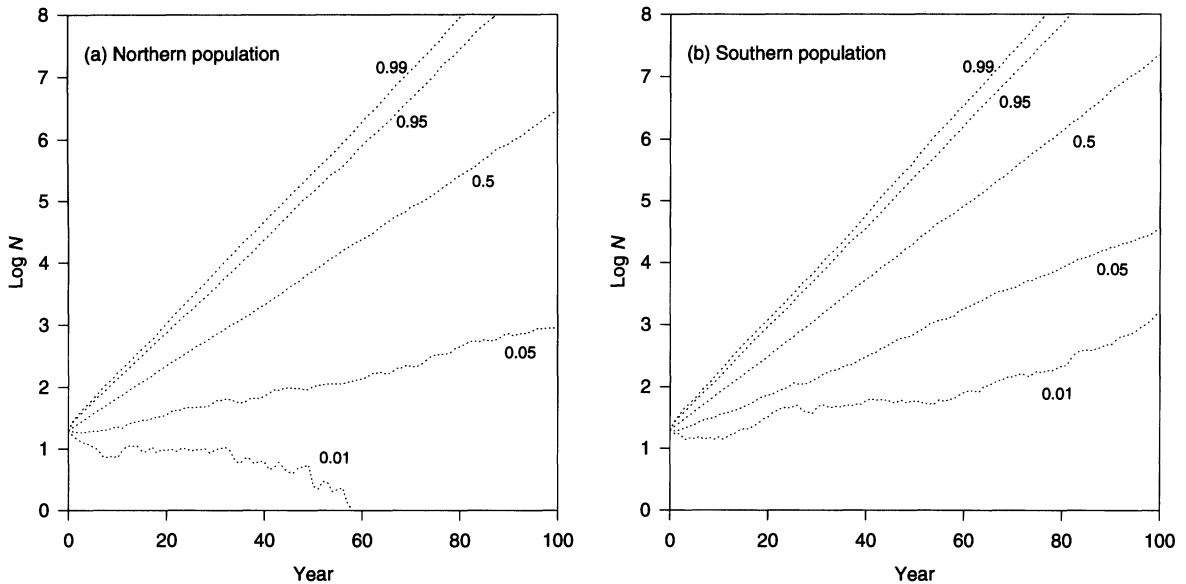
Fig. 5. Prediction interval of the population size in (a) the northern and (b) the southern population of the Scandinavian brown bear. The initial population size was 20 adult females.

American bear populations may be larger than 90% (Eberhardt et al. 1994, Boyce 1995, Hovey and McLellan 1996).

We have based our analysis on data collected from radio-collared animals. This assumes that those individuals comprise an unbiased sample from the population. This is most likely not the case. Hunting mortality was probably lower for our radio-marked bears because hunting for bears is allowed, on average, on 75% of the area within municipalities with bear hunting in Sweden, but 67% of our radio-marked bears were in areas closed to hunting during the hunting season (Swenson et al. 1994). This was because hunting is not allowed in the national parks in the north and because several large timber companies have a very restrictive policy regarding bear hunting on their land in the south. In addition, we have strong indications that our research activities have resulted in a lower rate of illegal killings in our study areas than is the case elsewhere, and that this is most pronounced in the north (Swenson et al. unpubl.). Because of this, our estimates of minimum viable population size must be considered to be conservative underestimates.

Uncertainty and population viability

Our viability analyses are based on the assumption that population fluctuations can be described by a diffusion process. Theoretical analyses have shown that this is possible if the population growth rate is not too high

(Dennis et al. 1991, Engen et al. unpubl.) and the stochasticity is not too large (Lande and Orzack 1988, Ludwig 1996, Engen et al. unpubl.). The similarity between the population growth rate in the diffusion (Fig. 3) and individual-based simulation model (Fig. 4) suggests that the diffusion approximation is reasonable even for small population sizes. One great advantage of describing the population growth by a diffusion process is that it makes it possible to obtain analytical expressions for several parameters that determine the viability of a population (Foley 1994, Lande et al. 1995, Engen et al. 1998, unpubl.). Furthermore, the diffusion approximation also can be used to estimate essential parameters from data (Sæther et al. 1996, 1998, Engen et al. 1998). In many of the simulation models currently used in population viability analyses, it is often necessary to use unknown input variables based more or less on guesses, and parameters that are not estimated from data (Boyce 1992, Caughley 1994, Sæther et al. 1998). Accordingly, Mills et al. (1996) found very large differences among four commonly used models in the predictions of the viability of an artificial grizzly bear population, even though the analyses were based on the same data set.

In our viability analysis we have assumed exponential population growth, i.e. we have assumed no density dependence. The form of density dependence may have a strong effect on the predictions from viability analyses (Ginzburg et al. 1990, Mills et al. 1996), but will be extremely difficult to describe quantitatively in a long-lived species such as the brown bear. Accordingly, Mills et al. (1996) suggested that all results from viability
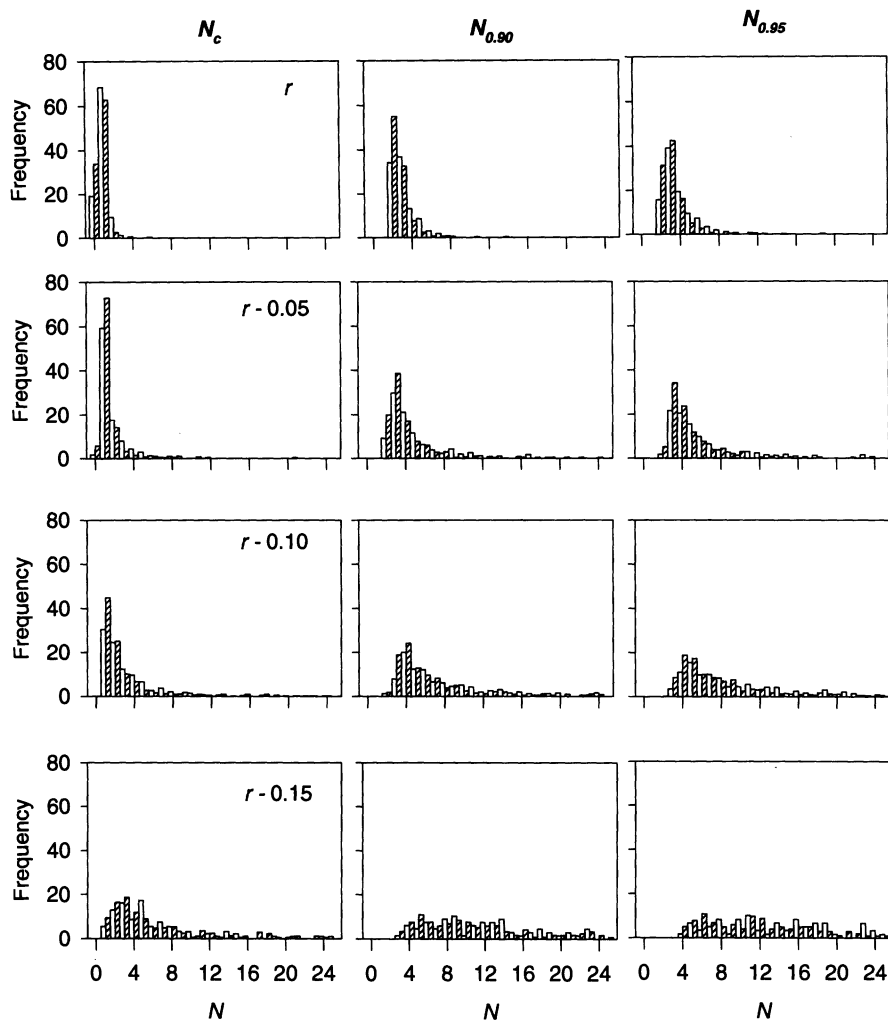
Fig. 6. The bootstrap distribution of the estimates of the critical population size (N_c) of the two populations of the Scandinavian brown bear, and the population size when the probability that the population will survive is 90% ($N_{0.90}$) and 95% ($N_{0.95}$), respectively, for different harvest rates. Critical population size is the minimum population size where the growth rate will be positive (see text for explanation). The critical population sizes are given only for populations where any potential density-dependent effects is assumed to be of minor importance ($N < 25$, see Table 2). Open bars: the northern population. Cross-hatched bars: the southern population.

analyses should be presented with and without the presence of density dependence. Considering the small size of the current Norwegian brown bear population (Swenson et al. 1995), the presence of density dependence will appear at much larger densities than will be encountered in Norway for many years and will be of little practical importance. In addition, the populations were growing rapidly, suggesting that they were not close to the carrying capacity. We have therefore restricted our analyses to calculations of the risk of extinction of relatively small populations. Any presence of density dependence will reduce the estimated life expectancy of the population, however, and increase the size necessary for a viable population.

As expected from the general theory (May 1974, Leigh 1981, Goodman 1987, Lande 1993), variation in

Table 2. The percentage of the bootstrap replicates that is greater than 25 individuals for the critical population size (N_c), and the population size where the probability that the population will survive is 90% ($N_{0.90}$) and 95% ($N_{0.95}$), respectively, for different harvest rates in the two populations. Density-dependent factors may have an effect for populations larger than 25 females.

Harvest rate	N_c		$N_{0.90}$		$N_{0.95}$	
	North	South	North	South	North	South
r	1.4	0.0	7.8	4.6	7.8	5.0
$r - 0.05$	6.0	1.6	14.2	11.0	13.1	9.8
$r - 0.10$	36.8	17.6	48.1	30.9	44.9	29.1
$r - 0.15$	82.6	59.0	88.5	71.0	87.2	79.0

Table 3. The reduction in age-dependent expected survival rates of the northern and the southern populations caused by reduction in the population growth rate by 0.05, 0.10 and 0.15, respectively, when a similar proportion is removed in each age class.

Age	$r - 0.05$		$r - 0.10$		$r - 0.15$	
	North	South	North	South	North	South
0	0.9133	0.7344	0.8687	0.6985	0.8264	0.6645
1	0.9053	0.8273	0.8611	0.7869	0.8191	0.7486
2	0.8957	0.8767	0.8520	0.8340	0.8104	0.7933
3	0.8843	0.9043	0.8411	0.8602	0.8001	0.8183
4 +	0.8707	0.9213	0.8202	0.8763	0.7878	0.8336

the population growth rate strongly affected the risk of extinction of the Scandinavian brown bear (Figs 2, 3, 6). Changes in the average mortality rate will also strongly influence the growth rate (Table 3). For instance, if we assume that an equal proportion of each age class is removed, a reduction in the adult survival rate from 0.9685 to 0.9213 will reduce the population growth by 5% in the south. This shows that the population growth rate is very sensitive to change in the mortality rate, and that the viability of the Scandinavian brown bear will be influenced by changes in the mortality rate. Thus, the prediction of a high viability of even small Scandinavian brown bear populations in the present study is highly dependent on the maintenance of a high survival rate. Relatively small increases in the mortality rate from the estimates in the present study will give low viability predictions even for very large brown bear population sizes. This is in accordance with the results from viability studies of other bear populations (Shaffer 1983, Suchy et al. 1985, Stenseth and Steen 1987, Boyce 1995) and other large mammals (Burgman et al. 1993, Ranta et al. 1996).

A common assumption in most population viability analyses is that a precise estimate of all necessary parameters can be obtained. The large standard deviations in the distribution of the bootstrap replicates of r, s_d^2 and s_e^2 (Fig. 1), even in our data-set, which is based on a relatively large sample of radio-collared individuals, indicates that uncertain parameter estimates will be a general problem in most population viability analyses. Our analyses demonstrate that these uncertainties, in combination with demographic and environmental stochasticity, strongly reduce our ability to correctly predict the population size in the future (Fig. 5). It is important to consider these large uncertainties when making predictions about viable population sizes. Our results illustrate that such predictions may be very imprecise (Fig. 6). According to the precautionary principle, the predicted viable population size should be larger than the population size considered to be viable if there had been no uncertainty in

the population parameters. This is illustrated in Fig. 6, where we have chosen a viable population size larger than the most likely value of $N_{0.90}$. It will be a great challenge for conservation biologists to develop quantitative criteria for assessing the risk of extinction that include uncertainties in parameter estimates.

Our estimates of minimum viable size, 6–7 females in the south and 8–9 in the north, is lower than previous estimates based on bear data from North America (see references in Boyce 1995). However, the finding that even small populations of brown bears can be viable agrees with historical data from Scandinavia. After an intense eradication effort in both Norway and Sweden in the last century, Sweden protected the brown bear, gradually increasing protection from 1893 to 1927 (Swenson et al. 1995). Around 1930, there were perhaps only about 130 bears in total left, divided among the four remnant populations that have survived in Sweden (Swenson et al. 1995). These populations have increased to about 1000 bears in total today (Swenson and Sandegren unpubl.). However, several other populations, extant in 1910–1920, are now extinct. They were mostly in Norway, where the eradication efforts continued much longer than in Sweden (Swenson et al. 1995).

References

Boyce, M. S. 1992. Population viability analysis. – Annu. Rev. Ecol. Syst. 23: 481–506.
– 1995. Population viability for Grizzly bears (*Ursus arctos horribilis*): a critical review. – Report to the Interagency Grizzly Bear Committee.
Bunnell, F. L. and Tait, D. E. N. 1985. Mortality rates of North American bears. – Arctic 38: 316–323.

Burgman, M. A., Ferson, S. and Akçakaya, H. R. 1993. Risk assessment in conservation biology. – Chapman & Hall, London.

Caughley, G. 1994. Directions in conservation biology. – J. Anim. Ecol. 63: 215–244.

Cohen, J. E. 1977. Ergodicity of age structure in populations with Markovian vital rates, III: finite-state moments and growth rate; an illustration. – Adv. Appl. Prob. 9: 462–475.

– 1979. Comparative statics and stochastic dynamics of age-structured populations. – Theor. Popul. Biol. 16: 159–171.

Dennis, B., Munholland, P. L. and Scott, J. M. 1991. Estimation of growth and extinction parameters for endangered species. – Ecol. Monogr. 61: 115–123.

Eberhardt, L. L., Blanchard, B. M. and Knight, R. R. 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. – Can. J. Zool. 72: 360–363.

Engen, S., Bakke, Ø. and Islam, A. 1998. Demographic and environmental stochasticity: concepts and definitions. – Biometrics 54: 39–45.

Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. – Cons. Biol. 8: 124–137.

Ginzburg, L. R., Ferson, S. and Akçakaya, H. R. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. – Cons. Biol. 4: 63–70.

Goodman, D. 1987. The demography of chance extinction. – In: Soulé, M. E. (ed.), Viable populations for conservation. Cambridge Univ. Press, Cambridge, pp. 11–34.

Goodman, L. 1967. The probability of extinction for birth-and-death processes that are age-dependent or phase-dependent. – Biometrika 54: 579–596.

Hovey, F. W. and McLellan, B. N. 1996. Estimating population growth of grizzly bears from Flathead River drainage using computer simulations of reproduction and survival rates. – Can. J. Zool. 74: 1409–1416.

IUCN 1994. IUCN Red List Categories. – IUCN Species Survival Commission, Gland, Switzerland.

Kaplan, E. L. and Meier, P. 1958. Nonparametric estimation for incomplete observations. – J. Am. Stat. Ass. 53: 457–481.

Karlin, S. and Taylor, H. M. 1981. A second course in stochastic processes. – Academic Press, New York.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity, and random catastrophes. – Am. Nat. 142: 911–927.

– and Orzack, S. H. 1988. Extinction dynamics of age-structured populations in a fluctuating environment. – Proc. Natl. Acad. Sci. USA 85: 7418–7421.

– , Engen, S. and Sæther, B.-E. 1995. Optimal harvesting of fluctuating populations with a risk of extinction. – Am. Nat. 145: 728–745.

Leigh, E. G., Jr. 1981. The average lifetime of a population in a varying environment. – J. theor. Biol. 90: 213–239.

Leslie, P. H. 1948. Some further remarks on the use of matrices in population mathematics. – Biometrika 35: 213–245.

Ludwig, D. 1996. The distribution of population survival times. – Am. Nat. 146: 506–526.

Mace, G. M. and Lande, R. 1991. Assessing extinction threats: toward an reevaluation of IUCN threatened species categories. – Cons. Biol. 5: 148–157.

May, R. M. 1974. Complexity and stability in model ecosystems, 2nd ed. – Princeton Univ. Press, Princeton, NJ.

McLellan, B. 1994. Density-dependent population regulation of brown bears. – In: Taylor, M. (ed.), Density-dependent population regulation of black, brown, and polar bears. Int. Conf. Bear Res. Manage. Monogr. 3: 15–24.

Mills, L. S., Hayes, S. G., Baldwin, C., Wisdom, M. J., Citta, J., Mattson, D. J. and Murphy, K. 1996. Factors leading to different viability predictions for a grizzly bear data set. – Cons. Biol. 10: 863–873.

Ranta, E., Lindström, J. and Kokko, H. 1996. Ecological risk analysis: the case of the Saima Ringed Seal. – Ambio 25: 363–365.

Reynolds, H. V. III. 1993. Evaluation of the effects of harvest on grizzly bear population dynamics in the northcentral Alaska Range. – Alaska Dept. Fish and Game, Federal Aid in Wildlife Restoration, Final Report, Project W-23-5. Juneau, AK.

Rogers, L. L. 1987. Effects of food supply and kinship on social behavior, movements, and population dynamics of black bears in northeastern Minnesota. – Wildl. Monogr. 97.

Sæther, B.-E. and Engen, S. 1997. Forvaltning av små bestander. En teoretisk undersøkelse. – NINA fagrapport 24: 1–39 (in Norwegian).

– , Ringsby, T. H. and Røskaft, E. 1996. Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. – Oikos 77: 217–226.

– , Engen, S., Swenson, J., Bakke, Ø. and Sandegren, F. 1997. Levedyktighetsanalyser av skandinavisk brunbjørn. – NINA fagrapport 25: 1–41 (in Norwegian).

– , Engen, S., Islam, A., McCleery, R. and Perrins, C. M. 1998. Environmental stochasticity and extinction risk in a population of a small songbird, the great tit. – Am. Nat. 151: 441–450.

Sagør, J. T., Swenson, J. E. and Røskaft, E. 1997. Compatibility of brown bear Ursus arctos and free-ranging sheep in Norway. – Biol. Cons. 81: 91–95.

Servheen, C. 1990. The status and conservation of the bears of the world. – Int. Conf. Bear Res. Manage. Monogr. 2: 1–32.

– et al. 1994. Report of the Northern Ecosystem researchers on grizzly bear population trends in the North and South Forks of the Flathead, and the Blackfeet Indian Reservation of the NCDE; the Cabinet-Yaak ecosystem; and the Selkirk ecosystem; and future data needs to improve trend estimates. – Report to the Interagency Grizzly Bear Committee.

Shaffer, M. L. 1983. Determining minimum viable population sizes for the grizzly bears. – Proc. Int. Conf. Bear Res. Manage. 5: 133–139.

Stenseth, N. C. and Steen, H. 1987. Små bestanders dynamikk med spesiell referanse til bjørn, jerv og ulv i Norge: Et teoretisk studium. – Viltrapport 45: 1–43 (in Norwegian).

Suchy, W. J., McDonald, L. L., Strickland, M. D. and Anderson, S. H. 1985. New estimates of minimum viable population size for grizzly bears of the Yellowstone ecosystem. – Wildl. Soc. Bull. 15: 223–228.

Swenson, J. E., Sandegren, F., Bjärvall, A., Söderberg, A., Wabakken, P. and Franzén, R. 1994. Size, trend, distribution and conservation of the brown bear Ursus arctos population in Sweden. – Biol. Cons. 70: 9–17.

– , Wabakken, P. Sandegren, F., Bjärvall, A., Franzén, R. and Söderberg, A. 1995. The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. – Wildl. Biol. 1: 11–25.

– , Sandegren, F., Söderberg, A., Bjärvall, A. and Franzén, R. 1997. Infanticide caused by hunting of male bears. – Nature 386: 450–451.

– , Franzén, R., Segerström, P. and Sandegren, F. (in press). The age of self-suffiency in Scandinavian brown bears. – Acta Theriol.

Taberlet, P., Swenson, J. E., Sandegren, F. and Bjärvall, A. 1995. Localization of a contact zone between two highly divergent mitochondrial DNA lineages of the brown bear Ursus arctos in Scandinavia. – Cons. Biol. 9: 1255–1261.

Turelli, M. 1977. Random environments and stochastic calculus. – Theor. Popul. Biol. 12: 140–178.

Williams, H. P., Bryan, P. F., Teukolsky, S. A. and William, T. W. 1988. Numerical recipes in C. – Cambridge Univ. Press, Cambridge.

414

Appendix 1

Let R_i be the individual contribution to the next generation for a population where all individuals have the same properties with respect to survival and reproduction. The contributions are defined as the number of offspring surviving to the next season plus 1, if the parent survives. Engen et al. (1998) have presented general definitions of demographic and environmental variances for this class of models. The demographic variance is

$$\sigma_d^2 (N) = \text{var} (R_i) - \text{cov} (R_i, R_j) = \frac{1}{2} \text{var}(R_i - R_j) \quad \text{(A1)}$$

for $i \neq j$, which in general may depend on the population size N. Provided that there is no intraspecific competition, the environmental variance is generally defined as the within-generation covariance between two contributions, that is

$$\sigma_e^2(N) = \text{cov} (R_1, R_j) \quad \text{(A2)}$$

for $i \neq j$. Writing ΔN for the change in the population size from one season to the next, it follows from these definitions that

$$\text{var} (\Delta N) = \sigma_d^2(N)N + \sigma_e^2(N)N^2. \quad \text{(A3)}$$

For a small time interval of length Δt, $E(\Delta N) = \mu(N)\Delta t + o(\Delta t)$, where $\mu(N)$ is the infinitesimal mean and $E(\Delta N)^2 = v(N)\Delta t + o(\Delta t)$, where $v(N)$ is the infinitesimal variance. Methods for approximating discrete processes by diffusions are given by Turelli (1977), Karlin and Taylor (1981: ch. 15) and Engen et al. (unpubl.). In biological literature the most common approach is the so-called Ito method, which is equivalent to choosing $\mu(N) = E(\Delta N)$ and $v(N) = \text{var} (\Delta N)$. Improved higher order approximations were proposed by Engen et al. (unpubl.).

Many biological processes may be approximated by processes with constant demographic and environmental variance and constant specific growth rate. However, especially in age-structured populations, there may be autocorrelations in the population growth. One way of overcoming this problem is to choose time steps for the discrete model consisting of several generations so that autocorrelations can be ignored in this new discrete process. Then, if this process can be accurately approximated by a diffusion, we also have a good diffusion approximation of the original model, with discrete time steps of one season.

Let the new and larger discrete time step have length t. Assume that $E(\Delta N) = \rho N$ and $\text{var} (\Delta N) = \sigma_d^2 N + \sigma_e^2 N^2$, where ΔN is the change in population size in the time interval. We now want to approximate this discrete process by a diffusion with infinitesimal mean $\mu(N) = rN$ and variance $v(N) = s_d^2 N + s_e^2 N^2$. Engen et

al. (unpubl.) has shown that the mean and variance of ΔN for this diffusion is

$$E(\Delta N) = (e^{rt} - 1)N$$

and

$$\text{var} (\Delta N) = s_d^2 e^{rt} \frac{e^{(s_e^2 + r)t} - 1}{s_e^2 + r} N + e^{2rt}(e^{s_e^2 t} - 1)N^2.$$

Hence, we obtain a diffusion model with the same mean and variance of ΔN over the time step t by choosing r, s_e^2, and s_d^2 to fit the equations

$$\rho = e^{rt} - 1 \quad \text{(A4)}$$
$$\sigma_e^2 = e^{2rt}(e^{s_e^2 t} - 1) \quad \text{(A5)}$$
$$\sigma_d^2 = s_d^2 e^{rt} \left(\frac{e^{(s_e^2 + r)t} - 1}{s_e^2 + r} \right). \quad \text{(A6)}$$

The solution of this set of equations is

$$r = \frac{1}{t} \ln (1 + \rho) \quad \text{(A7)}$$

$$s_e^2 = \frac{1}{t} \ln \left[1 + \frac{\sigma_e^2}{(1 + \rho)^2} \right] \quad \text{(A8)}$$

$$s_d^2 = \frac{1}{t} \sigma_d^2 \frac{\ln \left[1 + \rho + \frac{\sigma_e^2}{(1 + \rho)} \right]}{\rho(1 + \rho) + \sigma_e^2} \quad \text{(A9)}$$

which defines the relevant diffusion approximation to the discrete process.

The final problem is to find the relevant values of the three parameters (ρ, σ_d^2, σ_e^2) of the discrete process with time steps with length t for an age-structured population. Engen et al. (unpubl.) have proposed a method for computing these parameters by stochastic simulations for a very general class of age-structured models. This class of models includes models with only demographic stochasticity of the type analysed by Goodman (1967), as well as the models covered by the theory of stochastic Leslie matrices (Cohen 1977, 1979), which are essentially models with environmental variance only. Diffusion approximation for this type of model with small noise was proposed by Lande and Orzack (1988). The standard deterministic Leslie model (Leslie 1948) is also a special case. For a description of the computational method, the reader is referred to Todnem and Engen (unpubl.).

Appendix 2

The data showed no significant difference in reproduction and survival between the age-classes including 4 years and upwards. We therefore let these be defined as one age-class, for which surviving individuals remain in

the same class. The distribution of the number of offspring did not differ significantly between years (Swenson et al. unpubl.). Consequently, we only model the demographic component of reproduction assuming that all females produce a number of offspring independent of each other. Let $g(x, y)$ denote the probability that a female of age x produces y offspring, both sexes included. If the number of female offspring conditional on y is binomial with parameters $(y, 1/2)$, the distribution of the number of female offspring is

$$f(x, y) = \sum_{x=0}^{k} \binom{x}{y} \left(\frac{1}{2}\right)^z g(x, z),\qquad (A10)$$

where k is the maximum number of offspring. The distributions $g(x, y)$ may be estimated as $\hat{g}(x, y) = n(x, y)/\Sigma_y\, n(x, y)$, where $n(x, y)$ is the total number of females of age x observed during the whole period of sampling that produces y offspring. The estimator $\hat{f}(x, y)$ is then found by replacing $g(x, y)$ in (A10) by $\hat{g}(x, y)$.

Bootstrapping is performed by choosing at random with replacement from each age class.

The individual survivals are assumed to be independent when conditioned on the environmental conditions. However, the probabilities of survival may vary stochastically among years because of varying environmental conditions. If there is such a stochasticity, it will produce environmental variance s_e^2 in the diffusion approximation for the process. Let $p(x, t)$ denote the probability that an individual of age x in season t survives to age $x + 1$. We model the stochasticity in $p(x, t)$ by assuming that logit $[p(x, t)]$ is normally distributed and hence may be written as

$$\text{logit } [p(x, t)] = \phi(x) + \psi(x)U_t,\qquad (A11)$$

where $\phi(x)$ and $\psi(x)$ are functions of the age x, and U_t is a sequence of independent standard normally distributed variables. The expectation and standard deviation of logit $[p(x, t)]$ is then $\phi(x)$ and $\psi(x)$, respectively. Alternatively, eq. (A11) may be written as

$$p(x, t) = \frac{e^{\phi(x) + \psi(x)U_t}}{1 + e^{\phi(x) + \psi(x)U_t}}.\qquad (A12)$$

The expectation $\phi(x)$, as well as the standard deviation $\phi(x)$, are expected to depend slightly on the age x. This can be approximated by linearization, writing

$$\phi(x) = \alpha + \beta x\qquad (A13)$$

$$\ln [\psi(x)] = \gamma + \delta x.\qquad (A14)$$

We have chosen to use $\ln [\psi(x)]$, that is, to adopt a loglinear model for $\psi(x)$, because the standard deviation is always non-negative. Hence, the model is well defined for any values of the four parameters. The likelihood function for these parameters is calculated by first considering the survivals as independent for a given sequence $U_1, U_2 \ldots$ and then integrate over the distribution of $U_1, U_2 \ldots$, which is a product of standard normal densities. A Pascal program computes this likelihood function by numerical integration. Then, finally, the likelihood function is maximised numerically with respect to the four parameters by the downhill simplex method (Pascal procedure is given by Williams et al. 1988).

Bootstrapping is performed by parametric simulations from the estimated model. The best approach is to simulate independent sets of data of the same size as the original set of data. Bootstrap replicates of the parameters of the diffusion approximation (r, s_d^2, s_e^2) are finally computed from the estimated bootstrap replicates for the model parameters. These computations are performed by the Monte Carlo technique of Engen et al. (unpubl.) described in Appendix 1. Altogether we have computed 500 bootstrap replicates for the northern and southern population.

416