

Harvesting strategies for conserving minimum viable populations based on World Conservation Union criteria: brown bears in Norway

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The World Conservation Union (IUCN) defines populations as vulnerable if the probability of extinction is larger than 10% within the next 100 years. With the objective of minimizing problems with predation on domestic livestock and, at the same time, conserving a viable population, we consider different threshold harvesting strategies for a small population of brown bear, based on a population dynamics model with growth rate and demographic and environmental variances estimated from the present Swedish population. Taking into account uncertainties in present estimates of the demographic parameters and in population size, we show that the population can be harvested when the population size exceeds 34 female bears aged one year and older, if the entire population exceeding the threshold is harvested. To minimize the expected long-term population size, however, we show that it is optimal to harvest only a proportion equal to 35% of the population exceeding a lower threshold of 12 female bears. This strategy gives an expected long-term population size of around 20 female bears. If the growth rate of the population is reduced by *ca.* 3%, the threshold must, under some conditions, be doubled. We argue that the small thresholds are mainly a result of the high intrinsic growth rate of the population considered in the present paper. However, the analysis also suggests that IUCN's criterion might allow a rate of extinction that is too high.

Keywords: threshold harvesting; minimum viable population size; stochasticity; *Ursus arctos*; extinction; IUCN's Red List categories; predation

1. INTRODUCTION

At present, many species are declining in numbers and may soon become extinct, mainly due to overharvesting marine species and the conversion of terrestrial ecosystems into alternative land uses considered more profitable by land owners. For example, in many countries large land areas are being used to support widespread domestic and semi-domestic livestock. This has caused a reduction in the size of many populations of large carnivores occupying the same areas because of predation on livestock and because current husbandry practices are to a great extent incompatible with the presence of these large predators (Fuller & Kittredge 1996). One example is the Scandinavian brown bear (*Ursus arctos*) population, which was persecuted for several centuries mainly due to its predation on sheep and semi-domestic reindeer. The national governments of Norway and Sweden encouraged this persecution with generous bounties. As a result, the bear was exterminated in Norway, and as few as around 130 individuals survived in Sweden (Swenson *et al.* 1995).

Swedish authorities initiated management actions to save the species at the turn of the century. These actions were successful, and the population increased gradually to approximately 620 individuals in the early 1990s (Swenson *et al.* 1994). Currently, there might be around 1000 bears in Sweden and Norway. The bears in Norway have immigrated from neighbouring countries, primarily Sweden (Swenson *et al.* 1998). These immigrating bears cause serious problems in Norway, in part because the livestock breeders, when there were few or no predators, adopted a less intensive husbandry, which made the livestock more vulnerable to predation after the re-establishment began (Sagør *et al.* 1997). At present, sheep are untended; 6–10% of the ewes are killed in some areas, and the rate of predation is increasing with the number of bears, even though there are still few bears in Norway (Sagør *et al.* 1997). This has led to strong political and public pressure to limit the size of the bear population through hunting and killing the individuals that kill many sheep.

At the same time, a reduction in the size of small populations in general increases the risk of extinction (Sæther *et al.* 1998) and can easily result in a conflict with the obligations of the Convention of Biodiversity to secure viable populations. The World Conservation Union (IUCN) has defined several categories used in Red

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Listings of threatened species (IUCN/SSC 1994). These categories are meant to serve as a guide for managers in setting conservation priorities; conservation action is needed if a species is listed in one of the 'high risk' categories. The IUCN follows Mace & Lande (1991) and considers extinction to be a chance event resulting from the intrinsic stochastic nature of the population dynamics. For given demographic parameters, a species is defined as 'vulnerable' (the lowest 'high risk' category) if the probability of extinction is larger than 10% within the next 100 years. Otherwise, a species is classified as belonging to the 'lower risk' category, and is considered to be viable.

Here we consider management strategies for conserving a future re-established brown bear population in Norway, with the objective of minimizing costs related to predation on domestic livestock, under the constraint that the population should be viable by IUCN's criteria. We therefore seek strategies for which the probability of extinction in the next 100 years is less than 10%.

We consider one form of management: a threshold harvesting strategy (Lande *et al.* 1995, 1997), in which the population is harvested down to a threshold c . Below the threshold there is no harvest. As we have described for the brown bear, the conservation of many species might be in conflict with other interests in a society. To reduce the conflict level it is therefore of interest to compute the smallest possible value of c satisfying the criteria of the IUCN.

For most threatened and vulnerable species, however, a quantitative analysis of the extinction risk involves uncertain parameter estimates. For instance, the uncertainties in several demographic parameters of two Scandinavian brown bear populations, on which our analysis is based, are quite large (Sæther *et al.* 1998). Accordingly, the threshold c , being a function of the demographic parameters, will itself be uncertain. Here, as advocated by the IUCN (IUCN/SSC 1994), we adopt the precautionary principle and choose the largest critical threshold c that, with 95% confidence, gives an extinction risk in the next 100 years of less than 10%.

Many management strategies of harvested species are based on population censuses that often involve considerable errors in the estimates of population size (Buckland *et al.* 1993). In those cases we show that a larger threshold should be used. We also show that harvesting only a proportion q above the threshold, so-called proportional threshold harvesting (Engen *et al.* 1997), will be a preferable strategy in such cases.

Although one particular species is used to illustrate the approach, a complete viability analysis for any endangered species will necessarily involve many of the same decisions with respect to how different forms of uncertainty should be treated, and how different costs and benefits should be balanced. The analysis presented here also illustrates some of the implications of basing conservation strategies on IUCN's criteria when applied to threatened species in general.

2. METHODS

(a) *The model*

As shown by Engen *et al.* (1999), provided that there is no density dependence at low densities, the long-term dynamics of

age-structured models with demographic and environmental stochasticity, applicable to populations of brown bear, can be approximated by simple diffusion models with infinitesimal mean (growth rate)

$$\mu(x) = rx, \quad (1)$$

and infinitesimal variance

$$\sigma^2(x) = \sigma_d^2 x + \sigma_c^2 x^2, \quad (2)$$

where x is the number of female bears in the population. Precise definitions of σ_c^2 and σ_d^2 are given by Engen *et al.* (1998).

In addition to the intrinsic dynamics of the population, defined by equations (1) and (2) we assume that the size of the population is regulated each year, at discrete time intervals, through harvesting of the population when some threshold c is exceeded. This regulation is based on censusing the population before each harvest, resulting in an unbiased estimate of the population size, \hat{X}_t , with variance $\theta^2 X_t$. This dependence of the variance on X_t arises in, for example, line-transect sampling (Seber 1982). In capture-recapture studies, the variance depends on the number of marked individuals and the number of recaptures, which can vary from year to year (Eberhardt 1990). In the study by Swenson *et al.* (1994), typical values of θ ranged up to 1.6. These estimates, however, included only breeding females, and the uncertainty in total population size might therefore be somewhat larger. For other methodologies, typical coefficients of variation of \hat{X}_t are between 0.04 and 0.5 (Engen *et al.* 1997, table 1), which, for a population of, say, 30 bears, corresponds to $0.21 \leq \theta \leq 2.73$.

Engen *et al.* (1997) have shown that so-called proportional threshold harvesting, in terms of maximizing the cumulative yield before extinction, is preferable to pure threshold harvesting when there is uncertainty in the population estimates. The rationale behind this strategy is that it will be advantageous, when there is large uncertainty in the estimate of the population size, to combine the actual estimate with the additional information contained in the quasi-stationary distribution of the underlying true population size (Lande *et al.* 1997). This results in a strategy that involves harvesting each year only a fraction, q , of the estimated excess above the threshold c , so that the quantity harvested becomes

$$Y(\hat{X}; c, q) = \begin{cases} q(\hat{X} - c) & \text{for } \hat{X} \geq c, \\ 0 & \text{for } \hat{X} < c. \end{cases} \quad (3)$$

(b) *Numerical analysis*

Under the model defined by equations (1), (2) and (3), the probability of extinction before $t_0 = 100$ years is a function of the model parameters ($r, \sigma_d^2, \sigma_c^2, c, q, \theta$), and the initial size of the population at $t = 0$, which we assume to equal the population size K at which the expected growth equals zero,

$$K = \frac{c}{1 - r/q}. \quad (4)$$

By using simulation and regression methods (see Appendix A) we can now estimate an approximate formula for the critical threshold c , satisfying the criterion that the probability of extinction before $t_0 = 100$ years is 0.10, as a function of the other model parameters,

$$\hat{c}(r, \sigma_d^2, \sigma_c^2, q, \theta). \quad (5)$$

Table 1. Estimates \pm standard errors of the growth rate and the environmental and demographic variance in the northern and southern Swedish brown bear populations

population	r	σ_c^2	σ_d^2
northern	0.12 ± 0.03	0.003 ± 0.003	0.180 ± 0.033
southern	0.15 ± 0.03	0 ^a	0.155 ± 0.023

^a Not statistically significant from zero.

(c) **Parameter estimates**

By using demographic data from two Swedish populations of brown bear, Sæther *et al.* (1997) estimated the parameters of the diffusion approximation given by equations (1) and (2), applied to the female component of the population. The point estimates of these parameters are given in table 1. The corresponding uncertainties in the parameter estimates were found by parametric bootstrapping from the age-structured model. The analysis here is based on 560 bootstrap replicates (r^* , σ_d^{2*} , σ_c^{2*}) for each of the two populations. The demographic parameters are known to be quite different between these established populations and peripheral, establishing populations, such as the present Norwegian population (Swenson *et al.* 1998). It will therefore be necessary to re-estimate the parameters with more data from a future restored population in Norway. Given our present state of knowledge, however, the best that we can do is to assume that a future Norwegian population, once it has become established, will come from the same ‘meta-distribution’ as the two Swedish subpopulations. This meta-distribution can be reconstructed approximately non-parametrically (Efron & Tibshirani 1993) by sampling from each of the two populations with probability 0.5. Taking into account uncertainty in the parameters within each region, this is equivalent to basing the analysis on the two bootstrap distributions combined into one distribution of 1120 replicates. Histograms of the bootstrap replicates for each parameter are shown in figure 1.

3. RESULTS

(a) **The critical threshold**

For each bootstrap replicate (r_i^* , $\sigma_{d,i}^{2*}$, $\sigma_{c,i}^{2*}$) of the population parameters we can now obtain, by using the estimated formula (equation (5)), a corresponding bootstrap replicate of the threshold $c_i^*(q, \theta) = \hat{c}(r_i^*, \sigma_{d,i}^{2*}, \sigma_{c,i}^{2*}, q, \theta)$. A reasonable choice of c is the upper 95% quantile, $c_{0.95}$, of the distribution of $c^*(q, \theta)$. This choice will be precautionary in the sense that the correct threshold c will be larger than $c_{0.95}$ in *ca.* 5% of repeated realizations of the data on which estimation of the population parameters was based. This is in agreement with IUCN’s recommendation, which states that ‘it is legitimate to apply the precautionary principle and use the estimate (providing it is credible) that leads to listing in the category of highest risk’ (IUCN/SSC 1994, § II.7).

This 95% quantile is shown, as a function of q and θ , in figure 2a. There are two major points to notice. First, as θ , the uncertainty in the population size estimates, increases, c has to be increased if the population is to avoid extinction with the prescribed probability. Secondly, if we choose to harvest a smaller proportion, $q < 1$, of the difference between the population estimate and the threshold, we can begin to harvest at a somewhat lower population size.

(b) **Minimizing costs related to predation**

From the conservation point of view, the points on each curve in figure 2a each represent alternative management decisions, all giving the same probability of extinction with *ca.* 95% confidence. If the goal of the harvest is to reduce the impact of the bear population (for example a sheep farmer’s point of view), it would be desirable to minimize the expectation of the loss experienced by the sheep farmer. Assuming that the loss is an increasing function of the bear population size and that the fluctuations in bear population size are small, minimizing the expectation of the loss is, to a good approximation, equivalent to minimizing the equilibrium population size given by equation (4). Because the population parameters are uncertain, we take an average of $K(r, q, \theta)$ over the bootstrap replicates of r . This average, again as a function of q and θ , is shown in figure 2b.

As expected, when there is no uncertainty in the population estimates ($\theta = 0$), the strategy corresponding to the strongest form of population regulation, $q = 1$, harvesting the entire population above the threshold gives the smallest expected equilibrium. However, when θ increases and the true population size is not known with certainty, the threshold has to be raised considerably if we are to avoid extinction with the prescribed probability. Also, harvesting only an intermediate proportion $q < 1$ leads to a smaller equilibrium population size (see figure 2). For $\theta = 4$, the optimal choice of q , minimizing the equilibrium population size, is as small as 0.3. If we assume that $\theta = 2$ is a realistic value, we see from figure 2 that the harvesting proportion should be set to around $q = 0.35$ and the threshold to $c = 12$. With this management strategy, the population will fluctuate around an expected equilibrium of approximately $K = 20$ female bears.

The effect of applying pure threshold harvesting ($q = 1$) instead of the optimal value of q is also large; the threshold then has to be set to 34, which gives an expected equilibrium of $K = 39$ female bears (see figure 2). Note that if $q < r$, the threshold will not exist. Consequently, the curves in figure 2b are shown only for values of q larger than the largest bootstrap replicate of r .

(c) **Reductions in r**

In North America, lower growth rates of bear populations have been recorded than in Scandinavia (Sæther *et al.* 1998). It is therefore of interest to analyse the effects on the population viability of a reduction in the growth rate of the Scandinavian population. It might also be desirable to allow a small selective offtake of a proportion, s , each year of those individuals in the population that kill most sheep, also when the overall population size is below the threshold, to decrease further the predation rate on untended sheep. Such a practice, as well as illegal hunting, would represent a similar reduction in the growth rate (Sæther *et al.* 1998).

In figure 3 the upper 95% quantile of the critical threshold is shown as a function of the reduction in growth rate s for different values θ and $q = 0.35$. As expected, as the reduction increases, the general threshold has to be raised if the population is to remain viable. For $\theta = 0$, a small reduction of only $s = 0.03$ requires almost a doubling of the threshold.

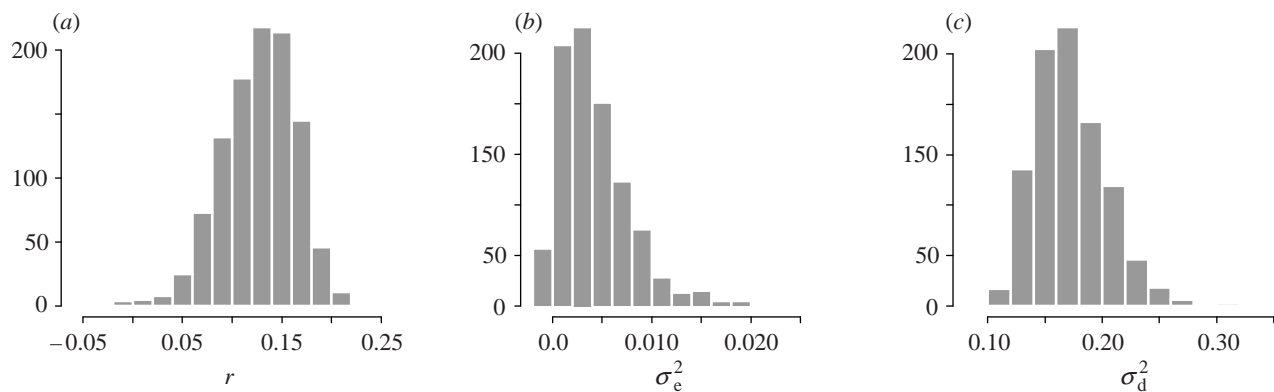


Figure 1. Histograms of the bootstrap replicates of (a) r , (b) σ_e^2 and (c) σ_d^2 taken from Sæther *et al.* (1997).

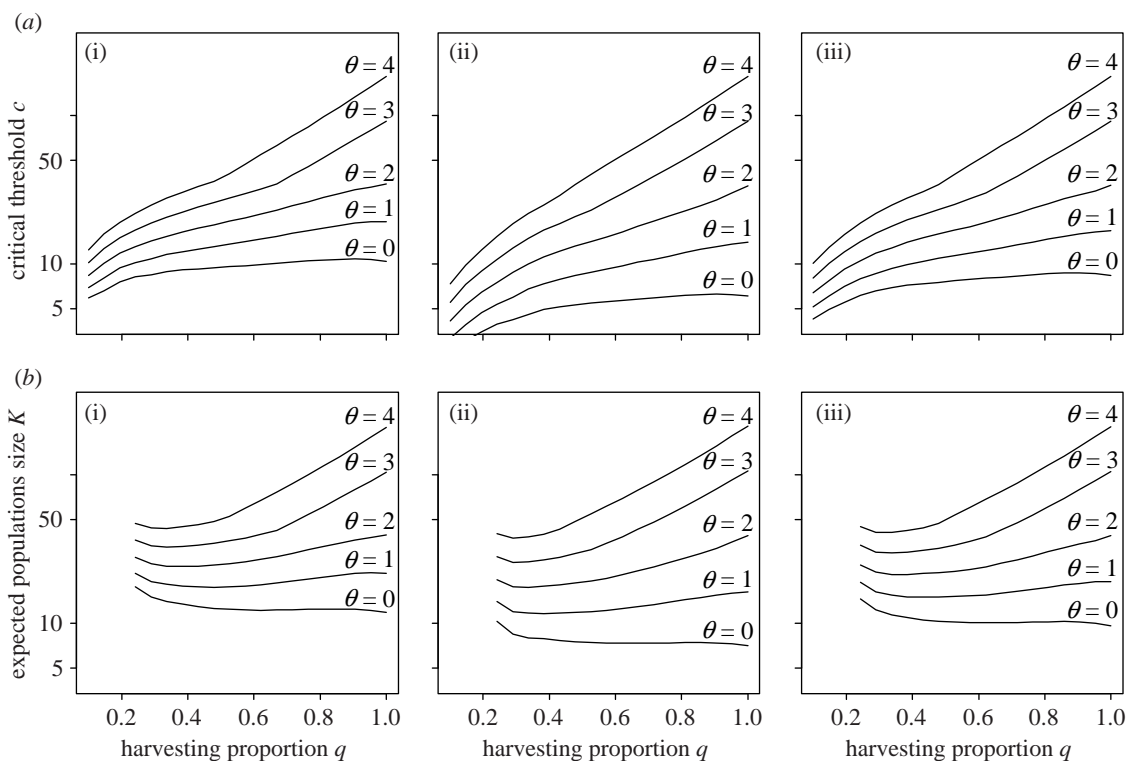


Figure 2. The upper 95% quantile of the critical threshold c as a function of the proportion q harvested for $\theta = 0, 1, \dots, 4$ (a), and the expected population equilibrium (equation (4)), again as a function of q and for different values of θ (b), in the (i) northern and (ii) southern (Swedish), and (iii) predicted (Norwegian) populations.

4. DISCUSSION

Conservation biology differs from ecology and other pure sciences in that it has a value-laden objective: to conserve biological species, communities and ecosystems because these are considered to represent various forms of utilitarian, intrinsic and existence values (Meffe & Carroll 1994). This entails balancing several, often conflicting, goals of a conservation problem to meet this major objective. Here we have presented one approach for choosing between different strategies for managing a population of a large carnivore, in this case a Norwegian population of brown bear.

It is important to note that our analysis involves a number of quite arbitrary choices, all implicitly representing different forms of values. The criterion of the

IUCN that the probability of extinction should be less than 10% within the next 100 years can be said to reflect the value that a non-extinct population of brown bear represents, in part, for the world community. The conservation value of a bear population implicitly also entered the analysis when the confidence level, considering the uncertainty in the threshold c , was set at 95%. Only when choosing between alternative harvesting proportions q did the values (or costs) related to predation enter the analysis. Overall, however, the entire strategy of limiting the population gives heavy priority to the costs related to predation. The resulting strategy does not seem to be very precautionary; a population of, on average, only around 20 female bears seems rather small. This is in part because the population does have a quite high growth rate and also a small demographic variance that

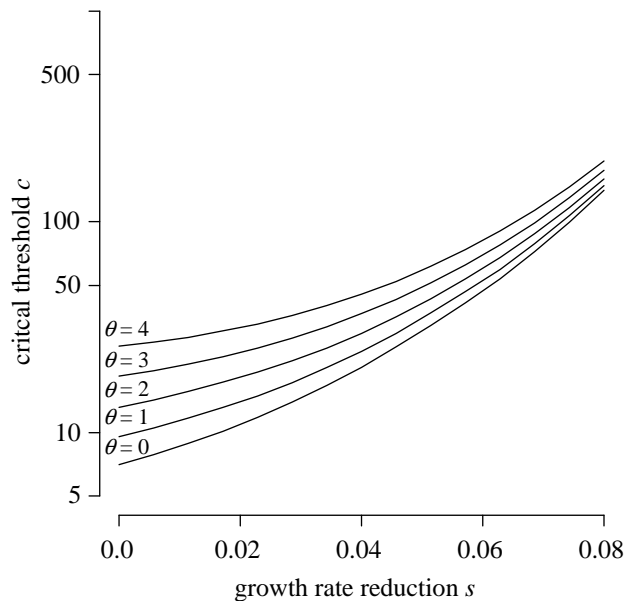


Figure 3. The critical threshold as a function of the reduction in the growth rate, s , for $\theta = 0, 1, \dots, 4$ and $q = 0.35$.

reduces the risk of extinction at low population densities. It is, however, also a result of the fact that IUCN's criterion allows a quite high rate of extinction.

The analysis has been based on a very specific interpretation of the criteria of the IUCN for classifying species as viable. Whereas the obligations of the Convention of Biodiversity can be satisfied in a narrow sense if one accepts the interpretation adopted here, there are several problems with the approach if regarded as a general procedure for choosing the management strategy. The various underlying costs and benefits of possible outcomes of the alternative actions are only crudely represented by a few prescribed probabilities and confidence levels. For example, in setting an acceptable probability of extinction α to 0.10, we are being indifferent between all values of α less than and larger than 0.10. This makes the overall procedure for choosing the management strategy somewhat inflexible. For example, the threshold does not depend on the actual magnitude of the costs related to predation on domestic animals nor on the magnitude of the value that a non-extinct population represents.

Despite this, it is not clear whether an alternative, more decision-theoretical approach would lead to more optimal management. One such approach is Bayesian decision theory, which essentially states that one should choose the action with the highest expected utility. Although a Bayesian analysis in theory might be preferable to the analysis presented here (see, for example, Berger 1985; Ferguson 1967, § 1.4), it is clear that such an approach would also involve several major difficulties. It is, for example, not clear how to quantify the utility of, say, different bear population sizes, including the utility (or cost) of an extinct population, how (and whether) the utility assigned to the future presence of some form of biodiversity should be discounted, and how to consistently assign utility to different geographical abundance patterns.

Until these questions have been resolved, it seems advisable to rely on simpler criteria such as that used in the analysis presented here. It seems necessary, however,

to apply such criteria with great care and only as an absolute minimum requirement. It is also questionable whether a probability of extinction equal to 0.10 during 100 years really corresponds to what most people find acceptable. It can be noted that the current global species extinction rate, which is considered highly unacceptable by many people, according to some estimates (Wilson 1992) is of the same order of magnitude as the rate of extinction allowed by IUCN's criterion. One can therefore argue that IUCN's criterion needs to be adjusted, for example by reducing the acceptable probability of extinction from 0.10 to 0.05, as proposed by Sæther & Engen (1997), or to some smaller value. It must be emphasized, however, that choosing an acceptable rate of extinction is not a scientific question but mainly a political one.

We have focused only on the level at which to set the harvesting threshold so as to meet the management goals. In reality the effort allocated to censusing the population is also subject to decisions. The results show that the bear population size (and costs related to predation) can be maintained at a considerably lower level by allocating more resources to censusing. For example, if increasing these resources such that θ is reduced from 4 to 1, a viable population can be maintained at an equilibrium of approximately 15 instead of 45 female bears (see figure 2). If one assumes that losses are directly proportional to the bear population size, this would represent a threefold reduction of the costs.

It is, however, uncertain how effective harvesting is in reducing losses (Sagør *et al.* 1997). It is therefore important to focus also on how the problem can be reduced, for example by introducing effective measures for protecting sheep from predation, by requiring the use of these measures before farmers can be fully compensated for losses to bears, by promoting the change in agricultural production from sheep farming to other forms of production in areas with bears, or by changing the livestock subsidy system to discourage agricultural practices that are not compatible with bears. Although this has been recognized by the Norwegian Parliament (Miljøverndepartementet 1997), very little progress has been made in this area in Norway. From society's point of view there might be some costs associated with all of these alternatives, but the total costs might become smaller than the costs experienced by livestock breeders that adopt current husbandry practices. With a change in these practices a somewhat larger population of bears might be optimal.

Turning to the biological assumptions that have gone into our analysis, it is clear that a number of important demographic and genetic processes that can influence the probability of extinction have been ignored. For instance, for certain patterns of environmental change, a certain amount of genetic variation must be present if a population is to be able to track changes in the optimum phenotype and avoid extinction (Lande & Shannon 1996). As a result of genetic drift, such genetic variation is lost at a higher rate in small populations. In addition, to avoid erosion of fitness by the accumulation of mildly detrimental mutations, large effective population sizes are necessary. For models in which the genetic variance is maintained by a balance between mutation, stabilizing selection and genetic drift, Lande (1995) has shown that

an effective population size of around 5000 individuals might be necessary to maintain typical levels of genetic variation. With immigration, this figure would be considerably lower; however, given that the size of the Swedish population at present is only around 1000 bears, Lande's model at least implies that the the total Swedish–Norwegian population would have to be increased to assure long-term viability on the basis of genetic factors.

In addition, in small populations such as that considered here, Allee effects (see, for example, Dennis 1989) might be present owing to difficulties of finding mates, for example as a result of large stochastic variation in the sex ratio at low population sizes. This could, in principle, be incorporated as density dependence in the demographic variance in equation (2). This would increase the extinction risk and lead to a higher harvesting threshold.

Another example is that population dynamics models for organisms without male parental care often rely on the assumption that only the female component of the population is important in determining the dynamics, because males never limit population growth. Recent studies of the Scandinavian brown bear population, however, suggest that immigrating males that take over the territory of a resident adult male shot by hunters might kill the young to shorten the interval to the female's next conception (Swenson *et al.* 1997). These authors estimate that the effect of killing one adult male has a population effect equivalent to killing between 0.5 and one adult female.

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APPENDIX A. NUMERICAL METHODS

The probability of extinction, for given model parameters, can be found with the desired accuracy by simulating, say, $n = 500$ realizations of the process up to $t = t_0$, and counting the number of extinctions m . One realization i of the process can be generated by simulating a sequence of standard normal variates $U_i = (U_{i1}, U_{i2}, \dots, U_{ik})$. In practice, in the discrete approximation of the diffusion, we found that time-steps of one year would suffice. Dropping model parameters other than c for brevity, for a given set of realizations of the process, $U = (U_1, U_2, \dots, U_n)$, an estimate of the probability of extinction is given by $\hat{\alpha}(c, U) = m(c, U)/n$. If we keep the stochastic element U fixed, which in practice is easily done by reinitializing the seed of the pseudo-random number generator used to some fixed constant for each computation of $\hat{\alpha}$, an estimate of the threshold \hat{c} at which $\alpha(c) = 0.1$, can be found by solving $\hat{\alpha}(c, U) = 0.10$ with respect to c by using some numerical root-finding algorithm.

This gives us a method for obtaining the threshold as a function $\hat{c}(r, \sigma_d^2, \sigma_e^2, q, \theta)$. We want to do this for different bootstrap replicates of $(r, \sigma_d^2, \sigma_e^2)$ and for different harvesting proportions q and uncertainties θ . It is therefore

desirable to find some approximate formula for c as a function of all these parameters that can be quickly evaluated.

Note that the rescaled process defined by $X'(t) = X(t)/\sigma_d^2$, by the transformation formulas for diffusions (Karlin & Taylor 1981, p. 173), will have demographic variance $\sigma_d'^2 = 1$, growth rate $r' = r$, environmental variance $\sigma_e'^2 = \sigma_e^2$, harvesting threshold $c' = c/\sigma_d^2$, harvesting proportion $q' = q$, and parameter characterizing the uncertainty in the population estimates $\theta' = \theta/\sigma_d$. Hence, we have

$$\hat{c}(r, \sigma_d^2, \sigma_e^2, q, \theta) = \sigma_d^2 \hat{c}'(r, 1, \sigma_e^2, q, \theta/\sigma_d), \quad (\text{A1})$$

which reduces the number of parameters to work with to four. To obtain a formula for the right-hand side of equation (A1), we computed, using the simulation method above, \hat{c}' at 2000 points throughout relevant parts of the parameter space and fitted $\ln(\hat{c}' + 1)$ to a fourth-order polynomial in $(r', \sigma_e'^2, q', \theta')$ by using ordinary least-squares linear regression. This gave a reasonably close fit and no systematic discrepancies in plots of the residuals against independent variables.

For $q \leq r$, the equilibrium used as the initial population size in the simulations does not exist; c must therefore be treated separately for these parameter values. Note that when $q \rightarrow r^+$, the equilibrium population size in equation (4) tends to infinity, implying that the threshold must tend to zero. We therefore choose to set $c = 0$ for $q \leq r$.

REFERENCES

- Berger, J. O. 1985 *Statistical decision theory and Bayesian analysis*. New York: Springer.
- Buckland, S. T., Anderson, D. R., Burnham, K. & Laake, J. L. 1993 *Distance sampling*. London: Chapman & Hall.
- Dennis, B. 1989 Allee effects: population growth, critical density, and the chance of extinction. *Nat. Res. Model.* **3**, 481–538.
- Eberhardt, L. L. 1990 Using radio-telemetry for mark-recapture studies with edge effects. *J. Appl. Ecol.* **27**, 259–271.
- Efron, B. & Tibshirani, R. J. 1993 *An introduction to the bootstrap*. London: Chapman & Hall.
- Engen, S., Lande, R. & Sæther, B.-E. 1997 Harvesting strategies for fluctuating population based on uncertain population estimates. *J. Theor. Biol.* **186**, 201–212.
- Engen, S., Bakke, Ø. & Islam, A. 1998 Demographic and environmental stochasticity—concepts and definitions. *Biometrics* **54**, 840–846.
- Engen, S., Bakke, Ø. & Todnem, T. 1999 Diffusion approximations to discrete population models. (In preparation.)
- Ferguson, T. S. 1967 *Mathematical statistics—a decision theoretic approach*. New York: Academic Press.
- Fuller, T. K. & Kittredge, D. B. 1996 Conservation of large forest carnivores. In *Conservation of faunal diversity in forested landscapes* (ed. R. M. DeGraaf & R. I. Miller), pp. 137–164. London: Chapman & Hall.
- IUCN/SSC 1994 *IUCN Red List categories*. Gland, Switzerland: IUCN/SSC. Available on the Internet. URL: <http://www.iucn.org/themes/ssc/redlist/ssc-rl.c.htm>
- Karlin, S. & Taylor, H. M. 1981 *A second course in stochastic processes*. New York: Academic Press.
- Lande, R. 1995 Mutation and conservation. *Conserv. Biol.* **9**, 782–791.
- Lande, R. & Shannon, S. 1996 The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution* **50**, 434–437.

- Lande, R., Engen, S. & Sæther, B.-E. 1995 Optimal harvesting of fluctuating populations with a risk of extinction. *Am. Nat.* **145**, 778–745.
- Lande, R., Sæther, B.-E. & Engen, S. 1997 Threshold harvesting for sustainability of fluctuating resources. *Ecology* **78**, 1341–1350.
- Mace, G. M. & Lande, R. 1991 Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. *Conserv. Biol.* **5**, 148–157.
- Meffe, G. K. & Carroll, C. R. 1994 *Principles in conservation biology*. Sunderland, MA: Sinauer Associates.
- Miljøverndepartementet 1997 *Om Rovviltforvaltning, St Meld. Nr 35*. Oslo, Norway: Departementet.
- Sæther, B.-E. & Engen, S. 1997 *Forvaltning av små bestander: en teoretisk bakgrunn* (NINA Fagrappport no. 024). Trondheim, Norway: Norwegian Institute for Nature Research.
- Sæther, B.-E., Engen, S., Swenson, J., Bakke, Ø. & Sandegren, F. 1997 *Population viability analysis of Scandinavian brown bears* (NINA Fagrappport no. 025). Trondheim, Norway: Norwegian Institute for Nature Research.
- 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.
- Sagør, J. T., Swenson, J. E. & Røskaft, E. 1997 Compatability of brown bear *Ursus arctos* and free-ranging sheep in Norway. *Biol. Conserv.* **81**, 91–95.
- Seber, G. A. F. 1982 *The estimation of animal abundance and related parameters*. London: Griffin.
- Swenson, J. E., Sandegren, F., Bjärvall, A., Söderberg, A., Wabakken, P. & Franzén, R. 1994 Size, trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. *Biol. Conserv.* **70**, 9–17.
- Swenson, J. E., Wabakken, P., Sandegren, F., Bjärvall, A., Franzén, R. & 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.
- Swenson, J. E., Sandegren, F., Söderberg, A., Bjärvall, A., Franzén, R. & Wabakken, P. 1997 Infanticide caused by hunting of male bears. *Nature* **386**, 450–451.
- Swenson, J. E., Sandegren, F. & Söderberg, A. 1998 Geographic expansion of an increasing bear population: evidence for presaturation dispersal. *J. Anim. Ecol.* **67**, 819–826.
- Wilson, E. O., 1992 *The diversity of life*. Cambridge, MA: Belknap Press of Harvard University Press.

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