

From: [Conor McGowan](#)
To: [Nelson, Marjorie](#)
Cc: [Justin Shoemaker/R6/FWS/DOI](#)
Subject: Re: Wolverine meeting in Denver?
Date: Monday, January 9, 2017 11:41:16 AM
Attachments: [jwmq%2E79.pdf](#)
[0022-541x%282005%29069%5B1001%3Amsftwi%5D2%2E0%2Eco%3B2.pdf](#)

Thanks Marj. What Kind of a role are you and Justin looking for me to play here on this project. Most of what I bring to the table are quantitative modeling skills and to a lesser extent elicitation. With such a limited time line there is not a lot of wiggle room to put together expert meetings and build robust quantitative analyses, so my strengths are not super useful. Having said that...I think that we can get a few useful and defensible things accomplished in 2 months. In my view, if it hasn't already been done, it to pull together a useful conceptual model of the population dynamics and it's ecology. This will guide how the rest of the SSA shapes up and help us focus on what kind of analyses or assessment can be completed. The second/concurrent step would be to very quickly assess the data that are available to use for use in this SSA. I've read two papers (both attached) that offer potentially useful frame works for analysis and assessment, but it is highly dependent on the type and quality of data. I can work with my grad student to get the data analyzed. She is really good and will get it done quickly and done well.

Take care,

Conor

On Mon, Jan 9, 2017 at 10:54 AM, Nelson, Marjorie <marjorie_nelson@fws.gov> wrote:

looping Conor in.

[Marjorie Nelson](#)
Chief, Division of Ecological Services
Mountain-Prairie Region
U.S. Fish and Wildlife Service
[303-236-4258](tel:303-236-4258)

----- Forwarded message -----

From: **Shoemaker, Justin** <justin_shoemaker@fws.gov>
Date: Mon, Jan 9, 2017 at 8:30 AM
Subject: Wolverine meeting in Denver?
To: "Grizzle, Betty" <betty_grizzle@fws.gov>, Jodi Bush <jodi_bush@fws.gov>
Cc: Seth Willey <seth_willey@fws.gov>, Marjorie Nelson <marjorie_nelson@fws.gov>, Caitlin Snyder <caitlin_snyder@fws.gov>

Betty, Jodi, Caitlin,

Those of us in the RO would like to get some of the wolverine team together in person for a few days to discuss the analysis in late Jan if possible, or early Feb. At this point I'm just checking availability to see what is possible. Can you let me know what day's you cannot travel between Jan 22 and Feb 10?

This may also line up w/ results from NOAA, in which case we will arrange for a meeting

with the NOAA folks as well to discuss. I'm waiting to hear back from John or Steve on timing of this, but the modeling is behind schedule a bit.

I imagine we will extend and invite to the core team as well, once we get some date options together. And Conor if needed.

Justin Shoemaker
Senior Listing Biologist
U.S. Fish and Wildlife Service, Region 6
1511 47th Avenue, Moline, IL 61265
Phone: [309-757-5800](tel:309-757-5800) ext. 214
Email: justin_shoemaker@fws.gov

--

//-----

Conor P. McGowan, Ph.D.
Assistant Leader and Associate Research Professor
USGS, Alabama Cooperative Fish and Wildlife Research Unit
School of Forestry and Wildlife Sciences,
Auburn University
Auburn, AL 36849-5418

EM:cmcgowan@usgs.gov
Ph:334 844 9231
www.auburn.edu/~cpm0014

//-----

Density Estimation in a Wolverine Population using Spatial Capture-Recapture Models

Author(s): J. Andrew Royle, Audrey J. Magoun, Beth Gardner, Patrick Valkenburg and Richard E. Lowell

Source: Journal of Wildlife Management, 75(3):604-611.

Published By: The Wildlife Society

URL: <http://www.bioone.org/doi/full/10.1002/jwmg.79>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.



Research Article

Density Estimation in a Wolverine Population Using Spatial Capture–Recapture Models

J. ANDREW ROYLE,¹ USGS Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD 20708, USA

AUDREY J. MAGOUN, Alaska Department of Fish and Game, P.O. Box 667, Petersburg, AK 99833, USA

BETH GARDNER, USGS Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD 20708, USA

PATRICK VALKENBURG, Alaska Department of Fish and Game, P.O. Box 115526, Juneau, AK 99833, USA

RICHARD E. LOWELL, Alaska Department of Fish and Game, P.O. Box 667, Petersburg, AK 99833, USA

ABSTRACT Classical closed-population capture–recapture models do not accommodate the spatial information inherent in encounter history data obtained from camera-trapping studies. As a result, individual heterogeneity in encounter probability is induced, and it is not possible to estimate density objectively because trap arrays do not have a well-defined sample area. We applied newly-developed, capture–recapture models that accommodate the spatial attribute inherent in capture–recapture data to a population of wolverines (*Gulo gulo*) in Southeast Alaska in 2008. We used camera-trapping data collected from 37 cameras in a 2,140-km² area of forested and open habitats largely enclosed by ocean and glacial icefields. We detected 21 unique individuals 115 times. Wolverines exhibited a strong positive trap response, with an increased tendency to revisit previously visited traps. Under the trap-response model, we estimated wolverine density at 9.7 individuals/1,000 km² (95% Bayesian CI: 5.9–15.0). Our model provides a formal statistical framework for estimating density from wolverine camera-trapping studies that accounts for a behavioral response due to baited traps. Further, our model-based estimator does not have strict requirements about the spatial configuration of traps or length of trapping sessions, providing considerable operational flexibility in the development of field studies. © 2011 The Wildlife Society.

KEY WORDS Bayesian, capture–recapture, density, *Gulo gulo*, motion-detection cameras, spatial models, wolverine.

The wolverine (*Gulo gulo*) is an elusive species that occurs at low densities (Lofroth and Krebs 2007), maintains large home ranges (Persson et al. 2009), and at times undertakes long movements (Inman et al. 2004). For these reasons, estimating density for wolverines has been problematic and early attempts lacked measures of accuracy and precision (review by Lofroth and Krebs 2007). More recently, Golden et al. (2007) estimated wolverine density based on aerial track surveys in winter in open habitats. Mulders et al. (2007) and Fisher et al. (2009) used DNA from hairs collected at bait sites to estimate wolverine density. Lofroth and Krebs (2007) used capture–recapture estimates of density from live-trapped wolverines and were the first to publish density estimates using photographs of wolverines captured on motion-detection cameras. None of the methods above that used capture–recapture approaches considered the spatial context of the data.

Closed population models are widely used to estimate abundance or density of animal populations from fixed arrays of traps or other devices that obtain information on encounter history (Borchers et al. 2002). Direct interpretation of population density obtained from such models is difficult because the sampled area of trap arrays is not a well-defined

concept in that, although one may delineate a geographic area for the placement of traps, it is not usually possible to delineate the effective sampled area (i.e., that area from which captured individuals are drawn). The difficulty in determining the effective sampled area has long been recognized in the literature (e.g., Dice 1938, Stickel 1954, Wilson and Anderson 1985, Efford 2004). Authors have used different approaches to resolve the problem of defining the effective area, most often drawing polygons around trapping arrays, buffering, and adjusting estimates of population size obtained from closed population models (Karanth and Nichols 1998). The problem with this approach is that it is ad hoc. Rules for buffering (e.g., mean maximum distance moved) are arbitrary and not consistent among studies, and such approaches induce uncertainty into estimates of density that have not been accommodated formally into density estimation. Moreover, the spatial organization of traps within the resulting buffered area suggests heterogeneity in encounter probabilities among individuals, which this method does not formally accommodate.

Recent developments of spatial capture–recapture (SCR) models (Efford 2004, Borchers and Efford 2008, Royle and Young 2008) provide a formal method for inference from capture–recapture studies by allowing for density estimation. These models extend standard closed population models (e.g., Otis et al. 1978, Borchers et al. 2002, Lukacs and Burnham 2005) to include a spatially explicit model for distribution of individuals in space. These models are

Received: 18 February 2010; Accepted: 29 July 2010

¹E-mail: aroyle@usgs.gov

spatially explicit in that they are parameterized in terms of a spatially indexed, individual random effect. The trap-specific encounter probabilities are modeled as a function of distance between traps and individual activity centers. These models have proved useful for estimating density in several carnivore sampling problems including small cats (Gardner et al. 2010a), bears (*Ursus americanus*; Gardner et al. 2010b), and tigers (*Panthera tigris*; Royle et al. 2009a,b). Our objective was to develop a spatially explicit capture–recapture model for estimating density, using data from a camera-trapping study of wolverines in Southeast Alaska.

STUDY AREA

The study area comprised 2,140 km² of coastal tidelands, temperate rainforest, muskeg, alpine habitats, and glaciers

in the Tongass National Forest on the mainland of Southeast Alaska (Fig. 1) near Petersburg (56°48.67602'N, –132°57.07452'W). Elevation in the study area ranged from sea level to 2,164 m. Temperatures at sea level during the camera-trapping sessions ranged from –4°C to 7°C but were considerably colder at higher elevations, although rarely falling below –23°C. Precipitation (mainly as snow) was heavy during the study, exceeding 4-m snow depth at higher elevations. Sitka spruce (*Picea sitchensis*) or Western hemlock (*Tsuga heterophylla*) dominated the overstory on productive forest sites, but poorly drained sites supported mountain hemlock (*Tsuga mertensiana*) and Alaska-yellow cedar (*Chamaecyparis nootkatensis*). The forested habitat where we deployed cameras occurred within 50 km of the coast of Frederick Sound, which bordered the study area on the

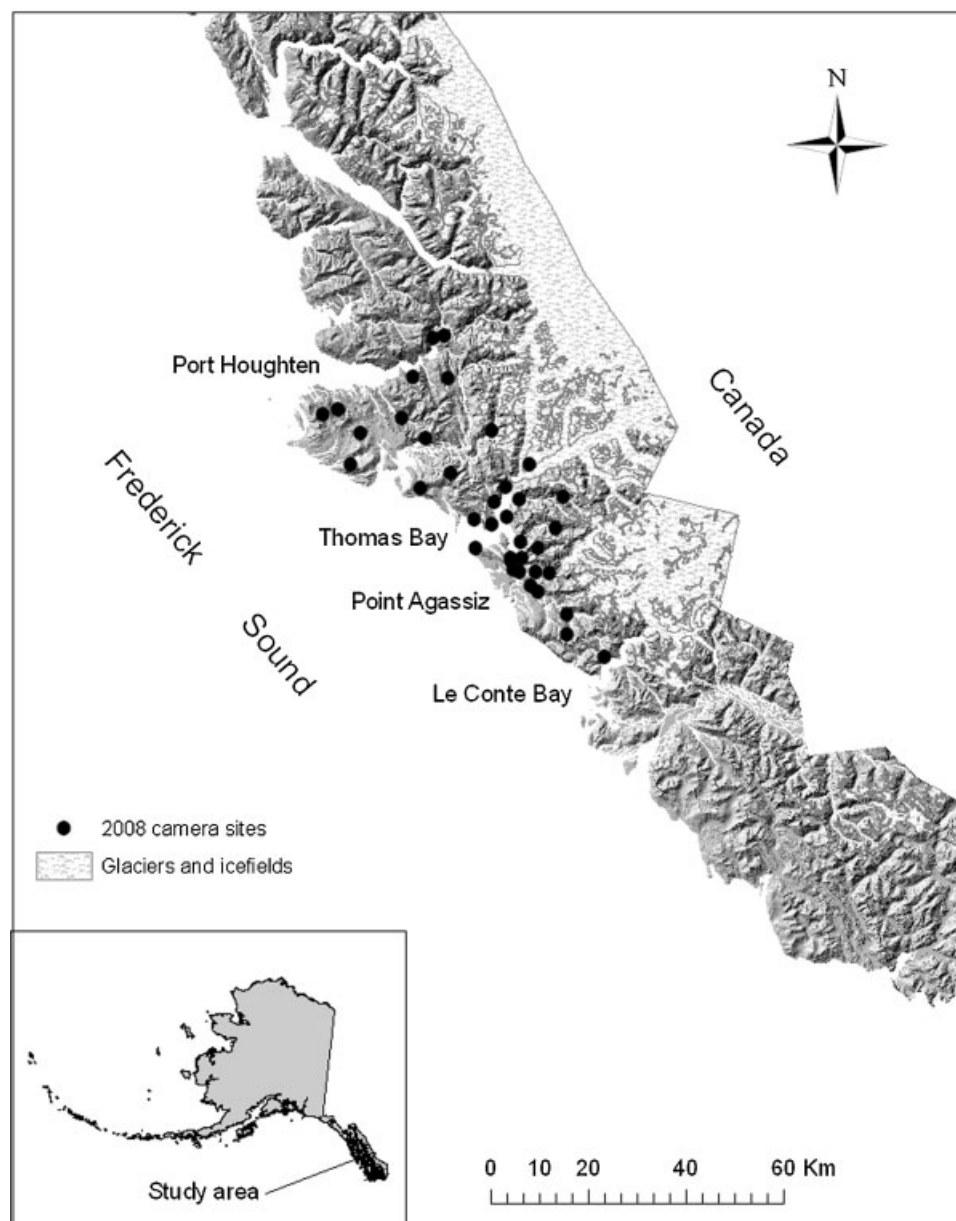


Figure 1. Study area on the mainland of Southeast Alaska near Petersburg showing location of camera and hair snag (C&H) stations (black dots) we used in 2008 for detecting wolverines. Stippled area indicates the extent of the Stikine Icefield to the Canadian border. The C&H array is largely surrounded by ocean and icefields except for a 20-km-wide forested area at the head of Port Houghton.

west. To the north the study area was bordered by Port Houghton, on the south by Le Conte Bay, and on the east by the Stikine Icefield. These geographic barriers limited movements of wolverines into the study area (Frances 2008). Prior to our study, fur trappers targeted wolverines along low-elevation forestry roads and along beaches but, in cooperation with our study, they refrained from setting traps for wolverines. Other than wolverines, the three species that triggered our camera traps most often, in order of frequency in photographs, were American marten (*Martes americana*), bald eagle (*Haliaeetus leucocephalus*), and black bear (*Ursus americanus*).

METHODS

Camera Trapping

Individual wolverines have a unique pattern of light-colored pelage on their ventral surface and this ventral pattern can be used to identify individuals from photographs, much as stripes and spots have been used to identify individual wild cats from photographs (Karanth and Nichols 1998, Soisalo and Cavalcanti 2006, Balme et al. 2009). Technique development with captive wolverines and radio-tagged wild wolverines demonstrated that this pattern remains the same over the lifetime of the individual (Magoun et al. 2011). To photograph the ventral pattern, we lured wolverines to camera traps using remnants of moose (*Alces alces*), deer (*Odocoileus hemionus*), and beaver (*Castor canadensis*) donated by hunters and trappers. We selected trap sites (Fig. 1) based on recommendations of local fur trappers, our knowledge of

suitable wolverine habitat, and logistical constraints of accessing mountainous terrain in our study area.

For camera sites accessed by helicopter, we fabricated run poles by mounting a 107-cm-long piece of 2×4 (38 mm \times 89 mm) dimensional lumber onto a 25-cm-long piece of 4×6 (89 mm \times 140 mm) dimensional lumber (Fig. 2; left panel). For camera sites accessed on the ground, we used either the same type of run pole or one fashioned from logs found on site. We suspended bait from a horizontal cable stretched between 2 trees 3–4 m apart. We attached a run pole to one of the trees at 1–2 m above ground or snow with the distal end of the run pole extending toward the other tree, on which we mounted a digital motion-detection camera (Trailwatcher[®], Monticello, GA). We suspended the bait 0.5–1.0 m above the end of the run pole. To access the bait, a wolverine would have to walk out to the end of the run pole, thereby triggering the camera while the animal was looking up at the bait exposing the ventral pattern (Fig. 2; right panel).

We set cameras to take photographs whenever there was motion in front of the camera. With the flash on all the time, cameras took photos approximately every 4 s when an animal was on the run pole. Each photograph file included the date and time the photograph was taken. We considered each 24-hr period a trapping session. We attempted to visit trap sites at least every 2 weeks to change batteries and flash cards and to rebait the sites, but this was not always possible due to weather and logistical constraints. If cameras were inoperable when we revisited the sites, we used the last day a photograph was taken to calculate the total number of days the camera was operational (i.e., number of trapping sessions).



Figure 2. Location of camera and hair snag (C&H) stations on the mainland of Southeast Alaska near Petersburg that we used for detecting wolverines in 2008. The left panel shows the configuration of the run pole, bait, and camera. The camera was approximately 3 m from the distal end of the run pole. We set the motion-detection camera to take photographs whenever an animal moved in front of the camera and with the flash on both day and night. The right panel shows a wolverine photographed at C&H station number 31 showing the ventral pattern we used to identify the wolverine in the photograph.

Statistical Methods

Data from a SCR study consist of the individual and trap-specific encounter histories $y_{i,j,k}$ for individual $i = 1, 2, \dots, n$; traps $j = 1, 2, \dots, J$; and sample periods $k = 1, 2, \dots, K$. In practice, sample periods are daily intervals and thus we obtain a conventional encounter history (i.e., a sequence of 0 s and 1 s) for each individual and trap. In our study, traps were operational for variable lengths of time. The temporal nature of encounter histories is important when time effects, such as date of the sample or behavioral response, are of interest (Gardner et al. 2010b). When explicit temporal effects are not relevant, we can summarize encounter histories by individual and trap-specific frequencies (i.e., y_{ij} , the number of times that individual i was encountered by trap j out of K_j sample periods).

The key idea in SCR models is that they formally relate the encounters of individuals to where these individuals spend time over the trapping period. In particular, if we imagine that an individual occupies a defined area for a given period of time (i.e., a seasonal home range or use area) and its activities are centered in that area for that period, then it is natural to expect that the probability of an individual encountering a trap is a function of the distance between that individual's activity center and the trap. Efford (2004) introduced this concept, which was formalized in a likelihood framework by Borchers and Efford (2008). Royle and Young (2008) developed a Bayesian hierarchical formulation of a similar class of models. Here we assume that encounter probability is related to distance between each activity center and trap according to:

$$p_{i,j} = 1 - \exp \left[-\lambda_0 \times \exp \left(\frac{-d_{ij}^2}{\sigma^2} \right) \right]$$

where $d_{ij} = \|s_i - x_j\|$ is the distance between activity center of individual i , s_i , and location of trap j , x_j . This specific form of the detection function is justified as the probability of at least one encounter under a Poisson model where the encounter rate declines with distance according to a normal probability kernel with scale parameter σ (Royle et al. 2009b). To interpret this, suppose that it was feasible to deploy a very dense, regular grid of traps such that individuals are encountered frequently at many locations. Then, under the model, encounter frequencies would resemble a histogram approximation to a bivariate normal density around an individual's activity center. However, in practice we only observe individuals at a small fixed number of traps and thus such a pattern will typically not be evident. The parameter σ can be related formally to movement in that it corresponds to the standard deviation of locations under a bivariate normal model, if space is uniformly sampled (Royle and Young 2008).

We can express this model for detection probability as a linear model on the complementary log-log scale:

$$\text{cloglog}(p_{i,j}) = \log(\lambda_0) - b1 \times d_{ij}^2$$

where $b1 = (1/\sigma^2)$. Thus, alternative detection functions arise by modifying either the choice of link function or

the linear predictor. For example, a linear distance term corresponds to an exponential detection function, which is not widely used in distance sampling applications because it does not have a shoulder at distance zero, and resulting estimates can be sensitive to rounding or sparse data (Buckland et al. 2001).

The encounter probability model indicates the structural similarity between SCR models and classical heterogeneity models (so-called Model Mh). Namely, distance is an additive random effect on a transformed scale, resulting in individual heterogeneity in encounter probability. Heterogeneity models can be extremely sensitive to choice of heterogeneity distribution, which can have severe consequences in the context of Model Mh (Link 2003). However, in our case the latent variable (distance) is partially observed because trap locations are fixed, so we might expect that SCR models are less sensitive than ordinary heterogeneity models considered by Link (2003).

Because we can formulate the model as a binary regression model in this fashion, useful extensions of the model are straightforward. For example, primarily a scavenger in winter, the wolverine tends to return repeatedly to a food source to remove food to caching sites (Banci 1994). As such, it is reasonable to assume that once a wolverine has found a baited camera site, the same wolverine is likely to visit the site repeatedly. Thus, we consider the possibility of a behavioral response (referred to as Model Mb in classical capture-recapture), which for our model involves adding one regression term to the model and defining a regression variable, say $x_{ijk} = 1$ if individual i was captured previous to sample session (day) k . In the context of SCR models, it is natural to define the behavioral response to be trap-specific (Royle et al. 2009b, Gardner et al. 2010b). That is, $x_{ijk} = 1$ if individual i has previously been captured in trap j . Thus, if an individual is captured in a specific trap, then the probability of subsequent encounter is increased or decreased only for that trap. We consider this a local behavioral response in contrast to what we could consider a global behavioral response as in the standard model (Model Mb) that is, a behavioral response that does not depend on where the individual was encountered. The latter type of response would be unrealistic in most spatial sampling situations. Because the covariate is time-dependent, we require a definition of the model in terms of individual Bernoulli trials, $y_{i,j,k}$, with probability of encounter p_{ijk} with

$$\text{cloglog}(p_{i,j,k}) = \log(\lambda_0) - b1 \times d_{ij}^2 + b2 \times x_{ijk}$$

Note that distance d_{ij} is a function of individual activity center s_i , which is an unobserved random effect. The model thus appears similar to so-called individual covariate models (e.g., Royle 2009). Because the individual activity centers are latent variables, we specify a probability distribution for them. The standard assumption is that s_i are uniformly distributed in space (Efford 2004, Borchers and Efford 2008, Royle and Young 2008). As such, we note that the model is essentially a standard, closed population model, but augmented with a spatial random effect that

describes the juxtaposition of individuals with the trap array.

With this additional model assumption for random effects, we can analyze the model using methods standard for analyzing generalized linear mixed models. In particular, models with random effects are conveniently analyzed by Bayesian methods using a technique known as data augmentation (Royle et al. 2007). Royle and Gardner (2011) and Gardner et al. (2010a,b) implement similar models in WinBUGS (Gilks et al. 1994) and provide the R and WinBUGS scripts to fit the models. In addition, a native R implementation developed from Royle et al. (2009a,b) provides a more efficient Markov chain Monte Carlo (MCMC) implementation in some cases. We used these R programs, which are now available in the freely available R package SPACECAP.

Bayesian analysis proceeds using a simulation-based method (i.e., MCMC; Link et al. 2002), which requires that we simulate realizations of the underlying point-process. To do this we must specify the region over which points are distributed (called the state-space of the point process), a geographic region that we denote by the set S . In general, we must specify the state-space regardless of whether one adopts a Bayesian or frequentist (e.g., Borchers and Efford 2008) approach to inference. In the latter case, we must integrate the random variables (activity centers) out of the conditional- s_i likelihood. When the state-space of the point process is precisely defined, it in turn defines the parameter N as the number of individual activity centers located within the prescribed state-space. We estimate the parameter N (see below). Density is a derived parameter $D = N/\text{area}(S)$, where N is the parameter of the model and $\text{area}(S)$ is the known area of the prescribed state-space. Although N is arbitrary in that it necessarily increases with the size of S , which we prescribe, the density of points $N/\text{area}(S)$ is invariant to S as long as S is sufficiently large, which we can verify by conducting a trial MCMC run.

That N is unknown is accommodated by imposing a discrete uniform prior on the integers $[0, M]$ where M is a large integer. If the posterior mass for N is concentrated away from M , then we can conclude that the posterior distributions are insensitive to M . As a technical matter, using the data augmentation formulation of the problem (Royle et al. 2007), the data set is augmented with $M - n$ all-zero encounter histories and we conduct the analysis on this augmented data set, which has a fixed number of M observations. The augmented data set induces a reparameterization of the model in which N is replaced as a formal parameter by a sequence of indicator variables z_i for $i = 1, 2, \dots, M$ indicating whether an individual is a member of the population (with probability ψ) or not (with probability $1 - \psi$). Formally, the z_i variables are binary latent variables having a Bernoulli distribution and we estimate N as a derived parameter, computed as the sum of the latent variables: $N = \sum z_i$. To obtain a posterior sample of N , we compute this sum at each iteration of the MCMC algorithm using the current values of each z_i . This construction of the model for the augmented data set induces the uniform prior

for N on the integers $[0, M]$ and also facilitates analysis of the model by MCMC (Royle et al. 2007).

In a Bayesian analysis, the size and configuration of the state-space requires careful consideration because the model is analyzed conditional on the underlying point process. That is, the point process is explicitly simulated, and thus we must describe the state-space precisely. There are two basic approaches to choosing the state-space. We might consider describing the geographic region containing the traps only where habitat is suitable. Alternatively, we can define a regular polygon (e.g., rectangle) containing the trap array without differentiating unsuitable habitat. Although defining the state-space to be a regular polygon has computational advantages (e.g., we can implement this more efficiently in WinBUGS and cannot for irregular polygons), a regular polygon induces an apparent problem of admitting into the state-space regions that are distinctly non-habitat (e.g., oceans, large lakes, ice fields). It is difficult to describe complex sets in mathematical terms that can be admitted to this spatial model. As an alternative, we can provide a representation of the state-space as a discrete set of points that will allow us to delete specific points or not depending on whether they represent habitat, which is primarily necessary to provide control over the geometry and morphology of what we consider to be suitable habitat. We analyzed the camera data using both approaches. In the first analysis, we defined the state-space to be a regular continuous polygon (a rectangle) but did not clip out non-habitat. To define the continuous state-space we overlaid the trap array (Fig. 1) on a rectangular region extending 40 km beyond the traps in each cardinal direction. In the second set of analyses, we used a discrete representation of the state-space but then deleted points that were not over land. For that approach we used two grid resolutions (2 km and 8 km) before clipping out unsuitable points to evaluate the relative influence of grid resolution on estimated density because coarser grids will be more efficient from a computational stand-point and so are preferable unless there is a strong influence on estimated density.

We chose priors customarily used to reflect little prior information. We used a uniform prior on $[0, 1]$ for the data augmentation parameter ψ (a probability), which implies a discrete uniform prior for N on the integers $[0, M]$ (Royle et al. 2007). For the regression parameters (intercept, coefficient on distance, and behavioral response), we used constant priors (default priors in the R library SPACECAP).

RESULTS

We operated 37 camera sites (Fig. 1) over a 165-day period during January–May 2008. Cameras were operational for variable periods (min. = 5 days, max. = 108 days, median = 45 days). Cameras captured 21 unique individuals 115 times. Individual encounter frequencies (Table 1) ranged from one capture (four individuals) to one individual captured 14 times, in three unique traps.

For the 2-km and 8-km discrete state-space models (Table 2), posterior summaries of model parameters and related quantities were similar. Densities were 8.6 individuals

Table 1. Individual frequencies of capture for wolverines captured in camera traps in Southeast Alaska in 2008. Rows index unique trap frequencies and columns represent total number of captures (e.g., we captured 4 individuals 1 time, necessarily in only 1 trap; we captured 3 individuals 3 times but in 2 different traps).

No. traps	No. captures									
	1	2	3	4	5	6	8	10	13	14
1	4	1	0	0	0	0	0	0	0	0
2	0	0	3	2	0	2	1	2	0	0
3	0	0	1	1	0	0	0	0	0	1
4	0	0	0	0	0	0	0	0	1	0
5	0	0	0	0	1	0	0	0	0	0
6	0	0	0	0	0	0	0	0	1	0

Table 2. Posterior summary statistics from the spatial capture–recapture models fitted to the 2008 wolverine camera-trapping data from Southeast Alaska. Models considered were: 1) a discrete approximation to the state-space using an 8-km grid, 2) a discrete state-space using a 2-km grid with no behavioral response, and 3) a behavioral response added to the second model; D is density per 1,000 km². λ_0 is the baseline encounter rate, $\sigma = 1/b1$, where $b1$ is the coefficient on distance-squared in the model for encounter probability, and N is the population size for the prescribed state-space.

Model	Parameter	Mean	SD	2.50%	50%	97.50%
Discrete 8-km	D	8.195	1.592	5.474	8.061	11.644
	λ_0	0.045	0.007	0.033	0.045	0.061
	σ	6.812	0.472	5.982	6.774	7.845
	$b1$	0.011	0.001	0.008	0.011	0.014
	N	82.343	16.001	55	81	117
Discrete 2-km	D	8.591	1.689	5.677	8.414	12.267
	λ_0	0.048	0.008	0.034	0.048	0.065
	σ	6.322	0.489	5.426	6.298	7.342
	$b1$	1.273	0.197	0.928	1.261	1.698
	N	84.737	16.66	56	83	121
Discrete 8-km and behavioral effect	D	9.6688	2.3255	5.872	9.355	15.028
	λ_0	0.0087	0.0022	0.005	0.008	0.0137
	σ	9.8356	1.335	7.484	9.743	12.747
	$b1$	0.0055	0.0015	0.003	0.005	0.0089
	$b2$	2.5988	0.2652	2.088	2.595	3.1326
	N	97.152	23.367	59	94	151

and 8.2 individuals per 1,000 km², respectively, consistent with that fact that the finer resolution grid accommodates higher levels of heterogeneity in detection probability (Link 2003). To improve computational efficiency, we used the 8-km discrete state-space to develop the behavioral response model (Table 2). Consistent with our expectations, there was a large positive effect of previous capture in a trap and an increase in estimated density under that model (posterior mean: 9.7 individuals/1,000 km²) compared to the model without the behavioral response.

DISCUSSION

The model based on the continuous state-space resulted in a much lower density estimate than that based on the discrete grid approximations to the state-space because most of the stated area of the continuous state-space lay over water. Thus the model distributed some individual activity centers over water, resulting in a corresponding decrease in apparent density compared with the discrete representation that allowed for water area to be removed. We noted little difference in estimated density and other model parameters between the 2-km and 8-km grids and thus we feel that, as an operational compromise, the coarser grid provided adequate estimates of density.

Integrating the trap identity information explicitly into the model allowed for consideration of more realistic models of the behavioral response. The intuitively appealing model we fitted to our data, in which the behavioral response operates on individual traps (what we referred to as a local behavioral response), has not been considered in the standard capture–recapture context. The model without a behavioral effect estimated a density of about 8.2 wolverines/1,000 km² with an estimated detection scale parameter (σ) of 6.8 km. In contrast, the estimated density was 9.7 wolverines/1,000 km² and $\sigma = 9.8$ km when we included the behavioral response. This strongly positive, trap-specific behavioral response indicated a tendency for individuals to revisit camera traps subsequent to their initial visit, a result that is unsurprising when traps are baited and successive captures are not independent. The apparent encounter probability was artificially high in the presence of a behavioral response and was properly adjusted downward when a behavioral response was added to the model, yielding a corresponding increase in estimated density.

By using SCR models for estimating wolverine density, we avoided several problems inherent in non-spatial models for species that are hard to detect and yield small sample sizes. Logistical constraints of operating in northern wilderness

environments in winter usually make it impossible to ensure that the number of trap sessions among camera sites is the same, but trapping sessions of equal length are not a requirement of the SCR models. For non-spatial models it is not at all obvious how to condense such variable trap-specific encounter histories into standard encounter histories that ignore trap identity, therefore, excess recaptures (i.e., wolverines captured multiple times at a unique site in a session) are discarded or pooled in some fashion, resulting in loss of information about the encounter process. An obvious problem with pooling data from a trap array into discrete periods to create non-spatial encounter histories is that it is not obvious how to do this when trap operation is staggered in time and deployed traps are operational for varying lengths of time. Pooling of data was not necessary in our SCR models because they are based on trap-level encounters of individuals.

The SCR models resolve two specific problems inherent in the application of non-spatial, closed population capture-recapture models. First, it is not necessary to use ad hoc methods to devise an effective sample area to which we applied the estimated N because, instead, we regard the location and number of individual activity centers (s) as unknown parameters (random effects) to estimate. Secondly, SCR models account for individual heterogeneity in encounter probability that is necessarily induced by juxtaposition of individuals with traps. In particular, the model assumes that encounter probability is a function of distance between traps and activity centers, and thus encounter probability decreases to zero as distance from the trap array increases.

As with all closed population models, the SCR models we used assume demographic closure (i.e., no permanent additions or removals from the population during the trapping period). The closure assumption in the SCR model is manifest in the static nature of the individual activity centers. Although each individual has its own activity center, the model assumes that activity centers are static over the trapping period. To the extent that non-closure is due to the presence of transients, such non-closure could perhaps be effectively modeled as an individual-specific encounter probability scale parameter, σ , accommodating apparent variability among individuals in home range size. We are currently devising methods for fitting such models. Extensions of the model that allow for mortality and recruitment have also recently been developed (Gardner et al. 2010a). In addition to accounting for explicit violation of the closure assumption due to population dynamics, such models can accommodate non-static activity centers, such as may be necessary in multi-year studies as individual home ranges shift due to resource variability, behavioral interactions, and other biological phenomena.

We also plan further extensions to this basic SCR model by adding covariates that could address other sources of heterogeneity in individual capture probabilities. For example, based on the smaller average size of home ranges for female wolverines (Persson et al. 2009), we expect that the sex of individuals influences average distances between activity centers and encountered traps for males and females. Sex of wolverines can be determined using camera-trapping

techniques (Magoun et al. 2011), as well as from DNA, and could easily be incorporated as an individual covariate in our models. Moreover, we suspect that camera traps visited by female wolverines, particularly lactating females in March and April, may indicate prime habitat where wolverines are concentrated across the landscape (A. Magoun, Alaska Department of Fish and Game, unpublished data). Therefore, we suggest a trap-specific covariate that considers visits by females. Finally, Copeland et al. (2010) showed that late spring snow cover may be correlated with suitable wolverine habitat, suggesting another covariate that could be incorporated into the SCR models for study areas that are heterogeneous for spring snow cover.

MANAGEMENT IMPLICATIONS

The SCR models we developed remove several mathematical and logistical problems that arise in estimating density of wolverines and other cryptic, low-density species. The SCR models can be applied to any capture-recapture technique that provides individual and trap-specific encounter histories. Besides incorporating spatial data and thereby avoiding ad hoc derivations of an effective area, the SCR models permit formal mathematical testing of assumptions regarding capture probabilities. Furthermore, the capability of the SCR models to incorporate variables that affect encounter probability provides managers the flexibility to modify camera-trapping techniques in ways that improve capture success (e.g., using multiple cameras at trapping stations or adjusting camera activation periods to accommodate species-specific activity). Finally, methods for estimating density of species are most useful when they accommodate the realities of working under rigorous and unpredictable field conditions on species that are difficult and expensive to study.

ACKNOWLEDGMENTS

Our research was funded by the Alaska Department of Fish and Game, Alaska Trappers Association, American Wildlife Conservation Foundation, Inc., Campion Foundation, D. Pedersen, Milwaukee Zoo, Minnesota Zoo, Norcross Wildlife Foundation, Inc., Seattle Sportsman's Conservation Foundation-Safari Club International, The Wolverine Foundation, Inc., Wilburforce Foundation, Wildlife Conservation Society Canada, and Wildlife Research and Management, WRAM. D. Benitz provided logistical support, assistance in the field, and expertise in wolverine trapping. S. and F. Nelson shared information on wolverines in the study area. We thank J. Long for administration of grants and assistance with data management. D. Watts provided GIS expertise. M. Meucci, W. O'Brocta, and W. Malcom provided logistical support and assistance in the field. We thank trappers and hunters who provided bait for our traps. Any use of trade, product, or firm names is for descriptive purposes only and does not constitute endorsement by the United States government.

LITERATURE CITED

Balme, G. A., L. T. B. Hunter, and R. Slotow. 2009. Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management* 73:433-441.

- Banci, V. 1994. Wolverine. Pages 99–127 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, W. J. Zielinski, editors. The scientific basis for conserving forest carnivores, American marten, fisher, lynx and wolverine in the Western United States. General Technical Report RM-254. U.S. Department of Agriculture Forest Service Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Borchers, D. L., and M. G. Efford 2008. Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics* 64:377–385.
- Borchers, D. L., S. T. Buckland, and W. Zucchini. 2002. Estimating animal abundance: closed populations. Springer-Verlag, London, United Kingdom.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, United Kingdom.
- Copeland, J. P., K. S. McKelvey, K. B. Aubry, A. Landa, J. Persson, R. M. Inman, J. Krebs, E. Lofroth, H. Golden, J. R. Squires, A. Magoun, M. K. Schwartz, J. Wilmot, C. L. Copeland, R. E. Yates, I. Kojola, and R. May. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? *Canadian Journal of Zoology* 88:233–246.
- Dice, L. R. 1938. Some census methods for mammals. *Journal of Wildlife Management* 2:119–130.
- Efford, M. 2004. Density estimation in live-trapping studies. *Oikos* 106:598–610.
- Fisher, J. T., S. M. Bradbury, A. C. Fisher, and L. Nolan. 2009. Wolverines on the edge of Alberta's Rockies. Alberta Research Council, Edmonton, Alberta, Canada.
- Frances, J. 2008. Spatial structure and demographic history of wolverines in North America with emphasis on peripheral populations. Thesis, University of New Mexico, Albuquerque, USA.
- Gardner, B., J. Reppucci, M. Lucherini, and J. A. Royle. 2010a. Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. *Ecology* 91:3376–3383.
- Gardner, B., J. A. Royle, M. T. Wegan, R. E. Rainbolt, and P. D. Curtis. 2010b. Estimating black bear density using DNA data from hair snares. *Journal of Wildlife Management* 74:318–325.
- Gilks, W. R., A. Thomas, and D. J. Spiegelhalter. 1994. A language and program for complex Bayesian modelling. *The Statistician* 43:169–177.
- Golden, H. N., J. D. Henry, E. F. Becker, M. I. Goldstein, J. M. Morton, D. Sr. Frost, and A. J. Poe. 2007. Estimating wolverine *Gulo gulo* population size using quadrat sampling of tracks in snow. *Wildlife Biology* 13(Suppl. 2): 52–61.
- Inman, R. M., R. R. Wigglesworth, K. H. Inman, M. K. Schwartz, B. L. Brock, and J. D. Rieck. 2004. Wolverine makes extensive movements in greater Yellowstone ecosystem. *Northwest Science* 78:261–266.
- Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852–2862.
- Link, W. A. 2003. Nonidentifiability of population size from capture–recapture data with heterogeneous detection probabilities. *Biometrics* 59:1123–1130.
- Link, W. A., E. Cam, J. D. Nichols, and E. G. Cooch. 2002. Of BUGS and birds: Markov chain Monte Carlo for hierarchical modeling in wildlife research. *Journal of Wildlife Management* 66:277–291.
- Lofroth, E. C., and J. Krebs. 2007. The abundance and distribution of wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71:2159–2169.
- Lukacs, P. M., and K. P. Burnham. 2005. Review of capture–recapture methods applicable to noninvasive genetic sampling. *Molecular Ecology* 14:3909–3919.
- Magoun, A. J., C. D. Long, M. K. Schwartz, K. L. Pilgrim, R. E. Lowell, and P. Valkenburg. In press. Integrating motion-detection cameras and hair snares for wolverine identification. *Journal of Wildlife Management*.
- Mulders, R., J. Boulanger, and D. Paetkau. 2007. Estimation of population size for wolverines *Gulo gulo* at Daring Lake, Northwest Territories, using DNA based mark–recapture methods. *Wildlife Biology* 13(Suppl. 2): 38–51.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:1–135.
- Persson, J., P. Wedhholm, and P. Segerström. 2009. Space use and territoriality of wolverines (*Gulo gulo*) in northern Scandinavia. *European Journal of Wildlife Research* 55:547–551.
- Royle, J. A. 2009. Analysis of capture–recapture models with individual covariates using data augmentation. *Biometrics* 65:267–274.
- Royle, J. A., and B. Gardner. 2011. Hierarchical spatial capture–recapture models for estimating density from trapping arrays. Pages 163–190 in A. F. O'Connell, J. D. Nichols, K. U. Karanth, editors. Camera traps in animal ecology: methods and analyses. Springer, New York, New York, USA.
- Royle, J. A., and K. Young. 2008. A hierarchical model for spatial capture–recapture data. *Ecology* 89:2281–2289.
- Royle, J. A., R. M. Dorazio, and W. A. Link. 2007. Analysis of multinomial models with unknown index using data augmentation. *Journal of Computational and Graphical Statistics* 16:67–85.
- Royle, J. A., J. D. Nichols, K. U. Karanth, and A. M. Gopalaswamy. 2009a. A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology* 46:118–127.
- Royle, J. A., K. U. Karanth, A. M. Gopalaswamy, and N. S. Kumar. 2009b. Bayesian inference in camera trapping studies for a class of spatial capture–recapture models. *Ecology* 90:3233–3244.
- Soisalo, M. K., and S. M. C. Cavalcanti. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biological Conservation* 129:487–496.
- Stickel, L. F. 1954. A comparison of certain methods of measuring ranges of small mammals. *Journal of Mammalogy* 35:1–15.
- Wilson, K. R., and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. *Journal of Mammalogy* 66:13–21.

Associate Editor: Kevin McKelvey.

MANAGEMENT STRATEGIES FOR THE WOLVERINE IN SCANDINAVIA

Author(s): BERNT-ERIK SÆTHER, STEINAR ENGEN, JENS PERSSON, HENRIK BRØSETH, ARILD LANDA, and TOMAS WILLEBRAND

Source: Journal of Wildlife Management, 69(3):1001-1014.

Published By: The Wildlife Society

DOI: [http://dx.doi.org/10.2193/0022-541X\(2005\)069\[1001:MSFTWI\]2.0.CO;2](http://dx.doi.org/10.2193/0022-541X(2005)069[1001:MSFTWI]2.0.CO;2)

URL: <http://www.bioone.org/doi/full/10.2193/0022-541X%282005%29069%5B1001%3AMSFTWI%5D2.0.CO%3B2>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

MANAGEMENT STRATEGIES FOR THE WOLVERINE IN SCANDINAVIA

BERNT-ERIK SÆTHER,¹ Department of Biology, Norwegian University of Science and Technology, Realfagbygget, N-7491 Trondheim, Norway

STEINAR ENGEN, Department of Mathematical Sciences, Norwegian University of Science and Technology, Realfagbygget, N-7491 Trondheim, Norway

JENS PERSSON, Department of Animal Ecology, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden

HENRIK BRØSETH, Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway

ARILD LANDA, Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway

TOMAS WILLEBRAND, Department of Animal Ecology, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden

Abstract: The use of Population Viability Analysis has recently been criticized mainly because uncertainties in population predictions are often ignored. We analyzed the viability of Scandinavian wolverine *Gulo gulo* populations that allow for the inclusion of uncertainties in parameter estimates and stochastic effects on population dynamics. We used the insight gained from analyses of stochastic population models to quantitatively analyze different management options for the wolverine. These management options were based on data from an individual-based demographic study in the Sarek National Park, Sweden, and data from monitoring schemes in Norway and Sweden. Stochastic components in population dynamics of the wolverine were large. Strong density regulation occurred around the carrying capacity. According to the World Conservation Union (2001), the carrying capacity of populations must exceed 46 sexually mature (≥ 3 -yr-old) females to be considered not vulnerable. Continuation of the current levels of offtake in Norway will lead to extinction of the wolverine over large parts of the country. Hence, current rates of mortality of female wolverine make the northern population endangered, whereas the southern population is classified as vulnerable. Management plans allowing harvest of individuals should be based on a proportional threshold harvest strategy. Only 40–60% of the surplus individuals exceeding a certain threshold for harvesting should be removed. Our analyses emphasized the importance of including estimates of precision in parameter estimates, including stochastic factors in recommendations based on Population Viability Analysis, and examining the robustness of the conclusions against variation in crucial parameters by sensitivity analyses.

JOURNAL OF WILDLIFE MANAGEMENT 69(3):1001–1014; 2005

Key words: density dependence, *Gulo gulo*, Population Viability Analysis, risk of extinction, Scandinavia, stochastic effects, wolverine.

Population Viability Analysis (PVA) has wide application in the management of threatened and vulnerable species (Beissinger and Westphal 1998, Groom and Pascual 1998, Sjøgren-Gulve and Ebenhard 2000, Beissinger and McCullough 2002). The predictions from such analysis have recently received severe criticism (Ludwig 1996, 1999; Fieberg and Ellner 2000; Ellner et al. 2002). There are 3 major problems with many PVAs: (1) For most threatened or vulnerable species few demographic data are often available. Even when 20–30 years of high-quality data are available, the uncertainties in the parameter estimates are still large (Sæther et al. 2000; Sæther and Engen 2002a,b). (2) In many cases, available data are inappropriate for estimating crucial parameters for describing dynamics and may even result in biased estimates. For instance, the specific growth rate at low densities is often difficult to estimate in many time series of population fluctuations because interpolation over a wide range of population sizes is often necessary (Taylor 1995, Aanes et al. 2002). (3) The

stochastic effects on the population dynamics are often not properly estimated and modeled (Sæther and Engen 2002a), resulting in biased estimates of the risk of extinction. As a consequence, the validity of predictions based on PVA has been seriously questioned (Ludwig 1999).

Recently, great advances have been made in our understanding of stochastic effects on the dynamics of fluctuating populations (Lande et al. 2003). An important step was the development of precise definitions of the stochastic components (Engen et al. 1998) that permitted estimation of demographic and environmental stochasticity from field data (Sæther et al. 2000, 2002a; Engen et al. 2001). Demographic stochasticity is due to random variation in individual fitness, whereas environmental stochasticity arises from random variation that affects the whole or parts of the population similarly. These methods allow us to separate stochastic effects on population dynamics from deterministic components (e.g., due to density dependence or life history variation).

In PVA, development of projections for future population fluctuations is necessary for calculating the risk of extinction or the probability of reaching

¹ E-mail: Bernt-Erik.Sather@bio.ntnu.no

some critical lower population size. Such analyses must model the deterministic influence and the stochastic effects on the population dynamics and take into account uncertainty in population parameters (Sæther and Engen 2002a). After the highly influential paper of Mace and Lande (1991), the World Conservation Union (2001) included criteria based on quantitative analyses into their risk classification of threatened or endangered species. Thus, according to World Conservation Union (2001), only populations with $\leq 10\%$ risk during 100 years will not be considered vulnerable to extinction.

Many large carnivores became vulnerable or threatened because of human persecution (Swenson et al. 1994). For instance, the Scandinavian wolverine population was persecuted from the mid-19th century when harvest increased due to the introduction of state bounties. The main reason for this intense persecution was predation by wolverines on domestic sheep and reindeer (*Rangifer tarandus tarandus*), a conflict still present today in many parts of Scandinavia. As a consequence, harvest of individuals is important to consider as an option in management plans and is often a prerequisite for local acceptance. In such cases, stochastic factors must be estimated and modeled to obtain a proper understanding of the effects on the viability of the population (Lande et al. 1995, 1997, 2001; Tufto et al. 1999).

Our objective was to use recent advances in the theory of stochastic population ecology to perform a PVA of the Scandinavian wolverine. We combined data from long-term population studies with data on individual variation in reproductive success and survival to obtain estimates of the stochastic components in the population dynamics. We then provided analyses of factors influencing the time to extinction. We used this insight to quantitatively analyze different management strategies. By means of sensitivity analysis, we focused on how uncertainty in parameter estimates and imprecise population estimates affect the choice of management actions.

Wolverines in Fennoscandia

Historically, the wolverine was found throughout mountainous and forested areas in Norway and from the south-central to the northern parts of Sweden (Johnsen 1929, Lönnberg 1936). From the mid 19th century the Scandinavian wolverine population decreased due to human persecution until the species became protected in Sweden in 1969, in southern Norway in 1973, and in the remaining parts of Norway in 1982 (Landa et al. 2000). In the beginning

of the 1980s, the distribution of wolverine was limited to the mountain range along the Swedish–Norwegian border. The population increased in both countries slowly during the first decades after protection. The estimates of total population size in 1998–2000 were 326 (± 45) individuals in Sweden and 269 (± 32) individuals in Norway (Landa et al. 2001). The Swedish population was protected, whereas in Norway offtake of individuals through regular harvest or killing of litters has become an important tool in wolverine population management.

Population Model

The dynamics of all populations have a deterministic (predictable) and a stochastic (unpredictable) component that operate simultaneously. The deterministic component can be mathematically defined as the expected change of the log population size during the next year, the mean value of $\Delta X_t = X_{t+1} - X_t$ conditioned on X_t , or alternatively, it can be defined as the mean change in population size, where N_t is the population size in year t and $X_t = \ln N_t$. The theta-logistic model is a very general class of models specifying the deterministic component (Gilpin and Ayala 1973; Gilpin et al. 1976; Sæther et al. 1996, 2000, 2002b; Lande et al. 2003):

$$\Delta N = rN[1 - (N/K)^\theta], \quad (1)$$

where the time index is omitted to simplify the notation. Here θ denotes the form of the density regulation. Large values of θ show strong density regulation around the K . For a positive value of the parameter θ , r is the specific growth rate at small population sizes, formally the growth rate obtained in the limit as N approaches zero. The carrying capacity for this model is K , which means that the expected change in population size when $N = K$ is zero. For small and moderate changes between 2 years, $\Delta N/N \approx \Delta \ln N = \Delta X$ giving:

$$\Delta X \approx r[1 - (N/K)^\theta]. \quad (2)$$

Because all methods for parameter estimation from data are based on the use of log population size, we prefer to use eq (2) rewritten as an exact equation as our basic model. If we define extinction to occur at $N = 1$, the smallest possible specific growth rate is actually the growth rate at $N = 1$, $r_1 = r[1 - K^{-\theta}]$. Using r_1 rather than r in eq (2), the model may be rewritten as:

$$\Delta X = r_1[1 - (N^\theta - 1)/(K^\theta - 1)] = r_1[1 - h(N, \theta)/h(K, \theta)], \quad (3)$$

where $h(N, \theta) = (N^\theta - 1)/\theta$. An advantage with this formulation of the theta-logistic model is that a well-defined model is obtained as θ approaches zero and even when θ is negative. Considering the limit as θ approaches zero, $h(N, 0) = \ln N = X$. Hence, for $\theta = 0$, we obtain a form of density regulation that is linear on the log scale,

$$\Delta X = r_1(1 - X/k), \quad (4)$$

where $k = \ln K$ is the carrying capacity on the log scale. This is called the Gompertz type of density regulation. Alternatively, this may also be written as:

$$X_{t+1} = r_1 + (1 - r_1/k)X_t \quad (5)$$

a linear model frequently used in time series analysis of population fluctuations (Royama 1992). Another special case is the logistic model obtained as $\theta = 1$, giving a second-degree polynomial on the right side of eq (1) and a linear expression in N in eq (2).

When studying small fluctuations around the carrying capacity a simple linear approximation on the absolute scale a linearization of $E(\Delta N | N)$ is often used (Lande et al. 2002). Such a linear form is also a special case because if $\theta = -1$, then:

$$\Delta N = \frac{r_1 K}{K-1} \left[1 - \frac{N}{K} \right]. \quad (6)$$

Another special case of the theta-logistic model that is often used for territorial species is the ceiling model (Lande 1993) that has no density regulation (i.e., exponential growth) for population sizes smaller than K . The ceiling at $N = K$ is then a reflecting barrier preventing the population size from exceeding K . Equation (3) demonstrates that this is exactly the model we obtain in the limit as θ approaches infinity.

The expected time to extinction is computed by adopting the diffusion approximation to the process on the logarithmic scale (Lande et al. 2003). The infinitesimal mean and variance is then $\mu(N) = r_1 N [1 - h(N, \theta)/h(K, \theta)]$ and $v(N) = \sigma_e^2 N^2 + \sigma_d^2 N$. The expected time to extinction is calculated numerically by first calculating the Green function for the diffusion process (Karlin and Taylor 1981; Lande et al. 1995, 2003):

$$G(N, N_0) = \begin{cases} 2m(N)S(N) & \text{for } 1 \leq N \leq N_0 \\ 2m(N)S(N_0) & \text{for } 1 \leq N_0 \leq N \end{cases} \quad (7)$$

where

$$S(N) = \int_1^N s(z) dz, \quad s(N) = \exp \left[-2 \int_1^N \frac{\mu(z)}{v(z)} dz \right]$$

and $m(N) = 1/v(N) \times s(N)$. We then integrate this function numerically from the extinction barrier at $N = 1$ to infinity. For the ceiling model of Lande (1993) we consider the limiting form as θ approaches infinity. This is equivalent to a model with reflecting barrier, a ceiling, at population size K , and exponential growth with stochastic growth rate r_1 below K . The Green function of eq (7) for this process must be equal to zero for $X > \ln K$. Expected time to extinction can then be written as:

$$ET = \int_1^K G(N, K) dN.$$

for $N_0 = K$. Because the Green function does not depend on K except that $G(N, K) = 0$ for $N > K$, we find that

$$dET/dK = G(N, K), \quad (8)$$

which then takes the form

$$dET/dK = 1/r_0 K \left[\left(\frac{K+\delta}{1+\delta} \right)^\gamma - 1 \right], \quad (9)$$

where $r_0 = r_1 - \sigma_e^2/2r_0/\sigma_e^2 - 1$ and $\delta = \sigma_d^2/\sigma_e^2$ (Lande et al. 2003). This expression can easily be integrated numerically to give ET .

In Scandinavia, wolverines kill domestic, free-ranging sheep and semidomestic reindeer that graze in mountain ranges. As a consequence, there is a strong demand for the reduction of wolverine population size through individual offtake. A central aim of offtake is to minimize its effect on the expected time to extinction. We suggest, based on theoretical studies (Engen et al. 1997, Tufto et al. 1999, Aanes et al. 2002, Lande et al. 2003), that 2 types of harvest strategies be considered: proportional harvesting and proportional threshold harvesting.

Proportional harvesting means removing a fixed proportion of the population each year, giving the annual yield:

$$y = bN, \quad (10)$$

where b is the proportion harvested. In fisheries, this strategy is often carried out by assuming that a given harvesting effort leads to harvesting a given proportion of the population (Quinn and

Deriso 1999). The optimal proportion to harvest depends on the dynamics of the populations (e.g., the form of the density regulation; Beddington and May 1977, May et al. 1978, Jonzén et al. 2002). Unfortunately, this commonly employed harvesting strategy leads to higher risk of extinction than threshold harvesting (Lande et al. 1995, 1997); i.e., harvesting occurring only when the population size exceeds a certain threshold c .

The wolverine population size is difficult to assess, so uncertainty in population estimates should be considered when choosing a harvest strategy (Engen et al. 1997, Quinn and Deriso 1999). If \hat{N} is the estimated population size and q is the proportion of the estimated surplus, individuals above the threshold c that can be removed. Engen et al. (1997) proposed that proportional threshold harvesting that is defined as:

$$y(\hat{N}, q, c) = \begin{cases} q(\hat{N} - c) & \text{for } \hat{N} > c \\ 0 & \text{otherwise} \end{cases}, \quad (11)$$

will reduce the effect on population viability by overestimating the actual population size and thereby causing animal offtake to be too high.

A reasonable assumption about the sampling variance in the estimated population size \hat{N} is that it is proportional to the expected population size:

$$\text{var} \hat{N} = \varepsilon^2 EN, \quad (12)$$

where ε determines the sampling error. The coefficient of variation in \hat{N} $CV = \varepsilon / \sqrt{E/(N)}$ then becomes dependent on N . If we assume binomial sampling (Seber 1982) with probability p of detecting an animal, $\varepsilon = \sqrt{(1-p)/p}$. Thus, $p = 0.5$ corresponds to $\varepsilon = 1$.

The expressions for the infinitesimal mean and variance to be applied in the diffusion approximation for this process are given by Engen et al. (1997). The derivation of these functions was based on the assumption that the estimate of the population size is unbiased and normally distributed. When the population size is not known exactly, harvesting also introduces an additional term in the infinitesimal variance that must be incorporated (Engen et al. 1997).

STUDY AREA

We studied individual variation in reproductive success and survival in Sarek National Park and surrounding areas in Norrbotten County (hereafter referred to as Sarek) in northern Sweden (67°00'N 17°40'E; Fig. 1). The climate was continental with cold winters (−10 to −13°C in Jan), and

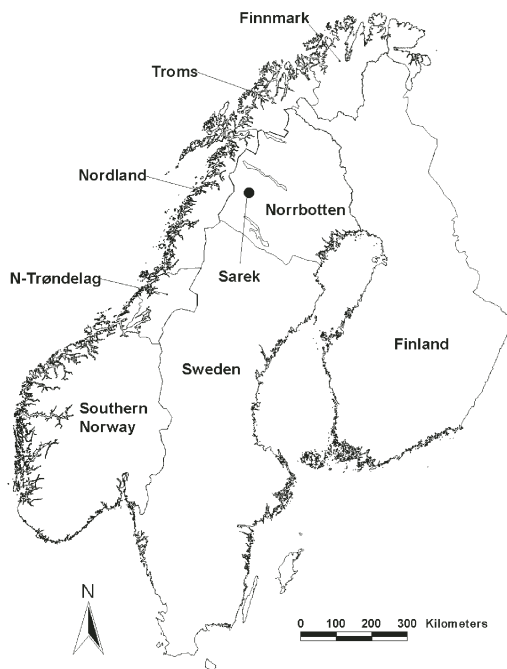


Fig. 1. The location of study areas in Fennoscandia to examine wolverine ecology.

the annual precipitation was 500–1,000 mm. Snow usually covered the ground from October to May. The area is characterized by deep valleys, glaciers, and mountain plateaus with peaks reaching above 2,000 m above sea level. The valleys forests were dominated by mountain birch (*Betula pubescens*) and scots pine (*Pinus sylvestris*). The tree line was formed by mountain birch and reached a maximum of 600–700 m above sea level. Semidomesticated reindeer managed by the indigenous Sámi were numerous in Sarek.

METHODS

Our analysis was based on data from 37 radio-collared, adult females. The females were equipped with an intraperitoneally implanted transmitter. We radiotracked individuals from the ground or air approximately once every 2 weeks. In this way we determined whether the female and her offspring survived to the following reproductive season that was assumed to start on 1 March.

We also used helicopters and snowmobiles to search an area of approximately 6,000 km² in Sarek from 1995 to 2002 for dens during winter and spring. We assumed that this extensive fieldwork and the numerous radiocollared individuals allowed us to accurately estimate the annual variation in the Sarek breeding population. During

Table 1. The number of active dens and the number of age-determined adult (>1-yr-old) females harvested in different parts of Fennoscandia, 1979–2002.

Year	Norway								Sweden		
	Southern Norway ^a		N-Trøndelag and Norrland County		Troms County		Finnmark County		Sarek		Norrbotten County
	Dens	Harvest	Dens	Harvest	Dens	Harvest	Dens	Harvest	Dens	Harvest	Dens
1992	4		9		1	0	7				
1993	4		5	0	7	1	3				
1994	5		7	1	17	5	3	0			
1995	8	0	11	1	13	2	9	1	11	0	
1996	5	2	11	1	11	5	6	0	16	0	50
1997	5	0	7	1	6	5	9	1	9	2	47
1998	8	3	12	3	10	2	9	0	13	1	40
1999	8	1	10	4	9	0	10	2	14	1	37
2000	10	2	8	4	15	4	7	9	12	0	28
2001	12	8	13	1	7	1	5	0	15	0	38
2002	8		12		7		3		19		37

^a In southern Norway, the number of recorded dens each year was (dens/year): 3/1979, 2/1980, 3/1981, 3/1982, 2/1983, 3/1984, 3/1985, 2/1986, 4/1987, 3/1988, 4/1989, 4/1990, and 2/1991.

the study period, the number of dens fluctuated between 9 and 19 active dens (Table 1).

Population Censuses

In Scandinavia, annual censuses of wolverine breeding population were conducted over larger parts of its distributional range (Fig. 1; Table 1). Likely den localities were visited several times during late winter and early spring by experienced persons who searched for typical characteristics of a natal den (for a more detailed description of the den characteristics, see Magoun and Copeland 1998 and Andersen et al. 2001). In addition, established routes were driven by snowmobiles to search for wolverine tracks in many areas. When a track was detected, it was followed to see if it led to a denning area. In this way, an estimate of the minimum number of reproductive females was obtained.

In Sarek, the mean proportion of the radiocol-lared adult females that bred each year was 0.57 ($n = 6$ yr). Thus, the number of active dens (Table 1) represents an underestimate of the actual number of sexually mature females in the population.

In southern Norway (Fig. 1), an increase in numbers occurred during the last years (Table 1). In the northern parts of the country, no clear trend was present in population fluctuations. In contrast, we recorded a decline in the number of dens in Sweden during the study (Table 1). This decline was mainly due to a decline in Norrbotten County, which had the largest number of wolverines.

Since 1990, female wolverines (≥ 1 yr old) were killed by humans over larger parts of their distributional range (Table 1). In Norway, the wolverine population was managed by 2 regional manage-

ment boards: 1 covering the 4 northernmost counties (Nord-Trøndelag, Nordland, Troms, Finnmark; Fig. 1) and 1 for southern Norway. These 2 boards had heavy representation from various user groups. The annual quota was determined by the boards.

Estimation of Parameters

We estimated the demographic variance (σ_d^2) and the environmental variance (σ_e^2) from individual-based data from Sarek. We let $R_{i,j}$, $i = 1 \dots n_j$, $j = 1, 2, \dots, t$, denote observations of the contribution by the females to the following generation, where j was the year and n_j was the number of females for which data were available in a given year. The total contribution of female i in year j ($R_{i,j}$) was the number of female offspring born during the year that survived for 1 year plus 1 if the female survived to the next year (Sæther et al. 1998a). If \mathbf{Z} was a stochastic vector describing the environment influencing R , the variance in R could be partitioned into 2 components (Engen et al. 1998):

$$\text{var}(R) = \text{Evar}(R|\mathbf{Z}) + \text{var}(\text{ER}|\mathbf{Z}), \tag{13}$$

where $\text{Evar}(R|\mathbf{Z}) = \sigma_d^2$ and $\text{var}(\text{ER}|\mathbf{Z}) = \sigma_e^2$ is the demographic and the environmental variance, respectively. For a given population size N , the variance in the change in population size to the next year will then be:

$$\text{var}(\Delta N|N) = \sigma_d^2 N + \sigma_e^2 N^2. \tag{14}$$

We let \bar{R}_j denote the mean value of the contributions in year j , and let \bar{R} be the mean of all recorded contributions. The major part of the information in

the environmental variance came from the variation between years, whereas the variation in R_{ij} within years contained information about the demographic variance. Sæther et al. (1998a) showed that:

$$\hat{\sigma}_e^2 = \frac{1}{n-t} \sum_{j=1}^t \sum_{i=1}^{n_j} (R_{ij} - \bar{R}_j)^2 \quad (15)$$

was an unbiased estimator for the demographic variance, where

$$n = \sum_{j=1}^t n_j.$$

Usually, σ_e^2 was estimated from time series of fluctuations in ΔN (Sæther et al. 1998a, 2000, 2002a). A problem with this approach is that the environmental stochasticity is extremely difficult to separate from the effects of sampling errors in the population estimates (De Valpine and Hastings 2002). Thus, in many cases it is better to estimate σ_e^2 from the individual variation in fitness. Engen et al. (1998) showed that the fitness contributions can be written in the form $R_{ij} = ER + e_j + d_{ij}$, where e_j and d_{ij} are independent, $\sigma_e^2 = \text{var}(e_j)$ and $\sigma_d^2 = \text{var}(d_{ij})$. In general, we have the relationship:

$$\text{var}(\bar{R}_j - \bar{R}) = \text{var}(\bar{R}_j) + \text{var}(\bar{R}) - 2\text{cov}(\bar{R}_j, \bar{R}). \quad (16)$$

From eq (13), it then follows:

$$\text{var}(\bar{R}_j) = \sigma_e^2 + \sigma_d^2/n_j, \quad (17a)$$

$$\text{var}(\bar{R}) = \sigma_d^2/n + \sigma_e^2 \sum n_j^2/n^2 \quad (17b)$$

and:

$$2\text{cov}(\bar{R}_j, \bar{R}) = 2(\sigma_d^2 + n_j \sigma_e^2)/n. \quad (17c)$$

This gives:

$$E \sum_{j=1}^t (\bar{R}_j - \bar{R})^2 = \sigma_e^2(t-2 + t \sum n_j^2/n^2) + \sigma_d^2[\sum(1/n_j) - t/n],$$

which leads to the estimation equation:

$$\sum_{j=1}^t (\bar{R}_j - \bar{R})^2 = \hat{\sigma}_e^2(t-2 + t \sum n_j^2/n^2) + \hat{\sigma}_d^2[\sum(1/n_j) - t/n], \quad (18)$$

that combined by eq (15) determines $\hat{\sigma}_e^2$. We used equal weights in eq (18) on $(\bar{R}_j - \bar{R})^2$ because this was optimal for large values of n_j that gave $\bar{R}_j \approx e_j$.

Estimation of the variance components for wolverine in Sarek was also complicated because

radiocollared females did not represent a random sample of the population because only females that had a den were captured in the first year. We, therefore, did not include the results from the year of capture in the analyses. In this way we obtained data from 28 females from 1995 to 2001.

The Specific Population Growth Rate r_1

The specific population growth rate was a problematic parameter for us to estimate because the population must spend periods at low population sizes to avoid interpolation over a large range of population sizes (Taylor 1995, Sæther and Engen 2002a, Aanes et al. 2002). Thus, we followed Sæther et al. (2002b) and used demographic data to get information about this parameter. Female wolverines may attain sexual maturity at about 15 months, but previous studies reported varying proportions of pregnant, 2-year-old females (Rausch and Pearson 1972, Liskop et al. 1981, Banci and Harestad 1988). Information from reproductive tracts showed that a very high proportion of adult females (≥ 3 years old) were pregnant each year, but observations of radiocollared wolverines indicated that the proportion of females actually reproducing was much lower (Banci and Harestad 1988). However, in an area where females were given supplemental food, 83% of the females gave birth to a litter (Persson 2003). The mean litter size of litters dug out soon after birth was 2.77 (Pulliainen 1968), which was significantly higher than the litter size at the time of radiomarking in Sarek ($\bar{x} = 1.9$; Persson 2003) and than sizes recorded in North America (Magoun 1985, Copeland 1996). This reduction was probably due to losses from infanticide, starvation, predation, or disease (Persson et al. 2003). At low population densities we assumed these losses were reduced by 25%, giving a litter size of 2.12 at weaning. Assuming a slightly female-biased sex ratio at birth (55% females; Persson et al. 2003) and a juvenile survival rate of 0.81, this represents an annual recruitment rate of 0.78 juvenile females to the next generation. If we assumed reproductive onset at 3 years and an adult survival rate of 0.92 (Willebrand et al. 1999), the specific population growth rate at low density was $r_1 = 0.27$.

The Form of Density Regulation θ

We estimated the form of density regulation for the population in Sarek, where the population estimates were assumed to be reasonably accurate. We estimated by maximum likelihood, assuming the population process was a Markov process and ΔN normally distributed with mean $\mu(N) = r_1 N[1 - h(N, \theta)]/h(K, \theta)$ and variance $v(N) = \sigma_e^2 + \sigma_d^2/N$.

We estimated a large value of θ for the Sarek population ($\hat{\theta} = 12.5$) that indicated a strong density regulation around the carrying capacity K and weak regulation below K . However, as expected from the short study duration, the estimate of θ was very uncertain with a relatively high proportion of the bootstrap-replicates at very large values ($q > 25$) (Sæther et al. 2003). In relation to their body size, wolverines have

very large home ranges, and the females occupy distinct home ranges that overlap to a small extent (Powell 1979, Magoun 1985, Copeland 1996), whereas adult males occupy larger home ranges than females and can encompass several female home ranges (Banci 1994). This suggests that the ceiling model of Lande (1993) describes the form of the density regulation of the wolverine reasonably well. Hence, we used this model of density regulation in the following analyses.

Time to Extinction

When we assumed that the ceiling model of Lande (1993) was valid and used the transformation formulas for diffusion (Karlin and Taylor 1981), the infinitesimal mean and variance for the process $X = \ln N$ was $r_1 - 1/2 \sigma_e^2 - 1/2 \sigma_d^2 e^{-X}$ and $\sigma_e^2 + \sigma_d^2 e^{-X}$ for $X \leq \ln K$, respectively. We estimated the risk of extinction by simulating this model using 1,000 sample paths (Sæther et al. 2003).

RESULTS

The range of variation in the individual contributions of females R was from zero to 4 (Sæther et al. 2003) with 1 as the modal value. The estimated demographic variance was $\sigma_d^2 = 0.571$, whereas the environmental variance was $\sigma_e^2 = 0.154$. A problem with this approach using eqs (16–18) is that variation in R will also be dependent on fluctuations in population size through the effects of density regulation. Thus, our estimate of σ_e^2 may represent an upper level for the environmental variance in Sarek.

We examined the dynamic characteristics of the population in Sarek by simulating 1,000 sample paths from this population model (eq 6). We assumed that the number of active dens recorded represented only 50% of the sexually mature fe-

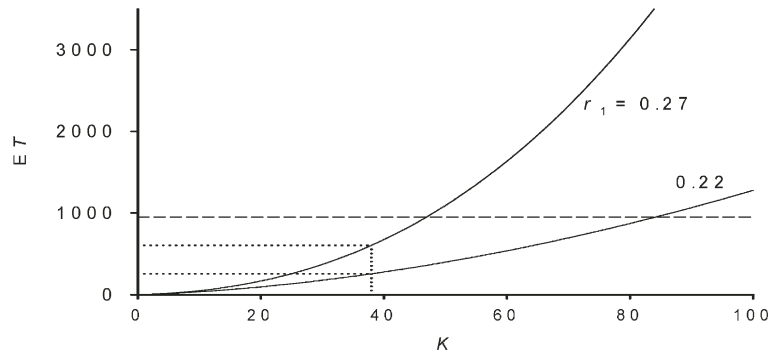


Fig. 2. Expected time to extinction ($E T$) in relation to the carrying capacity (K) in the ceiling model of Lande (1993) for different values of the specific growth rate r_1 for the wolverine population in Sarek, northern Sweden (see Fig. 1). The dashed line indicates the expected time to extinction for a population that is considered vulnerable according to World Conservation Union's (2001) classification. The dotted line indicates the estimates for the Sarek population

males actually present in the population (see Methods). We found that a population at an initial population size of $N = K = 38$ adult (≥ 3 -yr-old) females had a 10% probability of becoming extinct after 137 years, and there was only a 50% probability that the population would be present after 898 years. These results were very sensitive to the estimate of the environmental variance σ_e^2 . If we assume $\sigma_e^2 = 0.075$, the population would not be considered vulnerable according to World Conservation Union's (2001) classification.

The distribution of the time to extinction of the Sarek population, using the ceiling model (eq 6) and assuming an initial population size of $K = 38$ (≥ 3 -yr-old) females, closely resembles an exponential distribution. Thus, the probability of extinction will be highest during the first years. Assuming the population parameters as estimated for the Sarek population, we found that the expected time to extinction increased curvilinearly with carrying capacity K (Fig. 2). The expected time to extinction of the Sarek population was 604 years (Fig. 2) when assuming a ceiling model with K equal to twice the highest number of dens we recorded ($K = 38$ [≥ 3 -yr-old] females) with $r_1 = 0.27$. This means that the wolverine population in Sarek must be recorded as vulnerable according to World Conservation Union's (2001) classification if no individuals immigrate. Only populations with a carrying capacity > 46 adult (≥ 3 -yr-old) females can be considered not vulnerable according to this classification (Fig. 2). As expected (Lande 1993, Sæther et al. 1998a), this critical population size is strongly influenced by the value of r_1 (Fig. 2). A decrease in r_1 by 0.05 increased the necessary carrying capacity for the population not to be considered vulnerable to $K = 85$. In contrast, if $\sigma_e^2 = 0.075$ this critical carrying capacity was reduced to only $K = 18$.

We used the ceiling model to examine the different harvest strategies and assumed an initial population $N_0 = K = 60$ sexually mature (≥ 3 -yr-old) females. Furthermore, we required that the harvest strategy give an expected lifetime of the population > 952.3 years; thus, this satisfied the criteria of World Conservation Union (2001) for populations that are not considered vulnerable when the time to extinction is approximately exponentially distributed. No offtake is permitted when $E T < 952.3$ years. If $T > 952.3$ without harvesting, we consider harvesting strategies (c, q) that keep T constant equal to 952.3 years. When the population surveys are accurate, but environmental stochasticity is large, only small values of q can be permitted for relative thresholds c/K up to approximately 0.8, resulting in a very low annual offtake of individuals (Fig. 3). When c/K approaches 1, about half of the individuals in excess of the threshold can be removed, giving a low expected population size after the hunt but with harvest only permitted for a few years (Fig. 3). When the precision in the population estimates is improved, q increases for larger values of c/K (Fig. 3).

These patterns were extremely sensitive to the estimates of the environmental variance σ_e^2 , as expected from theoretical analysis of harvesting models (Sæther et al. 1996, Lande et al. 1997, 2001). When we assume a lower estimate of σ_e^2 , all individuals above the threshold can be removed for $c/K > 0.37$. With reduced bias in the population estimates, this critical threshold can be reduced (Fig. 3). The number of animals that can be removed and the expected population size after the hunt depend on the particular combinations of c/K and q chosen (Fig. 3). Lowest expected population size after the hunt was found for values of c/K between 0.3 and 0.4, dependent on the census accuracy. In contrast, the highest offtake of animals occurred at $c/K = 0.59$. We also found that population dynamics were strongly influenced when all excess individuals were removed (Fig. 3).

We then applied the insight gained by analysis of the Sarek population to the development of management strategies of the Norwegian wolverine. However, the application of the ceiling model of Lande (1993) requires an estimate of the carrying capacity for the different regions in Fig. 1. We assumed that continuous areas > 50 km² situated 600 m above sea level (or 300 m above sea level in the 2 northernmost counties) represented suitable wolverine habitat. Scandinavian home range studies have shown that the mean size of a female's annual home range varies from 274 km² in Snøhetta in southern Norway (Landa et al.

1998) to 322 km² in Sarek (J. Persson, University of Umeå, unpublished data). Because these estimates were obtained in areas likely to represent very suitable habitats for wolverine, we assumed that an average Norwegian female wolverine requires an area of 400 km². Dividing the total area of available wolverine habitat with the mean home range size, the rough estimate of K is 166, 48, 26, and 46 sexually mature (≥ 3 -yr-old) females in southern Norway, Nordland (including Nord-Trøndelag), Troms, and Finnmark, respectively (Fig. 1). These estimates are based on that nonreproductive territorial 2-year-old females (Vangen et al. 2001) comprise 30.5% of the adult (≥ 2 -yr-old) females in the population (Landa et al. 2001).

In all parts of Norway, adult (> 1 -yr-old) female wolverine were killed almost every year (Table 1) due to different forms of human activities such as legal hunting, illegal killing, and control of individuals that kill semidomestic reindeer or sheep.

We examined the consequences of this mortality on future wolverine population dynamics by assuming that removal of individuals during a period could be approximated by a constant harvest strategy where the number of animals removed each year has a constant mean and variance. We assumed that the future harvest in southern and northern Norway would be equal to the harvest during past years (Table 1). We also assumed that the number of active dens represented only 50% of the sexually mature females present. In both regions, our simulations showed that continuation of the current level of harvest of females will, with 10% probability, cause extinction of the wolverine within 20 years (Fig. 4). The probability of absence of the wolverine in northern Norway in 243 years is higher than the probability of its presence. Our simulations also showed that time to extinction was relatively independent of the estimates of the carrying capacity. For instance, an increase in K by reducing the required home range size from 400 km² to 200 km² in all regions had $< 5\%$ influence on the expected time to extinction. Thus, prolonging the current harvest of wolverine in Norway is likely to cause extinction of the species in the near future. Hence, if the current rate of killing female wolverines continues, the northern population will be classified according to World Conservation Union's (2001) criteria as endangered, whereas the southern population will be considered vulnerable (Fig. 4). The classification of the southern population is sensitive to the estimate of N_0 . For instance, for $N_0 = 20$ the southern population will also be considered endangered.

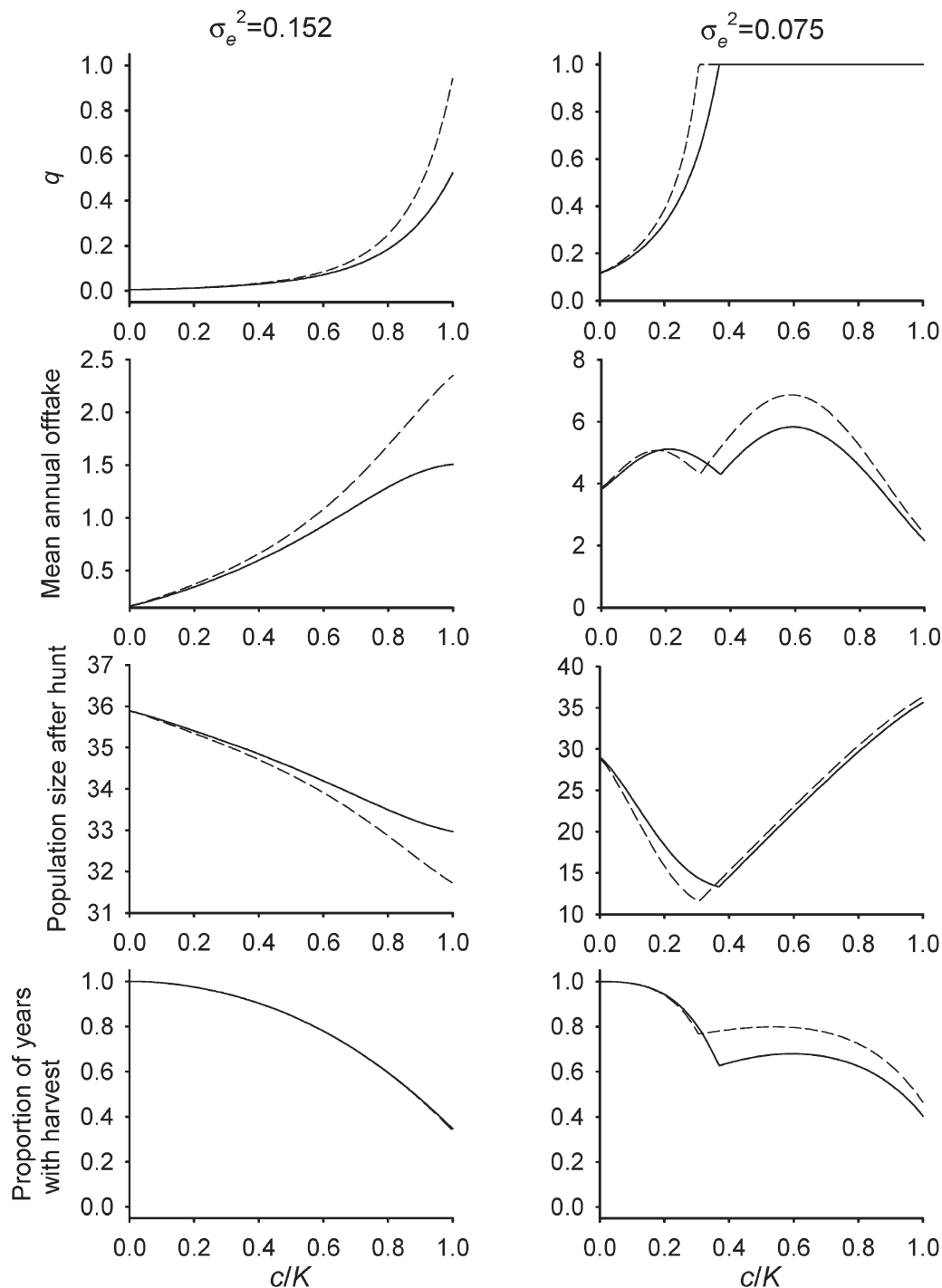


Fig. 3. The proportion of wolverines in excess above the threshold c that can be removed (q), the mean annual harvest of individuals, the expected population size after the hunt, and the proportion of years when harvest is allowed in relation to the threshold c/K for different levels of uncertainty in the population estimates (dashed line: $\epsilon = 0.01$, solid line: $\epsilon = 1$, see (12) in the text) for 2 values of environmental stochasticity under the constraint of an expected time to extinction of 952.3 years, thus satisfying the criteria that the population would not be classified as vulnerable according to World Conservation Union (2001). The population model is the ceiling model of Lande (1993). Other parameters were $r_1 = 0.27$, $\sigma_d^2 = 0.571$, and initial population size was $N_0 = K = 60$.

To determine a sustainable strategy for offtake of wolverine, we examined the threshold c/K in the different regions of Norway, under the constraints that the expected time to extinction

should be 952.3 years. Thus, the population should not be considered vulnerable according to the criteria of World Conservation Union (2001). We used $q = 0.4$, representing a strategy to mini-

imize expected population size after hunt, and $q = 0.6$, a strategy aimed to maximize the mean annual offtake of animals (Fig. 3). Using the parameter estimates from the Sarek population and an initial population size of $N_0 = K$, harvest could only be allowed in populations with $K > 47$ sexually mature females if the expected time to extinction was long enough to consider the population as nonvulnerable. For increasing values of K , the threshold could decrease, reaching 10–15% of K in very large populations (Fig. 5). These patterns were very sensitive to environmental stochasticity. For lower estimates of σ_e^2 , harvesting could start at much lower population sizes, and lower thresholds could be selected for a given q (Fig. 5).

DISCUSSION

We demonstrated that the carrying capacity K of wolverines in Scandinavia must be >46 sexually mature (≥ 3 -yr-old) females (Fig. 2) for a population to be considered not vulnerable by the World Conservation Union (2001), assuming that the demographic characteristics of the Sarek population were typical for most populations in Scandinavia. This implies that the current population in Sarek is not viable (Fig. 2) with-

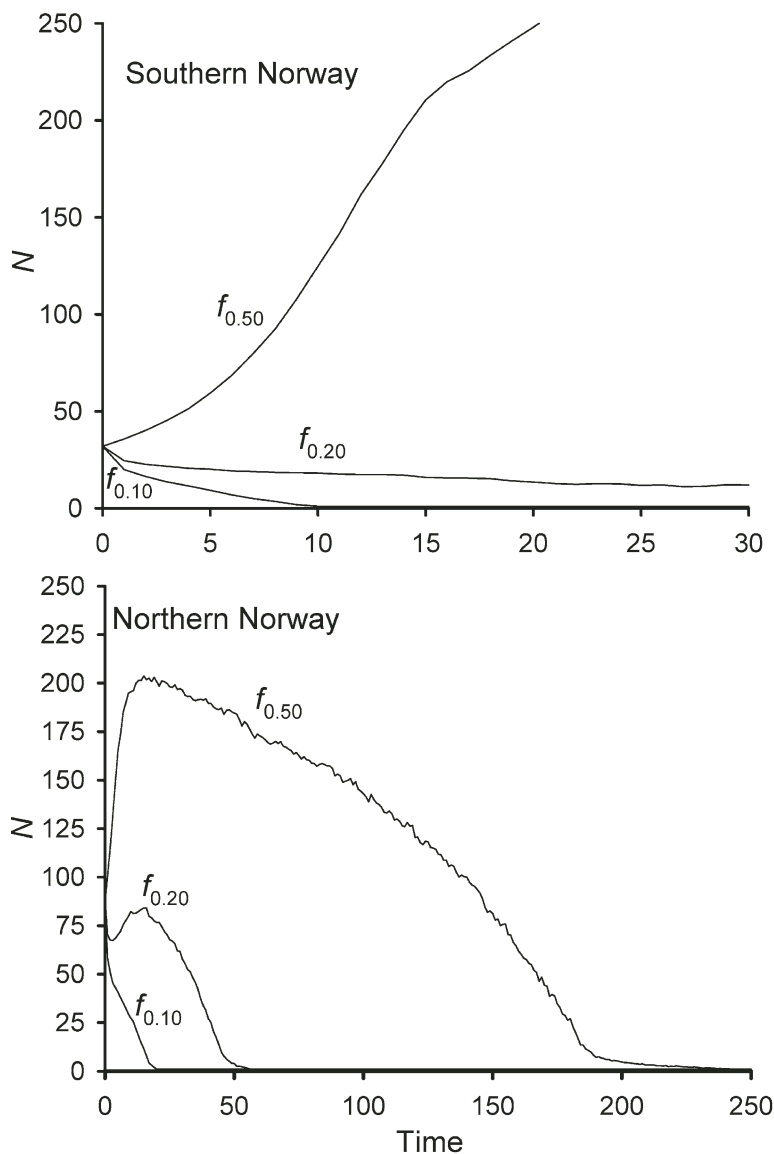


Fig. 4. Simulation of the effects of harvesting on wolverine populations in the southern and northern Norway (counties N-Trøndelag, Nordland, Troms, Finnmark; Fig. 1) with parameters estimated for the Sarek population (solid line) for $\sigma_e^2 = 0.154$. In the distribution of the simulated population sizes resulting from 1,000 sample paths, the 50%, 20%, and 10% quantiles are denoted by $f_{0.5}$, $f_{0.20}$, and $f_{0.10}$, respectively. The population size of sexually mature (≥ 3 -yr-old) females was set to twice the estimated number of active dens in 2002, assuming no sampling errors in the estimates. Because many killed females were not age-determined, we included the complete adult (≥ 1 -yr-old) female segment of the population in the analyses. We assumed that 1- and 2-year-old individuals comprised 50.5% of the population (Landa et al. 2001). This gave $N_0 = 32$ and $K = 332$ in southern Norway and $N_0 = 88$ and $K = 240$ in northern Norway. A constant harvest was assumed, specified by the mean and variance in the number of adult females harvested in the region over the past years (Table 1). The carrying capacity was determined from an assessment of the areas with available wolverine habitat. Other parameters were $r_1 = 0.27$ and $\sigma_d^2 = 0.571$.

out immigration from surrounding areas. Furthermore, we demonstrated that the rate of loss of wolverines in Norway due to various kinds of human activities will likely lead to rapid wolverine extinction (Fig. 4), provided that no immigration occurs from neighboring countries.

Our analyses were based on several simplifying assumptions. Our estimate of the specific growth rate $r_1 = 0.27$ was based on all females being mature at age 3. In general, this is not the situation in Scandinavian populations where only 33% of 3-year-old females reproduce.

The average age at first reproduction among females monitored to their first reproduction was 3.4 years (Persson 2003). Similarly, we assumed very small losses of offspring before weaning (see Methods). A problem with these estimates is that the demographic study was undertaken in an area with a high density of animals that is likely to represent a favorable habitat for the wolverine. Thus, our choice of parameter values for calculating the mean growth rate at small population sizes was likely to overestimate r_1 in other areas. In general, a reduction in r_1 will have a strong influence on time to extinction (Lande 1993; Sæther et al. 1998a,b; Lande et al. 2003; Sæther and Engen 2003), as was the case for the wolverine population in Sarek (Fig. 2). Furthermore, we assumed that the recorded number of active dens represented only half of the number of sexually mature females present in the population. However, there was large annual variation in the proportion of females breeding. If the large number of dens recorded in Sarek in 2002 (Table 1) was due to a high breeding propensity among the females that particular year, we may have overestimated the carrying capacity for the area. This suggests that our estimates of the time to extinction of the Sarek population (Figs. 2, 3) are likely to represent overestimates.

Reliable estimates of density regulation require long-time series of precise population estimates (Sæther et al. 1998b, 2000, 2002a,b), far longer

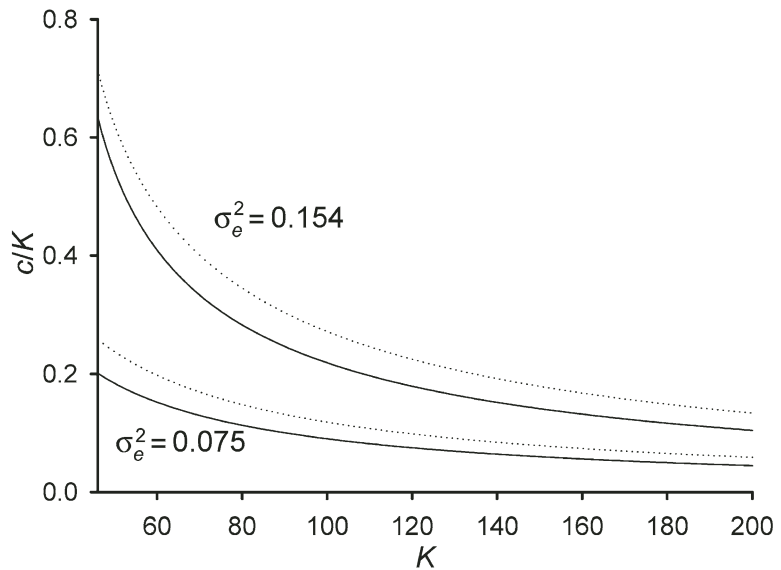


Fig. 5. The threshold c/K in relation to the carrying capacity K for different choice of q and environmental variance σ_e^2 that gives an expected time to extinction of 952.3 years and thus satisfies the criteria that the wolverine population would not be classified as vulnerable according to World Conservation Union (2001). The solid lines represents $q = 0.4$, and the dotted line represents $q = 0.6$. Other parameters were $r_1 = 0.27$, $\sigma_d^2 = 0.571$, and initial population size was $N_0 = 40$.

than available for any Scandinavian wolverine population. Thus, in most of the analysis, we assumed the ceiling model of Lande (1993) with a very simplified description of the density regulation. The uncertain estimates of θ in the Sarek population (Sæther et al. 2003) do indicate strong density regulation around K , which supports the choice of this model. This type of population dynamic seems typical for many solitary vertebrates that defend territories (Lande 1987, Sæther et al. 2002b).

Stochastic factors strongly influence the population dynamics of the wolverine. Our estimate of the demographic variance σ_d^2 in the wolverine population in Sarek was higher than those previously estimated in most vertebrate populations (Lande et al. 2003). Similar values have only been recorded in some small passerine birds (Lande et al. 2003). This is related to the combination of relatively high survival rate of the adult females but highly variable recruitment success (Sæther et al. 2003). Previous studies have indicated high losses of offspring after the denning period that were probably related to intra-specific predation (Persson et al. 2003). However, these estimates of recruitment could also be an artifact of the sampling procedure because, during the first year, only breeding females were radiocollared. Accordingly, we included only females that already had been followed 1 year in the estimates of recruitment success. However, including

all adult females or selecting only females followed over 2 years gave a small change (<5%) in $\hat{\sigma}_d^2$. This suggests that large demographic stochasticity is an important characteristic of wolverine population dynamics. Theoretical analyses have shown that the demographic stochasticity strongly influences the time to extinction of small populations (Lande 1993; Lande et al. 1998, 2003; Sæther and Engen 2003). Thus, the results of our calculations of the expected time to extinction (Fig. 2), the simulations of future population trajectories (Fig. 4), and our analysis of different harvest strategies (Figs. 3, 5) are all likely to be influenced by such a high estimate of σ_d^2 . This illustrates the importance of incorporating analysis of demographic stochasticity, especially when considering management options for small populations (Sæther and Engen 2002a).

Environmental stochasticity is another important component of the population dynamics of the wolverine. Usually, we estimate this from time series of population fluctuations (Dennis and Otten 2000; Sæther and Engen 2002b; Sæther et al. 2000, 2002b). In the Sarek population, we used the among-year variation in the individual fitness contributions, using the method of variance partitioning described in Engen et al. (1998). We then assumed that the annual fluctuations in population size were only due to stochastic fluctuations around K and were not related to density dependence. Thus, $\hat{\sigma}_e^2$ probably represented an upper limit for the environmental variance σ_e^2 . However, large environmental stochasticity was expected in the population dynamics of the wolverine because the demography was presumably influenced by highly variable food availability, such as the abundance of ungulate carrion (Persson 2003) and rodents (Landa et al. 1997). Therefore, we performed all analyses using $\hat{\sigma}_e^2 = 0.154$ and $\hat{\sigma}_d^2 = 0.075$. As expected from theoretical analysis (Lande 1993, 1998; Lande et al. 2003; Sæther and Engen 2003), variation in this parameter strongly influenced the expected time to extinction and the choice of harvest strategy for larger populations (Fig. 3). However, predictions of the future development of wolverine populations in Norway were relatively independent of the estimates of σ_e^2 (Fig. 4); this was probably because the harvest of individuals (Fig. 3) affected the deterministic dynamics by reducing r_1 . It is therefore important to continue long-term individual-based population studies of the wolverine to improve precision in the estimates of r_1 and σ_e^2 .

Theoretical analysis of harvesting models has shown that proportional threshold harvesting has some useful properties in reducing the variance in

the annual yield, compared to a pure threshold strategy (Engen et al. 1997; Lande et al. 1997, 2001). We are then left with 2 options, determining the threshold and determining the proportion of individuals above the threshold that can be removed, q . When we kept the expected time to extinction constant, we found that, for large values of the environmental stochasticity, the annual yield was maximized and the expected population size after the hunt was minimized for high thresholds c/K (Figs. 3, 5). In contrast, when environmental stochasticity was smaller, the chosen values c and q depend on the optimization criteria. If the expected population size after the hunt should be minimized, a smaller threshold c/K should be chosen than for maximization of the annual off-take as optimization criterion. Irrespective of the value of σ_e^2 , higher values of q could occur when the precision in the population estimates is improved (Fig. 3). Thus, larger off-takes were permitted for small sampling errors than for larger sampling errors (Tufto et al. 1999); this strongly emphasized the need for the investment in precise population censuses for a sustainable harvest strategy for wolverine. A central focus for such schemes should be to obtain estimates of the nonbreeding part of the population (i.e., by using modern DNA techniques to obtain individual identification from samples of feces or urine samples collected from tracks [Flagstad et al. 2004]). Such data can be analyzed by capture-recapture techniques to provide information on the precision in the censuses (Seber 1982, Mills et al. 2000) and estimates of important demographic variables (Lebreton et al. 1992).

MANAGEMENT IMPLICATIONS

Our analyses have shown that the Norwegian management boards have given quotas that are too high to secure viable wolverine populations in Norway according to the World Conservation Union's (2001) criteria (Fig. 4). Thus, if the current practice is continued, this is likely to lead to extinction of the wolverine over the larger parts of Norway within a relatively short period (Fig. 4). Assuming the demographic characteristics of the Sarek population are typical of most Norwegian populations, our estimates of K , though admittedly very rough, suggest that harvest should not be permitted before the populations exceed 22 sexually mature females in both northern and southern Norway. This calculation is based on $q = 0.4$ and the initial population size of sexually mature (≥ 3 -yr-old) females; that is twice the number of active dens in the 2 regions in 2002 (Table 1). When the estimated population size exceeds this value,

40–60% of the excess individuals can be removed (Fig. 3). Thus, the current population size must be increased before harvesting should be permitted in the southern Norwegian management region. In northern Norway, a limited offtake can be permitted. However, this assumes strong regulation of the offtake with no harvest below the threshold.

A central element in a management strategy would be to reduce the number of animals killed illegally that is likely to occur even in the protected Sarek area (Table 1). A consequence of this will be an increase in the specific growth rate and a reduction in the stochastic influences on the population. This will strongly increase the expected time to extinction (Fig. 2) and improve viability of the species.

ACKNOWLEDGMENTS

This study was financially supported by grants from the Norwegian Directorate for Nature Management. The field study of wolverines in Sarek was financed by the Swedish Environmental Protection Agency, World-Wide Fund for Nature, and Norwegian Directorate for Nature Management. P. Segerström and T. Wiklund conducted the fieldwork in Sarek.

LITERATURE CITED

- AANES, S., S. ENGEN, B.-E. SÆTHER, T. WILLEBRAND, AND V. MARCSTRÖM. 2002. Sustainable harvest strategies of willow ptarmigan in a fluctuating environment. *Ecological Applications* 12:281–290.
- ANDERSEN, R., A. LANDA, H. BRØSETH, AND J. D. C. LINELL. 2001. Instruks for yngleregistrering av jerv. A: Bakgrunnsinformasjon og overvåkingsmetodikk. Norwegian Institute for Nature Research, online report. [In Norwegian.]
- BANCI, V. 1994. Wolverine. Pages 99–123 in L. F. Ruggerio, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, editors. *The scientific basis for conserving forest carnivores: American marten, fisher, lynx and wolverine in the western United States*. U.S. Forest Service General Technical Report RM-254. Fort Collins, Colorado, USA.
- , AND A. S. HARESTAD. 1988. Reproduction and natality of wolverine *Gulo gulo* Yukon. *Annales Zoologici Fennici* 25:265–270.
- BEDDINGTON, J. R., AND R. M. MAY. 1977. Harvesting populations in a randomly fluctuating environment. *Science* 197:463–465.
- BEISSINGER, S. R., AND D. R. MCCULLOUGH. 2002. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- , AND M. I. WESTPHAL. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821–841.
- COPELAND, J. P. 1996. *Biology of the wolverine in central Idaho*. Thesis, University of Idaho, Moscow, USA.
- DENNIS, B., AND M. R. OTTEN. 2000. Joint effects of density dependence and rainfall abundance of San Joaquin kit fox. *Journal of Wildlife Management* 64:388–400.
- DE VALPINE, P., AND A. HASTINGS. 2002. Fitting population models incorporating process noise and observation error. *Ecological Monographs* 72:57–76.
- ELLNER, S. R., J. FIEBERG, D. LUDWIG, AND C. WILCOX. 2002. Precision of population viability analysis. *Conservation Biology* 16:258–261.
- ENGEN, S., R. LANDE, AND B.-E. SÆTHER. 1997. Harvesting strategies for fluctuating populations based on uncertain population estimates. *Journal of Theoretical Biology* 186:201–212.
- , Ø. BAKKE, AND A. ISLAM. 1998. Demographic and environmental stochasticity—concepts and definitions. *Biometrics* 54:830–836.
- , B.-E. SÆTHER, AND A. P. MØLLER. 2001. Stochastic population dynamics and time to extinction of a declining population of barn swallows. *Journal of Animal Ecology* 70:789–797.
- FIEBERG, J., AND S. R. ELLNER. 2000. When is it meaningful to estimate an extinction probability? *Ecology* 81:2040–2047.
- FLAGSTAD, Ø., E. HEDMARK, A. LANDA, H. BRØSETH, J. PERS-SON, R. ANDERSEN, P. SEGERSTRÖM, AND H. ELLEGREN. 2004. Colonization history and noninvasive monitoring of a reestablished wolverine population. *Conservation Biology* 18:676–688.
- GILPIN, M. E., AND F. J. AYALA. 1973. Global models of growth and competition. *Proceedings of the National Academy of Sciences USA* 70:3590–3593.
- , T. J. CASE, AND F. J. AYALA. 1976. θ -selection. *Mathematical Biosciences* 32:131–139.
- GROOM, M., AND M. A. PASCUAL. 1998. The analysis of population persistence: an outlook on the practice of viability analysis. Pages 4–27 in P. L. Fiedler and P. Kareiva, editors. *Conservation biology*. Second edition. Chapman and Hall, New York, USA.
- JOHNSEN, S. 1929. Rovdyr og rovfuglstatistikken i Norge. *Naturvidenskabelig Årbok* 2. Bergen Museum, Bergen, [In Norwegian.]
- JONZÉN, N., J. RIPA, AND P. LUNDBERG. 2002. A theory of stochastic harvesting in stochastic environments. *American Naturalist* 159:427–437.
- KARLIN, S., AND H. M. TAYLOR. 1981. *A second course in stochastic processes*. Academic Press, New York, USA.
- LANDA, A., O. STRAND, J. E. SWENSON, AND T. SKOGLAND. 1997. Wolverine and their prey in southern Norway. *Canadian Journal of Zoology* 75:1292–1299.
- , ———, J. D. C. LINNELL, AND T. SKOGLAND. 1998. Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. *Canadian Journal of Zoology* 76:448–457.
- , ———, ———, M. LINDÉN, J. E. SWENSON, E. RØSKAFT, AND A. MOKSNES. 2000. Conservation of Scandinavian wolverines in ecological and political landscapes. Pages 1–20 in H. I. Griffiths, editor. *Mustelids in a modern world*. Backhuys, Netherlands.
- , J. TUFTO, R. ANDERSEN, AND J. PERSSON. 2001. Aktive ynglehi som bestandsestimator basert på nye data om alder for første yngling. *NINA Notat* 2001:1–10. [In Norwegian.]
- LANDE, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911–927.
- , S. ENGEN, AND B.-E. SÆTHER. 1995. Optimal harvesting of fluctuating populations with a risk of extinction. *American Naturalist* 145:728–745.
- , B.-E. SÆTHER, AND S. ENGEN. 1997. Threshold

- harvesting for sustainability of fluctuating resources. *Ecology* 78:1341–1350.
- , AND ———. 2001. Sustainable exploitation of fluctuating populations. Pages 67–86 in G. M. Mace, J. P. Reynolds, K. H. Redford, and J. G. Robinson, editors. *Conservation of exploited populations*. Cambridge University Press, Cambridge, United Kingdom.
- , S. ENGEN, AND B.-E. SÆTHER. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford, United Kingdom.
- , ———, F. FILLI, E. MATTHYSEN, AND H. WEIMERSKIRCH. 2002. Estimating density dependence from population time series using demographic theory and life history data. *American Naturalist* 159:321–337.
- LEBRETON, J. D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- LISKOP, K. S., R. M. F. S. SADLEIR, AND B. P. SAUNDERS. 1981. Reproduction and harvest of wolverine (*Gulo gulo*) in British Columbia. Pages 469–477 in J. A. Chapman and B. P. Pursley, editors. *Proceedings of the worldwide furbearer conference*. Worldwide Furbearer Conference, Frostburg, Maryland, USA.
- LÖNNBERG, E. 1936. Bidrag till järvens historia i Sverige. Kungliga Svenska Vetenskapsakademiens Skrifter i Naturskyddsärenden 32:1–38. [In Swedish.]
- LUDWIG, D. 1996. Uncertainty and the assessment of extinction probabilities. *Ecological Applications* 6:1067–1076.
- . 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80:298–310.
- MACE, G. M., AND R. LANDE. 1991. Assessing extinction threats: towards a reevaluation of IUCN species threatened categories. *Conservation Biology* 5:148–157.
- MAGOUN, A. J. 1985. Population characteristics, ecology and management of wolverines in north-western Alaska. Dissertation, University of Alaska, Fairbanks, USA.
- , AND J. P. COPELAND. 1998. Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management* 62:1313–1320.
- MAY, R. M., J. R. BEDDINGTON, J. W. HORWOOD, AND J. G. SHEPHERD. 1978. Exploiting natural populations in an uncertain world. *Mathematical Biosciences* 42:219–252.
- MILLS, L. S., J. J. CITTA, K. LAIR, M. SCHWARTZ, AND D. TALLMON. 2000. Estimating animal abundance using non-invasive DNA-sampling: promise and pitfalls. *Ecological Applications* 10:283–294.
- POWELL, R. A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. *Zeitschrift Tierpsychologie* 50:153–165.
- PERSSON, J. 2003. Population ecology of Scandinavian wolverines. Thesis, Swedish University of Agricultural Sciences, Umeå, Sweden.
- , T. WILLEBRAND, A. LANDA, R. ANDERSEN, AND P. SEGERSTRÖM. 2003. The role of intraspecific predation in the survival of juvenile wolverines *Gulo gulo*. *Wildlife Biology* 9:21–28.
- PULLIAINEN, E. 1968. Breeding biology of the wolverine (*Gulo gulo* L.) in Finland. *Annales Zoologici Fennici* 5:338–344.
- QUINN, T. J., AND R. B. DERISO. 1999. Quantitative fish dynamics. Oxford University Press, New York, USA.
- RAUSCH, R. A., AND A. M. PEARSON. 1972. Notes on the wolverine in Alaska and the Yukon territory. *Journal of Wildlife Management* 36:249–268.
- ROYAMA, T. 1992. Analytical population dynamics. Chapman and Hall, London, United Kingdom.
- SÆTHER, B.-E., AND S. ENGEN. 2002a. Including uncertainties in population viability analysis. Pages 191–212 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- , AND ———. 2002b. Pattern of variation in avian population growth rates. *Philosophical Transactions of the Royal Society London Series B* 357:1185–1196.
- , AND ———. 2003. The routes to extinction. Pages 218–236 in T. Blackburn and K. Gaston, editors. *Macroecology*. Blackwell, United Kingdom.
- , ———, AND R. LANDE. 1996. Density-dependence and optimal harvesting of fluctuating populations. *Oikos* 76:40–46.
- , ———, A. ISLAM, R. MCCLEERY, AND C. PERRINS. 1998a. Environmental stochasticity and extinction risk in a population of a small songbird, the great tit. *American Naturalist* 151:441–450.
- , ———, J. E. SWENSON, Ø. BAKKE, AND F. SANDEGREN. 1998b. Assessing the viability of Scandinavian brown bear, *Ursus arctos*, populations: the effects of uncertain parameter estimates. *Oikos* 83:403–416.
- , ———, R. LANDE, P. ARCESE, AND J. N. M. SMITH. 2000. Estimating time to extinction in an island population of song sparrows. *Proceedings of the Royal Society London Series B* 267:621–626.
- , ———, C. BOTH, AND M. E. VISSER. 2002a. Density dependence and stochastic variation in a newly established population of a small songbird. *Oikos* 99:331–337.
- , ———, AND E. MATTHYSEN. 2002b. Demographic characteristics and population dynamical patterns of solitary birds. *Science* 292:2070–2073.
- , ———, J. PERSSON, H. BRØSETH, A. LANDA, AND T. WILLEBRAND. 2003. Levedyktighetsanalyser av skandinavisk jerv. NINA Fagrapport 62:1–28. [In Norwegian.]
- SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. MacMillan, USA.
- SJÖGREN-GULVE, P., AND T. EBENHARD. 2000. The use of population viability analysis in conservation planning. *Ecological Bulletin* 48:1–203.
- SWENSON, J. E., F. SANDEGREN, A. BJÄRVALL, A. SÖDERBERG, P. WABAKKEN, AND R. FRANZÉN. 1994. Size, trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. *Biological Conservation* 70:9–17.
- TAYLOR, B. L. 1995. The reliability of using population viability analysis for risk classification of species. *Conservation Biology* 9:551–558.
- TUFTO, J., B.-E. SÆTHER, S. ENGEN, J. E. SWENSON, AND F. SANDEGREN. 1999. Harvesting strategies for conserving minimum viable populations based on World Conservation Union criteria: brown bears in Norway. *Proceedings of the Royal Society London Series B* 266:961–967.
- VANGEN, K. M., J. PERSSON, A. LANDA, R. ANDERSEN, AND P. FAGERSTRÖM. 2001. Characteristics of dispersal in wolverines. *Canadian Journal of Zoology* 79:1641–1649.
- WILLEBRAND, T., M. LINDÉN, J. PERSSON, AND P. SEGERSTRÖM. 1999. Överlevnad och dödsorsaker hos märkta järv i Sarek. Page 146 in Anonymous, editor. *Sammanhållen rovdjurspolitik. Slutbetänkande av rovdjursutredningen. Statens Offentliga Utredningar 1999. Fakta Info Direkt*, Stockholm. [In Swedish.]
- WORLD CONSERVATION UNION. 2001. IUCN Red List categories. Gland, Switzerland.