Native predators reduce harvest of reindeer by Sámi pastoralists

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Abstract. Contemporary efforts to protect biological diversity recognize the importance of sustaining traditional human livelihoods, particularly uses of the land that are compatible with intact landscapes and ecologically complete food webs. However, these efforts often confront conflicting goals. For example, conserving native predators may harm pastoralist economies because predators consume domestic livestock that sustain people. This potential conflict must be reconciled by policy, but such reconciliation requires a firm understanding of the effects of predators on the prey used by people. We used a long-term, large-scale database and Bayesian models to estimate the impacts of lynx (*Lynx lynx*), wolverine (*Gulo gulo*), and brown bear (*Ursus arctos*) on harvest of semi-domesticated reindeer (*Rangifer tarandus*) by Sámi pastoralists in Sweden. The average annual harvest of reindeer averaged 25% of the population (95% credible interval = 19, 31). Annual harvest declined by 96.6 (31, 155) reindeer for each lynx family group (the surveyed segment of the lynx population) in a management unit and by 94.3 (20, 160) for each wolverine reproduction (the surveyed segment of the wolverine population). We failed to detect effects of predation by brown bear. The mechanism for effects of predation on harvest was reduced population growth rate. The rate of increase of reindeer populations declined with increasing abundance of lynx and wolverine. The density of reindeer, latitude, and weather indexed by the North Atlantic Oscillation also influenced reindeer population growth rate. We conclude that there is a biological basis for compensating the Sámi reindeer herders for predation on reindeer.

Key words: Bayesian hierarchical model; brown bear; density dependence; lynx; North Atlantic Oscillation; population dynamics; predator–prey interactions; Rangifer tarandus; *reindeer management units; Sámi pastoralism; Sweden; wolverine.*

INTRODUCTION

In many areas of the world, efforts to conserve biological diversity have shifted from a historic emphasis on protecting single species to approaches that emphasize maintaining intact landscapes and fully functioning food webs (Grumbine 1994, Liddicker 1995, Boyd et al. 2008). Because indigenous human consumers have been a part of these food webs for millennia, sustaining the livelihoods of indigenous people alongside the biota has emerged as an important conservation goal. Often, traditional uses of land by people assure the landscape is maintained in a state that is far more hospitable to biological diversity than would be the case if these traditional economies were replaced by more intensive uses of the land. However, landscape-level conservation is demanding because it often creates conflicting goals that must somehow be reconciled. For example, restoration and conservation of large mammals, particularly large predators, is a laudable conservation objective, but it has the potential to harm human livelihoods that may be vital to sustaining semi-wild landscapes (Thirgood and Rabinowitz 2005). This problem is particularly acute for lands inhabited by people whose well-being depends on harvesting prey species that are also consumed by predators. When conflicts between predators and people occur, they must be remedied by management. This management can be costly and must be justified on the basis of understanding impacts of predators on prey shared with human users of the land (Sillero-Zubiri and Laurenson 2001).

The Sámi people have lived on the landscapes of Fennoscandia for at least 5000 years (Jorner et al. 1999). Reindeer husbandry is central to their culture and livelihood. During the last two millennia, domesticated reindeer have been used for meat, hides, transportation, milking, and to lure wild reindeer to sites for capture. Today, Sámi pastoralists allow their reindeer herds to migrate across large distances unimpeded by fences, gathering them only a few times a year (Jorner et al. 1999).

The area of land devoted to reindeer husbandry covers approximately half of the area of Sweden and offers vital habitat for the Eurasian lynx (*Lynx lynx*), wolverine (*Gulo gulo*), and brown bear (*Ursus arctos*). The main prey for lynx and wolverine is now the semi-domestic reindeer, and reindeer husbandry is believed to

suffer, at least locally, from the effects of this predation. As a consequence, policy makers in Fennoscandia face a problem of compromising between competing management goals.

Policy on management of large predators in Sweden and Norway is guided by international agreements that simultaneously require sustaining the livelihood of the Sámi people as well as assuring the viability of populations of large carnivores (Nilsson-Dahlström 2003). In Sweden the national government compensates reindeer herders for assumed damage caused by predators. The yearly cost of compensation for all predators together was about 57 million Swedish kronor (kr) (about 6.3 million euros; or about 8.6 million U.S. dollars) in 2009 (Sámi Parliament web site),[4] kr 33 million (~€3.6 million or ~US $4.9 million) of which was paid to offset effects of lynx predation and kr 21 million (~€2.3 million or ~US $3.1 million) was compensation for predation by wolverine.

The Swedish scheme for compensation is based on risk of economic loss by herders (Schwerdtner and Gruber 2007), and risk, in turn, is estimated from the number of predators present within a reindeer-grazing district. In 2008, the compensation was kr 200 000 (~€20 000 or ~US $29 000) for each lynx family group found within a reindeer-grazing district (i.e., an adult female with her kittens of the year; the surveyed segment of the population) and the same amount for each wolverine reproduction (the surveyed segment of the population). Under this compensation scheme, the reindeer owners accept some losses to predators and, in return, the Swedish government attempts to give full compensation for the financial losses due to reduced slaughter and other costs caused by the predators, for example, increased herding costs caused by disturbance.

The fairness of this system is controversial. The system is based on assuming a one-to-one relationship between losses to predators and number of predators; thus, doubling the number of predators should double the losses of reindeer. However, current rates of compensation of the number of reindeer that fall prey to predators are based on rough estimates of consumption rates and conservation values (Naturvårdsverket 1991). These estimates are not derived from any comprehensive, large-scale analysis of effects of predators on reindeer population dynamics or harvest. Consequently, expenditures for compensation are difficult to justify politically. Thus, there is a pressing need to understand effects of predators on reindeer to support decisions on compensation for losses to predators.

The reindeer husbandry system also provides an unusual opportunity to gain basic insight into population dynamics of large herbivores. Unlike domesticated livestock, reindeer are free ranging and, as a result, are fully exposed to effects of predators and weather.

Annual gathers of animals by herders assure that populations are censused repeatedly under similar conditions. As described in more detail below (see *Materials*), records from the reindeer husbandry system offer a time series of population observations replicated extensively along a latitudinal gradient. This time series creates an opportunity to address a fundamental question in population ecology: "How does the growth of populations of large herbivores respond to the environmental context, to external forcing from predation and weather, and to internal forcing from density dependence?" This question has engaged researchers all over the world (Skogland 1990, Aanes et al. 2000, Coulson et al. 2000, Mysterud et al. 2000, Jacobson et al. 2004, Hebblewhite 2005, Post 2005, Owen-Smith and Mills 2006, Wang et al. 2006, 2009, Tyler et al. 2008). However, most previous studies have gained insight by observing temporal variation in populations at a single location; research in population ecology that simultaneously analyzes variation in space and time is less common (Post 2005, Wang et al. 2006, Melis et al. 2009, Wang et al. 2009). Work that has considered spatio-temporal variation has been done at coarse spatial scales; fine-scale variation has not been widely considered.

Here we report an analysis of the effects of predation by lynx, wolverine, and brown bear on reindeer harvest and population growth rate in Sweden. Our work focused on two objectives: to determine if predators have a measurable, long-term impact on reindeer harvest and to evaluate the magnitude of the effects of predators on reindeer population growth relative to other sources of variation, including density dependence, latitudinal gradients in climate and resources, and annual variation in weather. The approach we offer provides a broadly applicable model for decision support needed to achieve compromises between goals for conservation of traditional livelihoods and goals for conservation of large, native predators.

Study Area

The reindeer husbandry area covers 230 000 km^2 of the land area of Sweden, spanning the three northernmost counties, Norrbotten, Västerbotten, and Jämtland, as well as parts of Dalarna and Västernorrland counties (Fig. 1).

Semi-domestic reindeer support the livelihoods of indigenous Sámi pastoralists in Sweden's reindeer husbandry area. The area is divided into 51 reindeer management units, most of which ($n = 33$ units) are defined by river valleys extending northwest–southeast. In these areas animals are herded along rivers between winter ranges in the forest (southeast) and summer ranges in the mountains (northwest), areas that are 100 to 300 km apart (Bjärvall et al. 1990). The remaining management units ($n = 18$) are primarily forested. In these areas, herds do not migrate. The total number of reindeer after harvest in December has been 220 000–
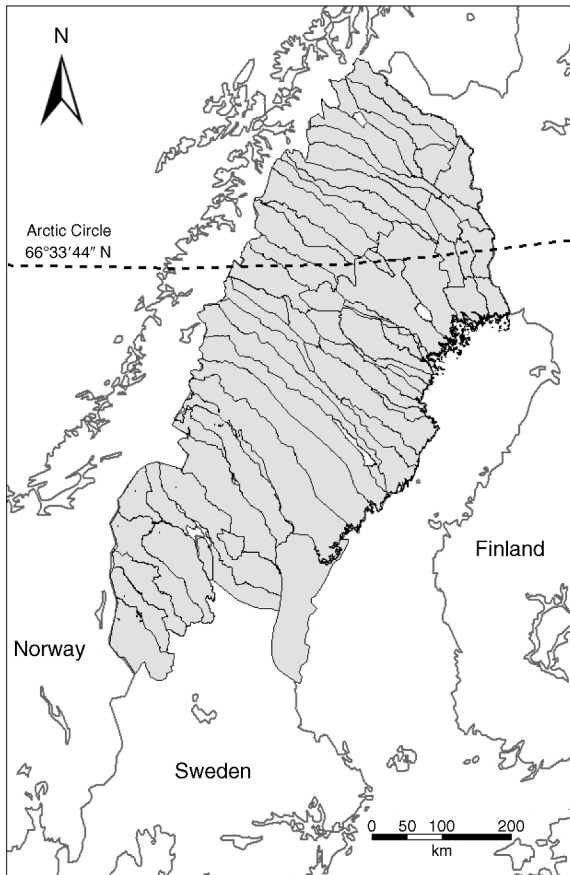
[4] http://www.sametinget.se/1131

FIG. 1. The reindeer husbandry area of Sweden (shaded area in the map), divided into 51 management units. Some management units are overlapping and are therefore partly hidden in the map. Some areas in northern Sweden are excluded from the reindeer husbandry area (shown as white areas or black dots embedded in the shaded area)

260 000 animals and yearly harvest was 47 000–74 000 animals during the last 10 years (official data from Sámi Parliament; see footnote 4).

Several large predators prey upon semi-domesticated reindeer. Eurasian lynx and wolverine are believed to have the greatest impacts on reindeer production. During 2009, lynx accounted for 57% of the compensation paid to pastoralists, while wolverine accounted for 36% (Sámi Parliament; see footnote 4). Based on surveys of lynx family groups and wolverine reproductions (see *Materials*, below), the estimated population size of these predators within the Swedish reindeer husbandry area during the last 10 years was 500–900 lynx (Andrén et al. 2010) and 310–650 wolverine (Persson and Brøseth 2011). Brown bear and golden eagle (*Aquila chrysaetos*) are also common. The estimated population sizes of brown bear is about 2000 individuals (Kindberg et al. 2009); golden eagles number ~550 breeding pairs (Tjernberg and Svensson 2007). Current Swedish policy does not allow resident wolf packs in the reindeer husbandry area. Successful enforcement of this policy means that there are only a few individual wolves and no wolf packs present there (Wabakken et al. 2009).

MATERIALS

We analyzed observations of reindeer population size, reindeer harvest, and results of predator surveys from 51 reindeer management units in Sweden during 1996–2008 (Sámi Parliament [Kiruna, Sweden], *unpublished data*). The number of reindeer harvested in each management unit and the post-harvest population size are recorded during September–December each year when reindeer populations are gathered by herders for slaughter. The reindeer data in our analysis are based on these annual records of herd numbers, composition, and harvest as reported by reindeer owners. We used official survey data on lynx and wolverine from the Swedish Environmental Protection Agency and County Administration Boards from 1996 to 2009.

County Administration Boards have monitored lynx and wolverines within the reindeer husbandry area since 1996. The aim of the survey is to find all lynx family groups and wolverine reproductions within the reindeer husbandry area each year. Therefore, the County Administration Boards organize the surveys mainly through field personnel, but a network of reindeer herders within the 51 management units also contribute. As the compensation system is based on these surveys, there is a very strong incentive for reindeer herders to report tracks of lynx family groups and wolverine den sites to the County Administration Boards. These reports are verified by field personnel from the County Administration Boards.

The lynx survey is performed during January and February by snow-tracking and identifying family groups consisting of adult females with kittens approximately nine months old. Tracks in the snow from two or more lynx traveling together during January and February almost always indicate presence of a family group. Criteria based on observed home-range sizes and movement rates (Linnell et al. 2007) are used to assure that counts of family groups are distinct. These surveys provide an index of all lynx in the district. On average, one lynx family group represents 6.1 ± 0.44 (mean ± SD) lynx in an area (Andrén et al. 2002).

The wolverine survey is performed during March to May and is based on documentation of den sites or tracks of females with cubs of the year after den abandonment (Swedish Environmental Protection Agency, *unpublished report*). The number of wolverine reproductions in a reindeer-grazing district is assumed to be proportionate to the total population size; on average, there are 6.4 (±0.8) wolverines in the population for each reproduction (Landa et al. 2001).

Abundance of brown bears is based on an observation index averaged over nine years (1998–2006; Kindberg et al. 2009). During the first week of the moose hunt in September and October, moose hunters record all observations of brown bear, generating an index

(observations per 1000 h) covering almost all of Sweden. The bear observation index is based on about 2.5 million observation hours and around 1000 bear observations annually.

ANALYSIS

Harvest model

We conducted two analyses to meet two distinct objectives. Our first objective was to estimate long-term effects of predators on the average harvest of reindeer in Sweden. To meet this objective, we analyzed the 13-year averages of the number of reindeer harvested in relation to 13-year averages in predator abundance across 51 reindeer management units. We used the following simple Bayesian model:

$$\mu_i = b_0 + b_1 R_i + b_2 L_i + b_3 W_i + b_4 B_i + b_5 G_i \quad (1)$$

$$\Pr(\mathbf{b}, \sigma \,|\, \mathbf{h})$$

$$\propto \prod_{i=1}^{51} \text{lognormal}[\bar{h}_i \,|\, \log(\mu_i), \sigma] \quad (2)$$

$$\times \prod_{j=0}^{5} \text{normal}(b_j \,|\, 0, 10^{-8}) \text{gamma}(\sigma^{-2} \,|\, 0.0001, 0.0001)$$

where $\mathbf{b}$ is a six-element vector of regression coefficients, σ is the standard deviation of the estimate on the log scale, and $\mathbf{h}$ is a 51-element vector of mean harvest, averaged over 13 years. The subscript i indexes reindeer management units ($i = 1 \ldots 51$). Thus, the $\bar{h}_i$ is the 13-year mean harvest for management unit i, excluding rare missing values, and μ_i is the model prediction of the median of the distribution of the average harvest. Independent variables are 13-year means for the total number of reindeer (R_i), the number of lynx family groups (L_i), the number of wolverine reproductions (W_i), and the bear index (B_i). The predictor G_i is the latitude at the centroid of the management unit (converted to a continuous number of kilometers from Swedish National Grid; RT90). We included a north–south gradient as an explanatory variable to account for latitudinal differences in climate and primary production (Lundqvist et al. 2009). This gradient was centered on 0 by subtracting the mean latitude from all observations. We used a lognormal likelihood function for the probability of the data conditional on the model parameters because the observations of harvest were strictly positive and were right-skewed. Prior distributions were chosen to be uninformative.

We analyzed the model (Eq. 2) in three ways: (1) with untransformed data, (2) with predator abundance indices converted to density indices by dividing the abundance indices by the area of year-round pasture in each management unit, and (3) with standardized independent variables. We chose the area of year-round pastures as a basis for estimating density indices because winter pastures are not used every year. The year-round

pastures averaged 45% ± 4% (mean ± SE) of the total area of the reindeer management units. The total areas of management units were positively correlated with areas of year-round pastures ($n = 51$ units, $r = 0.32$, $P = 0.02$). Independent variables were standardized by subtracting their means and dividing by their standard deviations to allow comparison of the magnitude of the effects of regression coefficients (Gelman and Hill 2009).

The regression coefficients in Eq. 1 are interpreted as follows. Because the north–south gradient was centered on 0, the intercept is the offset in production that occurs at the average latitude of the management areas. The coefficient b_1 is the number of reindeer harvested per reindeer. The predation coefficients (b_2, b_3, b_4) give the change in average reindeer harvest per unit change in predator abundance, and b_5 gives the change in reindeer harvest per kilometer of latitude along the north–south gradient. When coefficients were standardized, they represent the change in harvest per 1 SD change in an independent variable.

Population model

Our second objective was to evaluate the effects of predation on reindeer population growth relative to effects of density, weather, and latitude. To meet this objective, we portrayed reindeer population growth for each management area using a Bayesian, state-space model:

$$\log(\lambda_{i,t})$$

$$= (B_0 + B_1 L_{i,t} + B_2 W_{i,t} + B_3 G_i + B_4 O_t + B_5 O_t)\Delta t \quad (3)$$

$$\eta_{i,t} = \lambda_{i,t} N_{i,t-1} - h_{i,t} \quad (4)$$

$$\Pr(\mathbf{N}, \mathbf{B}, \sigma \,|\, \mathbf{y}, \mathbf{h}, \mathbf{X})$$

$$\propto \prod_{i=1}^{41} \prod_{t=1}^{13} \text{Poisson}(y_{i,t} \,|\, N_{i,t})$$

$$\times N_{i,1} \prod_{i=1}^{41} \prod_{t=2}^{13} \text{lognormal}[N_{i,t} \,|\, \log(\eta_{i,t}), \sigma]$$

$$\times \text{gamma}(N_{i,1} \,|\, 0.001, 0.001) \prod_{j=0}^{5} \text{normal}(B_j \,|\, 0, 10^{-6})$$

$$\times \text{gamma}(\sigma^{-2} \,|\, 0.001, 0.001). \quad (5)$$

Forty-one management units had complete data for covariates for at least 14 years. For each management unit (indexed by i) and each year (indexed by t), $y_{i,t}$ is the observed number of reindeer post-harvest, $h_{i,t}$ is the observed number of animals harvested, $N_{i,t}$ is the unobserved, true number of reindeer; $\eta_{i,t}$ is the deterministic estimate of the median of the distribution of $N_{i,t}$ and σ is the process standard deviation on the log scale, representing all of the influences on the true population size that are not represented in the deterministic model (Eq. 3). The coefficient B_0 estimates the

intrinsic rate of increase (r_{max}, time^{-1}) and the other coefficients give the change in the rate of population growth per unit change in a covariate. Covariates used to model $\lambda_{i,t}$ (represented collectively as the matrix **X**) were $L_{i,t}$, the number of lynx family groups influencing reindeer population growth during $t - 1 \rightarrow t$; $W_{i,t}$, the number of wolverine reproductions influencing reindeer population growth during $t - 1 \rightarrow t$; $G_{i,t}$, the latitude of the centroid of the management unit (in kilometers), $D_{i,t}$, the observed density of reindeer on year-round pasture (per 100 km^2); and $O_{i,t}$, the index of North Atlantic Oscillation (NAO). Normal priors on the model coefficients (**B**) and gamma priors on initial conditions ($N_{i,1}$) and σ were uninformative (Eq. 5). As above, we analyzed the model (Eq. 3) in three ways: (1) with untransformed data, (2) with predator-abundance indices converted to density indices by dividing the abundance indices by the area of year-round pasture in each management unit, and (3) with standardized independent variables.

Estimation

Posterior distributions of parameters and states (Eqs. 2 and 5) were estimated using Markov chain Monte Carlo (MCMC) methods implemented in JAGS 3.1.0 (Plummer 2003, 2011a) using the rjags package (Plummer 2011b) of the R computing environment (R Development Core Team 2011). To promote convergence, nonstandardized observations were centered by subtracting their means and estimates of the intercepts were recovered to their non-centered values (McCarthy 2007). Four chains were computed for each parameter with initial values chosen to be diffuse relative to posterior distributions (Brooks and Gelman 1997). After discarding the first 10 000 iterations, we accumulated 25 000 samples from each chain. Convergence was assured by visual inspection of trace plots to assure stationarity and homogeneous mixing, and by the diagnostics of Gelman (Brooks and Gelman 1988, 1997) and Heidelberger (Heidelberger and Welch 1983) implemented in the coda package (Plummer et al. 2010) in R. Autocorrelation function plots were observed to assure autocorrelation in chains was 0 by lag 10.

Model evaluation

Posterior predictive checks.—The most basic approach to checking the fit of a model is to compare replicated data sets simulated from the model to the data that were used to estimate the model's parameters (Gelman et al. 2004, Gelman and Hill 2009). The failure of the distribution of simulated data to mimic the distribution of the real data is diagnostic of structural deficiencies in the deterministic core of the model and/or problems in the choices of probability distributions used to represent stochasticity. To evaluate model fit, we used posterior predictive checks (Gelman et al. 2004, Gelman and Hill 2009). Posterior predictive checks use a test statistic calculated from the observed data (T^{obs}) and from

replicated data sets simulated from the posterior predictive distribution (T^{rep}). To test for lack of fit, we calculate the Bayesian P value, P_B, defined as the probability that the simulated data are more extreme than the observed data (Gelman et al. 2004):

$$P_B = \Pr[T^{rep}(y^{rep}, \theta) \geq T^{obs}(y, \theta) \,|\, y] \tag{6}$$

where θ is the vector of the parameters in the model. Eq. 6 is a two-tailed probability, which means a model shows lack of fit if P_B is close to 0 or 1 (Gelman et al. 2004). For the harvest model, we used the test statistics

$$T^{obs} = \sum_{i=1}^{51} \frac{(\bar{h}_i - \mu_i)^2}{\mu_i} \qquad T^{rep} = \sum_{i=1}^{51} \frac{(\bar{h}_i^{rep} - \mu_i)^2}{\mu_i} \tag{7}$$

where the 51-element vector $\mathbf{h}^{rep}$ is drawn from the posterior predictive distribution and other parameters are as defined above (Eq. 2). For the population model, we used

$$T^{obs} = \sum_{i=1}^{41} \sum_{t=1}^{13} \frac{\left(\dfrac{y_{i,t}}{y_{i,t-1}} - \lambda_{i,t}\right)^2}{\lambda_{i,t}}$$

$$T^{rep} = \sum_{i=1}^{41} \sum_{t=1}^{13} \frac{\left(\dfrac{y_{i,t}^{rep}}{y_{i,t-1}} - \lambda_{i,t}\right)^2}{\lambda_{i,t}}. \tag{8}$$

Consequences of observation uncertainty in predator indices.—Data were not available to assess sampling error or bias in estimates of indices of predator abundance. However, we can be sure that there is some uncertainty in the predator predictor variables. To assess the consequences of this uncertainty, we conducted simulations for all predator coefficients for which the upper 95% credible interval was <0. We assumed observation standard deviations (σ_{obs}) equaled the index value (x_{obs}) multiplied by coefficients of variation ranging from 0.1 to 1.0 and that the true value of the predictor (x_{true}) was distributed as

$$x_{true} \sim \text{gamma}\left(\frac{x_{obs}^2}{\sigma_{obs}^2}, \ \frac{x_{obs}}{\sigma_{obs}^2}\right). \tag{9}$$

For each coefficient of variation and corresponding value of σ_{obs}, we estimated the probability that the predation coefficient value was less than zero using the empirical cumulative distribution of the converged MCMC chains. This allowed us to examine if conclusions on predator effects were robust to assumptions on observation uncertainty.

Why we avoided model selection

We chose to avoid model selection in our analysis for philosophical and operational reasons. Our choice was motivated philosophically by Gelman and Rubin (1995), Clark (2007), and Knape and de Valpine (2011) who argued that, under many circumstances, objectives for insight from the model, rather than the use of model selection statistics, should guide the choice of model
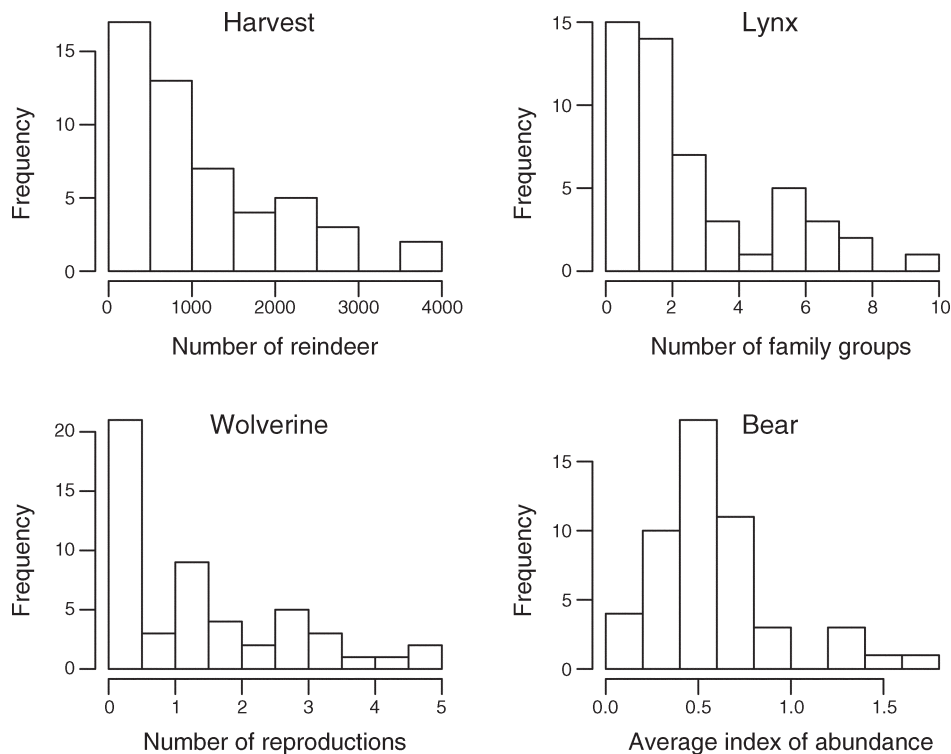
Fig. 2. Frequency distributions of observations of average annual reindeer harvest and indices of predator abundance for the 51 reindeer management areas in Sweden. Categories are means of 13 years of observations. The calculation of the bear index is explained in the text (see *Analysis: Harvest model*).

structure. We can reasonably decide a priori to include a parameter in a model if there is a firmly established biological mechanism that stands behind the operation of the parameter and if the objective of the modeling is to estimate the parameter's value and to evaluate its importance relative to other mechanistic parameters.

Our choice was motivated operationally by the subjectivity that is required by current methods for estimating model weights. There is substantial ambiguity in the statistical literature on how to select best models from a set of candidates (reviewed by Kadane and Lazat 2004). Different approaches to multi-model inference can lead to dramatically different conclusions (Link and Barker 2006, 2010). Moreover, all current methods are sensitive to the choice of the assumed prior distribution of model weights and to the choice of shape parameters in vague priors (Royle and Dorazio 2008, Link and Barker 2010), a problem that is not avoided in the likelihood framework (Link and Barker 2006). Widely used information-theoretic methods do not solve the problem of model over-fitting when many covariates are considered (Knape and de Valpine 2011). Rather than choosing subjectively among model-selection methods and priors on model weights, we chose to use full but relatively simple models with well-established, biological foundations. We chose to examine main effects alone, without considering interactions. Adding interactions among

predictors would dramatically expand the number of parameters to be estimated. Our choice to use a single model for inference means that the inferences we offer are conditional on the model we analyzed.

To assess the relative importance of model coefficients, we compared standardized coefficients (Gelman and Hill 2009) and examined overlap of their posterior distributions with 0. Coefficients that broadly overlapped 0 were considered unimportant to the process being modeled (e.g., Mysterud et al. 2008).

Results

Frequency distributions of observations of average annual harvest and predator abundance were strongly skewed (Fig. 2) such that most observations were smaller than the mean, justifying the use of lognormal distributions for likelihoods.

Posterior predictive checks showed that the harvest model (Eq. 2) and the population model (Eq. 5) were able to simulate data that were consistent with the observations (Fig. 3).

Harvest model

Regressions based on predator abundance (Table 1, Fig. 4) revealed that the average number of reindeer harvested annually from a management unit was 25% of the average population size ($b_1 = 0.25$, 95% credible
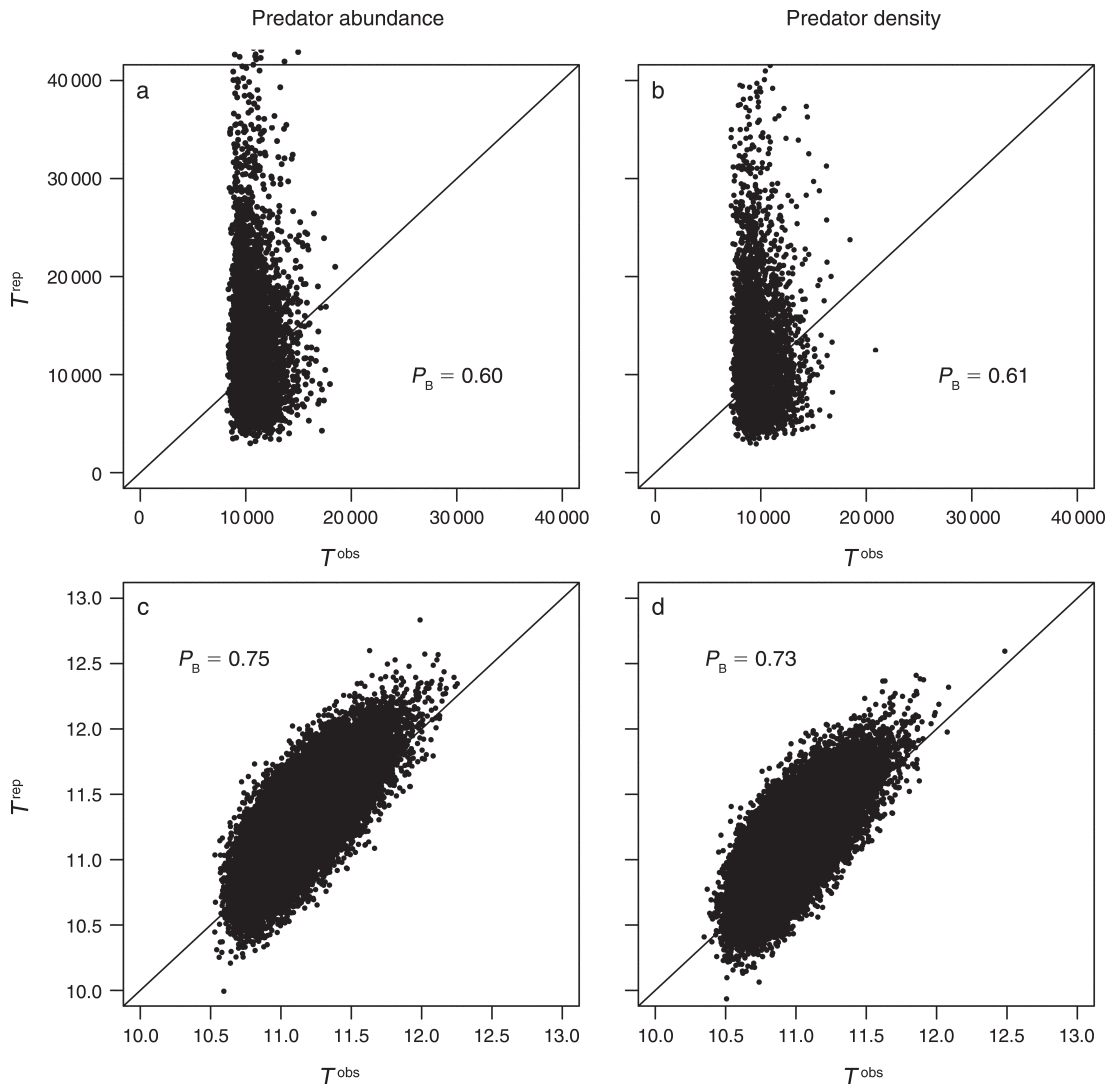
FIG. 3.   Posterior predictive checks of (a, b) the harvest regression model and (c, d) the population model using predator abundance (left column) and density (right column) for covariates. Test statistics calculated from the observed (T^{obs}) data plotted against replicated (T^{rep}) test statistics calculated from simulated data bracket a line with intercept 0 and slope = 1, indicating adequate model fit. The proportion of points above the line give Bayesian P values (P_B). Values of P_B near 1 or 0 indicate lack of fit.

interval (CI) = 0.19, 0.31). Estimates of regression coefficients (predation coefficients b_2, b_3, b_4) representing the change in harvest resulting from predation showed that the annual, average harvest in a management unit was reduced by almost 100 reindeer per lynx family group ($b_2 = -96.6$, 95% CI = -155, -31) and by almost 100 reindeer per wolverine reproduction ($b_4 = -94.3$, 95% CI $= -160$, -20.3). This corresponds to an annual reduction in harvest by about 15 reindeer per lynx and 15 reindeer per wolverine because, on average, a lynx family group represents 6.1 lynx, and a wolverine reproduction represents 6.4 wolverines. Effects of brown bear on reindeer harvest were not evident; CIs broadly spanned 0.

Reindeer harvest was reduced at northern latitudes relative to southern ones by about two reindeer per

kilometer along the north–south gradient. Estimates of effects of predation based on predator density (indices/ area of year-round pasture) were consistent with those based on abundance (Table 1).

Comparisons of standardized regression coefficients (Table 1) showed that variation in reindeer population size had the greatest impact on reindeer harvest among the variables studied and that variation in latitude had roughly half the effect of variation in reindeer numbers. Increases in lynx abundance exerted effects on growth rate that were about 1/3 of the effect of reindeer population size, and the effect of variation in wolverine abundance was about half as large as the effect of lynx. Effects of brown bear were minor relative to the other predators.

TABLE 1. Estimates of parameters in harvest models (Eq. 2), including the upper and lower bounds of a 95% credible interval (CI).

Coefficient	Mean	SD	2.5% CI	97.5% CI
Abundance model†				
Intercept	198	89	21.2	373
Reindeer number	0.25	0.0303	0.191	0.311
Lynx index	−96.6	31.1	−155	−30.6
Wolverine index	−94.3	35.6	−160	−20.3
Bear index	47.2	86.4	−96.8	240
Latitude	−2.33	0.362	−3.03	−1.6
Density model‡				
Intercept	401	113	180	628
Reindeer number	0.178	0.0224	0.136	0.224
Lynx index/area	−732	241	−1190	−232
Wolverine index/area	−1450	662	−2680	−28.6
Bear index/area	−100	647	−1220	1320
Latitude	−2.68	0.401	−3.5	−1.89
Standardized model§				
Intercept	1030	69.8	900	1170
Reindeer	753	92.3	577	939
Lynx	−232	74.3	−368	−77
Wolverine	−132	49.6	−226	−31
Bear	16.3	29.8	−33.3	84
Latitude	−443	69.1	−574	−300

Notes: The 95% CI estimates the interval between the 0.025 and 0.975 quantiles of the posterior distribution. Reindeer number is the annual count of reindeer in a reindeer management unit. Interpretations of coefficients in each model are given in *Analysis: Harvest model.*

† The independent variables for predators in the abundance model are unadjusted indices of numbers of predators in a reindeer management unit; the density model uses abundance indices per 100 km^2 of year-round pastures; and the standardized model uses standardized predictors [i.e., $(x_i - \mu)/\sigma$].

‡ The density model uses abundance indices per 100 km^2 of year-round pastures.

§ The standardized models uses standardized predictors [i.e., $(x_i - \mu)/\sigma$].

Population model

We estimated the intrinsic rate of increase of reindeer populations was 0.35 reindeer/yr (95% CI = 0.32, 0.38; Table 2, Fig. 5). On average, an increase of one lynx family group in a management area reduced the rate of population growth by 0.0079 yr^{-1} (95% CI = −0.014, −0.0017) and an increase of one wolverine reproduction in a reindeer management unit reduced the rate of growth by 0.015 yr^{-1} (95% CI = −0.023, −068). We observed similar effects of predators on reindeer population growth when predator abundance was expressed as density rather than number per management unit (Table 2). Comparisons of regression coefficients for standardized data showed that the effect of latitude was roughly 4–5 times stronger than individual effects of predation, density, or NAO (North Atlantic Oscillation), and that individual effects of predators, density dependence, and the NAO were similar.

Simulations of observation uncertainty

We found that predation by lynx and wolverine reduced reindeer harvest and population growth rate. However, this result depends on the unrealistic assumption that indices of predator abundance reflect the true abundance without uncertainty. Simulations revealed that our overall conclusion on predator effects was robust to unbiased observation uncertainty that might arise, for example, from sampling error (Fig. 6). Even when assumed coefficients of variation for predator indices approached 1, there was substantial weight of evidence in the posterior distribution of coefficients supporting the conclusion that predators reduce harvest and retard population growth (Fig. 6).

DISCUSSION

Predation effects on long-term harvest

Using a large-scale database and Bayesian regression, we demonstrated a depressing effect of predators on reindeer harvest and population growth rate in Sweden. Analysis revealed that average annual harvest per reindeer management unit was reduced by 97 reindeer per surveyed lynx family group. This reduction in harvest is somewhat lower than what would be expected based on kill rate by lynx based on radio telemetry studies, assuming that predation is largely additive to other sources of mortality (Mattisson et al. 2011*b*). In our analysis, we used lynx family groups as an index of the total number of lynx in a management area. On average, a lynx family group during the winter survey also represents the presence of males and single females (Andrén et al. 2002). Furthermore, lynx kill rate on reindeer varies due to seasonal variation in reindeer density and density of alternative prey (Sunde et al. 2000, Mattisson et al. 2011*b*). Thus, there were factors
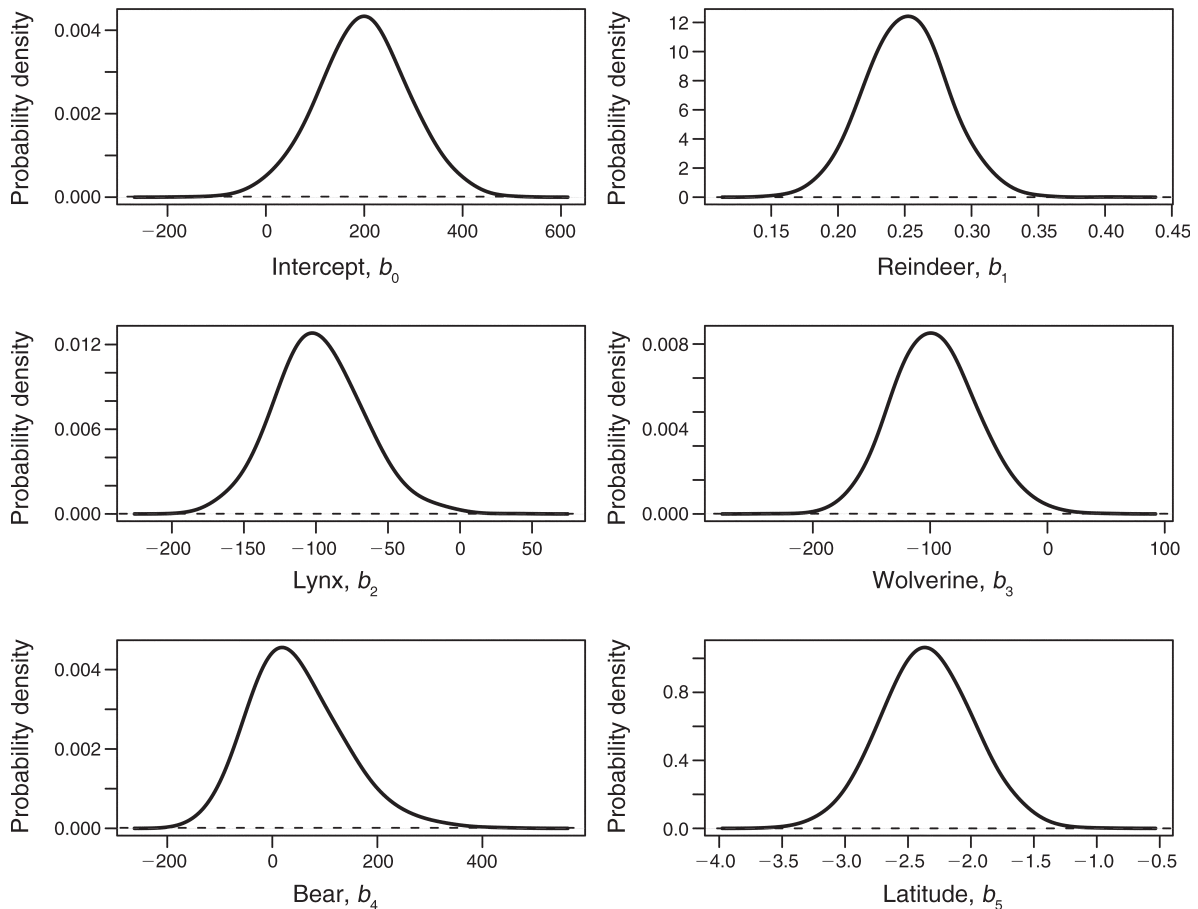
FIG. 4. Harvest model results. Posterior (solid line) and prior (dashed line) distributions of coefficients in the harvest regression model (Eq. 1) using unstandardized covariates. The intercept (b_0) is the offset in production that occurs at the average latitude of the management areas. The coefficient for reindeer (b_1) is the number of reindeer harvested per reindeer. Coefficients for the predation covariates, lynx (b_2), wolverine (b_3), and bear (b_4), give the change in average reindeer harvest per unit change in predator abundance and latitude(s) gives the change in average reindeer harvest per kilometer of latitude along the north–south gradient.

influencing kill rate that were not possible to take into account in our large-scale study.

Given a mean abundance of lynx family groups per management area (2.53 groups) and mean population size of reindeer (4701 animals), we estimate that herders at the average latitude could harvest 247 fewer reindeer as a consequence of lynx predation alone or 82% of what could be harvested if there were no lynx. However, estimates based on averages may offer an overly optimistic view of effects of predation on reindeer production because distributions of the number of reindeer in a management unit and the number of lynx family groups are highly skewed (Fig. 2). The data and model imply the greatest impacts of lynx predation on reindeer harvest when lynx abundance is high and when the population size of reindeer is low. In these cases, our analyses show that the reduction in harvest resulting from lynx predation can be disproportionately greater than would be predicted from average lynx and reindeer abundance (Fig. 7). Assuming average lynx numbers and below-average reindeer numbers, harvest in the

presence of lynx could reasonably be expected to range between 50% and 80% of harvest from predator-free herds (Fig. 7). However, if lynx abundance is above average (i.e., at the 75% quantile of the data = 3.87 surveyed lynx family groups per management unit), then harvest from reindeer management units with less than the average herd size is expected to fall between 20% and 70% of the predator-free harvest (Fig. 7). These results show that levels of lynx abundance well within the range of the observed data could cause dramatic reductions in harvest from reindeer populations and that the magnitude of these reductions is amplified when reindeer populations are small. We caution, however, that the highest posterior density intervals on all of these estimates are broad (Fig. 7). Hence, we cannot rule out effects of predation on harvest that could be substantially smaller or substantially greater than the mean estimates.

Kill rates of reindeer by wolverine have not been estimated directly from field data. However, using radio telemetry observations, Mattisson et al. (2011a) estimat-

TABLE 2.   Estimates of parameters in population models (Eq. 5).

Coefficient	Mean	SD	2.5% CI	97.5% CI
Abundance model†				
Intercept	0.35	0.017	0.317	0.384
Lynx index	−0.00777	0.00316	−0.0139	−0.0016
Wolverine index	−0.0149	0.00412	−0.023	−0.00687
Latitude	−0.0000591	4.34×10^{-5}	−0.000676	−0.000506
Reindeer density	−0.000229	7.31×10^{-5}	−0.000374	-8.82×10^{-5}
NAO	−0.0114	0.00478	−0.0207	−0.00204
Density model‡				
Intercept	0.349	0.0169	0.316	0.382
Lynx index/area	−0.109	0.029	−0.165	−0.0527
Wolverine index/area	−0.361	0.0826	−0.523	−0.2
Latitude	−0.000661	4.40×10^{-5}	−0.000749	−0.000575
Reindeer density	−0.000224	6.95×10^{-5}	−0.000361	-8.67×10^{-5}
NAO	−0.0111	0.00476	−0.0201	−0.00169
Standardized model§				
Intercept	0.253	0.00697	0.239	0.266
Lynx	−0.0208	0.0083	−0.037	−0.00425
Wolverine	−0.0267	0.00739	−0.041	−0.0123
Latitude	−0.11	0.00811	−0.126	−0.0939
Reindeer	−0.0263	0.00848	−0.0428	−0.00955
NAO	−0.0207	0.00869	−0.0379	−0.00343

Notes: Reindeer density is the annual count of reindeer in a reindeer management unit per 100 km^2 of year-round pastures. Interpretations of coefficients in each model are given in *Analysis: Population model.*

† The independent variables for predators in the abundance model are unadjusted indices of numbers of predators in a reindeer management unit.

‡ The density model uses abundance indices per 100 km^2 of year-round pastures.

§ The standardized model uses standardized indices of numbers of predators in a reindeer management unit (i.e., $[x_i - \mu]/\sigma$).

ed that kill rates of reindeer by lynx were much higher than kill rates of reindeer by wolverine, a finding at odds with our result that the average number of reindeer killed per surveyed lynx family group is approximately the same as the number killed per surveyed wolverine reproduction. The wolverine kill rate was from an area where lynx and wolverine coexist. Wolverines frequently scavenge reindeer killed by lynx (Mattisson et al. 2011*a*), so the expected kill rate of reindeer by wolverines is higher in areas without lynx (Andrén et al. 2011). Moreover, the 97.5% quantile of the posterior distribution of the ratio of lynx/wolverine kill rates was 4.42, which is more in line with the field estimate. We observed the same nonlinearities in effects of wolverine on reductions in reindeer harvest as we observed for lynx (Fig. 7). Again, effects of predation were disproportionately great when wolverine abundance was above average and reindeer population size was below average.

Comparisons of standardized coefficients suggested that variation in reindeer numbers and variation along a latitudinal gradient exerted much stronger effects on average annual harvest than variation in predator abundance.

Role of predation in limiting population growth

Our estimates of the intrinsic rate of increase of reindeer ($r_{max} = 0.35$, 95% CI = 0.31, 0.38) agreed closely with estimates based on allometric scaling for ungulates. Assuming an average approximate reindeer body mass

(M) of 80 kg (averaged across all age and sex classes), predicted r_{max} for reindeer is $1.37M^{-.31} = 0.35$ (Sinclair 2003).

Results from the state-space model reinforced the conclusions of the regression model and provided a mechanistic explanation for diminished harvest in reindeer management units where lynx and wolverine were abundant. Parameter estimates from the state-space model suggest that predators caused meaningful reductions in the annual increment in reindeer population size that, in turn, reduced the harvestable surplus. It is possible that our findings of effects of predators on population growth and harvest depend on our implicit assumption that predation does not compensate for other sources of mortality that might result, for example, from density-dependent feedbacks. If predation partially substitutes for density-dependent mortality, then predation effects may be overestimated. However, we reduced this possibility by including a separate term for density dependence in the population model.

Realized rates of increase in reindeer populations were shaped by a composite of forces, including density dependence, predation, weather, and latitude. Standardized regression coefficients revealed roughly equivalent effects of predation, density, and winter weather (indexed by the North Atlantic Oscillation, NAO). Changes in latitude exerted effects that were 4–5 times as great as predation, density, or weather. We suggest
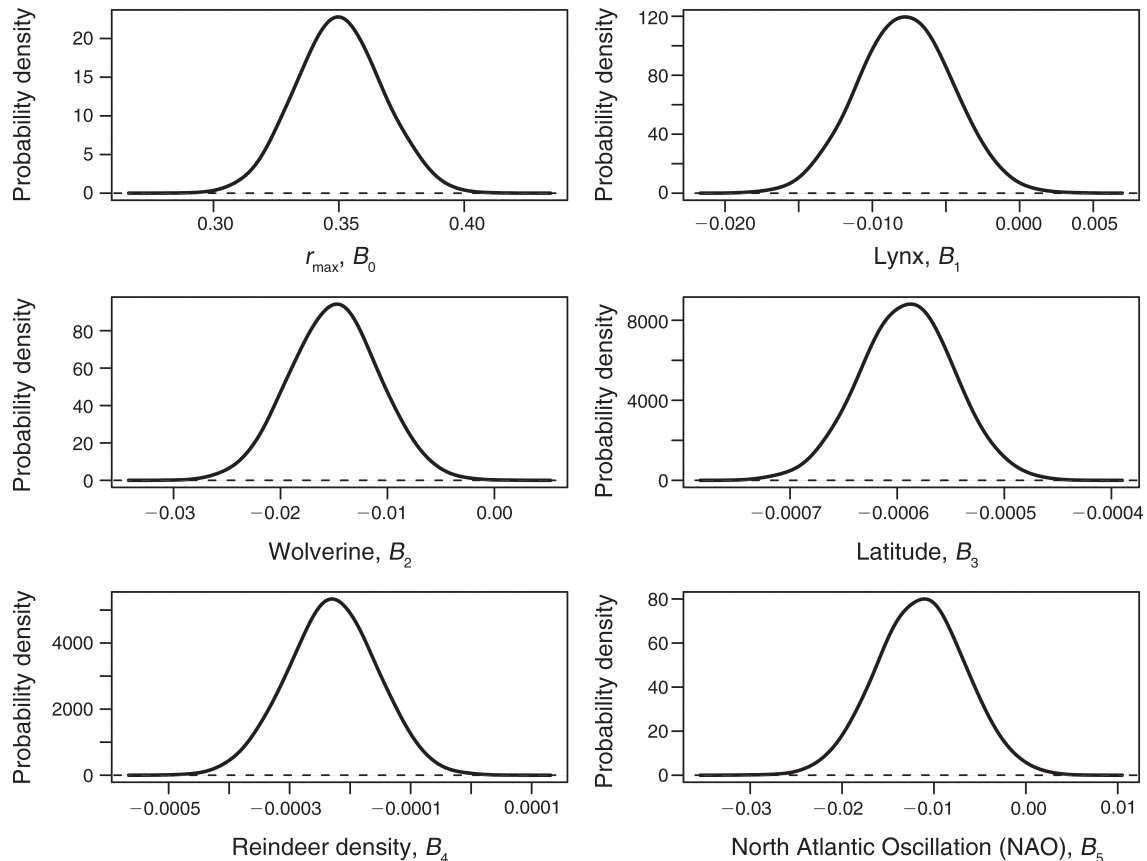
FIG. 5. Population model results. Posterior (solid line) and prior (dashed line) distributions of coefficients in the population model (Eq. 3) using unstandardized covariates. The intrinsic rate of increase (r_{max}, time^{-1}) of population growth per unit change in a covariate is estimated by the intercept (B_0), and the other coefficients give the change in the rate of population growth per unit change in a covariate. Covariates and their coefficients were lynx (B_1), the number of lynx family groups influencing reindeer population growth during $t - 1 \rightarrow t$; wolverine (B_2), the number of wolverine reproductions influencing reindeer population growth during $t - 1 \rightarrow t$; latitude (B_3), the latitude of the centroid of the management unit (in kilometers); reindeer (B_4), the density of reindeer on year-round pasture (per 100 km^2); and the index of North Atlantic Oscillation (B_5).

that the particularly strong effects of latitude resulted in part from increasing weather severity and diminished primary productivity at northern latitudes. However, there also may be an effect of differences in husbandry. Management units at the southern end of the gradient tended to have larger proportions of adult females in the population (linear regression, $P = 0.0001$, $r^2 = 0.25$). This is likely a reflection of differences in harvesting practices that favor maintaining more adult males in the northern populations, which would reduce rates of increase.

Findings on responses of ungulate populations to effects of winter weather indexed by the NAO have been inconsistent (Post and Stenseth 1999, Grotan et al. 2005, 2008, Weladji and Holand 2006). Body condition, fecundity, and reproductive rate have shown both positive and negative relationships to NAO, suggesting that under some circumstances warm, wet winters are favorable to animals, producing a positive correlation with NAO, while in others cold dry winters are favorable, producing a negative relationship similar to

the one we observed. Although these conflicting observations have been explained by differences between maritime and mainland climates, inconsistencies remain (e.g., compare Grotan et al. 2005, Weladji and Holand 2006) that may result from the inability of time-series data to resolve causal effects of weather on population dynamics (Knape and de Valpine 2011).

Our work adds to a growing body of evidence (e.g., Skogland 1990, Aanes et al. 2000, Coulson et al. 2000, Owen-Smith and Mills 2006, Wang et al. 2006, 2009, Melis et al. 2009) that population dynamics of large herbivores respond to multiple forces, including intrinsic effects of density-dependent competition for resources and extrinsic effects of weather and predation. We show that density dependence, predation, and weather were implicated as controls on population growth rate of reindeer and that these influences were roughly equal in strength. In particular, our findings resemble those of Jacobson et al. (2004) who found evidence for density dependence in populations of mountain sheep that were harvested and preyed upon. It is sometimes said that

populations that are routinely harvested should not show effects of density on population growth rate because they are maintained well below the carrying capacity of the environment. However, if feedbacks from population density to per capita population growth rate are approximately linear (as is the assumption in logistic population growth), then we would expect that effects on per capita growth rate would be observable at all densities.

In contrast to our observations, others have failed to see effects of density dependence in ungulates in the far north, particularly in populations exposed to predation (Aanes et al. 2000). It is becoming clear that the spatial context can modify the effects of predation and density dependence on ungulate population dynamics (Post 2005). Our results reinforce the findings of Lundqvist et al. (2009) who showed that relatively fine-scale differences in latitude can exert strong effects on the productivity of reindeer. These effects of spatial context appear to result from multiple influences including spatial variation in primary production, weather, and differences in husbandry.

Implications for future work

A weakness of our work is the assumption that abundance of predators is estimated without error, although our fundamental conclusion about effects of predators appeared to be robust to this assumption (Fig. 6). Nonetheless, substantial improvements could be made in our ability to estimate and forecast effects of predators on reindeer by including uncertainty in these estimates. We strongly urge the development of statistically rigorous methods for estimating predator abundance, methods that would allow a proper observation model for the predator data. Similarly, estimates of reindeer numbers could be enhanced by methods that would allow assessment of variance in observations and potential bias in census.

For example, given that animals are handled a few times per year, it would be relatively easy to implement a mark–recapture design to estimate total numbers and vital rates. These data would enable development of age- and sex-structured models, which we believe are particularly needed given our observation that variation in husbandry practices, mediated through demography, may be at least partially responsible for variation in harvest along the north–south gradient. Age-structured models are needed to better explain the operation of density dependence (Bonenfant et al. 2009). In earlier work we attempted to develop these models, but the absence of data on the sex composition of the calf harvest proved to be an impediment that could not be overcome because the proportion of calves in the harvest could trade-off with the unobserved parameter of calf survival, making these parameters inestimable. Adding observations of the sex ratio of the calf harvest to the reindeer database could markedly enhance future
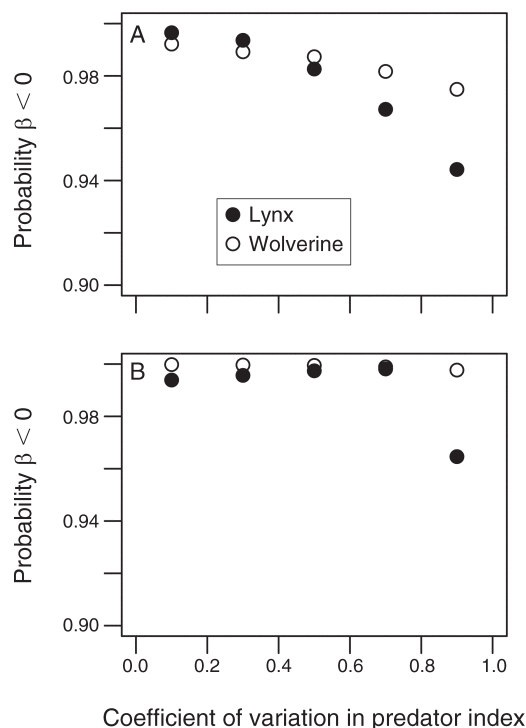

FIG. 6.   Simulations of effects of observation error on the conclusion that lynx and wolverine (A) reduce harvest and (B) retard population growth. The x-axis is the assumed coefficient of variation in predator indices resulting from observation uncertainty. The y-axis is the proportion of estimates in the MCMC chain for which the estimate of the predation coefficient, β, is less than zero, indicating a depressing effect of predators on harvest or population growth.

models of predator impacts with virtually no added expense for sampling.

Implications for policy

Throughout Scandinavia, there are conflicting goals for sustaining the pastoral livelihoods of indigenous people while restoring and conserving native predators that prey on reindeer. This conflict is reconciled by environmental policy in Sweden (SOU 1999) that provides monetary compensation to Sámi pastoralists to offset losses of productivity of reindeer resulting from effects of native predators. Owners of predator-killed livestock are usually compensated based on documented losses (ex post facto compensation; Schwerdtner and Gruber 2007), whereas the Swedish system is based on risk. In a risk-based compensation the reindeer herders can focus on reindeer husbandry, instead of searching for predator-killed reindeer. There is also an incentive for reindeer owners to invest in mitigation measures to reduce losses, e.g., keeping reindeer females in enclosures during calving and a few weeks thereafter. A risk-based compensation scheme excludes the need to directly observe predator kills, but nonetheless requires defensible estimates of damage.
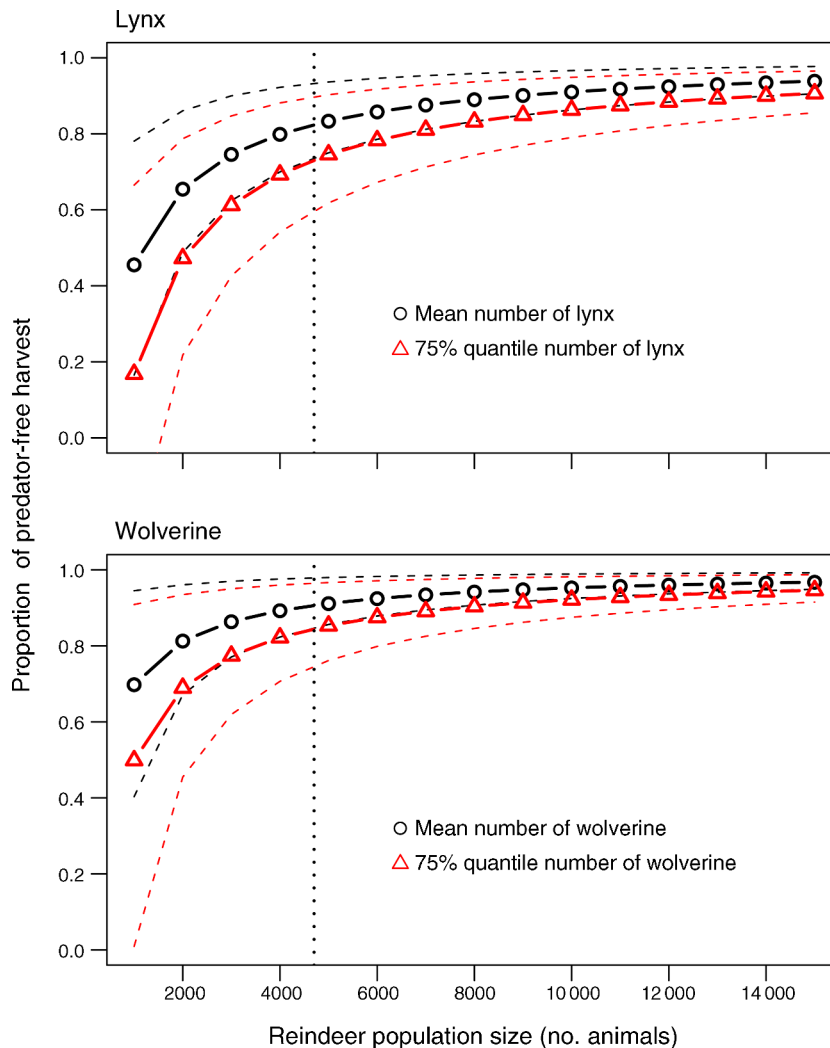
FIG. 7. Model predictions of the proportional change in harvest attributable to lynx and wolverine predation as a function of reindeer population size. Two levels of predator abundance were used in predictions, the mean level and the upper 75% quantile. Dashed lines give 95% credible intervals (i.e., the 95% highest posterior density intervals) on model predictions. The vertical dotted line indicates the mean reindeer population size.

Heretofore, the Swedish risk-based system was not based on quantified effects of predators on reindeer, and as a result, could be criticized as an unjustified subsidy. Mattisson et al. (2011*a*) used individual lynx kill-rate on reindeer as an estimate of losses that could be used for setting compensation levels. We offer evidence that native predators meaningfully reduce the number of reindeer that could be harvested relative to harvests that would occur in the absence of predators. However, we also show that although the absolute impacts of predation on reindeer harvest are proportionate to predator abundance in a reindeer management unit, the relative impacts are disproportionate. Proportional reductions in potential harvests within management units were relatively small where reindeer populations were large (Fig. 7), while these reductions were large when reindeer populations within a management unit were small.

In conclusion, we provide evidence that native predators reduce harvest of reindeer by Sámi pastoralists by reducing reindeer population growth rate. This evidence provides a biological justification for Sweden's risk-based compensation policy.

LITERATURE CITED

Aanes, R., B. E. Sæther, and N. A. Oritsland. 2000. Fluctuations of an introduced population of Svalbard

reindeer: the effects of density dependence and climatic variation. Ecography 23:437–443.

Andrén, H., J. D. C. Linnell, O. Liberg, P. Ahlqvist, R. Andersen, A. Danell, R. Franzen, T. Kvam, J. Odden, and P. Segerstrom. 2002. Estimating total lynx *Lynx lynx* population size from censuses of family groups. Wildlife Biology 8:299–306.

Andrén, H., J. Persson, J. Mattisson, and A. C. Danell. 2011. Modelling the combined effect of an obligate predator and a facultative predator on a common prey: lynx and wolverine predation on reindeer. Wildlife Biology 17.

Andrén, H., L. Svensson, O. Liberg, H. Hensel, N. T. Hobbs, and G. Chapron. 2010. The Swedish lynx population 2009–2010 and forecasts for 2011–2012. Survey Report 2010 4, Swedish Wildlife Damage Center. Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, Ridderhyttan, Sweden.

Bjärvall, A., R. Franzén, M. Nordqvist, and G. Ålunan. 1990. Renar och rovdjur. Technical report. [In Swedish.] Tryck-industri, Solna, Sweden.

Bonenfant, C., J. M. Gaillard, T. Coulson, M. Festa-Bianchet, A. Loison, M. Garel, L. E. Loe, P. Blanchard, N. Pettorelli, N. Owen-Smith, J. Du Toit, and P. Duncan. 2009. Empirical evidence of density-dependence in populations of large herbivores. Advances in Ecological Research 41:313–357.

Boyd, C., T. M. Brooks, S. H. M. Butchart, G. J. Edgar, G. A. B. da Fonseca, F. Hawkins, M. Hoffmann, W. Sechrest, S. N. Stuart, and P. P. van Dijk. 2008. Spatial scale and the conservation of threatened species. Conservation Letters 1:37–43.

Brooks, S. P., and A. Gelman. 1988. Alternative methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics 7:434–455.

Brooks, S. P., and A. Gelman. 1997. General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics 7:434–455.

Clark, J. M. 2007. Models for ecological data. Princeton University Press, Princeton, New Jersey, USA.

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

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian data analysis. Chapman and Hall/CRC, London, UK.

Gelman, A., and J. Hill. 2009. Data analysis using regression and multilevel/hierarchical modeling. Cambridge University Press, Cambridge, UK.

Gelman, A., and D. B. Rubin. 1995. Avoiding model selection in Bayesian social research. Sociological Methodology 25:165–173.

Grøtan, V., B. E. Sæther, S. Engen, E. J. Solberg, J. D. C. Linnell, R. Andersen, H. Broseth, and E. Lund. 2005. Climate causes large-scale spatial synchrony in population fluctuations of a temperate herbivore. Ecology 86:1472–1482.

Grøtan, V., B. E. Sæther, F. Filli, and S. Engen. 2008. Effects of climate on population fluctuations of ibex. Global Change Biology 14:218–228.

Grumbine, R. E. 1994. What is ecosystem management? Conservation Biology 8:27–38.

Hebblewhite, M. 2005. Predation by wolves interacts with the North Pacific Oscillation (NPO) on a Western North American elk population. Journal of Animal Ecology 74:226–233.

Heidelberger, P., and P. Welch. 1983. Simulation run length control in the presence of an initial transient. Operations Research 31:1109–1044.

Jacobson, A. R., A. Provenzale, A. Von Hardenberg, B. Bassano, and M. Festa-Bianchet. 2004. Climate forcing and density dependence in a mountain ungulate population. Ecology 85:1598–1610.

Jorner, U., E. Baer, and Ö. Danell. 1999. Reindeer husbandry in Sweden. Technical report. Swedish Statistical Bureau, Stockholm, Sweden.

Kadane, J. B., and N. A. Lazat. 2004. Methods and criteria for model selection. Journal of the American Statistical Association 99:279–209.

Kindberg, J., G. Ericsson, and J. E. Swenson. 2009. Monitoring rare or elusive large mammals using effort-corrected voluntary observers. Biological Conservation 142:159–165.

Knape, J., and P. de Valpine. 2011. Effects of weather and climate on the dynamics of animal population time series. Proceedings of the Royal Society B 278:985–992.

Landa, A. J., R. Tuftø, and J. Persson. 2001. Aktive ynglehi hos jerv som bestandsestimator basert på nye data om alder for første yngling. Technical report, [In Norwegian.] NINA notåt. Norwegian Institute for Nature Research, Trondheim, Norway.

Liddicker, W. Z. 1995. Landscape approaches in mammalian ecology and conservation. University of Minnesota Press, Minneapolis, Minnesota, USA.

Link, W. A., and R. J. Barker. 2006. Model weights and the foundations of multimodel inference. Ecology 87:2626–2635.

Link, W. A., and R. J. Barker. 2010. Bayesian inference with ecological applications. Academic Press, San Diego, California, USA.

Linnell, J. D. C., et al. 2007. Distance rules for minimum counts of Eurasian lynx *Lynx lynx* family groups under different ecological conditions. Wildlife Biology 13:447–455.

Lundqvist, H., L. Norell, and O. Danell. 2009. Relationship between biotic range characteristics and productivity of reindeer husbandry in Sweden. Rangifer 29:1–24.

Mattisson, J., H. Andrén, J. Persson, and P. Segerström. 2011a. The influence of intraguild interactions on resource use by wolverine and Eurasian lynx. Journal of Mammalogy 92:1321–1330.

Mattisson, J., J. Odden, E. B. Nilsen, J. D. C. Linnell, J. Persson, and H. Andrén. 2011b. Factors affecting Eurasian lynx kill rates on semi-domestic reindeer in northern Scandinavia: Can ecological research contribute to the development of a fair compensation system? Biological Conservation 144:3009–3017.

McCarthy, M. A. 2007. Bayesian methods for ecology. Cambridge University Press, Cambridge, UK.

Melis, C., et al. 2009. Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. Global Ecology and Biogeography 18:724–734.

Mysterud, A., N. G. Yoccoz, R. Langvatn, N. Pettorelli, and N. C. Stenseth. 2008. Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. Philosophical Transactions of the Royal Society B 363:2359–2368.

Mysterud, A., N. G. Yoccoz, N. C. Stenseth, and R. Langvatn. 2000. Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. Journal of Animal Ecology 69:959–974.

Naturvårdsverket. 1991. Förslag till nytt ersättningssystem för rovdjursdödade renar. Naturvårdsverket Rapport 3899. Technical report. [In Swedish.] Sjöfartsverket, Norrköping, Sweden.

Nilsson-Dahlström, A. 2003. Negotiating wilderness in a cultural landscape: predators and Saami reindeer herding in the Laponian World Heritage Area. Volume 32 of Uppsala studies in cultural anthropology. Uppsala University Library, Uppsala, Sweden.

Owen-Smith, N., and M. G. L. Mills. 2006. Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. Ecological Monographs 76:73–92.

Persson, J., and H. Brøseth. 2011. The Scandinavian wolverine population – status and distribution 1996–2010. Technical report, NINA Report 732. Norwegian Institute for Nature Research, Trondheim, Norway.

Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In K. Hornik, F. Leisch, and A. Zeileis, editors. DSC Working Papers, Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), 20–23 March 2003, Technische Universität, Wien, Vienna, Austria. http://www.ci.tuwien.ac.at/Conferences/DSC-2003/

Plummer, M. 2011a. JAGS version 3.0.0 user manual. http://sourceforge.net/projects/mcmc-jags/files/Manuals/3.x/jags_user_manual.pdf

Plummer, M. 2011b. rjags: Bayesian graphical models using MCMC. R package version 3.1.0. http://CRAN.R-project.org/package=rjags

Plummer, M., N. Best, K. Cowles, and K. Vines. 2010. coda: Output analysis and diagnostics for MCMC. R package version 0.14-4. http://CRAN.R-project.org/package=coda

Post, E. 2005. Large-scale spatial gradients in herbivore population dynamics. Ecology 86:2320–2328.

Post, E., and N. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80:1322–1339.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations, and communities. Academic Press, London, UK.

Schwerdtner, K., and B. Gruber. 2007. A conceptual framework for damage compensation schemes. Biological Conservation 134:354–360.

Sillero-Zubiri, C., and M. Laurenson. 2001. Interaction between carnivores and local communities: conflict or coexistence? Pages 282–312 in J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. Wayne, editors. Carnivore conservation. Cambridge University Press, London, UK.

Sinclair, A. R. E. 2003. Mammal population regulation, keystone processes and ecosystem dynamics. Philosophical Transactions of the Royal Society of London B 358:1729–1740.

Skogland, T. 1990. Density dependence in a fluctuating wild reindeer herd; maternal vs. offspring effects. Oecologia 84:442–450.

SOU [Statensoffentliga utredningav]. 1999. A coherent predator policy. SOU [Swedish Government technical report] 1999:146. Information Rosenbad, Regeringskansliet, Stockholm, Sweden. http://www.regeringen.se/sontent/1/c4/26/46/1928d026.pdf

Sunde, P., T. Kvam, J. P. Bolstad, and M. Bronndal. 2000. Foraging of lynxes in a managed boreal–alpine environment. Ecography 23:291–298.

Thirgood, W. R. S., and A. Rabinowitz. 2005. The impact of human–widlife conflict on human lives and livelihood. Pages 13–26 in R. Woodroffe, S. Thirgood, and A. Rabinowitz, editors. People and wildlife: Conflict or coexistence? Cambridge University Press, London, UK.

Tjernberg, M., and M. Svensson. 2007. Swedish red data book of vertebrates. Technical report, Swedish Species Information Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Tyler, N. J. C., M. C. Forchhammer, and N. A. Oritsland. 2008. Nonlinear effects of climate and density in the dynamics of a fluctuating population of reindeer. Ecology 89:1675–1686.

Wabakken, P., Å. Aronson, T. Strømseth, H. Sand, E. Maartman, L. Svensson, and I. Kojola. 2009. The wolf in Scandinavia: status report of the 2008–2009 winter. Technical report 4. Hogskilen I Hedmark, Evenstad, Norway.

Wang, G. M., N. T. Hobbs, R. B. Boone, A. W. Illius, I. J. Gordon, J. E. Gross, and K. L. Hamlin. 2006. Spatial and temporal variability modify density dependence in populations of large herbivores. Ecology 87:95–102.

Wang, G. M., N. Hobbs, S. Twombly, R. Boone, A. Illius, I. Gordon, and J. Gross. 2009. Density dependence in northern ungulates: interactions with prédation and resources. Population Ecology 51:123–132.

Weladji, R. B., and O. Holand. 2006. Influences of large-scale climatic variability on reindeer population dynamics: implications for reindeer husbandry in Norway. Climate Research 32:119–127.