

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: Predator-prey, population dynamics, pastoralism, Bayesian hierarchical model, lynx, wolverine, brown bear, density dependence, North Atlantic Oscillation

1 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. However, 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 60 MSEK (about 6 M€ or about 8.6 M\$) in 2008 (Swedish Environmental Protection Agency, unpublished), 29 MSEK (about 2.9 M€ or about 4.1 M\$) of which was paid to offset effects of lynx predation and 20 MSEK (about 2.0 M€ or about 2.9 M\$) was compensation for predation by wolverine. The Swedish scheme for compensation is based 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 200,000 SEK (about 20,000 € or about 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.

No assessment has been done whether this system is “fair”. 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 described above 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 (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; Hebblewhite, 2005; Mysterud et al., 2000; Jacobson et al., 2004; Post, 2005; Owen-Smith and Mills, 2006; Wang et al., 2006; Tyler et al., 2008; Wang et al., 2009). 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). Moreover, 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.

2 Study Area

The reindeer husbandry area covers 230,000 km² of the land area of Sweden, spanning the three northernmost counties, Norrbotten, Västerbotten, Jämtland, as well as parts of Dalarna and Västernorrland counties (Figure).

[Figure 1 about here.]

Semi-domestic reindeer are part of a pastoral production system where reindeer are herded by indigenous Sámi people. The reindeer husbandry area is divided into 51 reindeer management units, most of which (n=33) 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 (Björvall 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

117 between 220,000-260,000 and yearly harvest between 47,000-74,000 during the last 10 years
118 (official data from Swedish Board of Agriculture and Sámi Parliament).

119 Several large predators prey upon semi-domesticated reindeer. Eurasian lynx and wolver-
120 ine are believed to have the greatest impacts on reindeer production. During 2008, lynx
121 accounted for 48% of the compensation paid to pastoralists, while wolverine accounted for
122 33% (Swedish Environmental Protection Agency and Sámi Parliament). Based on surveys of
123 lynx family groups and wolverine reproductions (see Materials, below), the estimated popu-
124 lation size of these predators within the Swedish reindeer husbandry area during the last 10
125 years was 500-900 lynx (Andrén et al., 2010) and 310-650 wolverine (Persson and Brøseth,
126 2011). Brown bear and golden eagle (*Aquila chrysaetos*) are also common. The estimated
127 population sizes within the Swedish Reindeer husbandry area are about 2000 bear individuals
128 (Kindberg et al., 2009) and around 550 pairs of breeding eagles (Tjernberg and Svensson,
129 2007). Current Swedish policy does not allow resident wolf packs in the reindeer husbandry
130 area. Successful enforcement of this policy means that there are only a few individual wolves
131 and no wolf packs present there (Wabakken et al., 2009).

132 **3 Materials**

133 We analyzed observations of reindeer population size, reindeer harvest, and results of predator
134 surveys from 51 reindeer management units in Sweden during 1996 – 2008 (Swedish Board
135 of Agriculture and Sámi Parliament, unpublished). The number of reindeer harvested in
136 each management unit and the post-harvest population size are recorded during September
137 – December each year when reindeer populations are gathered by herders for slaughter. The
138 reindeer data in our analysis are based on these annual records of herd numbers, composition,
139 and harvest as reported by reindeer owners. We used official survey data on lynx and wolverine

140 from the Swedish Environmental Protection Agency and County Administration Boards from
141 1996 to 2009.

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

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

157 The wolverine survey is performed from March to May and is based on documentation
158 of den sites or tracks of females with cubs of the year after den abandonment (Swedish En-
159 vironmental Protection Agency, unpublished). The number of wolverine reproductions in a
160 reindeer-grazing district is assumed to be proportionate to the total population size; on av-
161 erage, there are 6.4 (± 0.8) wolverines in the population for each reproduction (Landa et al.,
162 2001).

163 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 observation 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.

4 Analysis

4.1 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 simple Bayesian model,

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

$$\begin{aligned} \Pr(\mathbf{b}, \sigma | \mathbf{h}) &\propto \prod_{i=1}^{51} \text{lognormal} \left[\bar{h}_i \mid \log(\mu_i), \sigma \right] \times \\ &\quad \prod_{j=0}^5 \text{normal} \left(b_j \mid 0, 10^{-8} \right) \text{gamma} \left(\sigma^{-2} \mid .0001, .0001 \right), \end{aligned} \quad (2)$$

where \mathbf{b} is the 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 ($i=1\dots 51$). 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 lognormally distributed (Fig. 2). Priors were chosen to be uninformative.

We analyzed the model (Equation 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 were on average 45 % (± 4 % S.E.) of the total area of the reindeer management units, and the two measurements were also correlated ($n = 51$, $r = 0.32$, $p = 0.02$). 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 Equation 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_4 gives the change in reindeer harvest per km of latitude along the north-south gradient. When coefficients were standardized, they represent the change in harvest per one standard deviation change in an independent variable.

205 4.2 Population model

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

$$\log(\lambda_{i,t}) = (B_0 + B_1 D_{i,t-1} + B_2 L_{i,t} + B_3 W_{i,t} + B_4 G_i + B_5 O_t) \Delta t \quad (3)$$

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

$$\begin{aligned} \Pr(\mathbf{N}, \mathbf{B}, \sigma \mid \mathbf{y}, \mathbf{h}, \mathbf{X}) &\propto \prod_{i=1}^{41} \prod_{t=1}^{13} \text{Poisson}(y_{i,t} \mid N_{i,t}) \times \\ &N_{i,1} \prod_{i=1}^{41} \prod_{t=2}^{13} \text{lognormal}[N_{i,t} \mid \log(\eta_{i,t}), \sigma] \times \\ &\text{gamma}(N_{i,1} \mid .001, .001) \prod_{j=0}^5 \text{normal}(B_j \mid 0, 10^{-6}) \times \\ &\text{gamma}(\sigma^{-2} \mid .001, .001). \end{aligned} \quad (5)$$

209 Forty one management units had complete data for covariates for at least 14 years. For each
 210 management unit (indexed by i) and each year (indexed by t), $y_{i,t}$ is the observed number
 211 of reindeer unit post-harvest, $h_{i,t}$ is the observed number of animals harvested, $N_{i,t}$ is the
 212 unobserved, true number of reindeer; $\eta_{i,t}$ is the deterministic estimate of the median of the
 213 distribution of $N_{i,t}$ and σ is the process standard deviation on the log scale, representing all
 214 of the influences on the true population size that are not represented in the deterministic
 215 model (Equation 3). The coefficient B_0 estimates the intrinsic rate of increase (r_{max} , time^{-1})
 216 and the other coefficients give the change in the rate of population growth per unit change
 217 in a covariate. Covariates used to model $\lambda_{i,t}$ (represented collectively as the matrix \mathbf{X}) were
 218 $D_{i,t}$, the observed density of reindeer on year-round pasture (100 km^{-2}); $L_{i,t}$, the number of
 219 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 km) and $O_{i,t}$, the index of North Atlantic Oscillation. Normal priors on the model coefficients (\mathbf{B}) and gamma priors on initial conditions ($N_{i,1}$) and σ were uninformative (Equation 5).

4.3 Estimation

Posterior distributions of parameters and states (Equations 2,5) 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, non-standardized 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.

4.4 Model evaluation

4.4.1 Posterior predictive checks

The most basic approach to checking the fit of a model is to compare replicated datasets 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 datasets simulated from the posterior predictive distribution (T^{rep}). To test for lack of fit, we calculate P_B , defined as the probability that the simulated data are more extreme than the observed data (Gelman et al., 2004),

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

where θ is the vector of the parameters in the model. Equation 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:

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

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

$$T^{obs} = \sum_{i=1}^{41} \sum_{t=1}^{13} \frac{(y_{i,t} - N_{i,t})^2}{N_{i,t}}, \quad T^{rep} = \sum_{i=1}^{41} \sum_{t=1}^{13} \frac{(y_{i,t}^{rep} - N_{i,t})^2}{N_{i,t}}.$$

4.4.2 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

260 predator coefficients for which the upper 95% credible interval was < 0 . We assumed obser-
 261 vation standard deviations (σ_{obs}) equaled the index value (x_{obs}) multiplied by coefficients of
 262 variation ranging from 0.1 to 1.0 and that the true value of the predictor (x_{true}) was distributed
 263 as

$$x_{true} \sim \text{gamma}\left(\frac{x_{obs}^2}{\sigma_{obs}^2}, \frac{x_{obs}}{\sigma_{obs}^2}\right). \quad (8)$$

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

268 4.5 Why we avoided model selection

269 We chose to avoid model selection in our analysis for philosophical and operational reasons.
 270 Our choice was motivated philosophically by Gelman and Rubin (1995), Clark (2007), and
 271 Knappe and de Valpine (2011) who argued that under many circumstances, objectives for
 272 insight from the model, rather than the use of model selection statistics, should guide the
 273 choice of model structure. We can reasonably decide *a priori* to include a parameter in a
 274 model if there is a firmly established biological mechanism that stands behind the operation
 275 of the parameter and if the objective of the modeling is to estimate the parameter's value and
 276 to evaluate its importance relative to other mechanistic parameters.

277 Our choice was motivated operationally by the subjectivity that is required by current
 278 methods for estimating model weights. There is substantial ambiguity in the statistical liter-
 279 ature on how to select best models from a set of candidates (reviewed by Kadane and Lazat,
 280 2004). Different approaches to multi-model inference can lead to dramatically different con-
 281 clusions (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 (Link and Barker, 2010; Royle and Dorazio, 2008), 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 (Knappe 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).

5 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 (Equation 2) and the population model (Equation 5) were able to simulate data that were consistent with the observations (Fig. 3).

[Figure 2 about here.]

[Figure 3 about here.]

5.1 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 ($b_1 = .25$, 95% CI = .19, .31). Estimates of regression coefficients representing the change in harvest resulting from predation showed that 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 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; credible intervals broadly spanned 0.

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

[Figure 4 about here.]

[Table 1 about here.]

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

327 about half as large as the effect of lynx. Effects of brown bear were minor relative to the other
328 predators.

329 [Figure 5 about here.]

330 5.2 Population model

331 We estimated the intrinsic rate of increase of reindeer populations was $.35 \text{ yr}^{-1}$ (95% CI =
332 $.32, .38$, Table 2, Fig. 5). On average, an increase of one lynx family group in a management
333 area reduced the rate of population growth by $.0079 \text{ yr}^{-1}$ (95% CI = $-.014, -.0017$) and
334 an increase of one wolverine reproduction in a management unit reduced the rate of growth
335 by $.015 \text{ yr}^{-1}$ (95% CI = $-.023, -.068$). We observed similar effects of predators on reindeer
336 population growth when predator abundance was expressed as density rather than number
337 per management unit (Table 2). Comparisons of regression coefficients for standardized data
338 showed that the effect of latitude was roughly four to five times stronger than individual effects
339 of predation, density, or NAO and that individual effects of predators, density dependence,
340 and the NAO were similar.

341 [Table 2 about here.]

342 5.3 Simulations of observation uncertainty

343 A central finding was that predation by lynx and wolverine reduced reindeer harvest and
344 population growth rate. However, this conclusion depends on the unrealistic assumption that
345 indices of predator abundance reflect the true abundance without uncertainty. Simulations
346 revealed that our overall conclusion on predator effects was robust to unbiased observation
347 uncertainty that might arise, for example, from sampling error (Figure 6). Even when assumed
348 coefficients of variation for predator indices approached 1, there was substantial weight of
349 evidence in the posterior distribution of coefficients supporting the conclusion that predators

350 reduce harvest and retard population growth (Figure 6).

351 [Figure 6 about here.]

352 6 Discussion

353 6.1 Predation effects on long-term harvest

354 Using a large-scale database and Bayesian regression, we demonstrated a depressing effect of
355 predators on reindeer harvest and population growth rate in Sweden. Analysis revealed that
356 average annual harvest per management unit was reduced by 97 reindeer per surveyed lynx
357 family group. This reduction in harvest is somewhat lower than what would be expected
358 based on kill rate by lynx based on radio telemetry studies, assuming that predation is largely
359 additive (Mattisson et al., 2011b). In our analysis, we used lynx family groups as an index of
360 the total number of lynx in a management area. On average a lynx family group during the
361 winter survey also represents the presence of males and single females (Andrén et al., 2002).
362 Furthermore, lynx kill rate on reindeer varies due to seasonal variation in reindeer density
363 and density of alternative prey (Sunde et al., 2000; Mattisson et al., 2011b). Thus, there were
364 factors influencing kill rate that were not possible to take into account in our large-scale study.

365 Given a mean abundance of lynx family groups per management area ($= 2.53$) and mean
366 population size of reindeer ($= 4701$), we estimate that herders at the average latitude could
367 harvest 247 fewer reindeer as a consequence of lynx predation alone or 82% of what could be
368 harvested if there were no lynx. However, estimates based on averages may offer an overly
369 optimistic view of effects of predation on reindeer production because distributions of the
370 number of reindeer in a management unit and the number of lynx family groups are highly
371 skewed (Fig. 1). The data and model imply the greatest impacts of lynx predation on reindeer
372 harvest when lynx abundance is high and when the population size of reindeer is low. In these

373 cases, our analyses show that the reduction in harvest resulting from lynx predation can be
 374 disproportionately greater than would be predicted from average lynx and reindeer abundance
 375 (Fig. 7). Assuming average lynx numbers and below-average reindeer numbers, harvest in
 376 the presence of lynx could reasonably be expected to range between 50-80% of harvest from
 377 predator free herds (Fig. 7). However, if lynx abundance is above average (i.e., at the 75%
 378 quantile of the data = 3.87 surveyed lynx family groups per management unit), then harvest
 379 from reindeer management units with less than the average herd size are expected to fall
 380 between 20-70% of the predator-free harvest (Fig. 7). These results show that levels of lynx
 381 abundance well within the range of the observed data could cause dramatic reductions in
 382 harvest from reindeer populations and that the magnitude of these reductions is amplified
 383 when reindeer populations are small. We caution, however, that the credible intervals on all
 384 of these estimates are broad (Fig. 7). Hence, we cannot rule out effects of predation on harvest
 385 that could be substantially smaller or substantially greater than the mean estimates.

386 Kill rates of reindeer by wolverine have not been estimated directly from field data. How-
 387 ever, using radio telemetry observations, Mattisson et al. (2011a) estimated that kill rates of
 388 reindeer by lynx were much higher than kill rates of reindeer by wolverine, a finding at odds
 389 with our result that the average number of reindeer killed per surveyed lynx family group
 390 is approximately the same as the number killed per surveyed wolverine reproduction. The
 391 wolverine kill rate was from an area where lynx and wolverine coexist. Wolverines frequently
 392 scavenge reindeer killed by lynx (Mattisson et al., 2011a), so the expected kill rate of reindeer
 393 by wolverines is higher in areas without lynx (Andrén et al., 2011). Moreover, the 97.5%
 394 quantile of the posterior distribution of the ratio of lynx / wolverine kill rates was 4.42, which
 395 is more in line with the field estimate. We observed the same non-linearities in effects of
 396 wolverine on reductions in reindeer harvest as we observed for lynx (Fig. 7). Again, effects

397 of predation were disproportionately great when wolverine abundance was above average and
398 reindeer population size was below average.

399 [Figure 7 about here.]

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

403 6.2 Role of predation in limiting population growth

404 Our estimates of the intrinsic rate of increase of reindeer ($r_{max} = 0.35$, 95% CI = 0.31, 0.38)
405 agreed closely with estimates based on allometric scaling for ungulates. Assuming an average
406 approximate reindeer body mass (M) of 80 kg (averaged across all age and sex classes),
407 predicted r_{max} for reindeer is $1.37M^{-.31} = .35$ (Sinclair, 2003).

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

418 Realized rates of increase in reindeer populations were shaped by a composite of forces,
419 including density dependence, predation, weather, and latitude. Standardized regression coef-

420 ficients revealed roughly equivalent effects of predation, density, and winter weather (indexed
421 by the NAO). Changes in latitude exerted effects that were four to five times as great as pre-
422 dation, density or weather. We suggest that the particularly strong effects of latitude resulted
423 in part from increasing weather severity and diminished primary productivity at northern
424 latitudes. However, there also may be an effect of differences in husbandry. Management
425 units at the southern end of the gradient tended to have larger proportions of adult females in
426 the population (linear regression, $P=.0001$, $r^2 = .25$). This is likely a reflection of differences
427 in harvesting practices that favor maintaining more adult males in the northern populations,
428 which would reduce rates of increase.

429 Findings on responses of ungulate populations to effects of winter weather indexed by the
430 NAO have been inconsistent (Post and Stenseth, 1999; Grotan et al., 2005; Weladji and Holand,
431 2006; Grotan et al., 2008). Body condition, fecundity, and reproductive rate have shown both
432 positive and negative relationships to NAO, suggesting that under some circumstances warm,
433 wet winters are favorable to animals, producing a positive correlation with NAO, while in
434 others cold dry winters are favorable, producing a negative relationship similar to the one we
435 observed. Although these conflicting observations have been explained by differences between
436 maritime and mainland climates, inconsistencies remain (e.g., compare Grotan et al., 2005;
437 Weladji and Holand, 2006) that may result from the inability of time series data to resolve
438 causal effects of weather on population dynamics (Knape and de Valpine, 2011).

439 Our work adds to a growing body of evidence (e.g., Skogland, 1990; Aanes et al., 2000;
440 Coulson et al., 2000; Owen-Smith and Mills, 2006; Wang et al., 2006, 2009; Melis et al., 2009)
441 that population dynamics of large herbivores respond to multiple forces, including intrinsic
442 effects of density dependent competition for resources and extrinsic effects of weather and
443 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 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.

6.3 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 (Figure 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

468 predator data. Similarly, estimates of reindeer numbers could be enhanced by methods that
469 would allow assessment of variance in observations and potential bias in census.

470 For example, given that animals are handled a few times per year, it would be relatively
471 easy to implement a mark-recapture design to estimate total numbers and vital rates. These
472 data would enable development of age and sex structured models, which we believe are partic-
473 ularly needed given our observation that variation in husbandry practices, mediated through
474 demography, may be at least partially responsible for variation in harvest along the north-
475 south gradient. Age-structured models are needed to better explain the operation of density
476 dependence (Bonenfant et al., 2009). In earlier work we attempted to develop these models,
477 but the absence of data on the sex composition of the calf harvest proved to be an impediment
478 that could not be overcome because the proportion of calves in the harvest could trade-off with
479 the unobserved parameter of calf survival, making these parameters inestimable. Adding ob-
480 servations of the sex ratio of the calf harvest to the reindeer database could markedly enhance
481 future models of predator impacts with virtually no added expense for sampling.

482 **6.4 Implications for policy**

483 Throughout Scandinavia, there are conflicting goals for sustaining the pastoral livelihoods of
484 indigenous people while restoring and conserving native predators that prey on reindeer. This
485 conflict is reconciled by environmental policy in Sweden (SOU, 1999) that provides monetary
486 compensation to Sámi pastoralists to offset losses of productivity of reindeer resulting from
487 effects of native predators. Owners of predator-killed livestock are usually compensated based
488 on documented losses (ex post fact compensation; Schwerdtner and Gruber, 2007), whereas the
489 Swedish system is risk-based. In a risk-based compensation the reindeer herders can focus on
490 reindeer husbandry, instead of searching for predator-killed reindeer. There is also an incentive
491 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.

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. (2011a) 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 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 population growth rate. This evidence provides a biological justification for Sweden's risk-based compensation policy.

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Table 1: Estimates of parameters in harvest models (Equation 2). 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 km² of year-round pastures, and the standardized models uses standardized predictors [i.e., $(x_i - \mu) / \sigma$]. Reindeer number is the annual count of reindeer in a management unit. Interpretations of coefficients in each model are given in the text.

Coefficient	Mean	SD	2.5% CL	97.5% CL
<u>Abundance model</u>				
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
<u>Density model</u>				
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
<u>Standardized model</u>				
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

Table 2: Estimates of parameters in population models (equation 5). 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 km² of year-round pastures, and the standardized models uses standardized indices of numbers of predators in a reindeer management unit [i.e., $(x_i - \mu)/\sigma$]. Reindeer number is the annual count of reindeer in a management unit. Interpretations of coefficients in each model are given in the text.

	Mean	SD	2.5% CL	97.5% CL
<u>Abundance model</u>				
Intercept	0.35	0.0173	0.316	0.385
Lynx index	-0.00786	0.00309	-0.0138	-0.00175
Wolverine index	-0.0149	0.00419	-0.0232	-0.00676
Latitude	-0.000592	4.45E-05	-0.00068	-0.000505
Reindeer density	-0.023	0.00737	-0.0377	-0.00855
NAO	-0.0114	0.00482	-0.0208	-0.002
<u>Density model</u>				
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	4.40E-05	-0.000749	-0.000575
Reindeer density	-0.000224	6.95E-05	-0.000361	-8.67E-05
NAO	-0.0111	0.00476	-0.0201	-0.00169
<u>Standardized model</u>				
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

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688		The vertical dotted line indicates the mean reindeer population size.	41

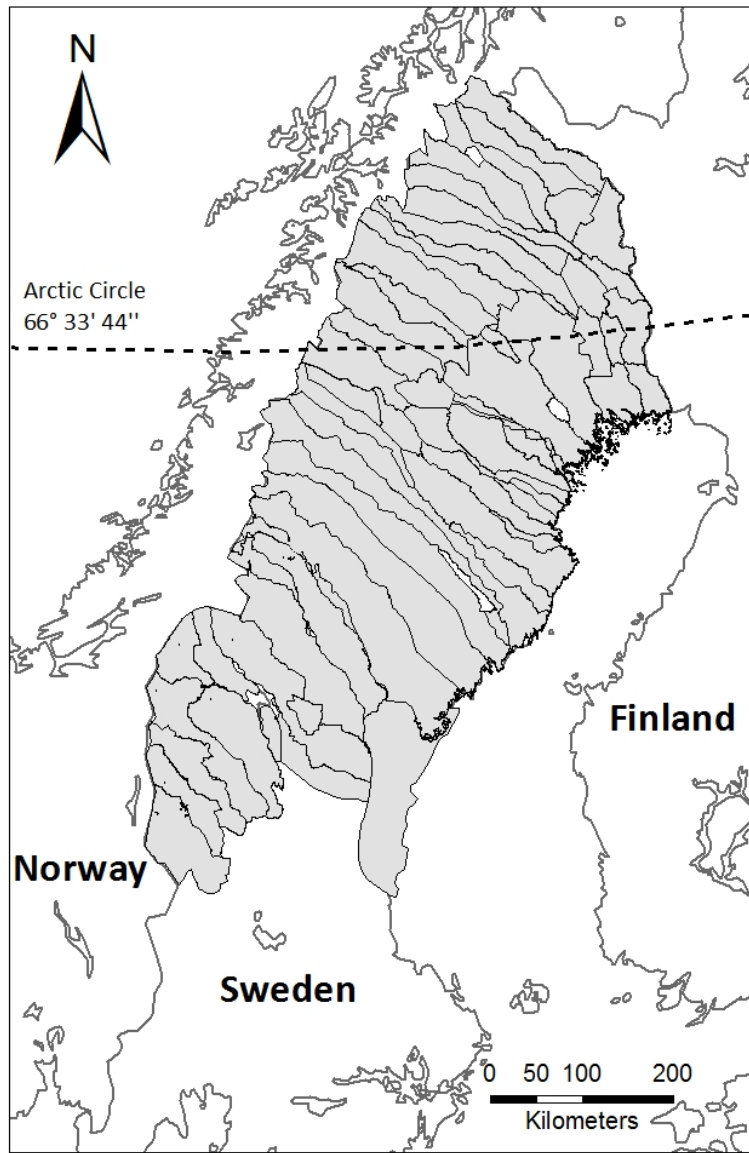


Figure 1: The reindeer husbandry area of Sweden (shaded area in the map), divided into 51 management units. Some management units are overlapping and are therefore partly hidden in the map. Some areas in northern Sweden are excluded from the reindeer husbandry area (shown as white areas or black dots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

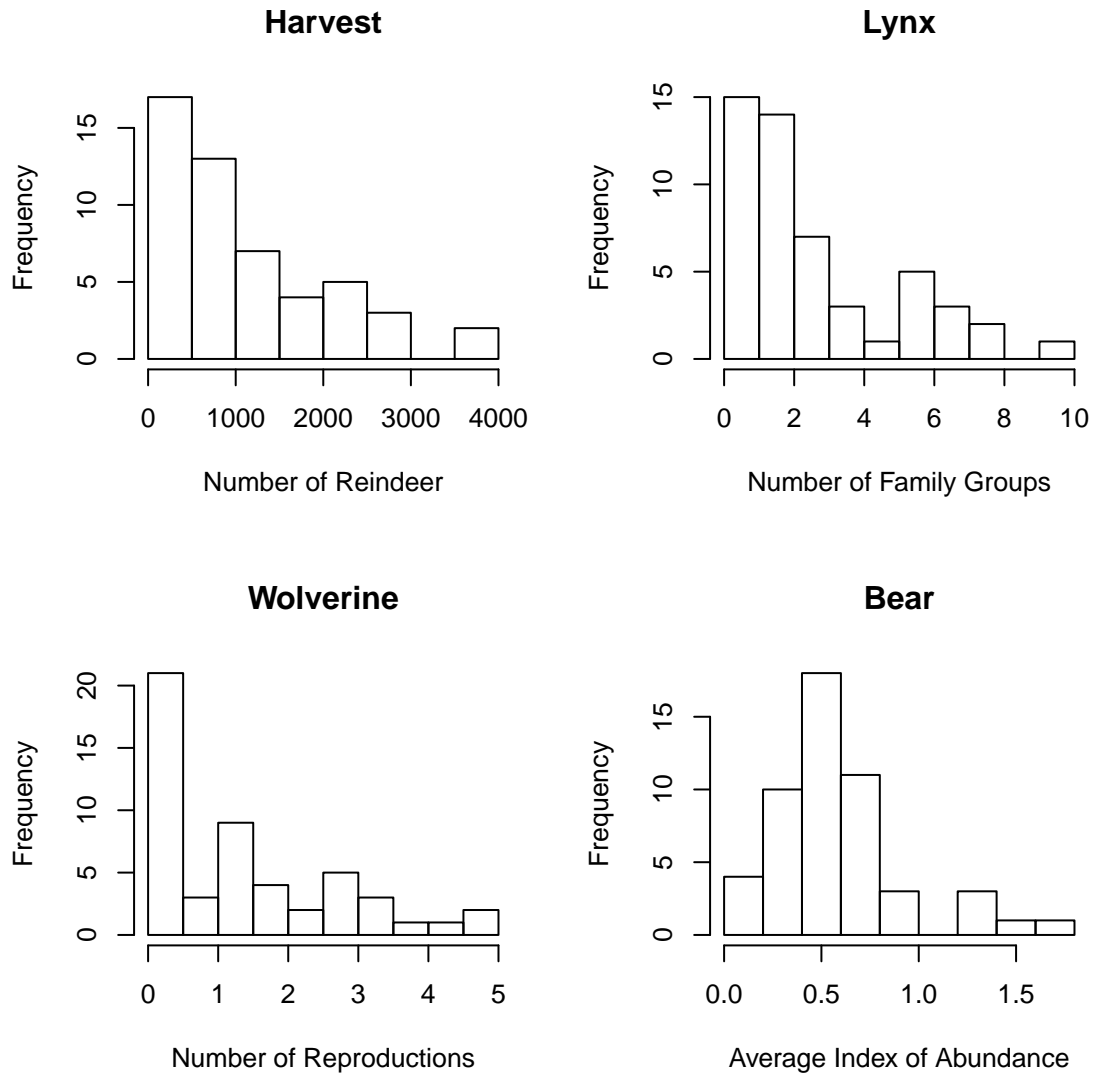


Figure 2: Frequency distributions of observations of average annual harvest and indices of predator abundance for 51 reindeer management areas in Sweden.

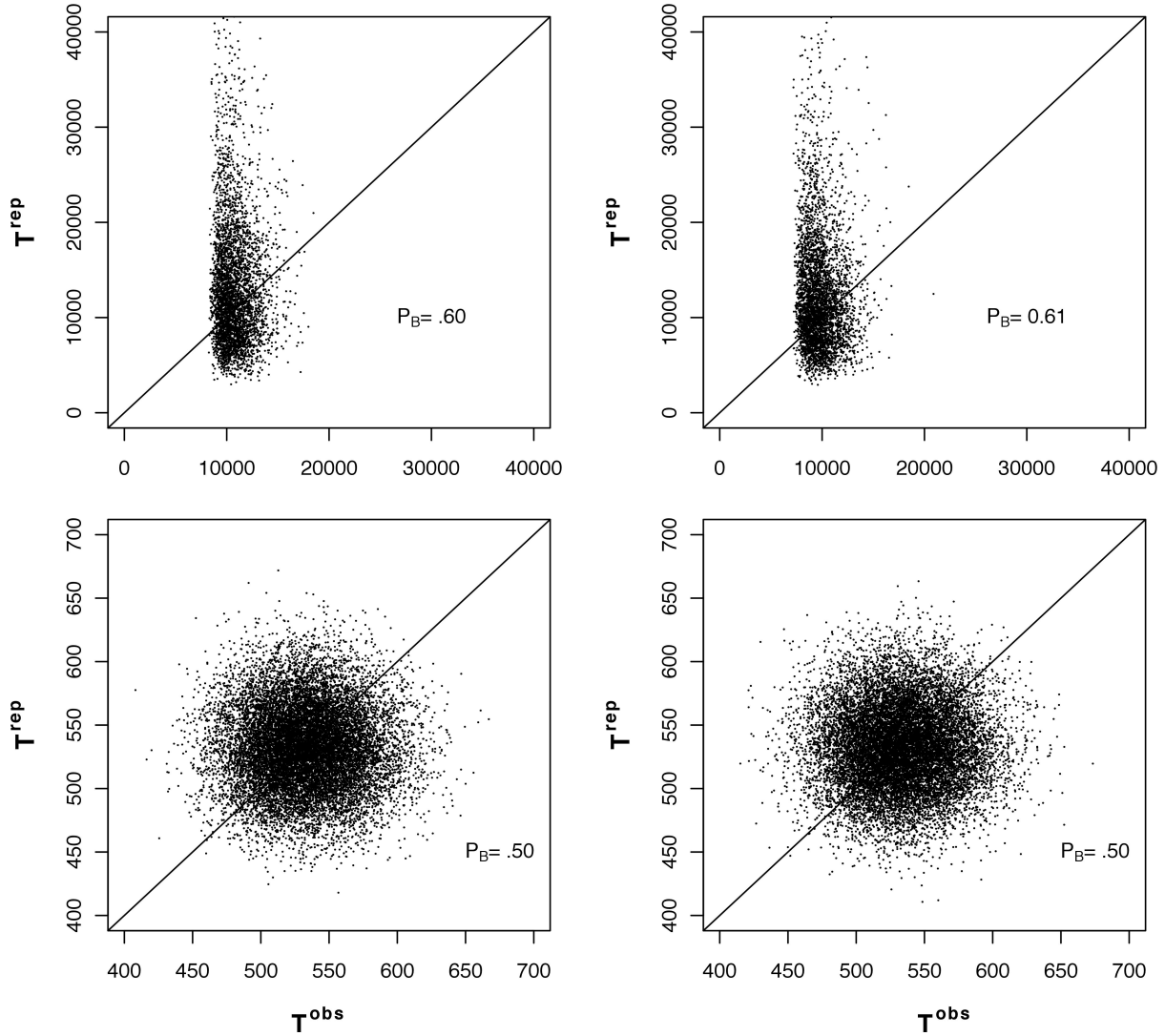


Figure 3: Posterior predictive checks of the harvest regression model (upper panels) and the population model (lower panels) using predator abundance (left column) and density (right column) for covariates. Test statistics calculated from the observed data plotted against test statistics calculated from 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.

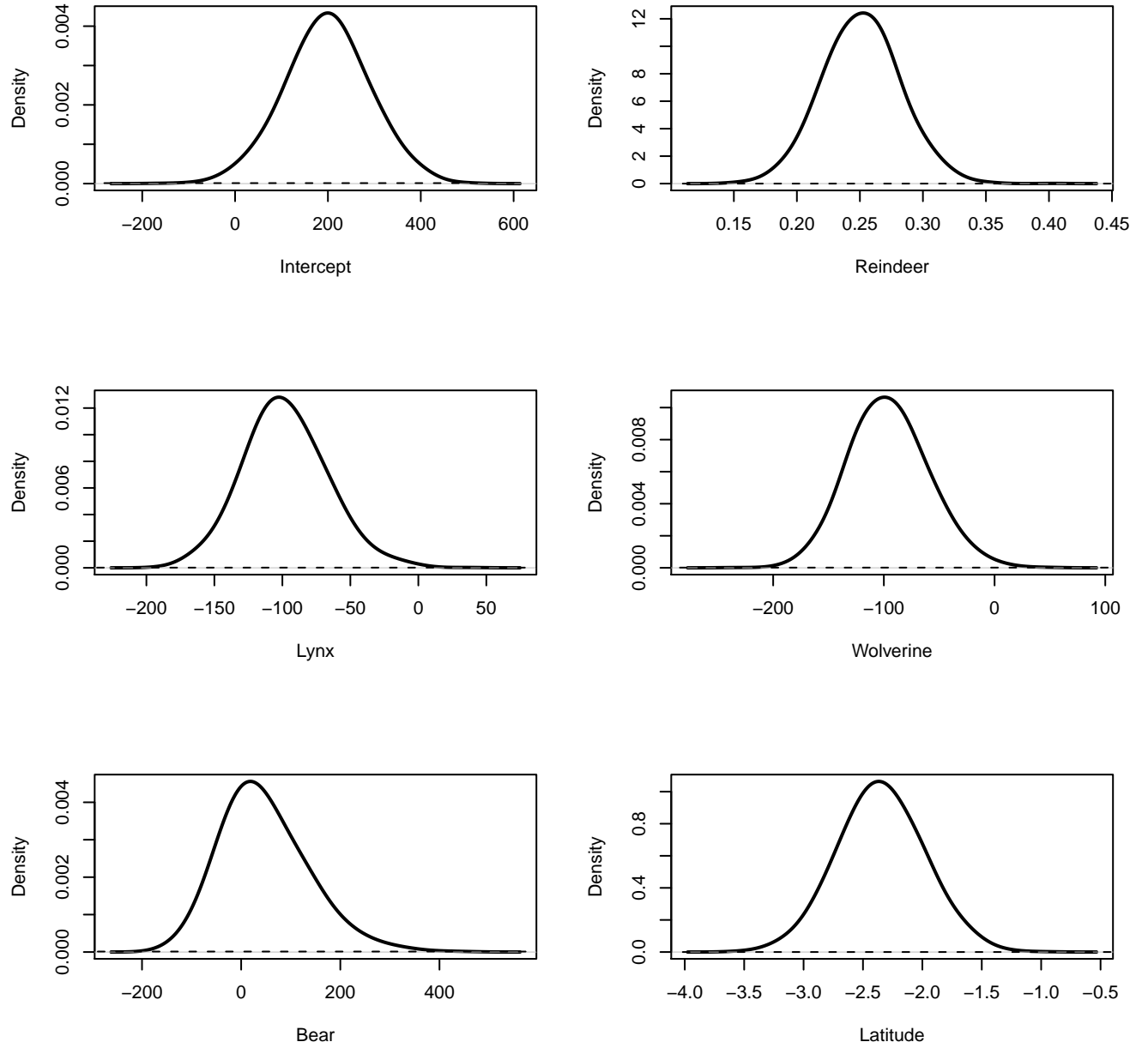


Figure 4: Posterior (solid line) and prior (dashed line) distributions of parameters in the harvest regression model using indices of predator abundance as independent variables.

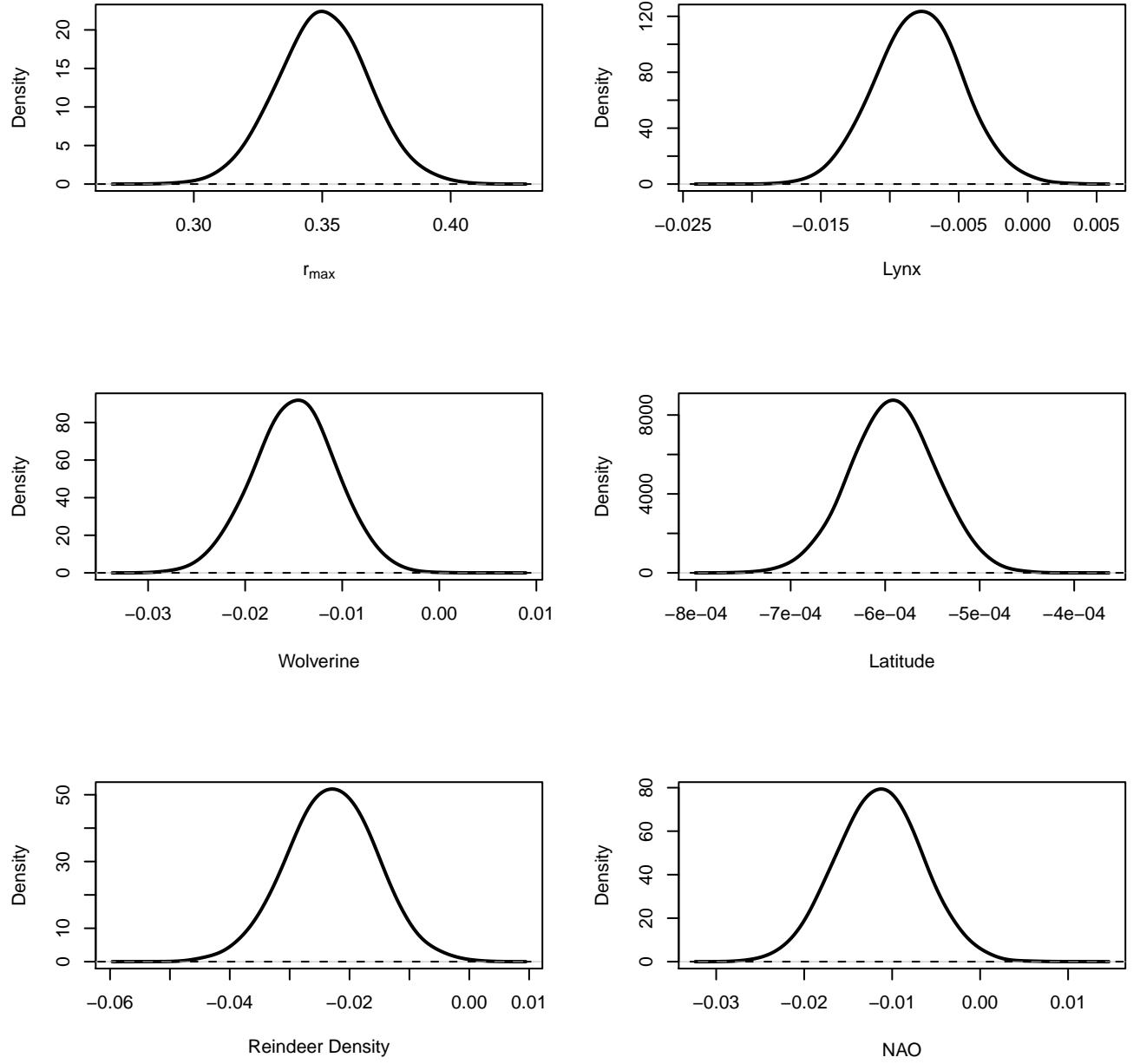


Figure 5: Posterior (solid line) and prior (dashed line) distributions of parameters in the population model using estimates of indices of predator abundance as independent variables.

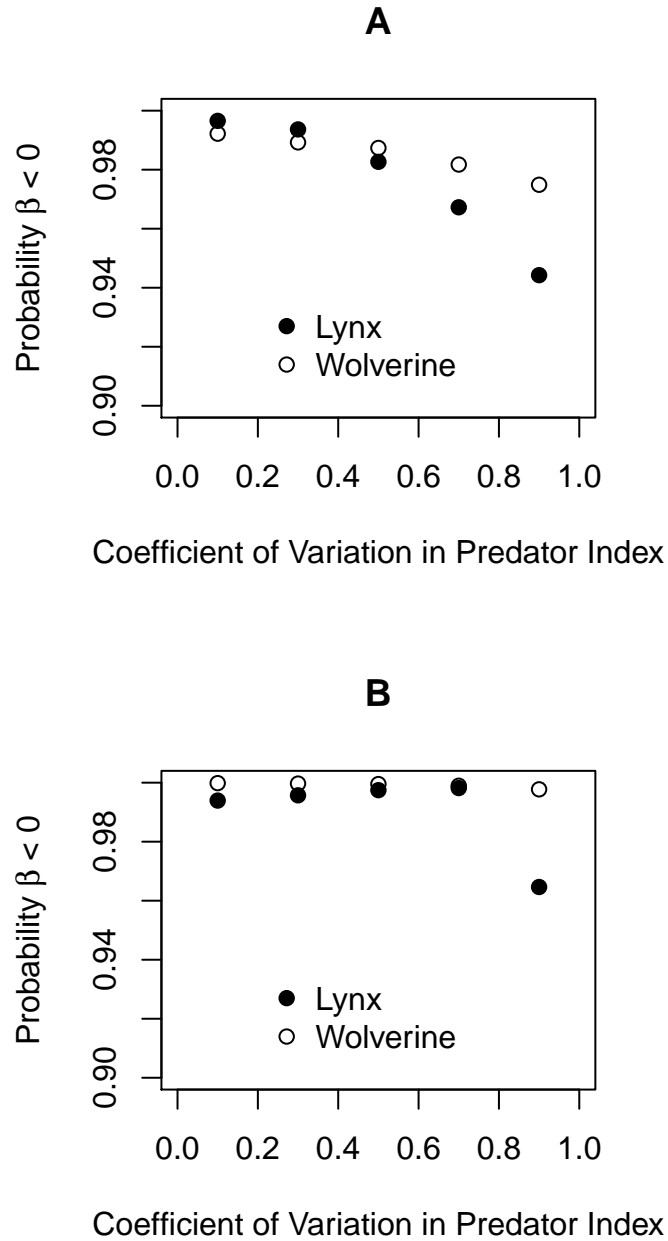


Figure 6: Simulations of effects of observation error on the conclusion that lynx and wolverine reduce harvest (A) and retard population growth (B). The x-axis is the assumed coefficient of variation in predator indices resulting from observation uncertainty. The y-axis is the proportion of estimates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

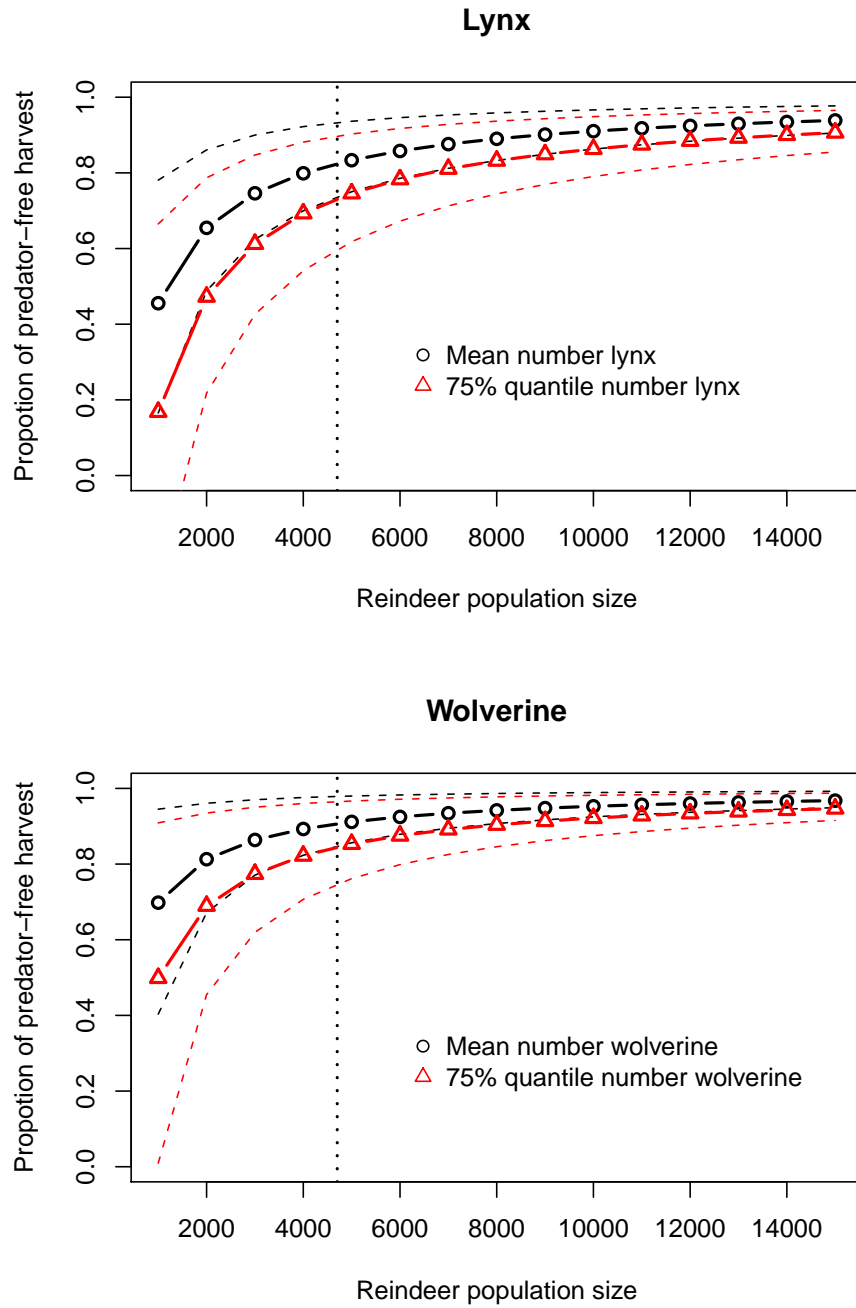


Figure 7: Model predictions of the proportional change in harvest attributable to lynx and wolverine predation as a function of reindeer population size. Two levels of predator abundance were used in predictions, the mean level and the upper 75% quantile. Dashed lines give 95% credible intervals on model predictions. The vertical dotted line indicates the mean reindeer population size.