

Estimating Sustainable Harvest in Wolverine Populations Using Logistic Regression

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ABSTRACT Population viability analysis (PVA) is a common tool to evaluate population vulnerability. However, most techniques require reliable estimates of underlying population parameters, which are often difficult to obtain and PVA are, therefore, best used in a qualitative context. Logistic regression is a powerful alternative to traditional PVA methods but has received surprisingly limited attention. Logistic regression fits regression equations to binary output from PVA models at a specific point in time to predict probability of a binary response over a range of parameter values. We used logistic regression on output from stochastic population models to evaluate the relative importance of demographic parameters for wolverine (*Gulo gulo*) populations and to estimate sustainable harvest in a wolverine population in Alaska. Our analysis indicated that adult survival is the most important demographic parameter to reliably estimate in wolverine populations because it had a greater effect on population persistence than did both fecundity and subadult survival. In accordance with this, harvest rate had a greater effect on population persistence than did any of the other harvest- and migration-related variables we tested. Furthermore, a high proportion of harvested females strengthened the effect of harvest. Hypothetical wolverine populations suffered high probabilities of both extinction and population decline over a range of realistic population sizes and harvest regimes. We suggest that harvested wolverine populations must be regarded as sink populations and that source populations in combination with sufficient dispersal corridors must be secured for any wolverine harvest to be sustainable. (JOURNAL OF WILDLIFE MANAGEMENT 72(5):1125–1132; 2008)

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The wolverine (*Gulo gulo*) is a large terrestrial mustelid with a circumpolar distribution, primarily inhabiting tundra and taiga of northern latitudes (Wilson 1982). Small and fragmented populations both in the contiguous United States and in Scandinavia have recently generated attention to management and research on the species (Weaver et al. 1996, Landa et al. 2000, Rowland et al. 2003, Flagstad et al. 2004, Ruggiero et al. 2007). The United States Fish and Wildlife Service has proposed to list wolverines as endangered in the lower 48 States. Wolverines are also listed as a species of concern in western Canada and as endangered in eastern Canada (Committee on the Status of Endangered Wildlife in Canada 2007).

Similar to many other large carnivores, wolverines are difficult to study because of their large area requirements and naturally low abundance. The wolverine is also the least known species among the large boreal carnivores (Weaver et al. 1996, Landa et al. 2000, Ruggiero et al. 2007). This lack of information stands in unfortunate contrast to an increased need to evaluate the effects of human impacts such as landscape fragmentation (Cegelski et al. 2003, Rowland et al. 2003) or human persecution or harvest (Landa et al. 2000, Sæther et al. 2005, Golden et al. 2007a, Lofroth and Ott 2007) on persistence of wolverine populations. Despite this lack of information, substantial harvest of wolverines occurs in Montana and Alaska, USA, and western Canada (Golden et al. 2007a, Lofroth and Ott 2007, Squires et al. 2007).

Population viability analysis (PVA) has provided a powerful framework for estimating vulnerability of specific

populations or to assess relative estimated effects of different management strategies (reviewed in Beissinger and McCullough 2002). However, reliability of any PVA is dependent on the quality of demographic information that is available at the time of model parameterization. For species like the wolverine, such information is still far from sufficient to enable construction of reliable PVA models on most populations, with the notable exception of the wolverine population in northern Scandinavia (Sæther et al. 2005). Furthermore, although the relative importance of different population parameters on extinction risk can be inferred by sensitivity analyses, most techniques do not account for uncertainty in these parameters (Mills and Lindberg 2002). Therefore, PVA models have been recommended as a qualitative rather than a quantitative tool, which has its main strength in its ability to compare hypothetical populations under different management scenarios and with different demographic characteristics (Beissinger and Westphal 1998).

Logistic regression is a powerful method to analyze data with binary response variables (Vittinghof et al. 2005). Logistic regression has been suggested as an alternative approach to traditional sensitivity analysis if output from PVA models are expressed in a binary format (for instance extinct vs. nonextinct; McCarthy et al. 1995, McCarthy et al. 1996, Cross and Beissinger 2001). Logistic regression relates binary output from the PVA models at a specific point in time to the model parameters using a logit linearization of the binary response. Despite the relative lack of attention paid to this technique, logistic regression is potentially powerful because it has the ability to test a wide

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range of parameter values as well as interaction effects between parameters and nonlinear parameter effects.

We used binary output from a simple stochastic population model in combination with logistic regression to 1) estimate the relative importance of the basic population parameters fecundity and survival to guide priority decisions for future field efforts, and 2) explore sustainable harvest levels in a population of wolverines in the western Brooks Range, Alaska. This population lies within the administrative units of Western Arctic National Parklands (WEAR) of the United States National Park Service. We will hereafter refer to this population as the WEAR population. The WEAR is mandated to actively manage for the long-term viability of wildlife within its administrative boundaries but also to meet requirements from native communities with regard to land use, which includes harvest of furbearers. There are currently 3 main questions related to management of this population: 1) what is the effect of population size on population viability? 2) how is wolverine population viability affected by different harvest regimes? and 3) how are these effects influenced by dispersal patterns?

METHODS

Population Model and Model Parameters

We used a temporally discrete, stochastic population model with a simple sex and age structure as the basis for our modeling. The model has the structure

$$P_i = AM_i + AF_i + SM_i + SF_i + J_i \quad (1)$$

where P_i , AM_i , AF_i , SM_i , SF_i , and J_i are population size, number of adult males and females, number of subadult males and females, and number of juveniles at year i , respectively. We regard adults as animals ≥ 2 years, subadults as 1–2 years, and juveniles as young of the year (see Krebs et al. 2004, Dalerum et al. 2007). We calculated number of animals in each age and sex category:

$$J_i = AF_i \times f_i \quad (2)$$

$$\begin{aligned} SM_i &= 0.5 \times J_{i-1} \times js_i + MMS_i: \\ SF_i &= 0.5 \times J_{i-1} \times js_i + FMS_i \end{aligned} \quad (3)$$

$$\begin{aligned} AM_i &= AM_{i-1} \times mas_i + SM_{i-1} \times mss_{i-1} + MMA_i: \\ AF_i &= AF_{i-1} \times fas_i + SF_{i-1} \times fss_{i-1} + FMA_i \end{aligned} \quad (4)$$

where f_i is annual birth rate (no. of kits/F/yr; we estimated postweaning to weaning sex ratio to be 1:1), js_i is juvenile survival, MMS_i and FMS_i is net number of migrant males and females, respectively, mss_i and fss_i is subadult survival for males and females, respectively, mas_i and fas_i is adult mortality for males and females, respectively, and MS_i and MA_i is net number of subadult and adult immigrants, respectively.

We evaluated relative effects of fecundity and survival on probability of extinction and population decline in hypothetical populations of 1,000 animals without any migration

or harvest. For each simulated year, we drew model parameters from normal distributions independently from each other. In these simulations, we used the exhaustive approach to logistic sensitivity explained by McCarthy et al. (1995) and sequentially altered the means from which we drew each parameter so that we covered a wide range of possible parameter values to generate robust estimates of the relative beta coefficients. We divided each parameter into 6 increments and ran simulations over the full range of possible parameter combinations (i.e., $6^3 = 216$). For each parameter combination, we ran 1,000 simulations.

Persson et al. (2006) estimated a 95% confidence interval of wolverine birth rate (no. of kits/F/yr) to lie between 0.33 and 1.14, with a mean of 0.75 and a standard deviation of 0.38. We varied means of the normal distribution from which we drew fecundity (f_i) between 0.1 and 1.5, with a fixed standard deviation of 0.38. We drew both adult (mas_i and fas_i) and subadult survival (mss_i and fss_i) from normal distributions with means ranging from 0.1 to 0.99, and we fixed standard deviations to 0.26 and 0.22 for adult and subadult, respectively, estimated from Krebs et al. (2004). We assumed equal survival for males and females and for juveniles and subadults.

When estimating relative effects of population size, migration, and harvest on probability of extinction and population decline, we included additional stochasticity in the model by assigning a quality index (q_i) to each year, using a discrete ordinal scale with 3 levels, poor, medium, and good. We drew the q_i for each year from a multinomial distribution with probabilities 0.15, 0.7, and 0.15 so that on average 14 of 20 years will be medium and 3 of 20 years will be good and poor, respectively.

We drew fecundity and baseline survival from normal distributions with q_i specific means with fixed standard deviations (Table 1). We let average fecundity for normal years be 0.75 and we fixed standard deviation to 0.38 for all years based on Persson et al. (2006). We used pooled survival estimates for untrapped populations in Krebs et al. (2004) for mean adult (0.88) and subadult (0.85) survival for normal years, and we fixed standard deviations to 0.26 and 0.22, for adults and subadults, respectively. For both fecundity and survival, we adjusted means for normal years up and down with 25% for good and poor years, respectively (Table 1). We used the same survival estimates for juvenile survival as for subadult survival and assumed equal survival among males and females. We let the remaining population parameters vary within plausible ranges, described below. Variable parameters included initial population size, total harvest, which was drawn independently from survival estimates (i.e., estimating additive harvest mortality), age structure of harvest, harvest sex ratio, total immigration, age structure of immigrants, and migration sex ratio. Following McCarthy et al. (1995), we generated 1,000 parameter combinations by drawing each parameter independently from uniform distributions and ran 10 simulations for each parameter combination, thus generating 10,000 different population trajectories.

Table 1. Parameters used for modeling effects of population size, migration, and harvest on extinction risk and probability of population decline in wolverines.

Parameter	$\bar{x}$			SD
	Poor ^a	Normal ^b	Good ^c	
Fecundity ^d	0.56	0.74	0.93	0.38
Ad survival ^c	0.99	0.88	0.77	0.26
Subad survival ^c	0.99	0.85	0.64	0.22
Range				
Initial population size (n)	300–1,500			
Migration				
Net immigration				
(% of population size)	0–25			
Age structure (% ad)	25–75			
Sex ratio (% M)	50–100			
Harvest				
Net harvest (no. animals)	10–100			
Age structure (% ad)	0–100			
Sex ratio (% M)	50–100			

^a Average used for a poor yr.

^b Average used for a normal yr.

^c Average used for a good yr.

^d Mean for a normal yr and SD estimated from Persson et al. (2006).

^e Ad and subad survival estimated by the pooled untrapped survival given by Krebs et al. (2004).

The WEAR population covers an area of approximately 100,000 km². Although population density for this area is unknown, Golden et al. (2007b) reported densities of approximately 10 animals/1,000 km² for a Canadian population in a similar environment, which would give an approximate population of 1,000 animals in our area. However, because this estimate is highly uncertain, we used a conservative range of 300–1,500 individuals, which reflects a realistic range of animals within the area.

A recent genetic study suggested a high level of gene flow in this population (Dalerum et al. 2007), which is supported by other population genetic studies throughout the wolverine's range (Kyle and Strobeck 2001, 2002; Cegelski et al. 2003; Chappell et al. 2004; Tomasik and Cook 2005). However, such patterns may develop even without large numbers of dispersing individuals. In the absence of direct estimates of inter population dispersal, we used a conservatively large range of migrants. We only included effects of immigration, and we let number of immigrants range between 0% and 20% of total population size.

We did not let the age and sex structure of migrants follow that of the main population, but we altered the age structure of immigrants to range from 25% to 75% adults. Although Dalerum et al. (2007) failed to find genetic evidence for sex-biased dispersal, previous studies found male-biased dispersal both within and among wolverine populations (Vangen et al. 2001, Cegelski et al. 2003, Chappell et al. 2004). Therefore, we also varied the sex ratio of immigrants from 50% to 100% males.

Exact harvest rate in the focal population is unknown, but between 10 and 30 animals have been registered/year for the area since the early 1990s (Alaska Department of Fish and Game 2004). However, not all harvested wolverines are

registered. To gather population information on this population, 139 wolverine carcasses were salvaged from hunters from 1996 to 2003 (ranging from 2 carcasses/yr to 53 carcasses/yr; e.g., Dalerum 2005; Dalerum et al. 2005, 2007). Although this collection was not systematic enough to provide us with direct correction factors for official harvest statistics, when combined with official harvest statistics it allowed us to create likely boundaries for wolverine harvest in the area, which we set to vary from 10 animals/year to 100 animals/year.

There was a strong bias towards young animals among our collected carcasses, with 75% of animals estimated as subadults based on tooth annuli counts and tooth wear. Although this estimate is supported by official harvest statistics, it is highly uncertain because age determination of wolverines is difficult. Therefore, we let harvest age structure vary within the conservative range of 0–100% adults.

There also was a sex bias among our collected carcasses, which similarly is supported by official harvest statistics. In our sample, 65% of harvested animals were males. Because sex is more accurately determined than age, we used a less conservative range of sex ratios than for age structure and let sex ratio vary from 50% to 100% males.

Logistic Regression Analyses

For each simulation, we recorded population size after 25 years, 50 years, and 100 years of population projection and coded it as either extinct ($P_{25,50,100} < 1$) or nonextinct ($P_{25,50,100} > 1$) and as negative ($P_{25,50,100} < P_0$) or nonnegative ($P_{25,50,100} > P_0$) growth. We used these arbitrary points in time (i.e., 25 yr, 50 yr, and 100 yr) because they reflect a compromise over time spans that are long enough to capture demographic processes and short enough to be viable for management purposes and to minimize projection error (Bessinger and Westphal 1998). We used logistic regression models to calculate probability of extinction and population decline over the range of parameter values at each of these time points. We constructed generalized linear models using the raw frequencies of each pair of output categories (i.e., extinct vs. not extinct and negative growth vs. positive growth) as dependent variables and the varied population parameters as predictors. We used a logit link function but fitted models using a quasi-binomial error structure rather than binomial to account for overdispersion (Crawley 2002).

To evaluate the effect of uncertainty in fecundity and mortality estimates, we did not include any interaction terms but fitted models only containing the main effects of fecundity, adult survival, and subadult survival as predictors. To evaluate effects of population size, harvest, and migration we fitted models containing all possible 2-way interaction terms including the altered population variables.

For statistical analyses on simulated data such as these, traditional statistical inference is somewhat inappropriate because it is mainly conditioned on the sample size that is arbitrarily determined (i.e., in our case, no. of simulation runs/parameter combination; see McCarthy et al. 1995). Furthermore, raw regression coefficients do not directly reflect the relative importance of specific terms, because they

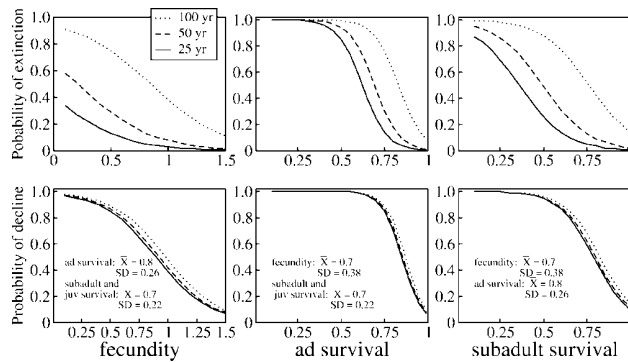


Figure 1. Probabilities of extinction and of population decline after 25 years, 50 years, and 100 years of simulations of hypothetical wolverine populations of 1,000 animals with the initial age structure of 60% adults, 30% subadults, and 10% juveniles and a 1:1 sex ratio over a range of fecundity and age specific survival values. We fixed mean adult survival to 0.8 (SD = 0.26) for the graphs describing effects of fecundity and subadult survival (A, B, E, F), we fixed mean subadult survival to 0.7 (SD = 0.22) for the graphs describing effects of fecundity and adult survival (A, B, C, D), and we fixed mean fecundity to 0.7 (SD = 0.26) for the graphs describing effects of adult and subadult survival (C, D, E, F). We estimated fecundity and age specific survival from Persson et al. (2006) and Krebs et al. (2004).

depend on the units used to measure the independent variables (Selvin 1998). Instead, standardized regression coefficients calculated as the raw coefficients divided by their standard errors more accurately measure the relative importance of predictor variables (McCarthy et al. 1995, Cross and Beissinger 2001). We have reported these standardized regression coefficients to permit evaluation of the relative importance of predictor variables on probabilities of population extinction and population decline. Finally, we used the estimated logistic regression equations to calculate probability of extinction and population decline after 50 years of simulation for hypothetical populations within realistic ranges of population sizes, immigration, and harvest regimes. We conducted both the population modeling and statistical analyses using the statistical software R version 2.4.0 for Linux (R: A language and environment for statistical computing; R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Simulations of closed populations of 1,000 individuals indicated that adult survival had a greater effect on probability of extinction than did fecundity and subadult survival (standardized $\beta_{\text{fecundity}} = -6.93$, standardized $\beta_{\text{adult survival}} = -9.94$, standardized $\beta_{\text{subadult survival}} = -8.60$), although there were fewer differences between effects of fecundity and survival on probability of population decline (standardized $\beta_{\text{fecundity}} = -7.75$, standardized $\beta_{\text{adult survival}} = -9.22$, standardized $\beta_{\text{subadult survival}} = -8.97$). Length of projection had a greater effect on probability of extinction (standardized $\beta_{\text{time}} = 5.86$) than on probability of population decline (standardized $\beta_{\text{time}} = 0.88$). To visualize these differences in demographic effects we applied the logistic regression equations (extinction: $\text{logit}[p] = 15.4 + 0.04 \times$

time $- 3.14 \times \text{fecundity} - 14.4 \times \text{ad survival} - 7.48 \times \text{subad survival}$; decline: $\text{logit}[p] = 25.5 + 0.005 \times \text{time} - 4.37 \times \text{fecundity} - 17.8 \times \text{ad survival} - 10.0 \times \text{subad survival}$) to fixed mean fecundity and survival values (mean fecundity = 0.7, mean ad survival = 0.8, and mean subad survival = 0.7). Probability of extinction and population decline declines more drastically with increasing survival compared to fecundity values, and length of projection affects probability of population extinction much more than probability of population decline (Fig. 1).

In our simulations testing for the relative effects of population size, harvest and migration on population viability, length of projection was influential on probability of extinction as well (standardized $\beta = 19.55$) but had similarly less effect on probability of population decline (standardized $\beta = 3.99$). Number of harvested animals had the highest relative effect of the demographic variables we included, both on probability of extinction (standardized $\beta = 12.33$; Table 2) and on probability of population decline (standardized $\beta = 13.54$; Table 3). Furthermore, the effect of harvest appear to be influenced by the sex ratio of harvested animals (harvest $\times$ harvest sex ratio; probability of extinction: standardized $\beta = -9.09$, probability of decline: standardized $\beta = -11.18$), with a higher relative effect of harvest as the proportion of males among harvested animals declined. In contrast to harvest sex ratio, the effect of harvest was not influenced by the age structure of harvested animals for effects of probabilities of neither extinction (standardized $\beta = 1.19$; Table 2) nor population decline (standardized $\beta = 1.14$; Table 3). Apart from harvest, initial population size, migration and migration sex ratio, and migration age structure also had large relative effects on extinction probability (standardized $\beta_{\text{initial population size}} = -5.44$, standardized $\beta_{\text{migration}} = -8.57$, standardized $\beta_{\text{migration sex ratio}} = 4.14$, standardized $\beta_{\text{migration age structure}} = -3.14$; Table 2) and population decline (standardized $\beta_{\text{initial population size}} = -6.16$; standardized $\beta_{\text{migration}} = -9.14$, standardized $\beta_{\text{migration sex ratio}} = 4.12$, standardized $\beta_{\text{migration age structure}} = 3.01$; Table 3). After 50 years of simulation, populations without net immigration suffered extinction probabilities above zero at harvest rates of approximately 5–10% (with a harvest age structure of 25% ad and a sex ratio of 65% M) across the range of population sizes (Fig. 2A) and high probabilities of population decline even at moderate harvest levels (e.g., a 20% risk of decline with a harvest of 10 out of 1,500 animals [0.7% harvest rate]; Fig. 2D). However, probabilities of extinction and population decline decreased substantially in populations with 10% immigration (Fig. 2B, E) and remained close to zero even at low population sizes with high harvest rates and a 20% immigration (Fig. 2C, F).

Populations of 500 animals with a harvest rate of 50 animals/year (10% harvest rate) suffered high risks of both extinction (Fig. 3A) and population decline (Fig. 3D) after 50 years of simulation if the proportion of harvested males was $< 80\%$ of total harvest and there was no immigration. Sex ratio of harvested animals still had a great effect on both probability of extinction (Fig. 3B) and on probability of

Table 2. Relative effects of length of projection, initial population size, migration, and harvest parameters as well as possible combinations of 2-way interaction terms on probability of population extinction in simulated wolverine populations. Relative effects are indicated by standardized β coefficients generated from a generalized linear regression model on binary output from stochastic population models. Coefficients for sex ratio are given for percent males and coefficients for age structure are given for percent adults.

Parameter	β -coeff.	Standardized β	Rank
Length of projection	1.40×10^{-2}	19.55	1
Harvest	1.12×10^{-1}	12.33	2
Population size $\times$ migration	-2.03×10^{-2}	-10.01	3
Migration sex ratio $\times$ migration age structure	10.3	9.31	4
Harvest $\times$ harvest sex ratio	-7.77×10^{-2}	-9.09	5
Migration	-45.9	-8.57	6
Harvest sex ratio $\times$ migration	33.1	7.83	7
Harvest age structure	4.52	6.57	8
Population size	3.71×10^{-3}	-5.44	9
Harvest sex ratio	-6.63	-4.82	10
Population size $\times$ harvest sex ratio	3.11×10^{-3}	4.78	11
Migration sex ratio	-5.41	-4.14	12
Migration $\times$ migration age structure	15.8	3.83	13
Harvest sex ratio $\times$ harvest age structure	-2.45	-3.80	14
Harvest $\times$ migration	9.02×10^{-2}	3.63	15
Population size $\times$ harvest	1.28×10^{-5}	-3.51	16
Migration age structure	-4.37	-3.14	17
Harvest age structure $\times$ migration sex ratio	-1.55	-2.76	18
Harvest age structure $\times$ migration age structure	-1.26	-2.27	19
Migration $\times$ migration sex ratio	-9.18	-2.20	20
Harvest sex ratio $\times$ migration age structure	-2.87	-2.08	21
Harvest sex ratio $\times$ migration sex ratio ^a	2.20	1.62	22
Population size $\times$ harvest age structure ^a	-4.42×10^{-4}	-1.57	23
Harvest $\times$ migration age structure ^a	-1.09×10^{-2}	-1.42	24
Harvest $\times$ harvest age structure ^a	4.36×10^{-3}	1.19	25
Harvest age structure $\times$ migration ^a	-1.72	-0.88	26
Population size $\times$ migration sex ratio ^a	2.57×10^{-4}	0.44	27
Population size $\times$ migration age structure ^a	9.82×10^{-5}	0.17	28
Harvest $\times$ migration sex ratio ^a	-3.60×10^{-4}	-0.05	29

^a Term not statistically significant at $\alpha = 0.05$.

decline (Fig. 3E) in populations with an immigration of 10%. In populations with 20% immigration, probability of both extinction and population decline remained close to zero across the tested range of harvest sex ratio and age structures (Fig. 3C, F).

DISCUSSION

By applying the logistic regression equations to the best estimates of fecundity and natural mortality we had available, we were able to estimate probabilities of extinction and population decline over a range of population sizes, immigration levels, and harvest scenarios. Our simulations indicated that populations without an influx of immigrating individuals suffer high risks of extinction and almost certain risks of population decline over 50 years, which suggests that harvested populations should be regarded as sink populations that rely on influx of animals from neighboring areas. Similar conclusions have now independently been reached by several studies (Krebs et al. 2004, Sæther et al. 2005, Golden et al. 2007a), suggesting that wolverine harvest may only in exceptional circumstances be viable on a local scale.

Wolverines appear to avoid areas of high human population and road density, so dispersal is likely to occur along undisturbed segments of the landscape (Rowland et al. 2003, Copeland et al. 2007). Securing dispersal corridors and assessing their effectiveness around harvested segments

of populations should, therefore, be of high priority. Studies further identifying characteristics of such corridors will likely be important for our abilities to manage wolverine populations sustainably. We also need basic information on dispersal rates for wolverine populations. The maximum dispersal rate we used, net immigration corresponding to 20% of population size, is likely a high estimate for a species such as the wolverine. However, by including high dispersal estimates in our analyses we were able to show that high dispersal rates can mitigate negative effects of harvest. Furthermore, dispersal representing approximately 10% of local population size has been estimated for cougars (*Felis concolor*; Logan and Sweanor 2001), indicating that the range of 0–20% that we tested may be a realistic range for large carnivores. Prior to obtaining knowledge about dispersal patterns and what ecological factors drive them, harvest in fragmented populations such as the populations in Idaho and Montana, USA (e.g., Cegelski et al. 2006, Squires et al. 2007) must be conservative. For northern Canada and Alaska, on the other hand, migration is not likely to be limited due to large areas of undeveloped land and high connectivity (Chappell et al. 2004, Dalerum et al. 2007), and harvest is likely sustainable on a regional level (Lofroth and Ott 2007). Even so, if dispersal rates are naturally low, high harvest could have substantial demographic effects locally.

Table 3. Relative effects of length of projection, initial population size, migration, and harvest parameters, as well as possible combinations of 2-way interaction terms on probability of population decline in simulated wolverine populations. Relative effects are indicated by standardized β coefficients from a generalized linear regression model on binary output from stochastic population models.

Parameter	β -coeff.	Standardized β	Rank
Harvest	1.03×10^{-1}	13.54	1
Harvest $\times$ harvest sex ratio	-7.35×10^{-2}	-11.18	2
Population size $\times$ harvest sex ratio	5.23×10^{-3}	10.76	3
Population size $\times$ harvest	-2.85×10^{-5}	-10.29	4
Migration	-44.5	-9.14	5
Migration sex ratio $\times$ migration age structure	8.91	8.85	6
Population size $\times$ migration	-1.20×10^{-2}	-7.1	7
Harvest age structure	3.79	6.19	8
Population size	-3.42×10^{-3}	-6.16	9
Harvest sex ratio $\times$ migration	19.4	5.22	10
Migration $\times$ migration age structure	18.7	4.89	11
Harvest sex ratio	-47.4	-4.24	12
Migration sex ratio	-4.65	-4.12	13
Length of projection	2.59×10^{-3}	3.99	14
Harvest $\times$ migration	8.62×10^{-2}	3.91	15
Harvest age structure $\times$ migration age structure	-1.81	-3.64	16
Migration age structure	-3.65	-3.01	17
Harvest age structure $\times$ migration sex ratio	-1.49	-2.99	18
Harvest sex ratio $\times$ harvest age structure	-1.50	-2.87	19
Population size $\times$ harvest age structure	-5.77	-2.63	20
Migration $\times$ migration sex ratio	-9.71	-2.57	21
Harvest $\times$ migration age structure	-1.46×10^{-2}	-2.25	22
Harvest $\times$ migration sex ratio	1.33×10^{-2}	2.18	23
Harvest sex ratio $\times$ migration age structure ^a	-1.71	-1.52	24
Population size $\times$ migration sex ratio ^a	5.71×10^{-4}	1.26	25
Harvest $\times$ harvest age structure ^a	3.47×10^{-3}	1.14	26
Harvest age structure $\times$ migration ^a	1.32	0.73	27
Population size $\times$ migration age structure ^a	1.67×10^{-4}	0.37	28
Harvest sex ratio $\times$ migration sex ratio ^a	1.48×10^{-1}	0.14	29

^a Term not statistically significant at $\alpha = 0.05$.

For all our simulations, length of population projection was influential on risk of extinction within the time frame we used. The arbitrary thresholds in time, 25 years, 50 years, and 100 years, are in ecological terms a relatively short time

span of only approximately 5–20 generations for an animal like the wolverine. The great differences between extinction risks over these 3 intervals highlight that the time frame for which conservation and management actions are scheduled

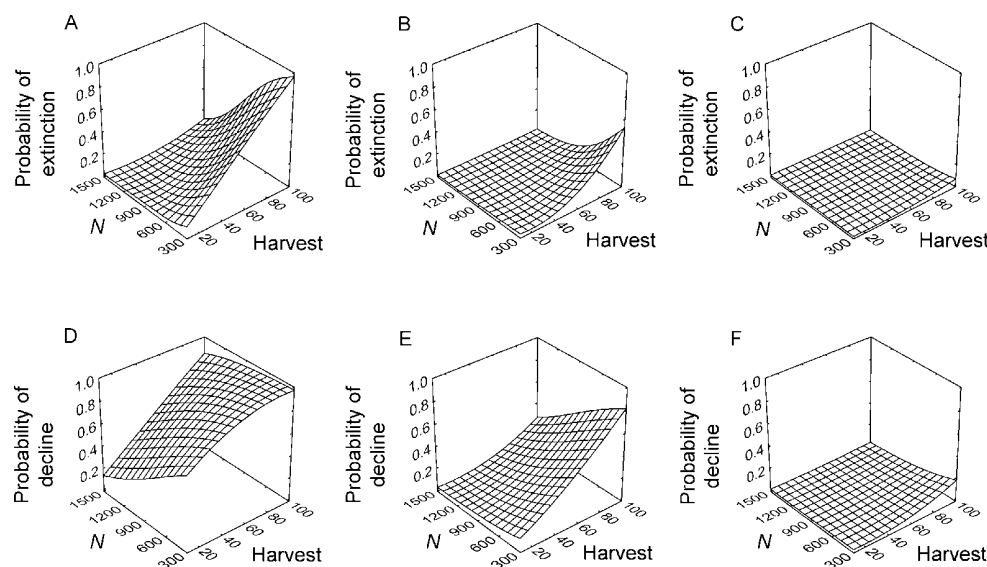


Figure 2. Effects of population size and harvest rates of wolverines on probabilities of wolverine population extinction in closed wolverine populations (A), in wolverine populations with 10% immigration (B), in wolverine populations with 20% immigration (C), and on probabilities of wolverine population decline for the same range of immigration values (D, E, F). We set sex ratio of harvested animals to 65% males and age structure of harvested animals to 25% adults. Probability values are given after 50 years of simulation.

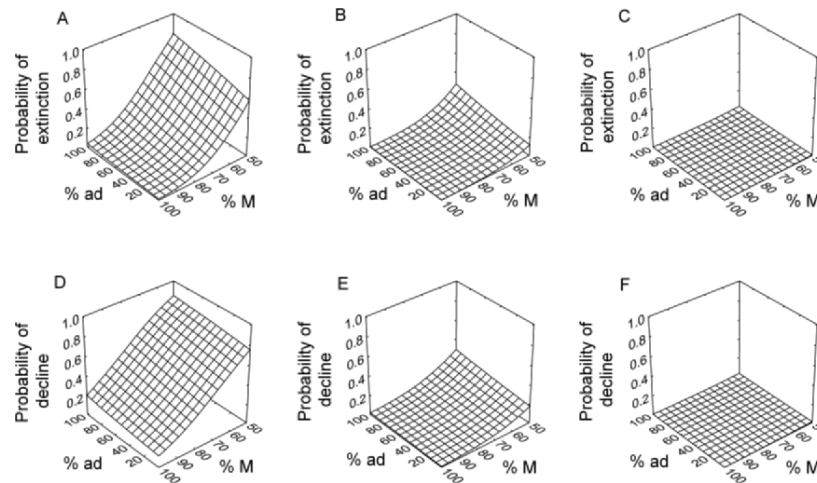


Figure 3. Effect of sex ratio and age structure of harvested wolverines on probabilities of wolverine population extinction in closed wolverine populations (A), in wolverine populations with 10% immigration (B), in wolverine populations with 20% immigration (C) and on probabilities of population decline for the same range of immigration values (D, E, F). We set population size to 500 animals and harvest to 50 animals/year. Probability values are given after 50 years of simulation.

is important for their long-term effectiveness. However, time scale of management actions is often a neglected aspect of resource management, and even the shortest time period we used, 25 years, is longer than what is in use for most current wildlife management plans.

Wolverines have low reproductive rates and high natural survival (Krebs et al. 2004, Persson et al. 2006). Therefore, it is not surprising that our models indicated that adult survival had a greater impact on wolverine population viability than did fecundity. However, the management implications are significant. Firstly, for a meaningful assessment of population viability, it will be more important to derive reliable estimates of survival than of fecundity for specific wolverine populations, which means that field studies, which are often limited in time and resources, should prioritize collection of survival data before data on reproductive rates. Secondly, in practical management it may be more important to control factors affecting survival than factors affecting reproduction and reproductive rates, which could, for instance, include limiting the level of sexually selected infanticide or controlling legal and illegal harvest (Persson et al. 2003, Sæther et al. 2005).

In line with the finding that adult survival is the most influential demographic parameter for wolverine populations, harvest was the most influential term in our simulations, which highlights that accurately estimating harvest levels must be an integral and prioritized component of wolverine population management. If such data cannot be reliably obtained harvest should be eliminated or substantially curtailed or the population under consideration should reside near a significant source population (see above). Furthermore, the effect of harvest seems to be influenced by harvest sex ratios, with a stronger effect of harvest on population persistence if the proportion of harvested females was high. However, because wolverine harvest generally seems to be male-biased, sex ratios may not be a concern in

most harvested populations (Lofroth and Ott 2007). Nonetheless, we suggest that sex ratio of harvested animals be routinely monitored and possibly controlled if harvest sex ratio approaches 50% females, for instance by a system with separate female quota restrictions (e.g., Swenson et al. 1994).

Our study adds to the growing number of efforts that use population modeling to evaluate population management and sustainable harvest in wolverines (Krebs et al. 2004, Sæther et al. 2005, Lofroth and Ott 2007). Although our conclusions to a large extent overlap with previous efforts, logistic regression has some distinct advantages because it provides a robust and simple statistical framework to compare different management and population scenarios within. Such a qualitative approach has been suggested as the most fruitful way of using PVA techniques (Bessinger and Westphal 1998), and we suggest an increased use of logistic regression techniques for modeling approaches to large carnivore management, which applies particularly to species where field data collection is expensive and logistically difficult. However, we must stress that exploratory modeling such as ours must not be regarded as a decision-making tool, but rather as one component of a decision support toolset (i.e., Starfield 1997).

MANAGEMENT IMPLICATIONS

The apparent impact of harvest on closed populations as well as effects of dispersal on local population persistence indicates that a spatial approach to harvest management may be required for wolverines, where refuge areas must be secured adjacent to harvested populations along with secure dispersal corridors. We emphasize that achieving accurate estimates of adult survival, including accurate estimates of harvest levels and of harvest sex ratio, must be a prioritized component of wolverine population management, as well as achieving reliable estimates of dispersal rates between and within populations.

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