Journal of Wildlife Management 74(8):1894–1903; 2010; DOI: 10.2193/2009-386

Tools and Technology Article

Coarse-Scale Distribution Surveys and Occurrence Probability Modeling for Wolverine in Interior Alaska

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ABSTRACT We determined wolverine (*Gulo gulo*) distribution and occurrence probabilities using aerial surveys and hierarchical spatial modeling in a 180,000-km^2 portion of Interior Alaska, USA. During 8 February–12 March 2006, we surveyed 149 of 180 1,000-km^2 sample units for wolverine tracks. We observed wolverine tracks in 99 (66.4%) sample units. Wolverine detection probability was $\geq$69% throughout the survey period. Posterior occurrence probabilities of whether a wolverine track occurred in a sample unit was dependent on survey timing, number of transects flown, number of neighboring sample units with detected tracks, percentage of the sample unit with elevation $\leq$305 m, and human influences. Our model indicated strong evidence of occurrence (>0.80) in 72% of the 180 survey units, strong evidence of absence (<0.20) in 12%, and weak evidence of occurrence or absence (0.20–0.80) in 16%. Wolverine area of occupancy made up 83% of the study area. Simulations illustrated that 2–4 survey routes were necessary for the survey technique to provide strong evidence of wolverine presence or absence in Interior Alaska if a track was not identified along the first route. The necessary number of survey routes depends on the occurrence probability in a sample unit. We provided managers with a map of wolverine distribution in Interior Alaska and an efficient and lower-cost method to detect coarse-scale changes in wolverine distribution. Our technique was effective in both Interior Alaska and Ontario, Canada, suggesting it would be effective throughout most of the boreal forest range of wolverines where tracks can be readily observed from the air. The technique requires a certain skill level in recognizing tracks; it is essential that tracks are identified correctly and training may be necessary depending on surveyor experience.

KEY WORDS detection probability, distribution mapping, *Gulo gulo*, hierarchical spatial modeling, Interior Alaska, occurrence probability, track survey, wolverine.

Wolverines (*Gulo gulo*) are found throughout Interior Alaska, USA (Manville and Young 1965), but little is known about local distribution and the habitat factors that affect wolverine occurrence. As a result, wolverine management in Interior Alaska is based on inferences from harvest data and incidental observations by biologists and trappers. Sole reliance on these sources of information is problematic because an unknown number of harvested wolverines are taken for subsistence purposes and are not reported, locations of harvest or observations are not verified, and there is no measure of trapper effort and relationship of effort to harvest levels (Alaska Department of Fish and Game 2007, McKelvey et al. 2008). The lack of empirical information on wolverine populations and distribution compromises science-based wolverine management and makes it difficult to assess the effects of changing land use patterns and harvest pressure on wolverine populations in Interior Alaska.

Wolverine distribution can be affected by habitat quality and availability (Carroll et al. 2001, Copeland et al. 2007, Krebs et al. 2007), predation risk (Copeland et al. 2007, Krebs et al. 2007), harvest (Krebs et al. 2004, Dalerum et al. 2007, Squires et al. 2007), and human disturbance including roads, recreation, and infrastructure (Carroll et al. 2001, Rowland et al. 2003, May et al. 2006, Krebs et al. 2007, Lofroth and Krebs 2007). In Interior Alaska, the current greatest management concerns for wolverine distribution contraction are trapping effects and increasing industrial development.

Wolverine trapping occurs at different intensities in both urban and remote areas throughout Interior Alaska (Golden et al. 2007*a*). Harvest from trapping is an additive source of mortality and sustained trapping can cause wolverine populations to decline without immigration from untrapped populations (Krebs et al. 2004, Dalerum et al. 2007, Squires et al. 2007). In Interior Alaska, the wolverine trapping season is 1 November–28 February in most areas, with no bag limit. Managers use reported harvest, percentage of males in the harvest, and availability of known refugia (i.e., national parks and other areas with no or light harvest) to monitor harvest effects and to make regulatory adjustments.

Human-caused landscape change has occurred and more is anticipated in Interior Alaska, which will reduce the quality and quantity of wolverine habitat and increase human access. Since the mid 1990s, Interior Alaska has experienced an increase in resource exploration and development, especially near Fairbanks and Delta Junction, Alaska, USA (Fig. 1; U.S. Environmental Protection Agency 2003, Fairbanks Gold Mining 2004). Future industrial growth may include agricultural development and oil, gas, and coal-bed methane extraction at numerous sites throughout Interior Alaska (Alaska Department of Natural Resources

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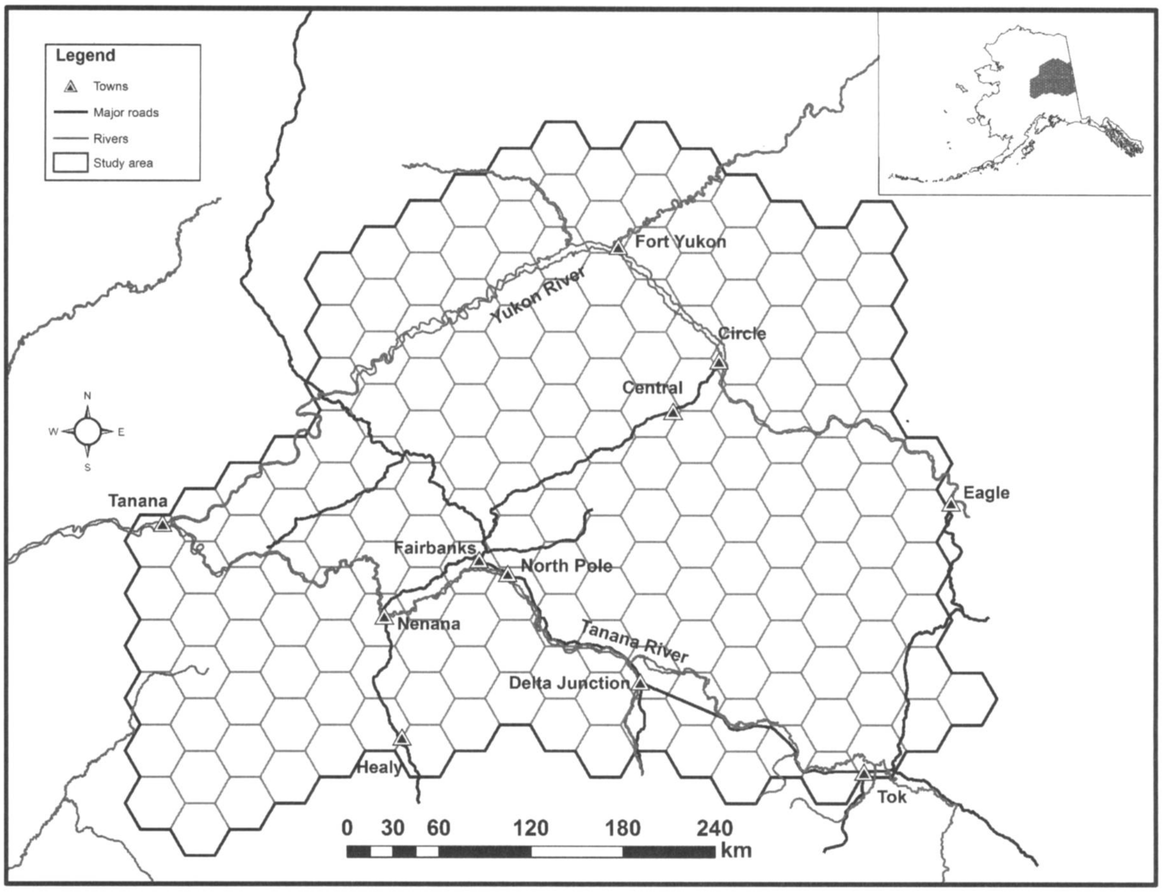

Figure 1. Wolverine distribution study area including hexagon sample units in Interior Alaska, USA, February–March 2006.

2004). Roads are being constructed and more are planned as industry and human habitation increases (Alaska Department of Labor and Workforce Development 2009), mostly into remote country that historically had limited human access and served as refugia from trapping for wolverines and other furbearers.

Because wolverines naturally occur at low densities, are difficult to see, and range widely, monitoring wolverines over large, remote areas the size of Interior Alaska, USA, is a challenging task for managers (Banci 1994). Magoun et al. (2007) delineated the extent of distribution and area of occupancy for wolverines in a 60,000-km^2 area in Ontario, Canada, using aerial surveys of tracks in snow and hierarchical spatial modeling. We modified the technique by Magoun et al. (2007) to survey a larger area (180,000 km^2) in Interior Alaska. Interior Alaska is an ideal location to conduct track surveys because alpine habitat and open canopy forests are common, allowing tracks to be easily located and identified from the air by trained observers (Magoun et al. 2007, Koen et al. 2008). Our objectives were to 1) establish a baseline map of wolverine distribution over a 180,000-km^2 area in central and eastern Interior Alaska, 2) model wolverine distribution and occurrence probabilities within the study area, and 3) identify habitat covariates and develop a sampling protocol to improve the models. Our goal was to improve wolverine management in Interior Alaska by providing a quantifiable and scientifically defensible methodology as the basis for management decisions and future research needs. In addition, we provide insight on the influence of human activity (harvest and infrastructure) on wolverine distribution.

STUDY AREA

Our study area was located in the subarctic boreal forest zone in central and eastern portions of Interior Alaska (63–67°N and 141–153°W; Fig. 1). Elevations ranged from 120 m to 2,000 m above sea level. Topography in the study area varied from flat lowlands to rugged alpine areas. At Fairbanks, Alaska, near the center of the study area, average snow cover and temperatures during mid-February and mid-March (1949–2005) were 53 cm and 51 cm of snow and −20.0° C and −11.7° C, respectively (National Oceanic and Atmospheric Administration 2009). Dominant trees included black spruce (*Picea mariana*), white spruce (*Picea glauca*), paper birch (*Betula papyrifera*), and aspen (*Populus tremuloides*). Primary shrub species were dwarf birch (*Betula* spp.), willow (*Salix* spp.), and alder (*Alnus* spp.). Tree line was at approximately 600 m elevation. Alpine vegetation was dominated by dwarf shrubs including dryas (*Dryas* spp.), dwarf willow (*Salix* spp.), blueberry (*Vaccinium uliginosum*), cranberry (*Vaccinium vitis-idaea*), and bearberry (*Arctostaphylos* spp.). Alpine tundra, waterways, and other open habitats (meadow systems, recent burns, and sparse forest) composed ≥48% of the study area (U.S. Geological Survey 2009*a*). The remainder of the area included open and closed forests;

<25% of forest stands had dense enough canopies to block aerial view of the forest floor.

Most human activity and development were located along the 5 highways that traversed the area. There were 4 communities with >1,000 inhabitants (Tok, Delta Junction, North Pole, and Fairbanks) in the southern portion of the study area (Fig. 1). The largest human population (approx. 87,000; U.S. Census Bureau 2006) was in the Fairbanks–North Pole area. Road densities were ≥0.44 km/km^2 in the Fairbanks–North Pole area and <0.2 km/km^2 in the remainder of the study area (Fig. 1). The only extensive agricultural area was located in the Tanana and Delta River valleys near Delta Junction. Other descriptions of ecological attributes of the area were provided in Gasaway et al. (1983, 1992), Bertram and Vivion (2002), and Ducks Unlimited (2002).

METHODS

We partitioned the study area into a grid of 180 1,000-km^2 hexagon-shaped sample units (Fig. 1), basing sample unit size on the approximate home range size for male wolverines (Gardner 1985, Magoun 1985, Whitman et al. 1986, Banci 1987). Koen et al. (2008) recommended 1,000-km^2 sample units for survey areas >100,000 km^2 because cost and logistical constraints of conducting the survey are considerable when sample units are small. In addition, such a large survey area precluded multiple visits (repeat surveys) to a sample unit to estimate detection probability. Therefore, we planned to survey each sample unit one time, using 1–4 survey routes during this single visit to estimate detection probability. We flew one survey route through each unit and, if we did not detect a wolverine track during this flight, we flew additional routes until we detected a track or until we completed 4 routes (i.e., removal method sensu MacKenzie 2005, MacKenzie and Royle 2005).

Hexagon-shaped sample units were efficient to survey because the 6 edges were equidistant from the center point providing multiple choices for survey routes, approaches, and exits (Fig. 2). The first 3 survey routes through a sample unit were from the midpoints of one of the sides through the center-point of the hexagon (Fig. 2). If we flew a fourth route, we did not pass through the center-point but included the segments travelling from the midpoints of the edges (Fig. 2). In each sample unit, there were 6 possible routes to choose from. Each route line was 32 km long. When we flew multiple routes through a sample unit, we completed them the same day to reduce the chance of changing detection probabilities (MacKenzie and Royle 2005). Optimal elevation for observing tracks varied with terrain, vegetation cover, and light intensity.

We followed the sampling protocol outlined by Magoun et al. (2007), which allows survey teams to deviate from the flight path to open habitats or forest stands to minimize time spent over areas of dense forests or wind-hardened snow where track detection was improbable. For this reason, actual flight distances and time spent in sample units differed slightly among units. Using a 2-tailed *t*-test (Zar 1984), we compared survey times along the first survey routes in sample units where we found wolverine tracks to those in sample units where we did not find tracks. We flew surveys on days with good lighting conditions and we did not survey ≤24 hours after either widespread snowfall ≥3 cm or windstorms with average winds >50 km per hour. There was no upper limit for number of days following snowfall or wind.

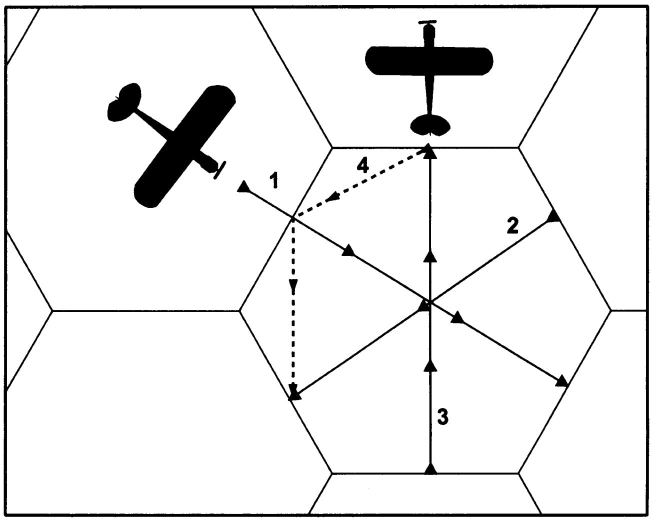

Figure 2. We surveyed sample units in Interior Alaska, USA, February–March 2006, by flying ≤3 transects using midpoint coordinates of the hexagon edges and the center point. The fourth transect included the segments traveling between the midpoints of the edges.

During 8 February–7 March 2006, we surveyed sample units using PA-18 Piper Super Cubs (Piper Aircraft Corporation, Lock Haven, PA) by flying low (100–250 m above ground level) and slow (approx. 120 km/hr) looking for tracks in the snow. We used 3 pilots (residents of Interior AK), each with >20 years of experience with aerial snow-tracking of wolverines, wolves, and other furbearers (2 of whom participated in the Magoun et al. 2007 study) and 2 observers (C. Gardner and J. Lawler) each with ≥3 years experience snow-tracking wolverines, wolves, and other furbearers. Teams spent as much time as needed to verify track identity to ensure against either false positives or negatives. Evidentiary standards we used were to follow any questionable tracks until we observed the 3-track diagnostic lope of wolverines or determined that the track was not made by a wolverine (McKelvey et al. 2008). In some situations we landed the plane for a ground inspection. We did not use tracks that remained questionable in our analysis (Sargeant et al. 2005). We considered a wolverine detected if we observed wolverine tracks in the survey unit in any of the 4 survey routes. To account for possible differences in pilot–observer teams, we included pilot–observer pairs as a covariate in our models of wolverine detection probability.

We used human influences (Carroll et al. 2001, Rowland et al. 2003, May et al. 2006, Krebs et al. 2007, Lofroth and Krebs 2007) and elevation (Copeland et al. 2007) as habitat covariates in our model. We recorded presence of snow machine trails and human development along the survey route. Because of the uncertainty of harvest data in portions of the study area we did not include it as a separate covariate.

However, harvest is part of human influences because harvest densities generally follow human population density patterns (Golden et al. 2007*a*). We summarized reported harvest during 1987–2006 at the watershed level to evaluate potential patterns with wolverine distribution. We categorized harvest as low (0–10; <0.5/yr), medium (11–21), and high (>21; >0.9/yr). We used total harvest instead of harvest density because harvest locations within a watershed were unknown and because watershed sizes varied (Golden et al. 2007*a*). For example, areas smaller than wolverine home ranges often had seemingly high harvest densities that were not biologically feasible.

To summarize available elevations in each sample unit, we used a 2-arc second digital elevation model (DEM; U.S. Geological Survey 2009*b*). We used ArcMap 9.3 to project the DEM into Albers 154 using the North American Datum 1927 and determined, based on the majority of 50-m pixels, the percentage of each sample unit $\leq$305 m. We considered elevations 1) $\leq$305 m to be "lowlands," which encompassed all the flat lands associated with large river valleys; 2) $\geq$915 m to be "high elevation," which included the higher, more rugged mountains; and 3) 306–914 m to be "midrange," consisting primarily of rolling hills.

To evaluate the possible preference of wolverines for steeper terrain, we used the Surface Areas and Ratios from the Elevation Grid version 1.2 extension (Jenness Enterprises ArcView 3.x, <http://www.jennessent.com/>, accessed 15 Jul 2010) and the Spatial Analyst extension in ArcView 3.2 to calculate a measure of terrain ruggedness for each pixel in the DEM. Terrain ruggedness is the ratio of the surface area to the planimetric area (Jenness 2004). We characterized terrain ruggedness for each sample unit by the mean ruggedness value for all pixels within the sample unit.

Data Analysis

To examine the validity of absence based on non-detections in sample units, we modeled the probability of wolverine occurrence in each unit based on landscape and human influence covariates and the detection of wolverine tracks in adjacent units. This allowed us to model probability of false negatives.

Our statistical methods followed Magoun et al. (2007), with some modifications. We let the observed occurrence of a track be y_{ij} for the jth transect (one flight transect across the sample unit, $j = 1, \ldots, n_i$) of the ith sample unit (sample unit, $i = 1, \ldots, N$), where $y_{ij} = 1$ if we observed a wolverine track and 0 otherwise. Our main concern was accounting for undetected wolverine presence in a sample unit. We used a hierarchical modeling framework (see a review by Cressie et al. 2009), where $\{y_{ij}\}$ forms the data model for the observation process and the variable x_i is 1 for true presence of a wolverine track and a 0 for track absence. In the language of Cressie et al. (2009), $\{x_i\}$ forms the ecological model that is our main interest. We set up our model hierarchically, where

$$P(\mathbf{y} \mid \mathbf{x}) = \prod_{i=1}^{N} \prod_{j=1}^{n_i} (x_i \theta_{ij})^{y_{ij}} (1 - x_i \theta_{ij})^{1-y_{ij}}.$$

If $x_i = 0$, then $P(0 \mid 0) = 1$ is a degenerate distribution where $y_{ij} = 0$ is the only outcome. However, if $x_i = 1$, then probability of observing the track follows a Bernoulli distribution, where probability of sighting is determined by the parameter θ_{ij}. Magoun et al. (2007) used a binary covariate (a before–after certain date covariate) to allow θ_{ij} to be affected by covariates. We used a continuous function of time for our model, because we did not see a reason for a sharp cutoff in date,

$$\text{logit}(\theta_{ij}) = \gamma_0 + \gamma_1 d_{ij}$$

where d_{ij} is the date (no. of days from 20 Feb) and γ_0 and γ_1 are parameters. We also had 3 pilots and 2 observers that occurred in 4 combinations (one observer only flew with one pilot and one pilot–observer pair only flew early in the survey period), so we included an effect for each pilot–observer pair. This factor was not significant (i.e., credibility interval did not include zero) and was somewhat confounded with date. Therefore, we removed it from the model.

We viewed $\{x_i\}$ as a spatial hierarchical model, allowing for autocorrelation. Classical statistical models assume independence among sample units; however, in our case nearby sample units might be similar for reasons including tracks crossing neighboring borders, proximity in space having similar habitats, and population dynamics such as dispersal. Unlike Magoun et al. (2007), we explicitly included additional covariates in this part of the model. Let

$$x_i \mid z_i, h_i \sim \text{Bernoulli}(\xi_i),$$

where

$$\text{logit}(\xi_i) = \alpha_0 + \alpha_1 \nu_i + \alpha_2 \phi_i + \sigma_z z_i,$$

and ν_i is the percentage of the sample unit $\leq$305 m elevation, ϕ_i is the log-mean of a Poisson regression model of human influences (e.g., roads–major trails, buildings, mines) observed within each sample unit, and z_i is a spatially autocorrelated random effect. We added the z_i term because autocorrelation will affect hierarchical occupancy models in much the same way as any spatial statistical model, affecting estimates and precision of those estimates. We computed ν_i for all sample units, including unsampled ones, from a DEM. However, we did not have counts of human influence (h_i), for unsampled units, so we used a spatially autocorrelated model to predict its value at unsampled units:

$$h_i \mid s_i \sim \text{Poisson}(\exp(\phi_i))$$

where $\phi_i = \omega + s_i$. Note that, through the hierarchical model, h forms a multivariate model with all other data and uncertainty in prediction of missing values is accounted for by the estimation method (below).

We took both $\{z_i\}$ and $\{s_i\}$ to have a conditionally autoregressive (CAR) model (see review in Cressie 1993) and the use of a CAR model as a random effect. The CAR model is specified conditionally,

$$z_i \mid \mathbf{z}_{-i} \sim \text{N}(\mu_i, \tau_i^2),$$

where

$$\mu_i = \frac{\beta_z}{|B_i|}\sum_{j\in B_i} z_j \quad \text{and} \quad \tau_i^2 = \frac{1}{|B_i|},$$

with B_i representing the set of neighbors of the ith sampling unit and $|B_i|$ as the number of neighbors. In our model, if any 2 sample units shared a border, we defined them as neighbors. Hence, an interior sample unit had 6 neighbors. The conditional specification resolved into a spatially autocorrelated multivariate normal distribution that we denoted $P_{CAR}(\mathbf{z}|\beta_z)$. Likewise, we have $P_{CAR}(\mathbf{s}|\beta_s)$ formulated in the same way, and we assume that $\mathbf{z}$ and $\mathbf{s}$ are independent of each other. Initially, we tried other covariates in the model one at a time, including presence–absence counts of potential prey and predator species sampled as well as snow machine tracks and a terrain ruggedness index. Of those, besides elevation and human influences covariates, only snow machine tracks and terrain ruggedness showed significant effects. However, snow machine tracks were collinear with human influence counts ($r = 0.58$) and terrain ruggedness was collinear with percent elevation ≤305 m ($r = 0.79$). When we added either of these to the model, neither the covariate nor its collinear pair were significant, so we only included human influences and elevation in the final model. We found that presence–absence data without a measure of abundance were not adequate to detect effects of predator–prey species on wolverine distribution and we did use them in the model.

To summarize, we have the following joint distribution formulated through the hierarchical model:

$$\begin{aligned} &P(\mathbf{y},\mathbf{x},\mathbf{z},\mathbf{h},\mathbf{s} \mid \boldsymbol{\gamma},\boldsymbol{\eta},\boldsymbol{\alpha},\boldsymbol{\beta},\sigma_z,\omega) \\ &\quad = P(\mathbf{y} \mid \mathbf{x},\boldsymbol{\gamma},\boldsymbol{\eta})P(\mathbf{x} \mid \mathbf{z},\mathbf{h},\boldsymbol{\alpha},\sigma_z) \\ &\qquad P_{CAR}(\mathbf{z} \mid \beta_z)P(\mathbf{h} \mid \mathbf{s},\omega)P_{CAR}(\mathbf{s} \mid \beta_s). \end{aligned}$$

In a Bayesian hierarchical model, we complete the full joint distribution by putting prior distributions on all parameters, $\pi(\boldsymbol{\gamma},\boldsymbol{\eta},\boldsymbol{\alpha},\boldsymbol{\beta},\sigma_z,\omega)$, so we obtain

$$\begin{aligned} &P(\mathbf{y},\mathbf{x},\mathbf{z},\mathbf{h},\mathbf{s},\boldsymbol{\gamma},\boldsymbol{\eta},\boldsymbol{\alpha},\boldsymbol{\beta},\sigma_z,\omega) \\ &\quad = P(\mathbf{y},\mathbf{x},\mathbf{z},\mathbf{h},\mathbf{s} \mid \boldsymbol{\gamma},\boldsymbol{\eta},\boldsymbol{\alpha},\boldsymbol{\beta},\sigma_z,\omega)\pi(\boldsymbol{\gamma},\boldsymbol{\eta},\boldsymbol{\alpha},\boldsymbol{\beta},\sigma_z,\omega). \end{aligned}$$

We only have observed data $\mathbf{y}$, so the desired posterior distribution of all quantities, given the observed data $\mathbf{y}$, is

$$\begin{aligned} &P(\mathbf{x},\mathbf{z},\mathbf{h},\mathbf{s},\boldsymbol{\gamma},\boldsymbol{\eta},\boldsymbol{\alpha},\boldsymbol{\beta},\sigma_z,\omega \mid \mathbf{y}) \\ &\quad = \frac{P(\mathbf{y},\mathbf{x},\mathbf{z},\mathbf{h},\mathbf{s} \mid \boldsymbol{\gamma},\boldsymbol{\eta},\boldsymbol{\alpha},\boldsymbol{\beta},\sigma_z,\omega)\pi(\boldsymbol{\gamma},\boldsymbol{\eta},\boldsymbol{\alpha},\boldsymbol{\beta},\sigma_z,\omega)}{P(\mathbf{y})} \end{aligned}$$

where $P(\mathbf{y})$ is the marginal distribution of $\mathbf{y}$ obtained by integrating over all other quantities in the joint distribution. This is an intractable analytical problem, but Markov chain Monte Carlo (MCMC) methods allow us to sample from the posterior distribution. To be complete, the prior distributions on the parameters were all $y_i \sim N(0,10)$, all $\eta_i \sim N(0,10)$, all $\alpha_i \sim N(0,10)$, all $\beta_i \sim UNIF(0,1)$, $\sigma_z \sim UNIF(0,10)$, and $\omega \sim N(0,10)$. Note that these are all broad but not excessive priors, because the logit function uses the exponential function, which can cause overflow or underflow in computing when values are too large or small. We considered these to be diffuse priors. Also note that we followed Magoun et al. (2007) and constrained spatial autocorrelation parameters β_i to be positive, because we did not expect any negative spatial autocorrelation.

We fit the model using MCMC sampling in OpenBUGS (Version 3.0.3 within BRugs package, Version 0.4-1, R, <http://www.r-project.org./>, accessed 13 Jul 2010). Markov chain Monte Carlo draws an autocorrelated sample from the posterior distribution. To avoid any dependence on starting values we used a burn-in of 10,000 iterations followed by 100,000 iterations (Link et al. 2002), where for storage purposes we only kept every 20th sample, yielding 5,000 MCMC samples from the posterior distribution of each quantity.

Following Sargeant et al. (2005), we characterized the estimated occurrence probabilities as strong evidence of occurrence (>0.80), strong evidence of absence (<0.20), and weak evidence of occurrence or absence (0.20–0.80). We investigated sampling intensities necessary to minimize the number of sample units with probabilities indicating weak evidence of occurrence or absence. We used our model to estimate the sampling effort needed to obtain strong evidence of occurrence or absence in 5 sample units (i.e., 189, 190, 220, 553, and 581) that had ambiguous results following our survey (Fig. 3a). The sample units we chose for simulation all had neighbors that we sampled. Sample units 189, 190, and 553 were near sample units in which we found strong evidence of wolverines being absent. Sample units 220 and 581 were surrounded by units with detected wolverine but were either connected to or close to a road system and were within 80 km of Fairbanks. We fixed the survey date at 20 February, the midpoint of our survey, for these simulations.

To determine effectiveness of our methodology for detecting wolverine population contraction in specific areas, we simulated survey intensities necessary to avoid false negative survey error at the 0.05–0.20 level; assuming we found no evidence of wolverines. We simulated changes in specific areas (sample units 611 and 202) within the original data set (Fig. 3a). Sample unit 611 had no human development, 100% of its elevation was >305 m, there was low reported harvest, and it was surrounded by 6 sample units where we detected wolverines. Sample unit 202 had 38% of its elevation ≤305 m, included a lightly travelled road, was within 45 km of Minto Village, Alaska, (population 258; U.S. Census Bureau 2006) and 72 km of Fairbanks, had low to moderate reported harvest, and was surrounded by 4 neighbors in which we detected wolverines. We maintained the fixed date of 20 February for these analyses.

RESULTS

From 8 February to 12 March 2006, we surveyed 10 days (6 days in Feb and 4 in Mar) and completed 149 of 180 sample units (83%). We did not sample remaining units because of weather or funding restraints. Of the 149 sample

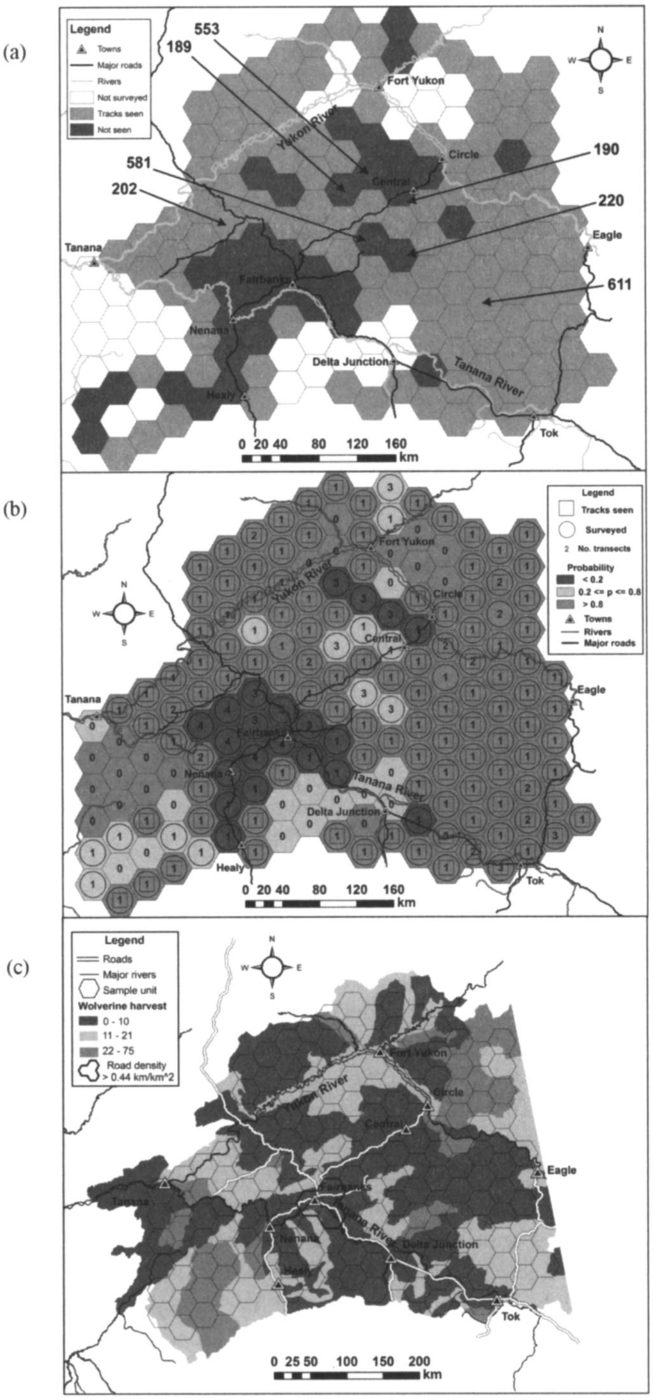

Figure 3. Results of the wolverine track survey in Interior Alaska, USA, in February–March 2006, illustrating (a) observed wolverine occurrence based on track sightings, (b) wolverine distribution based on modeled probability of occurrence, and (c) wolverine distribution based on historical trapping records, 1984–2007.

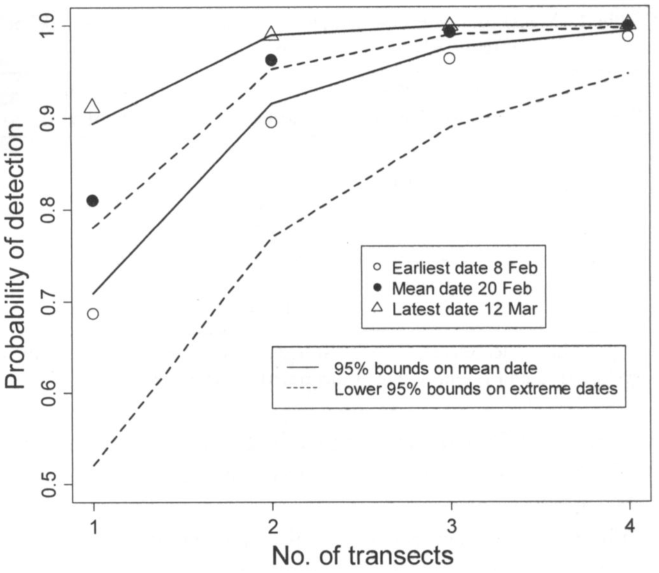

Figure 4. Probability of wolverine detection in 1,000-km^2 sample units in Interior Alaska, USA, during February and March 2006, based on number of transects and survey date.

units surveyed, we surveyed 118 (79%) once, 11 (7%) twice, 14 (9%) 3 times, and 6 (4%) 4 times. Average flight time per survey route was 22.3 minutes (SD = 6.25). There was no difference between time flown per survey route in sample units with detected wolverines compared to sample units where we did not detect wolverines ($P = 0.19$; $t_{(2)} = -1.29$).

We observed wolverine tracks in 99 (66%) sample units. Wolverine distribution was mostly contiguous. Notable absences occurred near Central, Alaska, along the Parks Highway from Nenana to Healy, and Fairbanks–North Pole (Fig. 3a). We detected wolverines in 58% of sample units during the first transect through each unit. By surveying a unit a second and third time, wolverine detections in all survey units increased to 64% and 66%, respectively. We did not identify any additional occupied sample units by conducting a fourth transect. We found evidence of human influences, excluding snow machine trails, in 22% of the 149 sample units surveyed. The area with the greatest amount of human impact in terms of development and access routes occurred near Fairbanks–North Pole. We categorized elevation in 77 (43%) sample units as lowland ($\leq$305 m). High elevation constituted 8% of the study area ($n = 15$) and was limited to the Alaska Range. The number of sample units with elevations in the midrange was 88 (49%).

Modeling results indicated that wolverine detection probability was >70% throughout the survey period. We also found that detection improved later in the survey period. We computed detection probability as the posterior distribution of

$$f(t;d_0)=1-\left(1-\frac{\exp(\gamma_0+\gamma_1 d_0)}{1+\exp(\gamma_0+\gamma_1 d_0)}\right)^t$$

where t is the number of transects, and d_0 is a specified date. There was a 0.81 probability (95% credibility interval 0.72–0.90) of detecting a track, given one was present, with one transect on the mean date of 20 February (Fig. 4). Detection probability approached 100% for $\geq$3 transects, with little improvement if we searched a sample unit 4 times compared to 3. In comparison, probability of detecting a wolverine track with one transect in an occupied sample unit was 69% (95% credibility interval 0.52–0.83) on 8 February and 91% (95% credibility interval 0.78–0.99) on 12 March (Fig. 4). Based on 95% credibility intervals for the extreme dates, to

Table 1. Model parameters estimating wolverine presence in a 1,000-km^2 sample unit in Interior Alaska, USA, 2006.

Parameter[a]	Lower 95% credible interval	Estimate	Upper 95% credible interval
γ_0	0.890	1.486	2.134
γ_1	−0.0001	0.0543	0.118
α_0	−0.908	1.306	4.045
α_1	−8.880	−4.907	−1.753
α_2	−4.117	−2.104	−0.881
β_z	0.033	0.579	0.987
β_s	0.827	0.944	0.996

[a] γ_0 is the model intercept, γ_1 is survey date, α_1 is elevation, α_2 is human development, and β_z and β_s are autocorrelation parameters.

ensure a >90% detection rate we had to fly ≥3 transects on 8 February, compared to 2 transects if we surveyed on 12 March.

The posterior occurrence probability of whether there was actually a wolverine track in a sample unit where we observed no tracks was dependent on survey timing (γ_1), number of transects flown, number of neighboring sample units with detected tracks, percentage of the sample unit with elevations ≤305 m, and modeled number of human influences in the sample unit (Table 1). Model results indicate that the odds ratio of occurrence probability significantly decreased by 0.085 with each percentage increase in lowlands (α_1). The odds ratio of wolverine occurrence probability also significantly decreased by around 0.98 with each number of human influences (α_2). Elevation and human influences were not correlated (Spearman's Rank correlation $P = 0.96$, $(r_s)_{0.05(2),158} = -0.004$). The autocorrelation parameter β_z was not different than the prior distribution, ranging from near zero to near 1, with a mean near 0.5 indicating little spatial pattern left in the random effects **z** after we accounted for the covariates elevation and human influences. The autocorrelation parameter β_s was near 1, with a range ≥0.8, indicating the human influences covariate was highly autocorrelated in space. For units not sampled, the estimated occurrence probability increased with number of neighbor sample units with wolverines but decreased with presence of human influences.

Using the occurrence probability model, we found strong evidence of occurrence in 72% (129, SE = 0.03) of 180 survey units, strong evidence of absence (<0.20) in 12% (22, SE = 0.02), and weak evidence of occurrence or absence (0.20–0.80) in 16% (29, SE = 0.03; Fig. 3b). We did not survey 22 (76%) of the sample units that had weak evidence of occurrence or absence. Overall, 84% of units showed either strong evidence of occurrence or strong evidence of absence. Observation data and modeled occurrence probabilities were consistent in indicating strong evidence of wolverine absence near Fairbanks–North Pole, along the Parks Highway from Nenana to Healy, and areas south and west of Circle (Fig. 3a, b). We found that harvest records were not a good indicator of wolverine distribution. Areas of low (53%), medium (33%), and high (14%) harvest were distributed throughout the study area with no clear association to strong evidence of presence or absence of wolverines (Fig. 3c).

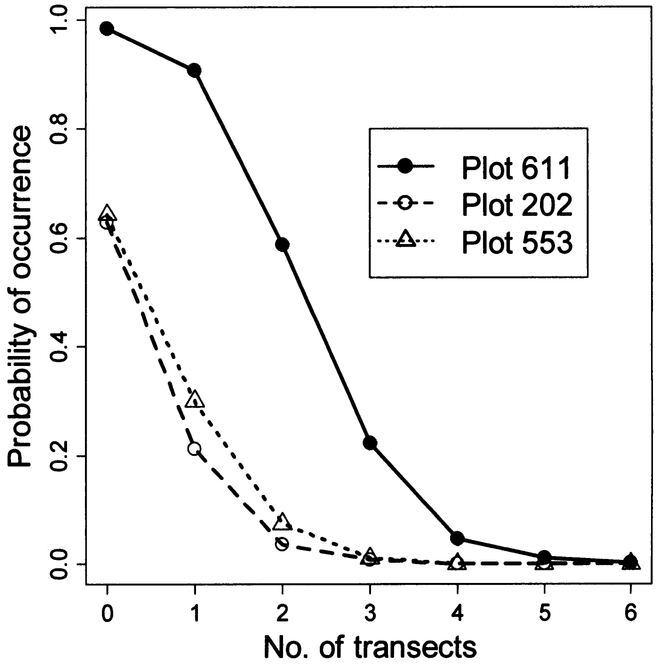

Figure 5. Simulated number of transects needed to detect changes in wolverine distribution from present to absent (sample units 611 and 202) and necessary sampling intensity to change from an ambiguous probability of occurrence (0.4) to a strong evidence of absence (sample unit 553) based on occurrence data collected during February and March 2006 in Interior Alaska, USA.

Sample units with ambiguous occurrence probabilities were most common in the southwest and southern portions of the study area and west of Central (Fig. 3b). In the south and southwest portions, we either did not sample or surveyed most sample units only once because of weather or funding restraints. In addition, we did not sample 1–5 of their neighbors. In contrast, we sampled units 189, 190, and 553 (Fig. 3a), west of Central, either 1 or 3 times but found either weak evidence of occurrence or absence. All 3 sample units had low reported historical wolverine harvest. Of neighboring units, the 4 units adjacent to the north had strong evidence of wolverine absence (Fig. 3b) and the 4 units to the northwest had high historical harvest (Fig. 3c). We surveyed sample unit 189 (probability of occurrence = 0.22) 3 times, and it had zero human developments, it was hilly and had 32% of its elevation >305 m, and 5 of its neighbors had strong evidence of wolverines. We surveyed sample unit 190 (probability of occurrence = 0.69) once, and it had limited human developments (one sparsely travelled road), 85% of its elevation >305 m, and 3 neighbors with strong evidence of wolverines. We surveyed sample unit 553 (probability of occurrence = 0.40) once, and it had limited human development (few structures), 97% of its elevation >305 m, and 2 neighbors with detected wolverines. Assuming we did not find evidence of wolverines, simulations estimated that 4, 3, and 2 transects were required for sample units 189, 190, and 553, respectively, to verify a probability of occurrence <0.20 (Fig. 5).

Sample units 220 and 581 (Fig. 3a) also had ambiguous occurrence probabilities of 0.29 and 0.24, respectively. We surveyed both sample units 3 times, and both had zero human developments recorded, 100% of elevation >305 m, and 5 neighbors with strong evidence of wolverines. Reported historical harvest was low in sample unit 581 and moderate in sample unit 220. Simulations indicate we needed to fly these areas 4 times without detecting wolverines to get occurrence probabilities <0.2.

Simulations testing our ability to detect substantial contraction (areas of occupancy becoming absent of resident wolverines) in wolverine distribution found that 4 transects without detecting wolverines were needed in sample unit 611 to declare strong evidence of absence (Fig. 5). Estimated probability of occurrence based on neighbor, elevation, and human influence covariates was 0.98 in sample unit 611 prior to any surveys. In comparison, in sample unit 202, probability of occurrence was 0.63. Sample unit 202 was bordered by 2 units with strong evidence of wolverine absence. Simulations required only 2 transects without detection to declare this unit had a strong probability of absence.

DISCUSSION

We modified the Magoun et al. (2007) sampling protocol in 2 ways: 1) we increased the size of sample units to 1,000 km^2 from 100 km^2 and 2) we surveyed using a removal design instead of a standard design (MacKenzie and Royle 2005). Our sample unit size approximated the home range of a resident male wolverine. Based on documented home range sizes from Alaska and Yukon, Canada (Gardner 1985, Magoun 1985, Whitman et al. 1986, Banci 1994), the 1,000-km^2 area we used could support ≥1 resident male, 3–5 resident females, and variable numbers of subordinate or transient wolverines. Completing 4 survey routes through a 1,000-km^2 sample unit subdivided the unit into 166.7-km^2 blocks. Resident female home range sizes from other wolverine studies averaged 100–400 km^2 and were smaller than those of resident males and transient animals (Banci 1994). Therefore, the larger sample unit size we used ensured that we detected occupancy, regardless of the sex or age class of the wolverine in residence (MacKenzie 2005), and followed the recommendation of Koen et al. (2008) to maximize survey efficiency.

We used the removal method of sampling following the recommendation of MacKenzie (2005) for sampling rare species. Based on results from Magoun et al. (2007), and because we used larger sample units, we expected detection probability to be >0.5 for any single survey route (Field et al. 2005, MacKenzie 2005, MacKenzie and Royle 2005). Because of our high detection probability (≥69%), surveying 3–4 survey routes in a sample unit without detecting a wolverine provided strong evidence of wolverine absence.

Our survey technique provided sufficient statistical power to estimate wolverine occurrence in a 180,000-km^2 area of Interior Alaska in just 13 survey days. Based on criteria proposed by Sargeant et al. (2005), we achieved an unambiguous estimate of wolverine distribution in Interior Alaska by having >70% of sampling units with either strong evidence of presence (>0.80) or strong evidence of absence (<0.20). Using occupancy probability limits (>0.50) defined by Magoun et al. (2007), the core area of occupancy for wolverines was 83% of the study area, illustrating that wolverines are distributed throughout Interior Alaska. Our results indicate that managing wolverines over a large area using harvest data (the current management system in Interior AK) can give erroneous results; historical low harvests may be associated with areas devoid of wolverine and areas of high harvests may still support resident wolverines.

Wolverine presence was positively associated with elevation and negatively associated with human influences. Others have reported that wolverines are commonly associated with high-elevation habitats (Copeland et al. 2007, May et al. 2008) and avoid areas of human development and use (Carroll et al. 2001, Rowland et al. 2003, May et al. 2006, Krebs et al. 2007). Copeland et al. (2007) noted the possibility that spatial separation of wolverines and human infrastructure was not a cause–effect relationship but rather due to wolverines' tendency to select for high-elevation remote habitats generally inhospitable to human development. Our study, however, lends evidence that wolverines prefer higher habitats and also avoid human influences, based on our observation that both elevation and human influence had significant effects on wolverine occurrence probabilities and yet were not correlated. Our sampling design did not allow us to identify what aspects of human influences were correlated with wolverine distribution but we contend it was most likely a combination of development intensity and harvest.

Our methodology allowed us to estimate wolverine presence (72%) or absence (12%) with a high degree of confidence. Areas with strong evidence of occurrence were distributed throughout the study area (Fig. 3b) and included all elevation categories. There were 2 distinct areas that did not support resident wolverine: the road system between Fairbanks–North Pole to Healy and around Circle–Central (Fig. 3b). These areas were primarily low elevation and differed from other low elevation areas with high probabilities of wolverine occurrence in the amount of human influences that occurred. The Fairbanks–North Pole area included the highest levels of human presence and development and historically low harvest (Fig. 3c). West of Fairbanks, along the Parks Highway between Nenana and Healy (Fig. 3b), the magnitude of human development was small, consisting of 4 small communities (population = 1,170; U.S. Census Bureau 2006) and few roads. However, this area was intensively trapped during 1984–2006 (Fig. 3c). The area around Circle and Central had little human development. Harvest records indicated few wolverines were caught in these sample units during 1984–2006 (Fig. 3c), although known but unreported subsistence harvests of wolverines make it difficult to determine the actual take (Alaska Department of Fish and Game 2010). This comparison of low elevation areas indicates that wolverines in Interior Alaska can persist even in lower-quality lowland habitats except where harvest and human influences are high.

For this survey and modeling technique to be most valuable for managers the number of sample units with ambiguous results needs to be small. In our survey, 25 sample units (13.9%) had weak evidence of absence or presence. In all cases, this ambiguity would have been eliminated by increasing the number of survey routes flown. Our simulations (Fig. 5) illustrated that, depending on the occurrence probability in a sample unit, 2–4 transects were necessary for this technique to provide strong evidence of wolverine presence or absence in Interior Alaska if we did not identify a track along the first survey route. This level of survey intensity agrees with simulations conducted by MacKenzie and Royle (2005) and Field et al. (2005).

All 4 sample units with ambiguous results after completing 3 transects were mostly surrounded by units with high occurrence probabilities and had zero to little human influences. Furthermore, 3 of the 4 units offered high elevation habitats. Collectively these conditions favor wolverine presence and, coupled with a high detection rate, would require ≥4 transects without observing evidence of wolverines to infer absence and guard against a false negative.

Our technique has a variety of safeguards to ensure against incorrectly classifying presence or absence. Spatial autocorrelation between sample units, elevation, human influence, and number of survey routes all significantly influenced wolverine occurrence probability for a sample unit and helped minimize the chance of false negatives. Furthermore, surveyors and track identification criteria met evidentiary standards to confirm detection (McKelvey et al. 2008).

In areas such as Interior Alaska where managers need to identify occupied and unoccupied wolverine ranges on a large scale (180,000 km^2) our survey technique proved effective in developing a map of wolverine occupancy. Success of this technique in Ontario, Canada, and Interior Alaska also suggests the technique is appropriate for monitoring wolverine distribution in mixed boreal forest and tundra habitats where sightability is adequate.

MANAGEMENT IMPLICATIONS

We provided managers a map of wolverine distribution in Interior Alaska and an efficient and lower cost method to detect coarse-scale changes in wolverine distribution. Using commercial operators we surveyed 149,000 km^2 for US$0.11/km^2 (2006 dollars; Super Cub rates at US$185.00/hr) during 13 survey days. This technique was effective in both Interior Alaska and Ontario, Canada, suggesting it would be effective throughout most of the boreal forest range of wolverines where tracks can be readily observed from the air. The technique requires that tracks are identified correctly and therefore training may be necessary, dependent on surveyor experience.

Our simulations suggest that a conservative monitoring strategy would include 4 sample routes per sample unit to ensure at ≥80% confidence that tracks are truly absent. However, the use of covariates allows a more efficient strategy in which sampling effort can be focused in areas favorable for track occurrence (up to 4 routes) and less effort (2 routes) in units that are less favorable. Managers should attempt to sample all sample units, but if situations arise that prevent some from being completed then it is better to spread the unsampled units across the study area to maximize the benefits of spatial autocorrelation. Although we fixed the survey date at 20 February for these simulations, our results indicate additional efficiency could be gained by surveying in March rather than February provided snow conditions do not deteriorate.

We found that this technique could detect distribution contraction following intensive sampling at <5% probability of occurrence (Fig. 5). However, because the technique had such a high detection rate, managers may not recognize distribution contraction until the area is essentially absent of wolverines. We thus conclude that high detection rates of wolverines in Interior Alaska and informative covariates make this technique effective for detecting large-scale (e.g., study area) contraction in wolverine distribution but is inadequate for portraying fine-scale (e.g., 100 km^2) changes in occupancy. If contraction in a specific location is a management concern, then managers should use a technique that provides better estimates of wolverine numbers. We suggest resurveying using smaller sample units (100 km^2; Magoun et al. 2007) or using alternative methods such as the population survey of Becker et al. (2004) or Golden et al. (2007*b*).

ACKNOWLEDGMENTS

The National Park Service and Federal Aid in Wildlife Restoration Project 7.21 under grant W-33-3 provided financial support. We thank B. Taras, S. Brainerd, L. McCarthy, G. Roloff, and 2 anonymous referees for their editorial comments to this manuscript. N. Pamperin assisted constructing the figures. We particularly want to thank M. Webb, P. Valkenburg, and P. Zaczkowski for many hours of safe flying and discussions on wolverine movements.

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Associate Editor: Roloff.