Modeling Wolverine Occurrence Using Aerial Surveys of Tracks in Snow

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ABSTRACT We designed a novel approach to determining extent of distribution and area of occupancy for wolverines (*Gulo gulo*) by using aerial surveys of tracks in snow and hierarchical spatial modeling. In 2005 we used a small, fixed-wing aircraft with pilot and one observer to search 575 of 588 survey units for wolverine tracks in approximately 60,000 km^2 of boreal forest in northwestern Ontario, Canada. We used sinuous flight paths to scan open areas in the forest in the 100-km^2 survey units. We detected tracks in 138 (24%) of the 575 sampled units. There was strong evidence of occurrence (probability of occurrence >0.80) in 30% of the 588 survey units, weak evidence of occurrence (0.50–0.80) in 12%, weak evidence of absence (0.20–0.50) in 15%, and strong evidence of absence (<0.20) in 43%. Wolverine range comprised 59% of the study area and area of occupancy was 33,400 km^2. With information on probability of occurrence and core areas of occupation for wolverines in our study area, resource managers and others can examine factors that influence wolverine distribution patterns and use this information to formulate best management practices that will maintain wolverines on the landscape in the face of increasing resource development. Comparing future survey results with those of our 2005 survey will provide an objective way to assess the efficacy of management practices. (JOURNAL OF WILDLIFE MANAGEMENT 71(7):2221–2229; 2007)

DOI: 10.2193/2006-372

KEY WORDS distribution map, *Gulo gulo*, hierarchical spatial modeling, occupancy, Ontario, track survey, wolverine.

In 2004 the Ontario Ministry of Natural Resources (OMNR) listed the wolverine (*Gulo gulo*) as threatened on the Species at Risk list for the province, in part because historic accounts, fur-trapping records, and incidental observations (sightings and animals killed on roads) indicated that wolverine range had receded from southern portions of the province by about 1900 and from portions of northern Ontario, Canada, since about 1955 (Dawson 2000). However, fur-trapping records may not reflect actual distribution of wolverines because of a number of factors including uneven distribution of trappers and differences in trapping effort. Moreover, historic records and unverified sightings are often unreliable and may overestimate species distribution (Frey 2006, Aubry et al. 2007). Concerns about the possible effects of proposed resource development on wolverine distribution in northern Ontario (Dawson 2000) prompted us to develop a method for modeling distribution of wolverines using aerial surveys of tracks in snow, the only feasible means of detecting wolverines over large, remote regions of northern Ontario. Unlike other methods that require tracking wolverines in winter from aircraft (Becker 1991, Becker et al. 2004), a survey technique for northern Ontario must be efficient and economical to apply over large areas (>50,000 km^2) of forested habitat and cannot require that all fresh wolverine tracks be detected and followed forward and backward. Furthermore, the modeling approach must deal with imperfect detection of tracks and autocorrelated data. Because we knew of no published method of surveying wolverines that fit these specifications, we designed a new aerial survey technique and used readily available software to implement a hierarchical spatial model that estimates probability of occurrence. Specifically, our objectives were to 1) model probability of occurrence of wolverines using tracks in snow in forested habitat in northwestern Ontario, 2) produce a map of wolverine distribution in our study area, and 3) define extent of occurrence and area of occupancy as objective metrics of distribution. This information would serve as a baseline reference with which to compare future patterns of wolverine distribution following large-scale habitat change as human developments expand farther into wolverine range.

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STUDY AREA

Our study area (approx. 60,000 km^2) was located in the Boreal Shield Ecozone of northwestern Ontario (49–51° N and 90–96° W; Fig. 1a). Mean elevation in the study area is 390 m (SD = 29; range = 300–520 m). The main tree species were white and black spruce (*Picea glauca* and *Picea mariana*, respectively), jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), tamarack (*Larix laricina*), birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*). Lichens, shrubs, or forbs dominated the ground cover, depending on the forest community. Water bodies comprised approximately 20% of our study area, and other open habitat types included open fen, treed fen, open bog, treed bog, sparse coniferous forest, sparse deciduous forest, recent cutovers, and recent burns.

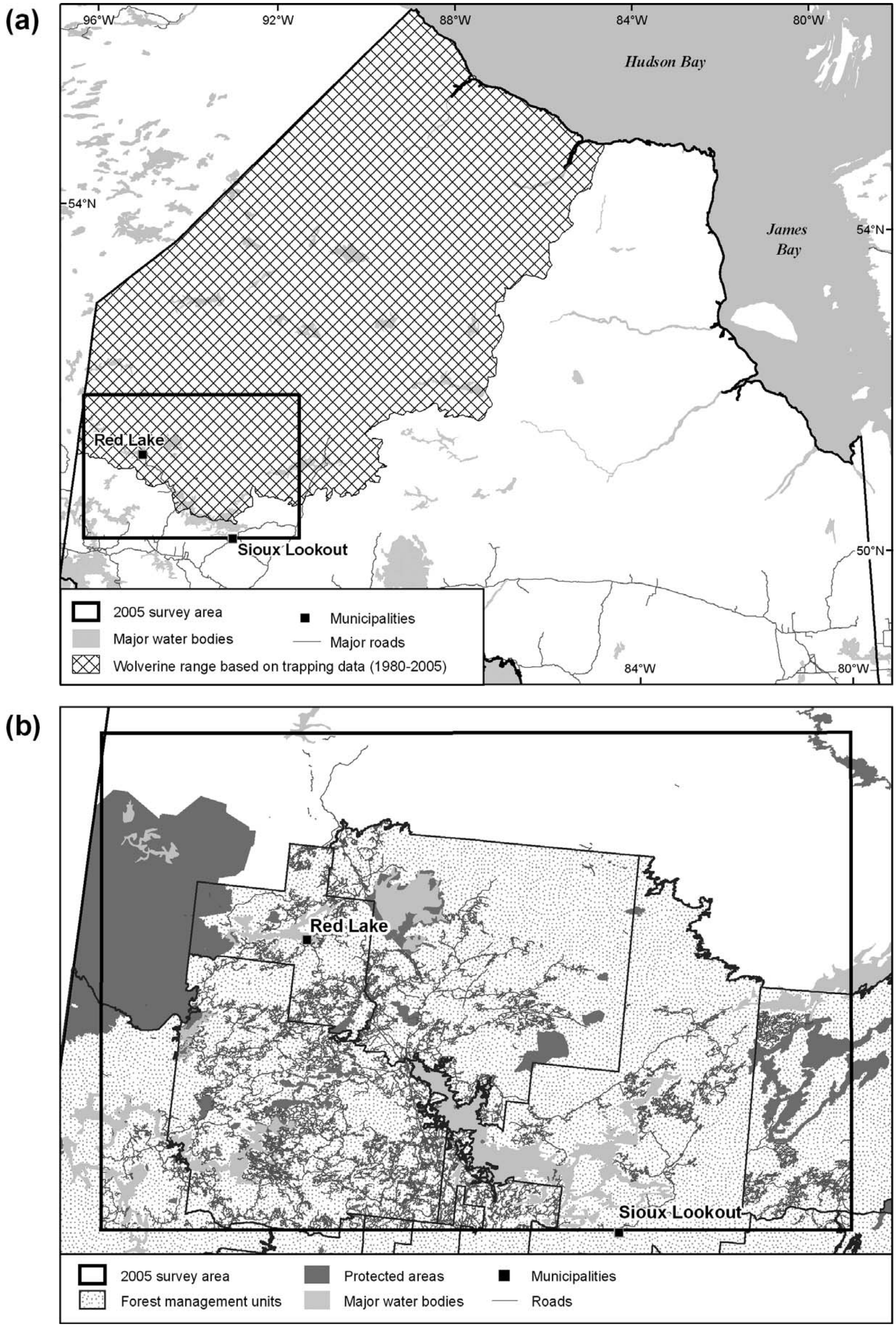

Figure 1. Location of our wolverine track survey in northern Ontario, Canada in 2005 showing (a) location of the study area in relation to wolverine distribution based on fur-trapping data (Ontario Ministry of Natural Resources) from 1980–2005, and (b) land classifications and human footprint in the survey area.

These open habitats where wolverine tracks were detectable were well-distributed across our study area and comprised >50% of the area (OMNR Ontario Provincial Land Cover; Landsat Thematic Mapper imagery compiled in 2000). Forest stands with canopies dense enough to block the view of the forest floor from survey aircraft comprised <25% of our study area. These stands were mature jack pine or a mix of jack pine and white and black spruce with trees >10 m tall and a stocking density >70%. Roads, logging, mining, and other human developments were most numerous in the southwest portion of the study area (Fig. 1b). Mammals, other than wolverine, for which tracks in snow were detectable from survey aircraft included moose (*Alces alces*), caribou (*Rangifer tarandus*), white-tailed deer (*Odocoileus virginianus*), wolf (*Canis lupus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), lynx (*Lynx canadensis*), river otter (*Lontra canadensis*), fisher (*Martes pennanti*), marten (*Martes americana*), mink (*Neovison vison*), beaver (*Castor canadensis*), and snowshoe hare (*Lepus americanus*). Tracks of fisher, which were most similar to those of wolverine, were concentrated in the western half of the study area and particularly in the southwest quadrant. Details on vegetation, physiography, climate, forest succession, and other ecological attributes of the region are provided in Perera et al. (2000).

METHODS

In January–March of 2005, we used a PA-18 Super Cub (Piper Aircraft Corporation, Lock Haven, PA) equipped with wheel-skis, with a survey team comprised of the pilot and one observer, to search for wolverine tracks. We chose this 2-seat, tandem aircraft because of its proven suitability for wolverine track surveys in Alaska, USA (Becker 1991, Becker et al. 2004) and the ability of both pilot and observer to see the ground on both sides of the aircraft. The aircraft was highly maneuverable with a tight turning radius and slow stall speed. Groundspeed was usually 110–140 km per hour. Survey altitude was approximately 200 m above the ground but varied between 100–300 m over hilly terrain. We waited $\geq$24 hours before flying survey routes after widespread snowstorms that deposited $\geq$3 cm of fresh snow or after windstorms with average wind gusts of >50 km per hour. We flew on days with sunny or bright overcast skies when wind conditions were favorable for circling over tracks and safely maneuvering the aircraft at low levels. We had no upper limit for number of days after a fresh snowfall and we considered all detected wolverine tracks as evidence of occurrence regardless of track age or condition.

We divided the study area into a tessellation of 100-km^2 hexagons, which allowed for up to 6 neighboring units of equal distance from the sampled unit and with boundaries of equal length. We based our survey unit size on what we considered a minimum home range size of resident female wolverines in Ontario. A radiocollared resident female in our study area had a home range of about 300 km^2 (95% min. convex polygon) in 2004 (F. N. Dawson, OMNR, unpublished data) but home ranges of resident females in other study areas averaged 100–400 km^2 and were smaller than those of resident males or young transient animals (Banci 1994). Use of larger survey units would have resulted in higher occurrence probabilities given the same occurrence distribution (MacKenzie et al. 2006) but would have provided lower resolution of spatial characteristics of occurrence. Given our survey unit size, all home ranges had the potential to be included in a survey route. Prior to beginning the surveys, we plotted flight routes through the centers of survey units and determined the coordinates of the centers (ArcGIS Version 9.0). A flight route entered one side of a unit, passed through the center, exited another side (not necessarily the opposite side), and then entered the next unit on a heading toward the center of that unit. Because of the hexagonal shape of the units, we had 6 compass headings to choose from when establishing flight routes. Whenever possible, we aligned routes along a long line of survey units to avoid having to frequently adjust headings during the survey. The distance across a survey unit was about 10 km but pilots used a sinuous flight path to maneuver the aircraft over open habitats or forest stands where the forest floor was visible, minimizing time over forest canopies where track detection was not possible. The mean and median sizes of these stands were only 45 ha and 8 ha (SD = 338), respectively, so circumventing the stands during the survey flights did not cause large deviations from the designed flight paths. Deviations were not >1 km and were usually much less because of the amount and distribution of openings where tracks could be detected. We recorded the location of wolverine tracks using the Global Positioning System (GPS).

The length, shape, and direction of a flight route depended on local weather conditions on the day of the flight, day length, location of airstrips with aviation fuel, and number of times we had surveyed units previously. A priori knowledge of wolverine distribution from trapping records (Dawson 2000) suggested wolverines were less abundant in the southern portion of our study area and possibly in the eastern portion as well, so we aligned survey routes to sample northern and southern or eastern and western portions of the study area (or both) on the same day whenever possible. In that way, regions of the study area with different levels of wolverine abundance were likely to be surveyed under similar tracking conditions, thereby breaking any correlation with sources of variation in detection probability caused by variable tracking conditions (MacKenzie and Royle 2005). We determined potential flight routes before beginning the survey, distributing them evenly across the study area in space and time. Weather conditions often dictated which route we could survey and whether we could complete it on any particular day. If we could not complete the survey route in its entirety, we noted the GPS location where the flight ended and used it to determine the last sampled unit for that route. We could then select another survey route where conditions were suitable. To use flight time efficiently and obtain the largest possible number of samples (both sampled units and repeated surveys of sampled units) given the time and money available for the survey, we minimized ferry time to and from survey routes, using most flight time for surveys and surveying all units along the routes, regardless of the number of times we had surveyed units previously. When we flew a unit twice on the same day (i.e., the route crossed back over itself), we used a different heading through the unit in order to survey a different area of the unit. We surveyed up to 50 units per day and plotted track locations only after we completed the route. While flying a particular heading, we did not know which unit we were surveying except for the first and last unit on that leg. Therefore, previous track history in a sampling unit did not influence detection on subsequent surveys of the unit.

Members of the survey team were experienced at locating wolverine tracks from the air. The pilot (P. Valkenburg) was a professional wildlife biologist with >25 years experience snow-tracking wolverines and other wildlife from aircraft in Alaska and 3 months experience tracking in forested areas of northern Ontario in 2004. Both persons alternating as observers (A. Magoun and J. Ray) had 2 seasons tracking wolverines in the study area prior to the survey. To identify tracks, we used a combination of track size, shape, depth, and gait but most importantly track pattern, which included changes in types and spacing of different gaits because of different habitats and snow conditions. In addition, we used body print patterns in deeper snow and behavior of the animal to help identify tracks. We spent as much time as needed to verify the identity of tracks, including circling tracks, following tracks to observe changes in track pattern or behavior, following fresh tracks until we saw the wolverine, and landing the aircraft to investigate tracks on the ground. For the experienced survey team, wolverine tracks were usually easier to identify from the air than from the ground, especially if tracks were not fresh or were following or mixed in with tracks of other species. Long segments of track were visible from the air making it easier to discern track patterns, and tracks could be followed at a rate of >1 km per minute to observe changes in track patterns and behavior of the animal. The 3× lope (Halfpenny et al. 1995) with different stride lengths (depending on rate of travel) is the most common gait that wolverines use. Wolverines also use a 2× track pattern, a walking gait, and, less commonly, a galloping gait and a bounding gait in deep soft snow. When we observed the latter gaits, we followed the tracks until we saw the characteristic 3× lope. Fishers have a similar range of track patterns but tracks of large male fishers in our study area were considerably smaller than tracks of small female wolverines. We could also distinguish fisher tracks from those of wolverines by more frequent changes in track pattern by fishers, differences in behavior (e.g., more frequent nonlinear travel by fishers), and a generally narrower track pattern for fishers. If there was any doubt about a track, we did not include it in our analysis to avoid false positives (Sargeant et al. 2005). After we investigated a track, we returned to the route heading.

We used a hierarchical spatial-modeling approach (Banerjee et al. 2004) to map probability of occurrence of wolverine tracks, which was similar to that of Sargeant et al. (2005) for modeling species distribution using ground-based track surveys. We also used a subset of our survey data to model the effects of reduced sampling effort (≤2 surveys/sampled unit) on pattern of occurrence. Because of similarities in modeling framework to that of Sargeant et al. (2005), we used the same notation for corresponding model components in the following description:

The variable x_i denotes the true presence or absence of a wolverine track in sampling unit $i = 1, \ldots, S$ (takes values 1 or 0, respectively). Rather than assume occurrence was constant (i.e., wolverine tracks were either always present or always absent in the sampling units during the survey), we assumed movement in and out of a sampling unit was random (MacKenzie et al. 2006). We also assumed that permanent immigration or emigration to and from the study area did not occur during the survey; none of 7 wolverines that we radiotracked in 2004 left the study area during the January–March period in 2004 (F. N. Dawson, unpublished data). Spatial association is expected to occur in the joint distribution of $\mathbf{x} = (x_1, \ldots, x_S)$ for 3 reasons. First, it is possible that wolverine tracks cross over into neighboring survey units and are detectable in >1 unit because a wolverine home range might overlap several units. Second, it is likely that survey units close in space share similar environments making it more likely that they will also possess or fail to possess wolverine tracks. Finally, offspring of resident females may live in or near their mother's home range for up to 28 months before dispersing (Magoun 1985, Vangen et al. 2001).

Sargeant et al. (2005) modeled spatial association in the joint distribution of $\mathbf{x}$ through use of an autologistic model (Besag 1974). We took a slightly different approach that is computationally simpler but similar in spirit. Instead of directly modeling the conditional distribution of x_i given occurrence values at all other sites, $\mathbf{x}_{-i}$, as in the autologistic model, we incorporated a latent continuously valued auxiliary variable vector $\mathbf{z} = (z_1, \ldots, z_S)$. The vector $\mathbf{z}$ can be thought of as a combination of several unobserved environmental covariates, such as cover type or prey density. (We used the term "auxiliary" because it can also be thought of as simply a tool to construct a distribution model for $\mathbf{x}$, which is easy to sample in a Markov Chain Monte Carlo [MCMC] context). Conditional on a realization of $\mathbf{z}$, we modeled the x_i as independent Bernoulli random variables with parameter logit $\xi_i = \alpha + \sigma z_i$. To induce spatial association in $\mathbf{x}$, we modeled the vector $\mathbf{z}$ with a conditionally autoregressive (CAR) distribution. The CAR model is defined by the conditional normal distributions

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

where

$$\mu_i = \frac{\beta}{|n(i)|} \sum_{j \in n(i)} z_j \text{ and } \tau_i^2 = \frac{1}{|n(i)|}.$$

The set $n(i)$ is the set of neighbors for sampling unit i and $|n(i)|$ is the size of the neighborhood set. We defined neighbors as survey units that share a border. The parameter β is a measure of spatial contagion between -1 and 1, with 0 indicating independence of the random effects. We assumed that spatial association in wolverine occurrence is positive due to the fact that environmental conditions in the sample units are similar for neighboring units. We restricted β to (0,1) to maintain positive spatial association. The complete model for the random effects and true occurrence values is

$$P(\mathbf{x}, \mathbf{z}|\alpha, \beta, \sigma) = P(\mathbf{x}|\alpha, \sigma, \mathbf{z}) \times P_{CAR}(\mathbf{z}|\beta),$$

where $P_{CAR}(\ )$ is the joint normal distribution that results from the defining conditional distributions (Banerjee et al. 2004). The spatial association within **x** results by integrating over the latent process **z** to obtain the marginal density of **x**

$$P(\mathbf{x}|\alpha, \beta, \sigma) = \int_{\mathbf{z}} P(\mathbf{x}|\alpha, \sigma, z) P_{CAR}(\mathbf{z}|\beta) d\mathbf{z}.$$

The marginal density of **x** will be spatially associated because **z** is a spatial process. Due to the nonlinear relationship of **z** to the distribution of **x**, the integral is not obtainable in closed form. Using MCMC methods, however, we can numerically evaluate the integral by including **z** in the updating scheme and then ignoring it when examining the results. The benefit of this model-based or hierarchical spatial approach is that all of the variables in the MCMC routine have tractable, and common, joint distributions. Sargeant et al. (2005) needed to use an approximation of the joint distribution for the autologistic model in their MCMC routine.

Because detection of tracks is imperfect, we could not directly measure the true presence or absence of wolverine tracks (x_i) in a particular sampling unit. Therefore, we used multiple surveys of sampled units to obtain a correction for detectability. The variable y_{ij} denotes whether we detected a wolverine track in unit i on survey j ($y_{ij} = 1$ if detected, 0 else). It follows that if $x_i = 0$ then $y_{ij} = 0$ with probability 1 for all j. If $x_i = 1$, however, then y_{ij} may be either 0 or 1 depending on the probability of detection. Therefore, given $x_i = 1$

$$y_{ij}|x_i = 1 \sim \text{Bernoulli } (\theta_{ij}),$$

where θ_{ij} is the probability that a wolverine track is detected in unit i on survey j given there is one present. Unlike Sargeant et al. (2005), we surveyed units repeatedly even after an initial detection occurred, allowing the Bernoulli model to be used where detection probability can vary through time. The geometric data model of Sargeant et al. (2005) assumes a constant detection probability through time.

Two ways to deal with heterogeneity in detection probability are to minimize its potential effect (MacKenzie and Royle 2005) or to include covariates in the model (MacKenzie et al. 2002). To avoid confounding the effects of wolverine abundance and heterogeneity resulting from differences in weather and snow conditions, we spread survey effort across the study area spatially and temporally to avoid surveying units where wolverines were more abundant during only the best or only the worst survey conditions. We minimized the effect of forest cover on detection probability by flying over habitats where tracks were detectable whenever possible. Finally, detection rate appeared higher in the period after 14 February, possibly due to increased activity of wolverines in late winter, increased density of snow in late winter facilitating movement, or accumulated experience of the tracking team. Therefore, we added this covariate, employing the detection model

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

where

$$d_{ij} = \begin{cases} 1 \text{ if survey } j \text{ of hex } i \text{ is conducted on or after 15 Feb} \\ 0 \text{ else} \end{cases}$$

If we assume that the observed occurrences y_{ij} are independent given the true occurrence x_i, we arrive at the conditional distribution model for the observed occurrence

$$P(\mathbf{y}|\mathbf{x}) = \left[\prod_{i=1}^{S} \prod_{j=1}^{N_i} (x_i\theta_{ij})^{y_{ij}} (1 - x_i\theta_{ij})^{1-y_{ij}}\right],$$

where **y** is the vector of all y_{ij} and N_i is the number of surveys of the ith sampling unit.

We took a Bayesian MCMC approach to parameter estimation due to a large amount of missing data, unknown parameter values, and complex nonlinear dependencies among data and parameters. The complete hierarchical model for analysis results from combining the occurrence model with the detection model to obtain

$$P(\mathbf{y}, \mathbf{x}, \mathbf{z}|\alpha, \beta, \sigma) = P(\mathbf{y}|\mathbf{x}, \gamma) P(\mathbf{x}, \mathbf{z}|\alpha, \beta, \sigma),$$

where $\boldsymbol{\gamma}$ is the vector of detection probability parameters and **z** is the vector of latent spatial variables. The posterior distribution of interest is

$$P(\mathbf{x}, \alpha, \beta, \sigma, \gamma|\mathbf{y}) \propto P(\mathbf{y}|\mathbf{x}, \gamma) \left[\int P(\mathbf{x}, \mathbf{z}|\alpha, \beta, \sigma) d\mathbf{z}\right] \pi(\alpha, \beta, \sigma, \gamma),$$

where $\pi(\ )$ represents the prior distribution of the model parameters.

The hierarchical formulation incorporates the detection model in order to produce an estimate of **x**, the occurrence field. The missing data arise both from units that we never surveyed (i.e., missing y_{ij} and x_i) and from units in which we never detected wolverine tracks (i.e., missing x_i). The MCMC routine updates the missing x_i as if they were parameters of the model. For sites where we observed tracks (i.e., $y_{ij} = 1$ for some j), $x_i = 1$ for all MCMC iterations. In this way the algorithm updates elements of **x** that are missing using the spatial association in the occurrence model and the units where $x_i = 1$. Thus, we can construct a seamless distribution map. Sargeant et al. (2005) provided a detailed description of the use of MCMC in hierarchical models for mapping occurrence. They needed to make use of custom code in order to execute their MCMC routine due to the intractability of the joint distribution of the autologistic model. The hierarchical approach of our spatial

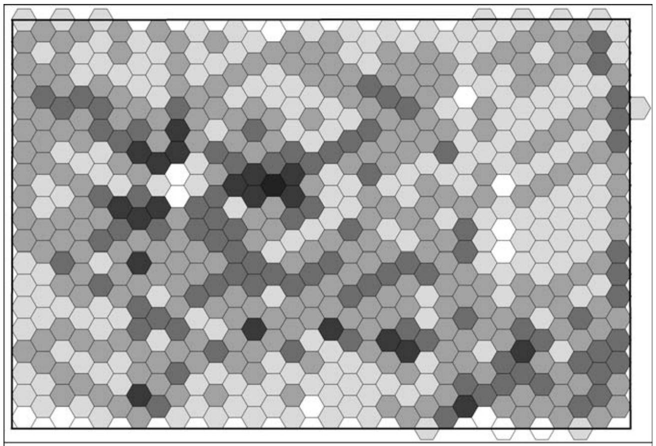

Figure 2. Distribution of survey effort (no. of survey flights/survey unit) for wolverine tracks in our study area in northern Ontario, Canada in 2005.

model resulted in conditional distributions for the Gibbs sampler, which were tractable. Therefore, we used the free software program OpenBUGS (Version 2.2.0) in BRugs (R interface to BUGS; Thomas 2004) to execute the MCMC analysis. We provide some details and OpenBUGS code in the Appendix. In each analysis, we chose the priors $\beta \sim$ uniform(0, 1), $\sigma \sim$ normal(0, 1.5^2), $\alpha \sim$ normal(0, 1.5^2), $\gamma_0 \sim$ normal(0, 1.5^2), and $\gamma_1 \sim$ normal(0, 1.5^2). Using normal(0, 1.5^2) for a quantity defined on the logit scale results in the transformed quantity that is distributed approximately uniform(0, 1). We ran the MCMC simulation for 50,000 iterations following a 10,000-iteration burn-in period. The chains visually converged in approximately 7,000 iterations. We based occurrence probabilities in our distribution maps on the means from the posterior distribution.

RESULTS

The pilot and one of the 2 observers flew 905 of 1,079 (84%) survey flights (total no. of flights resulting from repeated surveys in 575 sampled units). The same pilot and the other observer flew the remainder ($n = 174$) of the survey flights, with the principal survey team repeating surveys in the same sampled units. Because we used one survey team for most of the survey flights, we did not use survey team as a covariate in the model. We could not verify potential wolverine tracks in 5 sampled units and we did not include them in the analysis. Because fisher tracks that had melted on southerly exposures in late March resembled wolverine tracks when viewed from the air, the survey team checked fisher tracks on the ground 3 times to verify their identity. These were the only tracks checked on the ground during the survey. The survey team also followed one track from the air for visual verification of a wolverine. We terminated the survey in late March because of frequent freeze–thaw cycles and deteriorating tracking conditions.

We surveyed 575 of 588 survey units (98%) over 26 days, with 9 days in January, 15 days in February, and 2 days in March. Of the survey days, 46% fell on or after 15 February. Weather conditions at the Red Lake weather station (Fig. 1b) in 2005 in January, February, and March, respectively, were as follows: average temperature (° C), −19.8, −13.1, and −8.7; average snowfall (cm) per day, 2.8, 1.7, and 1.9; number of days with snowfall, 20, 9, and 11; number of days with ≥3 cm of fresh snow, 7, 2, and 2; and range of snow on the ground (cm), 59–85, 70–75, and 57–74. Only one day during the survey period had wind gusts >50 km per hour (in Feb).

Of the 575 sampled units, we surveyed 204 (35%) once, 260 (45%) twice, 90 (16%) 3 times, 20 (3%) 4 times, and 1 (<1%) 5 times (Fig. 2). Flight time per sampled unit averaged 10 minutes including verification of track identity. We detected wolverine tracks in 24% (138 of 575) of the units (Fig. 3a). In 88% of 138 units with detected tracks, detection occurred within the first 2 surveys of the unit. Cumulative units with detected tracks after the first, second, third, and fourth survey flights in the sampled units were 65 (11% of the 575 sampled units), 121 (21%), 133 (23%), and 137 (24%), respectively.

Units with detected tracks were in the northern portion of the study area (Fig. 3a) and units with occurrence probabilities >0.80 were concentrated in the north-central portion of the study area (Fig. 3b). There was strong evidence of occurrence (probability of occurrence >0.80; Sargeant et al. 2005) in 30% of the 588 survey units, weak evidence of occurrence (0.50–0.80) in 12%, weak evidence of absence (0.20–0.50) in 15%, and strong evidence of absence (<0.20) in 43%. Of the 588 units, 73% showed either strong evidence of occurrence or strong evidence of absence. Detection probability before 15 February was 0.23 (95% Bayesian CI (BCI) = [0.18, 0.29]) and afterwards, 0.54 (95% BCI = [0.42, 0.66]).

When we examined model results using ≤2 survey flights per sampled unit, we detected tracks in 21% (120 of 575) of the units and the highest occurrence probabilities were still concentrated in the north-central portion of the study area (Fig. 3c). The highest occurrence probability for units without track detections was 0.87 (SD = 0.34) compared to 0.91 (SD = 0.29) for the full survey. Detection probability before 15 February was 0.25 (95% BCI = [0.19, 0.33]) and afterwards, 0.62 (95% BCI = [0.46, 0.77]). This simulated reduction in survey effort decreased occurrence probabilities in 69% of the 588 survey units, but <1% of the units decreased by >0.20; there was an increase in occurrence probabilities in 11% of the survey units, all by <0.01. The percentage of the 588 units with occurrence probabilities >0.80 (strong evidence of occurrence) fell from 29% (n = 170) to 23% (n =135).

DISCUSSION

Our survey and modeling approach made it possible to determine distribution of wolverines on a scale appropriate to this wide-ranging species that naturally occurs at low densities on the landscape (Banci 1994). The survey technique allowed us to acquire large amounts of occurrence data over a large area in a relatively short period of time (26 d in a period of <3 months) and required a team of only 2 people. The technique was more flexible than other published aerial surveys for wolverines (Becker 1991, Becker et al. 2004) and used approximately 6 times less flying time than those techniques would have required for our study area (H. N. Golden, Alaska Department of Fish and Game, personal communication). All flight time undertaken in good survey conditions could be used for sampling and the technique did not require that we survey only routes and sampling units chosen a priori.

Probability of occurrence showed strong spatial structure with 73% of 588 survey units having either strong evidence of occurrence or strong evidence of absence. Even with reduced survey effort ($\leq$2 surveys/unit), the southern limit of wolverine distribution in the study area was evident (Fig. 3c), but increasing the number of repeated surveys to $\geq$3 (at a cost of approx. 10 min of flight time/surveyed unit) was necessary to adequately deal with detection probability (Mackenzie and Royle 2005) and to establish the general pattern of wolverine occurrence throughout the study area. To achieve a relatively unambiguous estimate of distribution (Sargeant et al. 2005), we suggest that $\geq$70% of sampling units should be units with either strong evidence of presence (probability of occurrence >0.80) or strong evidence of absence (<0.20). Otherwise, few (relative to the no. of survey units), widely spaced units with detections will result in weak evidence of occurrence in all units except the ones with detections.

Wolverine occurrence based on our track surveys in the study area generally agreed with occurrence patterns based on OMNR fur-trapping records from 1980 to 2005 (Fig. 1a). Trapping data, however, spanned a relatively long period, were only known at the scale of individual trap-lines or community trapping areas, and were influenced by the number and distribution of trappers. Our survey technique allowed us to assign locations to particular sampling units and provided an objective means to measure extent of distribution and area of occupancy using data we collected within a single year.

We defined the southern extent of distribution as a line below the southernmost survey units with >0.20 probability of occurrence. Using this definition, wolverine range comprised 59% of the study area (347 of 588 survey units) and no limit to distribution was evident in the north, west, or east (Fig. 3b). We defined area of occupancy as those survey units with occurrence probabilities >0.20, which comprised 33,400 km^2 (57% of the study area). We considered survey units with occurrence probabilities >0.50 (24,300 km^2; 41% of the study area) to be the core area of occupancy because clumping of units with high occurrence probabilities can identify areas on the landscape that are highly used (MacKenzie 2006, Wintle and Bardos 2006).

Populations of many wildlife species have intrinsic spatial structure that influences their distribution on the landscape (Wintle and Bardos 2006). In wolverine populations, intrinsic spatial structure arises from offspring sharing their mother's home range and home ranges of resident male wolverines overlapping those of resident females (Banci 1994). We suggest that relatively large groups of contiguous sampling units (e.g., $\geq$10) with high occurrence probabil-

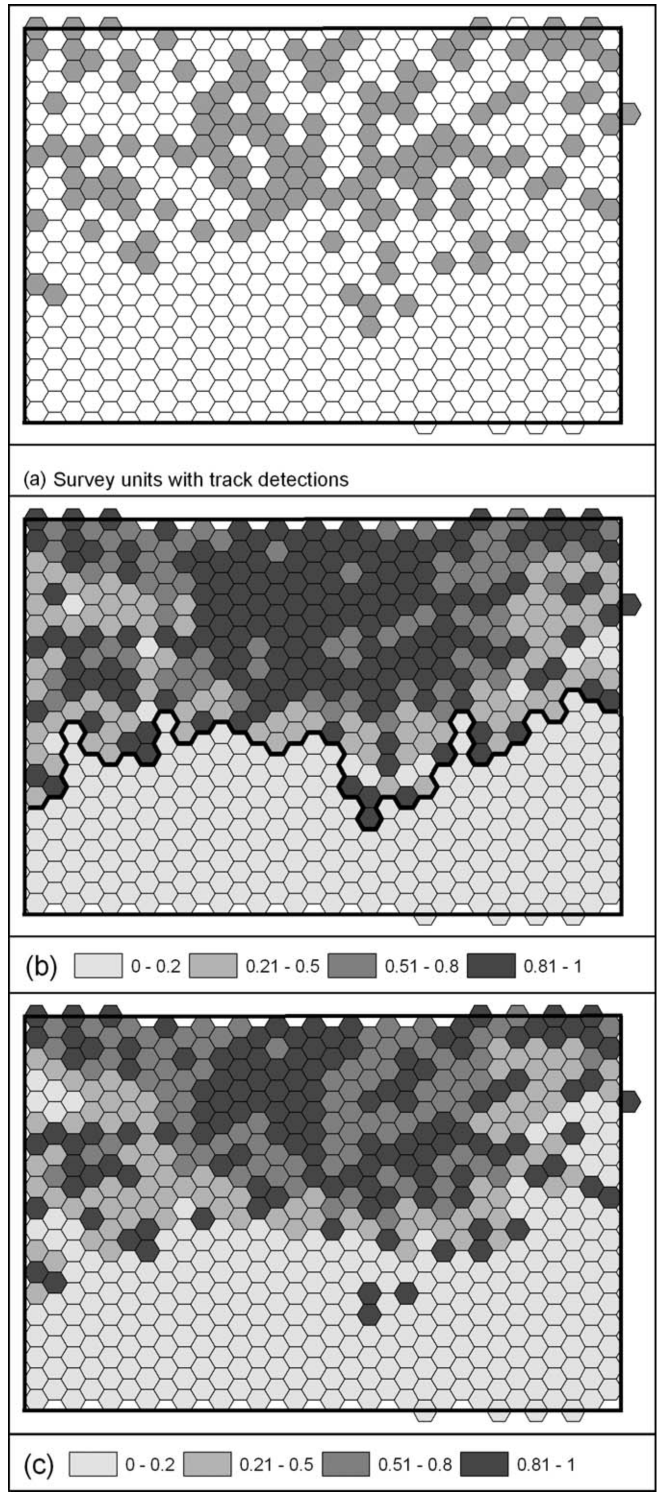

Figure 3. Results of the wolverine track survey in northern Ontario, Canada in 2005 showing (a) survey units with detected wolverine tracks, (b) pattern of occurrence probabilities based on all repeated surveys in the sampled units (the bold line indicates the southern extent of occurrence based on probabilities >0.20), and (c) pattern of occurrence probabilities when we used data from $\leq$2 surveys to simulate reduced survey effort (we used the first 2 surveys if there was >1 survey for the sampling unit).

ities (>0.80) in the northern region of the study area indicated areas with occupied home ranges. From a radiotelemetry study we conducted in 2004, we had evidence that wolverines were resident in the northern part of our study area and reproduced, at least in the north-central region of the study area where we located a natal den (F. N. Dawson, unpublished data). In contrast, smaller groups of contiguous survey units with occurrence probabilities >0.80 may represent areas where 1) transients were temporarily active, 2) resident animals were occupying patches of suitable but discontinuous habitat, or 3) immigrants were colonizing new areas. Units with high occurrence probabilities isolated from similar units may only provide information on extent of distribution and location of movement corridors.

Occupancy modeling must address heterogeneity in detection probability (MacKenzie et al. 2002, MacKenzie 2005). In our survey, the most practical ways to minimize the potential effects of heterogeneity on estimates of occurrence, other than that caused by differences in wolverine abundance, were to use one survey team for most of the survey, repeat flights in sampling units even after the first detection, and position survey routes and flight paths to break any correlation with sources of variation in detection probability (MacKenzie and Royle 2005). If multiple survey teams are used for surveys, all pilots must be experienced at identifying and tracking wolverines and experience of survey teams should be roughly equivalent whenever possible. In addition, teams should fly adjacent routes on the same days whenever possible so that team differences in ability to detect tracks are distributed similarly across the study area under similar conditions. One of the benefits of our modeling approach is that the model can accommodate variability in skill levels of survey teams by including survey team as a covariate, but it is best to minimize potential effects of this variability on detection probability by distributing skill levels equally across the study area and alternating teams in repeated surveys of the same unit (MacKenzie and Royle 2005). Finally, concentrating our survey effort over habitat types where it was possible to see wolverine tracks was an effective way to deal with potential heterogeneity in detectability due to forest cover.

MANAGEMENT IMPLICATIONS

Our survey method identified not only extent of wolverine distribution in our study area but also core areas of occupation, and it provided probability of occurrence for each sampling unit including those not surveyed. Using this information, resource managers and others can examine wolverine–habitat associations across the study area by comparing characteristics of occupied and unoccupied habitats and can track changes in wolverine distribution by comparing future surveys with our 2005 baseline survey. With an understanding of how distribution changes with changing habitat conditions, OMNR, conservation organizations, forest management companies, trappers, and others can cooperate in the development of best management practices targeted at maintaining wolverines on the landscape in the face of increasing resource development in the study area. We recommend repeating the survey in our study area at intervals sufficient to inform forest management plans (e.g., every 5 yr) and other resource development that could potentially alter wolverine distribution patterns.

ACKNOWLEDGMENTS

The Wildlife Conservation Society, OMNR, Canadian Boreal Initiative, Ontario Living Legacy Trust, Ontario Living Legacy Research Program, The Wolverine Foundation, the Endangered Species Recovery Fund (World Wildlife Fund—Canada & Environment Canada), Hunter Foundation, Forest Products Association of Canada, and Weyerhaeuser Corporation provided funding for the survey. The OMNR staff in Red Lake and Green Airways provided logistical support. G. Woolmer mapped and archived survey results and created the figures for this paper. K. Middel assisted with analysis of Landsat and Forest Resource Inventory data. C. Anderson and J. Zigouris assisted with ArcGIS and data entry. J. Ver Hoef advised us on Bayesian spatial modeling and J. Lawler, R. Powell, and anonymous reviewers provided constructive reviews of the manuscript.

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APPENDIX

Details of the Markov chain Monte Carlo (MCMC) routine and the OpenBUGS code follow.

MCMC Routine

OpenBUGS executes the MCMC in approximately the following manner (exact order of update is unknown but does not matter in obtaining a posterior sample), assuming independent prior distributions for the parameters of the model. Here the full conditional distributions for the Gibbs sampler are denoted by $P(\text{parameter} \mid \ldots)$.

- Update missing y_{ij} (y_{i1} is enough), using $d_{ij} = 1$, with a draw from the conditional distribution $P(y_{i1}|\ldots) = (x_i\theta_{i1})^{yi1}(1{-}x_i\theta_{i1})^{1-yi1}$. The actual N_i and d_{ij} used will not matter to the posterior distribution of the parameters.
- Update γ_k with a draw from the conditional distribution $P(\gamma_k \mid \ldots) \propto P(\mathbf{y} \mid \mathbf{x})P(\gamma_k)$ for $k = 0,1$. A Metropolis-within-Gibbs draw is required here (see Sargeant et al. [2005] for explanation). OpenBUGS uses a normal proposal.
- Update missing x_i (those sample units for which tracks were never seen) with a draw from $P(x_i|\ldots) = \xi_i^{x_i}(1-\xi_i)^{1-x_i}$.
- Update α with a draw from $P(\alpha \mid \ldots) \propto P(\mathbf{x} \mid \alpha,\mathbf{z})P(\alpha)$. A Metropolis-within-Gibbs draw is required.
- Update z_i, $i = 1, \ldots, N$, with a draw from $P(z_i \mid \ldots) \propto P(z_i \mid \mathbf{z}_{-i},\beta)P(x_i \mid \alpha,\sigma,z_i)$. A Metropolis-within-Gibbs draw is required.
- Update β with a draw from $P(\beta \mid \ldots) \propto P(\mathbf{z} \mid \beta)P(\beta)$. A Metropolis-within-Gibbs draw is required. Repeat this step for σ.

OpenBUGS Code

```
##################################################
#TotObs = sum_{i=1}^N N_i
# y[] = (TotObs x 1) vector [y_{ij}]
# d[] = (TotObs x 1) vector [d_{ij}]
# su[] = (TotObs x 1) vector of integer sample unit labels for
each element of y[]
# theta[] = TotObs x 1) vector [theta_{ij}]
##################################################
model
{
  # OBSERVATION MODEL P(y|x,gamma)
  for(k in 1:TotObs){
    y[k] ~ dbern(p[k])
      p[k] <- x[su[k]]*theta[k]
      logit(theta[k]) <- gamma0+gamma1*d[k]
}

# OCCURRENCE MODEL P(x|z,alpha,sigma)
for(i in 1:N){
  x[i] ~ dbern(xi[i])
  logit(xi[i]) <- alpha + sig*z[i]
  mu.z[j] <- 0
}

# LATENT SPATIAL PROCESS MODEL P(z|beta)
z[1:Nplots] ~ car.proper(mu.z[], C[], adj[],num[], M[], 1,
beta)

# DETECTION MODEL PARAMETER PRIORS
gamma0 ~ dnorm(0, 0.4)
gamma1 ~ dnorm(0, 0.4)

# OCCURRENCE MODEL PARAMETER PRIORS
alpha ~ dnorm(0, 0.4)
sig ~ dnorm(0,0.4)

# LATENT SPATIAL PROCESS PARAMETER PRIOR
beta ~ dunif(0, 1)

# DERIVED PARAMETERS
sd.z <- abs(sig)#      standard deviation of the z process
logit(theta0) <-       gamma0# Early season theta
logit(theta1) <-       gamma0+gamma1# Late season theta
}
```

Associate Editor: Alpizar-Jara.