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RESEARCH PAPER

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Modelling broad-scale wolverine occupancy in a remote boreal region using multi-year aerial survey data

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Abstract

Aim: We used data from aerial surveys of wolverine tracks collected in seven winters over a 10-year period (2003–2012) within a 574,287 km^2 study area to evaluate the broad-scale pattern of wolverine occurrence across a remote northern boreal forest region, identifying areas of high and low occupancy.

Location: Northern Ontario, Canada.

Taxon: Wolverine (*Gulo gulo* Linnaeus, 1758).

Methods: We collected wolverine tracks and observations in 100-km^2 hexagonal survey units, making a total of 6,664 visits to 3,039 units, visiting each 1–9 times. We used hierarchical Bayesian occupancy modelling to model wolverine occurrence, and included covariates with the potential to affect detection and/or occupancy probability of wolverines.

Results: we detected wolverines on 946 visits, 14.2% of total visits. Probability of detecting a wolverine varied among years and between the two ecozones in the study area. Wolverine occupancy was negatively related to two important covariates, the geographical coordinate Easting and thawing degree-days. A site occupancy probability map indicated that wolverine occupancy probabilities were highest, and standard error lowest, in the western and northern portions of the study area.

Main conclusions: The occupancy framework enabled us to use observation data from tracks of this elusive, wide-ranging carnivore over a vast, remote area while explicitly considering detectability and spatial autocorrelation, yielding a map of probable wolverine distribution in northern Ontario that would not be possible using other methods of detection across a large region. With resource development pressures increasing in this globally significant region in the face of a changing climate, it is important to monitor changes in distribution of species like wolverines that have low population growth rates, large spatial requirements and sensitivity to human disturbance. This study demonstrates a relatively cost-effective and non-invasive alternative to monitoring based on wolverine harvest records, which have not been available since 2009 in Ontario due to changes in the provincial regulatory regime for this threatened species.

KEYWORDS

Aerial survey, conservation biogeography, fur harvest, *Gulo gulo*, hierarchical modelling, imperfect detection, northern Ontario, probability of occupancy, spatial autocorrelation, wolverine

1 | INTRODUCTION

Areas of the world where industrial development and infrastructure are absent or at low levels are increasingly rare. Recent global analyses (e.g. Watson et al., 2016) highlight regions that remain large enough to be ecologically intact, and contain complete biotic assemblages and functioning ecological processes, thereby contributing to the global and regional persistence of biodiversity and ecosystem services (Potapov et al., 2017). However, the same characteristics that define the ecological value of these remote areas present challenges for the inventory and monitoring of resident faunal populations, largely due to the lack of road access and large distances between airports. Species with less resilience to environmental disturbances (Weaver, Paquet, & Ruggiero, 1996) require monitoring as changes within remote regions accelerate.

Canada's northern boreal forests have been identified as globally significant, in part because of their intactness, yet are experiencing increasing pressures from industrial development and climate change (Venier et al., 2014). Ontario's Far North comprises 42% of the province's land mass and has only one permanent road. There have, however, been increasing levels of mineral exploration since 2007 with the discovery of world-class chromite deposits in the "Ring of Fire" (Hjartarson, McGuinty, Boutileir, & Majernikova, 2014). In addition, commercial timber harvesting and hydroelectric development opportunities are under active consideration, heightening the imperative to measure and monitor the ecological impacts of current and future developments (Far North Science Advisory Panel, 2010).

The wolverine *Gulo gulo* (Linnaeus, 1758) is a large-bodied mustelid with a relatively slow population growth rate and large space requirements (Weaver et al., 1996). This species historically occurred throughout most of the province, but its range receded substantially between the mid-1800s and 1950s (Ontario Wolverine Recovery Team, 2013). Listed as threatened in Ontario (Government of Ontario, 2017), a number of inter-related factors have likely caused its decline, including harvest by humans, land use changes, reductions in prey species and climate change resulting in altered snow conditions (Ontario Wolverine Recovery Team, 2013). An estimate of current wolverine distribution and relative abundance is needed to track and compare future changes in occupancy and assess the effectiveness of management actions.

Standard approaches to assessing population and range status, such as mark–recapture or population counts, are not logistically or financially feasible for wolverines across broad spatial scales in remote regions like northern Ontario. Monitoring populations and assessing distribution through trapper harvest is more practicable across broad scales, but requires accurate reporting and is subject to variable and often undocumented trapper effort (Koen, Ray, Bowman, Dawson, & Magoun, 2008). Wolverine occurrence in Ontario traditionally has been evaluated using harvest data from registered traplines and incidental observations (Dawson, 2000; Ontario Wolverine Recovery Team, 2013). However, trapping of wolverines by non-Indigenous trappers was prohibited in 2001 through a zero-quota policy (i.e. no allocation for harvest), while sale, possession and purchase of wolverines by fur auction houses ended in 2009, following the passage of Ontario's *Endangered Species Act, 2007* and subsequent amendments to open season regulations under the provincial *Fish and Wildlife Conservation Act, 1997*.

Recently developed occupancy modelling approaches, such as Hierarchical Bayesian Occupancy Modeling (HBOM; Johnson, Conn, Hooten, Ray, & Pond, 2013), provides an alternative method of establishing species distribution and monitoring changes in distribution over time. Modelling probability of occupancy using detection or non-detection of wolverine tracks from aircraft within a sample of survey units (site) is possible if combined with relevant environmental variables (Magoun et al., 2007; Gardner, Lawler, Ver Hoef, Magoun, & Kellie, 2010). HBOM explicitly address imperfect detection of a species, a common confounding factor in wildlife surveys, and estimates the effects of factors that influence the detection of the species during surveys. It has the added advantage of being able to exploit spatial autocorrelation in observations and habitat variables in order to extrapolate occupancy of unsurveyed units based on habitat characteristics and occupancy status of neighbouring units (Johnson et al., 2013). Taking such factors into account during occupancy modelling reduces bias and increases precision of occupancy estimates and accuracy of species distribution models and mapping (Poley et al., 2014).

For wide-ranging species, broad spatial scales should be of highest interest for monitoring changes in their distribution over time. In this study, we considered cumulative surveys for wolverines conducted within a decadal timeframe at a provincial scale to be appropriate for determining the state of wolverine range occupancy because the return to previously occupied habitat can be a relatively slow process, even with full protection of the species (Persson, Rauset, & Chapron, 2015). Range expansion is most likely mediated by the spatial dynamics of territorial females and their female offspring, which preferentially occupy vacant home ranges near their natal areas rather than undergo long-range dispersal (Aronsson, 2017). Likewise, the tendency of some individuals, most often males, to occasionally engage in very long-distance movements (Packila, Riley, Spence, & Inman, 2017) can confuse understanding of distribution of reproductive populations. Yet wolverine lifespan and social structure should lead to a relatively consistent pattern of occupancy when examined over a 10-year period.

In this first attempt to model wolverine occurrence at a provincial scale, we used data from aerial surveys of wolverine tracks collected in seven winters over a 10-year period across northern Ontario, using an HBOM framework to create a single model of the probability of wolverine occupancy. We took into account factors affecting detection of wolverine tracks during aerial surveys as well as covariates that improve estimates of occupancy probability in unsurveyed sample units. The goal of this analysis was to identify the broad-scale pattern of wolverine occurrence and occupancy probability for comparison against future distribution in the face of anticipated change in the region.

2 | MATERIALS AND METHODS

2.1 | Study area

The total size of the study area (Figure 1a) is 574,287 km^2 (49 to 57°N, 79 to 96°W). This includes the Far North region (439,751 km^2, as defined by Ontario's *Far North Act*, *2010*), plus an adjacent area extending to the south (134,453 km^2) where commercial forest management is concentrated. There is one transmission corridor, one all-season road, one railway, two active mines and over 3,200 km of winter roads within the Far North portion of the study area (OMNRF, 2016). In the managed forest portion (22% of the study area), there are 19,600 km of roads, three railways and two active mines (Ontario Ministry of Natural Resources and Forestry (OMNRF), 2016).

The study area is comprised of two physiographic regions (terrestrial ecozones; Crins, Gray, Uhlig, & Wester, 2009): the Hudson Bay Lowlands (HBL) along the northern and eastern coastline, and the Boreal (Ontario) Shield (BSH) to the south and west of the HBL. These ecozones are characterized by different bedrock geology, land cover characteristics, climates and degrees of natural and anthropogenic disturbance. The BSH has more open water, deciduous forest, shorter fire regimes and a higher elevation gradient. By contrast, the HBL consists mainly of bog and fen habitats with longer natural fire regimes and is extremely flat (<50 m), except for local regions of higher elevation, and contains the largest wetland in North America (Crins et al., 2009). Forest composition is typical for northern boreal forests, dominated by black spruce (*Picea mariana*, particularly in lowland areas), followed by white spruce *(P. glauca*), jack pine (*Pinus banksiana*), trembling aspen (*Populus tremula*), tamarack (*Larix laricina*) and white birch (*Betula papyrifera*).

2.2 | Aerial surveys

We conducted aerial surveys of wolverine tracks in snow within a 304,668 km^2 portion of the study area, flying during the winter months (late January–early March) in seven non-consecutive years: 2003, 2004, 2005, 2008, 2009, 2010 and 2012 (Figure 1b; see Appendix S1, Figures S1–S3 in Supporting Information). In the first 2 years (2003 and 2004), our objective was to cover the area as extensively as possible to roughly assess where wolverines occurred on the landscape using 1,000-km^2 survey units, and we did not repeat surveys in the units for estimating detection probability. In subsequent years, we conducted more intensive surveys, covering smaller areas using 100-km^2 sample units (Magoun et al., 2007) and repeating surveys in some units to estimate detection probability (MacKenzie et al., 2002).

For all surveys, we used PA-18 Super Cub fixed-wing aircraft (Piper Aircraft Corporation, Lock Haven, PA, USA) equipped with wheel-skis, with a survey team comprised of a pilot with >10 years' experience tracking wolverines from the air and usually one experienced observer who took notes and helped spot wolverine tracks. The suitability of this two-seat, tandem aircraft for wolverine track surveys was demonstrated in Alaska, USA (Gardner et al., 2010) and Ontario (Magoun et al., 2007); it is highly manoeuvrable with a tight turning radius and slow stall speed, facilitating track verification. Over the 7 years, a total of five pilots and five observers flew the surveys. Groundspeed was usually 110–140 km per hour and survey altitude was approximately 200 m above the ground but varied between 100 and 300 m over hilly terrain. We waited ca. 24 hr before flying survey routes after widespread snowstorms that deposited >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 favourable for circling over tracks and safely manoeuvring the aircraft at low levels. We had no upper limit for number of days after a fresh snowfall and considered all detected wolverine tracks as evidence of occurrence regardless of track age or condition.

After 2004, we divided the survey areas into a tessellation of 100-km^2 hexagonal cells, which served as the sample units of analysis (see Appendix S2). In light of the potential increase in power to detect trends in the occupancy parameter when sample units are similar to home range size (Wilson & Schmidt, 2015), as well as our interest in capturing occupancy patterns of a reproductive population, the area of our sampling unit approximated that of the average home range of a lactating female wolverine (Persson, Wedholm, & Segerström, 2010). A hexagonal unit allowed for six neighbouring units that were equal distance from the sampled unit and had equal-length boundaries. We designed our flight paths to pass through the centre of units, with observers typically able to see animal signs several hundred meters to either side of the flight line through each site. Survey crews searched units for wolverine tracks, with multiple visits to a subset of units (see details in Magoun et al., 2007). Each aircraft passed through a mean of 45 units a day (range 3–112). This resulted in a series of known track observations, each associated with the sampling unit in which they were seen (i.e. presence), as well as possible absences (sample units with no detections). Because we used 1,000-km^2 units in 2003 and 2004 only, we rescaled the wolverine detections to the 100-km^2 grid used in subsequent years, effectively resampling these data by locating each observation in 2003 and 2004 in the 100-km^2 sample unit it fell completely within.

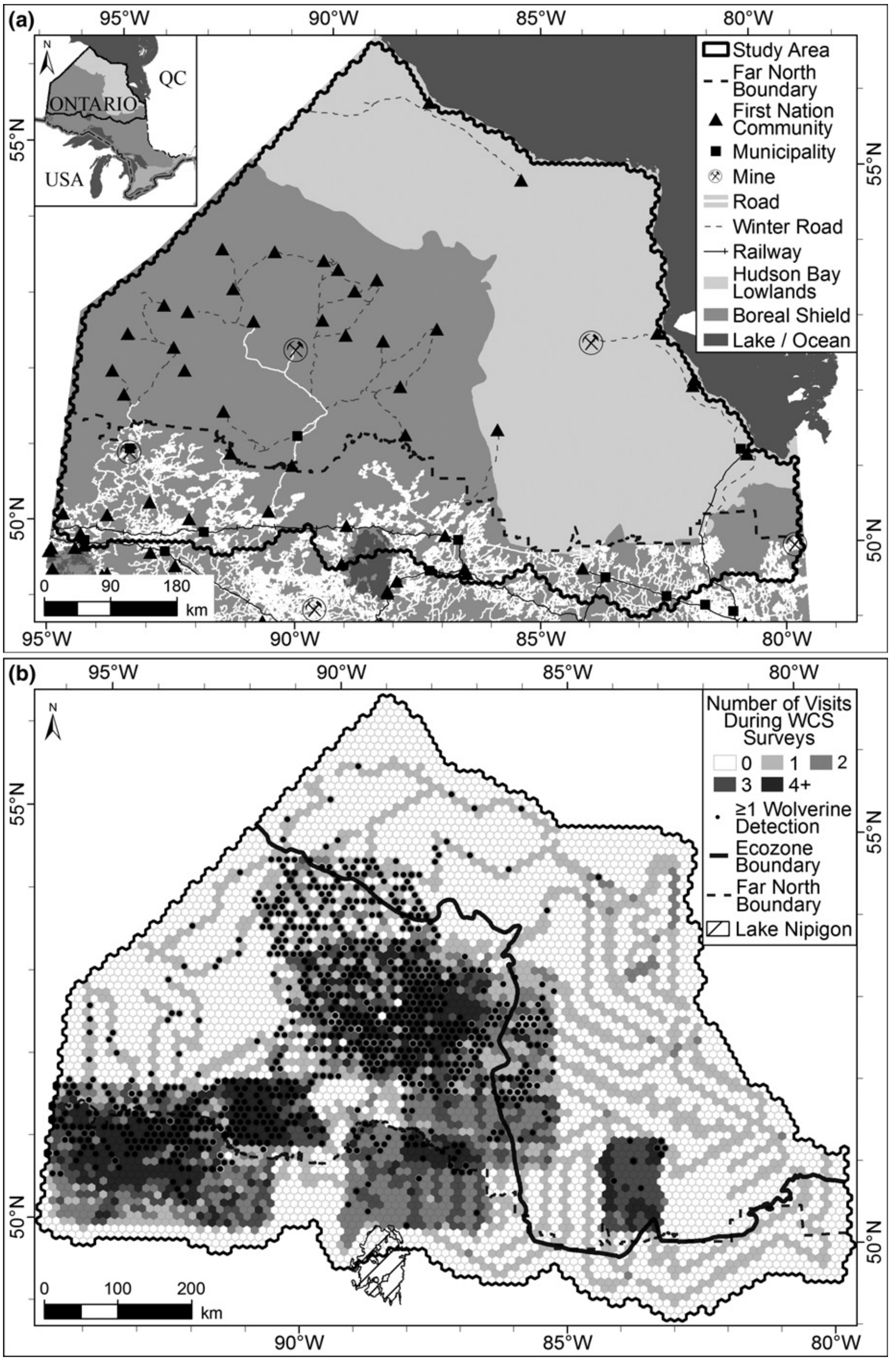

FIGURE 1 (a) Study area for wolverine occupancy analysis in northern Ontario encompassing the Far North Region. (b) All sampling units surveyed at least once during winter aerial surveys for wolverines in northern Ontario. Projection: NAD 1983 Ontario MNR Lambert

2.3 | Covariates

Covariates are measurable factors with the potential to affect detection and/or occupancy probability of wolverines in each sampling unit. These are generally consistent across visits but vary among units and are hypothesized to influence the probability of occurrence of the species of interest in each unit (Johnson et al., 2013). Detection probabilities may vary with conditions that influence the ability of observers to detect the species of interest and differ among visits to each sampled unit (MacKenzie et al., 2002).

We selected five occupancy covariates (see Appendix S3, Table S1) that we hypothesized provided suitable proxies for variables that influence wolverine habitat selection including: (1) geographic coordinates (Easting, Northing), (2) ecozone (HBL, BSH), (3) mean July temperature (MJT), (4) thawing degree-days (TDD; total number of days per year with mean temperature > 0° Celsius) and (5) road density (RD). To allow comparison among parameter estimates, we rescaled all covariates, except the categorical covariate ecozone, to a mean of 0 and standard deviation of 1.

We used the centre of each survey unit in NAD83 Ontario MNR Lambert Conformal Conic format (Easting, Northing) to address the spatial variation that occurs across the study area with respect to land cover, disturbance, climate and geology along north–south and east–west gradients. This captured broad-scale geographic changes in these environmental variables in contrast to the smaller scale of a sampling unit. While Easting and Northing captured potentially influential non-habitat variables that change along a gradient like harvest patterns and intensity, human development and potential dispersal from Manitoba, the ecozone boundary represents an abrupt shift, and we hypothesized this covariate may indicate the value of this boundary area. For example, in the same study area Poley et al. (2014) found the ecozone boundary to correspond to highest caribou occupancy. A sampling unit was considered to be within the ecozone when it contained >50% of the unit's area.

We obtained downscaled climate data at a resolution of 10 km from the Canadian Forest Service (CFS) North America Historical climate data (McKenney et al., 2011), interpolated using a thin-plate smoothing algorithm (ANUSPLIN) to develop spatially continuous climate models that reduce the predictive residual error across the surface (McKenney et al., 2013). We calculated the MJT (which has been used to understand broad-scale distribution patterns of mammals (e.g. Sans-Fuentes & Ventura, 2000) for each sampling unit during 1999–2013 because of the potential for an upper thermal limit to the broad-scale, circumpolar distribution of wolverines (Copeland et al., 2010). We calculated the 15-year average (1999–2013) of TDD for each sampling unit from the same climate data. Wolverines are closely associated with regions with snow cover persisting into late winter and spring (Copeland et al., 2010) and TDD is linked to persistence of snow with snow melting rapidly when TDD surpass some threshold (i.e. increased number of TDD means snow likely disappears sooner). At broad spatial and temporal scales, we assumed that some relatively high value for TDD could correlate with the southern limit of snow cover persistence for wolverine in Ontario.

Lastly, we included RD, calculated as length of winter-only and primary, secondary and tertiary roads (in meters) in the sample units based on spatial data on roads in Ontario (Ontario Ministry of Natural Resources and Forestry (OMNRF), 2016). Previous research demonstrated a negative association between road density and wolverines within a managed forest landscape south of Ontario's Far North, although the drivers of this relationship were not clear (Bowman, Ray, Magoun, Johnson, & Dawson, 2010). Research in Alberta lowland boreal forests showed that wolverines can be attracted to foraging opportunities provided by roads and seismic lines, but that these may also lead to increased mortality, depending on the type, scale and timing of human activities associated with roads and other linear features (Scrafford, Avgar, Abercrombie, Tigner, & Boyce, 2017).

We used three detection covariates (see Appendix S3, Table S1) in our model: year, ecozone and whether a survey flight occurred before February 15. We chose year because we flew surveys in seven winters over a 10-year period in different regions of the study area. By including year, changes in detection caused by factors that varied yearly among surveys (e.g. weather conditions, survey team make-up, region covered) were incorporated into the model. We included ecozone as a detection covariate because of the ecological differences between the HBL and BSH, particularly for tree cover (i.e. relative openness), which can affect observers' abilities to detect wolverine tracks. Lastly, past wolverine surveys have demonstrated that detection of wolverines increases as winter progresses (Magoun et al., 2007; Gardner et al., 2010). We chose February 15 (average start of the denning period; Inman, Magoun, Persson, & Mattisson, 2012) as the cut-off date to delineate early season (before Feb 15) from late season (≥ Feb 15) to assess whether detection probabilities differed between the two periods.

2.4 | Occupancy analysis

We used HBOM employing restricted spatial regression (RSR; Johnson et al., 2013) to model wolverine occupancy. HBOM uses an efficient Gibbs sampler Markov chain Monte Carlo method to make Bayesian inference about the detection and occupancy processes (Johnson et al., 2013). This method explicitly incorporates spatial autocorrelation in survey data while alleviating potential spatial confounding between the fixed effects and spatial portions of the model that hamper the estimation of intrinsic conditional autoregressive models, yielding a more stable algorithm for fitting spatially explicit occupancy models (Hughes & Haran, 2012; Johnson et al., 2013; Hanks, Schliep, Hooten, & Hoeting, 2015). Detailed descriptions and derivations of the HBOM approach can be found in Hughes and Haran (2012) and Johnson et al. (2013).

For each species-specific model, we set the threshold for detecting spatial structure in neighbouring sample units to 12,000 m—large enough to encompass all six neighbours of each hexagonal sample unit. We specified flat prior distributions for both the detection and occupancy coefficients and a Gamma (0.5, 0.0005) distribution for the spatial process following Johnson et al. (2013). We set the initial value of the smoothing parameter (restriction of eigenvectors in spatial portion of model) at 1/10th of the total number of units in the model, resulting in just under 600 eigenvectors being included in the smoothing process. Increasing the number of eigenvectors reduces the smoothing (Broms, Johnson, Altwegg, & Conquest, 2014; Hefley et al., 2017), creating a computationally more intensive model; however, in this case, reducing the smoothing also reduced the posterior predictive loss (PPL) values, indicating model fit increased with less smoothing in this region. The best models had a final smoothing parameter of 0.5 times the number of sample units in the model. We allowed the Markov chain to stabilize with a burn-in period of 10,000 iterations, which we then discarded, after which we ran the Gibbs sampler for 60,000 iterations. The thinning rate of the chain was 1/5, resulting in a total posterior sample of 12,000 for each model. To fit the models, we used the package "STOCC" (available from CRAN:

https://cran.r-project.org/web/packages/stocc/index.html) for the R statistical environment (3.1.1, R Core Team, 2016).

It is unlikely that all individual sample units in our study maintained the same occupancy status consistently across the 10 years we conducted surveys, which would be considered a violation of the closed-site assumption (i.e. site occupancy status is closed to changes during the survey period; MacKenzie et al., 2002). However, violations of closure do not always have detrimental effects on occupancy modelling, and biological context and inference objectives should be used to determine the relevant period over which sites should be considered "closed" (Royle & Dorazio, 2008). In this case, our interest in wolverine occupancy was not at the individual sampling unit level, but rather at the very broad spatial scale of provincial range occupancy of a reproductive population. Because wolverine range expansion is a slow process (Persson et al., 2015; Aronsson, 2017), we assumed the distribution was unlikely to change quickly and both the characteristics of the species (i.e. home range size of reproductive females) and objective of the study—to estimate province-wide range occupancy—guided choice of sampling unit size and survey frequency rather than avoiding the closure assumption.

2.5 | Model fit and selection

Similar to area under the curve (AUC), the PPL criteria characterizes predictive ability based on decision theory, and incorporates an estimate of model fit to the data along with a penalty for complex (over-parameterized) models (Johnson et al., 2013). Lower PPL values indicate better fit to the data. PPL is built into the "STOCC" package as the default method of model fit assessment. It has, however, been noted to be biased towards models with more parameters, occasionally resulting in inflated estimates of model fit for over-parameterized models (Broms et al., 2014). As such, we also assessed covariate importance using the Bayesian 95% credible intervals (CIs) surrounding each covariate's parameter estimates as well as the magnitude of parameter estimates. We considered covariates in the occupancy and detection models for wolverine to be important when the posterior 95% CI of the parameter estimate did not encompass zero, while we deemed covariates with CIs encompassing zero to have no relationship with occupancy. The magnitude of parameter estimates also indicates a covariate's relative importance, with larger values indicating a stronger influence on detection/occupancy (Broms et al., 2014).

We used a stepwise model selection procedure to determine the model that best fit the data. First, we fit separate models for each individual detection covariate, using a randomized constant value between 0 and 1 that had no important effect on wolverine occupancy as the only occupancy covariate. This allowed us to assess the contribution and importance of each detection covariate without having to simultaneously test occupancy covariates in the habitat portion of the model. Then we combined important detection covariates into one model. Once we determined the best combination of detection covariates, we kept these in the detection portion of the model while testing each occupancy covariate individually. We used a Pearson correlation test to assess multicollinearity among all habitat covariates prior to selecting occupancy covariates to include in the final model to avoid masking or direction switching that may occur when correlated covariates are included in the same model. Lastly, we combined the best-fitting and least-correlated occupancy and detection covariates into one model.

3 | RESULTS

3.1 | Surveys and detections

In seven wolverine surveys in northern Ontario, we made a total of 6,664 visits to 3,039 sample units (Table 1, Figure 1b, Appendix S3). This represents 51.4% of the overall study area to which models were applied, with 62.4% of the HBL and 36.0% of the BSH portions of the study area surveyed, respectively. We detected wolverines on 946 visits, 14.2% of total visits, 828 in the BSH and 120 in the HBL ecozones. The number of times we visited each survey unit varied considerably, ranging from 1 to 9 (mean 1.9; see Appendix S4, Table S2), for a total of 1,307 and 1,188 visits in BSH and HBL, respectively.

3.2 | Detection covariates

In the single covariate models, all detection covariates had CIs not encompassing zero, indicating they had an important influence on detection (Table 2). Year had a positive effect on wolverine detection, with higher probability of detection in later years. However, the parameter estimate was small compared to other covariates, indicating a relatively weak relationship. Wolverine detection was higher on survey days that took place on or after February 15 of each year. When we combined ecozone, year and February 15 into one model, they retained their sign direction and importance from the individual covariate models. The combined model had lower PPL than all other single covariate models (Table 2), suggesting it is a good combination of covariates for explaining differences in wolverine detection probability.

3.3 | Occupancy covariates

RD and TDD had a negative influence on wolverine occupancy (Table 3). Whether or not a survey unit fell within the HBL ecozone also had a negative influence, with higher probability of occupancy in the BSH. MJT did not have a significant influence, while Northing had a strong positive relationship and Easting a negative relationship with wolverine occupancy. Easting and Northing had the highest magnitude parameter estimates, followed by TDD, suggesting these covariates had relatively stronger influences on wolverine occupancy compared to RD, MJT or ecozone. TDD also had the lowest PPL value by a small amount.

MJT and TDD were strongly negatively correlated with Northing ($r > .7$), but less so with Easting ($r < .12$), while road density was negatively correlated with both ($r > .4$). Specifically, as Northing

Year or Ecozone	Units visited once (total visits)	# Detections (% of total visits)	# Non-detections (% of total visits)	# Routes Flown	Total kms Flown
2003	343 (714)	79 (11.1)	635 (88.9)	18	6,049
2004	686 (1165)	43 (3.7)	1,122 (96.3)	29	10,552
2005	531 (1296)	149 (11.5)	1,147 (88.5)	26	11,927
2008	101 (635)	123 (19.4)	512 (80.6)	10	6,120
2009	519 (821)	294 (35.8)	527 (64.2)	14	8,788
2010	393 (1184)	98 (8.3)	1,086 (91.7)	34	13,959
2012	466 (849)	160 (18.8)	689 (81.2)	16	12,145
Total	3,039 (6664)	946 (14.2)	5,718 (85.8)	147	69,540
HBL	887 (1334)	121 (9.1)	1,213 (90.9)	—[1]	—[1]
BSH	2,152 (5330)	825 (15.5)	4,505 (84.5)	—[1]	—[1]

[1]Not calculated because some flightlines surveyed both HBL and BSH ecozones.

TABLE 1 Survey years during winter aerial surveys for wolverine in Northern Ontario showing number of unique units visited at least once, total visits to all units, detections and non-detections by number and percentage of total units visited

TABLE 2 Comparison of posterior predictive loss (PPL) criterion, parameter estimates and plus and minus 95% credible intervals for detection covariates used in probability of occupancy models for wolverine in northern Ontario. Bold font indicates best-fitting model

		Detection				Occupancy			
Model	PPL	Parameter	Estimate	−95%	+95%	Parameter	Estimate	−95%	+95%
Year	1451.53	Intercept	−172.57	−204.91	−138.64	Intercept	0.45	0.08	0.86
		Year	0.09	0.07	0.10	Constant	−0.32	−0.86	0.31
Feb 15	1479.84	Intercept	−0.83	−0.91	−0.75	Intercept	0.09	−0.29	0.41
		Feb 15	0.17	0.08	0.27	Constant	−0.25	−0.92	0.31
Ecozone	1480.29	Intercept	−0.73	−0.80	−0.68	Intercept	−0.03	−0.43	0.41
		Ecozone	−0.22	−0.39	−0.03	Constant	−0.25	−0.83	0.22
Year +	**1441.23**	Intercept	−0.83	−0.91	−0.75	Intercept	0.23	−0.21	0.59
Feb 15 +		Ecozone	−0.46	−0.61	−0.30	Constant	−0.24	−0.76	0.29
Ecozone		Year	0.20	0.01	0.37				
		Feb 15	0.14	0.12	0.17				

increases (moves further north), MJT, TDD and RD all decrease. Given the importance of Easting and Northing in our occupancy models and the low correlation with other habitat covariates, we included Easting in the final model to capture variation in occupancy along the east–west gradient. In addition, other potentially influential factors, such as length of time between successive forest fire events, demonstrate a strong east–west gradient, with the HBL in the east having much longer periods between fires than the BSH in the west (Bridge, 2001). We also included TDD due to its importance in the individual covariate models and its high correlation with the other covariates occurring along the north–south gradient. These two covariates (Easting and TDD) resulted in a model with much lower PPL than any individual covariate model (Table 3) and both habitat covariates retained their sign and magnitude in the final model.

3.4 | Spatial patterns of occupancy

Wolverine occupancy based on the best-fitting model (detection covariates year + Feb 15 + ecozone and occupancy covariates TDD + Easting) showed that probabilities are highest in the western and northern portions of the study area (Figure 2a). There are also several "hot spots" occurring far from the contiguous areas of high occupancy in the centre of the study area as well as to the south in the BSH and south–east in the HBL. These are likely driven by pockets of isolated wolverine detections. By contrast, one obvious "cool spot" occurs in the centre of the study area close to the ecozone boundary. The most concentrated band of survey units with low standard errors (indicating a high degree of model confidence) lay in the northern and western parts of the study area where wolverine sign was consistently observed in all surveys since the first year of this study. The units where detections were inconsistent between surveys were located on the eastern edge of the high occupancy core (Figure 2b).

4 | DISCUSSION

Results from this study yielded a composite map of the probable distribution of wolverines in northern Ontario that likely reflects the relative abundance patterns of wolverines across the study area (i.e.

TABLE 3 Comparison of posterior predictive loss (PPL) criterion, parameter estimates and plus and minus 95% credible intervals for occupancy covariates used in probability of occupancy models for wolverine in northern Ontario. Bold font indicates best-fitting model resulting from combining individual occupancy covariates in one model

		Detection		Occupancy	
Model	PPL	Parameter	Estimate (−95%, + 95%)	Parameter	Estimate (−95%, +95%)
RD	1436.11	Intercept	−132.31 (−183.56, −80.89)	Intercept	0.02 (−0.31, 0.46)
		Ecozone	−0.53 (−0.69, −0.41)	Roads	−0.60 (−0.82, −0.39)
		Year	0.07 (0.04, 0.09)		
		Feb 15	0.30 (0.16, 0.45)		
MJT	1435.56	Intercept	−123.29 (−175.90, −75.58)	Intercept	0.05 (−0.14, 0.26)
		Ecozone	−0.54 (−0.67, −0.39)	MJT	0.16 (−0.18, 0.57)
		Year	0.06 (0.04, 0.09)		
		Feb 15	0.30 (0.15, 0.46)		
TDD	1434.63	Intercept	−120.44 (−172.22, −71.54)	Intercept	0.28 (−0.06, 0.58)
		Ecozone	−0.53 (−0.65, −0.40)	TDD	−1.49 (−1.84, −1.04)
		Year	0.06 (0.04, 0.09)		
		Feb 15	0.30 (0.15, 0.46)		
Ecozone	1436.55	Intercept	−123.62 (−172.88, −73.63)	Intercept	0.76 (0.41, 1.08)
		Ecozone	−0.54 (−0.65, −0.41)	Ecozone	−1.38 (−2.05, −0.58)
		Year	0.06 (0.04, 0.09)		
		Feb 15	0.31 (0.16, 0.47)		
Easting + Northing	1436.60	Intercept	−122.68 (−169.78, −64.10)	Intercept	−134.10 (−182.17, −85.50)
		Ecozone	−0.53 (−0.66, −0.41)	Easting	−2.05 (−2.87, −1.41)
		Year	0.06 (0.03, 0.08)	Northing	2.37 (1.43, 3.04)
		Feb 15	0.30 (0.14, 0.47)		
TDD + Easting	**1418.24**	Intercept	−0.83 (−0.91, −0.57)	Intercept	1.12 (0.51, 1.89)
		Ecozone	−0.46 (−0.61, −0.30)	TDD	−2.71 (−3.79, −1.63)
		Year	0.20 (0.01, 0.37)	Easting	−1.97 (−3.20, −1.02)
		Feb 15	0.14 (0.12, 0.17)		

RD: Road density; MJT: Mean July temperature; TDD: Thawing degree-days.

areas of higher abundance had a greater probability of detection) (Magoun et al., 2007; Dey et al., 2017). The HBOM framework allowed us to use survey data in a post hoc manner rather than design a broad-scale survey a priori—a reality in vast, remote areas where logistics bring many constraints and resources for inventory and monitoring are unpredictable. While harvest information traditionally offered a general understanding of wolverine distribution dynamics in the province (Dawson, 2000; Ontario Wolverine Recovery Team, 2013), these data did not extend across wolverine range in Ontario and have not been available since 2009.

The results from this study clearly demonstrate that the HBL ecozone is currently characterized by low wolverine occupancy probabilities compared to the BSH. Novak (1975) reported that this species no longer occurred in the HBL ecozone by the early 1970s, being restricted to a relatively small region in the northwest of the province about 400 km southwest of the northern coastline. Following this nadir, Dawson (2000) documented a marked increase in the annual harvests in the late 1970s. These were the highest recorded since records began in 1919–1920 (35; Dawson, 2000), although still not higher than 26 in a year and mostly confined to the BSH. Caribou aerial surveys conducted by the Ontario government in the Far North over several of the same winters as our surveys (2009–2011; Berglund et al., 2014) yielded 324 wolverine detections. While fewer than 17% of the these fell within survey units with a probability of occupancy of <0.5 as defined in our study, the north-eastern HBL ecozone showed the strongest difference between surveys, with a number of wolverine records collected in the later surveys (Berglund et al., 2014)—a possible reflection of range expansion. Our surveys yielded high SE values in the same areas, which is to be expected along the interface of reproducing populations and unoccupied range or areas of low abundance, whether or not expansion is occurring. Future surveys applying methods for modelling occupancy dynamics (MacKenzie et al., 2018) could corroborate whether wolverines are indeed reoccupying the HBL ecozone, potentially seeding recovery into Québec, where the last wolverine was confirmed in the 1970s (COSEWIC, 2014).

Relative availability of prey, which was not possible to measure in this study, may be a factor explaining the relatively low occupancy of wolverines in the HBL. Dawson (2000) pointed out that the increase in wolverine harvest records in the late 1970s corresponded

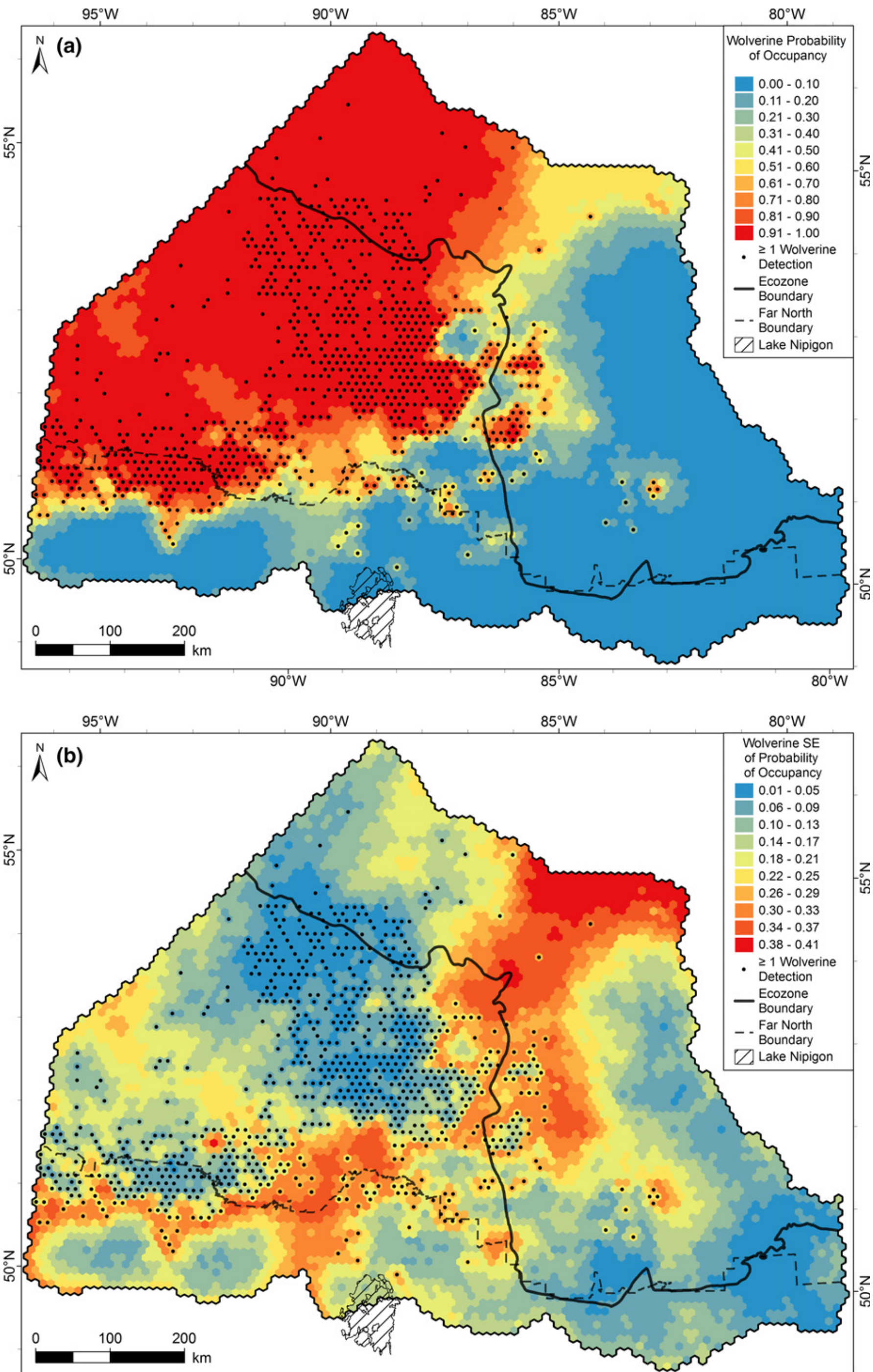

FIGURE 2 (a) Wolverine probability of occupancy and (b) standard error (SE) of probability of occupancy within the Northern Ontario study area from the model with detection covariates ecozone + year + Feb 15 and occupancy covariates TDD + Easting. Projection: NAD 1983 Ontario MNR Lambert [Colour figure can be viewed at wileyonlinelibrary.com]

to an increase in the Southern Hudson Bay migratory caribou herd (known at the time as Pen Islands), which grew from an estimated minimum population of 2,300 in 1979 to 10,798 in 1994 (Abraham & Thompson, 1998). Caribou observations made in the HBL suggest an increase in the occurrence of caribou in portions of the HBL since that time, following an eastward shift in occupancy and abundance to Cape Henrietta Maria (Magoun et al., 2005; Berglund et al., 2014), where they were reported as common in the 1940s and 50s (Novak, 1975).

As for the southern range limit of wolverines, food limitation is an unlikely driver, as moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), beaver (*Castor canadensis*) and other small prey—all favoured food items for wolverines in this area (Ontario Wolverine Recovery Team, 2013)—are relatively abundant within regenerating managed forests (Fisher & Wilkenson, 2005). Anthropogenic factors may be more important, as has been demonstrated in other studies (e.g. Krebs, Lofroth, & Parfitt, 2007; Lofroth, Krebs, Harrower, & Lewis, 2007). Three of seven radio-collared individuals in our study area were known to have been trapped or killed by a vehicle (Dawson, Magoun, Bowman, & Ray, 2010) and 15 additional reported deaths since 1990 resulted from vehicle (14) or train collisions (MNRF, unpublished data). Bowman et al. (2010) discussed the possible influence of industrial forestry activities and concurrent changes in ecosystem components (e.g. roads, wolf pack size, ungulate densities, % deciduous trees) on wolverine distribution in the southern portion of our study area. In lowland boreal forests of north-western Alberta, Scrafford et al. (2017) concluded that anthropogenic disturbance creates simultaneous risks and opportunities for wolverines, with habitat selection presenting trade-offs between predation risk and foraging opportunities.

The strong influence of the occupancy covariates TDD and Easting suggests that potential explanatory variables affecting wolverine occupancy not tested in this study may be more influential with a coincidental decrease in TDD (i.e. from south to north) and less influential with distance from the western border of Ontario (from west to east). While it may be tempting to consider the influence of TDD on the model results as proof that the persistence of spring snow is driving wolverine distribution (Copeland et al., 2010), we predict that TDD is also correlated with other variables such as summer temperature, soil temperature and moisture, forest cover types and human development, all of which could influence the occurrence and relative abundance of wolverines and their food resources. Magoun, Robards, Packila, and Glass (2017) provided evidence to suggest the resolution required to determine the relationship of wolverine distribution to snow may be most appropriately considered at the den site scale. Not to be overlooked is the possibility that wolverines are expanding their range to the east with dispersers sourced from the west, not only from high occupancy areas within Ontario, but also possibly from further west in Manitoba and beyond.

Without a clear understanding of how different environmental variables influence wolverine distribution and relative abundance, and lacking a reliable method of quantifying such variables at appropriate scales, we recommend using a minimum of covariates in occupancy models both to avoid over-parameterization and to make models more general, especially when using data from multiple seasons across very large areas. Although statistical methods such as cross-validation are available to determine appropriate model complexity among a set of scientifically justifiable models (Hooten & Hobbs, 2015), adding covariates for which effects on detection or occupancy are not fully understood may lead to biased conclusions and potentially misinformed or detrimental management actions (De Knegt et al., 2010). At the broad temporal (e.g. decades) and spatial (e.g. range) scales at which we examined wolverine occupancy in northern Ontario, we expect that the covariates we used in our final model will be sufficient to examine changes in wolverine distribution and occupancy over time, barring fast and/or broad-scale changes in ecosystems, harvest or development that are not presently captured in our model.

Fur harvest records have been unavailable from most of the wolverine range in Ontario since 2009, when the regulatory regime shifted to one where non-Indigenous trappers, fur dealers and fur auction houses cannot purchase, possess or sell wolverine in Ontario. As such, this standard means of monitoring wolverine distribution and relative abundance through harvest records and fur sales is no longer available. Repeated aerial surveys to record detections of wolverine, while expensive, provide a relatively cost-effective and non-invasive means to obtain the data necessary for assessing and monitoring the probability of occupancy of this wide-ranging, low-density species, including in areas with little to no trapping effort. Although this study has demonstrated that it is certainly possible to obtain results by combining a number of disparate surveys conducted in separate years and geographies, we nonetheless recommend designing surveys to cover the entire study area over one or two winters, taking into account heterogeneity in detection probability through adequate repeat visits (Magoun et al., 2007; Koen et al., 2008). As with sympatric caribou populations, the occupancy approach can provide a key means of measuring the effectiveness of recovery actions or mitigation measures for wolverine as industrial development and associated infrastructure move into the region along with the potential effects of climate change (Ontario Wolverine Recovery Team, 2013). The HBOM approach deployed in this study allows for addressing both species detectability and the inherent spatial structure of the data so as to minimize bias in occupancy estimates and increase accuracy in distribution mapping (Poley et al., 2014). We expect that cumulative changes in industrial development and/or climate change over broad areas could influence wolverine distribution and occupancy in the future and our results indicate that changes in distribution may be detectable if measured over a sufficient spatial and temporal scale using these results as a baseline measure.

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DATA AVAILABILITY

The datasets generated during and/or analysed during this study are available from the corresponding author on reasonable request.

BIOSKETCH

Justina Ray has been studying forest carnivores in North America and Africa for 20 years. This work is one component of the Ontario Wolverine Project, a collaboration among Wildlife Conservation Society Canada, the Ontario Ministry of Natural Resources and Forestry and The Wolverine Foundation in the earliest years.

Author contributions: J.C.R. and A.J.M. conceived the study and designed the surveys. J.C.R., A.J.M. and C.L.B.C. conducted the fieldwork and collected data, with additional material from F.N.D. and C.C.; L.G.P. conducted the occupancy modelling analysis; F.M.S. prepared the covariates and created the maps; and J.C.R., L.G.P. and A.J.M. led the writing, with assistance from F.N.D., C.L.B.C., F.M.S. and C.C.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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