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Occupancy patterns of large mammals in the Far North of Ontario under imperfect detection and spatial autocorrelation

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ABSTRACT

Aim An understanding of the factors that influence species distributions in heterogeneous landscapes is important when making decisions regarding conservation. Moreover, occupancy probabilities based on detection data can reveal important species–habitat relationships. Accounting for the spatial autocorrelation of detection data increases the statistical validity of occupancy models, but is not often considered. Using novel occupancy modelling that explicitly incorporates detectability and spatial autocorrelation, we assessed the influence of habitat on occupancy patterns of woodland caribou (*Rangifer tarandus caribou*), moose (*Alces alces*) and wolves (*Canis lupus*) across a broad biogeographical extent where fire is the dominant agent of disturbance.

Location Northern Ontario, Canada.

Methods We aerially surveyed 3851 sampling units, each covering 100 km², for woodland caribou, moose and wolves in February–March in 2009, 2010 and 2011, and visited 1663 units more than once to estimate detectability. We used restricted spatial regression to model occupancy probabilities of each species with respect to habitat factors in two ecozones, accounting for both imperfect detection and lack of independence of sampling units.

Results Covariates influencing species detection varied among ecozones and species. Caribou occupancy was positively related to bogs and negatively related to disturbed areas, while moose occupancy showed opposite responses to these covariates. Wolf occupancy was related to high prey occupancy. Explicitly accounting for spatial autocorrelation in detection data reduced the chance of type I error in occupancy estimates compared with non-spatial models.

Main conclusions Habitat relationships and occupancy patterns support the hypothesis that caribou remain spatially segregated from moose to reduce predation risk. The broad scale of analysis indicated changes in species–habitat relationships, suggesting that limiting factors vary across biogeographical gradients. The spatial pattern in caribou occupancy allowed us to identify important areas used by caribou across the region, including the ecotone between fire-driven boreal forests and peatland complexes. The evidence for significant relationships between caribou and land cover, predators and alternate prey underscores the need for careful planning of development and infrastructure in the area.

Keywords

Conservation biogeography, hierarchical modelling, imperfect detection, moose, northern Ontario, probability of occupancy, restricted spatial regression, spatial autocorrelation, wolf, woodland caribou.

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INTRODUCTION

An understanding of species distributions is central to biogeography. Combined with habitat variables, species distribution models are valuable in addressing ecological, biogeographical and evolutionary questions, especially for species of conservation concern (Guisan & Thuiller, 2005). They offer insights into the impacts of anthropogenic activities and environmental change, helping to identify areas of conservation priority and predicting the consequences of management activities (Chelgren *et al.*, 2011; Walpole *et al.*, 2012). Range reductions of many species have been linked to human disturbance (Lomolino & Channell, 1998; Ceballos & Ehrlich, 2002), and large, mobile mammals appear especially vulnerable because of their low recruitment rates and large home range sizes (Woodroffe & Ginsberg, 1998; Festa-Bianchet *et al.*, 2011). Among the first species to decline (Laliberte & Ripple, 2004), large mammals are regarded as sentinels of future biodiversity loss (Cardillo *et al.*, 2005). Conservation success in the coming decades, as human development expands into previously undisturbed areas, will depend on a sound understanding of the factors influencing species–habitat relationships and distributions and on accurate and precise monitoring.

Methods to build species distribution models have advanced rapidly. Models are frequently based on a species' presence or absence in a series of sample units, combined with environmental variables to estimate the probability of occupancy in each unit (MacKenzie *et al.*, 2002). Recent approaches address two longstanding problems: spatial autocorrelation and imperfect detection (Hoeting *et al.*, 2002; Magoun *et al.*, 2007; Chelgren *et al.*, 2011). The first reflects the intuitive idea that neighbouring sample units are more similar than those far apart. This lack of independence arises from population processes, such as herding behaviour or dispersal, or from environmental factors, such as the spatial structure of abiotic resources (Wintle & Bardos, 2006). Failure to account for spatial autocorrelation results in non-independence in residual errors, leading to overestimated precision in occupancy estimates (Legendre, 1993). To address this, a hierarchical, Bayesian approach to occupancy modelling has recently been developed; it has the attractive feature of partitioning the spatial component from environmental effects without assuming spatial independence, thus lending itself to improved inferences from survey data (Johnson *et al.*, 2013). The second problem, imperfect detection, represents a common feature of wildlife surveys. If not accounted for, it renders estimates of occupancy sensitive to variations in observers' detection abilities or to variations among surveys conducted at different times (MacKenzie, 2006). As a consequence, important inferences, such as the area occupied or the effects of habitat, may be biased (MacKenzie *et al.*, 2005; Kéry *et al.*, 2010). A common means to estimate the probability of detection for a species involves repeatedly visiting a subset of sample units to estimate the

likelihood of false absence, as well as incorporating covariates hypothesized to affect detectability into the models (MacKenzie, 2006; Johnson *et al.*, 2013).

Woodland caribou (*Rangifer tarandus caribou*, referred to hereafter as 'caribou') inhabiting the boreal forest represent an important application of occupancy modelling. Declines in populations at the southern edge of the caribou range have been linked to human-caused habitat alteration, leading to increased predation, especially from wolves (*Canis lupus*), in conjunction with apparent competition with other ungulate species (Festa-Bianchet *et al.*, 2011). Population declines and widespread range reduction have occurred across Canada, accounting for the threatened status of woodland caribou under Canada's Species at Risk Act (Environment Canada, 2012). In Ontario, where this species is also considered at risk (OMNR, 2009), caribou range has retracted on average 34 km per decade northwards (Schaefer, 2003).

Species occupancy is often measured in highly disturbed landscapes, where distribution patterns may already be altered (Yates & Muszika, 2006; Price *et al.*, 2010). The Far North of Ontario is largely undeveloped, although growing interest in natural resource exploitation portend expanding anthropogenic disturbance (Far North Science Advisory Panel, 2010). There is a need for broad-scale, long-term monitoring and understanding of woodland caribou distribution in advance of such expansion, but to date it is largely lacking (Magoun *et al.*, 2005). Using a novel method of occupancy modelling that accounts for both imperfect detection and spatial autocorrelation, we assessed the influences of habitat on caribou, wolf and moose (*Alces alces*) distributions across a vast landscape with minimal anthropogenic disturbance. In each occupancy model, we included specific habitat covariates that we hypothesized would have an influence on occupancy probabilities in the light of previously documented relationships with each species. We also tested for differences in the importance of habitat features to species occupancy estimates between two ecozones with prominent variations in land cover and natural disturbance patterns. Our methodology serves as a foundation for future assessments to distinguish between natural variation and anthropogenic effects, thereby improving management actions and the likelihood of positive conservation outcomes across large heterogeneous landscapes.

MATERIALS AND METHODS

Study area

The study area encompasses 385,100 km² of the Far North of Ontario, Canada, north of 50° N. It spans the Boreal Shield and Hudson Bay Lowlands ecozones, which have markedly different land cover characteristics, climates and degrees of natural disturbances. In particular, the Boreal Shield ecozone has greater areas of recently disturbed land cover, open water and more rugged terrain, while the

Hudson Bay Lowlands land cover consists mainly of bog and fen, and very little of it is disturbed (Appendix S1 in the Supporting Information). The Boreal Shield also has a greater human footprint than the Hudson Bay Lowlands, although overall human development is minimal; the total human population is fewer than 23,000, with few energy transmission corridors, one all-season road, one railway, and two active mines (Far North Science Advisory Panel, 2010).

The Hudson Bay Lowlands, 233,600 km² of the study area, consists mainly of poorly drained bog and fen complexes with areas of mudflats and marshes to the north, grading into tundra, taiga and finally boreal forest at the southern edge (Magoun *et al.*, 2005). The time between large fire events tends to be long compared with that in the Boreal Shield, and extensive fires are uncommon (Thompson, 2000). Nine human settlements are located within the Hudson Bay Lowlands, most along the Hudson and James Bay coasts, with a total population of about 4700 (Far North Science Advisory Panel, 2010).

The Boreal Shield Ecozone, 150,500 km² of the study area, is characterized by Precambrian Canadian Shield bedrock and thousands of glacially formed lakes. The plant community is dominated by hardy coniferous trees (Thompson, 2000). Where glacial scouring was intense, exposed bedrock remains, covered with lichens and mosses. The forests in this ecozone are renewed by large crown fires, encompassing areas of 10,000 to 100,000 ha, which constitute an important agent of regeneration (Beverly & Martell, 2005). There are 20 human settlements throughout the Boreal Shield, with a total population of about 18,000 (Far North Science Advisory Panel, 2010).

The study area includes the ranges of two caribou ecotypes. The more sedentary, forest-dwelling ecotype spends the year within the boreal forest, whereas the forest-tundra ecotype typically migrates from summer ranges in the tundra along the Hudson Bay coast to wintering areas in the boreal forest (OMNR, 2009; Berglund *et al.*, 2013). While only the forest-dwelling ecotype is designated provincially as threatened, the two ecotypes are known to share winter ranges in this study area (Magoun *et al.*, 2005).

Aerial surveys

Aerial surveys were conducted by the Ontario Ministry of Natural Resources (OMNR), and all flights followed a standardized protocol to keep flight patterns and parameters and observation methods as similar as possible among different flight crews (OMNR, unpublished report). The study area was divided into 100-km² hexagonal sample units, each adjacent to six other hexagons (see Magoun *et al.*, 2007). Their size and configuration were designed as a tradeoff between cost-effectiveness and resolution. Distribution models for wide-ranging vertebrate species tend to have the highest predictive power when the study unit is at the scale of the animal's home range (Carroll *et al.*, 2010), and in our study, individual caribou winter ranges were within the order of magnitude of the hexagon size (G.S.B., unpublished data).

Aerial surveys were conducted by OMNR personnel during three winters: 3 February–4 March 2009, 2 February–16 March 2010, and 3 February–7 March 2011 (Fig. 1). Survey flights were based at airports near communities and designed to pass through each hexagonal sample unit at least once. Repeat visits were conducted on a subset of sample units to estimate and account for imperfect detection; however, the number of repeat visits was limited by an interest in surveying each sample unit at least once. Each flight generally took 3 to 4 hours, at 100–200 m above ground level in fixed-wing aircraft. A navigator and at least two observers recorded observations of animals and signs of wolves, caribou and moose using Garmin GPSMAP 296 units (Garmin Ltd, Olathe, KS, USA).

Covariates

Detection covariates

Detection probabilities vary with conditions that affect the ability of observers to detect the species of interest (MacKenzie *et al.*, 2002). We hypothesized five variables to affect detectability, which we measured for each study unit during each survey and incorporated into occupancy modelling for each species: (1) Julian day; (2) average aboveground altitude of the aircraft; (3) mean speed of the aircraft; and (4) mean time of day. Models that included time also included a squared term, allowing the covariate to vary in a quadratic fashion (Boyce *et al.*, 2003). We calculated a covariate for (5) land cover openness by creating a 500-m buffer on either side of the flight path, the approximate limit of detection while in the aircraft. We calculated the percentage of open land cover within the buffer in each sample unit based on 12 'open' land cover classes from the Ontario Provincial Land-cover Classification. The classification was derived by the OMNR from Landsat-7 Thematic Mapper satellite scenes,

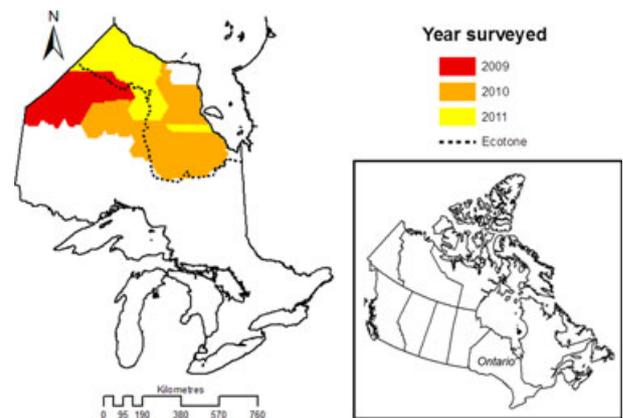


Figure 1 Study area in the Far North of Ontario, Canada, showing the sections surveyed for woodland caribou, moose and wolves in February–March 2009, 2010 and 2011. The dashed line represents the ecotone dividing the Boreal Shield (south and west) and the Hudson Bay Lowlands (north and east).

1999–2002, updated to reflect fire disturbance to 2008, and classified into 27 vegetated and non-vegetated land cover types at 25-m resolution.

Occupancy covariates

We included five occupancy covariates in our models for caribou and moose, and four for the wolf model. These a priori covariates were chosen to represent key habitat types or limiting factors for these species, and we hypothesized the direction of the response to each occupancy covariate (Table 1), based on documented habitat relationships for each species.

For caribou and moose, we chose terrain ruggedness, bog-type habitat (open and treed bog and fen), recent disturbances (burns and cuts, < 10 years old in 2008), open water, and distance to nearest human settlement, calculated for each hexagonal sample unit. Terrain ruggedness was represented by the standard deviation of elevation in each hexagon from a digital elevation model with a pixel size of 250 m, calculated for the province of Ontario using data from the Shuttle Radar Topography Mission (SRTM; Farr & Kobrick, 2000). We chose standard deviation because it provided a measure of variability within a sample unit, a more ecologically relevant variable than mean elevation given the overall flat nature of the landscape. Caribou have been found to be

Table 1 Hypothesized and modelled directions of relationships between woodland caribou, moose and wolf probability of occupancy and habitat covariates in the Boreal Shield ecozone (BSH), Hudson Bay Lowlands ecozone (HBL), or whole study area (WSA) in the Far North of Ontario, Canada. (+) indicates a positive relationship, (–) indicates a negative relationship, (/) indicates that no relationship was found (the credible interval of the covariate encompassed zero), and NA indicates that the covariate was not used in the occupancy model for that species. Bold direction signs indicate that the modelled covariate direction was consistent with the hypothesized covariate direction.

Model	Covariates*						
	W	R	D	B	S	CO	MO
Hypothesized caribou, BSH	(+)	(–)	(–)	(+)	(+)	NA	NA
Modelled caribou, BSH	(–)	(–)	(–)	(+)	(+)	NA	NA
Hypothesized caribou, HBL	(+)	(–)	(–)	(+)	(+)	NA	NA
Modelled caribou, HBL	(–)	(/)	(/)	(–)	(+)	NA	NA
Hypothesized moose, BSH	(–)	(+)	(+)	(–)	(–)	NA	NA
Modelled moose, BSH	(–)	(/)	(+)	(–)	(/)	NA	NA
Hypothesized moose, HBL	(–)	(+)	(+)	(–)	(–)	NA	NA
Modelled moose, HBL	(–)	(+)	(/)	(–)	(/)	NA	NA
Hypothesized wolf, WSA	NA	NA	NA	(–)	(+)	(+)	(+)
Modelled wolf, WSA	NA	NA	NA	(/)	(/)	(+)	(+)

*W, water; R, terrain ruggedness; D, disturbed; B, bog; S, distance to settlement; CO, caribou occupancy; MO, moose occupancy.

associated with less-rugged areas (James *et al.*, 2004). There was also a positive correlation across the study area between terrain ruggedness and mixed forest land cover ($r = 0.37$), a habitat type attractive to moose (Fortin *et al.*, 2008). Bog/fen complexes are commonly used by caribou and avoided by moose (James *et al.*, 2004), while disturbances such as forest cutovers or recent burns are generally avoided by caribou (Courtois *et al.*, 2008) but are good habitat for moose (Rempel *et al.*, 1997). Caribou will use frozen lakes and rivers as travel routes during winter (Schaefer & Pruitt, 1991); moose, on the other hand, tend to avoid ice in the winter as they are more prone to falling through than are the lighter caribou (G. Racey, OMNR, pers. comm.). Finally, we calculated the distance from the centroid of each study unit to the nearest human settlement. Caribou are known to avoid human disturbances (Smith *et al.*, 2000; Dyer *et al.*, 2001; Vors *et al.*, 2007); however, new growth in disturbed areas can be attractive to moose (Rempel *et al.*, 1997).

We chose a different set of occupancy covariates for wolves. As wolf distribution is strongly influenced by the location and biomass of their primary prey (Fuller, 1989), we used our estimated probability of occupancy of caribou and moose in each hexagonal sample unit as covariates in the wolf model. To avoid multicollinearity between caribou and moose occupancy probabilities and the other covariates, we used only two of the static habitat covariates in the wolf model, namely distance to settlement and bog-type habitat. We selected these because a Pearson product–moment correlation analysis indicated that these covariates had the lowest degrees of correlation with caribou and moose occupancy across the study area (caribou and bog: $r = -0.057$; caribou and settlement: $r = 0.039$; moose and bog: $r = -0.087$; moose and settlement: $r = -0.056$).

The variation in land-cover composition and configuration between ecozones led us to hypothesize that the influence of each land-cover covariate on species occupancy could differ in importance or even direction between the two ecozones. Therefore, we created separate caribou and moose models for each ecozone in order to identify any such geographical variation in covariate effects, and to identify covariates with opposite effects in each ecozone. For wolves, however, we did not achieve model convergence in ecozonal analyses, owing to the few repeated positive detections in sample units. We therefore analysed the wolf data in one model across the entire study area.

We deemed covariates in the occupancy and detection models for each species in each ecozone to be important when the posterior 95% credible interval of the parameter estimate did not encompass zero, while we deemed covariates with credible intervals encompassing zero to have no relationship with species occupancy.

Occupancy analysis

We used restricted spatial regression (RSR; Johnson *et al.*, 2013) to model the occupancy of each species in each

ecozone. The most common approach to occupancy modelling uses a product multinomial likelihood function, which allows detection and occupancy probabilities to be calculated accounting for measured external covariates hypothesized to influence these parameters (MacKenzie *et al.*, 2002). However, this approach produces unbiased estimates only when observations at nearby sample units are independent, a condition that is difficult to satisfy with ecological data, and residual spatial autocorrelation may result in overly precise confidence intervals around occupancy estimates, leading to type I error (Johnson *et al.*, 2013). In response to this, a growing number of studies have employed a Bayesian hierarchical spatial framework that explicitly incorporates spatial autocorrelation in occupancy models (Hoeting *et al.*, 2002; Magoun *et al.*, 2007; Chelgren *et al.*, 2011), but the computational time required to implement this method is prohibitive, making it impractical for processing large amounts of data from broad-scale or long-term monitoring programmes (Johnson *et al.*, 2013). There is also potential for confounding in spatial regression analyses between regression predictors, such as habitat covariates, and the spatial processes, leading to bias and inflated uncertainty in parameter estimates (Hodges & Reich, 2010; Hughes & Haran, 2012).

The RSR method was developed in response to these issues inherent in occupancy analyses, and allows the analysis of large occupancy data sets with spatial autocorrelation over large extents (Johnson *et al.*, 2013). RSR models use an efficient Gibbs sampler Markov chain Monte Carlo method to make Bayesian inference about the detection and occupancy processes, and explicitly incorporate spatial autocorrelation in survey data while solving issues of confounding between the fixed-effects and spatial portions of the model that hamper the estimation of intrinsic conditional autoregressive models (Hodges & Reich, 2010; Hughes & Haran, 2012). While previous hierarchical occupancy models employed a logit link function for relating measured covariates to occupancy and detection estimates, RSR models use a probit link function, resulting in increased computational efficiency that allows models to be fit over larger spatial domains (Johnson *et al.*, 2013). Detailed descriptions and derivations of the RSR model can be found in Hughes & Haran (2012) and Johnson *et al.* (2013).

We used the following settings for each species-specific model. We set the threshold for detecting spatial structure in neighbouring sample units to 12,000 m, which is large enough to encompass all six first-order neighbours of each hexagonal sample unit. We specified flat prior distributions for both the detection and occupancy processes, and a Gamma (0.5, 0.0005) distribution for the spatial process following Johnson *et al.* (2013). We allowed the chain to stabilize by running a burn-in period of 10,000 iterations, which were discarded, and then 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 species–ecozone model. The R package *stocc* (available from CRAN: <http://cran.r-project.org/web/packages/stocc/index.html>) for the R statistical

environment (R Development Core Team, 2012) was used to fit the models.

RESULTS

We surveyed a total of 3851 sample units, 1506 in the Boreal Shield and 2345 in the Hudson Bay Lowlands. During the flights, OMNR personnel surveyed 2188 (56.8%) sample units once, and 1663 (43.2%) between two and five times (Table 2). The proportion of sample units in which each species was detected at least once (Fig. 2) is the naïve occupancy estimate, representing the estimate of occupancy obtained without incorporating variations in species detectability or spatial autocorrelation (MacKenzie, 2005). Table 2 compares the naïve occupancy estimate for each model with the average calculated occupancy estimate.

No single detection covariate was important for all three species (see Table S1 in Appendix S2). Caribou detection in both ecozones was higher when terrain openness was high. In the Hudson Bay Lowlands, caribou detection was lower when the day of the year was higher, indicating that as the 6-week study period progressed, caribou detectability decreased. Caribou detection in this ecozone showed a quadratic relationship with time of day. Moose detection in both ecozones was lower when flight altitude was higher. In the Boreal Shield, moose detection was lower when aircraft speed was higher, and in the Hudson Bay Lowlands, moose detection was lower when the openness of the terrain around the flight path was greater. Wolf detection across the study area was lower when aircraft altitude, speed and terrain openness were high.

Table 2 Frequency distribution of the number of visits per sample unit (expressed as a percentage) in the whole study area and each ecozone in the Far North of Ontario, Canada; naïve species occupancy (percentage of study units where the species was detected at least once) of woodland caribou, moose, and wolves; and average modelled probability of occupancy (standard error), from each species-specific model incorporating all detection and habitat covariates and spatial autocorrelation.

	Whole study area (%)	Boreal Shield (%)	Hudson Bay Lowlands (%)
Number of surveys*			
1	55.8	54.7	56.8
2	31.6	32.6	32.3
3	7.9	7.5	7.4
4	3.5	2.8	1.9
5	1.2	2.4	1.6
Naïve occupancy			
Caribou	38.9	39.7	35.5
Moose	42.5	48.4	39.2
Wolf	19.7	19.1	20.1
Modelled occupancy			
Caribou	53.6 (14.1)	50.6 (12.2)	55.5 (15.2)
Moose	65.4 (12.8)	84.8 (7.7)	53.9 (15.9)
Wolf	59.4 (17.1)	69.9 (16.2)	53.2 (17.6)

*Sample sizes were: Boreal Shield, 1505 sample units; Hudson Bay Lowlands, 2346 sample units; whole study area, 3851 sample units.

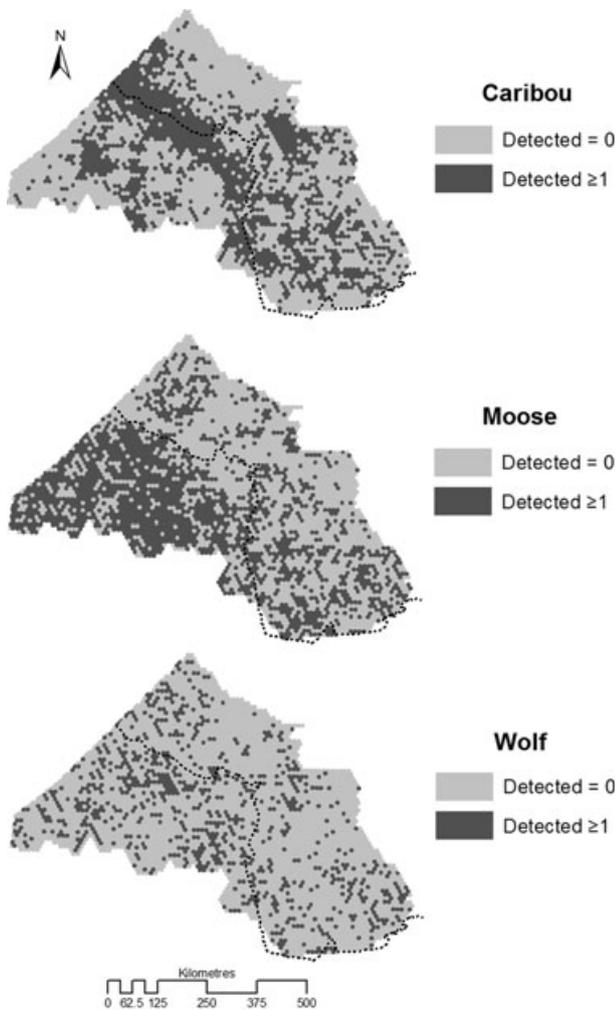


Figure 2 Study units in which woodland caribou, moose and wolves were detected at least once (dark grey), in February–March 2009, 2010 and 2011, in Ontario, Canada. The dashed line represents the ecotone dividing the Boreal Shield (south and west) and the Hudson Bay Lowlands (north and east).

Important occupancy covariates differed among species and ecozones (Table 1, and Table S2 in Appendix S2). Caribou occupancy in both ecozones was lower when the amount of water was more extensive, and was higher with increasing distance to settlements. In the Boreal Shield, caribou occupancy was lower when terrain ruggedness and disturbed habitat were more extensive, but high when the amount of bog in each sample unit was greater. In the Hudson Bay Lowlands, caribou occupancy was lower in sample units with more extensive bog. Moose occupancy in both ecozones was lower when the extent of water was greater. In the Boreal Shield, moose occupancy was lower when the amount of bog was more extensive, and was high when the amount of disturbed habitat was greater, while in the Hudson Bay Lowlands, moose occupancy was higher in sample units with greater terrain ruggedness. Wolf occupancy across the study area was higher in sample units with higher occupancy of both moose and caribou, and there was no evidence

of a relationship with distance to settlement or bog. Table 1 compares our hypothesized direction of relationship between habitat covariates and species occupancy with the modelled direction of relationship.

Each species' occupancy displayed clear spatial patterns across the study area (Fig. 3). Caribou occupancy was the highest along the boundary between ecozones (the ecotone), and lowest in the north-east area of the Hudson Bay Lowlands, along the Hudson Bay coast, and in the western Boreal Shield. Moose occupancy was very high overall across the Boreal Shield ecozone as well as in the southern portion of the Hudson Bay Lowlands, and low in the northern portion of the Lowlands ecozone. Wolf occupancy was not as clearly spatially patterned as that of the other species; areas of high occupancy did, however, appear to mirror the areas of highest occupancy of these prey.

For each model, the posterior distribution of the spatial variance parameter ($\sigma = 1/\sqrt{\tau}$) was far from zero, implying additional spatial correlation in the occupancy process beyond the variation produced by the habitat covariates (Table S3 in Appendix S2). The occupancy models incorporating spatial autocorrelation resulted in lower occupancy estimates and wider credible intervals around occupancy estimates for each species-ecozone model, compared to the occupancy models not taking spatial autocorrelation into account (Table 3).

DISCUSSION

Occupancy patterns across this vast, anthropogenically undisturbed landscape exhibited important differences among three large resident mammals. The variable patterns in caribou winter occupancy in the Far North lend support to the hypothesis that woodland caribou select habitats to minimize predation risk and to avoid apparent competitors (Cumming *et al.*, 1996; Rettie & Messier, 2000; Bowman *et al.*, 2010). Subsistence on lichen enables caribou to overwinter in 'refuge' areas that would not support other ungulates, such as bog and fen complexes (Thomas, 1995; Cumming *et al.*, 1996; James *et al.*, 2004), and caribou also avoid habitats, such as recently disturbed or mixed forests, that attract other ungulates (Courtois *et al.*, 2008; Fortin *et al.*, 2008), resulting in spatial segregation between caribou and alternate prey species and their associated predators. In keeping with this theory of spatial segregation, our hypotheses that caribou and moose would show opposing responses to habitat covariates were supported. However, the broad extent of our analysis allowed us to observe differences in occupancy and species-habitat relationships between the two ecozones, indicating that the habitat selection of caribou and moose changed across a gradient of habitat and resource availability.

Our hypothesis that caribou occupancy would be higher when bog-fen habitat was more extensive and lower where disturbed habitat was more common, and that moose occupancy would exhibit the converse, was supported to different degrees in the two ecozones (Table 1). Across the Boreal

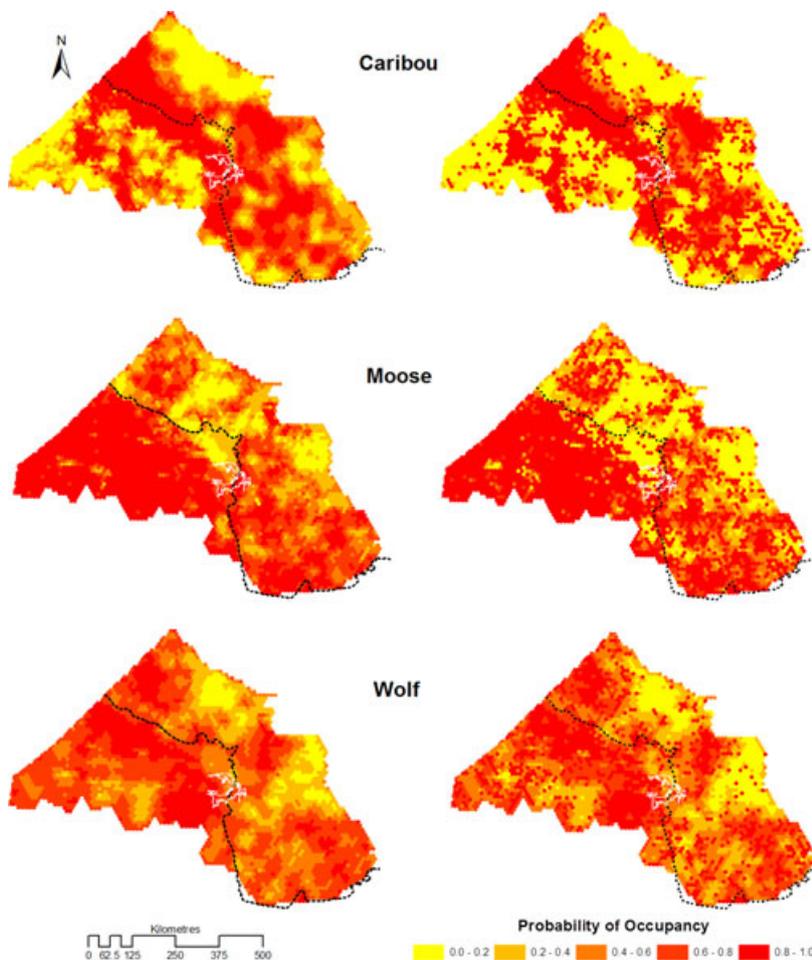


Figure 3 Derived probability of occupancy of woodland caribou, moose and wolves in the Far North of Ontario, Canada, from both spatial and non-spatial models. The dashed line represents the ecotone dividing the Boreal Shield (south and west) and the Hudson Bay Lowlands (north and east). Caribou and moose models were derived in each ecozone separately; the wolf model was derived across the whole study area. The left-hand side of the figure shows the spatial models (incorporating spatial autocorrelation in first-order neighbouring sample units), and the right side shows the non-spatial models (no spatial autocorrelation estimated). The region outlined in white on each map indicates staked claims in the Ring of Fire mineral deposit.

Table 3 Average probability of occupancy and standard error (SE) from spatial and non-spatial occupancy models, based on aerial survey data on woodland caribou, moose and wolves in the Far North of Ontario, Canada. Restricted spatial regression (RSR) models incorporated spatial autocorrelation, while non-spatial models did not. Caribou and moose models were calculated separately for each ecozone (BSH, Boreal Shield; HBL, Hudson Bay Lowlands); the wolf model was run for the whole study area (WSA).

	RSR models		Non-spatial models	
	Occupancy (%)	SE (%)	Occupancy (%)	SE (%)
Caribou (BSH)	50.6	12.2	54.2	3.21
Caribou (HBL)	55.5	15.2	64.7	3.72
Moose (BSH)	84.8	7.70	86.0	2.62
Moose (HBL)	53.9	15.9	58.1	4.70
Wolf (WSA)	59.4	17.1	67.4	6.53

Shield, where disturbed habitat was more common and bogs less common than in the Hudson Bay Lowlands, both species showed the hypothesized relationships. However, in the Hudson Bay Lowlands, disturbed habitat was rare and bog-type habitat was highly abundant, resulting in a negative influence of bogs on caribou occupancy in the Lowlands,

opposite to our hypothesized relationship. Moose occupancy, on the other hand, was still low in areas of high bog habitat but no longer exhibited any relationship with disturbed habitat. In Québec, Fortin *et al.* (2008) also observed a changing functional response to a gradient of resource availability: caribou selection of lichen, an important winter food, was strong when lichen cover was rare but decreased as lichen abundance increased. This relationship became negative when lichen abundance was sufficiently high to no longer limit caribou.

We found similar differences in the relationships between moose and caribou occupancy and terrain ruggedness (Table 1). Across the whole study area, terrain ruggedness was positively correlated with mixed forest, which is attractive to moose (Fortin *et al.*, 2008); associations between caribou and less rugged areas and between moose and more rugged areas have been previously documented (James *et al.*, 2004), and we hypothesized the same relationships with ruggedness in our study area. In the Boreal Shield, where bogs were less common and the probability of moose occupancy was high, caribou occupancy was lower in more rugged areas; in the Hudson Bay Lowlands, where moose occupancy was lower and bogs were abundant, no relationship between caribou and ruggedness was evident. Conversely, moose showed the hypothesized positive relationship with rugged

areas in the Hudson Bay Lowlands, whereas there was no such relationship in the Boreal Shield, where more disturbed habitat was available. The broad-scale variation in habitat availability probably drives these ecozone-specific differences in species occupancy and offers insight into the flexibility of habitat selection across spatial gradients.

Notwithstanding the benefit of the large spatial extent of our analysis for characterizing broad patterns, habitat relationships on a scale finer than our grain size of 100 km² may have been masked. For example, our hypothesis that moose occupancy would be low in areas with a high proportion of water was supported in both ecozones, as was our hypothesized positive relationship between caribou occupancy and distance to human settlements, consistent with previous reports on caribou avoidance of settlements and associated disturbances (Dyer *et al.*, 2001; Schaefer & Mahoney, 2007; Vors *et al.*, 2007; Vistness & Nellemann, 2008). However, the negative relationship between caribou occupancy and water area was contrary to our hypothesized positive relationship based on caribou selection of frozen lakes during winter (Ferguson & Elkie, 2005). We postulate that this unexpected relationship was a matter of spatial resolution: a smaller grain may have revealed whether caribou selected water near the shoreline while avoiding the centre of large lakes. Similarly, distance to settlement was not an important predictor of moose occupancy, although moose may have avoided settlements by distances smaller than the 9.8-km diameter of our sample units. Overall, the need for broad-scale monitoring of this extensive region outweighed the desire for finer spatial resolution in our study.

The strikingly different broad-scale occupancy patterns exhibited by caribou and moose provide further evidence for spatial segregation. High moose occupancy was found mainly in the more disturbed Boreal Shield ecozone. The area of highest caribou occupancy, on the other hand, formed a broad band (on average 110 km wide) straddling the ecotone in both ecozones, a pattern consistent with evidence from winter radio-telemetry data (Berglund *et al.*, 2013). The ecotone represents a transition between the fire-disturbed boreal forest and the peatland complexes characteristic of the Hudson Bay Lowlands, and evidence from this study and elsewhere (Schaefer & Pruitt, 1991) suggests that large expanses of recently burned forest west of the ecotone and extensive bog–fen complexes to the east offer less suitable winter caribou habitat conditions. Given that caribou tend to abandon winter ranges for years following human disturbance (Cumming & Beange, 1993), the ecotone appears to have markedly high conservation value. The Ring of Fire, a large mineral deposit with high economic potential (Far North Science Advisory Panel, 2010), is situated near the middle of our study area (Fig. 3). It is of particular interest in this context, falling as it does within the area of high caribou winter occupancy. This calls for careful planning of resource extraction and accompanying infrastructure in the area to minimize disturbance of caribou winter habitat.

Habitat selection of predators is strongly driven by the availability and location of prey (Karanth *et al.*, 2004; Walpole *et al.*, 2012). As such, the definition of ‘habitat’ in realistic species distribution models includes both the biotic and abiotic resources and conditions that limit species (Caughley & Gunn, 1995), and the incorporation of mechanisms such as interspecific interactions can make these models more ecologically accurate (Wisiz *et al.*, 2013). Although interspecific interactions can be difficult to measure and map owing to their dynamic nature (Johnson & Gillingham, 2005; Wisiz *et al.*, 2013), wolf numbers are generally predictable from ungulate biomass (Fuller, 1989), so we included the calculated probability of occupancy of the two ungulate species as unidirectional habitat covariates in our wolf model. Our results supported the hypothesized positive relationships between wolf and prey, but did not reveal any relationship between wolf occupancy and the two static habitat types (bog and distance to settlement) in the model (Table 1). However, given the comparatively low number of detections of wolves across the study area, a more flexible survey design (*i.e.* Patterson *et al.*, 2004; Magoun *et al.*, 2007), where flights are permitted to deviate from a straight path to search open areas, may be more efficient for detecting patchily distributed, relatively scarce carnivores. Improved wolf detection data would also allow more sophisticated methods of modelling species interactions to be used to describe multidirectional interactions or the strength of interactions between species, thus enhancing the predictive capabilities of the model (Kissling *et al.*, 2012).

By using the RSR method of occupancy modelling to incorporate both probability of detection and spatial autocorrelation, we were able to explicitly account for two factors which, if ignored, would have biased our results and reduced the ecological accuracy of our models (MacKenzie, 2005; Wintle & Bardos, 2006). The importance of incorporating detectability is evident when comparing the naïve occupancy with the average occupancy while taking detectability into account (Table 2; MacKenzie, 2005). The naïve occupancy was substantially lower than the modelled estimate, demonstrating that if probability of detection was not explicitly incorporated, occupancy would be underestimated. In addition, covariates strongly influencing the probability of detection varied among species and between ecozones, indicating that no single factor influenced the detectability of all three large mammals, and therefore that detectability could not be easily standardized among species by controlling for common detection covariates.

Spatial structure likewise proved to be important, as indicated by the strong spatial variance in each model. This means that the distribution of each species was spatially structured beyond what can be explained by measured and modelled habitat covariates. Compared with the non-spatial model, the RSR model had two main effects: a reduction in the average probability of occupancy, and an increase in the width of credible intervals around occupancy estimates (Table 3). We expected to see these effects, as it has been

shown that a lack of independence in residual errors within non-spatial models results in an overestimated precision of occupancy estimates (Legendre, 1993). Furthermore, a visual comparison of maps where analyses did and did not incorporate spatial autocorrelation between first-order neighbouring sample units indicated how the latter resulted in a smoother-looking map without lone sample units of high occupancy (Fig. 3). This is more biologically realistic: the spatial structure of habitat types across the study area implies that individuals are unlikely to occupy a single sample unit surrounded by sample units with low probabilities of occupancy and therefore low habitat quality. In sum, the benefits of using a hierarchical Bayesian approach to occupancy modelling were twofold: it allowed us to parcel out the variation related to species detectability and to address the inherent spatial structure of the data. The result was reduced bias in occupancy estimates and increased utility of our species distribution maps for conservation planning and long-term monitoring.

A fundamental premise in ecology is that the distribution of a species is influenced by habitat, now increasingly recognized as composed of both static and dynamic elements that change in space and time. Dealing with imperfect detection and spatial autocorrelation can enhance the predictive power of species distribution modelling, with implications for both study design and data analysis. Surveys should be designed to estimate and, if possible, control for variations in the detectability of species related to survey conditions or habitat factors; and models should account for spatial autocorrelation, incorporate both static and dynamic components of habitat, and be built at spatial and temporal scales that are biologically relevant to the species of interest. As demonstrated by our study, each of these factors has an important influence on our understanding of species distributions. Refined, more ecologically realistic models should improve our power to identify changes in species distributions, to inform land use planning, and to contribute to conservation.

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REFERENCES

- Berglund, N., Abraham, K., Brown, G., Pond, B., Racey, G. & Walton, L. (2013) *Woodland caribou* (*Rangifer tarandus caribou*) in the far north of Ontario: background information in support of land use planning. Technical Report Series, Ontario Ministry of Natural Resources, Thunder Bay, ON.
- Beverly, J.L. & Martell, D.L. (2005) Characterizing extreme fire and weather events in the Boreal Shield ecozone of Ontario. *Agricultural and Forest Meteorology*, **133**, 5–16.
- Bowman, J., Ray, J.C., Magoun, A.J., Johnson, D.S. & Dawson, F.N. (2010) Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. *Canadian Journal of Zoology*, **88**, 454–467.
- Boyce, M.S., Mao, J.S., Merrill, E.H., Fortin, D. & Turner, M.G. (2003) Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience*, **10**, 421–431.
- Canada, Environment (2012) *Recovery strategy for the woodland caribou* (*Rangifer tarandus caribou*), boreal population, in Canada. Species at Risk Act Recovery Strategy Series, Environment Canada, Ottawa, ON.
- Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L. & Purvis, A. (2005) Multiple causes of high extinction risk in large mammal species. *Science*, **309**, 1239–1241.
- Carroll, C., Johnson, D.S., Dunk, J.R. & Zielinski, W.J. (2010) Hierarchical Bayesian spatial models for multispecies conservation planning and monitoring. *Conservation Biology*, **24**, 1538–1548.
- Caughley, G. & Gunn, A. (1995) *Conservation biology in theory and practice*. Blackwell Science, Oxford.
- Ceballos, G. & Ehrlich, P.R. (2002) Mammal population losses and the extinction crisis. *Science*, **296**, 904–907.
- Chelgren, N.D., Adams, M.J., Bailey, L.L. & Bury, R.B. (2011) Using multilevel spatial models to understand salamander site occupancy patterns after wildfire. *Ecology*, **92**, 408–421.
- Courtois, R., Gingras, A., Fortin, D., Sebbane, A., Rochette, B. & Breton, L. (2008) Demographic and behavioural response of woodland caribou to forest harvesting. *Canadian Journal of Forest Research*, **38**, 2837–2849.
- Cumming, H.G. & Beange, D.B. (1993) Survival of woodland caribou in commercial forests of northern Ontario. *Forestry Chronicle*, **69**, 579–588.
- Cumming, H.G., Beange, D.B. & Lavoie, G. (1996) Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. *Rangifer*, Special Issue No. 9, 81–94.
- Dyer, S.J., Neill, J.P.O., Wasel, S.M. & Boutin, S. (2001) Avoidance of industrial development by woodland caribou. *Journal of Wildlife Management*, **65**, 531–542.
- Far North Science Advisory Panel (2010) *Science for a changing Far North. The report of the Far North Science Advisory Panel*. Ontario Ministry of Natural Resources, Thunder Bay, ON.
- Farr, T.G. & Kobrick, M. (2000) Shuttle radar topography mission produces a wealth of data. *EOS Transactions American Geophysical Union*, **81**, 583–585.
- Ferguson, S.H. & Elkie, P.C. (2005) Use of lake areas in winter by woodland caribou. *Northeastern Naturalist*, **12**, 45–66.

- Festa-Bianchet, M., Ray, J.R., Boutin, S., Côté, S.D. & Gunn, A. (2011) Conservation of caribou in Canada: an uncertain future. *Canadian Journal of Zoology*, **89**, 419–434.
- Fortin, D., Courtois, R., Etcheverry, P., Dussault, C. & Gingras, A. (2008) Winter selection of landscapes by woodland caribou: behavioural response to geographical gradients in habitat attributes. *Journal of Applied Ecology*, **46**, 1392–1400.
- Fuller, T.K. (1989) Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs*, **105**, 1–41.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Hodges, J.S. & Reich, B.J. (2010) Adding spatially-correlated errors can mess up the fixed effects you love. *American Statistician*, **64**, 325–334.
- Hoeting, J.A., Leecaster, A. & Bowden, D. (2002) An improved model for spatially correlated binary responses. *Journal of Agricultural, Biological, and Environmental Statistics*, **5**, 102–114.
- Hughes, J. & Haran, M. (2012) Dimension reduction and alleviation of confounding for spatial generalized linear mixed models. *Journal of the Royal Statistical Society: Series B*, **75**, 139–159.
- James, A.R.C., Boutin, S., Hebert, D.M. & Rippin, A.B. (2004) Spatial separation of caribou from moose and its relation to predation by wolves. *Journal of Wildlife Management*, **68**, 799–809.
- Johnson, C.J. & Gillingham, M.P. (2005) An evaluation of mapped species distribution models used for conservation planning. *Environmental Conservation*, **32**, 1–12.
- Johnson, D.S., Conn, P.B., Hooten, M.B., Ray, J.C. & Pond, B.A. (2013) Spatial occupancy models for large data sets. *Ecology*, **94**, 801–808.
- Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A. & Hines, J.E. (2004) Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences USA*, **101**, 4854–4858.
- Kéry, M., Gardner, B. & Monnerat, C. (2010) Predicting species distributions from checklist data using site-occupancy models. *Journal of Biogeography*, **37**, 1851–1862.
- Kissling, W.D., Dormann, C.F., Groeneveld, J., Hickler, T., Kühn, I., McNerny, G.J., Montoya, J.M., Römermann, C., Schiffers, K., Schurr, F.M., Singer, A., Svenning, J.-C., Zimmermann, N.E. & O'Hara, R.B. (2012) Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography*, **39**, 2163–2178.
- Lablerte, A.S. & Ripple, W.J. (2004) Range contractions of North American carnivores and ungulates. *BioScience*, **54**, 123–138.
- Legendre, P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology*, **74**, 1659–1673.
- Lomolino, M.V. & Channell, R. (1998) Range collapse, re-introductions, and biogeographic guidelines for conservation. *Conservation Biology*, **12**, 481–484.
- MacKenzie, D.I. (2005) What are the issues with presence-absence data for wildlife managers? *Journal of Wildlife Management*, **69**, 849–860.
- MacKenzie, D.I. (2006) Modelling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. *Journal of Wildlife Management*, **70**, 367–374.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew, J. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2005) *Occupancy estimation and modelling: inferring patterns and dynamics of species occurrence*. Elsevier, San Diego, CA.
- Magoun, A.J., Abraham, K.F., Thompson, J.E., Ray, J.C., Gauthier, M.E., Brown, G.S., Woolmer, G., Chenier, C.J. & Dawson, F.N. (2005) Distribution and relative abundance of caribou in the Hudson Plains Ecozone of Ontario. *Rangifer*, Special Issue No. 16, 4–6.
- Magoun, A.J., Ray, J.C., Johnson, D.S., Valkenburg, P., Dawson, F.N. & Bowman, J. (2007) Modelling wolverine occurrence using aerial surveys of tracks in snow. *Journal of Wildlife Management*, **71**, 2221–2229.
- OMNR (2009) *Ontario's woodland Caribou conservation plan*. Ontario Ministry of Natural Resources, Thunder Bay, ON.
- Patterson, B.R., Quinn, N.W.S. & Becker, E.F. (2004) Estimating wolf densities in forested areas using network sampling of tracks in snow. *Wildlife Society Bulletin*, **32**, 938–947.
- Price, S.J., Cecala, K.K., Browne, R.A. & Dorcas, M.E. (2010) Effects of urbanization on occupancy of stream salamanders. *Conservation Biology*, **25**, 547–555.
- R Development Core Team (2012) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org/>.
- Rempel, R.S., Elkie, P.C., Rodgers, A.R. & Gluck, M.J. (1997) Timber-management and natural-disturbance effects on moose habitat: landscape evaluation. *The Journal of Wildlife Management*, **61**, 514–524.
- Rettie, W.J. & Messier, F. (2000) Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*, **23**, 466–478.
- Schaefer, J.A. (2003) Long-term range recession and the persistence of caribou in the taiga. *Conservation Biology*, **17**, 1435–1439.
- Schaefer, J.A. & Mahoney, S.P. (2007) Effects of progressive clearcut logging on Newfoundland caribou. *Journal of Wildlife Management*, **71**, 1753–1757.
- Schaefer, J.A. & Pruitt, W.O. (1991) Fire and woodland caribou in southeastern Manitoba. *Wildlife Monographs*, **116**, 1–39.
- Smith, K.G., Ficht, E.J., Hobson, D., Sorensen, T.C. & Hervieux, D. (2000) Winter distribution of woodland caribou in relation to clear-cut logging in west-central Alberta. *Canadian Journal of Zoology*, **78**, 1433–1440.

- Thomas, D. C. (1995) A review of wolf–caribou relationships and conservation. *Ecology and conservation of wolves in a changing world* (ed. by L. N. Carbyn, S. H. Fritts and D. R. Seip), pp. 261–273. Canadian Circumpolar Institute, Edmonton, ON.
- Thompson, I. D. (2000) Forest vertebrates of Ontario: patterns of distribution. *Ecology of a managed terrestrial landscape: patterns and processes of forest landscapes in Ontario* (ed. by A. H. Perera, D. L. Euler and I. D. Thompson), pp. 54–73. University of British Columbia Press, Vancouver, BC.
- Vistness, I. & Nellemann, C. (2008) The matter of spatial and temporal scales: a review of reindeer and caribou response to human activity. *Polar Biology*, **31**, 399–407.
- Vors, L.S., Schaefer, J.A., Pond, B.A., Rodgers, A.R. & Patterson, B.R. (2007) Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. *Journal of Wildlife Management*, **71**, 1249–1256.
- Walpole, A.A., Bowman, J., Murray, D.L. & Wilson, P.J. (2012) Functional connectivity of lynx at their southern range periphery in Ontario, Canada. *Landscape Ecology*, **27**, 761–773.
- Wintle, B.A. & Bardos, D.C. (2006) Modelling species–habitat relationships with spatially autocorrelated observation data. *Ecological Applications*, **16**, 1945–1958.
- Wisz, M.S., Pottier, J., Kissling, W.D. *et al.* (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews*, **88**, 15–30.
- Woodroffe, R. & Ginsberg, J. (1998) Edge effects and the extinction of populations inside protected areas. *Science*, **280**, 2126–2128.
- Yates, M.D. & Muszika, R.M. (2006) Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. *Journal of Wildlife Management*, **70**, 1238–1248.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Habitat covariate differences among the Boreal Shield ecozone, Hudson Bay Lowlands ecozone, and the whole study area.

Appendix S2 Detection, occupancy, and spatial variance parameter estimates and credible intervals.

BIOSKETCH

Lucy Poley is a PhD student in the Department of Geography at the University of Calgary. Her research focus is on the conservation of large mammals, particularly ungulates and their associated predators, and the applications of remotely sensed data to assessing wildlife habitat use.

Author contributions: D.S.J. designed the statistical analysis; L.G.P. analysed the data and led the development of all drafts; all other authors contributed equally to the writing.

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