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

Lucy G. Poley1, Bruce A. Pond2, James A. Schaefer3, Glen S. Brown4, Justina C. Ray5 and Devin S. Johnson6

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.
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 (Schafer, 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 ecoregion 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 (Boye 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 Landcover Classification. The classification was derived by the OMNR from Landsat-7 Thematic Mapper satellite scenes.
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 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 (Schaef er & 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.

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, (I) 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.

<table>
<thead>
<tr>
<th>Model</th>
<th>Covariates*</th>
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<tbody>
<tr>
<td></td>
<td>W</td>
</tr>
<tr>
<td>Hypothesized caribou, BSH</td>
<td>(+)</td>
</tr>
<tr>
<td>Modelled caribou, BSH</td>
<td>(−)</td>
</tr>
<tr>
<td>Hypothesized caribou, HBL</td>
<td>(+)</td>
</tr>
<tr>
<td>Modelled caribou, HBL</td>
<td>(−)</td>
</tr>
<tr>
<td>Hypothesized moose, BSH</td>
<td>(−)</td>
</tr>
<tr>
<td>Modelled moose, BSH</td>
<td>(−)</td>
</tr>
<tr>
<td>Hypothesized moose, HBL</td>
<td>(−)</td>
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<tr>
<td>Modelled moose, IJBL</td>
<td>(−)</td>
</tr>
<tr>
<td>Hypothesized wolf, WSA</td>
<td>NA</td>
</tr>
<tr>
<td>Modelled wolf, WSA</td>
<td>NA</td>
</tr>
</tbody>
</table>

*W, water; R, terrain ruggedness; D, disturbed; B, bog; S, distance to settlement; CO, caribou occupancy; MO, moose 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; Magouln 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 biased 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](#)

<table>
<thead>
<tr>
<th>Number of surveys*</th>
<th>Whole study area (%)</th>
<th>Boreal Shield (%)</th>
<th>Hudson Bay Lowlands (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>55.8</td>
<td>54.7</td>
<td>56.8</td>
</tr>
<tr>
<td>2</td>
<td>31.6</td>
<td>32.6</td>
<td>32.3</td>
</tr>
<tr>
<td>3</td>
<td>7.9</td>
<td>7.5</td>
<td>7.4</td>
</tr>
<tr>
<td>4</td>
<td>3.5</td>
<td>2.8</td>
<td>1.9</td>
</tr>
<tr>
<td>5</td>
<td>1.2</td>
<td>2.4</td>
<td>1.6</td>
</tr>
</tbody>
</table>

**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.
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 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 eczone 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 ($\sigma = 1/\sqrt{s}$) 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 Shield...
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

Table 3

<table>
<thead>
<tr>
<th>RSR models</th>
<th>Non-spatial models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Occupancy (%)</td>
<td>SE (%)</td>
</tr>
<tr>
<td>Caribou (BSH)</td>
<td>50.6</td>
</tr>
<tr>
<td>Caribou (HBL)</td>
<td>55.5</td>
</tr>
<tr>
<td>Moose (BSH)</td>
<td>84.8</td>
</tr>
<tr>
<td>Moose (HBL)</td>
<td>33.9</td>
</tr>
<tr>
<td>Wolf (WSA)</td>
<td>59.4</td>
</tr>
</tbody>
</table>

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,
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 & Nellermann, 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; Wapole 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 (Wisz et al., 2013). Although interspecific interactions can be difficult to measure and map owing to their dynamic nature (Johnson & Gillingham, 2005; Wisz 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


**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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