

# Roads, logging, and the large-mammal community of an eastern Canadian boreal forest

Jeff Bowman, Justina C. Ray, Audrey J. Magoun, Devin S. Johnson, and F. Neil Dawson

**Abstract:** We evaluated hypotheses concerning the distributions of large mammals in a 60 000 km<sup>2</sup> study area that encompassed the contact zone between Ontario's roadless north and the postlogging southern landscape. We estimated occurrence probability in 575 sample units for woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)), wolverine (*Gulo gulo* (L., 1758)), gray wolf (*Canis lupus* L., 1758), moose (*Alces alces* (L., 1758)), and white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)). We used ordinations and spatial regressions to assess the contributions of parameters to species occurrence. Roads and cutovers were most abundant in the south, leading to an increased prevalence of deciduous forest. Mature coniferous forest, however, occurred most commonly in the north. Occurrence probabilities for moose and deer were greatest in the south, in close association with deciduous trees. Wolf occurrence was also greatest in the south, positively related to both deciduous forest and road density. Caribou occurrence, however, was positively related to mature coniferous forest and negatively related to both wolf occurrence and roads. Wolverine occurrence was negatively related to deciduous forest. Our surveys demonstrated distinct mammal communities in the northern and southern halves of our study area, a separation that appeared to be mediated by deciduous forest and roads.

**Résumé :** Nous avons évalué des hypothèses sur la répartition des grands mammifères dans une région d'étude de 60 000 km<sup>2</sup> qui chevauche la zone de contact entre les paysages sans routes du nord de l'Ontario et les paysages du sud affectés par la coupe du bois. Nous avons estimé les probabilités d'occurrence du caribou des forêts (*Rangifer tarandus caribou* (Gmelin, 1788)), du carcajou (*Gulo gulo* (L., 1758)), du loup gris (*Canis lupus* L., 1758), de l'orignal (*Alces alces* (L., 1758)) et du cerf de Virginie (*Odocoileus virginianus* (Zimmerman, 1780)) dans 575 unités d'échantillonnage. Des ordinations et des régressions spatiales ont servi à évaluer les contributions des variables à l'occurrence des espèces. Les routes et les zones coupées sont plus abondantes dans le sud, ce qui explique la prévalence plus importante de la forêt décidue. Cependant, la forêt de conifères mature est plus fréquente dans le nord. Les probabilités d'occurrence de l'orignal et du cerf sont supérieures dans le sud, en forte association avec les arbres décidus. L'occurrence du loup est aussi plus importante dans le sud, en relation positive avec la forêt décidue et la densité des routes. En revanche, l'occurrence du caribou est en relation positive avec la forêt de conifères mature et en relation négative avec l'occurrence du loup et des routes. L'occurrence du carcajou est en relation négative avec la forêt décidue. Nos inventaires démontrent l'existence de communautés distinctes de mammifères dans les moitiés nord et sud de notre région d'étude, une séparation qui semble s'expliquer par les forêts décidues et les routes.

[Traduit par la Rédaction]

## Introduction

Large mammals are often among the first species to disappear from a landscape following its settlement by humans (Weaver et al. 1996; Laliberte and Ripple 2004). Historically, extirpations of large mammals from settled landscapes in North America have occurred through overhunting, habitat loss, and predator control (Kellert et al. 1996; Lancaster et al. 2008). The pattern of mammal extirpation following human settlement has been repeated for

centuries so that today only 21% of the large, terrestrial mammal fauna on the planet remains intact (Morrison et al. 2007).

The boreal forest of northern Ontario, Canada, retains most of its presettlement community of large ungulates and their predators (Morrison et al. 2007). This is a vast, roadless, unlogged region; part of a larger complex of wilderness in northeastern North America that has been identified as one of the 10% most wild areas remaining on the planet (Sanderson et al. 2002).

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The human footprint in the south of Ontario's boreal forest was at first associated with settlement around the Canadian National Railroad in the early part of the 20th century, but since the 1920s has been most closely tied to logging activities that include road-building and fire suppression (Pinto and Romaniuk 2004). Prior to the occurrence of these activities, the region is typically characterized by large patches of coniferous forest that regenerate principally through stand-replacing fires, resulting in stands that tend to be even-aged (Frelich and Reich 1995). The return interval for a 10 000 ha fire in the region has been estimated at 5.2 years (Beverly and Martell 2005). Logging is initiated with the building of roads for accessing stands and hauling logs. These roads also provide opportunities for other resource users, such as trappers and hunters to access formerly inaccessible regions, leading to indirect effects of logging on mammal fauna (Rempel et al. 1997). Logging itself can change both the structure and composition of forests, which can lead to a variety of effects on animal species. One potentially important change is that logging tends to increase the prevalence of deciduous trees in boreal forest, because coniferous trees are typically what is sought by loggers, and most conifer-dominated forest in Ontario tends to regenerate following logging to mixed or deciduous-dominated stands (Carleton 2000). Fire suppression within commercially logged areas further contributes to this increased deciduous forest. Instead of large, stand-replacing fires occurring, other, smaller scale disturbances (e.g., windthrow, disease) create openings in stands, which can take on an uneven age structure and greater species diversity, including an increased prevalence of deciduous trees (Frelich and Reich 1995; Carleton 2000).

It is clear from numerous recent studies that the activities of road-building, logging, and fire suppression have some predictable effects on large mammals. Conversion of logged landscapes from coniferous to deciduous tree species can increase the abundance of ungulate species that forage on deciduous biomass (Hebblewhite et al. 2009). Smaller scale changes in vegetation that increase deciduous biomass along road corridors and the presence of salt on or near roads can also make roads attractive to these same ungulate species (Laurian et al. 2008). In Ontario, this means that moose (*Alces alces* L., 1758) and white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780); henceforth deer) should be more abundant in logged than in unlogged boreal forest. The abundance of gray wolves (*Canis lupus* L., 1758) is largely determined by the biomass of their ungulate prey (Fuller 1989; Messier 1995), which means that they should match the ungulate distribution and be more abundant in logged landscapes (Hebblewhite et al. 2009). Wolves also appear to benefit from living in landscapes with roads, as long as human density is low (Musiani and Paquet 2004), because roads can be used as efficient travel corridors (James et al. 2004). Thus, in Ontario, we expect that the human footprint of roads, fire suppression, and logging in boreal forest should result in greater moose, deer, and wolf abundance in logged compared with unlogged landscapes. These relationships can be confounded by human hunting and trapping activities that can reduce abundance of these species near roads (Rempel et al. 1997).

Two large-mammal species in northern Ontario of partic-

ular conservation concern, owing to their apparent sensitivity to human activities, are the woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788); henceforth caribou) and the wolverine (*Gulo gulo* (L., 1758)). The caribou is closely associated with late successional coniferous forests, which serve as a source for lichens and is their principal food in winter. Caribou are also associated with lakes and peatlands in winter, which may serve as refuges from predation (Bergerud 2000; Rettie and Messier 2000; Ferguson and Elkie 2005). Caribou once occupied most of the boreal forest in North America, but their range has contracted substantially (Hummel and Ray 2008). The boreal ecotype of woodland caribou is listed as threatened under both the Canadian *Species at Risk Act* and the Ontario *Endangered Species Act*. In Ontario, the range occupied by caribou has receded to the north by a rate of 34 km per decade since European settlement (Schaefer 2003). Several mechanisms limiting caribou have been suggested, which mostly relate to food supply or predation. The main bottom-up hypothesis has been that food limitation may occur in landscapes where too much old coniferous forest habitat has been logged (Wittmer et al. 2005). Lichens, which caribou use to survive winter, are highly sensitive to disturbance and most commonly found in mid- and late-successional conifer stands in the boreal forest. Recently, however, agreement has been coalescing around an alternative hypothesis: that predation is the most important direct explanation for the decline in caribou populations, driven by landscape-scale habitat changes (Bergerud and Elliot 1986; Rettie and Messier 1998; Courtois et al. 2007). Owing to low population densities and a slow rate of increase, caribou may be sensitive to predation by wolves, whose densities tend to be greater in early seral deciduous habitats where moose and deer are abundant (Bergerud 1974; Seip 1991; Wittmer et al. 2005; Bergerud et al. 2008). In unlogged forest, caribou appear to reduce predation to a sustainable level by separating themselves spatially from wolves and other ungulate species (Seip 1992; James et al. 2004). When boreal forest is logged, however, densities of wolves, moose, and deer are increased, leading to spillover predation on caribou that might cause population declines (Seip 1992).

The wolverine is listed as threatened in Ontario under the provincial *Endangered Species Act*. Although these elusive, large-bodied mustelids are characteristic of remote northern wilderness, they occurred historically throughout Ontario, only disappearing from the south of the province after human settlement (de Vos 1964). Across North America, the range of wolverine, like that of the caribou, has contracted (Laliberte and Ripple 2004). The wolverine has a relatively slow rate of population increase, and it may be that excessive mortality of adults at their southern-range boundary is a limiting factor. The major causes of death appear to be additive mortality associated with trapping or hunting and starvation (Krebs et al. 2004; Persson et al. 2009). Wolverine populations may not be able to sustain the high mortality that often is associated with relatively frequent human contact. Low to moderate wolf densities likely benefit wolverines by providing carcasses for food (van Dijk et al. 2008b). High wolf densities, however, may limit wolverines through predation, because wolves are known to prey upon wolverines (Krebs et al. 2004). Wolverines may spatially

separate themselves from wolves to reduce predation risk (May et al. 2008; van Dijk et al. 2008a). Availability of suitable den sites in logged landscapes might also limit wolverines. Human disturbance including trapping around natal and maternal dens may reduce their suitability (Magoun and Copeland 1998; May et al. 2006). Finally, recent studies have suggested that climate warming might limit wolverines through changes in snow conditions (Aubry et al. 2007; Copeland et al. 2010).

We carried out aerial surveys during winter in northern Ontario to evaluate the distribution of large mammals. Our surveys took place across a zone where the intact large-mammal fauna of the north, including caribou and wolverine, transitioned into a set of southern fauna and into a landscape characterized by human modifications. We were interested in the hypothesis that mammal distributions were determined, at least in part, by the presence of roads, fire suppression, and logging. More specifically, we were interested in testing whether the distributions of caribou and wolverine were limited by these activities. We evaluated the distribution of caribou and wolverine in relation to deer, moose, wolves, the regional road network, forest cover, and indices of disturbance history, including burns and cutovers. We used hierarchical spatial modeling to develop occurrence probabilities for each species (Magoun et al. 2007). We then used ordination methods to assess the relative contributions of spatial and environmental variables to species distributions. Finally, we tested our hypotheses for limiting factors of each species by evaluating spatial regression models, and comparing model fit to predicted relationships (Table 1).

## Materials and methods

### Study area

We established a nearly 60 000 km<sup>2</sup> study area that crossed the known southern-range limit of both caribou and wolverine in northwestern Ontario (Fig. 1). We selected our study area so that it also encompassed the northern limit of managed forest (and thus roads) in the province. The area was located in the Boreal Shield ecozone of northwestern Ontario (Ecological Stratification Working Group 1995). Dominant tree species were white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (P. Mill.) B.S.P.), jack pine (*Pinus banksiana* Lamb.), balsam fir (*Abies balsamea* (L.) P. Mill.), eastern larch (*Larix laricina* (Du Roi) K. Koch), paper birch (*Betula papyrifera* Marsh.), quaking aspen (*Populus tremuloides* Michx.), and balsam poplar (*Populus balsamifera* L.). Water bodies (mostly lakes) covered about 20% of the study area, whereas bogs, fens, sparse forest, recent burns, and recent cuts covered just over 30%. Coniferous forest stands with canopies dense enough to block the view of the forest floor from the survey aircraft composed <25% of the study area.

The northern limit of commercial logging in the province bisected the area in an east–west direction (Fig. 1). About 67% of the surveyed area fell south of this limit. Natural disturbances in the region tended to result in forests regenerating through large, stand-replacing fires, producing even-aged coniferous forest stands. Fire suppression occurred, however, especially within the commercially logged area. For example, only 5% of nearly 5000 fires suppressed in

northwestern Ontario during the 1990s occurred north of 52° latitude (Ontario Ministry of Natural Resources, unpublished data). Deciduous tree species were most prevalent within the managed forest portion of the survey area. Roads, logging, mining, fur harvest, hunting, and other human activities also occurred most frequently in the southern part of the study area, within the commercially managed forest. More details on the composition of the study area are provided by Magoun et al. (2007).

### Surveys

We divided the nearly 60 000 km<sup>2</sup> rectangular area into a tessellation of 588 hexagonal cells, each 100 km<sup>2</sup> in size. As the survey was originally designed as part of an ecological study on wolverines (Magoun et al. 2007), this survey-unit size was based on what we considered to be the minimum home-range size of adult female wolverines in the area (F.N. Dawson, unpublished data). During January to March 2005, we surveyed these cells using a PA-18 Super Cub (Piper Aircraft Corporation, Lock Haven, Pennsylvania, USA), a highly manoeuvrable aircraft with a tight turning radius and slow stall speed and equipped with wheel skis. An experienced team of one pilot (P. Valkenburg) and one observer (A. Magoun (84% of flight) or J. Ray (16%)) conducted the surveys at an altitude of approximately 200 m above the ground and a ground speed of usually 110–140 km/h. Details of these surveys are provided by Magoun et al. (2007). Briefly, we followed straight-line flight routes through the centres of survey units, surveying up to 50 units per day. We used the presence of either tracks in snow or actual individuals to confirm the occurrence of wolverine, caribou, wolves, moose, and deer in each of the cells. We verified the identity of tracks by circling and following tracks, and landing the aircraft to investigate tracks on the ground when necessary. When we observed animals, we counted individuals; for tracks it was possible to estimate group size of wolves only (A.J. Magoun, personal observation). Thus, following our aerial surveys, we had for each species a map of known occurrences and possible absences across nearly 588 hexagonal cells.

Our species of interest may have occurred in cells without being detected, as the detection probabilities of our survey were <1 (e.g., Magoun et al. 2007). Therefore, we could not be certain that our possible absences were true absences (MacKenzie and Royle 2005). To address this uncertainty, we used hierarchical spatial modeling to estimate the probability of occurrence of each species across the study area (Banerjee et al. 2004; Sargeant et al. 2005). This modeling method has been described in detail for the wolverines in our study area (Magoun et al. 2007). We used repeated surveys of cells (as many as 5 per cell) to facilitate estimation of detection probabilities for each species. We used conditional autoregression (CAR) to model spatial association. Finally, we used a Bayesian Markov chain Monte Carlo routine to estimate parameters to construct seamless distribution maps. The hierarchical spatial model was implemented with a Gibbs sampler in OpenBUGS (version 2.2.0). The end product of the modeling procedure was an estimate of occurrence probability for each species in each cell. Details of the procedure and OpenBUGS code are available (Magoun et al. 2007).

**Table 1.** Parameters tested for associations with occurrence probabilities of large mammals in logged and unlogged boreal forest in northern Ontario, Canada.

Species	Parameter (predicted direction of relationship)
White-tailed deer ( <i>Odocoileus virginianus</i> )	Deciduous forest (+)
	Mature coniferous forest (–)
	Recent cuts (+)
	Old cuts (+)
	Road density (–)
Moose ( <i>Alces alces</i> )	Deciduous forest (+)
	Mature coniferous forest (–)
	Recent cuts (+)
	Old cuts (+)
	Road density (–)
Gray wolf ( <i>Canis lupus</i> )	Deciduous forest (+)
	Deer (+)
	Moose (+)
	Old cuts (+)
	Road density (+)
Woodland caribou ( <i>Rangifer tarandus caribou</i> )	Mature coniferous forest (+)
	Moose (–)
	Deciduous (–)
	Road density (–)
	Wolf (–)
Wolverine ( <i>Gulo gulo</i> )	Caribou (+)
	Deciduous (–)
	Mature coniferous forest (+)
	Road density (–)
	Wolf (–)

**Note:** For each species, parameters were selected based on a priori hypothetical relationships derived from reviewing previous studies. Predicted directions of relationships between parameter and species are shown in parentheses. The parameters were used in model selection, where the set of all possible models ( $n = 31$  models for each species) were assessed to determine model averaged coefficients and parameter importance.

We identified and measured nine environmental variables related to our hypotheses. (Table 2). We compiled a map of all roads in the study area using Ontario Base Map aerial photographs (1 : 20 000 scale) updated as of 2003 (Ontario Ministry of Natural Resources, unpublished data). We estimated the density of roads in each 100 km<sup>2</sup> cell. For the purposes of this estimate, roads were all considered equally, whether they were primary, secondary, or tertiary — all of these roads were used to some extent during logging operations. The roads in our study were at the northern limit of the road network in Ontario. Some were paved, but the majority of roads were gravel logging roads. Logging occurred in both winter and summer. Most roads were travelled year-round.

We used both forest resource inventory (FRI) and Landsat thematic mapper (LTM) data from the study area to assess landcover patterns that were related to our hypotheses. The FRI data were vector-based digital coverages derived from interpreted aerial photography. Coverages were updated to 2003 or 2004, depending on forest management unit. The LTM data were raster-based satellite images from 2000 with a 25 m resolution. Because our study took place at the very northern edge of managed forests in Ontario, a small proportion (17.7%) of the 588 cells had no FRI and was omitted from subsequent modeling. Importantly, not all of the unmanaged forest in the area was without FRI, however,

as a large proportion of this area had been inventoried in advance of future management. Thus, we were able to include a large area of unmanaged, roadless forest in our study, which was important to the design.

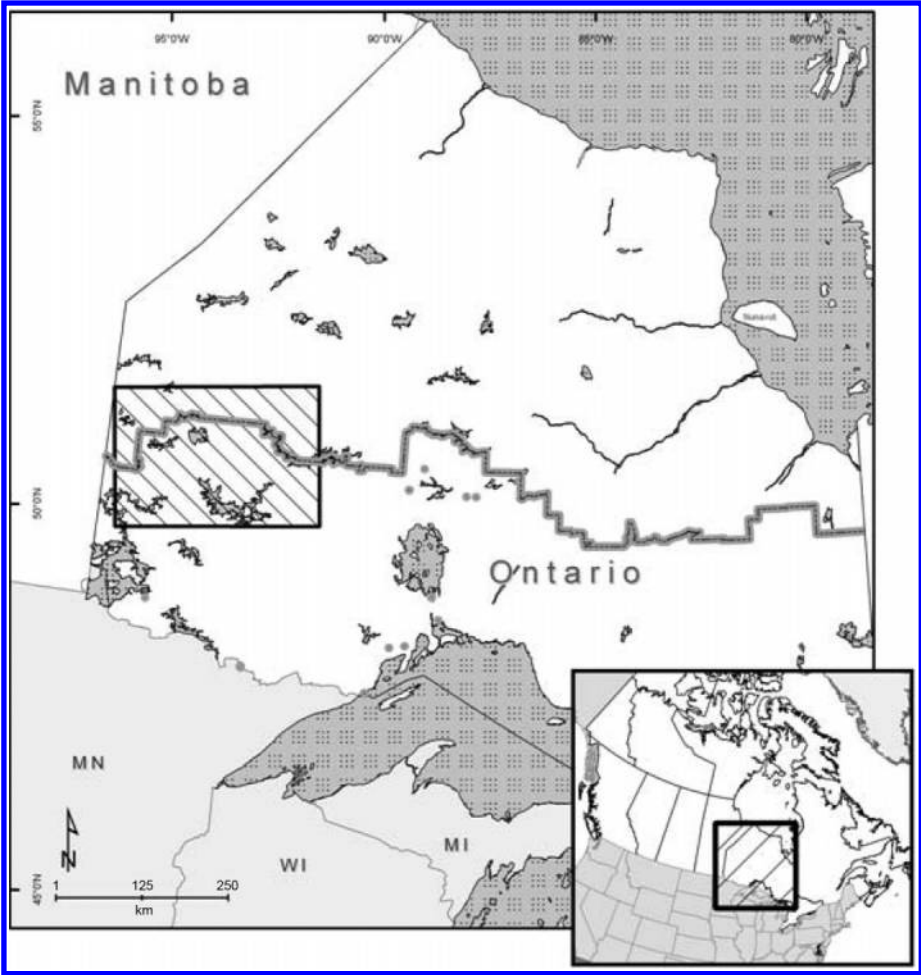
We estimated the proportion of each cell where the most prevalent tree species in a stand (termed working group in the FRI) was coniferous in a mature or older development stage (a categorical measure of stand age). This was our estimate of mature coniferous forest in each cell. We were also interested in deciduous forest of any age, as we considered an increased prevalence of deciduous forest in this region of the boreal forest to be associated with human impacts from road development, fire suppression, and logging (Frelich and Reich 1995; Carleton 2000). We tallied stands with a deciduous working group of any development stage to estimate the proportion of deciduous forest in each cell. We estimated the proportion of cutovers in each cell for two time periods: since 1990 (<15 years; hereafter recent cuts) or 1945–1990 (15–60 years; hereafter old cuts). The proportion of burns in each cell for these same two periods were estimated using data published previously describing northwestern Ontario’s fire history (Perera and Baldwin 2000). The proportion of bogs or lakes in each cell was estimated from the LTM data.

Although potentially important at large spatial scales (Aubry et al. 2007), we did not use snow cover as a predic-

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**Fig. 1.** Location of the study area in Ontario, Canada (inset), where aerial surveys of large mammals were conducted during winter 2005. The surveys occurred in the hatched rectangle. The northern limit of managed forest in the province is indicated by the gray line. North of that line occurs an unlogged, roadless landscape and an intact mammal fauna.



**Table 2.** A description of parameters sampled within 100 km<sup>2</sup> hexagonal cells surveyed in a northern Ontario, Canada, study area for the occurrence of large mammals during winter 2005.

Parameter	Description
Roads	Density (km/km <sup>2</sup> ) of primary, secondary, and tertiary roads in 100 km <sup>2</sup> cells
Mature coniferous forest	The proportion of each cell containing mature or older forest with a coniferous forest resource inventory (FRI) working group
Deciduous forest	The proportion of each cell containing forest of any development stage with a deciduous FRI working group
Recent cuts	The proportion each cell that had been cutover between 1990 and 2005 (within 15 years of the survey)
Old cuts	The proportion of each cell that had been cutover between 1945 and 1990 (15–60 years before the survey)
Recent burns	The proportion of each cell that had been burned between 1990 and 2005 (within 15 years of the survey)
Old burns	The proportion of each cell that had been burned between 1945 and 1990 (15–60 years before the survey)
Lakes	The proportion of each cell that was a lake
Bogs	The proportion of each cell that was treed or a treeless bog

**Note:** See text for description of source data.

tor in our models because it was only coarsely measured and not highly variable within our relatively small study area.

**Ordinations**

Our first step in data analysis was to explore how the large-mammal communities were structured in relation to both spatial location and environment, the latter referring to

the suite of species, vegetation, and landscape descriptors measured in each cell (e.g., deciduous forest and road density). We used the occurrence probabilities for each species estimated through hierarchical modeling as our response variable (Magoun et al. 2007). Matrices of these occurrence probabilities were compared with our environmental measures and spatial locations of cells in a redundancy analysis

(RDA; van den Wollenberg 1977). We used the method of partial constrained ordination (Borcard et al. 1992) to partition variation in the matrices into four parts: (1) variation related to environment and independent of any spatial effects; (2) variation related to space and independent of any environmental effects; (3) variation related to both spatial and environment effects (i.e., shared variation); and (4) unexplained variation. We examined a Pearson correlation matrix of our environmental variables and found the mean negative correlation was  $r = -0.18$  (SE = 0.03), whereas the mean positive correlation was  $r = 0.23$  (SE = 0.05). The maximum among all correlations was  $r = -0.48$  between mature coniferous forest and old cuts. Because we found no correlations where  $-0.5 > r > 0.5$ , we used the full set of nine variables in the RDA (Table 2). Spatial structure was estimated using a set of two-dimensional geographical coordinates representing cell centroids in a cubic polynomial (Borcard et al. 1992). The cubic polynomial was used because it has some ability to model nonlinearities, for example, when responses are not simply linear gradients. Thus, at the outset we had nine variables in both environmental and spatial data sets.

Partial constrained ordination was carried out using CANOCO version 4.0 (ter Braak and Šmilauer 1998). We used the full set of nine environmental variables in the ordinations. The spatial matrix exhibited multicollinearity, however, so we used a reduced set of variables after eliminating the less explanatory of the intercorrelated spatial coordinates. Partial ordinations were carried out by removing effects of the spatial model from the environment model and vice-versa. Significance of models was assessed using unrestricted Monte Carlo permutation tests with Bonferroni-corrected  $p < 0.05$ .

### Spatial regressions

Following the community-level ordination analyses, we used model selection to test alternative hypotheses relating to the distribution of each species. We assumed that at their northern- or southern-range boundaries, factors relating to occurrence probabilities for each species would be indicative of limiting factors. The occurrence probabilities that we estimated for each species tended to be spatially structured. This made good biological sense because we were sampling at or near the northern-range boundary of moose and deer, and the southern-range boundary of caribou and wolverine, and so we would expect spatial gradients in distribution probability. Thus, we used spatial regressions to compare occurrence probabilities to hypothetical limiting factors.

For each species we identified five parameters that had substantial literature support suggesting that they played some role in limiting the species. For each species and parameter, we identified the hypothetical direction of the relationship (Table 1). These five parameters then represented nonexclusive hypotheses of limitation. In general, we hypothesized that species in the study area would be distributed in relation to the human footprint as follows: (i) moose and deer would be most abundant in cells where deciduous forest was abundant; (ii) wolves would be most abundant in cells with moose and deer; and (iii) caribou and wolverines would be most abundant in unlogged cells with prevalent mature coniferous forest (Table 1).

For each species, we developed a set of all possible com-

binations of the five parameters, which resulted in 31 models per species. In all cases, correlations between the predictor variables were  $r < 0.5$ , so we did not view multicollinearity among predictors as an important problem. We used spatial regressions to model relationships to accommodate spatial structure in both the species distribution data and in the predictor variables. Based on a comparison of several methods where we evaluated spatial structure in residuals following model fit, we selected a lagged-predictor model as our best approach (Rangel et al. 2006). This model took the form  $Y = \rho WY + X\beta + WX\gamma + e$ , where  $\rho$  is an autoregression parameter of the response variable,  $W$  is a matrix of geographical distances,  $\beta$  is a vector of coefficients,  $\gamma$  is the autoregression parameters of each predictor variable, and  $e$  is an error term. These spatial models were implemented in the SAM package (Rangel et al. 2006). All response variables were  $\log_{10}$ -transformed for regression analyses. Models were evaluated using Akaike's information criterion adjusted for small sample size (AIC<sub>c</sub>) (Hurvich and Tsai 1989; Rangel et al. 2006). A set of candidate models was selected by sorting the models based on AIC weight in descending order and adding models to the suite until the sum of the weights was approximately 0.95, providing a 95% candidate model suite (Burnham and Anderson 2002). AIC weights are estimates of the probability that a model is the best model given the data and the model set. The candidate model suite was used to estimate model averaged coefficients. Parameter importance was calculated by summing AIC weights over the entire set of 31 models.

## Results

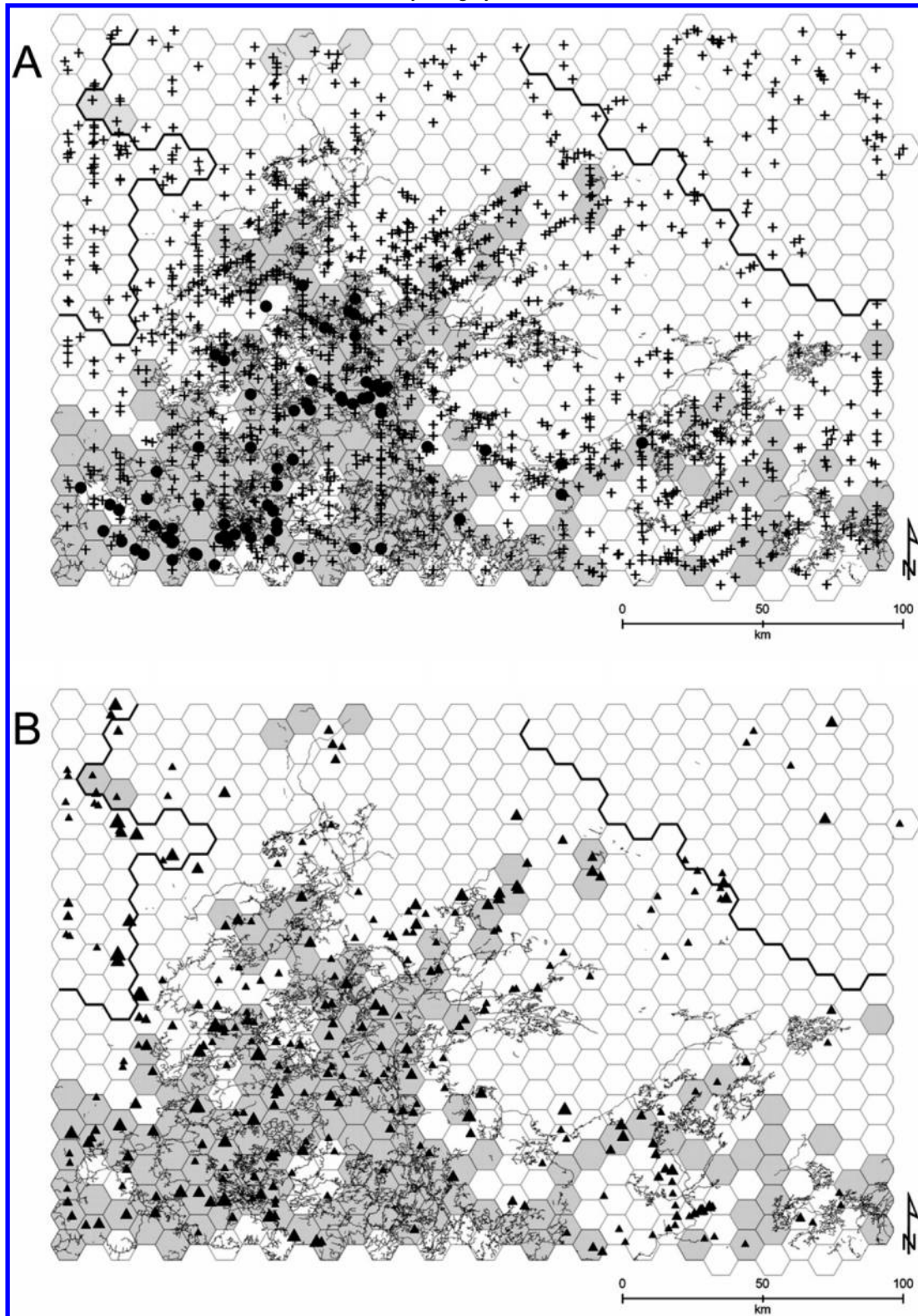
### Species distributions

We carried out 1079 flights through 575 of the 588 possible cells between late January and early March 2005. We surveyed 204 cells once (35%), 260 cells twice (45%), 90 cells three times (16%), 20 cells four times (3%), and 1 cell five times (<1%).

We observed moose or moose tracks at least once in 430 of the 575 cells (75%), but they appeared to be most common and abundant in the southern portion of the study area with roads (Fig. 2A). There was strong evidence of moose occurrence (probability of occurrence >0.80; Sargeant et al. 2005) in 77% of cells and strong evidence of moose absence (probability <0.20) in 6% of cells. Deer were exclusively found in the southern region with roads, occurring in only 46 cells (8%; Fig. 2A). There was strong evidence of deer occurrence in only 8% of cells and strong evidence of deer absence in 84% of cells. We observed wolves or their signs in 184 cells (32%), and like moose and deer, this species most commonly occurred in the portion of the survey area with roads. Moreover, group sizes also tended to be largest in the area with roads (Fig. 2B), with the largest observed group containing 19 individuals. There was strong evidence of wolf occurrence in 34% of cells and strong evidence of wolf absence in 29% of cells.

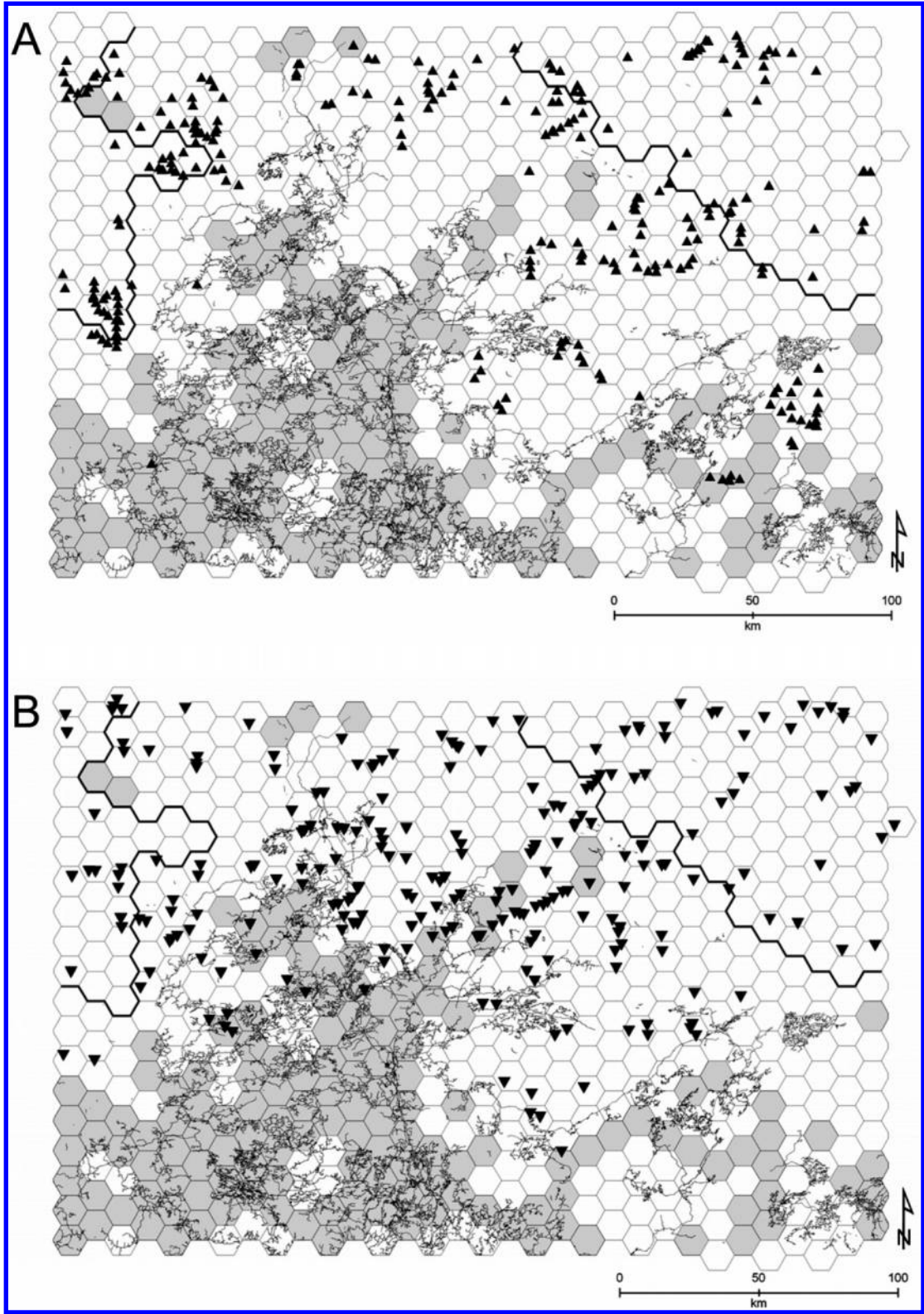
We recorded caribou or caribou tracks in 113 (20%) of the 575 cells. Caribou tended to be in the northern half of the survey area and also appeared to be clustered away from heavily portions of the landscape with roads (Fig. 3A). There was strong evidence of caribou occurrence in 20% of

**Fig. 2.** Observations of tracks or other signs of (A) moose (*Alces alces*; +) and white-tailed deer (*Odocoileus virginianus*; ●) and (B) wolves (*Canis lupus*; ▲) with wolf group size proportional to symbol size (range 1–19), resulting from aerial surveys during winter 2005 in a 6000 km<sup>2</sup> northern Ontario study area. Hexagonal cells were the sample unit for the survey and were each 100 km<sup>2</sup>. The northern boundary of available forest inventory maps is shown by the thick black lines. Shaded cells within the inventoried forest had at least 10% deciduous-tree-dominated stands. The road network is shown by the gray lines.





**Fig. 3.** Observations of tracks or other signs of (A) woodland caribou (*Rangifer tarandus caribou*; ▲) and (B) wolverine (*Gulo gulo*; ▼), resulting from aerial surveys during winter 2005 in a 6000 km<sup>2</sup> northern Ontario study area. Hexagonal cells were the sample unit for the survey and were each 100 km<sup>2</sup>. The northern boundary of available forest inventory maps is shown by the thick black lines. Shaded cells within the inventoried forest had at least 10% deciduous-tree-dominated stands. The road network is shown by the gray lines.





cells and strong evidence of caribou absence in 69% of cells. We observed wolverine signs in 138 cells (24%), also mostly in the northern half of the survey area (Fig. 3B). There was strong evidence of wolverine occurrence in 30% of cells and strong evidence of wolverine absence in 43% of cells.

### Ordinations

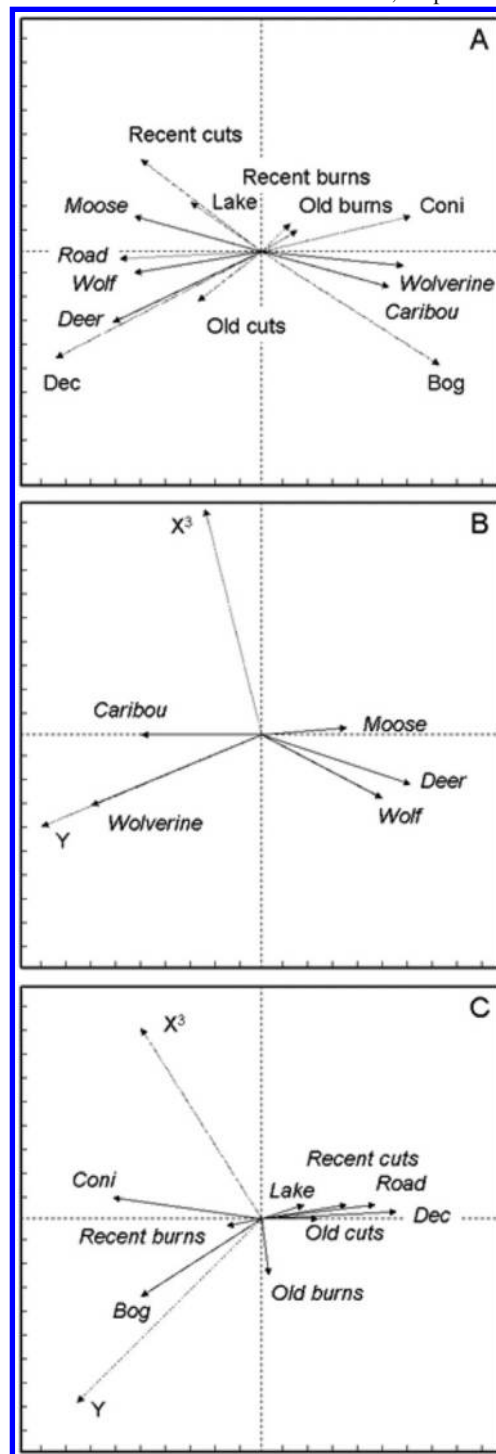
Owing to a lack of FRI data, we excluded 102 cells from further analysis, leaving 473 cells as our sample for ordination and regression analyses. In the first ordination, the matrix of species occurrence probabilities was significantly related to the suite of environmental variables ( $F = 27.49$ ,  $p = 0.002$ ). The sum of all canonical eigenvalues for this RDA was 0.348 (we refer to this below as ordination A). A biplot of the relationship between the species and environment shows that caribou and wolverine grouped with mature coniferous forest, burns, and bogs, whereas moose, deer, and wolves grouped with cutovers, deciduous forest, and roads (Fig. 4A). When the species matrix was constrained by spatial location rather than environmental variables ( $F = 145.64$ ,  $p = 0.002$ ), the sum of all canonical eigenvalues was 0.383 (ordination B). The biplot shows that caribou and wolverine tended to be in the north of the study area, whereas moose, deer, and wolf were in the south (Fig. 4B). Taken together, these first two analyses demonstrate that not surprisingly the environmental predictor variables were correlated with the spatial predictor variables. In fact, a biplot shows that mature coniferous forest, burns, and bogs tended to be in the north of the survey area, whereas cutovers, deciduous forest, and roads tended to be in the south (Fig. 4C).

To address the covariation between environmental and spatial predictor variables, we carried out a partial ordination where the species matrix was constrained by the environmental variables while covarying for spatial location. The sum of all canonical eigenvalues for this analysis was 0.080 (ordination C) ( $F = 7.62$ ,  $p = 0.015$ ). When we constrained the species matrix with spatial location, and covaried for environment, the sum of all canonical eigenvalues was 0.114 (ordination D) ( $F = 49.03$ ,  $p = 0.002$ ). We could use these four ordinations (A–D) to estimate the contribution to explained variation in the species matrix by the spatial and environmental matrices (Borcard et al. 1992). Eigenvalues for ordinations A + D = B + C = 0.463. Thus, 46.3% of variation in the species matrix was explained by the combination of spatial and environmental matrices, whereas  $100\% - 46.3\% = 53.7\%$  of variation in the species matrix was unexplained. Similarly,  $A - C = B - D = 26.8\%$ , which was the amount of variation in the species matrix that could be attributed to shared variation between spatial and environmental matrices. Finally, we could attribute 8% (ordination C) as being variation in the species matrix that was uniquely explained by the environmental variables, whereas 11.4% (ordination D) was uniquely explained by spatial location.

### Spatial regressions

For deer, the most important parameter among all spatial regression models was a positive relationship with the proportion of deciduous forest in a cell. It was the only parameter with coefficient confidence intervals that did not

**Fig. 4.** Ordination biplots for occurrence probabilities of large mammals in 100 km<sup>2</sup> cells ( $n = 473$ ) obtained from aerial surveys of a northern Ontario study area during winter 2005, along with spatial and environmental variables for the area. Biplots show (A) the species and environmental matrices; (B) the species and spatial matrices; and (C) the environmental and spatial matrices. Quantities in ordinations are either occurrence probability of species in each cell, proportion of land cover in each cell, or spatial co-ordinate of cell centroid. “Coni” and “Dec” are the proportions of coniferous and deciduous forest in each cell, respectively.



**Table 3.** Model selection results summarizing 31 models per species for occurrence of mammal species in northern Ontario, Canada, with parameters for each species listed in order of decreasing importance.

Species	Parameter	Estimate	SE	LCL	UCL	Importance
White-tailed deer ( <i>Odocoileus virginianus</i> )	<b>Deciduous</b>	<b>0.145</b>	<b>0.025</b>	<b>0.096</b>	<b>0.195</b>	<b>0.999</b>
	Road density	0.048	0.026	−0.002	0.099	0.448
	Old cuts	0.030	0.022	−0.013	0.073	0.227
	Recent cuts	−0.030	0.026	−0.081	0.021	0.214
	Coniferous	−0.029	0.025	−0.077	0.019	0.199
Moose ( <i>Alces alces</i> )	<b>Road density</b>	<b>0.114</b>	<b>0.058</b>	<b>0.001</b>	<b>0.227</b>	<b>0.552</b>
	<b>Deciduous</b>	<b>0.112</b>	<b>0.057</b>	<b>0.001</b>	<b>0.224</b>	<b>0.545</b>
	Old cuts	−0.089	0.051	−0.189	0.012	0.418
	Recent cuts	0.074	0.062	−0.048	0.196	0.257
	Coniferous	0.0003	0.060	−0.116	0.117	0.139
Gray wolf ( <i>Canis lupus</i> )	<b>Deciduous</b>	<b>0.127</b>	<b>0.044</b>	<b>0.040</b>	<b>0.213</b>	<b>0.893</b>
	<b>Road density</b>	<b>0.109</b>	<b>0.043</b>	<b>0.025</b>	<b>0.192</b>	<b>0.782</b>
	Moose	0.062	0.060	−0.056	0.180	0.367
	Old cuts	−0.048	0.039	−0.124	0.027	0.250
	Deer	0.004	0.048	−0.091	0.098	0.117
Woodland caribou ( <i>Rangifer tarandus caribou</i> )	<b>Coniferous</b>	<b>0.139</b>	<b>0.034</b>	<b>0.072</b>	<b>0.205</b>	<b>0.998</b>
	<b>Wolf</b>	<b>−0.121</b>	<b>0.034</b>	<b>−0.188</b>	<b>−0.054</b>	<b>0.987</b>
	<b>Road density</b>	<b>−0.115</b>	<b>0.033</b>	<b>−0.180</b>	<b>−0.050</b>	<b>0.981</b>
	Moose	−0.035	0.029	−0.091	0.022	0.207
	Deciduous	−0.022	0.036	−0.093	0.048	0.132
Wolverine ( <i>Gulo gulo</i> )	<b>Deciduous</b>	<b>−0.065</b>	<b>0.029</b>	<b>−0.122</b>	<b>−0.008</b>	<b>0.754</b>
	Caribou	−0.024	0.026	−0.075	0.028	0.195
	Road density	−0.013	0.027	−0.066	0.041	0.190
	Wolf	−0.016	0.025	−0.065	0.033	0.187
	Coniferous	−0.021	0.028	−0.077	0.035	0.176

**Note:** Estimates are model averaged coefficients for 95% candidate model set, or parameter importance for full set of 31 models. Values in bold-face type indicate parameters for which 95% CL of coefficients do not overlap 0. SE, standard error; LCL, lower confidence limit; UCL, upper confidence limit.

overlap 0, and was 2.2 times more important than the next most important parameter, road density (Table 3). Road density and deciduous forest were also the two most important parameters for moose occurrence probability. The positive coefficients for these two parameters were the only coefficients for moose occurrence with confidence intervals that did not overlap 0. Each of these parameters was about 1.3 times more important than the next most important parameter, old cuts (Table 3). Similarly, wolf occurrence was positively related to both the proportion of deciduous forest and road density, and these two parameters were the only ones with coefficient estimates not overlapping 0. Deciduous forest and road density were 2.4 times and 2.1 times more important than moose occurrence, respectively (Table 3).

The most important regression models explaining caribou occurrence probability were those depicting a positive relationship with mature coniferous forest, or negative relationships with either the occurrence probability of wolves or road density. These three parameters were about equally important and were each nearly 5 times more important than the next most important parameter, i.e., moose occurrence probability (Table 3). Wolverine occurrence probability was negatively related to the proportion of deciduous forest in a cell. This parameter was at least 3.9 times more important than any other parameter.

**Discussion**

Our survey results were consistent with the hypothesis that the distributions of caribou and wolverine in Ontario’s boreal forest are limited by human activities. More specifically, we found that both species were negatively associated with logged landscapes, whereas three other species (moose, deer, and wolves) appeared to be more abundant in logged landscapes. The spatial separation between these two groups of species appeared to be mediated by the presence of deciduous forest and roads.

The ordination biplots illustrated the footprint of human activities such as road-building, fire suppression, and logging in the southern half of our study area (Figs. 4A, 4B, 4C). Roads, cutovers, and the concomitant deciduous forest were clustered in the south, whereas mature coniferous forest and burns occurred in the north. An effect of this appeared to be an increase in the southern part of the study area in the abundance of two ungulate species (moose and deer) known to benefit from increased deciduous browse availability (Krefting and Phillips 1970; Rempel et al. 1997). This increased ungulate biomass was associated with an increase in both wolf occurrence probability and pack size in the south. The largest of these packs was equivalent to a recently observed record pack size in northwestern Ontario (Vors and Wilson 2006). Caribou and wolverine were

most commonly found in the northern, unlogged portion of the study area. Thus, the correlated distributional relationships from our surveys were consistent with the hypothesis that the caribou and wolverine are limited to the south by human activities, including road-building, fire suppression, and logging. This is consistent with the suggestions of other researchers that the ranges of many mammal species have been greatly reduced around the world owing to human disturbance (Ceballos and Ehrlich 2002; Laliberte and Ripple 2004; Morrison et al. 2007).

Determining the cause of these correlated relationships is complicated by the inherent spatial structure in species distribution data at range boundaries (e.g., Vors et al. 2007). The animal species of interest, as well as the environmental predictors we assessed, were all spatially structured in a north–south gradient. Some of this structure was a result of natural, biogeographic variability. For example, it was colder in the north of the study area. Some of the spatial structure was, however, a result of the spatial pattern of human disturbance. Overall, we were able to attribute 11.4% of variation in the species data to spatial location, which most likely resulted from a combination of spatial population processes (e.g., Bowman et al. 2001; Betts et al. 2009) and climate variation. We could attribute 8% of the variation to the environmental variables, which included anthropogenic disturbances such as roads and cutovers along with natural variation in habitats. Finally, 26.8% of the variation in the species data could not be disentangled between spatial location and environmental variability. For example, anthropogenic disturbances such as roads were clustered in the south of the study area (Fig. 4C). It is worth noting here that explained variation in direct gradient analysis is interpreted differently than in typical regression analysis. Unexplained variation in ordinations is over-represented compared with linear regressions and should not be interpreted as a result of poor model fit (Økland 1999).

The model selection analyses demonstrated that among the model parameters, a relatively small set was important for all five species. Deciduous forest was the most important parameter for the occurrence of deer, wolf, and wolverine, and was second in importance for moose. On the other hand, mature coniferous forest was the best predictor for caribou. Road density was among the top three parameters explaining the probability of occurrence for all five species. Cuts per se were never among the variables for which 95% confidence limits did not overlap 0. Taken together, these relationships suggest a cascading effect of human activities in the region that begins with road-building, fire suppression, and logging and leads to indirect effects on mammal species. We suggest a mechanism as follows. Where deciduous forest cover is increased, then ungulate biomass is increased. This in turn leads to an increase in wolves and a reduction in caribou. Caribou may be reduced directly through predation (Bergerud 1974, 2000; Seip 1991; Wittmer et al. 2005) or behavioural avoidance of wolves or logged landscapes (Duchesne et al. 2000; James et al. 2004).

Wolverines also appeared to avoid deciduous forest in the study area. It may be that this pattern did not represent an aversion to deciduous tree species per se, but rather the effects of a set of abiotic or biotic factors associated with this forest type, none of which were measured directly in this

study. For example, snow tends to accumulate more during winter or experience faster rates of snowmelt in spring under deciduous canopy cover (Jost et al. 2007). There is some evidence that wolverines are limited at their southern distribution by the availability of suitable spring snow cover (Aubry et al. 2007; Copeland et al. 2010). Reproductive female wolverines frequently make use of snow for dens; low snow cover in spring may reduce the availability of den sites. We were unable to test this hypothesis directly, however, as there was insufficiently resolved snow data available within our study area. Variation in spring snow depth was not great, however, across the relatively small area. The higher productivity deciduous-forest environments can also lead to a diverse and abundant predator and scavenger community that could limit wolverines through competition. We also recognize that our estimates of caribou distribution were limited to the winter season; the summer caribou distribution may have an effect on wolverine occurrence that we did not measure.

Our surveys suggest that a key concern regarding the conservation of northern Ontario's intact mammal fauna is the prevalence of deciduous forest, because of its influence on ungulate biomass and subsequently on the predator community. Previous research (e.g., Frelich and Reich 1995; Carleton 2000; Friedman and Reich 2005; Pinto et al. 2008; Boucher et al. 2009) has demonstrated landscape-scale shifts in tree species composition since the onset of industrial logging in the 20th century. Most relevant to our research findings has been the regional-scale increase in the prevalence of deciduous trees, which seems to occur as a result of both logging and fire suppression in boreal forest (Frelich and Reich 1995; Carleton 2000).

Road density serves as a proxy for the extent of the human footprint, as resource development is generally accompanied by a transportation network. Indeed, much of the roadless portions of this study area were either in the wilderness-class protected area (Woodland Caribou Provincial Park), in areas where logging is planned but has not yet taken place, or outside of the legal limit of commercial forestry. The lack of intercorrelation with other model parameters implied that roads themselves were an important factor determining distribution patterns of large mammals in this study. Moose, deer, and wolves were positively associated with roads, whereas the relationship was negative for both wolverine and caribou. Numerous studies have identified road density as potentially limiting to wolf populations owing to increased mortality risk associated with human presence, and have identified a threshold road density of about 0.6 km/km<sup>2</sup> beyond which wolves have a high probability of extirpation (Jensen et al. 1986; Fuller et al. 1992; Musiani and Paquet 2004; Person and Russell 2008). However, not only were road densities in our study somewhat lower than this threshold (mean = 0.37 km/km<sup>2</sup>, 95% CL = 0.33–0.42, maximum = 2.25), but human densities were low. Both factors suggest why in the context of our study area wolves could have a positive relationship with roads. Likewise, our survey results were not consistent with the idea that improved hunter or trapper access along roads limits the distribution of moose or deer in the area.

Caribou and wolverines were largely absent from the southern portion of the study area. This is consistent with



the broader patterns of range recession experienced by both species in Ontario over the past 150 years concomitant with the northward spread of human-driven land-use change (e.g., Schaefer 2003). Avoidance of areas with roads by caribou is well-documented (Dyer et al. 2001; Vors et al. 2007). The added negative association of wolves with caribou in this study provides support to the hypothesis that caribou-range contraction is related to landscape-scale changes that increase wolf abundance, which in turn increase predation on caribou (e.g., James et al. 2004). Although there has been no legal harvest of caribou in the province since 1929 (other than through treaty rights), because we did not directly measure hunting pressure, we were unable to address the extent to which facilitated access to hunters is a contributing factor in shaping the current caribou distribution.

We were similarly unable to assess the effects of trapping on the wolverine distribution in the study area. Because of their low reproductive rates, limited range and distribution, and large home ranges, wolverines have a low resilience to trapping or hunting pressure. Human harvest is generally an additive mortality agent and replacement of removed animals is a slow process, if it occurs at all (Banci and Proulx 1999). In a review of mortality patterns across North American wolverine populations, Krebs et al. (2004) found that immigration from untrapped areas is often required to sustain wolverines in trapped areas. Although wolverine harvest has been illegal in Ontario since 2001 (except through treaty rights), 1–4 wolverines are accidentally harvested each year in the study area in traps set for other species. All of this incidental harvest is clustered within the landscape with roads at the southern-range limit of the species.

Our aerial surveys in this remote region of northwestern Ontario demonstrated that the distributions of two species of conservation concern, the caribou and the wolverine, were negatively associated with the footprint of human activities in the study area. Although our data were correlational, they were consistent with prevailing hypotheses explaining the northward contraction of both species' ranges. For caribou, our results suggest that as roads and logging change the environment by increasing moose and deer densities, the numerical or behavioral response of caribou to predation or predation risk is related to range contraction. For wolverines, it appears that habitat alteration is among the important limiting factors at the southern-range boundary.

Given the global conservation importance of the roadless landscape of northern Ontario (Sanderson et al. 2002), containing a mostly intact large-mammal fauna (Morrison et al. 2007), it is important to plan carefully any future land use. It appears from our data, as well as from other studies, that both caribou and wolverines are sensitive to community changes arising from human modification of landscapes, such as road-building and logging. Consequently, appropriate planning that recognizes the reality of risks to caribou and wolverine of these activities will be of utmost importance for conservation of these large mammals. Our data suggest that an important component of land-use planning in northern Ontario is the maintenance of a large roadless area with a natural fire regime.

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