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Authors: Montgomery, Robert A., Roloff, Gary J., Millspaugh, Joshua J., and Nylen-Nemetchek, Marcy

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Living amidst a sea of agriculture: predicting the occurrence of Canada lynx within an ecological island

Robert A. Montgomery, Gary J. Roloff, Joshua J. Millspaugh and Marcy Nylen-Nemetchek

R. A. Montgomery (montg164@msu.edu) and J. J. Millspaugh, Dept of Fisheries and Wildlife Sciences, Univ. of Missouri, 302 Natural Resources Building, Columbia, MO 65211, USA. – RAM and G. J. Roloff, Dept of Fisheries and Wildlife, Michigan State Univ., 480 Wilson Road, Room 13 Natural Resources Building, East Lansing, MI 48824, USA. – M. Nylen-Nemetchek, Natural Resources Inst., Univ. of Manitoba, Winnipeg, MB, R3T 2N2, Canada

Carnivore populations are increasingly confined to reserves surrounded by anthropogenic development. The boundaries of ecological islands are risky because of habitat loss and human–carnivore conflict. From snow track survey data collected over a 5-winter period we developed a population-level resource selection function for Canada lynx *Lynx canadensis* in Riding Mountain National Park, Canada. This park has been characterized as an 'ecological island situated amidst a sea of agricultural land' and while lynx are protected within the park, they are subject to harvest outside of the park. Winter resource selection of lynx increased with higher elevation and in highly suitable habitat for snowshoe hare *Lepus americanus* and decreased in habitat with greater proportions of agriculture and grasslands, both of which are common along the edge of the park. Habitat with medium to high relative probabilities of lynx occurrence tended to be distributed in the interior of the park. However, the highest relative probability of lynx occurrence was associated with habitat near the southeast border of the park in close proximity to a human community and a lake where snowmobiling, skiing, and snowshoeing are common recreational pursuits. We attribute this relationship to a 25-year old fire which presently created successional habitat highly suitable for snowshoe hare and correspondingly for lynx in this area. Our results suggest that Canada lynx occurrence tends to be associated with habitat that is highly suitable for their primary prey even if that habitat is located near to sources of human recreational activity.

The habitat use of carnivores is at least partially informed by the availability and accessibility of foraging rewards and prevailing risks to fitness (Lima and Dill 1990). Sources of risk include competition, disease, injury and malnutrition (Wilmers et al. 2006, Galentine and Swift 2007, Campomizzi et al. 2008, Durner et al. 2011). Increasingly, risks to carnivores are anthropogenic in origin. The distribution and traffic levels of roads, landscape fragmentation, climate change and human persecution all affect carnivore habitat use (Kramer-Schadt et al. 2004, Nielsen et al. 2004, Whitman et al. 2007, Chapron et al. 2008). Rapid infrastructure development and the conversion of native vegetation communities for agriculture have increasingly confined carnivores to ecological islands within fragmented landscapes (Woodroffe and Ginsberg 1998, Kolowski and Holekamp 2006, Crooks et al. 2011). Human-dominated habitat bordering ecological islands often act as 'traps' where carnivore fitness is reduced (Robertson and Hutto 2006, Northrup et al. 2012, van der Meer et al. 2013). These traps not only affect the vitality of individual carnivores, but the viability of carnivore populations more broadly (Woodroffe and Ginsberg 1998).

Carnivore response to the edges of ecological islands or wildlife reserves is complex and tends to be informed by anthropogenic risk and foraging reward. For instance, snow leopards *Uncia uncia* in Sagarmatha National Park, Nepal are risk-averse as topography and relative proximity to human networks have a greater effect on habitat selection than the distribution of their primary prey (Wolf and Ale 2009). African leopards *Panthera pardus* in the Phinda Private Game Reserve, on the other hand, tend to use areas surrounding the reserve despite increased mortality rates in those habitats (Balme et al. 2010). Leopard selection of habitat around this reserve is attributed to productive foraging and reduced density-dependent competition (Balme et al. 2010). Areas around ecological islands are often associated with increased human–carnivore interaction which can be detrimental to carnivore vitality (i.e. reduced fecundity and mortality) and human interests (i.e. depredation and property damage; Ogada et al. 2003, Treves and Karanth 2003). Thus, effective conservation and management of carnivore populations and mitigation of human–wildlife conflict depends on the ability to predict carnivore habitat use within ecological islands. The habitat use of

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carnivores, with respect to foraging reward and sources of risk, is often assessed through examination of resource selection (Mao et al. 2005, Hebblewhite and Merrill 2008, Basille et al. 2009, Valeix et al. 2009, Hebblewhite et al. 2011). These models predict animal occurrence through associations with resource features and can be used to evaluate the riskiness of carnivore selection.

Lynx spp. are a highly valued furbearer species and overexploitation has been associated with lynx population declines throughout the world (Bailey et al. 1986, Breitenmoser 1998, McKelvey et al. 2000, Andrén et al. 2006, Bunnefeld et al. 2006). Canada lynx *Lynx canadensis* inhabit Riding Mountain National Park (RMNP), Manitoba, which has been described as an 'ecological island situated amidst a sea of agricultural land' (Parks Canada 2002), and while protected within the park they are subject to hunting and trapping pressure in areas surrounding the park. The distribution of snowshoe hare *Lepus americanus*, the primary prey of Canada lynx (Koehler 1990, Hodges et al. 2001, O'Donoghue et al. 2001), is a critical determinant of lynx habitat use (Fuller et al. 2007, Squires and Ruggiero 2007, Maletzke et al. 2008, Keim et al. 2011). Additionally, lynx habitat use is known to be affected by human activity (Apps 2000, Poole 2003, Bunnell et al. 2006). What remains unclear is whether Canada lynx selection of highly suitable snowshoe hare habitat is affected by sources of human disturbance within and outside of ecological islands. Our objective was to determine the factors influencing resource selection of the Canada lynx population within this ecological island.

Material and methods

Study area

Riding Mountain National Park (RMNP, 3089 km^2) is located in southwestern Manitoba, Canada (Fig. 1). Elevation within the park ranges from 315–750 m. This park is one of the largest tourism destinations in Manitoba with >250 000 visitors annually (Parks Canada 2007). Approximately 25% (n~63 000) of these visitors come to RMNP during the winter months (October–March; unpubl.). Wasagaming and Clear Lake, on which the town sits (Fig. 1), are hubs of winter recreation including snowmobiling and ice fishing. Relatively little is known about the RMNP lynx population (formal studies include Carbyn and Patriquin 1983, Nylen-Nemetchek 1999). Records on the lynx population within the park date back to the beginning of the 20th century. However, lynx were apparently absent in the park between 1910 and 1932 (Green 1932) but by the 1950s a small number of lynx were again using the park (Soper 1953). During the 1970s five lynx were successfully captured and studied in the park (Carbyn and Patriquin 1983). Habitat-based models predict that the park can support upwards of 170 viable lynx home ranges (Nylen-Nemetcheck 1999).

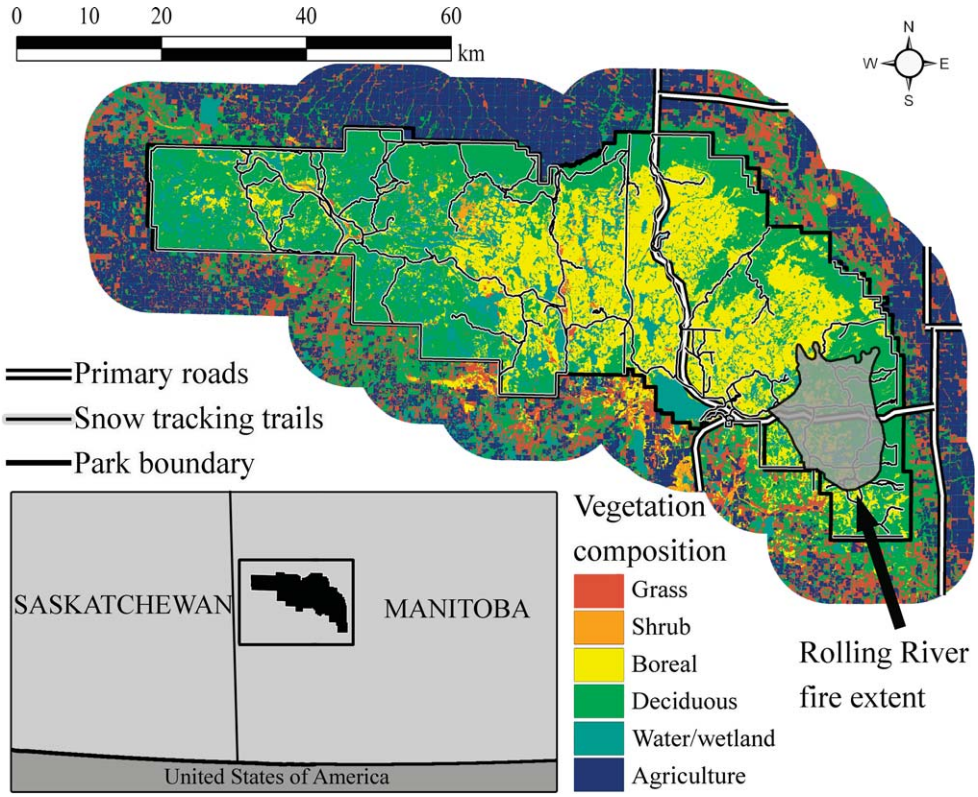


Figure 1. The vegetation communities within Riding Mountain National Park, Canada and in a comparable-sized area around the park (9 km buffer around the park). Primary roads, the extent of the Rolling River fire from 1980 and the snow tracking trails used to survey Canada lynx between 1997 and 2002 are also depicted.

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Riding Mountain National Park is an island ecosystem with extensive agricultural development outside of the park where oilseed, cereals, and hay are common crops (Brook and McLachlan 2006). Additionally, over 50 000 beef cattle *Bos primigenius* are grazed on ranches within 50 km of the park (Statistics Canada 2002, Brook and McLachlan 2006, Brook 2009). Concerns over human–wildlife conflict, specifically the transmission of tuberculosis *Mycobacterium bovis* from wild cervids to domesticated bovids, informed proposals by farmers to fence the boundary of RMNP (Brook and McLachlan 2003), but these measures have not yet been adopted. Nonetheless, the fencing-disease issue demonstrates that the park boundary receives considerable attention from farmers and resource managers. Vegetation structure inside and outside the park sharply contrasts. To facilitate a comparison of the Greater RMNP system we tabulated characteristics (i.e. area in km^2 and percent area) of each vegetation type within RMNP, around the periphery of the park, in the interior of RMNP, and near the edge of RMNP (Table 1). A 9 km buffer around the park provided a comparable sized-area (i.e. ~3000 km^2) to compare to RMNP (Fig. 1). To divide habitat between interior and edge regions of RMNP we quantified movement parameters of Canada lynx. Winter movement rates of Canada lynx tend to average 2–6 km day^{-1} between the northerly and southerly extent of the species range, respectively (Ward and Krebs 1985, Apps 2000, Squires et al. 2013). While movement rates have not been rigorously quantified for RMNP lynx, we anticipated that 3 km would delineate habitat within approximately one day's travel of the edge of this ecological island. Therefore, we classified edge habitat as that within 3 km of the park boundary and considered interior habitat to be > 3 km from the park boundary (Table 1).

There are four primary vegetation communities within the park; grasslands, shrublands, boreal mixed-wood forests and deciduous forests (Fig. 1). The grassland communities include a mix of native and herbaceous grasses. The shrublands are composed primarily of willow *Salix* spp., alder *Alnus* spp. and saskatoon *Amelanchier alnifolia* (Wang 1995). Boreal mixed-wood forests contain bogs and fens with dominant tree species including white spruce *Picea glauca*, black spruce *Picea mariana*, balsam fir *Abies balsamea* and jack pine *Pinus banksiana* (Wang 1995). The deciduous forests include balsam poplar *Populus balsamifera*, white birch *Betula papyrifera* and trembling aspen *Populus tremuloides* (Wang 1995). The present composition of the vegetation communities, particularly in the southeast portion of RMNP, was influenced by fire disturbance. The Rolling River fire, which was likely of human origin, burned some 20 000 ha in the southeast portion of RMNP near the town of Wasagaming and Clear Lake in 1980 (Pyne 2007; Fig. 1).

Data collection

In collaboration with RMNP wardens we conducted winter (December–March) snow track surveys for a five-year period between 1997 and 2002 (in 2000 surveys were not conducted) to develop a population-level resource selection function (RSF) that could be used to map the relative probability of lynx occurrence in the park. Snow tracking was performed with snowmobiles on 830 km of trails (including roads, trails, and forest cutlines) throughout the full extent of RMNP (Fig. 1). Trails along the periphery and the interior of the park were sampled with comparable effort so our survey design was not biased to particular regions of the study area. Good tracking conditions were estimated to occur within 48 h of the most recent snowfall. When a lynx track was located the age (in hours) since last snowfall was assessed and tracks > 48 h old were eliminated from consideration. The majority (> 90%) of lynx tracks were marked using a handheld GPS device; locations of the remaining tracks were estimated by marking the position on paper maps and later converting to digital coordinates. Most lynx tracks represented trail crossings. In cases where lynx briefly followed a trail, the center-point of the lynx track was marked. Tracks of multiple individuals were recorded as one single location documenting lynx occurrence.

We compiled a suite of covariates to describe the study area. These covariates derive from five broad categories; temporal, vegetation, prey, topographic and anthropogenic (Table 2). Because our study spanned a five-winter period, our temporal covariate was a year effect (Table 2). We expressed vegetation as the proportion of each vegetation type within cells of a given resolution across the study area (Squires et al. 2013). We based the scale of these cells on the spatial extent of Canada lynx foraging bouts (0.3 km^2; Moen et al. 2012). We evaluated covariates at this resolution for two reasons. Firstly, the observed lynx tracks in this study tended to represent cases where lynx were crossing trails. Inferring on-trail use, in these cases, would mischaracterize lynx resource selection.

Table 1. Vegetation type within Riding Mountain National Park (RMNP), Manitoba, Canada, in a comparable sized area (~3000 km^2) surrounding the park, in the interior of RMNP, and near the edge of RMNP. This table depicts the area (in km^2) and the percent of each vegetation type with the greater RMNP system.

	Within RMNP		Outside RMNP		Interior RMNP		Edge RMNP	
Land cover type	Area	%	Area	%	Area	%	Area	%
Grassland	30	1	730	24	21	1	10	1
Shrubland	51	2	38	1	41	2	10	1
Boreal	1117	36	93	3	970	46	147	15
Deciduous	1272	41	636	20	644	30	628	64
Agriculture	4	0	1348	43	0	0	4	0
Other δ	615	20	260	8	434	21	181	19
Total	3089	100	3105	100	2110	100	980	100

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Table 2. Covariates applied to the RSF models for predicting the relative probability of Canada lynx occurrence in Riding Mountain National Park, Canada, 1997–2002.

Category	Covariate	Description	Source
Temporal	year	year of the study (n = 5)	
Vegetation[a]	grassland	native and herbaceous grasses	LandSat 5 imagery 1994
	shrubland	willow, alder, saskatoon	
	boreal	jack pine, spruce, balsam fir with bogs and fens	
	deciduous	trembling aspen, balsam poplar, and white birch	
	agricultural	cereals, oil seeds, and specialty crops	
Prey[b]	hare	habitat suitability for snowshoe hare	Nylen-Nemetchek 1999
Topographic	DEM	digital elevation model (m)	Manitoba Geologic Survey
	slope	slope (degrees)	
	water	distance to water (km)	
Anthropogenic	boundary	distance to park boundary (km)	
	roads	distance to park roads (km)	
	recreation	distance to sources of within-park winter recreation (km)	

[a]proportion at a 0.3 km^2 resolution by vegetation type
[b]average habitat suitability value at a 0.3 km^2 resolution

Therefore, our intent was to characterize habitat in the vicinity of each lynx track. Secondly, maintaining consistency of scale between the dependent and independent variables was necessary to ensure accurate prediction of the RSF model (Hebblewhite et al. 2011).

For our prey covariate we developed a habitat suitability map for snowshoe hare throughout RMNP. Snowshoe hares are habitat specialists and their habitat selection correlates to specific vegetation characteristics that cannot be accurately quantified by coarse land cover classifications (Litvaitis et al. 1985, Koehler 1990, Keith et al. 1993). Hence, the distribution of snowshoe hares is often predicted by mapping habitat suitability based on field measures of understory security cover and browse potential (Carreker 1985, Timossi et al. 1995, Linden et al. 2011). We measured security cover and browse potential within distinct ecological land units (n = 24) in RMNP which were defined by unique combinations of vegetation types (Table 1) and soil groups in ArcGIS (Environmental System Research Institute, Redlands, CA). Within each ecological land unit, we measured security cover and browse potential within three plots at each of three randomly placed sites (Wolff 1980, Thomas et al. 1997, Nylen-Nemetchek 1999).

We measured security cover and browse potential at both ground level (up to 3 m high) and overhead levels. To measure security cover and browse potential at the ground level, we used a cover board. The 1-m^2 cover board was divided into 64 squares, each 5 cm in size, with estimates of cover taken by an observer, in four directions within each plot (Nudds 1977, Squires et al. 2010), at a distance of 5 m from the cover board (Nylen-Nemetchek 1999). Security cover was calculated as the proportion of squares covered by live or dead vegetation. For browse potential we calculated the proportion of squares covered by palatable live vegetation <1 cm in diameter (Koehler and Brittell 1990). To estimate overhead security cover, we used a spherical densiometer with the concave mirror divided into 24 squares each consisting of four quadrants (i.e. 96 quadrants total; Thomas et al. 1997). We calculated vertical security cover based on the proportion of quadrants covered by live or dead vegetation and measured browse potential based on the proportion of quadrants covered by palatable live woody vegetation. We averaged security cover and browse potential measurements across plots and sites, within each ecological land unit, to provide specific values for each ecological land unit.

We derived HSIs for browse potential and security cover based on the arithmetic means of our field sampling measurements at both ground level and overhead scales. We then combined these two HSIs to estimate a snowshoe hare habitat suitability map throughout RMNP using the equation;

$$(\mathrm{HSI}_{browse} \times \mathrm{HSI}_{cover})^{0.5} = \text{Habitat suitability map}_{hare_winter} \quad (1)$$

The resulting HSI map provided a spatially explicit estimate of winter snowshoe hare habitat suitability, ranging from 0 to 100 (representing low to high suitability), which we used as the prey covariate in our model.

We considered topographic covariates including elevation, slope, and distance to sources of water (Squires et al. 2010, 2013). We estimated Euclidean distance to water and sources of anthropogenic risk for lynx using the 'spatial analyst' extension and the Euclidean distance tool in ArcMap 10.0. The primary sources of anthropogenic risk to lynx in RMNP are interactions with humans near the road networks, boundary of the park, and areas within the park that permit winter recreation activities. We modeled distance to primary roads because lynx tend to be negatively affected by factors associated with roads including disturbance from humans, occurrence of competing carnivores, and direct mortality (lynx–vehicle collisions; Brocke et al. 1991, Aubry et al. 2000, Kolbe and Squires 2007). Distance to park boundary was modeled because lynx can be legally hunted and trapped outside of RMNP (National Parks Act 1989) and the vegetation characteristics outside the park tend to be unsuitable for lynx (Carbyn and Patriquin 1983, Paquet and Brook 2004; Table 1). Lastly, we modeled distance to within-park winter recreation to account for human activity (namely snowmobiling and ice fishing). Since these activities are permitted on Clear Lake, which is accessed via Wasagaming, we calculated distance to the merged polygon boundaries of the lake and the town (Fig. 1).

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Resource selection modeling

Resource selection functions estimate the proportional probability of animal occurrence across environmental space through used–available or used–unused designs (Boyce and McDonald 1999, Manly et al. 2002, Millspaugh et al. 2013). We applied a used–available design where lynx track locations collected during our winter snow track surveys represented 'used' habitat and we randomly generated locations, in ArcMap 10.0, to represent 'available' habitat. We randomly generated 0.5 locations per km of surveyed trail to estimate available habitat (Hebblewhite et al. 2011). We enforced a minimum random distance between used and available locations of 400–1500 m, based on known movement patterns of *Lynx* spp. (Palomares 2001). This ensured that no random location was generated within at least 400 m of a location where a lynx had been observed to occur. Thereby, available locations were not wrongly connected with used locations (Gervasi et al. 2013). The used and available locations functioned as a binary response variable in a fixed-effects logistic regression model (Manly et al. 2002, Hebblewhite et al. 2011) which we developed in STATA 10 (StataCorp LP, College Station, TX). We evaluated a variety of mixed-effects including a random year effect and different covariance structures according to methods outlined by Zuur et al. (2009). These additional terms however, did not improve model performance and were not retained in the final model design.

We identified our final multivariate logistic regression model via established techniques (Hosmer and Lemeshow 2000, Squires et al. 2010, 2013). We first tested the strength of univariate models, as determined by Wald statistics, from all important ($p < 0.25$) predictor covariates (Hosmer and Lemeshow 2000). We then used Pearson correlation coefficients to assess collinearity amongst these covariates. When collinearity was documented ($|r| > 0.50$), we retained the stronger predictor based on Wald statistics. For the retained predictor covariates we used a manual forward selection procedure to iteratively evaluate multivariate models. The order of predictor covariate addition was based on the univariate strength (described above). The covariate was included when it improved the model log-likelihood leading to a significant ($\alpha < 0.05$) likelihood ratio test. We continued this exercise until the final model fit well with no signs of collinearity (Hosmer and Lemeshow 2000).

We evaluated model prediction using receiver operating curves (ROC) and the k-fold cross validation test (Hosmer and Lemeshow 2000, Boyce et al. 2002). The k-fold cross validation test was based on an 80:20 ratio of training to testing data (i.e. models were developed using 80% of the data and subsequently validated with the remaining 20%). We generated five random sets of validation data using this ratio. For each validation data set we categorized the predicted relative probabilities of lynx occurrence into 32 categories based on equal intervals. We then simplified these categories into 10 bins (Boyce et al. 2002). We used Spearman's rank correlation to compare the frequency of testing data in each RSF category to the frequency of training data in the corresponding category. A high correlation coefficient indicates agreement between the training and testing data sets. We interpreted the magnitude of effects for those parameters where the 95% confidence interval of the odds ratio did not overlap 1. Given that the units of each covariate in the final model tended to vary, we interpreted the odds ratio calculated from the exponent of the parameter estimate multiplied by the unit interval. Finally, using raster calculator in ArcMap 10.0 we produced a GIS raster representing the predicted relative probability of lynx occurrence in the park from the parameter estimates in the final model.

Results

Between 1997 and 2002 we documented 418 Canada lynx tracks throughout RMNP. We surveyed an average of 80% (660 km of 830 km) of the trail system annually. In comparison to these used locations, we generated 1635 random locations to represent available habitat. The results of our hare habitat suitability model identified that habitat with the highest suitability for snowshoe hare was located in regenerating jackpine and aspen woodlands on clay soil types (Fig 2; Nylen-Nemetchek 1999). Lowest hare habitat suitability was associated with open, grassy areas (e.g. low shrub grassland on clay soils) and mature, closed-canopy forests with sparse understories (e.g. closed coniferous on clay soils and sand–clay soils; Fig. 2; Nylen-Nemetchek 1999).

The final model predicting the relative probability of lynx occurrence in winter included elevation, snowshoe hare habitat suitability, distance to within-park winter recreation, proportion boreal mixed-wood forests, proportion agriculture and proportion grassland (Table 3). The relative probability of lynx occurrence increased with elevation and increased in habitat that was highly suitable for snowshoe hare (Table 3). Interpretation of the odds ratio revealed that for every 100 m increase in elevation the relative probability of lynx occurrence increased by 35% ($e^{0.003} \times 100$; Table 3). The estimated odds ratio for each 10 unit increase in the suitability of habitat for snowshoe hare indicated that the relative probability of lynx occurrence increased by 21% ($e^{0.019} \times 10$; Table 3). Additionally, the relative probability of lynx occurrence decreased in habitat with a greater proportion of agriculture and grassland vegetation types (Table 3). For instance, with every 0.10 increase in the proportion of the respective vegetation type, the relative probability of lynx occurrence decreased by 21% for proportion agriculture ($e^{-2.336} \times 0.10$) and decreased by 14% for proportion grasslands ($e^{-1.537} \times 0.10$; Table 3). Finally, the relative probability of lynx occurrence increased in habitat that was nearer to sources of within-park winter recreation associated with Clear Lake and the town of Wasagaming in the southeast portion of RMNP (Table 3). For every 100 m distance closer to Wasagaming and Clear Lake the relative probability of lynx occurrence increased by 7% ($e^{-0.007} \times 100$; Table 3). This final model performed better than random (area under the ROC curve was 0.67) and the k-fold cross validation tests indicated that the training and testing data were highly correlated (average $r_s = 0.979$).

The map resulting from implementing the final model in GIS predicted that the relative probability of lynx occurrence

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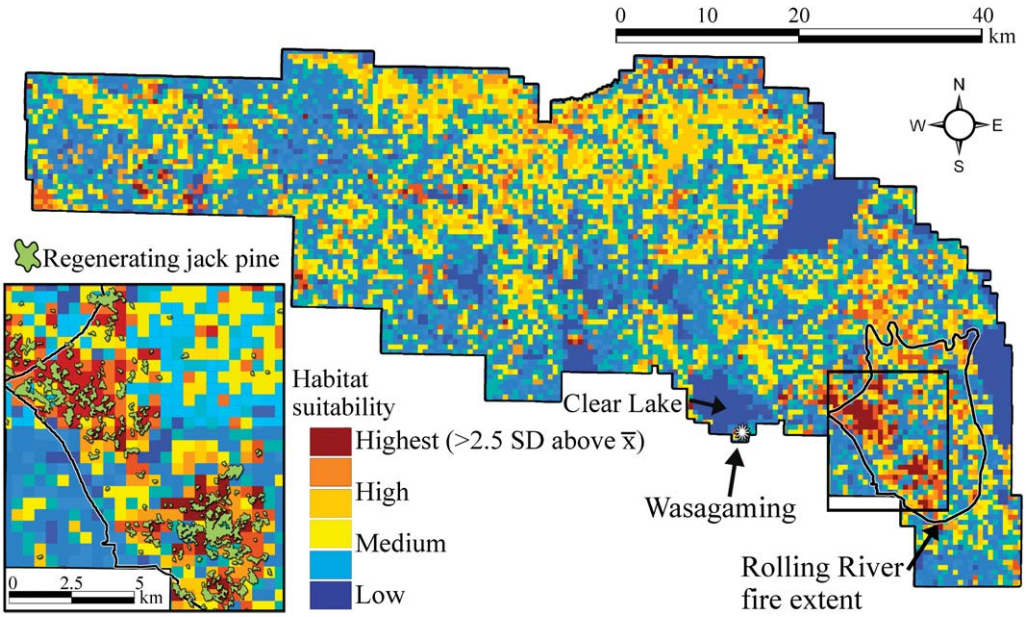


Figure 2. Snowshoe hare habitat suitability used as a covariate to predict the relative probability of Canada lynx occurrence in Riding Mountain National Park, Canada between 1997 and 2002. The inset portrays patches of regenerating jack pine forests within the extent of the Rolling River fire of 1980 located in the southeastern portion of Riding Mountain National Park.

was lowest near the park boundary, particularly along the agriculture-dominated northern and western edges (Fig. 1, 3). Habitats predicted to have medium to high relative probability of lynx occurrence tended to be located in the interior of RMNP (Fig. 3). The highest (>2.5 standard deviations (SD) above the mean) predicted relative probability of lynx occurrence was associated with habitat in the southeast portion of the park that tended to be at higher elevations and associated with the highest suitable snowshoe hare habitat (Fig. 3). This habitat with the highest probability of lynx occurrence had an average elevation of 662 m (SD = 14 m, range 645 m–734 m) which is >60 m above the average for RMNP ($\bar{x}$ = 599 m, SD = 77 m, range 315–750 m). Furthermore, over 90% (13.2 of 14.5 km^2) of this habitat intersected highly suitable snowshoe hare habitat. In turn, the suitability of habitat for snowshoe hare was greatly affected by regenerating jack pine forests (Fig. 2 inset). Over 92% of the highest suitable (>2.5 SD above the mean) snowshoe hare habitat was centered on patches of regenerating jack pine forests throughout RMNP. The majority (75%) of this habitat with the highest suitability for hare occurred in the southeastern portion of RMNP where the largest aggregation of patches of regenerating jack pine were located ($\bar{x}$ = 3.76 ha, min = 0.01 ha, max = 130 ha; Fig. 2 inset). Thus, the highest predicted relative probability of lynx occurrence was influenced by snowshoe hare habitat suitability and the underlying habitat heterogeneity in the southeast portion of RMNP associated with regenerating jack pine forests.

Discussion

We found that the predicted relative probability of lynx occurrence increased in habitat that was highly suitable for snowshoe hare, containing boreal mixed-wood forests at higher elevations, consistent with the established winter behavioral ecology of Canada lynx (Poole 2003, Koehler et al. 2008, Squires et al. 2008). Much of the medium to high predicted relative probability of lynx occurrence tended

Table 3. Logistic regression parameter estimates with standard errors (SE), corresponding p-values, and odds ratios with 95% confidence intervals for the environmental covariates in the final model explaining Canada lynx resource selection in Riding Mountain National Park, Canada, 1997–2002.

Environmental covariates[§]	Estimate (SE)	|z|	p>|z|	Odds ratio (95% CI)
Intercept	−3.309 (0.519)	6.4	<0.001	
DEM	0.003 (0.001)	3.2	<0.001	1.003 (1.000 to 1.004)
Hare	0.019 (0.005)	3.6	<0.001	1.019 (1.008 to 1.029)
Recreation	−0.007 (0.004)	1.8	0.07	0.993 (0.986 to 1.001)
Boreal	0.323 (0.193)	1.7	0.09	1.382 (0.947 to 2.016)
Agriculture	−2.336 (0.952)	2.5	0.01	0.097 (0.015 to 0.625)
Grassland	−1.537 (0.599)	2.6	0.01	0.215 (0.066 to 0.696)

[§]DEM = digital elevation model (m), Hare = snowshoe hare habitat suitability index, Recreation = distance to sources of within-park winter recreation (km), Boreal = proportion boreal in each cell, Agriculture = proportion agriculture in each cell, and Grassland = proportion grass in each cell.

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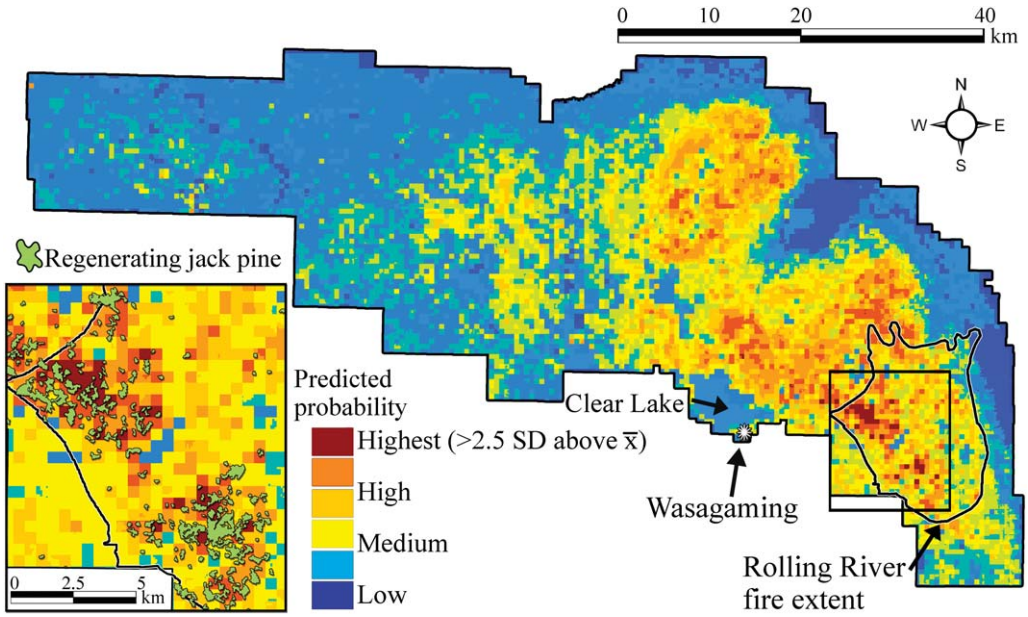


Figure 3. The predicted relative probability of Canada lynx occurrence in Riding Mountain National Park, Canada based on lynx track data collected between 1997 and 2002. The inset portrays patches of regenerating jack pine forests within the extent of the Rolling River fire of 1980 located in the southeastern portion of Riding Mountain National Park.

to be associated with interior habitat in RMNP (Fig. 3). Negative edge effects have been observed for other carnivores in diverse systems (Revilla et al. 2001, Balme et al. 2010, Burton et al. 2012, Northrup et al. 2012). However, the relationship between lynx occurrence and the boundary of RMNP was not consistent, as evidenced by the fact that the proximity to boundary covariate was not an important (i.e. $p > 0.25$) predictor of lynx resource selection. Agricultural and grassland vegetation types, both common along the periphery of the park (Table 1), are highly unsuitable for lynx and snowshoe hare during winter (Maletzke et al. 2008), yet that alone does not explain avoidance of the majority of habitat near the edges of this ecological island. The more likely explanation for this relationship relates to near-edge habitat also being relatively unsuitable for lynx. Comparison of the vegetation types in interior versus edge habitat of RMNP revealed that habitat near the edge of RMNP contains relatively little boreal mixed-wood forests (Table 1). Just 15% of habitat within 3 km of the RMNP boundary is characterized by boreal mixed-wood forests compared to 46% of interior habitat (Table 1). Boreal mixed-wood forests are known to be preferred habitat of Canada lynx and snowshoe hare (Thompson et al. 1989, Koehler and Brittell 1990). Thus, we contend that unsuitable habitat near to the RMNP boundary coupled with extensive landscape change, intensive farming, cattle grazing, and hunting/trapping in areas outside of RMNP (Brook and McLachlan 2006, Brook 2009) result in lynx tending to use insular areas of the park.

Despite general avoidance of near-edge habitat, we found that the predicted relative probability of lynx occurrence increased near Wasagaming and Clear Lake, which are focal areas for winter recreationists, in the southeastern portion of RMNP (Fig. 1, 3). We suggest that lynx tolerate winter recreation (skiing, snowmobiling, snowshoeing and ice fishing) in these areas because the habitat is highly suitable for their primary prey and these types of human activity are relatively non-threatening to lynx. Ninety-one percent of the highest (>2.5 SD above the mean) predicted relative probability of lynx occurrence intersected highly suitable snowshoe hare habitat in this area (Fig. 3 inset). Canada lynx tend to center their space use on high quality snowshoe hare habitat (McCann and Moen 2011) and are tolerant of sporadic human activity including snowmobile traffic (Mowat et al. 2000). Additionally, Canada lynx are least active during daylight periods when humans tend to participate in winter recreation (Poole et al. 1996, Mowat and Slough 2003, Kolbe and Squires 2007). Thus, we expect that the probability of lynx–human interaction in this region of RMNP is relatively low. Our observation of lynx using high quality foraging habitat in the vicinity of sources of human disturbance is congruent with research of lynx in other systems. Basille et al. (2009) determined that Eurasian lynx *Lynx lynx* used habitats with more human disturbance than average in pursuit of their primary prey. Bunnefeld et al. (2006) also found that Eurasian lynx selected day lairs and kill sites significantly closer to human communities, roads, and agricultural fields than what would be expected at random. While there was sex-specific variation in this response, the relationship between lynx winter habitat selection and sources of anthropogenic disturbance was attributed to roe deer *Capreolus capreolus* (primary prey) using habitat near to humans because of lower snow depths and artificial feeding taking place in these areas (Bunnefeld et al. 2006).

Winter snowshoe hare habitat suitability in RMNP was highest in regenerating jack pine consistent with established winter foraging preferences of snowshoe hare (Fox 1978, Koehler 1990). The distribution of regenerating jack pine forests in the southeastern portion of RMNP

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derived from the Rolling River fire of 1980 (Caners and Kenkel 1998; Fig. 2, 3 inset). The burn resulted in dense, regenerating jack pine that, 25 years post-fire, became high quality snowshoe hare habitat and correspondingly attracted lynx. This pattern indicates that the spatial distribution of lynx occurrence was ultimately affected by fire disturbance, consistent with the dynamics of lynx–hare systems in boreal zones (Fox 1978, Koehler and Brittell 1990, Hodson et al. 2011). Post-fire successional habitats tend to have vegetation characteristics (i.e. vertical and horizontal cover and increased plant biomass) that are preferred by snowshoe hare (Fox 1978, Koehler and Brittell 1990, Poole et al. 1996, Hodson et al. 2011). Additionally, regenerating conifer forests can support high densities of snowshoe hare and Canada lynx (Slough and Mowat 1996, Mowat and Slough 2003).

As these jack pine forests continue to mature they will become less desirable for snowshoe hare (Hodson et al. 2011) and correspondingly for lynx. Mature forests tend not to provide the dense understory which snowshoe hare select for cover in winter (Keith et al. 1984, Sievert and Keith 1985, Litvaitis et al. 1985, Wirsing et al. 2002, Fuller et al. 2007, Koehler et al. 2008). Abundance of snowshoe hare in the boreal forests of Canada is highest, as determined by fecal pellet counts, 40–50 years after fire/harvest disturbance (Hodson et al. 2011). Thus, it may be 15–25 years after this study before these habitats in the southeastern portion of RMNP are no longer preferred by snowshoe hare. Additionally, future forest fires could continue to shape the vegetation structure of RMNP. Our results suggest that as long as the distribution of highly suitable snowshoe hare habitat is coincident with areas used by humans in RMNP, the potential for lynx–human interaction persists.

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