

Ecological factors influencing the spatial pattern of Canada lynx relative to its southern range edge in Alberta, Canada

Erin M. Bayne, Stan Boutin, and Richard A. Moses

Abstract: We examined the spatial pattern of Canada lynx (*Lynx canadensis* Kerr, 1792) relative to its southern range edge at the boreal plains – prairie ecotone in Alberta, Canada. Relative to the original distribution of boreal forest in our study area, lynx range seems to have contracted up to 22%. In 100 km² sampling areas, lynx occupancy rate increased 1.93 times every 100 km farther (north) from the range edge that we sampled. An information–theoretic approach was used to evaluate 31 models to see which environmental factors were the best predictors of this spatial pattern. Lynx were strongly correlated with track counts of their primary prey, the snowshoe hare (*Lepus americanus* Erxleben, 1777), but this did not explain the observed increase in occupancy farther north. Rather, lynx occupancy was lower in areas with higher road densities and this effect was magnified in areas where coyote (*Canis latrans* Say, 1823) activity was highest. The inclusion of these effects rendered the south–north pattern no longer significant. The rapid pace of road building and associated development in Alberta’s boreal forest seems to be reducing habitat quality for Canada lynx, particularly at the southern edge of its range. This may be leading to range contractions for lynx in Alberta, much like has happened elsewhere in North America.

Résumé : Nous examinons la structure spatiale chez les lynx du Canada (*Lynx canadensis* Kerr, 1792) en relation avec la bordure sud de leur répartition au niveau de l’écotone plaines boréales – prairies en Alberta, Canada. Par rapport à la répartition d’origine de la forêt boréale dans notre zone d’étude, l’aire de répartition des lynx semble s’être rétrécie de jusqu’à 22 %. Dans des parcelles d’échantillonnage de 100 km², le taux d’occupation des lynx s’accroît par un facteur de 1,93 à chaque 100 km additionnel (vers le nord) depuis la bordure de l’aire que nous avons échantillonnée. Nous utilisons une méthodologie basée sur la théorie de l’information pour évaluer 31 modèles afin de voir quels facteurs environnementaux permettent le mieux de prédire ce patron spatial. Il y a une forte corrélation entre les lynx et les dénombrements de pistes de leurs proies principales, les lièvres d’Amérique (*Lepus americanus* Erxleben, 1777), mais cela n’explique pas l’augmentation de l’occupation notée plus au nord. Plutôt, l’occupation des lynx est plus faible dans les régions de plus forte densité de routes et cet effet est amplifié dans les zones dans lesquelles l’activité des coyotes (*Canis latrans* Say, 1823) est la plus grande. Les taux rapides de construction de routes et de développement associé dans la forêt boréale de l’Alberta semblent en train de réduire la qualité de l’habitat du lynx du Canada, particulièrement à la bordure sud de son aire. Cela peut mener à des rétrécissements de l’aire de répartition des lynx en Alberta, comme cela s’est produit ailleurs en Amérique du Nord.

[Traduit par la Rédaction]

Introduction

How organisms are distributed relative to the edges of their range and the environmental factors that influence these spatial patterns are fundamental questions in macroecology. Few species are uniformly distributed within their range (Brown et al. 1995) and there is a general belief that organisms are more abundant at the core of their range than at the edge (Guo et al. 2005). This paradigm, often referred to as the “abundant centre distribution”, was recently challenged by Sagarin and Gaines (2002) and Sagarin et al. (2006) who argued that few studies have explicitly measured

the abundance of organisms close to versus far from range edges. Of those, fewer still had results consistent with species being less abundant at range edges. This led them to conclude that spatial heterogeneity in climatic conditions, population demographics, community interactions, species plasticity, the strength of anthropogenic effects, and biogeographic differences at different range boundaries create far more complex patterns than the abundant centre distribution predicts. They challenged ecologists to not only better quantify spatial patterns of organisms relative to different range edges but to test specific hypotheses about the relative importance of these various environmental factors before concluding that a given spatial distribution fits the abundant centre hypothesis.

The Canada lynx (*Lynx canadensis* Kerr, 1792) is a mid-sized carnivore whose range is known to be concordant with the boreal forest of North America. Published density estimates suggest lynx are less abundant in the southern peninsulas of boreal forest that stretch into the conterminous United States relative to the more contiguous boreal forests

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of northern Canada (Boutin 2005; Mowat et al. 2000). Lalliberte and Ripple (2004) also suggest that lynx range has contracted 39% from its historic high across North America, with that contraction occurring at the edge of the boreal peninsulas. These declines have resulted in lynx being listed as threatened under the US Endangered Species Act. That contractions in lynx range have occurred at peninsular edges supports one prediction made by the abundant centre distribution (Sagarin et al. 2006). However, the lynx's range is spatially disjunct, requiring further investigation as to whether it is less abundant near all range edges. The Athabasca River basin of northern Canada has often been cited as a "hotspot" for lynx (Aubry et al. 2000) and lies north of the boreal plains – prairie ecotone, a known limit of lynx distribution in western Canada. The sharp range boundary that exists in this area provides a good opportunity to test whether lynx abundance is constant up to this ecotone or whether there is evidence of increasing abundance at greater distances from this clearly defined range edge.

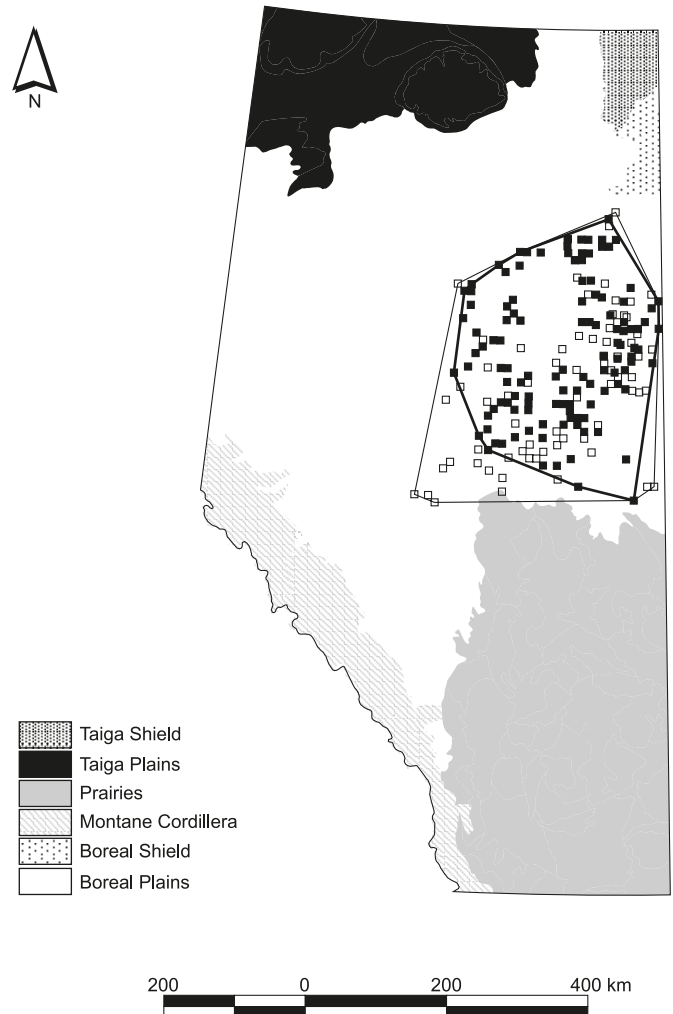
The primary objective of this study was to describe the spatial pattern of lynx distribution relative to the boreal plains – prairie ecotone in northeastern Alberta and to determine the relative importance of interspecific interactions and anthropogenic disturbance as factors explaining the patterns that we observed. Hengeveld (1990) argued that inclusion of environmental variables in statistical models should render spatial variables "nonsignificant" if gradients in resources or other environmental factors are the sole determinant of spatial patterns in species abundance. We hypothesized that (i) prey availability, (ii) intensity of interspecific competition, and (iii) mortality risk would be the best predictors of lynx occurrence. Lynx numbers fluctuate in response to the availability of their primary prey, snowshoe hare (*Lepus americanus* Erxleben, 1777). Hare tend to select conifer-dominated areas and areas with dense willow shrubs (Krebs et al. 2001), habitats typically more common farther north in the boreal plains. Hare also are thought to be less abundant in agricultural landscapes, which are more common in southern areas. Our second hypothesis was that coyotes (*Canis latrans* Say, 1823) may have a competitive effect on lynx (Buskirk et al. 2000; Boutin 2005). The coyote began expanding its' range into the boreal plains from the southern prairie roughly 100 years ago. This expansion may be leading to lynx densities decreasing southward. Thirdly, lynx have few natural predators, but humans can have a strong impact on lynx mortality through trapping and vehicle deaths. Both of those mortality factors are facilitated by roads (Kramer-Schadt et al. 2004) and road density is generally higher in the southern half of the boreal plains.

Materials and methods

Study area

The study was conducted in a 129 016 km² area (an area approximately the size of England) of the boreal plains in northeastern Alberta centred on the Alberta Pacific Forest Industries Inc. (ALPAC) Forest Management Area (Fig. 1). The study area is in the Athabasca River basin and was bounded by the prairie ecozone to the south and the boreal Canadian Shield to the north. Except for a few scattered hill systems, the study area had minimal topographic relief

Fig. 1. Location of the study area in Alberta, Canada. The thin solid line represents the 100% minimum convex polygon (MCP) around all sampled sites. The thick solid line indicates the 100% MCP around sites where lynx were detected. Each square is one township and is the primary sampling unit ($n = 202$). Canada lynx (*Lynx canadensis*) were detected in solid squares and were not detected in open squares.



(400–900 m). Pure and mixed stands of quaking aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) are most common in upland sites, although jack pine (*Pinus banksiana* Lamb.) predominates in drier areas. Lowland sites are characterized by open stands of black spruce (*Picea mariana* (P. Mill.) B.S.P), tamarack (*Larix laricina* (Du Roi) K. Koch), and peatland complexes. In ALPAC, there is 23 842 km² of potentially merchantable forest, as well as extensive oil and gas deposits. The forestry industry cuts approximately 160 km² of forest per year, while the energy sector clears approximately 110 km² per year, mainly for access routes. At the southern edge of the study area, 14 392 km² (11%) of the forested land has been converted to agriculture with cattle grazing and cereal grain farming being the most common activities. Agricultural "perforations" occur around settlements farther north but are less extensive than in the south. Forestry and energy sector activities are more common in the southern

half of the study area, although they are more uniformly distributed than agriculture. Temperature and snowfall vary slightly across the region with mean January temperatures of -18.8°C in the north and -14.9°C in the south. Snowfall in January averages 24.3 cm in the south and 27.0 cm in the north.

Field methods

Between 2002 and 2005 we collected data at 202 sites. Each year we sampled between 40 and 75 sites distributed throughout the study area and along the full length of the spatial gradient. Our definition of a site was a township, which is a legally defined spatial unit approximately $10\text{ km} \times 10\text{ km}$. Sites were selected using a stratified random design, using a GIS to randomly pick sites within strata. All townships in the study area were stratified a priori into a cumulative level of human impact and an equal number of townships in each cumulative effect strata were selected each year. An effort was made to balance the number of areas with high human impact between the north and the south, although we could not do this for areas with significant agricultural conversion. Given the relatively large size of our sampling transects we did not stratify by forest type, as all transects crossed multiple forest types. Instead, we sampled different forest types relative to their availability. We excluded from our statistical population all sites that were $>2\text{ h}$ by snowmobile from the nearest truck accessible road (approximately 15% of sites). Sites selected by the GIS that were within the Cold Lake Air Weapons Range (south-east portion of study area) were also excluded because of limits imposed on access.

To gather information on lynx and other mammals in this region, we counted the number of tracks left in the snow along 9 km triangular (3 km a side) transects or “triangles” (Lindén et al. 1996). Each triangle was centred on a township and oriented with the apex of the triangle pointing north. Hence, triangles were placed randomly with respect to forest type within a township. If any transect intersected $>3\text{ km}$ of open water, the position of the triangle was moved to reduce its exposure to “open water”. UTM coordinates were generated using GIS and downloaded to Global Positioning Systems (GPS) to allow observers to accurately move around the triangle. Each transect was divided into nine 1 km segments for purposes of data recording. In each segment, we recorded species and track type and tallied the number of “hits”. Hits were defined as tracks that intercepted the transect and may have included individuals that moved back and forth across transects (O’Donoghue et al. 1997). All surveys were done between 15 December and 15 March.

An important source of variation in our data was the time over which tracks were known to have accumulated or days since last snow (DSS). We attempted to minimize this variation by surveying transects between 3 and 10 DSS. Over 70% of transects surveyed were done between 3 and 6 DSS. Most of the observations $>6\text{ DSS}$ occurred in 2002 when fewer large snowfall events occurred. Snowfalls $>1\text{ cm}$ generally erased tracks and prohibited trackers from collecting reliable data, so the DSS count was “reset” at zero when any given township received a snowfall $>1\text{ cm}$. Regardless, we controlled for the effect of DSS in all analyses.

Statistical analyses

We assessed three aspects of the spatial distribution of lynx in northeastern Alberta. To determine if there was evidence of “range contraction”, we created a 100% minimum convex polygon (MCP) around the centroids of each township. This was the “potential range” of lynx, as all sampled townships were originally boreal forest prior to European settlement. We then generated a 100% MCP around townships where we found lynx tracks and calculated overlap between the potential range and the observed range. A jackknife analysis was also done 500 times to determine how removal of single townships influenced this estimate.

To determine whether lynx were patchily distributed, we calculated Moran’s I coefficient (spatial lag of 10 km with 10 lags). Moran’s I is a spatial autocorrelation statistic that estimates whether sites closer together were more likely to have lynx than sites farther apart. Probability values to determine the significance of each Moran’s I value were calculated using a randomization procedure in the program Rook Case (Sawada 1999). A sequential Bonferroni correction was applied to probability values when assessing the significance of Moran’s I at each lag distance.

To evaluate whether the occurrence of lynx showed a pattern of increase relative to range edge, we modelled the presence–absence of lynx against UTM northing coordinates divided by 100 000 (hereafter referred to as NORTH). Presence–absence data are typically modeled using logistic regression. However, species can go undetected in a sampling unit even when the species is present. Not accounting for such detection error could lead to an underestimation of the true level of occupancy, and hence biased inferences if detection error varied as a function of a variable of interest. Therefore, we used a modified version of logistic regression created by MacKenzie et al. (2002) to estimate occupancy rate (hereafter Ψ). Estimation was done within the program Presence. Occupancy rate is defined as the probability of occurrence corrected for detection error. Detection error is defined as the probability that we failed to detect a lynx in a township even though one was present (hereafter p). Hereafter detection error is referred to as detection probability (probability that lynx were detected given they were present). To estimate detection probability, we used each 1 km segment within a sampling triangle as a replicate survey for the township. In other words, we recorded whether lynx were detected or not in the township and the detection history for each of our nine 1 km segments (i.e., detection history of 010010000). This approach to sampling is recommended by MacKenzie and Royle (2005) for low density and highly mobile species that are likely to move out of a sampling area over time. While occupancy rate does not estimate density per se, this measure is increasingly being used as a surrogate for abundance, particularly in situations where the sample area is approximately the same size as the territory or home range of the animal of interest. While we do not know the mean home-range size for lynx in our study area, we assume that sample units 20 km apart were unlikely to detect the same individual.

The variable ROADS (total length divided by area of the township), which was our estimate of mortality risk owing to humans, was estimated for each township from the Alberta Base Features Layer (current to 2003). ROADS was

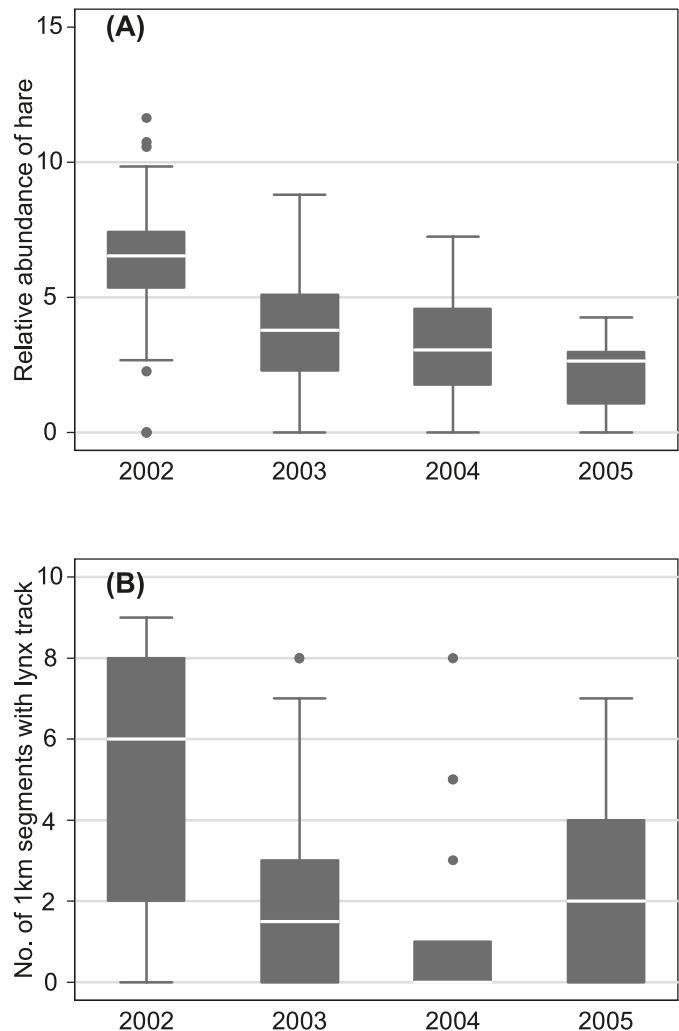
transformed prior to analysis ($x^{0.5}$). COYOTE, which was our measure of competition, and HARE, our measure of food abundance, were estimated from the winter tracking triangles. Total number of tracks per township of these species were divided by DSS and transformed ($x^{0.33}$) to approximate a normal distribution. We viewed the COYOTE variable as a measure of coyote activity and not a measure of abundance. For HARE, we viewed the track count as an index of relative abundance (O'Donoghue et al. 1997). We did not model year as a factor influencing lynx occupancy rate or detection probability because we could not directly estimate hare abundance, which we assumed is the most proximate explanation for variation in lynx numbers over time. The mean abundance of hare tracks in the study area varied threefold over the length of our surveys (Fig. 2A) and lynx detections tracked this change (Fig. 2B).

To determine if any combination of environmental variables could explain "away" the spatial patterns that we observed, a series of a priori models were fitted and compared using Akaike's information criterion (AIC). Akaike weights were used to assess the cumulative evidence for the hypothesis that spatial variation in environmental factors could explain spatial patterns in lynx occupancy rate. This was done by summing the weights from all models that contained NORTH and comparing these to models that did not contain NORTH. Prior to choosing AIC over quasi-AIC, overdispersion and other sources of lack of model fit were tested using methods outlined in MacKenzie and Bailey (2004).

There were a total of 31 models in the candidate set (Table 1). The variables we used to predict occupancy rate were HARE, ROADS, COYOTES, and NORTH. As the abundance of hare is known to be a very strong predictor of lynx occurrence, we included HARE in all models except the models used to describe spatial pattern. All other combinations of main effects (COYOTE and ROADS) were considered. We also examined models that included an interaction between HARE \times ROADS. When hare are rare, it can be difficult to detect effects of roads because lynx become rare across the entire landscape. This results in a flat relationship between lynx and roads simply because there are no lynx. Models that hypothesized an interactive effect of COYOTE \times ROADS were also considered. Our rationale was that coyote hunting success might be facilitated by roads, particularly during the winter, owing to snow packing (Bunnell et al. 2006, but see Kolbe et al. 2007). Where coyotes are more common, we postulated that roads might have a greater impact on lynx because greater hunting success in roaded areas by coyotes could increase their competitive ability over lynx.

The variables we used to model detection probability were NORTH and DSS. Our rationale for including DSS in detection probability was that the longer the time tracks could accumulate the higher the probability that each segment in our sampling would be crossed by a lynx. Various functional forms of DSS were examined, but a simple linear function fit the best. We also examined whether detection probability was influenced by NORTH. In more southerly regions, there are a greater number of open habitats (i.e., fields, clearcuts, etc.). Tracks do not last as long in open habitat (E.M. Bayne, unpublished data), thus it is possible

Fig. 2. Box plot showing (A) relative abundance (tracks per triangle corrected for DSS^{0.33}, where DDS is days since last snow) of snowshoe hare (*Lepus americanus*) per year in northeastern Alberta, Canada, and (B) mean number of 1 km segments where Canada lynx (*Lynx canadensis*) tracks were observed each year. Solid white lines represent medians, boxes represent 25th–75th quartile, and whiskers represent the upper and lower adjacent values. The upper adjacent value is equal to $1.5 \times$ interquartile range (IQR) and the lower adjacent value is equal to the smallest data value that is greater than or equal to the first quartile $- (1.5 \times$ IQR). Dots represent values outside the adjacent values. The number of townships sampled per year is between 40 and 75.



that we were less likely to detect lynx in the southern part of the study area even when lynx were present.

Results

Spatial patterns

Our naïve estimate of occurrence was 66%. The 100% MCP for the area we sampled was 106 890 km². The MCP for locations where lynx were observed was 83 193 km², a contraction of 22% from the assumed range. This estimate assumes that some time in the past lynx utilized all the areas sampled, which we do not know with certainty to be true. However, prior to European settlement this area was entirely

Table 1. Fit of a priori models predicting occupancy rate (Ψ) and detection error (p) of Canada lynx (*Lynx canadensis*) using Akaike’s information criterion (AIC).

Model	AIC	Δ AIC	AIC weight	K
$\Psi(\text{HARE} + \text{COYOTE} \times \text{ROADS}),p(\text{DSS} + \text{NORTH})$	1691.3	0	0.4185	8
$\Psi(\text{NORTH} + \text{HARE} + \text{COYOTE} \times \text{ROADS}),p(\text{DSS} + \text{NORTH})$	1692.8	1.6	0.1909	9
$\Psi(\text{HARE} \times \text{ROADS} + \text{COYOTE} \times \text{ROADS}),p(\text{DSS} + \text{NORTH})$	1693.2	1.9	0.161	9
$\Psi(\text{NORTH} + \text{HARE} \times \text{ROADS} + \text{COYOTE} \times \text{ROADS}),p(\text{DSS} + \text{NORTH})$	1694.7	3.5	0.0738	10
$\Psi(\text{COYOTE} + \text{HARE} + \text{ROADS}),p(\text{DSS} + \text{NORTH})$	1695.8	4.6	0.0424	7
$\Psi(\text{HARE} \times \text{ROADS}),p(\text{DSS} + \text{NORTH})$	1697.1	5.8	0.0228	8
$\Psi(\text{ROADS} + \text{HARE}),p(\text{DSS} + \text{NORTH})$	1697.2	6.0	0.0209	6
$\Psi(\text{COYOTE} + \text{HARE} + \text{ROADS}),p(\text{DSS} + \text{NORTH})$	1697.3	6.0	0.0205	8
$\Psi(\text{COYOTE} + \text{HARE}),p(\text{DSS} + \text{NORTH})$	1697.5	6.3	0.0181	7
$\Psi(\text{HARE} + \text{ROADS}),p(\text{DSS} + \text{NORTH})$	1698.4	7.2	0.0115	7
$\Psi(\text{HARD} \times \text{ROADS}),p(\text{DSS} + \text{NORTH})$	1698.6	7.3	0.0108	9
$\Psi(\text{COYOTE} + \text{HARE}),p(\text{DSS} + \text{NORTH})$	1699.9	8.7	0.0053	6
$\Psi(\text{HARE}),p(\text{DSS} + \text{NORTH})$	1700.9	9.7	0.0034	6
$\Psi(\text{HARE}),p(\text{DSS} + \text{NORTH})$	1708.7	17.5	0.0001	5
$\Psi(\text{NORTH}),p(\text{DSS} + \text{NORTH})$	1726.4	35.2	0	5
$\Psi(\cdot),p(\text{DSS} + \text{NORTH})$	1731.5	40.2	0	4
$\Psi(\text{NORTH}),p(\text{DSS})$	1781.9	90.6	0	4
$\Psi(\cdot),p(\text{DSS})$	1794.1	102.9	0	3

Note: Models with lowest Δ AIC values have the best fit to the data using the fewest number of parameters (K). Of the environmental models considered, only those containing $p(\text{DSS} + \text{NORTH})$, where DSS is days since last snow, are shown because models with $p(\text{DSS})$ had much poorer fit.

covered by boreal forest, so there is no reason to think that lynx would not have been present. Jack-knifed samples resulted in a mean (SD) observed range size of $82\,784 \pm 1\,169$ km², suggesting that no one sample location influenced this estimate strongly. The only statistically significant evidence of spatial autocorrelation occurred at the 20–30 km lag distance. However, the magnitude of the spatial autocorrelation was low ($I = 0.13$), suggesting little evidence for spatial clustering in lynx in northeastern Alberta.

Correcting detection probability for DSS, we found strong support that NORTH predicted the occupancy rate of lynx in the boreal plains of northeastern Alberta. The Δ AIC between the model containing $\Psi(\text{NORTH})$ and $p(\text{DSS})$ versus $p(\text{DSS})$ was 12.3. For every 100 km farther north, the occupancy rate of lynx in a township increased 1.93 times (odds ratio) (Fig. 3A). $\Psi(\text{NORTH}),p(\text{DSS})$ had a reasonable fit to the data with no strong evidence for lack of fit ($\chi^2 = 1056.5$, $P = 0.66$, $\hat{c} = 0.85$).

Environmental factors influencing spatial pattern

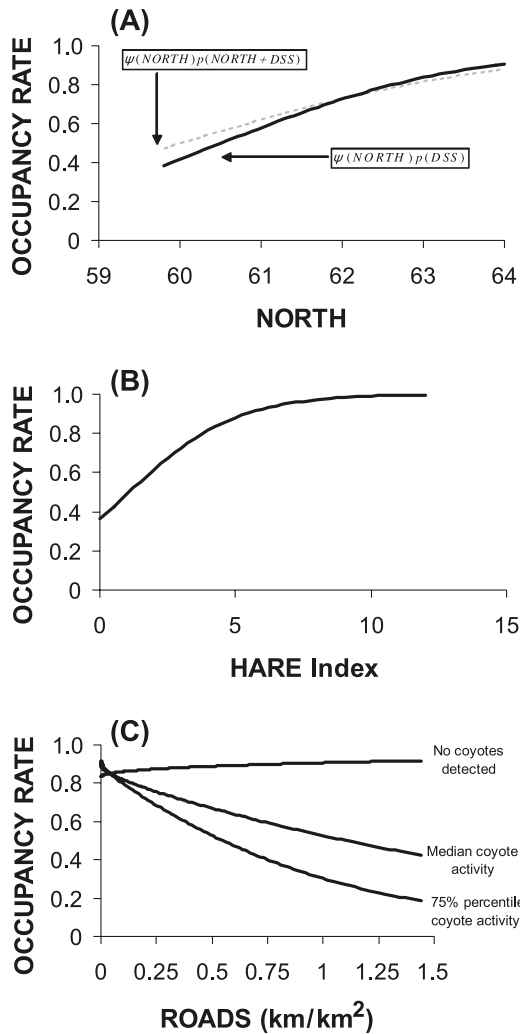
Including environmental variables in our models improved fit considerably as $\Psi(\text{NORTH}),p(\text{DSS})$ had a Δ AIC of 90.6 relative to the best fitting environmental model. Environmental variables seemed to explain “away” the spatial pattern in lynx, as models containing environmental factors but that excluded NORTH from occupancy rate had a combined Akaike weight of 0.671. The best fitting model was $\Psi(\text{HARE} + \text{COYOTE} \times \text{ROADS}),p(\text{DSS} + \text{NORTH})$. This model had an Akaike weight of 0.42. The model also had a good fit to the data, suggesting no adjustments to AIC owing to overdispersion were necessary ($\chi^2 = 1246$, $P = 0.40$, $\hat{c} = 0.98$). The same model that included NORTH as a variable influencing occupancy rate had an Akaike weight of only 0.19. The models that included NORTH as a factor

influencing detection probability were far more plausible than those that excluded NORTH from detection probability. The combined Akaike weight was 1 relative to models that excluded NORTH from detection probability. There was strong support that lynx occupancy rate was a positive linear function of HARE (Fig. 3B). There was also strong support for an interaction between COYOTE and ROADS. Where coyotes were more active, roads had a more substantial negative effect on lynx occupancy rate (Fig. 3C). Detection probability increased with DSS and NORTH (Figs. 4A, 4B). Model parameter estimates for the best fitting model are provided in Table 2.

Discussion

Our results show a clear pattern of increasing occupancy by lynx the farther we sampled from their southern range edge in boreal Alberta. Does this mean that lynx fit an abundant centre distribution? While consistent with the predictions of the abundant centre hypothesis, our partial range analysis (Blackburn et al. 1999) only allows us to draw conclusions about the influence of the southern range edge as a factor influencing lynx abundance. We do not know whether lynx occupancy rates decline in a similar fashion as you approach the northern range limit of lynx, which occurs several hundred kilometres north of our northern-most sampling point. We also cannot speculate on patterns of lynx abundance in an east–west direction where the range edge tends to be defined by oceans. The ultimate test of the abundant centre pattern occurs when species show a bell-shaped distribution relative to all range edges and is required to explicitly identify the core of the species range (Sagarin and Gaines 2002). It is possible that lynx may increase in abundance all the way to the boreal–tundra ecotone rather than showing a bell-shaped distribution. However, gathering

Fig. 3. Occupancy rates of Canada lynx (*Lynx canadensis*) per township (100 km²) in northeastern Alberta, Canada, relative to (A) NORTH using the models $\Psi(\text{NORTH}), p(\text{DSS})$ or $\Psi(\text{NORTH}), p(\text{DSS} + \text{NORTH})$; (B) HARE using the model $\Psi(\text{HARE} + \text{COYOTE} \times \text{ROADS}), p(\text{DSS} + \text{NORTH})$ with ROADS and COYOTES equal to 0; and (C) ROADS using the model $\Psi(\text{HARE} + \text{COYOTE} \times \text{ROADS}), p(\text{DSS} + \text{NORTH})$ with HARE equal to the median of 4.25 and COYOTE set at various levels.



quantitative data to test such a distribution for lynx is extremely difficult given the vast size and remote nature of much of the boreal ecosystem in which lynx are found.

The lower probability of occupancy we observed for lynx at the southern end of their range definitely suggests that habitat quality is lower here than in more northerly areas. Why areas near the edge of their southern range are less suitable does not seem to be caused by differences in food supply but interactions between lynx, roads, and coyotes. Relative to the spatial model that corrected both Ψ and p for NORTH, the inclusion of hare resulted in the greatest change in ΔAIC . This demonstrates that prey abundance is a dominant factor influencing lynx occurrence. However, the inclusion of hare did not remove the importance of NORTH as the model $\Psi(\text{HARE} + \text{NORTH}), p(\text{DSS} + \text{NORTH})$ had a better fit than $\Psi(\text{HARE}), p(\text{DSS} + \text{NORTH})$. In contrast, inclusion of the COYOTE \times ROADS term did

Fig. 4. Detection probability of Canada lynx (*Lynx canadensis*) per township (100 km²) in northeastern Alberta, Canada, relative to (A) DSS using the model $\Psi(\text{HARE} + \text{COYOTE} \times \text{ROADS}), p(\text{DSS} + \text{NORTH})$ with NORTH equal to 62 and (B) NORTH using the model $\Psi(\text{HARE} + \text{COYOTE} \times \text{ROADS}), p(\text{DSS} + \text{NORTH})$ with DSS equal to 6.

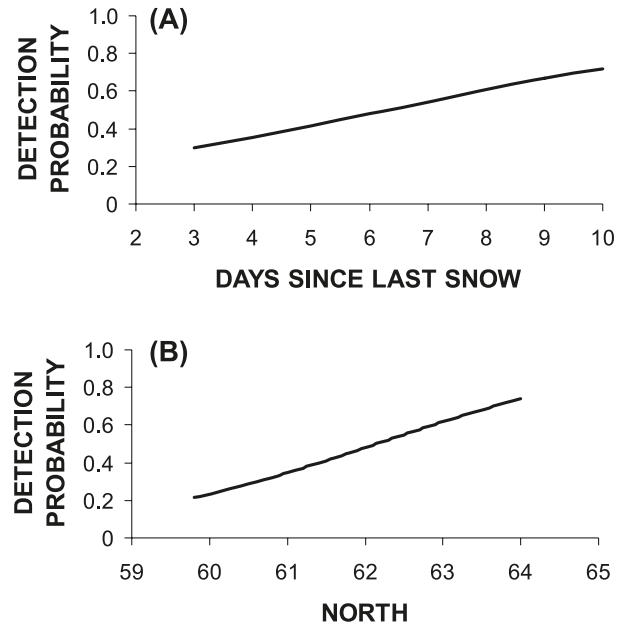


Table 2. Parameter estimates predicting Canada lynx (*Lynx canadensis*) occupancy rate and detection error based on the best fitting model containing environmental factors and best fitting spatial model.

Variable	Slope	SE
Best fitting environmental model		
$\Psi(\text{CONSTANT})$	-0.5514	0.5284
$\Psi(\text{ROADS})$	0.6611	1.2407
$\Psi(\text{COYOTE})$	0.4502	0.5000
$\Psi(\text{HARE})$	0.5090	0.1125
$\Psi(\text{COYOTE} \times \text{ROADS})$	-2.2564	0.9299
$p(\text{CONSTANT})$	-36.1961	0.2280
$p(\text{DSS})$	0.2566	0.0217
$p(\text{NORTH})$	0.5577	0.0033
Best fitting spatial model		
$\Psi(\text{CONSTANT})$	-29.7194	0.5480
$\Psi(\text{NORTH})$	0.4951	0.0088
$p(\text{CONSTANT})$	-35.7157	0.2571
$p(\text{DSS})$	0.2528	0.0220
$p(\text{NORTH})$	0.5504	0.0036

not result in as great a change in ΔAIC relative to the inclusion of HARE, but when included there was little support for including NORTH in the occupancy rate portion of the model. This suggests that the reduction in habitat quality at the edge of the lynx range is at least partially the result of human activity and the effects this has on competitive interactions with coyotes. This raises the question of whether the increase in lynx abundance farther from the range edge would exist if human activity and coyotes did not occur in our study area. Coyotes and roads both began to become common in this landscape within the last 50 years, suggest-

ing that the spatial patterns in lynx we observed may have developed quite recently.

The lack of spatial clusters for Canada lynx, as indicated by the small value of Moran's I statistic, is in distinct contrast to Iberian lynx (*Lynx pardinus* (Temminck, 1827)) in Spain, Eurasian lynx (*Lynx lynx* (L., 1758)) across their range, and Canada lynx in the conterminous United States. The restructuring of the internal structure of the Iberian lynx range has been well documented. In the last 35 years, Iberian lynx range has decreased 45% (Rodríguez and Delibes 2002). The change in range size for Iberian lynx occurred because of a contraction from the borders of the range, as well as increasing fragmentation within the range. Current patterns of Iberian lynx distribution are strongly autocorrelated as a result (Moran's $I = 0.434$ for first 10 km lag) (Rodríguez and Delibes 2002). Recovering or re-introduced populations of European lynx also are patchily distributed within their range (Schadt et al. 2002; Zimmermann et al. 2005). The absence of Canada lynx from much of the northeastern United States is believed to occur because they have been isolated from northern populations in Canada owing to land clearing along the St. Lawrence Seaway (McKelvey 2000). All areas where lynx species show strongly patchy structure share a significant level of habitat fragmentation, whereby intense human activity owing to urbanization or agriculture have isolated lynx populations into remnant "wilderness" areas (McKelvey 2000).

Lynx populations in Alberta's boreal forest do not currently suffer from isolation effects at large spatial scales, as agricultural conversion is mainly happening in the south. However, our data do suggest that lynx range may have contracted by up to 22%. Admittedly, this estimate is speculative, as we have no prior information on whether lynx used the southwest corner of our study area in previous time periods. However, the fact that the southwest corner of our study area is where lynx are absent and is the area where the highest amount of boreal forest has been converted to agriculture suggests that the size of the lynx's range in Alberta has contracted in response to human pressure, perhaps in concert with coyote invasion.

Recent changes in the distribution of many species have been attributed to climate change (Hampe and Petit 2005). Without a time series of lynx abundance to correlate with climatic variables, we cannot evaluate whether climate change per se could have created "new spatial patterns" for lynx. We suggest climate change is a less likely explanation for the spatial patterns of lynx that we observed than differences in food abundance, competition with coyotes, or human-caused mortality for two reasons. There has been an increase in winter (October–March) temperatures and decrease in snow depth between 1970 and 2000 in our study area. If the spatial patterns of lynx were created by a change in climate, then the rate of climate change should have been greater at southern weather stations. However, temperature and snow trends over time have been consistent from south to north with no interaction between time and latitude (H. Dalerum, unpublished data). Second, the kill rate of hares by lynx is highest when the snow depth is low and the snow is hard (Stenseth et al. 2004). Snow hardness is influenced by the frequency of warm and cold spells, with warm spells presumably becoming more common with

increases in winter temperatures over time. The southern portion of our study area is warmer overall, which means that hard crusty snow conditions should be more common in the south. Such conditions should benefit lynx through increased prey capture. If all of these assumptions were true, then the pattern of lynx should be reversed with lynx being more abundant in the south where snow, on average, might be getting harder and crustier.

Roads were not universally a negative predictor for lynx and depended on whether coyotes were using an area or not. Roads have been shown to alter the travel speed of coyotes because of snow packing, which may increase their ability to capture prey (Buskirk et al. 2000; Bunnell et al. 2006; but see Kolbe et al. 2007). This could increase the coyote's competitive effects on lynx. Unfortunately, we could not distinguish high versus low traffic volume roads or the level of snow packing that resulted, which would have provided the strongest support for this hypothesis. Coyotes have been found to be more common near roads than other carnivores, an affect often attributed to coyote's use of carrion (Thurber et al. 1992). Townships with roads but where coyotes were rare and lynx occurred may have had low traffic volume relative to sites where lynx were absent. However, whether coyotes being attracted to roads results in increased competition that forces lynx out has never been explicitly demonstrated. Coyotes may simply fill the vacant niche along roads when lynx are extirpated from areas with high road density. In such a scenario, road access may lead to increased human activity (i.e., trapping of lynx) whereby coyotes enter after lynx have already been reduced by human activity. Lynx also tend to be psychologically reluctant to cross roads with high traffic volume and may simply avoid roaded areas as a result (Apps 2000; but see Squires and Oakleaf 2005).

The higher detection rate of lynx in the northern portions of our study area suggests that "track" longevity may be an important factor influencing estimates of occupancy rate. However, track longevity may not be the only factor influencing detection rate. An alternative hypothesis that we cannot exclude is that there are more lynx per township in northern areas than in the south. Lynx are not strongly territorial and young lynx stay with their mother for extended periods of times. If more than one lynx was present in areas near our tracking triangles, we would expect that the probability of any 1 km segment having a track would also be higher for a given DSS exposure.

Whether our results support the existence of a "naturally occurring" abundant centre distribution for lynx remains unclear but is an area warranting future study. Without historical data, we cannot determine whether the patterns we observed existed prior to European settlement or whether range contraction per se has occurred. However, the transition zone between intact boreal forest and prairie has moved northward 50–100 km since European settlement and continues to do so in many areas of the boreal forest (Hobson et al. 2002). With increasing road access and industrialization of Alberta's boreal forest, more and more habitat perforations are beginning to occur in lynx range. If these human-disturbed areas continue to expand, it is possible that lynx in this region will also become patchily distributed as has happened to other felids around the world.

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