BROAD-SCALE PREDICTORS OF CANADA LYNX OCCURRENCE IN EASTERN NORTH AMERICA

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Abstract: The Canada lynx (*Lynx canadensis*) is listed as a threatened species throughout the southern extent of its geographic range in the United States. Most research on lynx has been conducted in the western United States and Canada; little is known about the ecology of lynx in eastern North America. To fill critical knowledge gaps about this species, we modeled and mapped lynx occurrence using habitat and weather data from 7 eastern states and 3 Canadian provinces. Annual snowfall, road density, bobcat (*L. rufus*) harvest, deciduous forest, and coniferous forest were compared at 1,150 lynx locations and 1,288 random locations. Nineteen a priori models were developed using the information–theoretic approach, and logistic regression models were ranked using Akaike's Information Criterion (AIC) and by our ability to correctly classify reserved data (Kappa). Annual snowfall and deciduous forest predicted lynx presence and absence for a reserved dataset ($n = 278$) with 94% accuracy. A map of the probability of lynx occurrence throughout the region revealed that 92% of the potential habitat (i.e., >50% probability of occurrence) was concentrated in a relatively contiguous complex encompassing northern Maine, New Brunswick, and the Gaspé peninsula of Quebec. Most of the remaining potential habitat (5%) was on northern Cape Breton Island in Nova Scotia. Potential habitat in New Hampshire, Vermont, and New York was small (1,252 km^2), fragmented, and isolated (>200 km) from known lynx populations. When federally listed as threatened in the contiguous United States in 2000, inadequate regulations on federal lands were cited as the primary threat to Canada lynx. However, the majority of potential lynx habitat in the eastern United States is on private lands and continuous with potential habitat in Canada. Therefore, lynx conservation in eastern North America will need to develop partnerships across national, state, and provincial boundaries as well as with private landowners.

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The Canada lynx was recently listed as threatened throughout the contiguous United States under the federal Endangered Species Act (USFWS 2000). The only known population of lynx in the eastern United States occurs in northern Maine (Litvaitis et al. 1991, Hoving et. al 2003); however, the species historically occurred throughout New England, New York, and the maritime provinces of Canada (McKelvey et al. 2000, Hoving et al. 2003). The listing cited inadequate regulations on federal lands as the single factor threatening lynx in the contiguous United States, including Maine, New Hampshire, Vermont, and New York (USFWS 2000). In Canada, the lynx is not listed federally (COSEWIC 2001), but it is listed as endangered in the provinces of New Brunswick and Nova Scotia. In a review of research needs for the conservation of lynx, Aubry et al. (2000*a*) highlighted the necessity for broad-scale studies of lynx–habitat relationships and the need for information on lynx–habitat associations in eastern North America.

Lynx likely relate to their habitat at several spatial and temporal scales. For this reason studies of habitat relationships at multiple scales are necessary. Because of their high mobility and dispersal potential, broad-scale factors could limit the distribution of lynx. The size of a home range at the southern edge of this species' distribution is approximately 100 km^2 (Aubry et al. 2000*a*). The maximum recorded dispersal of a lynx in the Northwest Territories of Canada was 930 km (Poole 1997). Further, 1 of 83 lynx released in the Adirondacks of New York in the early 1990s was subsequently shot in Plaster Rock, New Brunswick, which represents a straight-line movement of 780 km. Other lynx marked and released in New York were later recovered in Ontario, New Jersey, and Pennsylvania (Kent Gustafson, New Hampshire Fish and Game Department, personal communication).

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When studying population level responses to habitat conditions, the spatial scale of the study should coincide with the scale of the regional population (Goodwin and Fahrig 1998) and the temporal scale of at least 1 generation time (McArdle et al. 1990). Our study evaluated broad-scale habitat relation of lynx across a 512,000 km^2 region of eastern North America. Because recent analyses suggested that lynx populations in this region might be cyclic (McKelvey et al. 2000), a time period covering 1 full cycle (>10 years) was considered to be more important than 1 generation time.

Knowledge of lynx habitat is needed to evaluate limiting factors influencing future management and recovery efforts. A finer-scale study (Hoving et al. 2004) evaluated second-order habitat selection (Johnson 1980) of lynx in Maine, USA; lynx were more likely to occur in landscapes with much regenerating forest and relatively little partial harvest or mature forest. First-order habitat selection studies (Johnson 1980) evaluate the coarser-grained choices of animals at broader scales and may include variables such as climate, snowfall, and vegetation patterns across larger landscapes. Several environmental and habitat factors have been proposed to affect Canada lynx at the broad-scale, including snowfall (Ruggiero et al. 2000), roads (Aubry et al. 2000*b*) , competition with bobcats and other carnivores (Buskirk et al. 2000), and forest overstory characteristics (Aubrey 2000*b*, Buskirk et al. 2000). However, the existence and strength of relationships between these factors and patterns of lynx occurrence have not been quantified.

Snowfall has been hypothesized to be a habitat feature influencing the broad-scale distribution of several forest carnivores including martens (*Martes americana*), fishers (*M. pennanti*; Krohn et al. 1995, Krohn et al. 1997), and some species of weasels (*Mustela* spp.; Simms 1979). Patterns of regional snowfall may also affect the distribution of Canada lynx and bobcats (Parker et al. 1983; Hoving 2001) because of the morphological adaptations of lynx and their primary prey to deep snow (Murray and Boutin 1991, Krohn et al. 2004). On a geographic scale, bobcat and lynx are largely allopatric, and at least 2 historic instances of lynx populations declining as bobcat populations increased have been reported (Maine, Hoving et al. 2003; Nova Scotia, Parker et al. 1983). Because snowfall is only 1 of many possible explanations for spatial allopatry between lynx and bobcats, bobcat harvest density as an index to bobcat density was also considered as a habitat feature influencing lynx occurrence in a given landscape.

Road mortality appears to have been an important factor in the failure of an attempted reintroduction of Canada lynx to the Adirondack Mountains of New York (Brocke et al. 1991). A radiotelemetry study of lynx in the southern Rocky Mountains of Canada suggested that lynx avoided crossing or including divided highways within their home range (Apps 2000). Road density has been used to predict patterns of occupancy for wolves (*Canis lupus*; Mladenoff et al. 1995, Harrison and Chapin 1998, Mladenoff and Sickley 1998) and grizzly bears (*Ursus arctos*; Mace et al. 1999), and was, therefore, evaluated as a habitat feature that might influence patterns of occupancy by lynx.

Canada lynx have often been described as a boreal forest species (McCord and Cardoza 1982, Quinn and Parker 1987, Aubry et al. 2000*b*), and thus lynx would presumably be more likely to be found in landscapes with a high conifer component and rarely in landscapes dominated by deciduous forest. Forest composition also influences prey populations (Obbard 1987, Hodges 2000). Thus we evaluated whether forest overstory type was a significant predictor of the probability of habitat occupancy by lynx.

Spatial models using Geographic Information Systems (GIS) have been successfully used to quantify habitat relationships of other wide-ranging carnivores such as wolves (Mladdenoff et al. 1995, Corsi et al. 1999) and grizzly bears (Mace et al. 1999). Our objectives were (1) to determine which suite of habitat features were most closely associated with recent (1987–1999) patterns of spatial occupancy within the historic range of the Canada lynx (2) to develop and test a GIS-based model to map potential lynx habitat, and (3) to evaluate the consequences of the spatial arrangement of potential habitat on effective management and conservation of lynx in eastern North America.

STUDY AREA

We defined eastern North America as consisting of 3 Canadian provinces (Nova Scotia, New Brunswick, and Quebec south of the St. Lawrence Seaway) and 7 United States (Maine, Massachusetts, New Hampshire, Vermont, New York excluding Long Island, Connecticut, and Rhode Island). This 506,963 km^2 area included most of the historic range of lynx in eastern

North America (Hoving et al. 2003, McKelvey et al. 2000) and was primarily composed of a deciduous–hardwood overstory, including maple (*Acer* spp.) and beech (*Fagus* spp.) in the south, and a coniferous–softwood overstory in the north, including spruce (*Picea* spp.) and fir (*Abies* spp.). Mean annual snowfall ranged from 0.3 m to 5.9 m and increased with latitude and elevation.

METHODS

Lynx Presence and Absence

We compiled a database of spatially explicit observations of Canada lynx from state, provincial, and federal biologists for eastern North America (Fig. 1) from 1987 to 1999. In New Brunswick and Nova Scotia, locations of Canada lynx tracks, sightings, roadkills, and incidental kills were verified by biologists on maps of 1:250,000 or smaller (i.e., more detailed) scales; accuracy was <1 km^2. In Maine, observations were only used if verified by a biologist and mapped to <1 km accuracy on 1:24,000 to 1:100,000 scale-maps. In Quebec, which represented most of our positive occurrences, most observations were from legally trapped animals taken on registered traplines. Trappers were required to report locations of kills on map grids at a resolution of <1 km^2. We did not record data from other jurisdictions if not spatially explicit to <1 km^2 resolution. Based on this criterion, we did not omit observations from jurisdictions without verified lynx occurrences (i.e., Vermont, Massachusetts, Connecticut, New York); therefore, censoring of observations was unlikely to have biased our results. Because we simulated 100-km^2 landscapes around each lynx occurrence, slight inaccuracies in mapping the exact location of the center of that simulated circle would have a negligible effect on our quantification of descriptor variables.

Management status of lynx varies among states and provinces; therefore, occurrences included harvested individuals (in Quebec), road mortalities, tracks from surveys in Maine and Nova Scotia, and credible visual observations. For Canadian provinces, these data were compiled from government reports (Cumberland et al. 1998; Forbes et al., University of New Brunswick, unpublished report) or unpublished data on regular or incidental harvests archived by provincial wildlife biologists (Quebec and Nova Scotia). Records from Maine were predominantly track records from surveys conducted by the Maine Department of Inland Fisheries and Wildlife (MDIFW) and interviews with expert guides, woodsmen, and former game wardens that were conducted by the U.S. Fish and Wildlife Service. We also interviewed state biologists with management respon-

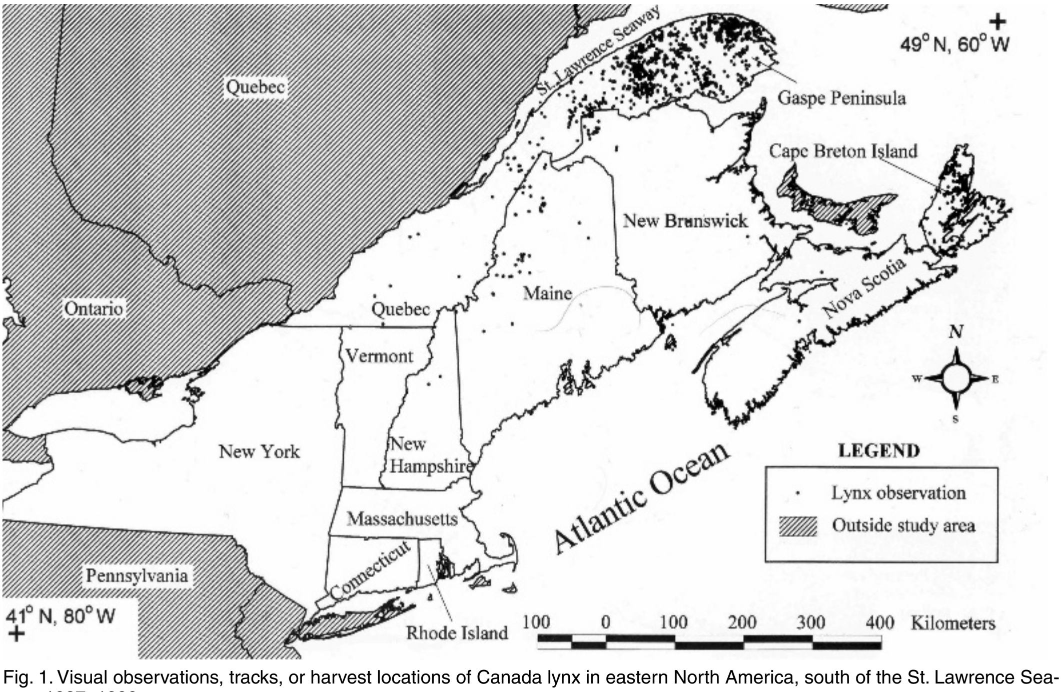

Fig. 1. Visual observations, tracks, or harvest locations of Canada lynx in eastern North America, south of the St. Lawrence Seaway, 1987–1999.

Table 1. Mean number (range) of mesocarnivores harvested per year in northeastern jurisdictions in Canada and the United States, south of Quebec, 1987–1988 to 1999–2000 (Northeast Furbearer Resources Technical Committee, unpublished data).

Province or state	Bobcat	Coyote	Fisher	Red fox
New Brunswick	180	924	379	1,400
	(40–317)	(239–1,633)	(103–824)	(522–2,434)
Nova Scotia	651	1,286	67[a]	1,138
	(311–1,103)	(1,031–1,276)	(3–215)	(627–1,741)
Maine	144	1,487	1,732	1,898
	(89–205)	(944–1,915)	(1,059–2,827)	(1,599–2,409)
Vermont	24	142	295	233
	(9–38)	(59–337)	(93–630)	(39–686)
New Hampshire	nos[b]	284	664	454
	(0–31)	(155–398)	(406–1,187)	(181–1,301)
New York	225	1,695	1,011	17,028
	(139–292)	(753–2,571)	(452–2,099)	(9,821–28,767)
Massachusetts	18	98	203	82
	(8–35)	(58–166)	(85–395)	(17–136)
Connecticut	nos[b]	102	nos[c]	83
		(54–166)		(40–236)
Rhode Island	nos[b]	generally 1–3	nos	8
		per year		(0–34)

[a] Accidental harvest occurs in addition to this recorded legal take.
[b] nos = No open season. Thirty and 31 bobcats were reported harvested in New Hampshire during open season in 1987–1988 and 1988–1989, respectively. Seasons were closed there beginning in 1989–1990, but 4–7 bobcats were reported during 1989–1990 through 1993–1994 harvest seasons for other furbearers.
[c] Some incidental take of this species is reported despite trapping closure.

sibility for lynx in New York, New Hampshire, Vermont, and Massachusetts and recorded occurrences that they considered reliable. Records of the 83 lynx that were marked and reintroduced to New York from the Yukon Territory in the early 1990s were not included in this analysis. Lynx occurrences were converted to a GIS point coverage (ARC/INFO 7.2.1, Environmental Systems Research Institute, Redlands, California, USA; use of trade names does not imply endorsement).

Our modeling effort was based on the premise that forest-dwelling mesocarnivores are harvested extensively throughout the region and that lynx, which are relatively easy to capture, would be taken and reported by fur harvesters or would be occasionally treed by hunters using hounds in pursuit of bobcats, which are frequently harvested throughout the region. In fact, bobcats are commonly harvested in 6 of the 9 jurisdictions within eastern North America, fishers are harvested extensively in 7 jurisdictions, and red fox (*Vulpes vulpes*) and coyotes (*C. latrans*) are harvested in all jurisdictions (Table 1). Our data were collected prior to special status designations for lynx at the federal or jurisdictional level in the United States or Canada, thus there was little disincentive for individuals who incidentally captured a lynx to report it to authorities. For example, incidentally captured bobcats were consistently reported in jurisdictions (e.g., Connecticut, New Hampshire) where seasons were closed (Table 1). Further, the Acadian forest, which dominates the region, is characterized by extensive forest harvesting and road densities that commonly exceed 1 km/km^2 (Harrison and Chapin 1998). Southern portions of the region have many paved roads and substantial human populations (Harrison and Chapin 1998) where lynx would likely be observed, captured incidentally, or suffer human-induced mortality if they occurred there. Although we could not ensure equal sampling effort throughout the region, we assumed that lynx would be frequently observed, captured, or killed in areas where they consistently occurred.

Habitat features within each 1-km^2 pixel associated with occurrences were compared to features within 1-km^2 pixels associated with random points that were located in areas where lynx were not verified to occur. Statistical comparisons between used and random pixels were evaluated using multiple logistic regression (Hosmer and Lemeshow 1989). Ideally, data on verified absence of lynx would have been desirable because the logistic regression model assumed that presence and absence were determined without error. Because the region was not systematically surveyed, random points were used *in lieu* of verified absences. We recognized that misclassifying random pixels as unused could increase the probability that models would be nonsignificant (i.e., elevated type II error), could decrease model fit, and could decrease our ability to correctly classify our reserved data as occurrences versus absences. Therefore, we restricted our conclusions to the variables that contributed to our best models and did not assume that variables that were not included in the best models were biologically unimportant.

We used 1,288 locations where lynx were not documented to occur as surrogates for lynx absences. Points were constrained to be >5.6 km (the diameter of a hypothetical 100 km^2 lynx home range) from each other and >16.8 km (3 times 5.6 km) from lynx occurrences to minimize potential overlap and spatial dependence. Excluding random points discarded because of spatial overlap and independence, all points within the landscape >16.8 km from lynx occurrences had an equal probability of being selected as unused. Random points were distributed on a roughly equal points/area basis throughout the portions of our study area without documented occurrences of lynx. Random points were determined using the Movement extension in ArcView 3.1 (Environmental Systems Research Institute, Redlands, California, USA).

Snowfall

We modeled and mapped mean annual snowfall (cm) for 1980–1990 based on a regression of weather station data using SYSTAT 9.0 (SPSS, Chicago, Illinois, USA) and ARC/INFO 8.0 (Hoving 2001). Weather station data were from Canadian Monthly Climate Data, purchased from Environment Canada, Atmospheric, Climate and Water Systems Branch, and Cooperative Summary of the Day, published by the National Oceanic and Atmospheric Administration, National Climatic Data Center. We determined elevation from 1:250,000 United States Geological Survey (USGS) Digital Elevation Models and 1:250,000 Natural Resources Canada Digital Elevation Data. In addition to elevation, latitude and longitude were also included in the regression model. The adjusted-r^2 of the model used to predict snowfall ($n = 590$) was 0.67 (Hoving 2001).

Road Density

We derived road densities from 1:100,000 USGS Digital Line Graphs (DLG) and 1:250,000 Geomatics Canada, National Topographic Data Base (NTDB) road layer. Because the cost of road data from Canada was calculated by km of road, areas in and immediately around Montreal were omitted from consideration as potential lynx habitat to reduce data costs.

We deleted all roads classified in the USGS DLGs as arbitrary line extensions, closure lines, processing lines, trails, limited access roads, class 5 roads (those designated for 4-wheel drive vehicles), or those that were not classified. The NTDB road data were available in 2 themes: roads and road network. Only the road network, which contains all roads passable by a 2-wheel drive vehicle, was acquired for the Canadian provinces. From these coverages, the density of roads was calculated using the ARC/INFO Grid command LINEDENSITY; this procedure calculated the number of km of road per km^2 within a 100-km^2 circle around each 1-km^2 cell.

Bobcat Density

The only data on bobcat abundance available for most of the study area was annual harvest (1993–1998) by county, township, or management unit (depending on jurisdiction). We converted data to harvest density for all 1-km^2 pixels within the relevant unit that we then averaged across the 100-km^2 area that was simulated around occurrences or random points. Bobcat data were absent for the states and provinces of Quebec, New Hampshire, Connecticut and Rhode Island where bobcats are protected from harvesting throughout the year. In Massachusetts, the trapping method (i.e., box trap only) was different from other states and provinces where foot-hold traps were permitted. Because harvests were restricted in states and provinces where bobcats are rare, bobcat density was considered to be zero for Quebec, New Hampshire, Connecticut, Rhode Island, and Massachusetts. The sensitivity of the models to these assumptions was tested by substituting bobcat harvest from adjacent regions for areas where harvest data were unavailable.

Land Use and Land Cover

We used the North America Land Cover Characteristics Data Base, a raster image of Advanced Very High Resolution Radar (AVHRR) imagery classified according to the USGS Land Use/Land Cover System (Anderson et al. 1976), obtained from the USGS Earth Resources Observation Systems. The satellite imagery was taken from April 1992 through March 1993 to classify land use and land cover worldwide. The image was converted to an ARC/INFO Grid with a cell size of 1 km^2. Two metrics were derived from the classified AVHRR imagery using the FOCALMEAN function in ARC/INFO Grid: the proportion of 1-km^2 grid cells dominated by deciduous forest and the proportion of grid cells dominated by coniferous forest within a 100-km^2 circular window.

Logistic Regression Models

The predicted snowfall (1980–1990), bobcat harvest density, road density, and the proportions of deciduous and coniferous forest within 100 km^2 were calculated for each lynx observation

Table 2. Data sources, years, and number of Canada lynx observations in the northeastern United States and eastern Canada, 1987–1999.

			Sources				
State or province	N	Years	Trapping	Tracks	Visual	Roadkill	Other
Quebec	909	1988–1999	823			8	78
Nova Scotia	167	1994–1999		45	45	~12[a]	77
Maine	50	1987–1999	2	30	8		10
New Brunswick	21	1992–1999	15	6			
New Hampshire	3	1987–1995			3		
Total[b]	1150	1987–1999	840	81	56	8	165

[a] Because locations of these roadkill were not available, they were not included as points in the analysis.
[b] Lynx reintroduced to New York, USA, from the Yukon Territory, Canada, were not included in these totals.

and random point. We could not justify the inclusion of a long list of other variables (e.g., human density or various landscape metrics) because inclusion of too many variables would likely result in spurious correlations and model over-fitting (Burnham and Anderson 2002). Other variables, such as prey density or forest stand composition, were either not available across the entire region or were inappropriate for consideration at the spatial scale of this study.

Independent (descriptor) variables were often estimated (e.g., snowfall) and were not always measured uniformly (e.g., bobcat harvest) throughout the region, which could increase uncertainty about broad-scale relationships. Although harvests occurred throughout the study, effort by hunters and trappers likely varied by place and by time. Further, systematic surveys by trained professionals occurred in northern and western Maine but not in other areas within the region. Again, we restricted our conclusions to unequivocal relationships between occurrence and descriptor variables that were statistically and biologically meaningful; we did not infer lack of statistical evidence as equating with biological unimportance.

We analyzed models (SYSTAT 9.0) using multiple logistic regression (Hosmer and Lemeshow 1989). All models were assessed for goodness-of-fit using McFadden's χ^2 (McFadden 1974). We evaluated regression models based on 2 criteria: (1) an information–theoretic approach (Anderson et al. 2000, Burnham and Anderson 2002) based on Akaike's (1973) Information Criterion (AIC) and (2) the model's success in correctly classifying 126 locations where lynx were known to be present and 152 random locations where lynx were assumed to be absent; this subset of occurrences and random locations were randomly withheld from model construction. We evaluated classification accuracy using Kappa (the proportion of specific agreement) that incorporates all of the information in the correct classification rate (CCR), false positive rate, and false negative rate (Fielding and Bell 1997). Nineteen models were developed and evaluated by analyzing combinations of variables considered likely to describe the system based on a priori scientific knowledge. The model with the greatest weight of evidence supporting it based on both criteria was subsequently used to predict and map the distribution of potentially occupied lynx habitat within eastern North America.

RESULTS

Lynx occurrences were concentrated on the Gaspé peninsula of Quebec and on Cape Breton Island, Nova Scotia. The density of locations decreased from north to south. Seventy-nine percent of all lynx occurrences ($n = 1{,}150$) were from Quebec ($n = 909$); most represented lynx that were harvested by trappers ($n = 840$, Table 2).

Habitat studies must recognize the interacting nature of multiple independent variables. We observed strong (Pearson $r > 0.50$) negative correlations between snowfall and roads and between snowfall and deciduous cover (Table 3). Areas with higher snowfall were generally associated with lower road densities and lower proportion of the landscape in deciduous forest relative to areas with lower snowfall.

The model that incorporated snowfall, deciduous forest, and conifer forest had the lowest AIC and was the best model according to the information theoretic approach. However, the simpler model containing the variables snowfall and deciduous forest had the greatest predictive power, had the third best AIC, and contained the 2 variables that were present in each of the top 6 models (ranked by AIC score). Canada lynx were positively associated with 10-year mean annual snowfall in each of the 11 models in which snowfall was included (Table 4). Lynx occurrences were negatively associated with the proportion of

Table 3. Correlation matrix among descriptor variables used to model lynx occurrences and random nonoccurrences in northeastern North America using multiple logistic regression.

Variable	Road density[a]	Snowfall[b]	Bobcat density[c]	Deciduous[d]	Conifer[e]
Road density	1.00				
Snowfall	–0.68	1.00			
Bobcat density	–0.06	–0.12	1.00		
Deciduous	0.45	–0.66	–0.09	1.00	
Conifer	–0.27	0.22	0.38	–0.42	1.00

[a] Number of km/km^2 of road passable by 2-wheel drive vehicle within a 100-km^2 circle around each 1-km^2 cell.
[b] Average snowfall predicted by logistic regression (Hoving 2001) averaged across a 100-km^2 window around each 1-km^2 cell.
[c] Average harvest density of bobcats/km^2 averaged across a 100-km^2 moving window around each 1-km^2 cell.
[d] Proportion of 1-km^2 grid cells dominated by deciduous forest within a 100-km^2 circular window around each 1-km^2 cell.
[e] Proportion of 1-km^2 grid cells dominated by coniferous forest within a 100-km^2 circular window around each 1-km^2 cell.

a 100-km^2 landscape in deciduous forest cover in each of the 9 models that included that variable. Models that included snowfall and deciduous cover had the lowest (best) ΔAIC (ΔAIC = 0–11, models 1–6 in Table 4); those models that included snowfall and lacked deciduous forest as a predictor variable had intermediate (ΔAIC = 117–119) ΔAIC (models 7–11 in Table 4), and the remaining models (12–19 in Table 4) performed poorly (ΔAIC > 725). Based on the ΔAIC rankings and Kappa, snowfall and deciduous forest had the strongest and most consistent effects.

The snowfall-deciduous forest model correctly classified 94% of 278 reserved data points (Table 5). Of the reserved points predicted to have lynx present (n = 126), 7% were absent (false positive rate); 4% of points predicted as absences (n = 152) had lynx present (false negative rate). The snowfall and deciduous forest model had a Kappa of 0.884, which denotes excellent agreement (Fielding and Bell 1997; Table 5).

The direction of the effects of conifer forest, road density, and bobcat harvest were inconsistent; these variables switched between positive and negative associations with lynx occurrences among different models. Relaxing the assumptions regarding bobcat density in areas where harvest was closed had no effect on model ranks or the predictive power of the models.

Table 4. Maximized log-likelihood [log(L)], number of estimable parameters (K), AIC, ΔAIC, Akiake weights (w_i), and McFadden's Rho^2 for logistic regression models comparing 1,150 presences and 1,288 random points in eastern North America where Canada lynx were not reported. Models were ranked by Akaike's Information Criterion (AIC).

Rank	Model	log(L)	K	AIC	ΔAIC	w_i	Rho^2
1	Deciduous (–), Snowfall (+), Conifer (–)[a]	–473.657	4	955.3	0	0.794	0.72
2	Deciduous (–), Snowfall (+), Bobcat (+), Roads (+), Conifer (–)	–473.151	6	958.3	3	0.177	0.72
3	Deciduous (–), Snowfall (+)	–478.609	3	963.2	8	0.015	0.72
4	Deciduous (–), Snowfall (+), Roads (+)	–478.410	4	964.8	10	0.005	0.72
5	Deciduous (–), Snowfall (+), Bobcat (+)	–478.534	4	965.1	10	0.005	0.72
6	Deciduous (–), Snowfall (+), Bobcat (+), Roads (+)	–478.308	5	966.6	11	0.003	0.72
7	Snowfall (+)	–534.264	2	1072.5	117	<0.001	0.69
8	Snowfall (+), Roads (–)	–533.342	3	1072.7	117	<0.001	0.69
9	Snowfall (+), Roads (–), Bobcat (+)	–532.541	4	1073.1	118	<0.001	0.69
10	Conifer (+), Snowfall (+)	–534.188	3	1074.4	119	<0.001	0.69
11	Conifer (0), Snowfall (+), Roads (–)	–533.342	4	1074.7	119	<0.001	0.69
12	Deciduous (–), Bobcat (–), Roads (–)	–836.810	4	1681.6	726	<0.001	0.53
13	Deciduous (–), Roads (–)	–954.233	3	1914.5	959	<0.001	0.46
14	Conifer (+), Bobcat (–), Roads (–)	–1039.597	4	2087.2	1132	<0.001	0.42
15	Deciduous (–)	–1084.854	2	2173.7	1218	<0.001	0.39
16	Conifer (–), Roads (–)	–1117.779	3	2241.6	1286	<0.001	0.37
17	Roads (–)	–1136.745	2	2277.5	1322	<0.001	0.36
18	Bobcat (–)	–1716.736	2	3437.5	2482	<0.001	0.04
19	Conifer (+)	–1758.687	2	3521.4	2566	<0.001	0.01

[a] Signs indicate direction of effect: (+) lynx are more likely to occur with higher values of that variable, (0) no effect, and (–) lynx are less likely to occur with higher values of that variable.

Table 5. Accuracy of logistic regression models to predict occurrences of Canada lynx in eastern North America derived from a building set of 2,160 (n = 1,024 presences, n = 1,136 absences) and a verification set of 278 (n = 126 presences, n = 152 absences). Models were ranked based on Akaike's Information Criterion (Table 4).

Rank	Model	CCR[a]	False positive	False negative	Kappa[b]
1	Deciduous (–), snowfall (+), conifer (–)[c]	0.94	0.07	0.06	0.877
2	Deciduous (–), snowfall (+), bobcat (+), roads (+), conifer (–)	0.94	0.07	0.05	0.884
3	Deciduous (–), snowfall (+)	0.94	0.07	0.04	0.884
4	Deciduous (–), snowfall (+), roads (+)	0.93	0.07	0.06	0.862
5	Deciduous (–), snowfall (+), bobcat (+)	0.94	0.07	0.06	0.870
6	Deciduous (–), snowfall (+), bobcat (+), roads (+)	0.94	0.07	0.05	0.877
7	Snowfall (+)	0.92	0.07	0.09	0.840
8	Snowfall (+), roads (–)	0.92	0.07	0.08	0.848
9	Snowfall (+), roads (–), bobcat (+)	0.92	0.08	0.07	0.848
10	Conifer (+), snowfall (+)	0.92	0.06	0.10	0.847
11	Conifer (0), snowfall (+), roads (–)	0.92	0.06	0.10	0.847
12	Deciduous (–), bobcat (–), roads (–)	0.85	0.16	0.14	0.697
13	Deciduous (–), roads (–)	0.81	0.31	0.06	0.618
14	Conifer (+), bobcat (–), roads (–)	0.76	0.36	0.10	0.527
15	Deciduous (–)	0.77	0.38	0.05	0.558
16	Conifer (–), roads (–)	0.77	0.30	0.15	0.544
17	Roads (–)	0.75	0.31	0.18	0.500
18	Bobcat (–)	0.64	0.55	0.13	0.306
19	Conifer (+)	0.51	0.25	0.77	–0.021

[a] CCR = correct classification rate, or the proportion of verification points correctly predicted from the model.
[b] A measure of classification accuracy derived from the confusion matrix per Table 2 in Fielding and Bell (1997).
[c] Signs indicate direction of effect: (+) lynx are more likely to occur with higher values of that variable, (0) no effect, and (–) lynx are less likely to occur with higher values of that variable.

Based on simplicity, consistency, low relative AIC score, and the highest Kappa, the snowfall and deciduous forest model was used to map the probability of lynx occurrence in eastern North America at a resolution of 1 km^2 (Fig. 2) according to the logistic regression formula:

$$P_{LYNX} = \frac{e^{-12.78 + 0.046X_{SNOW} + (-0.058)X_{DEC}}}{1 + e^{-12.78 + 0.046X_{SNOW} + (-0.058)X_{DEC}}}$$

where P_{LYNX} was the estimated relative probability of lynx occurrence on any 1 km^2 grid cell in eastern North America, x_{SNOW} was the mean annual snowfall at that grid cell, and x_{DEC} was the proportion of deciduous forest within 100 km^2 of that grid cell. Because we used random points to approximate absences of lynx, we categorized the absolute probabilities generated by the model into relative probability of lynx occurrence ranging from low (0.00–0.25 model probability) to high (0.75–1.00). The 2 regions with highest probabilities of occurrence by Canada lynx were (1) a 67,853-km^2 regional complex encompassing the Gaspé peninsula in Quebec, northern Maine, and northern New Brunswick; and (2) a 4,538-km^2 area on Cape Breton Island in Nova Scotia. During this study (1987–1999) there appeared to be relatively little potential habitat (generally low probability of lynx occurrence) in the Adirondack Mountains in New York (190 km^2), the Green Mountains in Vermont (11 km^2), and the White Mountains in New Hampshire (1,051 km^2). Although snowfall was relatively high in those areas, forest overstories were dominated by deciduous species.

When predictive power was considered by state and province, the models with the 2 best AIC scores had slightly better predictive power in New Brunswick but poorer predictive power in every other state and province (Table 6). The residuals of the model did not show systematic spatial patterning over the entire study area (Fig. 3). However, a few large negative residuals corresponded with potential habitat without lynx occurrences on the Northumberland plateau in north-central New Brunswick, which is a remote area with restricted human access and where little survey effort for lynx had occurred. Further, a few large positive residuals, corresponding to lynx observed in areas with low predicted probability of occupancy, occurred in southern Quebec.

DISCUSSION

The snowfall deciduous forest model had the most predictive power (Kappa = 0.884) but ranked third in AIC score. Analysis of regression residuals

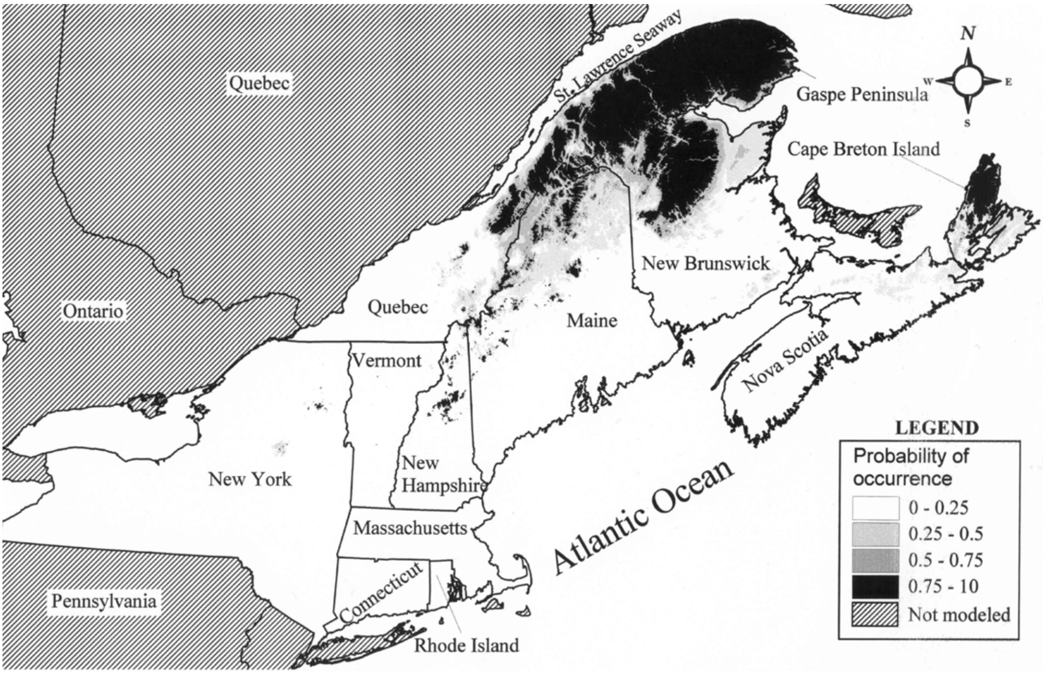

Fig. 2. Relative probability of Canada lynx occurrence based on snowfall and extent of deciduous cover throughout northeastern North America, south of the St. Lawrence Seaway, as determined from logistic regression modeling.

revealed that most false positives occurred in northern New Brunswick. Because poor model fit in 1 relatively small geographic region appeared to affect AIC rankings, we did not pursue model averaging (Anderson et al. 2000, Burnham and Anderson 2002). We caution that, although the information theoretic approach avoids many of the pitfalls of null hypothesis testing, it does not preclude the necessity of thorough interpretation.

The snowfall deciduous forest model did an excellent job (94% correct classification of reserved data) of predicting lynx occurrence throughout a large geographic region. The model overpredicted lynx occurrence in northern New Brunswick. This area had high snowfall, little deciduous forest, and was adjacent to known populations of lynx in Quebec and northern Maine but had not been searched systematically for Canada lynx (G. Forbes, University of New Brunswick, personal communication). In addition to its remoteness, much of this area had restricted

Table 6. A comparison of accuracy for 3 logistic regression models subset by states and provinces used to predict the occurrence of Canada lynx in eastern North America. Accuracy assessments were based on a building set of 2,160 (n = 1,024 presences, n = 1,136 absences) and a verification set of 278 (n = 126 presences, n = 152 absences).

Model	State or province	CCR[a]	False positive	False negative
Deciduous (–), snowfall (+), conifer (–)	Maine	0.86	0.07	0.43
	New Brunswick	0.82	0.19	0.00
	Nova Scotia	0.91	0.00	0.20
	Quebec	0.97	0.20	0.00
	Other states[b]	1.00	NA	0.00
Deciduous (–), snowfall (+), bobcat (+), roads (+), conifer (–)	Maine	0.88	0.07	0.29
	New Brunswick	0.82	0.19	0.00
	Nova Scotia	0.91	0.00	0.20
	Quebec	0.97	0.20	0.00
	Other states[b]	1.00	NA	0.00
Deciduous (–), snowfall (+)	Maine	0.89	0.07	0.29
	New Brunswick	0.79	0.23	0.00
	Nova Scotia	0.94	0.00	0.13
	Quebec	0.97	0.20	0.00
	Other states[b]	1.00	NA	0.00

[a] CCR = correct classification rate, or the proportion of verification points correctly predicted from the model.

[b] Connecticut, Massachusetts, New Hampshire, New York, Rhode Island, and Vermont had no actual or predicted locations. Thus, the false positive rate could not be calculated.

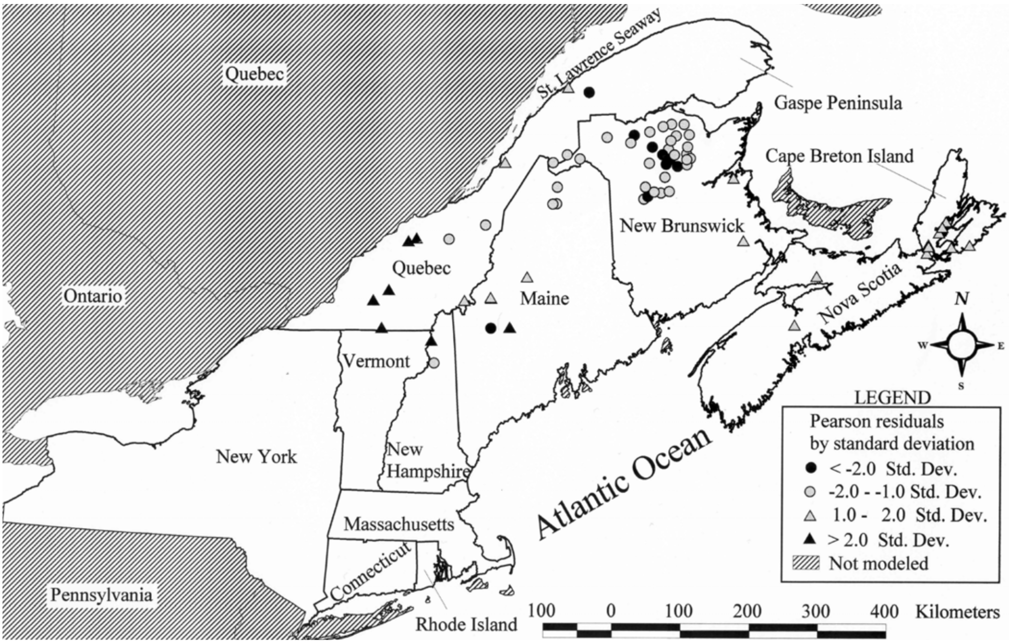

Fig. 3. Spatial distribution of Pearson residuals of the logistic regression model of mean snowfall and deciduous forest density. Triangles correspond to observations of Canada lynx in areas predicted to be poor habitat, based on probability contours, whereas circles represent a lack of observations in areas predicted to be good habitat, based on probability contours.

access and trapping, which were controlled by forest companies. Thus, we conducted a post-study interview with the Fish and Wildlife Manager for J. D. Irving, Limited, which was the predominant forest company in that region. He had observed 4 lynx during approximately 20 visitation days in a 1,730 km^2 district of northern New Brunswick during the summers of 2002 and 2003; he indicated that a single trapper typically releases 4–5 lynx annually in that area and that multiple tracks are often observed on a single day of fieldwork following fresh snowfalls (J. Gilbert, J. D. Irving, Limited, personal communication). These observations corroborate our findings and indicate that the model residuals are useful for directing additional survey efforts for lynx in our study area.

Snowfall and deciduous forest likely do not have a direct effect on lynx populations. Snowfall is probably an indirect proxy for prey densities or competition between lynx and other predators (Parker et al. 1983, Hoving 2001). Lynx have larger paws (Murray and Boutin 1991) and longer limbs relative to other predators (Krohn et al. 2004), and this likely gives lynx an advantage when pursuing prey in deep snow. The main prey of Canada lynx, the snowshoe hare (*Lepus americanus*), is also morphologically adapted to deep snow. Deciduous forest likely affects lynx via prey densities. The snowshoe hare and the lynx's secondary prey, the red squirrel (*Tamiasciurus hudsonicus*), are more likely to occur in landscapes with much (>75%) conifer or mixed forest and little deciduous forest (<25%; Hodges 2000, Obbard 1987). By using the information–theoretic approach, we can be more certain that the high predictive power of our model was not the result of spurious correlations than if we had used the traditional hypothesis testing approach (Burnham and Anderson 2002). Although the effects of snowfall and deciduous forest may be indirect, they reliably predict lynx occurrence at broad spatial scales in eastern North America.

Bobcat harvests were probably poor predictors of the potential for competition among bobcats and lynx because seasons were closed in some jurisdictions where bobcats occurred (e.g., Connecticut, New Hampshire), there were restrictions on harvest methodologies in Massachusetts, and harvest effort in the remaining jurisdictions was likely variable in time and space. Not surprisingly, bobcat harvest densities were also relatively poor predictors of lynx occurrence in this region. We recommend directed studies in the regions of overlap between bobcats and lynx (e.g., Cape Breton Island, Nova Scotia; Maine; New

Brunswick) to evaluate the spatial interactions and extent of sympatry among these felids at finer spatial scales.

Road density contributed little to our ability to discriminate between areas with and without lynx occurrences. Although lynx were absent from areas with high road densities, they were also absent from some areas with very low road densities, such as in the Adirondack Mountains region of New York, in northern New Hampshire, and in southern New Brunswick. Data on traffic volume over the entire region, if it had been available, probably would not have increased the predictive power of this variable. Traffic volume was relatively high on Cape Breton Island, but lynx occurred there. We do not mean to imply that roads do not limit lynx at other spatial scales but that density of roads passable by 2-wheel drive vehicles had a relatively small effect at the broad geographic scale of this study.

The reserved dataset included no Canada lynx presences in the United States other than Maine. The other states without lynx presences in our study area are within potential dispersal distances of lynx in the Maine-Maritime complex and within the historical geographic range of this species (McKelvey et al. 2000, Hoving et al. 2003). Furthermore, 83 lynx were reintroduced to the Adirondack region of New York, 1989–1991 (K. Gustafson, New Hampshire Fish and Game, personal communication), where this model predicted less suitable habitat area than would be needed to provide the hypothetical 100-km^2 home-range requirements for 2 lynx, assuming exclusive territories. Lack of suitable habitat at a broader scale may have contributed to the failure of that reintroduction attempt.

Snowfall was estimated from another model (Hoving 2001), and residuals of that model indicated that snow was underpredicted in a band stretching 50 km east of Lake Ontario and adjacent to the Bay of Fundy. Further, road density was used as a surrogate for estimating mortality risk, and bobcat harvests were a crude and indirect measure of potential competitive interactions. Imprecision in directly measuring independent variables warrants caution; lack of strong relationships (e.g., roads and bobcats) should not be inferred to mean that those variables are not biologically important. Despite these potential shortcomings, our models suggest that estimated snowfall and the extent of deciduous cover are reliable predictors of lynx occurrence in eastern North America and are the dominant factors influencing first-order (Johnson 1980) habitat selection at that geographic scale. These findings do not preclude the possibility that other factors (Hoving et al. 2004) may have greater influence on habitat occupancy by lynx at finer spatial scales.

MANAGEMENT IMPLICATIONS

Lynx occurrence at a broad-scale in eastern North America was highly correlated with 2 variables: average annual snowfall and the amount of deciduous forest on the landscape. Thus, lynx populations in this region are unlikely to occur in areas of low (<270 cm/year) snowfall, or in areas where the landscape is dominated by deciduous forests. Given that extant lynx populations in eastern North America occur near the southern extent of the lynx's geographic range, climate changes that alter snowfall distribution could greatly affect distribution of lynx. Further, forestry practices that shift forest composition from conifer and mixed forests to a deciduous-dominated landscape could adversely affect lynx. Areas such as the Adirondack Mountains of New York and the White Mountains of New Hampshire, which have been considered as focal areas for lynx conservation in the eastern United States, have insufficient area with sufficient snowfall and too much deciduous-dominated landscape to support viable populations of lynx.

Maintenance of lynx populations in eastern North America must include nonfederal forestlands. Almost all potential lynx habitat in the eastern United States occurs on privately owned, commercial forestlands. Further, most lynx habitat in the region straddles the United States–Canada border. Thus, successful recovery of the federally threatened lynx population in the eastern United States will require international cooperation and efforts to maintain large areas dominated by conifer and mixed forests on private lands.

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