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Canada lynx *Lynx canadensis* habitat and forest succession in northern Maine, USA

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The contiguous United States population of Canada lynx *Lynx canadensis* was listed as threatened in 2000. The long-term viability of lynx populations at the southern edge of their geographic range has been hypothesized to be dependent on old growth forests; however, lynx are a specialist predator on snowshoe hare *Lepus americanus*, a species associated with early-successional forests. To quantify the effects of succession and forest management on landscape-scale (100 km^2) patterns of habitat occupancy by lynx, we compared landscape attributes in northern Maine, USA, where lynx had been detected on snow track surveys to landscape attributes where surveys had been conducted, but lynx tracks had not been detected. Models were constructed *a priori* and compared using logistic regression and Akaike's Information Criterion (AIC), which quantitatively balances data fit and parsimony. In the models with the lowest (i.e. best) AIC, lynx were more likely to occur in landscapes with much regenerating forest, and less likely to occur in landscapes with much recent clearcut, partial harvest and forested wetland. Lynx were not associated positively or negatively with mature coniferous forest. A probabilistic map of the model indicated a patchy distribution of lynx habitat in northern Maine. According to an additional survey of the study area for lynx tracks during the winter of 2003, the model correctly classified 63.5% of the lynx occurrences and absences. Lynx were more closely associated with young forests than mature forests; however, old-growth forests were functionally absent from the landscape. Lynx habitat could be reduced in northern Maine, given recent trends in forest management practices. Harvest strategies have shifted from clearcutting to partial harvesting. If this trend continues, future landscapes will shift away from extensive regenerating forests and toward landscapes dominated by pole-sized and larger stands. Because Maine presently supports the only verified populations of this federally threatened species in the eastern United States, changes in forest management practices could affect recovery efforts throughout that region.

Key words: AIC, habitat, Lepus americanus, Lynx canadensis, Maine, model, regeneration, succession

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Around 1900, Canada lynx *Lynx canadensis* were commonly perceived to inhabit remote 'primeval' forests largely unoccupied by people (e.g. Hardy 1907, Seton 1929). This perception has changed little over the last hundred years. Popular literature (e.g. Kobalenko 1997) and a ruling by a federal judge have inferred that lynx require mature forests, and that industrial forest management degrades lynx habitat (United States Department of the Interior 1997). A scientific report recently contended that old growth forests provided temporally stable lynx habitat at the southern edge of their geographic range (Buskirk, Ruggiero, Aubry, Pearson, Squires & McKelvey 2000). Although this hypothesis might be consistent with patterns of habitat occupancy by lynx in the western United States, there is no evidence that lynx require old growth forest in the eastern United States where forests generally are younger, more mesic, diverse and structurally complex.

The Canada lynx is a specialist predator of snowshoe hare *Lepus americanus* (Saunders 1963, van Zyll de Jong 1966, Nellis, Wetmore & Keith 1972, Parker, Maxwell, Morton & Smith 1983). Although lynx will utilize alternative prey, such as red squirrels *Tamiasciurus hudsonicus* or Tetraonids (grouse), the percentage of snowshoe hare occurring in lynx scats can be as high as 97% (Parker et al. 1983), and in the core parts of their range, lynx populations cycle with a two to three year time lag behind snowshoe hare populations (Brand & Keith 1979, O'Donoghue, Boutin, Krebs, Zuleta, Murray & Hofer 1998). In the northern boreal forests of Canada and Alaska, USA, lynx are associated with habitats where hare are abundant (Parker et al. 1983, Koehler 1990, Staples 1995), although lynx seem to select slightly more open habitats than hare (O'Donoghue et al. 1998).

Snowshoe hare reach their highest densities in dense shrublands or dense immature forests (Tompkins & Woehr 1979, Pietz & Tester 1983, Orr & Dodds 1982), and select more for high understory density rather than for cover type or plant species (Litvaitis, Sherburne & Bissonette 1985, Long 1995). In Maine, USA, high densities of snowshoe hare are associated with dense regeneration that usually follows complete removal of overstory trees (i.e. clearcutting) at both the stand (Monhey 1986, Lachowski 1997, Fuller 1999) and statewide (Hoving 2001) scales. Because prey densities for lynx are highest in early successional forests, at least in the eastern United States, we predicted that lynx would be more likely to inhabit landscapes with much regenerating forest and little mature or old growth forest.

Habitat relationships can be difficult to quantify for wide-ranging animals; therefore, spatially explicit habitat models have become increasingly popular conservation tools (Turner, Arthaud, Engstrom, Hejl, Liu, Loeb & McKelvey 1995). Mladenoff, Sickley, Haight & Wydeven (1995) used locations of pack territories and unoccupied areas to build a predictive model of habitat occupancy for wolves *Canis lupus* in Wisconsin, USA, and then applied the model to predict areas in the states of Minnesota, Wisconsin and Michigan that wolves were likely to colonize as their populations expanded. They found that their model correctly predicted the locations of 18 of 23 new pack territories (Mladenoff, Sickley & Wydeven 1999). Logistic regression modeling was also used to predict grizzly bear *Ursus arctos* activity in the Swan Mountains of northwestern Montana, USA, relative to human activity, trails, and roads (Mace, Waller, Manley, Ake & Wittinger 1999). Broad-scale data have also been used to explore the habitat relationships of fisher *Martes pennanti* and interspecific relationships between fishers and marten *M. americana* in North America (Krohn, Elowe & Boone 1995, Krohn, Zielinski & Boone 1997). Further, Carroll, Zielinski & Noss (1999) used logistic regression to model and map fisher habitat in the northwestern United States.

The objective of our study was to develop and evaluate logistic regression models for Canada lynx in northern Maine, giving special attention to the effects of forest management and forest succession on the probability that lynx would occur in a landscape.

Study area

The 32,566 km^2 area considered in this study was delineated as the portion of Maine in which lynx were predicted to occur with > 10% probability based on a broad-scale model incorporating deep annual snowfall (> 268 cm) and low prevalence of deciduous forests (Hoving, Harrison, Krohn, Joseph & O'Brien in press). The state of Maine is located at the extreme northeastern corner of the United States, bordered by the Canadian provinces of Quebec and New Brunswick to the north, the state of New Hampshire to the west, and the Atlantic Ocean to the south and east. Maine is 90% forested. In the northern half of the state, large forest product companies own most of the forest lands. The forests of northern Maine are sub-boreal Acadian Forest; these forests feature high interspersion of spruce-fir and northern hardwood forests (Irland 1999). Typical species include: beech *Fagus grandifolia*, maple *Acer* spp., hemlock *Tsuga canadensis*, birch *Betula* spp., spruce *Picea* spp., and balsam fir *Abies balsamea*. The forests are mesic and have a relatively low fire frequency; most natural disturbances are small-scale wind and insect events (Lorimer 1977). Large-scale insect defoliation of mature spruce and fir caused by spruce budworm *Choristoneura fumiferana* and industrial forest harvesting are the large-scale disturbance regimes in this region (Hardy, Mainville & Schmitt 1985, Irland 1988). Nearly all of northern Maine has been harvested in the past 150 years, and old growth forests are essentially absent from the landscape (Critical Areas Program 1980). Northern Maine is also the only locality in the eastern United States with a verified population of the federally threatened Canada lynx (United States Fish and Wildlife Service 2000).

Material and methods

In December 1994, the Maine Department of Inland Fisheries and Wildlife (MDIFW) initiated an annual track survey in northern Maine to detect the presence of wolves or lynx. Private contractors used snowmobiles during the winter to record tracks of lynx, bobcats *L. rufus*, and the relative density of snowshoe hare along transect segments during 1994-1999. Each transect was divided into segments that were approximately 1 km in length, although there was some variation introduced by inconsistent snowmobile odometers. The locations of transects were recorded on copies of a DeLorme atlas (Anon. 1993) at a scale of 1:125,000.

Survey routes and the presence or absence of the aforementioned mammal tracks were digitized into Arc-Info (ESRI, Redlands, California, USA; use of trade names does not imply endorsement). United States Geological Survey (USGS) Digital Line Graphs (DLG) of roads, trails and water bodies were used as background coverages (i.e. digital maps) when digitizing transects. A coverage of township lines at the 1:250,000 scale, available from the Maine Office of Geographic Information Systems (GIS), was also used as a background coverage. Each transect was divided into segments to match the data sheets and maps.

Lynx are highly mobile and have large home ranges, which average about 100 km^2 in the southern boreal forest (Aubry, Koehler & Squires 2000). Therefore, lynx tracks occurring on adjacent segments might have resulted from double sampling of an individual lynx. However, tracks separated by > 5.6 km (the radius of a hypothetical, circular 100 km^2 home range) were unlikely to represent the same individual. Because lynx exhibit intrasexual territoriality, individual lynx on average will be 5.6 km apart. Some lynx could have been included in the model twice (Type I error). However, using a track separation of > 5.6 km would have increased the risk of not including individual lynx (Type II error). Thus, the 5.6 km separation seemed to best balance issues of pseudoreplication and loss of power, especially given the rarity of the species in this landscape. A subset of transect segments was selected at random to test the spatial distribution of the sampled lynx tracks. These random segments were also separated by at least 5.6 km.

The proportions of each vegetation type within 5.6 km of each selected segment with lynx presence or absence were calculated from the Maine Vegetation and Land Cover map (Hepinstall, Sader, Krohn, Boone & Bartlett 1999). The map was based on a classification of 1991 and 1993 Thematic Mapper (TM) satellite imagery, which was ground-truthed using low-altitude aerial videography, to represent 1993 conditions and was resolute to a 30 m^2 grid. This map was generalized to 90 m^2 cell size using RESAMPLE in ARC-INFO Grid because of limits on computer processing time, and to match the approximate resolution of field mapping of lynx occurrences.

We developed logistic regression models for the Canada lynx in northern Maine based on presence or absence in the snow track surveys. We evaluated nine *a priori* models that included variables deemed important to lynx or snowshoe hare based on a literature review, rather than using a statistical model to define the relationships. Statistical null hypothesis testing is prevalent in ecological literature, but may be uninformative in some modeling situations, especially when selecting descriptor variables for models (Anderson, Burnham & Thompson 2000). Testing a logistic regression model for lynx against a null model would not result in much new biological insight. The research question was not whether the variables had an effect significantly greater than zero (null hypothesis testing), but rather, which combination of variables best approximated the real biological system (model ranking). The information-theoretic approach is an alternative to model selection via null hypothesis testing (Burnham & Anderson 1998, Anderson et al. 2000). In the information-theoretic approach, models are constructed using different combinations of variables (i.e. different models) that are considered likely to describe the system based on *a priori* scientific knowledge. This approach avoids the inclusion of variables that have little or no justification in the model but might give spurious correlations to the pattern of interest.

The Maine Vegetation and Land Cover map delineated 37 vegetation types (Hepinstall et al. 1999). Based on a review of literature, a relatively small subset of types was considered likely to describe lynx habitat: recent clearcut, late regeneration, partial harvest, mature deciduous forest, mature conifer forest and forested wetland. Late regeneration forest was generally clearcut prior to 1991, and had > 50% overhead closure at a height of 1 m. Recent clearcut areas were generally harvested between 1991 and 1993 and contained little vegetation biomass in the overstory or understory. Partial harvest corresponded to a variety of silvicultural practices including improvement thinning, shelterwood and selection harvest. Deciduous species contributed to > 75% of the dominant cover in the mature deciduous forest type, and conifer species contributed to > 75% of the dominant cover in the mature conifer forest type.

The vegetation types were not developed from maps of known stand histories, but were based on reflectance patterns as captured in TM satellite data. Thus, the harvest classes did not represent stands of known age. The differences between early and late regeneration, for example, were structural and represented differences in biomass and reflectance patterns. The harvest classes were tested and corresponded to interpreted aerial videography (see Hepinstall et al. 1999 for details on accuracy), but the exact age and specific method of harvest were unavailable. Wetlands were incorporated into the Maine Vegetation and Land Cover map directly from the United States Fish and Wildlife Service, National Wetlands Inventory (Hepinstall et al. 1999). For this analysis, four forested wetland categories (deciduous forested, coniferous forested, deciduous scrub-shrub and coniferous scrub-shrub) were combined into one forested wetland vegetation type. Mean snowfall on each transect segment was also calculated (Hoving 2001).

Of the above variables, nine combinations were considered to have the greatest potential to be biologically meaningful (see Table 1). One model incorporated variables that predicted snowshoe hare abundance (Hoving 2001): late regeneration, partial harvest, forested wetlands, clearcut and mature deciduous forest. A model similar to a Canada lynx model developed and tested at a coarser and broader spatial scale (Hoving et al. in press) was also considered: mature deciduous forest and mean annual snowfall. A global model that included all variables (late regeneration, partial harvest, forested wetlands, clearcut, mature deciduous forest, mature conifer forest and snowfall) was also considered. A series of progressively simpler models were also considered by removing progressively less important variables based on the literature.

We built nine logistic regression models using the track transect data (Hosmer & Lemeshow 1989, Agresti 1996). Models were ranked according to their second order Akaike's Information Criterion (AIC_c) and ΔAIC_c (Burnham & Anderson 1998). The AIC_c is an AIC corrected for small sample size, and the ΔAIC_c is the difference between each model and the model with the lowest AIC_c: $\Delta AIC_{ci} = AIC_{ci}$ - minimum AIC_c. McFadden's ρ^2 (McFadden 1974), Hosmer Lemeshow P (Hosmer & Lemeshow 1989), sensitivity and specificity were calculated using SYSTAT 9.0 (SPSS, Chicago, Illinois, USA). The model with the lowest (i.e. best) mean ΔAIC_c was used to predict habitat at a 90 m^2 resolution for northern Maine.

To evaluate the predictive capabilities of the model, track locations from a snow track survey conducted in 2003 were compared to the predicted probabilities of occurrence on the landscape. Surveys were conducted from snowmobiles on snow covered roads. Locations were documented using GPS. Between mid-January and mid-March 2003, 1,713 km were surveyed in 20 townships predicted to have a high (> 0.66; N = 4), medium (0.66-0.33; N = 5), and low (< 0.33; N = 11) probability of lynx occurrence in northern Maine.

Table 1. Model performance in terms of AIC_c, ΔAIC_c, McFadden's ρ^2, Hosmer-Lemeshow P, sensitivity and specificity for nine logistic regression models of lynx presence and absence, based on transects where Canada lynx were present and absent in northwestern Maine. Vegetation types[1] were derived from the Maine Vegetation and Land Cover map (Hepinstall et al. 1999).

Model	AIC_c	ΔAIC_c	McFadden's ρ^2	Hosmer-Lemeshow P	Sensitivity	Specificity
C P L F D	73.98	0.00	0.310	0.590	0.380	0.911
C P L F	75.38	1.40	0.267	0.560	0.329	0.904
C P L F D Cn	76.20	2.22	0.311	0.622	0.381	0.911
C P L	76.73	2.75	0.228	0.421	0.309	0.901
P L F D	77.92	3.94	0.237	0.510	0.296	0.899
C P L F D Cn S	78.42	4.44	0.301	0.556	0.383	0.912
C L F	82.72	8.74	0.148	0.362	0.219	0.888
L	84.80	10.82	0.074	0.491	0.179	0.882
D S	90.87	16.89	0.034	0.428	0.146	0.878

[1] C = clear cut between 1991 and 1993, > 90% canopy removed;
P = heavy and light partial harvest, includes selection harvest, shelterwood and improvement thinning;
L = late regeneration forest harvested before 1991, sapling to poletimber with > 50% canopy closure;
F = deciduous or coniferous scrub-shrub or forested wetlands;
D = mature deciduous fores;
Cn = mature coniferous forest;
S = predicted 10-year mean annual snowfall during 1980-1990 from Hoving (2001).

Results

During 1995-1999, 2,664 segments of transect were surveyed for the presence or absence of lynx tracks. Lynx tracks were present on 66 (2.9%) segments, but using our spacing criteria, lynx were considered present on only 13 segments. Although lynx were not detected on 2,598 segments, only 108 segments were considered as absences because of our spacing criteria.

Models with $\Delta AIC_c < 2$ can be considered to give a roughly equivalent balance of data fit and parsimony (Burnham & Anderson 1998). Two models had $\Delta AIC_c < 2$, and were thus considered equivalent (Table 1). The logistic regression model with the lowest AIC_c incorporated clearcut (C), partial harvest (P), late regeneration (L), forested wetlands (F), and mature deciduous (D) forest (hereafter referred to as model CPLFD). A roughly equivalent model ($\Delta AIC_c = 1.4$) did not include mature deciduous forest (hereafter referred to as model CPLF). Model parameters, statistics and maps were similar for CPLFD and CPLF. To avoid redundancy we report only the parameters and map for model CPLFD, and note that the effect of mature deciduous forest was weak and ambiguous at this spatial scale.

The CPLFD model fit the data well (McFadden's $\rho^2 = 0.31$), and indicated that lynx were more likely to occur in 100 km^2 landscapes with much late regeneration, and relatively little recent clearcut, partial harvest, forested wetland or mature deciduous forest. Proportion of mature conifer and average snowfall in a landscape had no significant association with either lynx presence or absence at this spatial scale. The direction of effects was consistent across models (e.g. late regeneration had a positive effect in all models in which it was considered), regardless of AIC_c score. The Hosmer Lemeshow P statistic, which is the probability that the data fit a logistic curve (Hosmer & Lemeshow 1989), was moderately high (P = 0.76).

The probability of lynx occurrence (P_{lynx}) in northern Maine was mapped using the logistic regression model:

$$P_{lynx} = \frac{e^{2.33+(-64.33)x_C+(-43.01)x_P+(32.05)x_L+(-28.03)x_F+(-7.93)x_D}}{1+e^{2.33+(-64.33)x_C+(-43.01)x_P+(32.05)x_L+(-28.03)x_F+(-7.93)x_D}}$$

where x_C was the proportion of a 100 km^2 circle centered on a 90 m^2 grid cell that was clearcut between 1991 and 1993, x_P was the proportion that was partial harvest, x_L was the proportion that was late regeneration, x_F was the proportion that was forested wetland, and x_D was the proportion that was mature deciduous forest.

When the probability of occurrence was calculated for the entire study area (Fig. 1), potential lynx habitat (probability of occurrence > 50%) constituted < 5.5% of the study area. Potential habitat was distributed among several areas north and west of Moosehead Lake, one area of habitat west of Baxter State Park, and a complex in far northern Maine (see Fig. 1). Patches were separated by 25-80 km.

During the 2003 test survey, lynx tracks were present on 156 segments (9% of the 1,713 km surveyed). This represented 23 positive occurrences of lynx when randomly selected at a 5.6 km spacing. Lynx tracks were not present on 1,557 km, which represented 40 absences when randomly selected at a 5.6 km spacing. At a probability threshold of 0.5, the model correctly classified 63.5% of the selected transect segments. Sensitivity

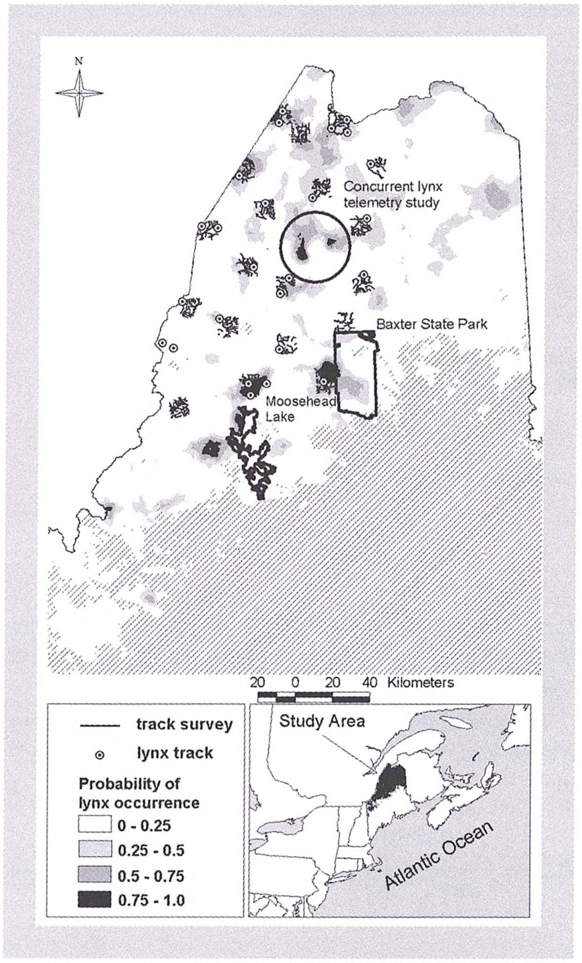

Figure 1. Probabilistic map of lynx occurrence derived from a logistic regression model of lynx presence/absence and the proportions of late regeneration, partial harvest, recent clearcuts, forested wetlands and mature deciduous forest in northern Maine, USA, during 1995-1999. Hatched areas were not included in the study area based on < 10% probability of lynx occupancy based on broader scale models developed for New England and eastern Canada (Hoving 2001). Lines and circled points represent test data from a winter survey in 2003. The circled area represents a concurrent radio telemetry study which was not surveyed in 2003, but where 30 lynx have been captured and monitored since 1999.

(the rate that presence was predicted correctly) was low (0.22), and specificity (the rate absence was predicted correctly) was high (0.88). The 0.5 threshold is not always the best cut-point; this is especially true of logistic regression models (Fielding & Bell 1997). At a probability threshold of 0.2, the correct classification rate was slightly higher (65.1%); sensitivity was moderate at 0.61, and specificity was similar at 0.68. Lynx occurrences that did occur in low probability areas tended to be adjacent to regions where lynx were predicted to occur (see Fig. 1).

Discussion

The model with the lowest AIC_c predicted an independent data set of lynx presence and absence with moderate success. The low sensitivity and bias toward lower thresholds were expected given the modeling methodology and recent changes in the lynx population in Maine. In logistic regression, probabilities tend to be biased toward the larger group (Fielding & Bell 1997). In the present case, absences far outnumbered presences due to the rarity of lynx within the study area.

The population of Canada lynx in northern Maine appears to have increased between the time that the tracks used to build the model were observed (1995-1999) and the time the test data were collected (2003). The proportion of segments with lynx tripled between the two surveys, and litter sizes during 2003 on a concurrent radio telemetry study in northern Maine were larger than any previously recorded in that state (MDIFW, unpubl. data). Because lynx are territorial, an increase in the population would likely result in some lynx using more habitats. This would be reflected in a drop in the sensitivity of the model, and a shift downward in the threshold value. Conversely, a decreasing population size likely would have resulted in a drop in specificity and an increase in the optimal threshold value. Thus, the low sensitivity of the model was consistent with an apparent increase in the lynx population on the study area during the 4-8 year interval separating the model-build and model-test data. Additionally, one of the highest probability areas (up to 94% probability of occurrence) was not surveyed during the model test year to avoid disturbing an on-going telemetry study (see Fig. 1), which may have further reduced our ability to correctly predict occupied habitat during that year. However, that 400 km^2 area was known to support resident lynx; 30 non-juvenile lynx and adult females with 39 kittens have been captured and monitored there as part of a companion radio-telemetry study (MDIFW, unpubl. data).

The recent increase in the lynx population may be related to a 10-year lynx-hare population cycle or unusually good habitat conditions for snowshoe hares in regenerating forests created by clearcutting in the 1970s and 1980s. In 2003, lynx populations in the Gaspé region of Quebec were high, which could result in increased emigration from that population into Maine. The extent of dispersal from Quebec to Maine is currently unknown. However, a thorough study of the historic record of lynx observation and harvest in Maine concluded that lynx populations fluctuate, but those snowshoe hare and lynx data were too sparse to document a regular cycle in Maine (Hoving, Joseph & Krohn 2003).

Lynx in northern Maine occurred most frequently in 100 km^2 landscapes with a disproportionately high amount of regenerating forest, predominantly even-aged forests that regenerated following clearcutting. A similar pattern has been reported for lynx on Cape Breton Island (Parker et al. 1983) and other northern boreal forests (Kesterton 1988, Staples 1995, Mowat, Poole & O'Donoghue 2000). Lynx presence was negatively associated with 100 km^2 landscapes dominated by recent clearcuts and partial harvests. Snowshoe hare showed the same positive associations with regenerating forest and negative associations with recent clearcuts and partial harvests in 0.46 km^2 landscapes (Hoving 2001), which suggests that lynx were exhibiting second order habitat selection (Johnson 1980) based primarily on abundance of principal prey.

Ecological scale can be measured in a variety of different ways (Peterson & Parker 1998), and organisms may show different habitat associations at different scales (Johnson 1980). Within a 506,963 km^2 area of eastern North America and at a 1 km^2 resolution, Canada lynx were strongly associated with areas of deep snowfall and with 100 km^2 landscapes comprised of little deciduous forest (Hoving et al. in press). However, lynx occurrences showed no significant association with snowfall and were weakly associated with deciduous forest within our 32,566 km^2 study area within eastern North America. Thus, the broad geographic distribution of lynx in eastern North America is greatly influenced by snowfall, but within areas of similarly deep snowfall, measures of forest succession become more important.

Potential habitat for lynx in northern Maine was rare, occurring on approximately 6% of the 32,566 km^2 study area. Furthermore, the patches of potential habitat were disjunct, and separated by 25-80 km. The distances between patches were considerably lower than the mean dispersal distance of 163 ± 209 km for Canada lynx in the Northwest Territories, Canada (Poole 1997). Thus, northern Maine appears to have discontinuous, rather than continuous, habitat for Canada lynx. Indeed, studies at broader spatial scales indicate that potential habitat in northern Maine was at the southern extremity of an international complex of potential habitat in eastern North America that encompasses northern Maine, Quebec and northern New Brunswick (Hoving et al. in press). Given the patchy and fragmented nature of potential habitat in northern Maine, lynx may be sensitive to changes in forest practices.

The proportion of partial harvest (which included thinning, selection cuts and shelterwood cuts) within 100 km^2 landscapes was negatively associated with both the presence of lynx and the relative abundance of snowshoe hare (Hoving 2001). At the scale of the forest stand, hares were one order of magnitude less abundant in one type of partial harvest, 3-4 years post-harvest, relative to regenerating forests (Fuller 1999). Based on our logistic regression model, the negative coefficient for partial harvest was stronger than the positive effect of late regeneration or the negative effects of forested wetland or mature deciduous forest.

Although lynx presence was positively associated with regenerating forest, it was negatively associated with recent clearcuts. Clearcutting was beneficial to lynx at a longer time scale because it produced a dense regenerating forest with abundant snowshoe hare, but clearcutting had a negative effect at shorter time scales. In Maine, lynx occurred in 100 km^2 landscapes that experienced relatively intensive (10-20% of a 100 km^2 landscape) clearcutting in the past 15-25 years, but relatively little clearcutting 0-15 years prior to our study. Extensive areas of even-aged management may mimic large-scale natural disturbances associated with lynx occurrence in boreal forest landscapes, such as fire or insect outbreaks (Poole, Wakelyn & Nicklen 1996, Paragi, Johnson & Katnik 1997).

During the 1990s there was a dramatic increase in partial harvesting, and an equally dramatic decrease in clearcutting in Maine. In 1989, clearcuts accounted for 45% of the land area harvested and partial harvests for 55% (Maine Forest Service 1995). In 1999, clearcuts accounted for only 3%, whereas partial harvests accounted for 96% of the forest area harvested in Maine (Maine Forest Service 2000). Much of the late regeneration on the landscape in the 1990s was a result of large-scale clearcutting during the 1970s and early 1980s that was associated with salvage harvesting from an epidemic of spruce budworm. Recent trends away from clearcutting in favour of partial harvest could have significant negative consequences on densities of snowshoe hare, and could affect an entire suite of carnivores that depend on hare, including the Canada lynx. Many types of forest practices are included under the term 'partial harvest', and these different forms of partial harvesting were not discernable from the Maine Vegetation and Land Cover Map. Therefore, further study is needed to better understand the effects of specific forms of partial harvesting on snowshoe hare and lynx.

In 1997 a federal judge stated that Canada lynx were threatened by "forest clearing and current timber management" (U.S. Department of the Interior 1997), and a recent review of the scientific knowledge of Canada lynx hypothesized that old growth forest may ensure more temporally stable habitat for lynx relative to earlier stages of forest succession (Buskirk et al. 2000). In the western United States, current timber management might reduce habitat suitability for lynx, depending on the structure that regeneration provides in that region. In Maine, however, different forms of timber management had different effects. Lynx were positively associated with 100 km^2 landscapes altered by clearcutting 15-25 years previously, but were less likely to use landscapes with partial harvesting or very recent clearcutting. The proportion of mature conifer forest in the landscape was not a powerful determinant of lynx occurrence, and the influence of mature deciduous forest on lynx occurrence was ambiguous. Although some forest harvest practices seem to harm lynx, some forms of harvesting that promote increased densities of snowshoe hare may be beneficial.

Canada lynx were sometimes abundant in Maine prior to the large-scale clearcutting of the late twentieth century (Hoving 2001). Though lynx occurred often in old burns (Audubon & Bachman 1852, Thoreau 1893), the pre-settlement frequency of fires appears to have been low in most of Maine (Coolidge 1963, Lorimer 1977) relative to the more conifer dominated boreal forests of Canada and Alaska. However, in extreme northwestern Maine fire frequency was notably higher (C. Cogbill, unpubl. data). Epidemic insect infestations, such as spruce budworm outbreaks, may account for periods of lynx abundance in pre-settlement forest. Spruce budworm outbreaks generally cause extensive mortality in mature balsam fir and lesser mortality in mature spruce (Blais 1985). Outbreaks in Canada appear to be cyclic with a period of 25-100 years, and occur over extensive areas (Blais 1983, Krause 1997). The most recent outbreak affected Ontario, Quebec, Maine, New Brunswick, Nova Scotia and Newfoundland (Hardy et al. 1985) in the 1970s and 1980s. Though there is some disagreement as to the proximate causes and frequency of spruce budworm outbreaks in Maine (Seymour 1992), budworm and spruce bark beetle *Dendroctonus rubipennis*, which affects mature spruce, likely caused mortality over large parts of Maine (Seymour 1992). Furthermore, snowshoe hare were more abundant in stands defoliated by the spruce budworm relative to mature forest in north-central Maine (Lachowski 1997). Thus, regeneration following periodic mortality of mature forest following insect infestations may have provided extensive areas of snowshoe hare habitat that met the landscape-scale requirements of Canada lynx in the pre-settlement forests of Maine.

Old growth forest does not currently exist as a functional component on the landscape in Maine (Critical Areas Program 1980). As such, this study can determine little about positive or negative associations of Canada lynx with old growth forest. Further, no benchmarks currently exist to evaluate the relative habitat quality of pristine versus managed forests for lynx in the eastern United States.

Trends toward partial harvesting seem to be the most immediate potential threat to the only population of lynx in the eastern United States. Partial harvests represented a large proportion of the annual area of forest logged in Maine when this study was conducted; however, partial harvests represented a small but increasing portion of the overall study area. Although our study was not designed to evaluate population level responses of lynx to partial harvesting, the negative stand-scale effects on snowshoe hares of one form of partial harvesting has been documented (Fuller 1999). Given recent trends toward partial harvest and away from forest management that creates large areas of regenerating forest, we recommend additional study of how different forms of partial harvest regenerate, and the effects through time of partial harvests on snowshoe hare and lynx.

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References

Agresti, A. 1996: An introduction to categorical data analysis. - John Wiley and Sons, New York, USA, 290 pp.

Anderson, D.R., Burnham, K.P. & Thompson, W.L. 2000: Null hypothesis testing: problems, prevalence, and an alternative. - Journal of Wildlife Management 64: 912-923.

Anonymous 1993: The Maine Atlas and Gazetteer. - DeLorme Mapping, Freeport, Maine, USA, 96 pp.

Aubry, K.B., Koehler, G.M. & Squires, J.R. 2000: Ecology of Canada lynx in southern boreal forests. - In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W. and others (Eds.); Ecology and Conservation of Lynx in the United States. University Press of Colorado, Boulder, Colorado, USA, pp. 373-396.

Audubon, J.J. & Bachman, J. 1852: Quadrupeds of North America, vol. 1. - V.G. Audubon, New York, USA, 348 pp.

Blais, J.R. 1983: Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. - Canadian Journal of Forest Resources 13: 539-547.

Blais, J.R. 1985: The ecology of the eastern spruce budworm: a review and discussion. - In: Sanders, C.J., Stark, R.W., Mullins, E.J. & Murphy, J. (Eds.); Recent advances in spruce budworm research. Proceedings of the CANUSA spruce budworm research symposium, Canadian Forest Service, Ottawa, Canada, pp. 49-59.

Brand, C.J. & Keith, L.B. 1979: Lynx demography during a snowshoe hare decline in Alberta. - Journal of Wildlife Management 43: 827-849.

Burnham, K.P. & Anderson, D.R. 1998: Model selection and inference: a practical information-theoretic approach. - Springer, New York, USA, 353 pp.

Buskirk, S.W., Ruggiero, L.F., Aubry, K.B., Pearson, D.E., Squires, J.R. & McKelvey, K.S. 2000: Comparative ecology of lynx in North America. - In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W. and others (Eds.); Ecology and Conservation of Lynx in the United States. University Press of Colorado, Boulder, Colorado, USA, pp. 397-417.

Carroll, C., Zielinski, W.J. & Noss, R.F. 1999: Using presence-absence data to build and test spatial habitat models of the fisher in the Klamath region, U.S.A. - Conservation Biology 13: 1344-1359.

Coolidge, P.T. 1963: History of the Maine Woods. - Furbush-Roberts, Bangor, Maine, USA, 805 pp.

Critical Areas Program 1980: Old growth forest inventory. - Critical Areas Program, Maine State Planning Office, Augusta, Maine, USA, 29 pp.

Fielding, A.H. & Bell, J.F. 1997: A review of methods for the assessment of prediction errors in conservation presence/absence models. - Environmental Conservation 24: 38-49.

Fuller, A.K. 1999: Influence of partial harvesting on American marten and their primary prey in northcentral Maine. - M.Sc. thesis, University of Maine, Orono, Maine, USA, 141 pp.

Hardy, M. 1907: Canada lynx and wildcat. - Forest and Stream 68: 1010-1011.

Hardy, Y., Mainville, M. & Schmitt, D.M. 1985: An Atlas of Spruce Budworm Defoliation in Eastern North America, 1938-80. - United States Department of Agriculture, Forest Service Miscellaneous Publication 1449, 52 pp.

Hepinstall, J.A., Sader, S.A., Krohn, W.B., Boone, R.B. & Bartlett, R.I. 1999: Development and testing of a vegetation and land cover map of Maine. - Maine Agriculture and Forest Experiment Station Technical Bulletin 173, University of Maine, Orono, Maine, USA, 104 pp.

Hodges, K.E. 2000: Ecology of snowshoe hares in southern boreal and montane forests. - In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W. and others (Eds.); Ecology and Conservation of Lynx in the United States. University Press of Colorado, Boulder, Colorado, USA, pp. 163-206.

Hosmer, D.W. & Lemeshow, S. 1989: Applied Logistic Regression. - John Wiley & Sons, New York, USA, 307 pp.

Hoving, C.L. 2001: Historical occurrence and habitat ecology of Canada lynx (Lynx canadensis) in eastern North America. - M.Sc. thesis, University of Maine, Orono, Maine, USA, 226 pp.

Hoving, C.L., Harrison, D.J., Krohn, W.B., Joseph, R.A. & O'Brien, M. in press: Broad-scale predictors of Canada Lynx occurrence in eastern North America. - Journal of Wildlife Management.

Hoving, C.L., Joseph, R.A. & Krohn, W.B. 2003: Recent and historical distributions of Canada lynx in Maine and the Northeast. - Northeastern Naturalist 10: 363-382.

Irland, L.C. 1988: The spruce budworm outbreak in Maine in the 1970's assessment and directions for the future. - Maine Agricultural Experiment Station, University of Maine, Orono, Maine, USA, 119 pp.

Irland, L.C. 1999: The Northeast's changing forest. - Harvard University Press, Petersham, Massachusetts, USA, 401 pp.

Johnson, D.H. 1980: The comparison and usage of availability measurements for evaluating resource preference. - Ecology 61: 65-71.

Kesterton, M.B. 1988: Lynx home range and spatial organization in relation to population density and prey abundance. - M.Sc. thesis, University of Alaska, Fairbanks, Alaska, USA, 66 pp.

Kobalenko, J. 1997: Forest cats of North America. - Firefly Books, Ontario, Canada, 128 pp.

Koehler, G.M. 1990: Population and habitat characteristics of lynx and snowshoe hares in north central Washington. - Canadian Journal of Zoology 68: 845-851.

Krause, C. 1997: The use of dendrochronological material from buildings to get information about past spruce budworm outbreaks. - Canadian Journal of Forest Resources 27: 69-75.

Krohn, W.B., Elowe, K.D. & Boone, R.B. 1995: Relations among fishers, snow, and martens: development and evaluation of two hypotheses. - The Forestry Chronicle 71: 97-105.

Krohn, W.B, Zielinski, W.J. & Boone, R.B. 1997: Relations among fishers, snow, and martens in California: results from small-scale spatial comparisons. - In: Proulx, G., Bryant, H.N. & Woodard, P.M. (Eds.); Martes: taxonomy, ecology, techniques, and management. Provincial Museum of Alberta, Edmonton, Alberta, Canada, pp. 211-232.

Lachowski, H.J. 1997: Relationships among prey abundance, habitat, and American marten in northern Maine. - M.Sc. thesis, University of Maine, Orono, Maine, USA, 73 pp.

Litvaitis, J.A., Sherburne, J.A. & Bissonette, J.A. 1985: Influence of understory characteristics on snowshoe hare habitat use and density. - Journal of Wildlife Management 49: 866-873.

Long, R.A. 1995: Annual survival and cause-specific mortality of white-tailed deer fawns, and relative abundance of snowshoe hare on Mount Desert Island, Maine. - M.Sc. thesis, University of Maine, Orono, Maine, USA, 83 pp.

Lorimer, C.G. 1977: The presettlement forest and natural disturbance cycle of northeastern Maine. - Ecology 58: 139-148.

Mace, R.D., Waller, J.S., Manley, T.L., Ake, K. & Wittinger, W.T. 1999: Landscape evaluation of grizzly bear habitat in western Montana. - Conservation Biology 13: 367-377.

Maine Forest Service 1995: 1994 Silvicultural Activity Report. - Maine Forest Service, Augusta, Maine, USA, 4 pp. Available at http://www.state.me.us/doc/mfs/pubs.htm.

Maine Forest Service 2000: 1999 Silvicultural Activity Report. - Maine Forest Service, Augusta, Maine, USA, 6 pp. Available at http://www.state.me.us/doc/mfs/pubs.htm.

McFadden, D. 1974: Analysis of qualitative choice behavior. - In: Zarembka, P. (Ed.); Frontiers in Econometrics. Academic Press, New York, USA, pp. 105-142.

Mladenoff, D.J., Sickley, T.A., Haight, R.G. & Wydeven, A.P. 1995: A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. - Conservation Biology 9: 279-294.

Mladenoff, D.J., Sickley, T.A. & Wydeven, A.P. 1999: Predicting gray wolf landscape recolonization: logistic regression models vs. new data. - Ecological Applications 9: 37-44.

Monthey, R.W. 1986: Responses of snowshoe hares, Lepus americanus, to timber harvesting in northern Maine. - Canadian Field Naturalist 100: 568-570.

Mowat, G., Poole, K.G. & O'Donoghue, M. 2000: Ecology of lynx in northern Canada and Alaska. - In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W. and others (Eds.); Ecology and Conservation of Lynx in the United States. University Press of Colorado, Boulder, Colorado, USA, pp. 265-306.

Nellis, C.H., Wetmore, S.P. & Keith, L.B. 1972: Lynx-prey interactions in central Alberta. - Journal of Wildlife Management 36: 320-329.

O'Donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L. & Hofer, E.J. 1998: Functional responses of coyotes and lynx to the snowshoe hare cycle. - Ecology 79: 1193-1208.

Orr, C.D. & Dodds, D.G. 1982: Snowshoe hare habitat preferences in Nova Scotia spruce-fir forests. - Wildlife Society Bulletin 10: 147-150.

Paragi, T.F., Johnson, W.N. & Katnik, D.D. 1997: Selection of post-fire seres by lynx and snowshoe hares in the Alaskan taiga. - Northwestern Naturalist 78: 77-86.

Parker, G.R., Maxwell, J.W., Morton, L.D. & Smith, G.E.J. 1983: The ecology of the lynx (Lynx canadensis) on Cape Breton Island. - Canadian Journal of Zoology 61: 770-786.

Peterson, D.L. & Parker, V.T. (Eds.) 1998: Ecological scale: theory and applications. - Columbia University Press, New York, USA, 615 pp.

Pietz, P.J. & Tester, J.R. 1983: Habitat selection by snowshoe hares in north central Minnesota. - Journal of Wildlife Management 47: 686-696.

Poole, K.G. 1997: Dispersal patterns of lynx in the Northwest Territories. - Journal of Wildlife Management 61: 497-505.

Poole, K.G., Wakelyn, L.A. & Nicklen, P.N. 1996: Habitat selection by lynx in the Northwest Territories. - Canadian Journal of Zoology 74: 845-850.

Saunders, J.K. 1963: Food habits of the lynx in Newfoundland. - Journal of Wildlife Management 27: 384-390.

Seton, E.T. 1929: Cats, wolves and foxes. - Lives of Game Animals, vol. 1, part 1. Doubleday, Doran and Company, New York, USA, 337 pp.

Seymour, R.S. 1992: The red spruce-balsam fir forest of Maine: evolution of silvicultural practice in response to stand development patterns and disturbances. - In: Kelty, M.J. (Ed.); The Ecology and Silviculture of Mixed-species Forests. Kluwer Academic, Netherlands, pp. 217-244.

Staples, W.R. 1995: Lynx and coyote diet and habitat relationships during a low hare population on the Kenai peninsula, Alaska. - M. Sc. thesis, University of Alaska, Fairbanks, Alaska, USA, 150 pp.

Thoreau, H.D. 1893: The Maine Woods. - Houghton Mifflin, The Riverside Press, Cambridge, Massachusetts, USA, 442 pp.

Tompkins, D.B. & Woehr, J.R. 1979: Influence of habitat on movements and densities of snowshoe hares. - Transactions of the Northeast Section of the Wildlife Society 36: 169-175.

Turner, M.G., Arthaud, G.J., Engstrom, R.T., Hejl, S.J., Liu, J., Loeb, S. & McKelvey, K.S. 1995: Usefulness of spatially explicit population models in land management. - Ecological Applications 5: 12-16.

United States Department of the Interior 1997: Endangered and threatened wildlife and plants: 12-month finding for a petition to list as endangered or threatened the contiguous United States distinct population of the Canada lynx. - Federal Register 63: 28653-28657.

United States Fish and Wildlife Service 2000: Endangered and threatened wildlife and plants; determination of threatened status for the contiguous U.S. distinct population segment of the Canada lynx and related rule; final rule. - Federal Register 65: 16052-16086.

van Zyll de Jong, C.G. 1966: Food habits of the lynx in Alberta and the Mackenzie District, N.W.T. - Canadian Field-Naturalist 80: 18-23.