HIERARCHICAL STRUCTURE OF CANADA LYNX SPACE USE AND HABITAT SELECTION IN NORTHEASTERN MINNESOTA

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DISSERTATION ABSTRACT

Limited knowledge about the ecology of the Canada lynx (*Lynx canadensis*) in the United States (U.S.), particularly its habitat requirements, resulted in the species being listed under the U.S. Endangered Species Act. I used global positioning system (GPS) collars to study the use of space and the habitat selection of 12 (6 male, 4 breeding female, and 2 non-breeding female) Canada lynx in northeastern Minnesota, U.S. Male home ranges (range = 29-522 km^2) and core areas (range = 6-190 km^2) were larger than the home ranges (range = 5-95 km^2) and core areas (range = 1-19 km^2) of females annually and during the denning season. The core areas of lynx were predicted by the 60% fixed-kernel isopleth in most seasons. Sensitivity analyses examining the effect of location frequency on home-range size suggest the smaller home-range sizes of breeding females are less sensitive to sample size than males. Some male lynx increased movements during March, the month most influenced by breeding activity. I used the core-area and home-range estimates to evaluate habitat selection with two habitat use metrics: (1) movement paths collected while following lynx trails with hand-held GPS units, and (2) locations recorded by the GPS collars worn by lynx. I modeled lynx habitat selection for both use metrics with 3 hierarchical spatial comparisons representing different intensities of use: (1) within core areas, (2) within territories, and (3) in areas adjacent to territories. Lynx consistently selected for 10-30 year-old successional forests, and sites where lynx foraged or rested were more common in these forests. Selection for successional forests was reduced within core areas because of the greater availability of successional forest in core areas. Core areas therefore appear to represent high quality habitat to lynx and represent valuable conservation tools, especially for lynx in southern populations with characteristically large territories. Although successional forest is important for lynx in Minnesota, lynx also responded to the distribution of mature forests. Lynx selected for the edges between patches of mature upland-conifer forest and successional forest. The more open understory in the mature upland-conifer portion of these edges may allow lynx to more efficiently hunt snowshoe hares (*Lepus americanus*) compared to the dense shrub and herbaceous understory occurring in the interior of successional forest patches. Most lynx consistently selected against mature lowland-conifer forests, but female lynx with 3-7 month-old kittens used these forests in proportion to their availability. These females with young kittens likely showed increased use of mature lowland-conifer forests because these forests contain protective cover for the kittens. Forest management to benefit lynx populations should consider the spatial distribution of 10-30 year old successional and mature coniferous forests to provide optimal habitat for foraging and denning. Timber-cutting patterns that mimic the large fires that controlled regeneration in boreal forests prior to human influence should benefit lynx.

DISSERTATION INTRODUCTION

Background and Motivation

The cyclic population dynamics occurring in the Canada lynx (*Lynx canadensis*) and its primary prey, the snowshoe hare (*Lepus americanus*), have interested ecologists since they were introduced to the scientific literature in the mid-20th century (Elton and Nicholson 1942). The lynx-hare system has been studied from empirical (Brand et al. 1976, Keith 1990, Krebs et al. 1995), theoretical (Akçakaya 1992, Ives and Murray 1997, King and Schaffer 2001), and statistical (Moran 1953, Bulmer 1974, Royama 1992, Ranta et al. 1997) perspectives. Despite this extensive literature, few telemetry-based field studies of lynx have been conducted in the conterminous United States (hereafter, U.S) (Mech 1980, Koehler 1990, Squires and Laurion 2000, Vashon et al. 2002), and the distribution, natural history, and status of Canada lynx populations in the U.S. remain poorly understood. Much of our current understanding of lynx ecology comes from field studies conducted in northern Canada (Nellis et al. 1972, Poole 1994, Murray et al 1995, Slough and Mowat 1996, O'Donoghue et al. 1998).

The limited knowledge of U.S. lynx populations precluded effective conservation and management planning and resulted in the listing of the Canada lynx as threatened under the U.S. Endangered Species Act (ESA) (USFWS 2000). In the final rule justifying the threatened listing, the United States Fish and Wildlife Service concluded that "the single factor threatening the contiguous U.S. distinct population segment of lynx is the lack of guidance for conservation of lynx and snowshoe hare habitat in National Forest

Land and Resource Plans and Bureau of Land Management Land Use Plans" (USFWS 2000). The habitat relationships of lynx have been studied in northern Canada (Murray et al. 1994, Poole et al. 1996, Mowat and Slough 2003), but in the U.S. the only telemetry-based study that investigated habitat was conducted in Washington (Koehler 1990, McKelvey et al. 2000a). Habitat analyses of other southern lynx populations are urgently needed to implement the conservation measures required by the ESA listing.

Minnesota is one of only 4-5 U.S. states with a consistent historical record of lynx presence (McKelvey et al. 2000b, Hoving et al. 2003). A previous telemetry study of lynx was conducted in Minnesota during the 1970s and 1980s (Mech 1980). This study was conducted during a large emigration of lynx from Canada into Minnesota (Mech 1973). Mech (1980) found the Minnesota lynx population was primarily composed of young animals with larger home ranges than lynx from northern populations. Mech (1977) also documented a distant movement of a lynx between Minnesota and Ontario. Such extensive movements are thought to be an adaptation to a fluctuating prey base and are characteristic of lynx throughout their range (Mowat et al. 2000).

Additional information about lynx in Minnesota is available from 20th century harvest records compiled by the Minnesota Department of Natural Resources (MNDNR) (Henderson 1978). These records show that > 400 lynx were regularly harvested in Minnesota during regional population peaks, but little or no harvest occurred during population lows. However, these harvest estimates should be viewed cautiously because lynx harvest was not regulated in Minnesota prior to 1975 and the pre-1975 harvest was estimated from mail surveys sent to registered trappers many years later (Henderson 1978). Nonetheless, when the estimated Minnesota harvest records are compared to those from the adjacent Canadian provinces of Ontario and Manitoba, spatial symmetry in regional population trends is apparent (Fig. 1). Peak populations in Minnesota typically lagged 1-2 years behind the provincial peaks, suggesting that the Minnesota population has been primarily composed of emigrants from Canada. The time-series of harvest records from Minnesota ended in the early-1980's after the anticipated peak failed to occur, and the lynx was reclassified as a protected species in the state. Little is known about the status of the lynx in Minnesota in recent decades, but harvests in Ontario and Manitoba have remained at reduced levels since the 1980s when compared to earlier in the 20th century (Fig. 1). Collectively, the harvest data and the telemetry study of Mech (1977, 1980) suggest that lynx occurring in Minnesota are primarily younger animals that fluctuate between relative abundance and scarcity similarly to the broader regional population in Canada.

The status of the lynx throughout the U.S. was reevaluated in association with the ESA listing in 2000. A nationwide lynx monitoring effort using a hair-snaring protocol was initiated in 1999 and included the north-central U.S. states of Michigan, Wisconsin, and Minnesota (Burdett et al. 2006). Although no lynx was detected with the hair-snare protocol, samples collected opportunistically along lynx snow trails indicated multiple lynx were present in Minnesota in the early 2000s (McKelvey et al. 2006). This finding initiated a new telemetry study in Minnesota in 2003. My dissertation represents the results of space-use and habitat analyses that were conducted during this research.

Research Objectives

My research represents one of the first uses of global positioning system (GPS) radiocollars on a medium-sized mammal. GPS telemetry systems have been previously restricted to large mammals (Moen et al. 1996, Moen et al. 1997, Merrill et al. 1998), but recent reductions in collar size and weight now allow this technology to be used on smaller mammals like the Canada lynx. All previously published lynx research has used very high frequency (VHF) radiocollars. GPS collars provide more frequent and accurate locations than VHF collars, which leads to more accurate depictions of animal movements and use of space (Arthur and Schwartz 1999, Belant and Follman 2002, Girard et al. 2002). GPS telemetry therefore allowed me to investigate patterns of space use and habitat selection in lynx at finer temporal and spatial scales than previous studies.

In chapter 1, I examine lynx movements and use of space in Minnesota. I use GPS collars to estimate home ranges over short periods that relate to the presence of snow and lynx reproductive biology. I perform a sensitivity analysis examining the effect of sample size on fixed-kernel and minimum-convex polygon estimates of lynx home ranges. I also objectively obtain estimates of lynx core areas, which I use in subsequent chapters for habitat-selection analyses. I conclude this chapter by relating my results to earlier studies and suggest causes for the differences in space use that occur between northern and southern lynx populations.

In chapter 2, I examine the hierarchical structure of fine-grained habitat selection in lynx using movement paths collected from 6 lynx wearing GPS collars. Using the results from chapter 1, I compare the forest types along actual lynx trails to random trails distributed within the core areas, home ranges, and areas immediately outside the home range. I provide a mechanistic foundation for lynx use of specific forest types by comparing behavioral sites where lynx rested and hunted, chased or killed prey to the forests preferred or avoided during movements. I also examine lynx movements relative to forest edges because of speculation that lynx preferentially move along forest edges (Mowat et al. 2000). Central to these analyses is my use of a stratified form of the logistic regression model which allowed me to use the trail as the sampling unit and model habitat selection while accounting for the paired nature of the actual and random trails in my sampling design.

In chapter 3, I also use a hierarchical sampling design to model habitat selection within lynx territories. However, chapter 3 utilizes locations obtained from GPS radiocollars. The large number of locations I obtained from my GPS collars allowed me to conduct more detailed studies of the effects of habitat on the within-territory space use of lynx. I developed models for individual lynx and also evaluated the effects of sex and season on lynx habitat selection patterns. Finally, I used these large telemetry datasets to further examine the relationship between lynx and forest edges by determining the specific types of edges preferred or avoided by lynx.

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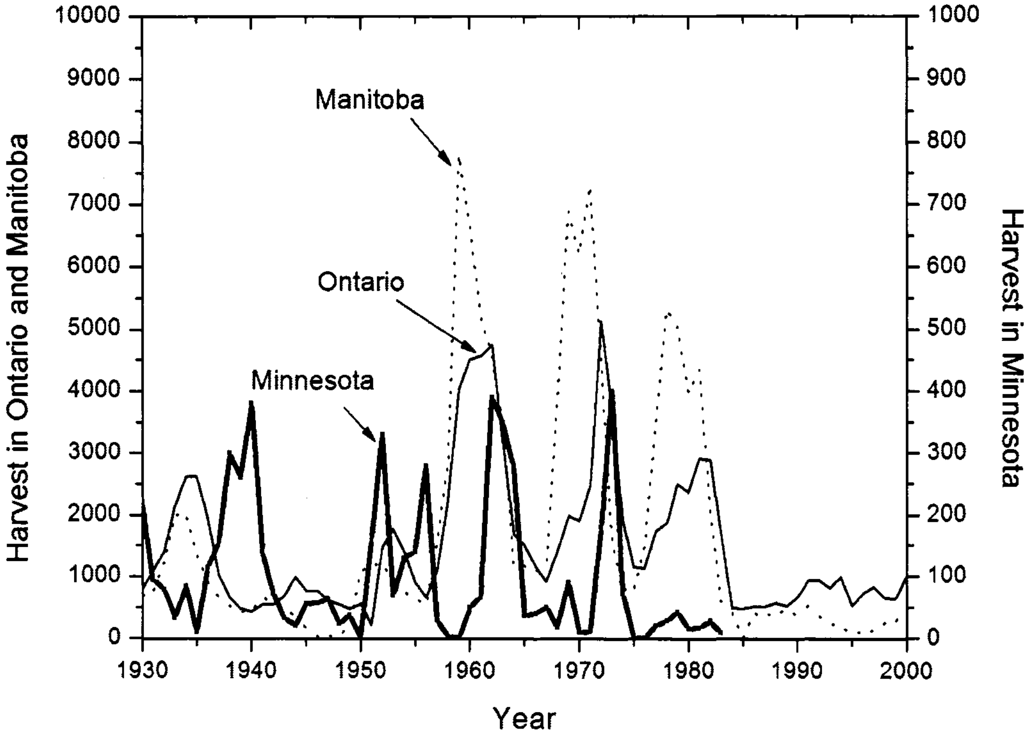

Figure 1. Twentieth-century harvest records for Canada lynx in Minnesota (bold straight line), Ontario (straight line), and Manitoba (dotted line). The size of the provincial harvests is shown on the left side of the figure and the size of the Minnesota harvest, which is an order of magnitude smaller than the provincial harvests, is shown on the right side of the figure.

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CHAPTER 1

Defining Canada lynx space use and movements with global positioning system telemetry

ABSTRACT

Space use and movements of Canada lynx (*Lynx canadensis*) are difficult to study with VHF radiocollars. I deployed global positioning system (GPS) collars on 11 lynx in Minnesota to study their seasonal space-use patterns. I estimated home ranges with minimum-convex polygon and fixed-kernel methods and estimated core areas with area/probability curves. Male fixed-kernel home ranges (range = 29-522 km^2) were significantly larger than those of females (range = 5-95 km^2) annually and during the denning season. Some male lynx increased movements during March, the month most influenced by breeding activity. Lynx core areas were predicted by the 60% fixed-kernel isopleth in most seasons. The mean core-area size of males (range = 6-190 km^2) was significantly larger than that of females (range = 1-19 km^2) annually and during denning. Most female lynx were reproductive animals with reduced movements whereas males often ranged widely between Minnesota and Ontario. Sensitivity analyses examining the effect of location frequency on home-range size suggest the home-range sizes of breeding females are less sensitive to sample size than males. Longer periods between locations decreased home-range and core-area overlap relative to the home range estimated from daily locations. GPS collars improve our understanding of lynx space use and movements by increasing the spatial extent and temporal frequency of monitoring and allowing home ranges to be estimated over short periods that are relevant to life-history characteristics.

INTRODUCTION

Canada lynx (*Lynx canadensis*) typically live in remote locations, persist at low densities, and range over large areas. These characteristics make it difficult to study lynx movements with VHF radiotransmitters. Consequently, many estimates of annual home-range size have been based on fewer than 60 locations per animal (Mech 1980, Ward and Krebs 1985, Koehler 1990, Poole 1994, Slough and Mowat 1996). GPS collars have previously been restricted to use on large mammals (e.g., Moen et al. 1996, Merrill et al. 1998, Arthur and Schwartz 1999), but are now small enough to deploy on Canada lynx. GPS collars collect locations in any weather, day or night, and over large geographic areas. The frequent locations available from GPS collars produce more accurate home-range estimates (Arthur and Schwartz 1999, Belant and Follmann 2002, Girard et al 2002). The increased sampling frequency also allows animal space-use patterns to be studied over short periods that correspond to life-history characteristics such as reproduction (Girard et al. 2002). Information on Canada lynx movements during denning or breeding is currently unavailable, despite important implications for conservation planning.

GPS collars also make it possible to use probability-based home range methods, such as the fixed-kernel estimator, which require large samples (Worton 1989, Seaman and Powell 1996, Seaman et al. 1999). Kernel estimators offer advantages over traditional home-range methods such as the minimum-convex polygon (MCP). Kernel estimators use telemetry locations to estimate the probability that an animal will be located within isopleths of varying percentages, providing information about how intensively portions of the home range are used (Powell 2000). Identifying intensively used core areas within animal home ranges has important applied uses (Seaman and Powell 1990, Bingham and Noon 1997, Seaman et al. 1999). Also, relative to the MCP method, kernel estimators are less biased by locations recorded during extraterritorial movements (Powell 2000). This is an important advantage because long-distance dispersal and extraterritorial movements are common in lynx (Mech 1977, Poole 1997, Mowat et al. 2000, Squires and Laurion 2000).

Lynx range throughout much of Canada, with southern range extensions into the U.S. Minnesota is one of only 4-5 states in the conterminous U.S with a consistent history of lynx presence (McKelvey et al. 2000, Hoving 2003). Lynx movements in Minnesota were studied decades earlier with VHF telemetry during a large emigration of lynx from Canada into the United States (Mech 1977, Mech 1980). Lynx were reported in prairie and agricultural landscapes far outside their normal range during the previous study (Mech 1973). This mid-1970s emigration is the last large regional population peak and subsequent lynx harvests from southwestern Ontario have been less than those from the mid-20th century. Similarly, snowshoe hare populations in Minnesota are believed to be smaller than those occurring after extensive timber harvest during the early-middle 20th century (Heinselman 1996). The causes for the exceedingly large mid-20th century fluctuations and recent decline in regional lynx and hare abundance have received little study and are poorly understood. Investigating current patterns of lynx space use relative to those from decades earlier may help interpret recent lynx population trends in Minnesota and southwestern Ontario.

I deployed GPS collars on Canada lynx in Minnesota. My first objective was to determine how the increased number of locations using GPS collars could improve descriptions of space use by a medium-sized carnivore such as the Canada lynx. I investigated the effect of sampling frequency on estimates of lynx home-range size by sex and season. I also compared overlap among kernel home-range isopleths estimated from different sampling intervals. My second objective was to estimate annual and seasonal home-range and core-area sizes for lynx and relate these results to previous Minnesota home-range estimates (Mech 1980). Finally, I evaluated monthly home-range sizes when lynx movements would have been strongly influenced by breeding activity.

Study Area

The study was conducted in the eastern and central sections of the Superior National Forest in St. Louis, Lake, and Cook counties in northeastern Minnesota (Fig. 1). The region consists of many lakes and little relief except for localized rocky ridges occasionally exceeding 600 m (Heinselman 1996). Regionally, forest composition is transitional between the southern boreal forests of southern Ontario and the temperate northern hardwood forests that occur farther south (Pastor and Mladenoff 1992). Currently, much of the landscape is composed of mixed forests dominated by quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) with numerous forested and non-forested wetlands of alder (*Alnus* spp.), willow (*Salix* spp.), black spruce (*Picea mariana*), and cedar (*Thuja occidentalis*). Northern hardwoods are common along ridges due to milder climate resulting from topography and proximity to Lake Superior (Flaccus and Ohmann 1964). Historically, most forest types in northeastern Minnesota experienced a 50-200 year disturbance regime with upland conifer-dominated stands typically having a shorter rotation period than upland-mixed or lowland-conifer forests (Heinselman 1996). Forest management has subsequently reduced the proportion of upland conifers (spruce and pine) in northern Minnesota forests (Frelich 2002, Wolter and White 2002). Managed stands often consist of regenerating hardwoods (primarily aspen) and red (*Pinus resinosa*) or jack pine (*P. banksiana*) plantations. Common understory vegetation includes beaked hazel (*Corylus cornuta*), mountain maple (*Acer spicatum*), fly honeysuckle (*Lonicera canadensis*), and saplings of common overstory trees including aspen, birch, balsam fir (*Abies balsamea*), and black spruce. Northern Minnesota has a continental climate with moderate precipitation, short warm summers, and long cold winters with snow cover usually present from December until April.

METHODS

Canada Lynx Capture and Data Collection

I captured lynx from February 2003 through March 2006 in custom-made cage traps (0.6 x 0.6 x 1.2 m) and anesthetized them by pole syringe with a mixture of ketamine hydrochloride (HCl) and xylazine HCl at 10.0 and 2.0 mg/kg (Kreeger et al. 2002). I monitored temperature, heart rate, and respiration rate of anesthetized animals at 10-minute intervals, sexed, weighed, and measured the animals, and fitted them with a radiocollar. I reversed the xylazine with yohimbine (0.11 mg/kg) after an injection of Dualcillin (9500 units/kg). I usually placed lynx in cages after handling and released them after recovery from anesthesia. The capture and handling protocol used in this study followed guidelines of the Animal Care and Use Committee (1998) of the American Society of Mammalogists and was approved by the Institutional Animal Care and Use Committee at the University of Minnesota (Code # 0301A39326).

Radiocollars used included VHF (Model 1960, Advanced Telemetry Systems, Isanti, MN) or 1 of 3 models of GPS collars (GPS_3300, Lotek Wireless, Inc., Newmarket, Ontario, and C200 or C300, Telemetry Solutions, Inc., Concord, CA). Lotek collars were programmed to attempt 4 to 12 locations per day. Telemetry Solutions (TS) collars were programmed to attempt 2 or 4 locations per day. Collars needed to be recovered to download data. I recaptured collared animals to recover Lotek collars, and a drop-off mechanism on TS collars was triggered by a low battery power condition. Output from all collar models included date, time, latitude, and longitude. TS collars only provide an index of location quality, while Lotek collars provided the number of satellites used for location estimates, search time, and the horizontal dilution of precision (HDOP) of each location (Moen et al. 1997). I screened my data for collars with extremely low fix rates that may indicate collar malfunction, the presence of improbable locations, and did not delete 2-D fixes to avoid potential bias and because little topographic relief occurs in my study area (D'Eon et al. 2002).

Home-Range and Core-Area Estimation

I used the Animal Movement Analyst extension (Hooge and Eichenlaub 2000) for ArcView 3.3 (ESRI, Redlands, CA) to calculate seasonal MCP and fixed-kernel home ranges. Home ranges were defined as the 95% isopleths of both estimators. For fixed-kernel home ranges, the resolution of the grid, or bandwidth, was determined with least-squares cross validation (Seaman and Powell 1996; Seaman et al. 1999). I considered 3 seasons relevant to lynx biology: winter, when snow is typically present in the study area (01 December-30 April), denning (01 May-30 June), and summer-fall (01 July-31 November), when snow is typically absent. I excluded seasonal home ranges that were > 1,600 km^2, which was approximately twice the size of the largest lynx home range described from previous studies (Bailey et al. 1986). These large home ranges that were excluded always involved lynx that made extraterritorial movements into Ontario. Lynx monitored for at least 50% of a season were included in the home-range analysis. I also calculated annual home ranges for lynx monitored at least 45% of the year following capture. All home ranges were calculated for approximately daily locations by sampling the GPS locations of individual lynx so that the mean time between locations was 24 hours. I standardized the sampling frequency to 1 location per day because this was the minimum sampling frequency common to all recovered GPS collars and also would provide accurate seasonal home-range estimates with kernel methods (Seaman et al. 1999). I summarized home-range sizes for combinations of sex and period (season or annual) and used *t*-tests on log-transformed values to detect intersexual differences in annual and seasonal home-range sizes.

I also investigated how breeding behavior affected lynx movements. I estimated fixed-kernel home ranges for March, the month with the most breeding activity in my study area, and also for January and February, other months when breeding behavior strongly influences lynx movements (Schmidt et al.1997). In contrast to the seasonal home-range analysis, I did not exclude lynx with home ranges > 1,600 km^2 in the monthly breeding-season analysis because I was specifically interested in the presence and extent of long-distance movements associated with breeding behavior. I used a two-factor analysis of variance on log-transformed home-range sizes to evaluate the effects of sex and month during January-March.

In a previous study of lynx in Minnesota (Mech 1980), locations were obtained from lynx wearing VHF collars every 9 days (*SD* = 10 days). I simulated this location frequency by randomly sampling locations from my GPS data with a mean location frequency of 9 days (*SD* = 10 days). The sample was drawn 10 times for each GPS collared animal. After censoring GPS collar locations that were beyond the search area and collar range of the previous study, I created 100% MCP home ranges for all GPS collared lynx with ≥ 18 locations, the minimum sample size used in the previous study

(Mech 1980). I tested for differences between male and female home-range sizes in these simulated home ranges with a *t*-test on log-transformed values.

I estimated the core areas of the annual and seasonal fixed-kernel home ranges with area/probability curves (Seaman and Powell 1990, Bingham and Noon 1997, Powell 2000). Area/probability curves are preferred over *ad hoc* core-area definitions because the method is objective and based on the spatial distribution of telemetry locations (Powell 2000). The null expectation of an area/probability curve is uniform use of all regions within a home range, represented as a linear relationship between the percentage of total home-range area and the probability isopleths (i.e., $y = x$). Area/probability curves are typically concave, indicating clustered use of space (Seaman and Powell 1990; Bingham and Noon 1997). I used daily locations from individual lynx to calculate fixed-kernel home ranges with isopleths at 5% increments from 5-95%. The area of the 18 interior-kernel isopleths was divided by the area of the 95% isopleth to determine the percentage of total area represented by each interior isopleth. I created area/probability curves by plotting the percentage of the total home-range area within each isopleth as a function of the isopleths. I transformed the percent of total home-range area for each isopleth by the natural logarithm and fit an exponential regression function ($y = e^{bx}$) forced through the origin to the transformed data (Bingham and Noon 1997). Regressions were performed on area/probability curves for individual lynx by season. I used the resulting regression coefficients (b_i) to determine the point (x) where the slope of the exponential regression curve was 1 by solving $x = \frac{\ln\left(\frac{1}{b_i}\right)}{b_i}$ for each lynx (Bingham and Noon 1997).

I summarized the isopleths predicting core area and the core-area size by sex and period. I used *t*-tests on log-transformed values to test for differences in annual and seasonal core-area sizes of male and female lynx. Because the denning season was 2 months long and the other seasons were 5 months long, I also estimated core areas for 10 2-month periods during the winter and summer-fall seasons to determine if the core-area isopleth was biased by the shorter duration of the denning season. These bimonthly winter and summer-fall core areas used for bias assessment were randomly selected from all available bimonthly non-denning intervals. Five bimonthly non-denning season estimates were evaluated for each sex.

Effect of Location Interval on Home-Range Area

I calculated seasonal MCP and fixed-kernel home ranges using locations obtained daily, on alternate days, twice weekly, weekly, bi-weekly, and monthly to determine how location frequency affected home-range size. These intervals represent common sampling frequencies in GPS or VHF telemetry studies. All sampling-frequency datasets were created by sampling the GPS locations of individual lynx so that the mean time between locations coincided with each of the 6 sampling intervals of interest.

Spatial Analyses of Home Range Overlap

I examined the extent of overlap among fixed-kernel home-range isopleths estimated from my simulated sampling frequencies to determine how the kernel estimate of internal home-range structure would change with less-intensive sampling. I estimated lynx home ranges with 5% isopleth increments using the daily, alternate day, twice weekly, and weekly locations. I restricted the overlap analysis to the 10-month winter and summer-fall seasons and excluded the bi-weekly and monthly home ranges to maintain sufficient sample sizes for kernel-based home-range estimation (Seaman et al. 1999). I used ArcGIS 9.1 (ESRI, Redlands, CA) to intersect the fixed-kernel home range estimated with daily locations (i.e., "maximum estimate") with home ranges estimated from alternate day, twice weekly and weekly locations. The degree of overlap among kernel isopleths was determined with a coincidence index (Cole 1949) adjusted to calculate area estimates of home range overlap (Ferreras et al. 1997):

$$C\% = \frac{2A \cap B}{A + B} \times 100$$

where A and B were home-range areas determined by sampling intervals and $A \cap B$ was the area of home-range overlap for a given kernel isopleth determined by intersecting the home ranges in ArcGIS. Coincidence indices were calculated for all kernel isopleths from 5-95% in 5% increments and results compared between sexes. Unless otherwise noted, all mean values are presented as mean ± *SE*.

RESULTS

Global Positioning System Collar Diagnostics

GPS collars were deployed on 11 different lynx. No lynx wore an active GPS collar throughout the entire study because of battery power limitations. Two males and 1 female were monitored during parts of 2004-2006. The GPS_3300 model was worn by 7 different lynx, the C200 model was worn by 1 lynx, and the C300 model was worn by 5 different lynx. Two lynx wore both Lotek and C300 collars. Of the 14 deployment periods with Lotek collars, I have yet to recover the last 3 Lotek collars. The drop-off mechanism on 1 TS collar was successful and I recaptured 3 lynx wearing TS collars for collar replacement before drop-off occurred. The drop-off mechanism failed in one TS collar and I only recovered the collar because the carcass was found in the spring (cause of death was incidental catch by a fur trapper). The other C200 collar was not recovered due to either transmitter failure or the collar being out of range.

Overall, 82% of 10,317 location attempts by the Lotek collar were successful, with 58% 3-D locations, 24% 2-D locations, and 18% failed attempts. The HDOP (± *SD*) from the Lotek collars was 5.0 ± 4.0 for 2-D fixes and 5.7 ± 4.1 for 3-D fixes. Of the 1,995 location attempts by the C200 and C300 collars, 69% were successful, with 52% 3-D locations, 16% 2-D locations, and 32% failed attempts. None of the collars had fix rates < 20% indicative of collar malfunction and < 0.1% of my locations were excluded as improbable.

Home-Range and Core-Area Estimation

I used data from every GPS collar that I recovered although some lynx could not be included in an analysis due to limited monitoring time within a season or because the lynx made long-distance movements. Ten (6 male, 4 female) of the 11 lynx that wore GPS collars were used for seasonal home-range estimates. The mean duration of the season that lynx were monitored was 79 ± 5% (range = 62–100%) for winter, 90 ± 5% (range = 58–100%) for denning, and 74 ± 11% (range = 54 – 100%) for summer-fall. I also calculated annual home ranges for 4 male and 2 female lynx monitored for 67 ±7% (range = 45-86%) of a year.

The mean log-transformed home-range size of males was larger than that of females during denning ($t = 5.48$, $d.f. = 6$, $P < 0.002$ for MCP and $t = 7.41$, $d.f. = 6$, $P < 0.001$ for fixed kernel) and annually ($t = 5.70$, $d.f. = 4$, $P < 0.005$ for MCP and $t = 4.04$, $d.f. = 4$, $P < 0.02$ for fixed kernel) but not winter ($t = 2.00$, $d.f. = 6$, $P < 0.09$ for MCP and $t = 1.65$, $d.f. = 6$, $P < 0.14$ for fixed kernel) (Table 1). I did not test for intersexual differences during summer-fall because only 2 males wore GPS collars during that season and only 1 of those 2 males consistently occupied a home range. For males, 2 of 5 winter and 3 of 5 denning season ranges included extraterritorial movements $\geq$ 30 km. Except for 1 winter home range, all females I monitored were either pregnant or raising kittens. Consequently, the female denning and summer-fall seasonal results represent the ranges of females with maternal dens or traveling with kittens $\leq$ 5 months old. The female summer-fall kernel home range was 3.4 times larger, and the female winter kernel home range was 7.0 times larger than the denning season kernel home range. Female summer-fall MCP home range was 1.5 times, and female winter MCP home range was 3.6 times larger than the denning MCP home range.

Random sampling of my GPS data with a similar location frequency as Mech (1980) created 42 (12 female, 30 male) home ranges from 8 (3 female, 5 male) individual lynx. Three lynx wearing GPS collars were not represented in my simulation results because they were monitored for insufficient time to meet my sampling criteria. Similarly, I did not create home ranges for the remaining 68 simulated location datasets because they had $\leq$ 18 locations. The 100% MCP annual home range sizes were 27-355 km^2 for males (mean = 134 ± 13) and 7-193 km^2 for females (mean = 56 ± 23). The simulated home ranges of males were larger than those of females ($t = 5.88$, *d.f.* = 40, $P < 0.001$). Previous lynx home range estimates in Minnesota were 145-243 km^2 for 4 males and 51-122 km^2 for 3 females (Mech 1980).

The seasonal core areas of the 10 lynx used for home-range estimates ranged from 1-63 km^2 (Table 2). The exponential function used for core-area estimation fit the data well with a mean R^2 of 0.95 ± 0.02 (range = 0.61–0.99) (Fig. 2). The mean seasonal core-area estimate pooled across sexes occurred at the 65 ± 2% fixed-kernel isopleth (range = 51–89%). The mean core-area isopleth increased for females during the 2-month denning period and also annually (Table 2). Excluding the denning season, the mean seasonal core-area estimate pooled across sexes was 60 ± 1% (range = 51-69%). Reducing the core-area isopleth to 60% for the 3 females monitored during the denning season did not result in the addition or deletion of any locations from the estimated core area for 2 of the 3 females. For males, removal of 1 potential outlier resulted in a mean male core-area isopleth of 60% for the other 4 males monitored during denning. The core-area isopleths of 2-month periods in the winter and summer-fall seasons did not show similar increases to those during the denning season, with mean core-area isopleths of 59 ± 1% for males (n = 5) and 60 ± 2% for females (n = 5). I therefore used the 60% isopleth for statistical tests.

Similar to home ranges, the log-transformed core-area size was larger for males than females annually ($t = 3.57$, *d.f.* = 4, $P < 0.02$) and during denning ($t = 6.98$, *d.f.* = 6, $P < 0.001$) but not during winter ($t = 1.63$, *d.f.* = 6, $P < 0.15$) (Table 2). During winter the only non-breeding female used a 19 km^2 core area, which was similar in size to most male core areas. In comparison, the mean winter core-area size for 3 breeding females was 4 ± 1 km^2 (range = 3-6). Male seasonal core areas averaged 24 ± 1% and female seasonal core areas averaged 23 ± 3% of the 95% fixed-kernel home range.

Eight individual lynx were used to evaluate the effect of sex and month for 28 monthly breeding-season home ranges. Three of the 8 lynx were monitored over multiple breeding seasons. Neither sex ($F = 1.89$, *d.f.* = 1, 24, $P < 0.18$) nor month ($F = 0.56$, *d.f.* = 2, 24, $P < 0.58$) had a significant effect on monthly home-range sizes from January-March. The monthly home-range size of adult female lynx changed little during the 3 breeding months but the home range of a sub-adult female decreased from 104 km^2 in February to 54 km^2 in March. Evidence along the snow trail of this sub-adult female indicated that she mated during late-March 2004 (C.L. Burdett, in litt.). Although the mean March home-range size for males was larger than the other breeding months, the non-significant results were due to variability in male home-range sizes during the breeding season (Fig. 3). Most of this variability resulted from long-distance movements that produced monthly home ranges of 392 km^2 and 4140 km^2 in 2 of the 5 males used in the breeding-season analysis.

Sensitivity Analysis on Location Frequency

Mean male home-range size was overestimated with the fixed kernel and underestimated with the MCP as time between locations increased (Fig. 4). Female home ranges showed little effect of sampling interval regardless of estimation method or season (Fig. 4). Both home-range estimators produced more variable estimates of home-range size with fewer locations, but the effect was largest for male fixed-kernel estimates.

Spatial Analyses of Home-Range Overlap

Coincidence among fixed-kernel isopleths decreased with decreasing location frequency (Fig. 5). My coincidence index indicated that overlap among both the fixed-kernel home range (95%) and the estimated core area (60%) declined about 10% for both sexes with each reduction in sampling frequency. Home ranges estimated from weekly locations overlapped 71 ± 3% of the maximum home-range estimate for males and 78 ± 3% for females. Core areas estimated from weekly locations overlapped 59 ± 6% of the maximum core-area estimate of males and 59 ± 2% for females. Females generally exhibited less overlap than males at all sampling frequencies, but this difference was not pronounced above the 60% core-area isopleth (Fig. 5).

DISCUSSION

Effect of Sample-Interval Size and Internal Structure of Home Range

Area/observation curve shapes varied between sexes. For males during the winter and denning seasons, the MCP home-range size increased with sample size while the kernel estimator decreased, similar to other mammals (Fritts and Mech 1981, Bekoff and Mech 1984, Arthur and Schwartz 1999, Belant and Follmann 2002, Girard et al. 2002). The large variability associated with reduced sampling frequency for male kernel home ranges likely results from the large sample requirements of kernel methods (Seaman et al. 1999). The area/observation curves of females showed far less sensitivity to location frequency. The home-range size of female lynx was affected by my use of reproductive animals. Although consistently smaller than male home ranges, female lynx reduced their movements further during the denning season, similar to other mammals with neonates (Girard et al. 2002).

The minimal effect of sampling frequency on female home-range estimates suggests that less-frequent locations are needed in areas where lynx have smaller home ranges. Lynx from northern populations often inhabit smaller home ranges during peaks of the snowshoe hare cycle (Ward and Krebs 1985; Slough and Mowat 1996). Alternate-day locations were needed to obtain MCP or fixed-kernel home-range estimates for male lynx in northeastern Minnesota within 20% of the maximum estimate based on daily locations. While female lynx also often required a similar location frequency to obtain home-range estimates within 20% of the maximum, the much smaller size of female home ranges created less extreme differences that may not be relevant for applied management. Weekly locations may be sufficient for describing the spatial extent of lynx home ranges < 30km^2.

The sampling frequencies typical of VHF studies seem more problematic when kernel methods are used to depict a home range's internal structure. Home ranges estimated with weekly locations showed less than 80% overlap with the maximum (i.e., daily) home-range estimate. Core areas using weekly locations overlapped less than 60% of the maximum core-area estimate. Weekly locations may be inadequate if core areas estimated from kernel-based estimators will be used in subsequent analyses. The large number of locations available from GPS collars should particularly help improve the accuracy of fine-grained habitat analyses based on home-range estimates (Marzluff et al. 2001).

Despite producing more accurate home-range estimates, GPS collars also provide new challenges for analyses of animal space-use and movements. For example, kernel home range estimates are strongly influenced by the technique used to define bandwidth, or level of smoothing applied during density estimation (Silverman 1986; Worton 1989; Seaman and Powell 1996; Seaman et al. 1999). Least-squares cross validation is commonly used to calculate bandwidth for fixed-kernel home ranges (Seaman and Powell 1996; Seaman et al. 1999). However, the least-squares cross-validation algorithm can fail for GPS datasets using > 3,900 locations per individual (Hemson et al. 2005). In addition, the presence of linear movements can bias kernel home ranges using least-squares cross validation (Silverman 1986, Blundell et al. 2001). I found that least-squares cross validation applied an appropriate level of smoothing to my data because most of my lynx home ranges consisted of ≤ 2 disjunct segments. I did not adjust bandwidth for two reasons. First, I did not experience failures in bandwidth calculation like Hemson et al. (2005) because I used daily locations and estimated home ranges on a seasonal basis. I did find during initial data analyses that there were several disjunct segments in kernel home ranges based on > 2,000 GPS locations, which likely underestimated home-range size. Second, I did not encounter serious problems with linear movements because I excluded wide-ranging lynx from my seasonal home-range analysis. The fixed-kernel home range of 1 male was affected by a linear movement of about 70 km. However, the movement occurred over approximately a 2 week time period and the fixed-kernel home range was still less than the 95% MCP home range. While my use of daily locations for maximum estimates minimized the potential drawbacks of least-squares cross validation in this study, I agree that bandwidth calculation methods currently available in most home-range software may be problematic for GPS datasets using multiple daily locations (Hemson et al. 2005).

Space Use of Canada Lynx in Minnesota

Core areas are valuable conservation tools because they represent the most intensively used portions of a home range (Seaman et al. 1999; Bingham and Noon 1997). Currently, much of the conterminous U.S. lynx population lives on land managed by the United States Forest Service (USFS). The USFS evaluates the effects of forest management on lynx populations with lynx analysis units (LAUs), which approximate the size of lynx home ranges (Ruediger et al. 2000). Current conservation strategies for

LAUs on USFS lands suggest that approximately 48 km^2 of quality lynx habitat should be present within an LAU (Ruediger et al. 2000). Although I did not evaluate habitat use, the core areas I defined for male and female lynx with GPS telemetry are generally within the spatial extent suggested by these LAU guidelines. Further validation of these conservation measures requires a better understanding of lynx habitat selection, factors controlling the landscape-level distribution of snowshoe hares, and spatial aspects of patch distribution within lynx home ranges.

The 60% fixed-kernel isopleth provided a reasonable generalized prediction for seasonal lynx core areas in northeastern Minnesota. The core areas of male (62.7%) and female (62.5%) Eurasian lynx in Switzerland were described by similar percentages (Breitenmoser et al. 1993). The higher core-area isopleths during the denning season had minimal effect on the specific GPS locations within the core area. However, the higher denning-season isopleths did not seem to be an artifact of the shorter sampling period. For females, the changes in core-area isopleth were likely related to the smaller denning-season home ranges and association with a den. Unlike females, the higher denning-season isopleths of males are not associated with reproductive behavior, suggesting that individual variation in the May and June movements of the males I monitored may have produced these patterns. The increased annual core-area isopleth of females may result from the greater site fidelity of females with kittens and the increased sample size of annual fixed-kernel estimates (Seaman et al. 1999). Further investigation of the area/probability technique to define core areas should address its sensitivity to the various biological and statistical factors that could affect its predictive ability.

My data support earlier descriptions of lynx having large home ranges in Minnesota (Mech 1980). However, the mean home-range sizes of the male and female lynx I studied were similar to the smallest home ranges found for both sexes 3 decades ago. This may result from the current lynx population having a different demography than the lynx studied by Mech (1980). The previous study found evidence of lactation in only 1 of 3 females, consisted mainly of younger animals, and occurred during a time when lynx and hare populations were likely larger and more widely distributed than during my study (Mech 1973, Mech 1980, Heinselman 1996). In contrast, the lynx I monitored were generally older and many adult females reproduced. The Minnesota lynx population is undoubtedly strongly influenced by periodic emigration from Canadian populations (Mech 1973, Mech 1980). However, some lynx having home ranges within Minnesota during my study also moved north into Ontario. As expected, this trend was more common among males.

The use of GPS collars improved my ability to obtain locations over a wide area, which produced seasonal-home range estimates for 2 of 5 male and 1 of 6 female lynx that were 2-10 times larger than those previously reported. Although my primary reason to exclude these animals from my home-range analysis was for consistency with other studies, these movements might not even represent actual home ranges (Burt 1943). However, movements at this scale are probably not unique to my study area, and lynx considered nomadic in earlier studies may have been moving over similar scales. Long-distance movements in adult lynx are often considered a behavioral response to low hare abundance (Ward and Krebs 1985). I found that animals making these long movements maintained a constant body mass after long movements, although I only examined them

1-5 times. The male lynx I studied were similar to most male felids that often have much larger home ranges than expected based on metabolic requirements defined by intersexual differences in body weight (Sandell 1989, Liberg et al. 2000). While I did not find weight loss among wide-ranging male lynx, these movements may still represent a behavioral response to low hare densities.

Alternatively, the large home ranges of the male lynx I studied may be a response to the distribution of resident females. Male home ranges are often larger in southern populations whereas female home ranges are relatively consistent between northern and southern populations (Table 3). When weighted by the number of animals monitored in each of these studies, the mean (±*SD*) male home-range size in northern populations ($\overline{X}$ = 74 ±78) is less than that of males in southern populations ($\overline{X}$ = 175 ± 91). Conversely, weighted mean (±*SD*) female home-range sizes are similar between northern ($\overline{X}$ = 67 ± 32) and southern ($\overline{X}$ = 74 ± 43) populations. Similar regional differences in home-range size patterns occurred in male and female American martens (*Martes americana*) (Buskirk and McDonald 1989). The density of resident females in southern lynx populations is likely less than northern populations due to the fragmented distribution of patches with sufficient prey to raise kittens (Keith et al. 1993). If male felids establish home ranges primarily on the distribution of females, their movements during the breeding season should be most representative of female distribution (Liberg et al 2000).

Male domestic cats typically increase their movements during the breeding season but this pattern has not been studied extensively in wild felids (Liberg et al. 2000). Male Eurasian lynx generally increase their movements during the breeding season (Breitenmoser et al 1993, Schmidt et al. 1997). However, Iberian lynx did not increase their home ranges in response to breeding activity, likely due to the lack of a well-defined breeding season for Iberian lynx (Ferreras et al. 1997). While 5 of my 7 comparisons showed larger March home-range sizes than other breeding months, these results were not significantly different because of limited sample size and the long-distance movements of two male lynx. One male made a > 70 km movement from Minnesota to Ontario, resulting in a March fixed-kernel home range of 4,140 km^2. While I can not be certain this male bred with females in both Minnesota and Ontario, a male lynx with a home range > 700 km^2 presumably mated with widely separated females in Alaska (Bailey et al. 1986). Regardless of whether this male bred females in both Minnesota and Ontario, his movements during March may indicate an attempt to do so and my use of GPS collars indicated how widely male Canada lynx can travel when breeding activity is at its peak. Although March is the most active breeding month for lynx in Minnesota, I found some male lynx traveling widely throughout January-March. However, the extraterritorial movements of the male lynx I monitored were not restricted to the breeding months and also occurred during the summer-fall season. The motivation for the timing of these movements has not been studied but may result from males regularly monitoring the availability of foraging habitat or females.

While some males moved long distances during the breeding months, others reduced their March movements. Lynx likely reduce their breeding-season movements when population density permits access to multiple females in small areas (Breitenmoser et al. 1993). I suspect one male had a March home range < 10 km^2 because of access to $\geq$ 2 females in this area. My data suggests male lynx may increase their movements during the peak of the breeding season but also may adjust their movements based on female density.

During my study, lynx in Minnesota appeared to have a social organization similar to lynx populations from more northerly regions and other solitary felids where females occupy home ranges with sufficient resources to raise young and the larger home ranges of males potentially provide access to multiple females (Eisenberg 1986; Poole 1995, Liberg et al. 2000). The frequent locations from my GPS collars allowed me to relate this pattern of social organization to lynx movements associated with reproduction. While males had a tendency to increase their home ranges during breeding months, female movements showed little change during the breeding months. However, female lynx with kittens consistently occupied small home ranges. This was most evident during the May-June denning season when the kernel home ranges of females with kittens were consistently (i.e., > 70% probability) within a 1-2 km^2 core area. Understanding the space-use of breeding females is clearly important for the conservation of U.S. lynx populations and GPS collars have allowed me to accurately estimate home ranges during the critical denning period. Females with kittens likely occupy similarly small areas throughout their geographic range. The use of GPS collars to evaluate the seasonal movements of male lynx in a northern lynx population with a greater density of females would further our understanding of lynx social organization and aid conservation planning in the species.

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Table 1. Summary statistics for 95% minimum convex polygon (MCP) and fixed-kernel home ranges (km^2) of resident male and female Canada lynx estimated with GPS telemetry in Minnesota, 2003-2005[a].

	N		Mean ± *SE*		Range	
	♂	♀	♂	♀	♂	♀
MCP						
Winter	5	3	162 ± 57	38 ± 23	96 - 348	10 - 82
Denning[b]	5	3	181 ± 55	11 ± 2	63 - 341	7 - 15
Summer-fall	1	2	55	16 ± 4	-	12 - 19
Annual[b]	4	2	267 ± 73	21 ± 2	146 - 439	19 - 23
Kernel						
Winter	5	3	128 ± 58	44 ± 26	29 – 324	13 - 95
Denning[b]	5	3	209 ± 81	6 ± 1	92 - 522	5 - 8
Summer-fall	1	2	68	21 ± 7	-	14 - 28
Annual[b]	4	2	160 ± 65	17 ± 4	86 - 354	13 - 21

[a] Home ranges > 1600 km^2 were excluded from this analysis.

[b] Home-range sizes are significantly different between sexes ($P < 0.05$).

Table 2. Summary statistics (mean ± *SE*) for fixed-kernel isopleth predicting core area and core-area size for male and female Canada lynx estimated with daily locations from GPS collars in Minnesota, 2003-2005[a].

	N		Isopleth (%)		Core Area (km^2)	
Season	♂	♀	♂	♀	♂	♀
Winter	5	3	60 ± 3	63 ± 3	27 ± 9	9 ± 5
Denning[b]	5	3	65 ± 6	78 ± 6	63 ± 33	1 ± 0
Summer-fall	1	2	69	56 ± 1	16	5 ± 2
Annual[b]	4	2	64 ± 3	72 ± 1	37 ± 15	5 ± 1

[a] Home ranges > 1600 km^2 were excluded from this analysis.

[b] Core-area sizes are significantly different between sexes ($p < 0.05$).

Table 3. Male and female home-range sizes for northern (> 50°N) and southern (< 50°N) lynx populations using mean annual minimum-convex polygon home-range sizes from individual studies.

	Latitude	Mean (Range)		n		Reference
Northern		♂	♀	♂	♀	
Alaska	65°N	20 (14 - 25)	13	2	1	Berrie 1973
Yukon	61°N	32 (14 - 255)	29 (7 - 33)	6	4	Ward and Krebs 1985
Northwest Territories	61°N	31 (3 - 68)	32 (7 - 91)	30	24	Poole 1994
Yukon	60°N	76 (12 - 498)	79 (3 - 775)	46	51	Slough and Mowat 1996
Alaska	60°N	424 (64 - 783)	70 (25 - 70)	2	2	Bailey et al. 1986
Nova Scotia	59°N	19	26	1	1	Parker et al. 1983
Manitoba	51°N	221	158 (138 - 177)	1	2	Carbyn and Patriquin 1983
Alberta/British Columbia	51°N	277 (224 - 357)	135 (44 - 276)	3	3	Apps 2000

Table 3. Continued.

Location	Latitude	Mean (Range)		n		Reference
Southern		♂	♀	♂	♀	
Washington	49°N	69 (56 - 99)	39 (38 - 41)	5	2	Koehler 1990
Minnesota[a]	48°N	194 (145 - 243)	87 (51 - 122)	3	4	Mech 1980
Minnesota[a,b]	48°N	267 (146 - 439)	21 (19 - 23)	4	2	This study
Montana	47°N	238 (20 - 534)	115 (15 - 164)	6	4	Squires and Laurion 2000
Wyoming	42°N	137	114	1	1	Squires and Laurion 2000

[a] Reproductive status of female lynx differs between Minnesota studies. See text for discussion.

[b] Home ranges > 1,600 km^2 were excluded.

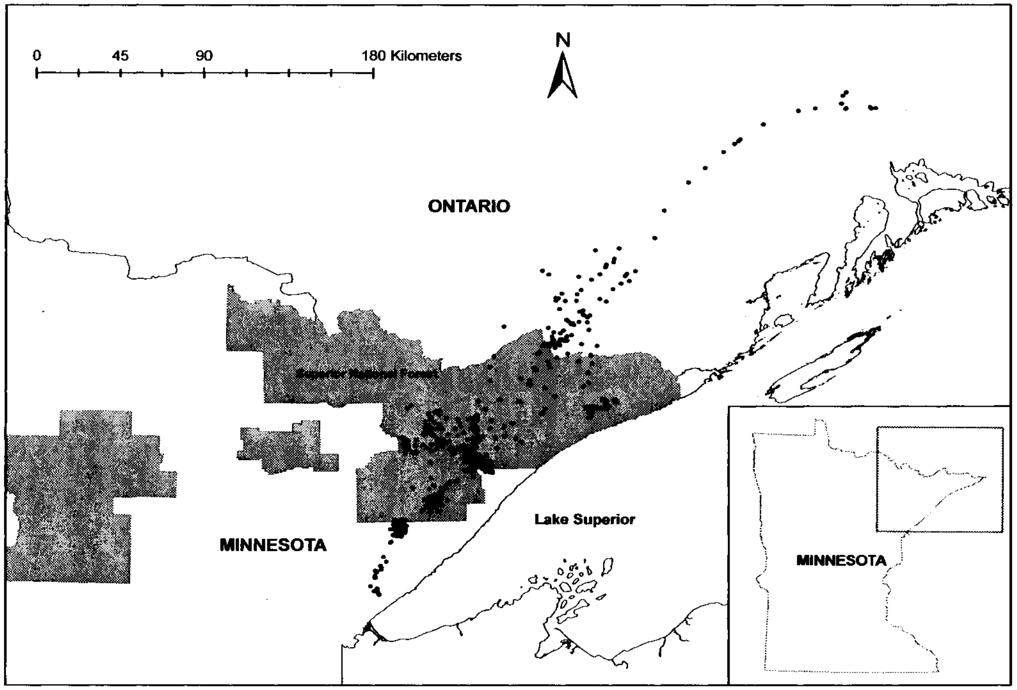

Figure 1. Canada lynx study area in Superior National Forest, Minnesota, U.S.A. Points represent the GPS locations of 11 Canada lynx wearing GPS collars in 2004-2005.

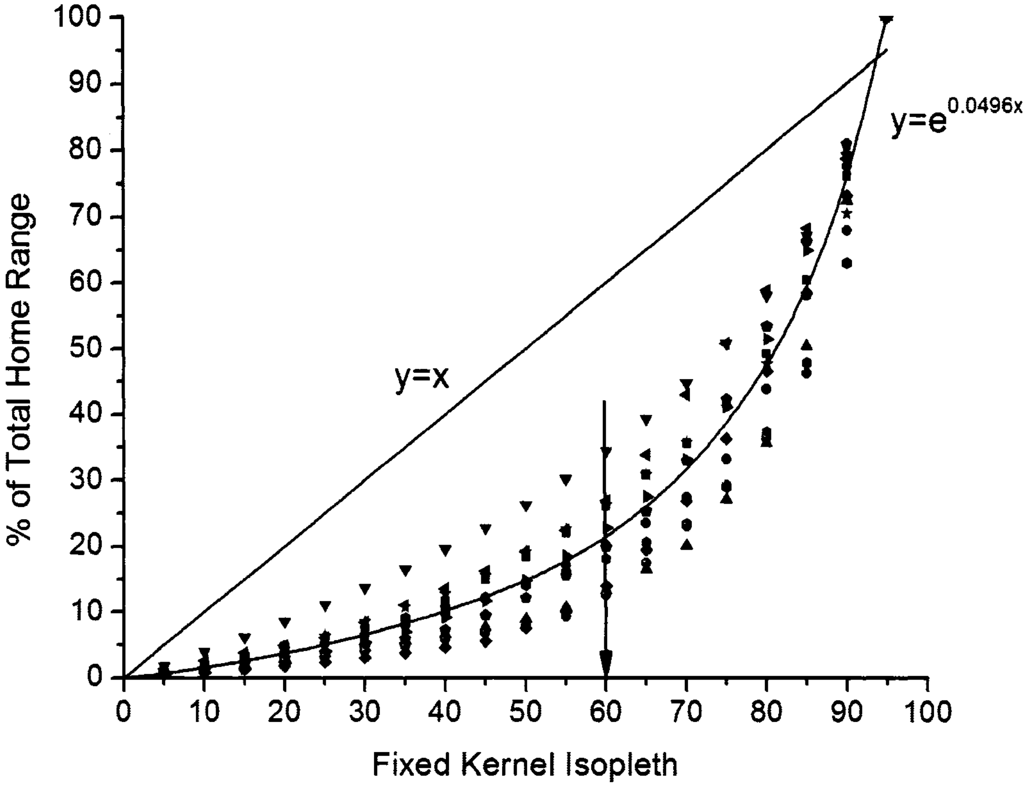

Figure 2. Area/probability curve estimating mean winter and summer-fall core areas of 8 Canada lynx wearing GPS collars in Minnesota, 2004-2005. Arrow depicts inflection point of exponential regression curve where slope of tangent line was equal to 1, predicting mean core area (60% isopleth) as area of uniform use among these 8 lynx. Two lynx were monitored during successive years or seasons.

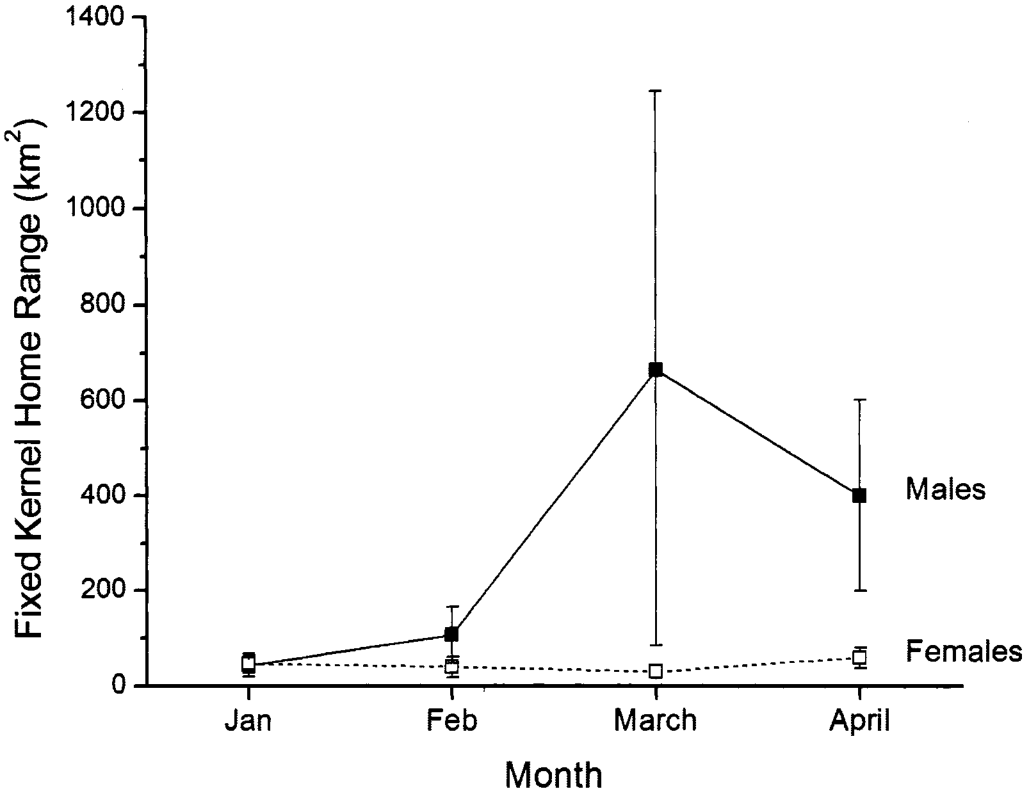

Figure 3. Monthly breeding season 95% fixed-kernel home ranges for January, February, and March. April was also included for comparison to preceding months with greater breeding activity. Mean values developed from 10 (5 male, 5 female) of 11 lynx monitored with GPS telemetry in Minnesota. Two males and one female were monitored over multiple winters.

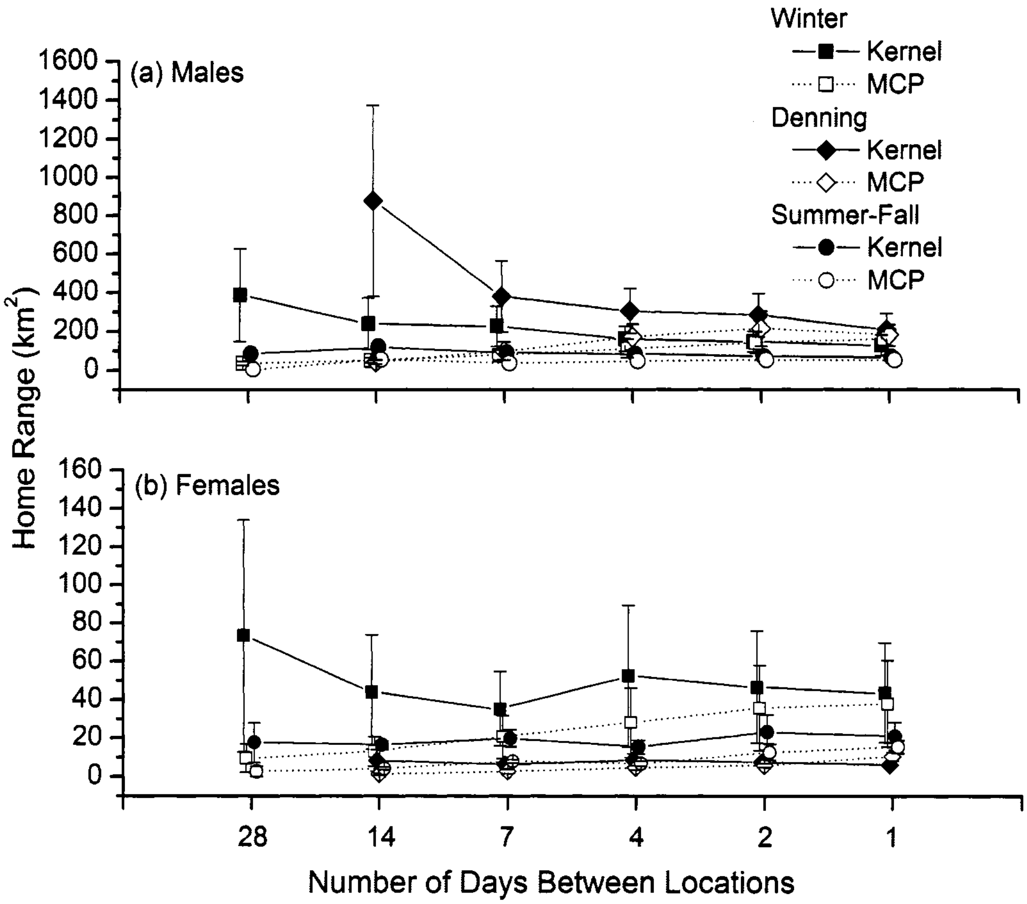

Figure 4. Home-range area (km^2) for Canada lynx in Minnesota by home-range estimator (95% minimum-convex polygon [MCP], 95% fixed kernel [Kernel]), season, and number of days between locations for males (a) and females (b). Note reversed x-axis and 10-fold increase in scale of y-axis for males. Ten individual lynx were used in home-range sensitivity analysis. Two lynx were monitored during successive winters. The x-axis was offset slightly to better show values and associated error bars (± *SE*).

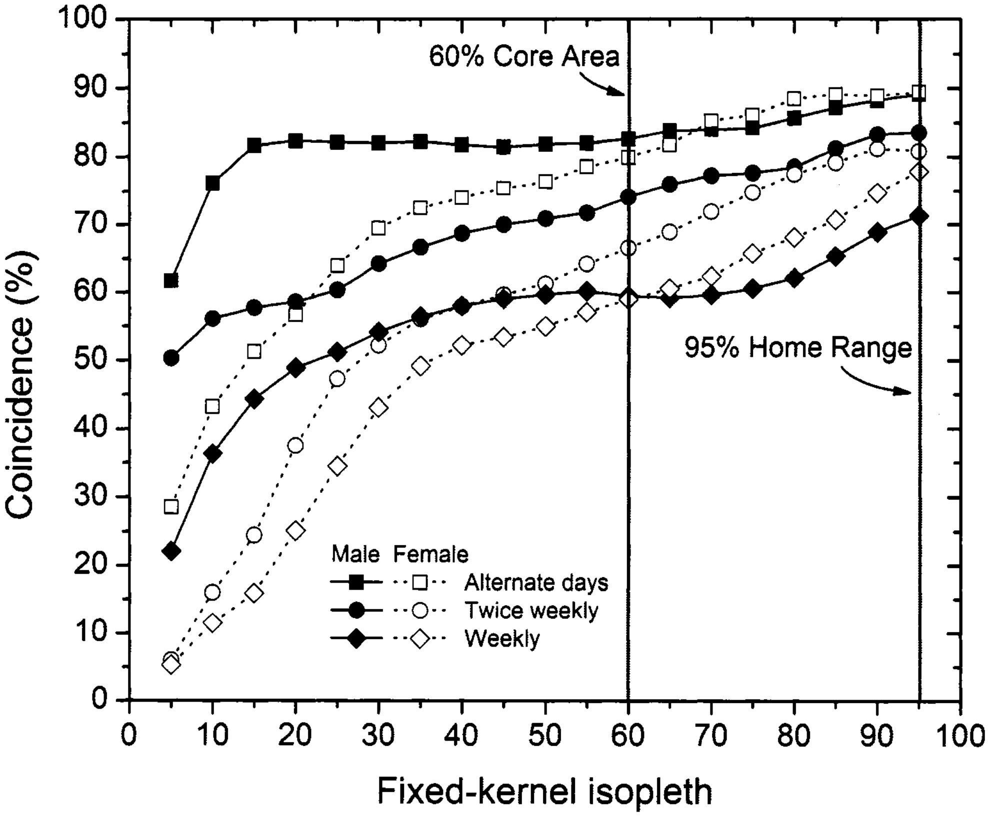

Figure 5. Percentage of coincidence (C%) between fixed-kernel Canada lynx home-range isopleths estimated from daily locations and 3 reduced location frequencies (alternate days, twice weekly, and weekly). Nine individual lynx were used in the coincidence analysis. Two lynx were monitored during successive winters.

CHAPTER 2

Evaluating fine-scale winter habitat selection of Canada lynx with movement paths

ABSTRACT

Many habitat-selection studies describe habitat use at coarse spatial and temporal scales. A movement path is an alternative habitat-use metric that can be used to examine fine-scale habitat use and the underlying behaviors that create habitat-selection patterns. I used hand-held GPS units to collect movement paths from 6 Canada lynx (*Lynx canadensis*) by following their snow trails. These movement paths were used to study the fine-scale winter habitat selection of lynx with a conditional logistic regression (CLR) model and a use-availability sampling design. I modeled lynx habitat selection with 3 hierarchical spatial comparisons representing different intensities of use determined from global positioning system (GPS) collars worn by the lynx I studied. Lynx movement paths were positively associated with areas having higher edge densities and negatively associated with lowland-conifer forests in all spatial comparisons. Regenerating forests were selected for in the best CLR model for areas immediately outside lynx home ranges. Regenerating forest was not an important variable within lynx core areas and home ranges because of the greater availability of regenerating forests in these areas. The results of my CLR models were consistent with sites chosen by lynx for hunting and resting. Evaluating lynx habitat selection with movement paths and a fine-grained

hierarchy of spatial comparisons showed the importance of contrasting use and availability and the need to analyze selection across spatial scales and behaviors.

INTRODUCTION

The Canada lynx (*Lynx canadensis*) is an obligate predator of snowshoe hares (*Lepus americanus*; Nellis et al. 1972, O'Donoghue et al. 1998a) and both species are typically associated with 20-40-year-old successional forests (Wolff 1980, Litvaitis et al. 1985, Koehler 1990, Mowat and Slough 2003, Hoving et al. 2004). Some Canada lynx habitat studies have been conducted at regional or landscape scales using telemetry locations, tracks, sightings, or trapping records (Koehler 1990, Poole et al. 1996, Carroll et al. 2001, Mowat and Slough 2003, Hoving et al. 2004, Hoving et al. 2005). Such broad-scale habitat analyses are valuable because they are conducted over the large areas typically advocated for conservation planning in carnivores (Carroll et al. 2001). The coarse spatial scale of these studies coincides with the coarse temporal scales of the units used to define habitat use. The time between telemetry locations or presence records prohibits inferences about the fine-scale behavioral decisions, such as those occurring during movement, that produce habitat-selection patterns. An alternative approach is to define habitat use with movement paths where the subject of analysis is the path that an animal takes as it moves from point x to point y. The movement paths of lynx can be recorded by following their snow trails. Many earlier studies using this technique examined the response of lynx to sub-stand level measurements such as canopy cover and understory density (Murray et al. 1994, O'Donoghue et al. 1998b, von Kienast 2003). Information about such fine-scale habitat features is rarely available over the large areas considered by forest-management planning based on the principles of landscape ecology and ecosystem management. Geographic information systems (GIS) permit habitat sampling over large areas, which can better characterize the habitat selection of wide-ranging species like lynx (Erickson et al.1998). An analysis of lynx habitat selection that applies a fine-scale measurement of habitat use such as a movement path within a GIS modeling environment would help link available knowledge about lynx behavior and microhabitat needs to land-cover classes over large areas. Movement paths are also ideal for examining the response of lynx to linear habitat features such as forest edges. Although lynx are thought to be attracted to forest edges (Kesterson 1988, Major 1989, Staples 1995, Mowat et al. 2000), edge use has not been quantitatively analyzed, despite important implications for lynx conservation.

The comparison of used to available habitat is a common sampling design in studies of resource selection. The area defined as available in habitat-selection analyses should be carefully defined because it strongly affects the subsequent interpretations (McClean et al. 1998, Garshelis 2000). Statistical models specifically designed for matched pairs or sets of binary use-availability data, such as conditional logistic regression or discrete-choice models, allow availability to vary for each unit of habitat use and provide the analytical tools to evaluate habitat selection at fine spatial or temporal scales (Arthur et al. 1996, Cooper and Millspaugh 1999, Compton et al. 2002, Manly et al. 2002). Fine-scale habitat selection for territorial mammals is often studied within an animal's home range. Few studies have sufficient data to compare fine-scale habitat selection within portions of the home range, such as the core area (Samuel et al. 1985, Powell 2000), that animals use with different intensities. Evaluating movements relative to intensity of use would help detect fine-scale heterogeneities that define habitat quality and improve my understanding of how animals structure their habitat use within their home ranges.

Minnesota is one of the few conterminous U.S. states with a consistent history of lynx presence and previous lynx research in Minnesota has focused on general ecology, space use, and broad-scale movements (Mech 1977, Mech 1980, Burdett et al. 2007). I conducted a GIS-based analysis of fine-scale winter habitat selection by Canada lynx in Minnesota. My analyses considered the 3rd (i.e., within home range) and 4th (i.e., selection of specific behavioral sites) orders of habitat selection (Johnson 1980). My first objective was to compare the habitat attributes along an actual lynx movement path to random duplicates of the actual path placed within or adjacent to the same lynx's home range. I studied lynx with known home ranges and core areas to analyze winter habitat selection along a gradient of 3 spatial comparisons that represented areas used by lynx with different intensities. My second objective was to examine the association between cover type and sites where lynx hunted or rested. I compared the habitat attributes of random sites within lynx home ranges to hunting and resting sites and used these results to help interpret the habitat-selection patterns associated with the movement paths of lynx.

Study Area

This study was conducted in the eastern and central sections of the Superior National Forest in Lake and Cook counties in northeastern Minnesota. Forests in northern Minnesota are transitional between Canadian boreal forests and temperate northern hardwood forests to the south (Pastor and Mladenoff 1992). The study area was dominated by mixed forests of white spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) with lowland habitats of alder (*Alnus* spp.), black spruce (*Picea mariana*), and cedar (*Thuja occidentalis*) occurring on hydric soils. Managed forests often consisted of regenerating aspen and red (*Pinus resinosa*) or jack pine (*Pinus banksiana*) plantations. Human land use, both historically and recently, has reduced the proportion of upland conifers (spruce and pine) in northern Minnesota forests (Frelich 2002, Wolter and White 2002). Understory vegetation was typically denser than western North American forests and consisted of various shrub species and saplings of overstory trees. Northern Minnesota has a continental climate with moderate precipitation, short warm summers, and severe winters. Snow cover was usually present from December through March.

METHODS

Data Collection

Field technicians followed the snow trails of radiocollared lynx during January-March of 2003-2006. The movement paths of these animals were recorded with handheld global positioning system (GPS) units (Garmin 12XL, V, or eTrex, Olathe, Kansas) set to obtain Universal Transverse Mercator (UTM) coordinates at 3-30 second intervals. The snow trails of these lynx were intercepted at road or snowmobile trail crossings. Lynx trails were usually backtracked but were also foretracked when the radiocollar signal indicated that tracking would not affect lynx behavior. The UTM coordinates were recorded for all kills, hunting beds, and resting beds encountered along the trails. The digitized trails and hunting and resting sites were imported into ArcView 3.3 (ESRI, Redlands, California) for spatial analyses. All lynx trailed during this study also wore GPS collars and their core areas and home ranges were estimated with kernel methods (Burdett et al. 2007). Capture and handling methods were described elsewhere (Moen et al. 2005, Burdett et al. 2007) and followed guidelines of the Animal Care and Use Committee (1998) of the American Society of Mammalogists and were approved by the Institutional Animal Care and Use Committee at the University of Minnesota (Code # 0301A39326).

Spatial Analyses and Sampling Design

My habitat data were derived from LANDSAT Thematic Mapper satellite imagery with a 30 m resolution (Minnesota Land Management Information Center, St. Paul, Minnesota). Land cover in my northeastern Minnesota study area was classified using satellite imagery from June 1994. Areas classified as regenerating habitat in 1994 were based on forest management occurring since 1973. Although this classification did not allow us to evaluate lynx response to recent timber harvest, it classified 10-30 year forests as regenerating forest, which is a successional stage frequently associated with Canada lynx (Koehler 1990, Poole et al. 1996, Mowat and Slough 2003). The overall classification accuracy of this data set was originally tested as $\geq$95% (Minnesota Land Management Information Center, St. Paul, Minnesota). I further evaluated this dataset during my study to examine the effect of recent timber harvest and found a classification accuracy of approximately 80% (C.L. Burdett, University of Minnesota, unpublished data).

I used my habitat map to evaluate 7 predictor variables that depicted the composition (i.e., proportion of 5 land-cover classes) and configuration (number of patches and edge density) of habitat associated with each lynx movement path (Table 1). The land-cover classes I selected for analysis, mature mixed coniferous-deciduous forest (MIX), mature lowland-conifer forest (LC), mature upland conifer forest (UC), 10-30 year old regenerating forests (REG), and non-forested areas (OP), are the same or similar to those used in previous habitat studies of lynx (Koehler 1990, Poole et al. 1996, Mowat and Slough 2003, Hoving et al. 2004, Hoving et al. 2005). The OP habitat classification combined land-cover classes depicting open, non-forested cover types associated with human development, upland and lowland grasslands, shrubby grasslands, and riparian habitat. The mean (± SE) percentage of my OP habitat classification within the home ranges of GPS-collared lynx was 7 ± 2%. I did not examine lynx response to deciduous forests because these forests comprised < 1% of the home ranges of the lynx I studied.

I analyzed habitat selection along lynx movement paths with a use-availability sampling design. My use samples were the actual movement paths of lynx that I recorded with handheld GPS units while following snow trails. I sampled availability separately for each movement path with three spatial comparisons that represented a gradient of use intensity. My availability sample sets were created by randomly relocating each actual movement path within each lynx's core area, home range, and the area in a 5 km buffer around the boundary of the home range (Fig. 1). The core area and home range were the 60% and 95% fixed-kernel isopleths estimated during winter (December-April) (Burdett et al. 2007). The area in the 5 km buffer represented an area that the lynx was likely familiar with, but rarely visited based on my 95% fixed-kernel home-range estimates. Whenever possible I created my random trails using the core-area and home-range estimate from the same winter that each actual trail was followed but used core-area and home-range estimates from other seasons when necessary.

I matched 10 random availability trails with each actual trail to better characterize habitat availability and because logistic regression models are robust to different samples of the binary response variable (Nielson et al. 2003). I generated a different set of availability trails for each spatial comparison. Availability trails maintained the relative Cartesian displacement of the actual trail but randomly altered the origin and orientation of the trail to create a set of alternate movement paths the lynx could have used instead of its actual path (Fig. 1). I used the Alternate Animal Movement Routes (AAMR) Extension for ArcView, version 2.1 (Jenness 2004), to create the availability trails within a GIS running ArcView 3.3 (ESRI, Redlands, CA). I buffered all actual and availability trails by 25 m to define my habitat variables along the movement paths. These 50 m wide strips controlled for the expected spatial error of lynx movement paths recorded on handheld GPS units under a forest canopy (DeCesare et al. 2005) and the resolution of my habitat data. I also used the AAMR extension to calculate the proportion of each cover type within each buffered trail. The AAMR extension can not calculate cover-type proportions along trails containing a loop so I manually tabulated habitat use on these trails with the clip and identity spatial analyses in ArcGIS 9.1 (ESRI, Redlands, California). I used Patch Analyst 3.0 (Rempel and Carr 2003) to calculate my habitat-configuration variables, the number of patches (NP) and edge density (m/ha) (ED), within the buffered trails, subtracting the artificial edge that was created by the buffer perimeter in a vector-based GIS environment.

Fine-Scale Winter Habitat-Selection Models

I investigated multicollinearity among predictor variables by examining Spearman correlation coefficients and did not include variables with $|r| > 0.6$ in my habitat models. I used conditional logistic regression (CLR) to create a set of candidate models that compared the habitat features between each lynx trail and its matched set of 10 random availability trails. Also known as case-control, matched-set, or fixed-effects logistic regression, CLR is a more powerful technique than standard unconditional logistic regression when data are stratified into paired observations or sets (Hosmer and Lemeshow 2000). The conditional form of the logistic-regression model is analogous to a discrete-choice model (McFadden 1974, Cooper and Millspaugh 1999) because the techniques share the same conditional likelihood function (Allison 1999). Conditional logistic regression allowed us to define habitat availability separately for each lynx trail and spatial comparison and also stratify my sampling across both lynx and trail, which reduced the potentially confounding influences of different trail lengths and different numbers of trails collected from individual lynx.

I developed a set of 41 candidate models that evaluated various combinations of 3 of my 7 predictor variables. I restricted my analysis to models with ≤ 3 parameters because my use of lynx trails as the experimental unit precluded a large sample. The use of all possible combinations was warranted by my use of few predictor variables, all of which have been relevant in previous habitat analyses of lynx (Koehler 1990, Poole et al. 1997, Mowat and Slough 2003, Hoving et al. 2004). I used Akaike's Information Criterion difference for small samples ($\Delta_i \text{AIC}_c$) to select the most parsimonious model and Akaike weights ($\text{AIC}_c\ w_i$) for relative comparisons among the candidate set. I then used all models with a $\Delta_i \text{AIC}_c$ value < 10 to calculate model-averaged coefficients, unconditional standard errors, and estimates of relative importance for the predictor variables ($w_+(j)$) included in final, averaged models of winter habitat selection for each of my spatial combinations. Importance estimates use the $\text{AIC}_c\ w_i$ values to depict the weight of evidence associated with a variable and are especially useful when no model in the candidate set is clearly superior (Burnham and Anderson 2002). To examine effect sizes appropriate for my sample, I conservatively defined selection with 95% confidence intervals (± 2*SE*) using the model-averaged coefficients and unconditional standard errors.

Because my sampling design used a gradient of increasing use and varying definitions of habitat availability, I further investigated the relationship between habitat use and availability in my models (Mysterud and Ims 1998, Garshelis 2000). I used linear regressions of proportional use and availability using my predictor variables to investigate if linear relationships existed between used and available habitat and if patterns varied across my spatial comparison. Used habitats were the cover-type proportion or configuration variable on the individual lynx trails. Availability was defined separately for each trail and spatial comparison using the mean of each predictor variable calculated from the matched set of 10 random trails.

Model Evaluation

Standard evaluation methods for logistic-regression models using the classification matrix are not valid for use-availability data (Boyce et al. 2002). Moreover, goodness-of-fit tests for CLR are complex and unavailable in commercial statistical software (Zhang 1999, Arbogast and Lin 2004). I therefore evaluated the best model for each spatial comparison with a *k*-fold cross-validation (Boyce et al. 2002). I split my dataset into 5 partitions, and used 4 as a training dataset to define coefficients and the remaining partition as a testing dataset to define the probability of selection with data not used for model development. I randomly subsampled each testing dataset to obtain a 1:1

use-availability ratio to ensure an adequate number of use records in the testing dataset and avoid distributing the probability of a negative outcome across multiple availability trails. I used 0.5 as the threshold value to classify a trail as available (≤ 0.5) or used (> 0.5) and performed 20 cross-validation iterations, using a different subset of trails for the testing and training partitions each time. Classification accuracy was evaluated as the mean percentage of correctly classified use or availability trails in the testing partitions.

Patch-Size Effects

I investigated potential factors affecting the response of lynx to forest edges. I performed linear regressions using edge density on a path as my response variable and mean patch size within a buffered path and proportions of abundant (i.e. mixed, coniferous, and regenerating forests) cover types as explanatory variables. Mean patch-sizes within buffered trails were calculated with Patch Analyst 3.0 (Rempel and Carr 2003). I conducted separate regressions for use and availabilities at the core-area and outside home-range scale. I log transformed edge-density values and examined standard regression assumptions with residual and normal-probability plots.

Behavioral Sites

I tested whether sites where lynx hunted or rested showed similar habitat relationships as my habitat models. I placed a 25 m buffer around all kill sites, hunting beds, and resting beds found while trailing lynx. Resting beds were ice-encrusted with the lynx resting in a curled position whereas hunting beds showed little ice crusting and the lynx positioned in a crouch (Parker et al. 1983, Murray et al. 1994, Murray et al. 1995). To obtain a larger sample, I used hunting and resting sites from 5 of the 6 lynx used in my habitat models (no behavioral sites were obtained from one of these lynx), 2 additional collared lynx, and some uncollared lynx. I compared the habitat features associated with the hunting and resting sites to 100 random locations from each home range of the seven collared lynx used for this analysis. I performed non-conditional univariate logistic regressions on each predictor variable to determine differences between behavioral and random sites. I accepted a significance level of $P \leq 0.10$ for the analysis of behavioral sites to emphasize detection of biological trends. I performed univariate logistic regressions on kill sites and hunting beds separately to determine if habitat differences existed among these hunting behaviors. Statistical analyses were performed with Stata Version 9.2 (2006).

RESULTS

I followed 38 trails totaling 63.2 km from 6 lynx (3M, 3F) wearing GPS collars. Trail distances varied from 0.5- 3.4 km (mean = 1.7 km, SD = 0.8 km) (Fig. 2). This mean distance approximated the mean net displacement of females during 24 hours (1.5 km/24 hours; SD = 0.2, n = 4) and 45% of the mean net distance moved by males during 24 hours (3.8 km/24 hours; SD = 1.3, n = 6) that was estimated from lynx wearing GPS collars (R. Moen, University of Minnesota, unpublished data). While the number of trails and total distance of trail for each lynx varied, the 6 lynx I studied were located in 3 widely-separated regions (i.e., activity centers) within my study area. The total trail distance was similar for 2 of these 3 activity centers and summary statistics show that the habitat present within the core areas and home ranges varied among individual lynx and among activity centers (Table 2). The availability trails for 29 of my 38 lynx trails (76%) were defined with core-area and home-range estimates from the same winter that the actual trail was recorded. The availability trails for the remaining lynx trails were defined with space-use estimates that were $\leq$ 12 months old but still reflected their home ranges during the period that their trails were recorded.

Number of patches was eliminated as a predictor variable in all models due to a high positive correlation with edge density ($0.56 < r < 0.64$ among all spatial comparisons). Mixed forest had high negative correlation with regenerating forest in the core area comparison ($r = -0.60$) but not in the home-range ($r = -0.35$) or outside home-range ($r = -0.42$) comparison so I did not eliminate candidate models in the core-area comparison that included both mixed and regenerating forests.

No model was strongly supported in comparisons for the intensively used core areas and home ranges but there was strong support for a best model for the outside home-range comparison (Table 3). Selection against lowland-conifer forests and selection for higher edge densities occurred consistently across all spatial comparisons (Table 4). Edge density (mean ± *SE*) on lynx trails was 253 ± 16 m/ha whereas edge density on the availability trails was 206 ± 6 m/ha within core areas, 219 ± 5 m/ha within home ranges, and 195 ± 6 m/ha in the areas immediately outside of home ranges. The importance of mixed forest and open habitat decreased with decreasing intensity of use and both of these habitats were consistently used in proportion to availability. Lynx selection for regenerating forest showed the opposite trend, increasing in importance in the comparisons of less intensively used areas. Regenerating forest was used in proportion to availability within the core area and home ranges but was selected for in the outside home-range comparison. Upland-conifer forests had small to moderate importance at any scale and use of these forests was always proportional to availability.

Although explaining little variation, positive linear relationships existed between proportional use and availability for the core-area and outside home-range comparisons for both regenerating (core area: $r^2 = 0.36$, $P < 0.001$; outside home range: $r^2 = 0.11$, $P < 0.04$) (Fig. 3) and mixed (core area: $r^2 = 0.12$, $P < 0.04$; outside home range: $r^2 = 0.24$, $P < 0.002$) forests. I detected no significant linear relationships between use and availability among the remaining predictor variables in any of my 3 spatial comparisons.

My *k*-fold cross-validation evaluated the classification accuracy of 180 pairs of used and available trails for my 3 spatial comparisons. Trails were correctly identified for 69%, 67%, and 78% of core-area, home-range, and outside home-range comparisons.

Patch-Size Effects

Edge density on lynx trails showed a negative linear relationship with mean patch size along the trail ($P < 0.001$, $r^2 = 0.33$) and proportion of regenerating forest ($P < 0.006$, $r^2 = 0.18$). Mean patch size also showed a negative linear relationship with edge density for the availability trails within the core area ($P < 0.001$, $r^2 = 0.50$) and outside the home range ($P < 0.001$, $r^2 = 0.53$). As expected, edge density and mean patch size showed strong negative correlations ($r = -0.56$ for use, $r = -0.65$ for core area and $r = -$

0.67 for outside). The distribution of mean patch sizes on the lynx trails showed distinct differences from the distribution of mean patch sizes on the availability trails (Fig. 4).

Behavioral Sites

I compared 77 lynx hunting behavior sites (26 kills, 51 hunting beds) to 700 random locations within lynx home ranges. Twenty-four of the 26 kills were snowshoe hares; the remaining 2 kills included 1 ruffed grouse (*Bonasa umbellus*) and 1 spruce grouse (*Dendragapus canadensis*). Collectively, lynx hunting behaviors occurred more often than expected in mixed ($\chi^2 = 3.96$, $P < 0.04$) and regenerating ($\chi^2 = 5.20$, $P < 0.02$) forests. Hunting beds occurred more frequently in mixed ($\chi^2 = 6.16$, $P < 0.01$) and regenerating forests ($\chi^2 = 2.95$, $\mathrm{P} < 0.07$) and less than expected in open habitats ($\chi^2 = 5.70$, $P < 0.06$). Kill sites occurred more than expected in regenerating forests ($\chi^2 = 2.62$, $P < 0.09$). No hunting beds or kill sites occurred in lowland-conifer forests despite this forest type comprising 15 ± 1% of the home ranges of lynx wearing GPS collars.

I located 60 resting beds and compared them to the 700 random locations within lynx home ranges. Resting beds occurred more than expected in regenerating forest ($\chi^2 = 15.33$, $P < 0.001$) and less than expected in lowland-conifer forests ($\chi^2 = 6.16$, $\mathrm{P} < 0.04$) and open ($\chi^2 = 3.52$, $P < 0.01$) habitats.

DISCUSSION

The most consistent trends emerging from my habitat models were selection for forest edges and selection against lowland-conifer forests. Previous research has described lynx use of forest edges (Kesterson 1988, Major 1989, Staples 1995, Mowat et al. 2000), but I found that lynx selected for edges during their movements. This association with forest edges may result from the interaction between the fine-scale habitat use of hares and the hunting behavior of lynx. Snowshoe hares often inhabit forest edges (Conroy et al. 1979, Wolff 1980, Pietz and Tester 1983, but see Potvin et al. 2005). While edge habitat may have a sufficiently dense understory to support hare populations (Keith 1990), hares may also leave the protective cover of successional forests to forage in adjacent stands. Regardless of whether hares are more abundant or simply more vulnerable to predation in forest edges, lynx would likely bias their movements to travel through these areas. Lynx often hunt in areas with less developed understories, even if prey is less abundant there, because of the difficulty of capturing hares in dense vegetation (O'Donoghue et al. 1998b, Fuller et al. 2007). Felids are often considered ambush predators but Canada lynx also regularly hunt hares by stalking (Murray et al. 1995). Lynx may stalk hares along edges if the patches adjacent to regenerating forests have more open understories that allow lynx to more easily detect and capture hares (Mowat et al. 2000). Lynx may also use the edges of regenerating forests for efficient travel through their home ranges.

Lynx did not use lowland-conifer forests for hunting or resting. This consistent selection against lowland-conifer forests was unexpected because lowland-conifer forests have traditionally been considered good habitat for snowshoe hares in the northern Great Lakes states (Buehler and Keith 1982, Pietz and Tester 1983, Fuller and Heisey 1986). Most lowland-conifer forests in my study area were black spruce-dominated wetlands that occurred on actively accumulating peat formations (Heinselman 1996). These forests characteristically were species poor and lacked the dense understory structure that hares prefer (Litvaitis et al. 1985, Keith 1990). Open, lowland-conifer bogs were similarly avoided by lynx in the Northwest Territories (Poole et al. 1996). The relationship between snowshoe hares and these forests during previous studies in the northern Great Lakes states may result from hares using more diverse lowland-conifer forests containing cedar, tamarack (*Larix laricina*), willow (*Salix* spp.), and alder (Fuller and Heisey 1986). It is also possible that the previous studies were conducted when hares were more abundant in the northern Great Lakes states (Heinselman 1996). Hare populations often show large fluctuations in sub-optimal habitat (Wolff 1980, Keith 1990), but during my study hares were most abundant in regenerating forests (McCann 2006). Hares may not have been abundant enough to colonize sub-optimal habitats like open black-spruce forests during my study. Despite lowland-conifer forests being poor foraging habitat, these forests are still an important component of lynx habitat in Minnesota because they contain the abundant blown-down mature timber that lynx use for denning (Moen et al. in review). My results show the importance of examining habitat use and selection relative to specific behaviors and suggest that general statements about the relative quality of lowland-conifer forests for hares and lynx in my region can be misleading.

It seems counter-intuitive to not see selection for regenerating forest in core areas and home ranges but this resulted from the abundance of these forests in the core areas and home ranges and my use of 95% confidence intervals ($\beta \pm 2SE$) to define selection. Lynx intensively used portions of their home ranges with regenerating forest, and all lynx I studied had a greater proportion of regenerating forest in their core areas than their home ranges. Because habitat selection is an inherently hierarchal process (Johnson 1980), the reduced importance of regenerating forests in core areas does not mean these forests are unimportant to lynx, but instead reflects the difficulty of defining selection for abundant habitat types (Mysterud and Ims 1998, Garshelis 2000). The standard null hypothesis of a use-availability sampling design is that habitat use is proportional to habitat availability, and that animals are more likely to use abundant habitat types (Garshelis 2000). I found that lynx use of regenerating forests showed a positive linear relationship with availability, suggesting that lynx increased their use of these forests when it was abundant. However, the slope of the regression lines became steeper with decreasing intensity of use and never accounted for > 36% of the total variation. The variability in my dataset precluded examining curvilinear relationships to detect asymptotic use of abundant habitat types (Garshelis 2000). Although the relationships were not strong, it is still informative that lynx increased their use of regenerating and mixed forests when these forest types became more common. The correlation between the proportion of regenerating and mixed forests in lynx core areas could indicate that lynx establish core areas in places where regenerating forests have replaced mixed forests. Although I conservatively defined selection with 95% confidence intervals, understanding habitat-selection patterns in intensively used areas of the home range may require large habitat-use samples. It may also be possible that lynx view the habitat within their core areas as relatively homogenous and, to an extent, use all patches there in proportion to their availability.

Lynx used upland-conifer and mixed forests and open areas in proportion to their availability. Both upland-conifer and mixed forests represented mature forests in my habitat classification. Lynx also did not select for mature forests in a snow-tracking study of lynx from northern Maine (Fuller et al. 2007). I saw little response by lynx to upland-conifer forests despite the previously reported association between coniferous forests and lynx and hares (Wolff 1980, Hoving et al. 2005). Although use of mixed forests was also proportional to availability, there were a greater number of hunting beds in these forests and use of mixed forests increased with increasing availability. Mixed forests of aspen, paper birch, balsam fir, and spruce >20 years old are the most abundant forest type in my study area and the effects of these forests on lynx behavior may result from their abundance.

Lynx consistently selected for regenerating forests when hunting and resting, which I believe reflects the greater abundance of hares in these forests (Conroy et al. 1979, Wolff 1980, Livaitis et al. 1985, Keith 1990, McCann 2006). Hare densities in my study area were estimated to be 0.3 – 2.0 /ha (McCann 2006), similar to hare densities from Montana and the Yukon (O'Donoghue et al. 1998a, Griffin 2004, Squires and Ruggerio 2007). It is unclear from research in Canada if lynx hunt more from beds when hares are abundant or scarce (Nellis and Keith 1968, O'Donoghue et al. 1998b), but most of my hare kills were short-distance chases that occurred during lynx movements and few kills originated from hunting beds. The increased use of hunting beds in mixed forests may indicate lynx used this hunting strategy more in areas where hares were less abundant. In northern Canada, red squirrels (*Tamiasciurus hudsonicus*) are an important alternate prey species for lynx when hares are scarce (O'Donoghue et al. 1998a), but lynx in my study area rarely preyed on red squirrels, similar to lynx in Montana (Squires and Ruggerio 2007). My results suggest that red squirrels or their habitat have little effect on the distribution of lynx in Minnesota.

Incorporating behavioral mechanisms into habitat analyses links habitat selection to life-history characteristics and provides conclusions that will better transfer across regions, studies, or datasets (Morrison 2001). My study describes a methodology that can be used to link animal behavior to GIS-based habitat analyses across large areas. Movement paths are a fine-scale, continuous metric of habitat use and are especially useful to detect animal response to linear features such as habitat edges. When movement paths are created by following snow trails, sites associated with specific behaviors can be found and used to help interpret the habitat use along movement paths. Because the lynx I studied also wore GPS radiocollars, I was able to accurately define availability relative to the space-use patterns of individual lynx. Such a sampling design was possible because of stratified statistical models such as CLR or discrete-choice that are ideal for paired data. These analytical techniques should see increasing use in wildlife-habitat studies because they avoid the common problem of analyzing paired data as independent samples (Thomas and Taylor 2006).

Management Implications

My results indicate that lynx locate their core areas and home ranges in areas with abundant regenerating forests and use these forests for hunting and resting. Therefore a key component of habitat management for lynx in Minnesota is the creation and maintenance of successional forest through timber harvest and natural or prescribed fires. Successional coniferous forests would likely be more beneficial than deciduous stands because hares typically prefer coniferous forests in Minnesota and elsewhere (Wolff 1980, Fuller and Heisey 1986, McCann 2006). Although lynx selected against lowland-conifer forests for foraging, these forests often provide denning habitat to lynx in my study area. The distribution and interspersion of lowland-conifer forests, or other types of mature forest that provide denning habitat, relative to the distribution of the regenerating forests lynx use for foraging is likely an important, but underappreciated, consideration for lynx habitat management.

The association between lynx movement and forest edges further indicates the importance of considering the spatial distribution of habitat patches when planning timber harvest to benefit lynx. The effect of spatial heterogeneity on lynx habitat selection warrants additional study because the amount of edge in a landscape can be easily manipulated by the distribution of timber-harvest blocks (Franklin and Foreman 1987, Baskent 1999). Lynx conservation should be implemented within an ecosystem management framework so that other species of concern are not negatively affected by habitat management for lynx and hares.

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Table 1. Predictor variables used in conditional logistic-regression models of fine-scale winter habitat selection of Canada lynx in Minnesota.

Variable name	Definition (units)
MIX	Mixed (coniferous and deciduous) forest (proportion)
LC	Lowland conifer forested wetland (proportion)
UC	Upland coniferous forest (proportion)
REG	Regenerating (coniferous and deciduous) forest (proportion)
OP	Non-forested (e.g., grass, shrub) areas (proportion)
ED	Edge density (m/ha)
NP[a]	Number of patches (count/trail)

[a] Not included in habitat models due to high correlation ($|r| > 0.60$) with ED.

Table 2. Percentage of cover type and edge density within the core area and home range, number of trails, distance, and activity center for each lynx used in habitat selection models.

Individual lynx[a]	M02	M05	M06	F07	F09	F14	Mean	*SD*
Home Range[b]								
MIX (%)	42	48	46	43	31	32	40	7
LC (%)	12	14	8	15	5	8	10	4
UC (%)	20	21	17	29	21	20	21	4
REG (%)	21	14	23	9	27	34	21	9
OP (%)	6	4	6	5	15	6	7	4
ED (m/ha)	223	202	211	240	157	252	215	34
Core Area[b]								
MIX (%)	40	51	45	48	35	15	39	13
LC (%)	7	8	3	13	4	13	8	4
UC (%)	21	21	21	25	14	14	19	4
REG (%)	28	19	24	12	40	55	30	14
OP (%)	5	1	6	2	7	4	4	2
ED (m/ha)	230	174	213	123	161	203	184	39
Number of trails	8	7	6	9	5	3	6	2
Total distance (km)	14	15	6	16	6	5	11	5
Activity center[c]	A	B	A	B	C	A		

Table 2. Continued.

[a] Individual lynx identified by sex (M=male, F = female) and study animal number.

[b] MIX = mixed deciduous-coniferous forest; LC = lowland-conifer forest; UC = upland-conifer forest; REG = 10-30 year-old regenerating forest; OP = non-forest; ED = edge density (m/ha)

[c] Lynx with same activity center had overlapping home ranges in disjunct portions of northeastern Minnesota study area.

Table 3. Model-selection results for top 5 candidate winter habitat-selection models for Canada lynx in Minnesota. Variables present in candidate models for each spatial comparison are indicated by its coefficient sign. The (+) or (–) sign does not incorporate effect size and does not necessarily reflect positive or negative selection.

	Predictor variables [a]								
Comparison	MIX	LC	UC	REG	OP	ED	AIC_c	ΔAIC_c	$w AIC_c$
Core area		-				+	171.6	0.000	0.309
		-			-	+	172.2	0.649	0.223
		-	+			+	173.2	1.663	0.135
		-		+		+	173.7	2.165	0.105
	+	-				+	173.8	2.205	0.103
Home range		-	-			+	162.7	0.000	0.318
		-				+	163.6	0.879	0.205
		-		+		+	163.7	0.952	0.198
	-	-				+	166.0	3.236	0.063
		-			-	+	166.0	3.242	0.063
Outside		-		+		+	154.2	0.000	0.859
	-	-				+	160.9	6.659	0.031
		-				+	160.9	6.696	0.030
		-			-	+	161.6	7.404	0.021
		-	-			+	162.8	8.565	0.012

Table 3. Continued.

[a] MIX = mixed deciduous-coniferous forest; LC = lowland-conifer forest; UC = upland-conifer forest; REG = 10-30 year-old regenerating forest; OP = non-forest; ED = edge density (m/ha)

Table 4. Model-averaged logistic-regression coefficients, unconditional standard errors (SE), and relative variable importance ($w_+(j)$; scaled 0 to 1) for fine-scale winter habitat selection of Canada lynx in Minnesota.

	CA			HR			OUT		
Variable[a]	β	*SE*	$w_+(j)$	β	*SE*	$w_+(j)$	β	*SE*	$w_+(j)$
MIX	-0.029	0.118	0.12	-0.007	0.076	0.10	-0.036	0.023	0.03
LC	-6.311	2.938	0.89	-9.001	2.926	1.00	-7.231	2.851	0.96
UC	-0.124	0.189	0.16	-0.558	0.419	0.36	-0.008	0.011	0.01
REG	0.058	0.118	0.13	0.255	0.194	0.24	1.904	0.691	0.87
OP	0.576	0.411	0.28	-0.024	0.128	0.10	-0.034	0.028	0.02
ED	0.006	0.002	0.97	0.004	0.002	0.85	0.005	0.002	0.95

[a] MIX = mixed deciduous-coniferous forest; LC = lowland-conifer forest; UC = upland-conifer forest;

REG = 10-30 year-old regenerating forest; OP = non-forest; ED = edge density (m/ha)

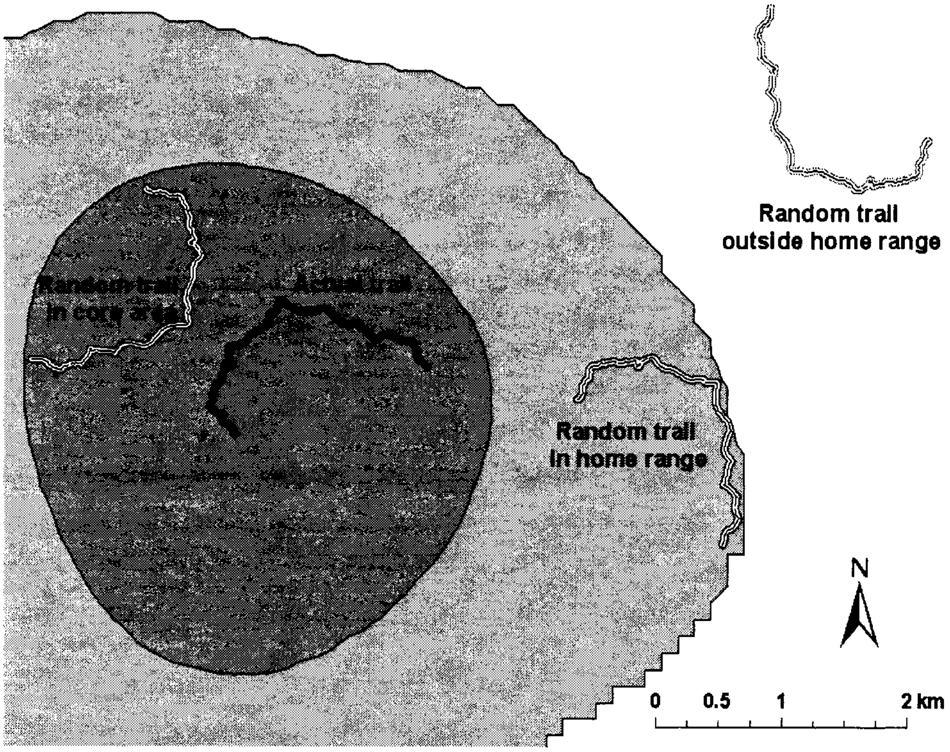

Figure 1. Generalized sampling design for evaluating habitat selection along Canada lynx movement paths. Only 1 of the 10 replicates of random trails in the core area, home range, and outside home-range area are shown for clarity.

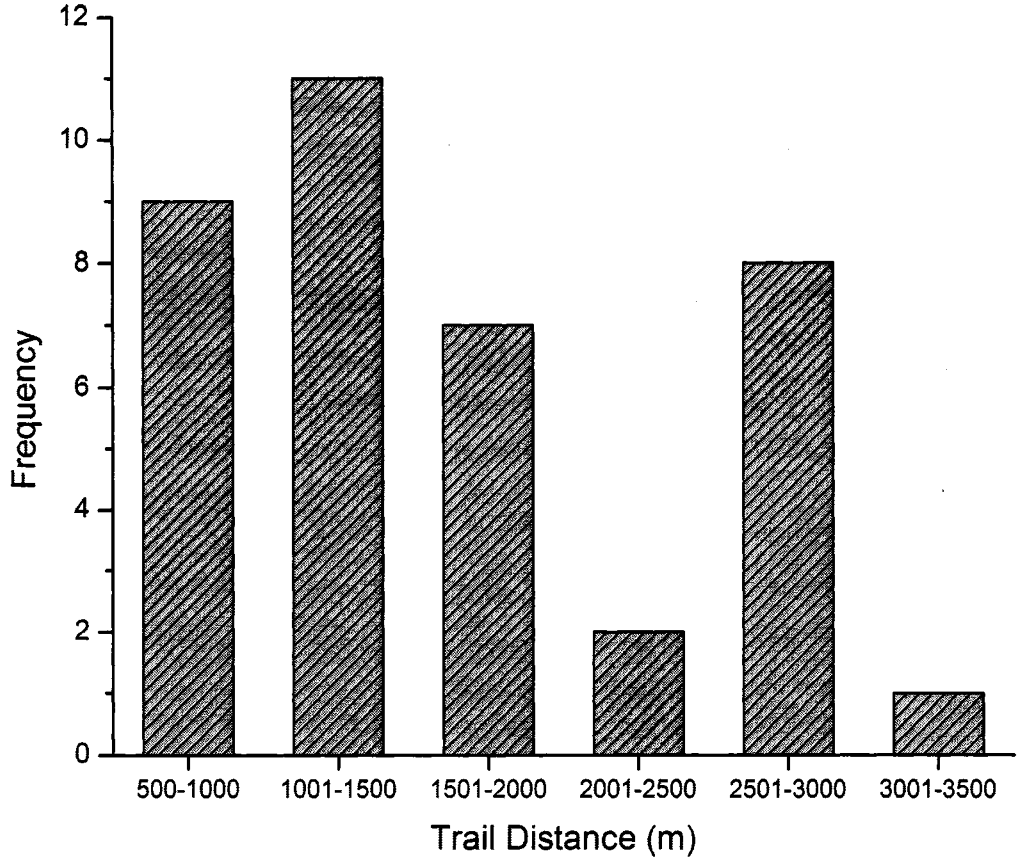

Figure 2. Frequency distribution showing distance of 38 Canada lynx trails used to analyze the fine-scale winter habitat selection of lynx in Minnesota.

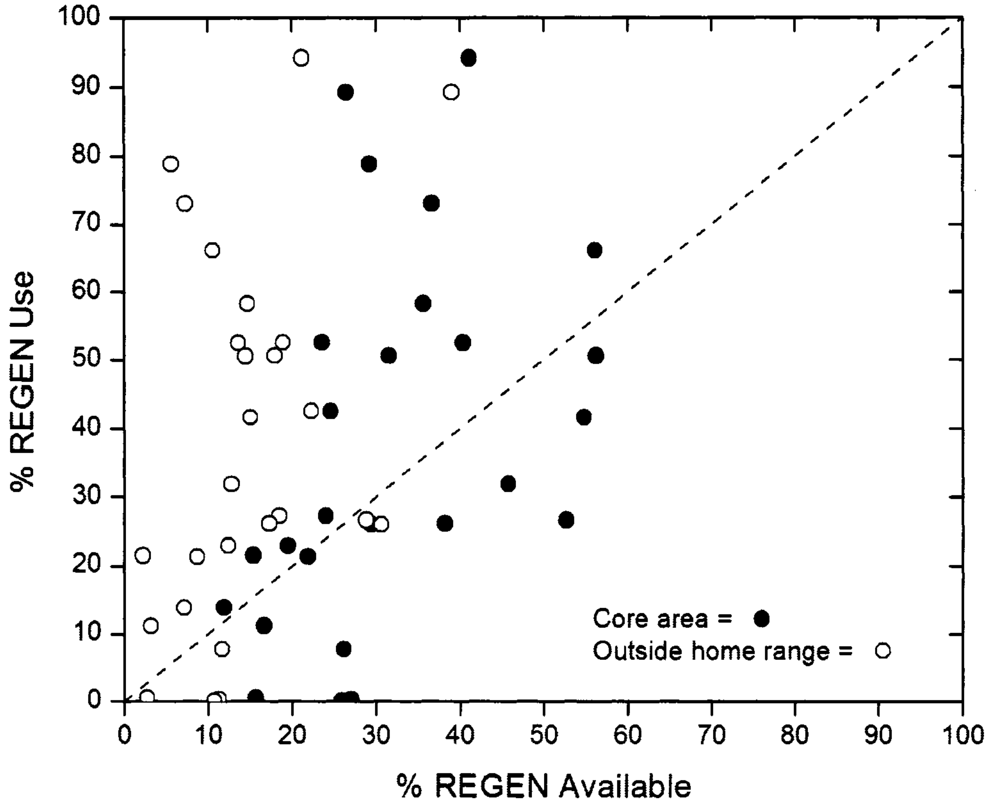

Figure 3. Comparison of the amount of regenerating forest within 25 m buffered lynx and availability trails within core areas (filled circles) and outside home ranges (open circles). Amount of regenerating forest on availability trails are mean values compiled from the set of 10 trails paired with each individual lynx trail. The dashed line indicates where use equals availability. Lynx trails with no use of regenerating forest are not shown.

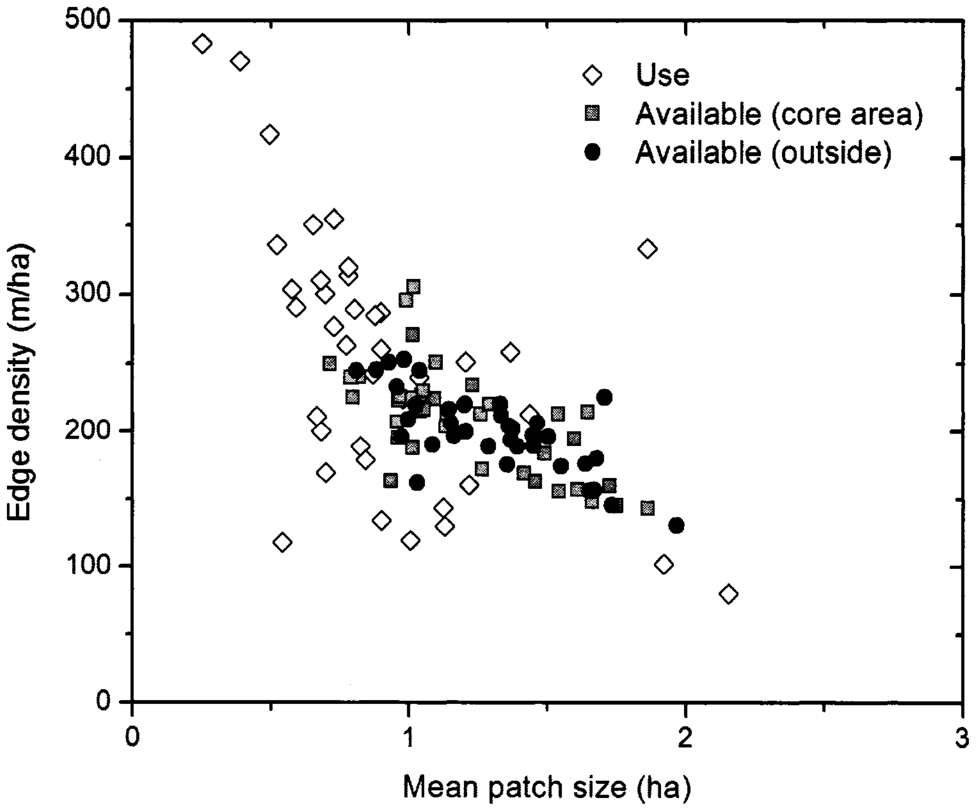

Figure 4. Relationship between edge density and mean patch size within 25 m buffered lynx (use) and availability trails for the core-area and outside home-range spatial comparisons. These mean patch-size values are not representative of actual patch sizes in the landscape, but may approximate patch size as perceived by a foraging lynx.

CHAPTER 3

Habitat effects on the within-territory space-use of Canada lynx in Minnesota

ABSTRACT

Habitat selection is a fundamental ecological process because the abundance and distribution of a species requires access to sufficient resources for survival and reproduction. Selection is often evaluated at multiple spatial scales, and GPS telemetry now allows habitat analyses at increasingly fine scales. I used daily locations from Canada lynx wearing GPS collars to investigate habitat use within their territories. I compared forest types used by lynx within their core areas to the availability of these forest types: (1) within core areas, (2) within territories, and (3) in areas adjacent to territories. Lynx consistently selected for 10-30-year-old (successional) forests except within their core areas. All lynx except females with young kittens showed neutral selection or selected against lowland-conifer forest. This finding suggests that maternal lynx select for coarse woody debris in lowland-conifer forests to conceal their kittens during the 2-5 months after leaving the den. Core areas of lynx territories seem to represent homogenous high-quality habitat so are valuable for applied conservation and management planning. Lynx also selected for the edges between successional and upland conifer forest, presumably because lynx can more efficiently forage for snowshoe hares along forest edges than in the dense shrub and herbaceous understory of successional forests. Lynx use of successional forests and forest edges has important implications for

the ecological management of southern boreal forests. Edge density can be controlled by forest-cutting patterns. Forest management that mimics the large fires that controlled regeneration in boreal forests prior to human influence should benefit lynx. Additional studies at broader spatial scales are needed to better understand how lynx and hares respond to spatial heterogeneity.

INTRODUCTION

Habitat selection is a fundamental ecological process because the abundance and distribution of a species requires access to sufficient resources for survival and reproduction (Southwood 1977, Morris 2003). Because habitat-selection patterns are often scale-dependent (Johnson 1980, Orians and Wittenberger 1991, Morris 2003, Ciarniello et al. 2007), many studies evaluate selection at multiple spatial scales (Miquelle et al. 1999, Saab 1999, Mosnier et al. 2003, Price et al. 2005, Boyce 2006). Habitat studies of territorial mammals often investigate selection within territories, and the distribution of territories within the study area. Habitat selection is rarely studied relative to how intensively areas are used within a territory. Such analyses have been limited because of logistic and technological constraints associated with intensively monitoring wide-ranging mammals in remote areas. Telemetry collars using global positioning system (GPS) satellites provide more accurate and frequent locations than very high frequency (VHF) radio collars (Moen et al. 1996, 1997), and are now available for medium-sized mammals (Burdett et al. 2007). When used with probability-based kernel home-range estimators (Seaman and Powell 1996, Seaman et al. 1999) and the rapidly-advancing technologies of geographic information systems (GIS) and remote sensing (Bolstad 2005), GPS collars enable analyses of the movements, space use, and habitat selection of wildlife at increasingly fine environmental scales. Fine-scale analyses can more clearly depict the ecological basis for habitat-selection patterns in carnivores (Fernández et al. 2003).

The most intensively used part of a territory is the core (Kaufmann 1962, Powell 2000). Cores are often defined visually or as a percentage of the most centrally-distributed locations. However, these subjective estimates lack a quantitative foundation and may poorly show patterns created by clusters of telemetry locations and the implicit biological information they represent (deSolla et al. 1999, Powell 2000). Objective techniques to estimate core areas (CAs) often involve quantifying the portion of territory that is used more than expected relative to a null model of uniform space use (Samuel et al. 1985, Seaman and Powell 1990, Bingham and Noon 1997). Core areas can be objectively defined with kernel estimators to determine the probability threshold that separates cores from the peripheral portion of the territory (Bingham and Noon 1997, Powell 2000). Kernel-based CA estimates become more precise with increasing location frequency, making this an ideal technique to use with GPS telemetry data (Burdett et al. 2007). Core areas have many applied uses, and they are especially useful for studying the habitat selection of wide-ranging animals (Samuel et al. 1985, Bingham and Noon 1997, Hodder et al. 1998, Seaman et al. 1999).

Habitat management is a key component of conservation planning for species listed under the U.S. Endangered Species Act (NRC 1995). The principal reason for listing the Canada lynx (*Lynx canadensis*), a medium-sized cat from the boreal forests of

North America, under the U.S. Endangered Species Act (ESA) was because the habitat needs of lynx occurring on land owned by the federal government were poorly understood (USFWS 2000). Few radiotelemetry-based studies of lynx habitat selection have been conducted in the U.S. (Koehler 1990, McKelvey et al. 2000), including states like Minnesota with a consistent history of lynx presence (Mech 1973, Henderson 1978, Mech 1980, McKelvey 2000, Burdett et al. 2007). The habitat selection of lynx has been studied in northern Canada (Poole et al. 1996, Mowat and Slough 2003), but differences in vegetation, prey density, and landscapes may limit the applicability of these results to U.S. populations. Factors that may affect lynx habitat-selection patterns, like sex or season, have not been studied in the U.S.

Hierarchy theory (Allen and Starr 1982) provides a conceptual framework to evaluate how animals respond to habitat at multiple spatial scales (Bissonette 2003). One hypothetical structure for hierarchical ecological systems suggests that mechanistic explanations for intermediate-level patterns exist at lower levels, whereas higher levels provide a context to interpret the intermediate-level patterns (King 1997). For habitat selection in most carnivores, this implies that behavioral choices at the microhabitat-scale are the mechanism governing habitat selection within a territory. Microhabitat selection in carnivores primarily involves foraging behavior, which has been well-studied in the Canada lynx (Murrary et al. 1995, O'Donoghue et al. 1998a, Fuller et al. 2007, Squires and Ruggerio 2007). The lynx is a specialist predator of snowshoe hares (*Lepus americanus*) (Elton and Nicolson 1942, Nellis and Keith 1968, Nellis et al. 1972, O'Donoghue et al. 1998b). Hares are often associated with the dense understories characteristic of 10-30 year-old forests (hereafter successional) (Wolff 1980, Wolfe et al.

1982, Pietz and Tester 1983, Litvaitis et al. 1985), and lynx habitat preferences are similar (Koehler 1990, Poole et al. 1996, Mowat and Slough 2003, Hoving et al. 2004). However, lynx may preferentially hunt in areas with more open understories, even if hares are less abundant there, because hares are more difficult to capture in dense cover (Murray et al. 1995, Mowat et al. 2000, Fuller et al. 2007). Lynx may also hunt along forest edges if differences in understory density between adjacent stands increase their ability to capture hares (Mowat et al. 2000). This fine-scale behavior and habitat use of lynx should be related to habitat preferences observed over larger areas that would be useful for management. Lynx territories, which often exceed 100 km^2 in the U.S. (Mech 1980, Burdett et al. 2007), are an ideal analytical scale because areas of this size are used for lynx conservation planning on federal land in the U.S. (Ruediger et al. 2000).

I deployed GPS radiocollars on Canada lynx to examine the effects of habitat on lynx space-use patterns at the southern edge of the species' range. First, I developed logistic-regression models that compared the habitat use of lynx within their CAs to habitat availability along a hierarchical use-intensity gradient (e.g., areas used intensively, frequently, and infrequently or not at all). I evaluated habitat selection for individual lynx and also explored differences in selection due to sex and season. Second, I examined lynx use of forest edges by evaluating selective use of specific forest-edge combinations (i.e., pairs of adjacent forest types) and determining if lynx locations were closer to selected edge types than a random expectation. I related my results to previous studies of lynx foraging, denning, and resting sites and the adaptive mechanisms that produce these habitat-selection patterns. Lastly, I discuss the implications of my results for forest management in southern boreal forests.

Study Area

I conducted my study in a 10,197 km^2 area in the eastern and central sections of the Superior National Forest in northeastern Minnesota (Figure 1). The forests of northern Minnesota are transitional between Canadian boreal forests and temperate northern-hardwood forests occurring further south (Pastor and Mladenoff 1992). My study area was dominated by mixed forests of quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*). Lowland-conifer forests of black spruce (*Picea mariana*), tamarack (*Larix laricinia*) and cedar (*Thuja occidentalis*) were common in poorly drained areas. Additional lowland habitats consisted of shrubs such as alder (*Alnus* spp.) or various grasses. Northern-hardwood stands of sugar maple (*Acer saccharum*) and basswood (*Tilia americana*) are generally uncommon but locally abundant on ridges near Lake Superior. Managed forests often consist of regenerating aspen and red (*Pinus resinosa*) or jack pine (*P. banksiana*) plantations. Logging, fire suppression, and other human actions have reduced the proportion of spruce and pine in northern Minnesota forests both historically and recently (Frelich 2002, Wolter and White 2002). Understory vegetation is typically denser than western North American forests and consists of various shrub species and saplings of overstory trees. Northern Minnesota has a continental climate with moderate precipitation, short warm summers, and severe winters. Snow cover is usually present from December to April.

Lynx have historically been more common in northeastern Minnesota than elsewhere in the north-central U.S. (Mech, 1973, Henderson 1978, Mech 1980).

Throughout much of the 20th century the regional lynx population has shown cyclic population fluctuations common in the species (Henderson 1978) (Figure 2). These fluctuations have diminished in recent decades, possibly due to concurrent declines in the regional snowshoe-hare population (Heinselman 1996, Burdett et al. 2007). In addition to its threatened status under the U.S. Endangered Species Act, the lynx has also been a protected species in Minnesota since 1984. Most mortality of radiocollared lynx during this study has been human-related, and included collisions with automobiles and trains, legal harvest in Ontario, and illegal harvest in Minnesota (Moen et al. 2005).

Snowshoe hares historically displayed cyclic population dynamics in Minnesota (Green and Evans 1940). However, hare population peaks in the early- to mid-20th century may have been larger than those occurring since about 1980 (Heinselman 1996). The Minnesota Department of Natural Resources has estimated hare population trends since 1974 by recording the number of hares seen during spring grouse drumming counts. Although $\geq$ 9-14 hares/100 km were counted from 1977-1981, counts from 1982-2004 have consistently remained between < 1-3 hares/100km (J. Erb, Minnesota Department of Natural Resources, unpublished report). It is unclear if hare populations cycle in many southern boreal forests (Keith et al. 1993, Murray 2000). Recently, hare densities in sites supporting lynx in northeastern Minnesota were estimated to be 0.3 – 2.0 hares/ha (McCann 2006). However, hare populations in northeastern Minnesota appear to be patchily distributed, being most consistently abundant in 10-30 year old regenerating forests (McCann 2006).

Other mesocarnivores in this study area that regularly consume snowshoe hares include the red fox (*Vulpes vulpes*), fisher (*Martes pennanti*), coyote (*Canis latrans*), and bobcat (*Lynx rufus*). Large mammals present in the study area include gray wolves (*Canis lupus*), black bears (*Ursus americanus*), white-tailed deer (*Odocoileus virginianus*), and moose (*Alces alces*).

METHODS

Canada Lynx Telemetry Data

The lynx used for these analyses were adult (> 2 years old) and sub-adult (1-2 years old) animals captured from 2003-2006, and fitted with one of three models of GPS radio collars (GPS_3300, Lotek Wireless, Inc., Newmarket, Ontario, and C200 or C300, Telemetry Solutions, Inc., Concord, CA). The collars were programmed to record 2–18 locations each day. I downloaded the location data after the collar drop-off mechanism was triggered, or when the lynx was re-trapped. The capture and handling protocol followed guidelines of the Animal Care and Use Committee (1998) of the American Society of Mammalogists and was approved by the Institutional Animal Care and Use Committee at the University of Minnesota (Code # 0301A39326). Additional details concerning animal handling and GPS collars are available elsewhere (Burdett et al. 2007, R. Moen, public communications).

I sub-sampled locations from the GPS collars using a mean location interval of 24 hours (i.e., daily locations). Occasional missed locations reset the sampling interval so that these daily locations were obtained throughout the 24-hour period. This maintained a standardized sampling frequency among the three collar models that reduced concerns about autocorrelation and independence among locations (Otis and White 1999, Fieberg 2007). I used 95% fixed-kernel territory estimates and 60% fixed-kernel CA estimates from two seasons (winter and summer-fall) to classify the locations relative to intensity of use (Burdett et al. 2007). I did not include data from females during the May-June denning season because the habitat features associated with denning habitat differ from those associated with non-breeding habitat (Slough 1999, Moen et al., in review). Each location was classified according to whether it was within the corresponding seasonal CA (< 60% kernel isopleth), or the peripheral zone of the territory, which is the term I used for the portion of the territory that is between the 60% and 95% kernel isopleths. Locations outside of the 95% kernel isopleth were not included in the use dataset because few locations were obtained there.

Study Design

I investigated the habitat selection of lynx within their territories by comparing the habitats used within lynx CAs to habitat availability: 1) within the CA, 2) within the peripheral zone of the territory (PZ), and 3) within areas adjacent to but outside of the 95% territory (OUT) (Figure 3). Thus, I defined habitat availability separately for each lynx territory and evaluated three hierarchical spatial comparisons, CA-CA, CA-PZ, and CA-OUT, in my habitat models. Habitat use was defined with locations within each lynx's CA. Availability locations were created for each spatial comparison by randomly generating points with the Animal Movement Analyst extension (Hooge and Eichenlaub 2000) for ArcView 3.3 (ESRI, Redlands, CA). For each spatial comparison, I created the same number of availability locations as use locations, but I created 2-4 sets of availability locations for the CA-PZ and CA-OUT spatial comparisons to better characterize habitat availability in the larger PZ and OUT regions. Each PZ and OUT availability location set was sampled from an area within the lynx's PZ or OUT region that was constrained to have a similar size (mean ± *SD* = 19.0 ± 19.5 km^2, range = 2.4 - 74.9 km^2) and shape as the corresponding lynx's CA. All use and availability locations were buffered by 25 m and the proportion of land-cover classes within each buffered point was recorded as a continuous variable. I censored any availability location whose buffer overlapped a use location to maintain independent use and availability samples.

I modeled habitat selection separately for each lynx because habitat analyses ideally use individual animals as the experimental unit (Otis and White 1999, Manly et al. 2002). I also pooled the data for all lynx to qualitatively examine the consistency of habitat-selection patterns and examine differences in habitat selection due to sex and season. These pooled models were also evaluated with my CA-CA, CA-PZ, and CA-OUT hierarchical sampling design.

Spatial Habitat Data and Variables

Habitat datasets were derived from LANDSAT Thematic Mapper satellite imagery with a 30 m resolution (Minnesota Land Management Information Center, St. Paul, Minnesota). Land cover from the study area was identified into 14 classes from images obtained during 1995-1996 (Table 1). Areas that had been disturbed in the previous 20 years were classified as successional forest. Although I could not evaluate lynx response to recent timber harvest with this habitat dataset, lynx rarely use stands < 10 years of age, and my classification of successional forest into a 10- to 30-year-old age-class is consistent with previous lynx studies (Koehler 1990, Poole et al. 1996, Mowat and Slough 2003). The overall classification accuracy of this data set is > 95% (Minnesota Land Management Information Center, St. Paul, Minnesota). I further evaluated this habitat dataset for recent timber harvest effects and found a classification accuracy of approximately 80% (C. Burdett, unpublished data).

I used my habitat map to evaluate selection by lynx for four forest types (mature mixed deciduous-coniferous forest, mature lowland-conifer forest, mature upland-conifer forest, and successional forest) that were similar to habitat variables examined in earlier studies of lynx habitat selection (Koehler 1990, Poole et al. 1996, Hoving et al. 2003, Mowat and Slough 2003, Hoving et al. 2004). These four forest types collectively comprise approximately 80% of the land cover in the study area. I did not evaluate lynx response to deciduous forests, water, lowland and upland grasslands, shrubby grasslands, and human development because these land-cover classes are uncommon within lynx territories and throughout the study area (Table 1). Water (8%) and deciduous forest (5%) were the only other land-cover classes that comprised ≥ 5% of the total land cover.

Model Building and Selection

I used logistic regression to model habitat selection within lynx territories (Hosmer and Lemeshow 2000, Manly et al. 2002). Prior to modeling, I used univariate Kruskal-Wallis rank tests to examine differences in the proportional area of my four forest-type variables within lynx CAs and PZs (Sokal and Rohlf 1995). I included multiple CA and PZ estimates from individual lynx monitored in different seasons or years because lynx often shifted the location of their CA.

I modeled habitat selection using the set of 15 candidate models that could be created from combinations of the four forest types. I used information-theoretic inference techniques to select the best model(s) for each of three spatial comparisons (Burnham and Anderson 2002). I used Akaike's Information Criterion (AIC) scores, AIC differences (Δ_iAIC), and AIC weights (AICw_i) to rank the 15 candidate models. I also calculated importance ranks for each forest type represented in models with Δ_i AIC < 10 (Burnham and Anderson 2002).

I used multi-model inference techniques to calculate model-averaged coefficients and unconditional-variance estimates for my individual-level and pooled models (Burnham and Anderson 2002). Model-averaging weights coefficients by the strength of evidence associated with each candidate model, and is especially useful in situations where no model is clearly superior (Burnham and Anderson 2002). The model-averaged coefficients were obtained by multiplying each forest-type coefficient by its associated AIC w_i and then summing the weighted coefficients from each candidate model. I also used the AIC w_i values to create unconditional-variance estimates because the model-selection process introduces additional uncertainty into estimated parameters (Burnham and Anderson 2002).

Logistic-regression coefficients can be used to infer habitat selection (Manley et al. 2002, Boyce et al. 2002). I used the estimated coefficients and a confidence interval of ± 2 *SE* to define positive selection (lower bound of confidence interval > 0), negative selection (upper bound of confidence interval < 0), or neutrality (confidence interval includes 0). I used the mean and *SE* estimates from the model-averaged coefficients from individual lynx for estimating selection. The individual lynx was the sampling unit, which accounted for variation in number of telemetry locations among individuals and defined confidence intervals relative to the number of study animals (Manly et al. 2002). Finally, I qualitatively assessed the generality of the selection patterns by comparing these individual-level results to the model-averaged coefficients and unconditional-variance estimates from the pooled model.

Model Evaluation

I examined how well the best models described the outcome data with overall and individual goodness-of-fit measurements and evaluated the predictive ability of each model with a validation analysis using additional telemetry locations from my study lynx that were not used for model building. I used the Hosmer and Lemeshow goodness-of-fit statistic, $\hat{C}$, to summarize overall model fit and the Pregibon $\Delta\hat{\beta}$ and the Hosmer and Lemeshow $\Delta\chi^2$ influence statistics to detect individual locations that had a large negative influence on model fit (Hosmer and Lemeshow 2000). I evaluated the influence of individual locations by plotting both influence statistics against the estimated probability of selection and examining specific locations whose $\Delta\hat{\beta}$ or $\Delta\chi^2$ values exceeded 1 (Hosmer and Lemeshow 2000).

I conducted a validation analysis with additional use locations that were not used for model building. While I did not use multiple locations from a single day for these validation datasets, the locations were not necessarily separated by > 24 hours relative to other locations. For each lynx, I used all of its remaining locations up to 100 to create the new use datasets. I reused the availability datasets from model-building because a different availability sample is not needed with this technique (Howlin et al. 2004). I used the best model with the lowest AIC score for evaluating the individual and pooled models for each spatial comparison. After estimating the predicted probabilities of selection for each availability location, I scaled each individual probability value by dividing it by the sum of all prediction probabilities and then multiplied it by the number of locations in the validation dataset. I then calculated the 5th to 100th percentiles for the availability locations and classified the availability locations into 20 equally-sized bins. The sum of the scaled probabilities for each bin represented the expected number of locations (Howlin et al. 2004). I obtained the observed number of locations by scaling the selection probabilities for the validation locations with the same procedure as the availability samples, classifying these locations into the bins previously defined for the availability samples, and then summing the number of validation locations in each bin. I evaluated the predictive ability of each model with a linear regression of the observed counts on the expected counts. The slope and confidence intervals resulting from the regressions were then used to classify the predictive performance of each model as good, acceptable, or unacceptable (Howlin et al. 2004) (Table 2).

Effects of Sex and Season on Habitat Selection

I used the pooled use and availability datasets to examine differences in habitat selection relative to sex and season. I stratified the pooled dataset by sex and season (winter and summer-fall), and used logistic regression to examine differences in selection for the four forest types among males and females in summer-fall and winter. I conducted these stratified selection analyses separately on the CA-CA and CA-PZ datasets. I evaluated selectivity similarly as my individual-level analysis with confidence intervals of ± 2 *SE* around the logistic-regression coefficients.

Lynx Relationship with Forest Edges

I investigated the response of lynx to forest edges with two analyses. First, I determined which edge combinations created by adjacent patches of the four forest types were most correlated with lynx use. Second, after determining preferences among forest-type combinations, I examined whether the actual lynx locations were closer to a preferred edge type than the availability locations.

I examined the relationship between forest edges and lynx habitat use using the use and availability locations from the habitat modeling. I screened these locations for those that contained > 1 forest type within its 25m buffer. I then converted the forest-type polygons into a polyline coverage to create forest edges in my habitat map and determined: 1) the forest type of each patch containing a use or availability location; and 2) the forest type of patches adjacent to patches containing a location. I eliminated all records where the forest type of a point was identical to the adjacent habitat type because > 88% of these were a processing artifact that resulted from adjacent polygons having separate, rather than shared, edges after being converted to a polyline coverage. I used logistic regression to examine differences between use and availability locations within all possible adjacency combinations among mixed, upland-conifer, lowland-conifer, and successional forests.

I also used logistic regression to evaluate if the use locations were closer to preferred edge types than the random availability locations. I measured the distance between my use and availability locations in all preferred edge-type combinations using the Nearest Features extension (version 3.8) for ArcView (Jenness Enterprises, Flagstaff, AZ). Separate regressions were performed for all preferred edge type locations within CAs, PZs, and all combined locations within the territory. I considered differences in the use and availability locations to be significant at the $P \leq 0.05$ level for both edge analyses. All statistical analyses were done with Stata Version 9.2 (StataCorp, College Station, TX).

RESULTS

I obtained sufficient data to investigate the habitat selection of 11 (6 adult M, 4 adult F, and 1 sub-adult F) lynx that wore GPS collars from 2003-2006. Three of the 4 adult females produced at least one litter during my study; the remaining adult female was not monitored during the May-June denning period. Seven of these lynx were monitored for multiple seasons and 3 were monitored for multiple years. The mean number of locations obtained from a CA was 102 (*SE* = 21, range = 12-255).

Kruskal-Wallis rank tests comparing the proportion of each of 4 forest types with lynx CAs and PZs showed that there was significantly less lowland conifer in CAs than PZs ($\chi^2_{1,21} = 3.90$, $P < 0.05$). The mixed ($\chi^2_{1,21} = 0.35$, $P > 0.55$) and upland-conifer ($\chi^2_{1,21} = 0.03$, $P > 0.86$) forests showed no significant differences, but there was a trend for more successional forest in CAs ($\chi^2_{1,21} = 2.80$, $P > 0.09$).

Habitat Models

Individual-level models –Selection estimated from the logistic-regression coefficients showed that lynx did not select for any forest type within their CAs (Figure 4). Habitat-selection patterns that emerged when habitat use within the CA was compared to areas used less intensively included selection for successional forests, use of mixed and lowland-conifer forests in proportion to their availability, and a trend for selection of upland-conifer forest with decreasing intensity of use (Figure 4).

Habitat-selection patterns showed some variability among individual lynx and spatial comparisons (Table 3). CA-CA models indicated most lynx showed neutral selection toward all forest types (Table 4). The CA-PZ and CA-OUT models showed more lynx selected for successional forest and selected against lowland-conifer forests. Selection for upland-conifer forests in lynx CAs only occurred for the CA-OUT comparison, and mixed forests were used in proportion to their availability in all spatial comparisons.

Neutral selection toward lowland-conifer forest was the most important selection pattern in all models within the CA, while selection for successional forest was the most important selection pattern within PZs and outside of the territory (Table 5). Across spatial comparisons, successional (+) and lowland-conifer forests (-) always ranked first or second in importance, while mixed and upland-conifer forests alternated between third or fourth.

Pooled models – The pooled models similarly showed the trends toward selection for successional forests and selection against lowland-conifer forests seen in the CA-PZ and CA-OUT comparisons for the individual-level models. However, the pooled models had smaller standard errors than selection estimates from the averaged individual coefficients, producing selection against lowland-conifer in all spatial comparisons rather then the neutral response to this forest type predicted by the averaged individual coefficients. Because the overall patterns between the pooled and averaged individual models were similar and the effect sizes small, I used the pooled models to evaluate patterns in model-selection inference parameters. The pooled models with the largest AICw_i were similar for all spatial comparisons. My best CA-CA model included lowland conifer and successional forests ($w_i = 0.485$), while lowland conifer, upland conifer, and successional forests were included in the best models for the CA-PZ ($w_i = 0.470$) and CA-OUT ($w_i = 0.628$) comparisons. The global model that included all four forest types was the second-ranked model for both the CA-PZ ($w_i = 0.212$) and CA-OUT ($w_i = 0.291$) comparisons.

Qualitative differences among the spatial comparisons were apparent in the Δ_iAIC values for the pooled models (Figure 5). For the CA-CA comparison, 12 of 15 candidate models had Δ_iAIC values < 10, indicating considerable uncertainty about which of the candidate models best fit the data. In contrast, only four of the 15 CA-PZ candidate models and three of the 15 CA-OUT candidate models had similar support as the best model at these scales. However, only three candidate models for the CA-CA and CA-PZ comparisons and two candidate models for the CA-OUT comparison had Δ_iAIC values > 2, which indicated some reduction in model fit (Burnham and Anderson 2002) (Table 6).

The averaged coefficients from the individual-level models obscured patterns associated with sex and season (Figure 6). For the two key forest types (lowland-conifer and successional forests), the models that evaluated the effects of sex and season consistently showed greater differences from the CA-CA to CA-OUT comparisons than the models for individual lynx. Male lynx during all seasons and female lynx during winter selected for successional forests in the CA-CA comparison. Sex and season had the strongest effect on lynx response to lowland-conifer forests. Female lynx showed neutral selection for lowland-conifer forests in summer-fall despite selecting against these forests during winter. Males selected against lowland-conifer forests in both seasons.

Model evaluation –All models had reasonable summary goodness-of-fit values for the CA-CA and CA-PZ comparisons. However, the pooled model ($\hat{C} = 15.3$, $P < 0.004$) and the individual-level models for M05 ($\hat{C} = 4.4$, $P < 0.04$), F07 ($\hat{C} = 24.2$, $P < 0.001$), F09 ($\hat{C} = 8.0$, $P < 0.02$), and F24 ($\hat{C} = 14.1$, $P < 0.02$) showed poor fit to these data for the CA-OUT comparison due to few covariate patterns relative to overall sample size of combined use and availability locations (mean = 499 ± 106, range = 54-1275). The

Pregibon $\Delta\hat{\beta}$ and the Hosmer and Lemeshow $\Delta\chi^2$ influence statistics showed that individual locations negatively influencing model fit were those that contrasted most with the predictions of the logistic-regression models.

Overall, validation indicated that both individual and pooled models were relatively robust. Only 10% of 36 models produced unacceptable results whereas 47% were good and 43% were acceptable. While the pooled models provided acceptable results for all comparisons, results for individual lynx were least successful predicting habitat use for the CA-CA comparison (Table 7).

Lynx Relationship with Forest Edges

Approximately 60% of all lynx locations (n = 1158 of 1928 total locations) were within 25m of a forest edge, but these locations were not significantly different between the use and availability locations for the CA-CA comparison ($z = 1.39$, $P > 0.17$), the CA-PZ comparison ($z = 0.19$, $P > 0.85$) or the PZ-PZ comparison ($z = 1.27$, $P > 0.20$). Lynx locations were more often near a forest edge than availability locations for the CA-OUT comparison ($z = 2.60$, $P < 0.009$).

When I considered specific combinations of edges among my 4 forest-type variables, I found significant selection of edges between upland-conifer and successional forests and avoidance of mixed and lowland-conifer forest edges (Table 8). The effect was more pronounced in the CA-PZ comparison than in the CA-CA comparison.

After I detected selection for edges between successional and upland coniferous forests, I investigated if actual locations were closer to this edge type than the random availability locations. Actual locations (mean ± *SE*=245 ± 19m, $n = 369$) were closer to the edge between upland-conifer and successional forests than random locations (mean ± *SE*=331 ± 9, $n = 1821$) within the entire territory ($z = -3.81$, $P < 0.001$). However, proximity to this edge type differed depending upon intensity of use within the territory. Within CAs, actual locations (mean ± *SE*=231 ± 20m, $n = 236$) were not significantly farther from upland-conifer/successional edges ($z = -0.96$, $P < 0.339$) than random locations (mean ± *SE*=252 ± 13m, $n = 492$). Within PZs, actual locations (mean ± *SE*=272 ± 38m, $n = 133$) were significantly closer to this edge type ($z = -2.27$, $\mathrm{P} < 0.023$) than random locations (mean ± *SE*=360 ± 12m, $n = 1329$).

DISCUSSION

Many factors influence the size of felid territories, including prey density, habitat features, climate, individual characteristics like sex, reproductive status, or body mass, and the distribution of conspecifics and competitors (Bertram 1979, Ward and Krebs 1985, Sandell 1989, Herfindal et al. 2005, Burdett et al. 2007). The ecological basis for differences in within-territory space use in carnivores is poorly understood (Young and Shivik 2006), but these same factors likely also exert strong influences on movements within carnivore territories. I studied how habitat affected the within-territory space-use of Canada lynx. The lynx is an ideal subject for such an analysis because its dependence on snowshoe hares creates dietary and habitat specialization, simplifying the habitat-selection patterns of lynx compared to those of generalist carnivores. Lynx located their territories in areas with abundant 10-30-year-old successional forests and then intensively used these forests within their territories. Land-cover classes like successional forest can provide a proximate indicator of habitat quality for lynx whereas the ultimate factor defining habitat quality for lynx, or any predator, is abundant prey. Snowshoe hares were also most abundant in successional forests in northeastern Minnesota (McCann 2006). These results agree with previous studies that described forests of this age class as a critical habitat component for Canada lynx (Koehler 1990, Poole et al. 1996, Mowat and Slough 2003).

Lynx also showed consistent patterns in how they responded to the mosaic of mature forest types occurring within their territories. Selection against mature lowland-conifer forest was nearly as important a predictor variable in my habitat models as lynx use of successional forest. Despite lynx generally selecting against these forests, lowland-conifer stands are used as denning habitat in Minnesota (Moen et al., in review), and breeding females continued to show increased use of these forests during summer and fall when kitten mobility remained limited. Core areas contained slightly more mature upland-conifer forest than areas used less frequently and lynx preferentially used the edges between these forests and younger stands. These results collectively indicate that the spatial arrangement of mature coniferous forests, especially relative to successional forests, influence the habitat selection of lynx. These findings were detected, in part, because of the fine-scale space-use patterns I obtained from GPS telemetry collars and my use of a hierarchical sampling design that evaluated habitat selection along a gradient of use intensity.

The proportion of the key successional and lowland-conifer forest types in CAs and PZs differed by only 3-5%, but my analyses suggest that the habitat in lynx CAs is distinct from that in the outlying territory and perhaps viewed as homogenous high quality habitat by lynx. First, most lynx showed neutral selection toward all forest types in my CA-CA models. The effect of habitat on animal movements often decreases in intensively used areas (Börger et al. 2006). If selection was defined with the more conservative ± 2 *SE* confidence intervals used here, lynx in northern Canada also would have shown neutral selection toward all forest types within entire territories (Poole et al. 1996). The smaller territories of lynx in the Poole et al. (1996) study may have been responsible for these neutral selection trends, similar to my analyses using CAs. Second, 12 of my 15 pooled candidate models had some support as the best CA-CA model, reflected by Δ_iAIC values < 10 (Burnham and Anderson 2002). Conversely, only 4 of the CA-PZ and 3 of the CA-OUT models had Δ_iAIC values < 10, indicating that many more candidate CA-CA models had a reasonable fit to the data than the CA-PZ and CA-OUT candidate models. Third, the reduced predictive ability of the CA-CA models indicates that the distribution of forest types in CAs was often too similar to the observed use to reliably predict lynx habitat selection within CAs. The improved predictive ability of my CA-PZ and CA-OUT models indicate that forest types in CAs were more consistently different from similarly sized areas within the PZs and outside the territory.

Previous studies have used the cores of carnivore territories to evaluate habitat use and selection (Poole et al. 1996, Potvin et al. 2000), but habitat-selection analyses evaluating differential use within territories are uncommon (but see Litvaitis et al 1986, Marzluff et al. 2004). Such analyses provide a more complete understanding of how habitat affects the space-use patterns of wide-ranging animals like lynx (Hodder et al. 1998, Marzluff et al. 2004, Börger et al. 2006). Territory size in carnivores typically scales to body size (McNab 1963, Lindstedt et al. 1986), but variability in the temporal and spatial distribution of prey can modify allometric scaling patterns (Stern 1998). Canada lynx have large territories relative to their body size, and their territories, especially those of males, are usually larger in southern populations (Mech 1980, Burdett et al. 2007). Although the distribution of breeding females will influence the territory size of males, southern lynx of either sex may require larger territories because of the patchy distribution and reduced abundance of hares at the periphery of their range (Burdett et al. 2007). Quality hare habitat is often more fragmented in southern boreal forests, which may diminish the magnitude of hare population cycles (Keith et al. 1993). Lynx in northern Canada will respond to low hare densities by increasing their territory size or abandoning their territories and traveling widely in search of prey (Ward and Krebs 1985). Although their space-use patterns change, lynx do not modify their habitat-selection patterns during prey declines (Mowat and Slough 2003). When resources like prey or habitat vary spatially or temporally, a focus on intensively used areas should enhance our understanding of how resource distribution affects the space use of carnivores. Core areas appear to represent relatively homogenous high-quality habitat for lynx in Minnesota. For southern lynx populations, and perhaps for northern lynx populations during lows in the hare cycle, the CA may be a better sampling unit for landscape-scale habitat analyses than the entire territory. The conventional use of 95% home ranges in habitat analyses should be reconsidered now that GPS telemetry systems, wide availability of remote sensing land-cover data, and advanced statistical modeling techniques like resource-selection functions (Boyce et al. 2002, Manley et al. 2002) allow animal movements and space-use to be defined and analyzed at finer spatial and temporal resolutions (Powell 2000).

Unlike previous studies of northern lynx populations (Poole et al. 1996, Mowat and Slough 2003), I found that sex and season modified the habitat-selection patterns of lynx. Lowland-conifer forests were consistently selected against by males, non-breeding females, and all lynx during winter, but females with 3-7 month-old kittens showed neutral use of these forests within their CAs and nearly selected for these forests in the CA-PZ comparison. Although I did not include locations from female lynx during the May-June denning season in my analyses, this result is consistent with lynx use of lowland-conifer forests for denning habitat in Minnesota (Moen et al., in review). The blown-down mature trees that characterize lynx denning habitat may continue to provide protective cover for reproductive females and their kittens during the 3-7 months after kittens begin traveling with their mother. It is possible that this effect of sex and season was discovered by the increased location frequency of GPS collars, and that similar patterns would have been observed if this technology had been used in other areas. Although it is reasonable to assume that females with young kittens have similar habitat requirements throughout lynx range, the more diverse mesocarnivore community in southern boreal forests may increase the importance of protective cover for lynx kittens that are less than 6 months old. The interspersion of mature forests for denning and young forest for foraging appears to be a critical consideration for lynx conservation planning.

Lynx Response to Forest Types

In Minnesota, lynx consistently selected for successional forest except within their CAs. Although somewhat counterintuitive, this finding resulted from the increased abundance and availability of successional forests in CAs. The association between lynx and successional forest is common throughout the U.S. and Canada (Koehler 1990, Poole et al. 1996, Mowat and Slough 2003, Hoving et al. 2004). In western North America, lynx occur in mountainous areas where fine-scale disturbances in old-growth forests may provide both moderate hare populations and high squirrel populations, thus providing access to multiple prey species in the same area (Buskirk et al. 2000). However, I found little evidence that such localized fine-scale disturbances influenced lynx movements or habitat selection in Minnesota. Lynx in Minnesota rarely hunted squirrels during winter (C. Burdett, unpublished data) and instead intensively used successional forests because hare populations were more abundant there (McCann 2006). The natural disturbance regime of northern Minnesota is more similar to that of northern Canada than to the western North American mountains, and the lynx I studied exhibited habitat-selection patterns that suggested adaptation to the frequent large fires that historically controlled succession in the boreal forest (Heinselman 1996).

I did not have the remote-sensing data to assess differences between deciduous and coniferous successional forests. Among successional forests, hares typically prefer coniferous to deciduous stands (Cook and Robeson 1944, Grange 1949, Wolff 1980, Wolfe et al. 1982). I therefore believe that the preferences for successional forests that lynx and hares show in Minnesota are primarily associated with conifer-dominated stands, although this needs to be confirmed with remote-sensing data that discriminates between these different successional forest types.

Although sex and season strongly affected lynx use of lowland-conifer forests, my finding of neutral selection for these forests at the population-level may underestimate the extent that most lynx select against these forests. Three lynx, M06, F09 (a non-reproductive female), and M12, never used this forest type even though it comprised 3, 4, and 10% of the area within their core areas. This lack of use precluded stable maximum-likelihood estimates for the lowland conifer regression coefficient. Because M06 and F09 had < 5% lowland-conifer forest within their CAs, and M12 had the least CA locations (*n* = 12) of the lynx I monitored, I chose not to use unstable maximum-likelihood estimates for the lowland-conifer variable, nor include these lynx in population-level estimates for selection for lowland-conifer forest (Fig. 4). I therefore caution that lynx may often select against these lowland-conifer forests to a greater extent than my results indicate. Despite the importance of lowland-conifer forests to reproductive females, lynx selection against these forests likely results from the low abundance of hares there (McCann 2006).

The poor quality of lowland-conifer forest as foraging habitat for lynx is somewhat surprising because previous studies in Minnesota have reported abundant hare populations in lowland-conifer forests, including the black spruce stands that comprise most of these forests in my study area (Pietz and Tester 1983, Fuller and Heisey 1986). This discrepancy may result from hares being more abundant in more diverse lowland-conifer forests with denser understories containing cedar, balsam fir, and deciduous shrubs such as alder that characterized the earlier studies (Conroy et al. 1979, Fuller and Heisey 1986), or regional hare populations during my study being lower than when these previous studies were conducted (Heinselman 1996). Studies from northern Canada and Maine also reported that lynx selected against lowland-conifer bogs (Poole et al. 1996, Hoving et al. 2004). Black spruce bogs are typically species poor, have low productivity, and have open understories lacking in cover. However, the importance of these forests for reproductive female lynx (Moen et al. in review) indicates that management of lynx- and hare-habitat should include lowland-conifer forest as a habitat component for this important life stage.

The remaining forest types, upland-conifer and mixed, were mature forests that lynx generally used in proportion to their availability. Lynx showed slight selection for upland-conifer forests in their CAs but only relative to the lesser amount present in infrequently used areas. Although lynx often select for conifer forests (Koehler 1990, Poole et al. 1996, Mowat and Slough 2003, Hoving et al. 2004), particularly at broad scales (Hoving et al. 2005), the effect of coniferous forests on lynx habitat selection appears to be dependent on factors like spatial scale, stand age, and perhaps latitudinal gradients. Unlike the spruce-dominated forests of northern Canada, mixed deciduous-coniferous forests were the most abundant forest type in northeastern Minnesota. Although I found neutral selection for these mixed forests, the increasing dominance of deciduous species in the most common, or matrix, forest type may indicate a decreasing gradient of habitat quality at lower latitudes if deciduous forest is a key factor limiting the southern distribution of lynx (Hoving et al. 2005).

Lynx Response to Forest Edges

Lynx travel along edges between different forest types (Mowat et al. 2000). I found this behavior to be primarily associated with edges between upland-conifer and successional forests. Lynx were closer to these edges than expected within PZs and entire territories, but not within CAs. The reduced selection for edges in CAs likely results from upland conifer-successional forest edge being more abundant in CAs than in less intensively used portions of territories, but additional analyses will be needed to better understand how lynx respond to forest edges and spatial heterogeneity at broader spatial scales.

Several felid species use edge habitats because they contain dense cover for ambush hunting (Logan and Sweanor 2001, Fernández et al. 2003, Hopcraft et al. 2005, Laundre and Loxterman 2007). Forest edges may have the opposite effect on Canada lynx with lynx preferentially hunting in stands with more open understories that are adjacent to successional stands. Lynx often avoid hunting in areas with dense understories, even if hares are more abundant there (Murray et al. 1995, Fuller et al. 2007). The anatomical adaptations of lynx for deep snow allow them to hunt in more open area than other mesocarnivores (Murray et al. 1995). These adaptations likely permit lynx to vary their hunting strategy according to the density of understory vegetation, stalking and chasing hares in more open areas and hunting from ambush beds in areas with dense cover (Murray et al. 1995). The relationship I found between lynx and forest edges is consistent with lynx using a stalking strategy in these areas because I found the edge relationship to be more prevalent when the lynx was in an upland-conifer patch that was adjacent to a successional stand, rather than vice-versa. Mature upland-conifer stands in southern boreal forests have a less-developed understory than successional stands (De Grandprè et al. 1993), and lynx may be able to stalk hares more efficiently when in the mature portion of the upland conifer-successional edge. Conversely, ambush hunting may be less effective in areas with relatively open understories. Rather than using edges for increased cover like many felids, lynx may use the edge between mature and successional forests as a better environment to hunt by stalking. If true, this supports the hypothesis that lynx often select foraging habitat based on the availability, rather than abundance, of hares (Fuller et al. 2007). Studies of the relationship between hares and forest edges often describe slight increases in abundance in edges, but the trend is inconsistent among studies (Conroy et al. 1979, Wolfe et al. 1982, Potvin et al. 2005).

Selection for edges has important implications for lynx conservation. Forest management to benefit lynx and hare populations could utilize relatively small patches of successional forest interspersed among mature forest to provide both dense understory cover for hares and foraging and denning habitat for lynx. The large fires that occur over much of the geographic range of lynx and hares typically contain many patches of unburned forest (Niemi and Probst 1990, Poole et al. 1996, Mowat et al. 2000, Mowat and Slough 2003). Designing timber harvests to mimic natural disturbance patterns has been advocated (Bergeron et al. 2001), and lynx would likely benefit from this management policy. However, the response of lynx to forest edges should be studied in other portions of their range. Lynx in the western mountains of North America often inhabit naturally heterogenous areas and may respond differently to habitat than lynx in boreal or sub-boreal forests where vegetation communities are less influenced by topography (Buskirk et al. 2000). For example, lynx may not select for edges where the transition between adjacent patches is abrupt, like between forest and non-forest. Also, due to differences in fire suppression and forest-management policies, selection for edges should be studied in northern Canada. Timber harvest has replaced fire as the dominant forest disturbance in northern Minnesota (Heinselman 1996). The negative public perception of clearcuts often reduces their size and creates more smaller patches of successional forest than occur after fires (Bergeron et al. 2001). Landscape patterns in areas of northern Canada without fire suppression likely differ from those in my study area. Although hares may be more abundant in large patches of successional forest like those resulting from fires (Keith et al. 1993), our current understanding of the factors affecting the landscape-scale distribution and abundance of snowshoe hares in southern boreal forests are too limited to draw clear conclusions about how hares respond to the composition and configuration of landscapes at broad spatial scales.

Similarly, the distribution of hares and lynx may also be affected by the greater dominance of deciduous vegetation occurring in southern boreal forests. Despite similarity in their selection for younger forests, southern lynx populations inhabit landscapes with a different vegetation matrix than northern populations. Both hares and lynx are broadly associated with coniferous forests (Wolff 1980, Wolfe et al. 1982, Hoving et al. 2005). In areas not influenced by topography, deciduous species become more abundant at the southern limit of boreal forest (Pastor and Mladenoff 1992). In this study area mixed deciduous-coniferous forests were the dominant habitat type, whereas lynx inhabit a matrix of coniferous forest in northern Canada. Their ability to persist in the southern portion of their range appears to be limited by the greater dominance of deciduous tree species (Hoving et al. 2005). Beyond these prey and habitat effects associated with human influence on forest succession and latitudinal gradients in the dominance of deciduous vegetation, southern lynx populations may be further limited by other factors like snow depth, climate change, and increased human-related mortality (Hoving et al. 2005, Carroll 2007).

My results show that technological advances like GPS telemetry allow more quantitative, focused, and biologically relevant analyses of animal space use and habitat selection. The capability to accurately define areas that animals intensively use represents an important new advantage for management because intensive use usually indicates the areas within an animal's territory that contain the abundant resources. Strict reliance on territory-scale habitat analyses may produce less accurate and meaningful results than those that consider different intensities of use, especially for wide-ranging animals like lynx. Nevertheless, while intensively used areas like cores are valuable for understanding habitat requirements, the entire territory remains a better choice for depicting the spatial requirements of threatened species like lynx because the portion of a territory outside of the core likely provides critical benefits. For example, the size, location, and composition of the territory periphery may reduce the negative impact of environmental variability (Börger et al. 2006). This concern is particularly relevant to Canada lynx because of their dependence on prey that exhibit large spatial and temporal fluctuations in abundance.

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Table 1. Mean (± *SE*) percentage of 14 land-cover classes defined from satellite imagery (Minnesota Land Management Information Center, St. Paul, Minnesota) for the core areas and peripheral zones of 11 Canada lynx territories in Minnesota.

Land-cover class	Core area (CA)	Peripheral zone (PZ)
Deciduous forest	< 1	< 1
Water	1 ± 0.4	2 ± 0.5
Upland grassland	< 1	< 1
Mixed forest	36 ± 2.8	38 ± 1.4
Lowland grassland	2 ± 0.3	3 ± 0.3
Lowland conifer	13 ± 2.2	16 ± 1.2
Agriculture	< 0.1	< 0.1
Upland conifer	24 ± 2.0	23 ± 1.8
Rural development	< 1	< 1
Shrub/grassland	2 ± 1.1	1 ± 0.6
Mining	< 1	< 1
Urban development	< 0.1	< 0.1
Successional forest	20 ± 2.3	15 ± 1.5
Bare rock	0	0

Table 2. Criteria for evaluating the predictive ability of lynx habitat models using out-of-sample model validation method of Howlin et al. (2004).

Slope (β)	95% C.I. on β	Predictive capability of model
β is either + or -	C.I includes 0	Unacceptable
0< β < 1	C.I. excludes 0 and 1	Acceptable
β > 1	C.I. excludes 0 and 1	Acceptable
β > 0	C.I. excludes 0 and includes 1	Good

Table 3. Model-averaged coefficients and unconditional *SE* estimates (in parentheses) based on AIC w_i for individual- and pooled candidate models with Δ_i AIC values < 10.

		Variable			
Lynx[a]	Comparison[b]	Mixed forest	Lowland conifer	Upland conifer	Regeneration
M2	CA-CA	-0.07 (0.07)	-0.22 (0.12)	0.08 (0.06)	0.40 (0.17)
	CA-PZ	0.29 (0.13)	-1.50 (0.50)	0.17 (0.11)	1.00 (0.38)
	CA-OUT	1.09 (0.39)	-0.51 (0.25)	1.31 (0.48)	1.91 (0.62)
M5	CA-CA	0.27 (0.15)	-1.25 (0.53)	-0.42 (0.22)	0.07 (0.11)
	CA-PZ	0.61 (0.30)	-0.67 (0.33)	-0.26 (0.21)	1.11 (0.44)
	CA-OUT	0.13 (0.06)	-1.80 (0.55)	0.01 (0.07)	0.13 (0.06)
M6	CA-CA	-0.22 (0.09)	not used[c]	0.05 (0.04)	-0.02 (0.03)
	CA-PZ	-1.01 (0.26)	not used[c]	0.02 (0.03)	0.00 (0.03)
	CA-OUT	-0.13 (0.06)	not used[c]	-0.44 (0.17)	0.15 (0.07)
F7	CA-CA	0.16 (0.08)	-0.36 (0.15)	-0.22 (0.10)	0.13 (0.07)
	CA-PZ	0.68 (0.19)	-0.05 (0.04)	-0.05 (0.04)	1.12 (0.29)
	CA-OUT	0.04 (0.09)	-0.23 (0.10)	0.44 (0.17)	0.52 (0.20)
F9	CA-CA	-0.19 (0.11)	not used[c]	-0.43 (0.22)	0.29 (0.14)
	CA-PZ	0.19 (0.10)	not used[c]	-0.79 (0.36)	1.47 (0.42)
	CA-OUT	0.03 (0.04)	not used[c]	-0.07 (0.05)	2.37 (0.36)

Table 3. Continued.

		Variable			
			Lowland	Upland	
Lynx[a]	Comparison[b]	Mixed forest	conifer	conifer	Regeneration
M10	CA-CA	-1.00 (0.41)	-0.13 (0.07)	0.15 (0.07)	0.37 (0.16)
	CA-PZ	-2.21 (0.53)	-0.17 (0.07)	2.00 (0.38)	1.11 (0.35)
	CA-OUT	-1.76 (0.51)	-0.10 (0.05)	2.82 (0.38)	2.00 (0.37)
M12	CA-CA	0.41 (0.35)	not used[c]	-2.15 (1.25)	0.87 (0.63)
	CA-PZ	0.51 (0.36)	not used[c]	-0.60 (0.42)	1.99 (0.98)
	CA-OUT	0.15 (0.15)	not used[c]	-0.16 (0.15)	1.89 (0.80)
F14	CA-CA	0.72 (0.56)	0.47 (0.30)	1.46 (0.94)	1.20 (0.79)
	CA-PZ	-0.01 (0.07)	-0.01 (0.08)	0.05 (0.07)	1.12 (0.40)
	CA-OUT	-0.61 (0.36)	-0.77 (0.46)	0.45 (0.48)	1.30 (0.52)
F24	CA-CA	0.02 (0.05)	-2.10 (0.81)	-0.15 (0.08)	0.42 (0.26)
	CA-PZ	-0.05 (0.08)	-1.54 (0.67)	0.78 (0.30)	0.91 (0.36)
	CA-OUT	-0.12 (0.07)	-0.39 (0.21)	0.89 (0.32)	1.02 (0.36)
M28	CA-CA	0.02 (0.21)	-0.43 (0.26)	0.82 (0.43)	0.80 (0.36)
	CA-PZ	0.13 (0.19)	-1.09 (0.47)	0.44 (0.24)	1.30 (0.49)
	CA-OUT	0.13 (0.10)	-1.05 (0.44)	0.11 (0.10)	1.61 (0.40)

Table 3. Continued.

		Variable			
			Lowland	Upland	
Lynx[a]	Comparison[b]	Mixed forest	conifer	conifer	Regeneration
F31[d]	CA-CA	-0.43 (0.38)	0.50 (0.26)	0.50 (0.26)	-1.25 (0.77)
	CA-PZ	0.05 (0.30)	1.45 (0.73)	1.65 (0.86)	-0.45 (0.22)
	CA-OUT	-0.13 (0.10)	1.03 (0.56)	1.26 (0.75)	-0.25 (0.10)
Pooled	CA-CA	0.00 (0.01)	-0.52 (0.16)	0.01 (0.02)	0.34 (0.16)
	CA-PZ	0.01 (0.02)	-0.77 (0.49)	0.16 (0.06)	0.89 (0.11)
	CA-OUT	0.06 (0.02)	-0.40 (0.12)	0.75 (0.12)	1.19 (0.11)

[a] M= male, F = female

[b] CA= core area, PZ = peripheral zone, OUT = outside territory

[c] No use locations were recorded in this forest type.

[d] Collinearity in the global model therefore not included in model averaging.

Table 4. Percentage of 11 Canada lynx exhibiting neutrality, positive selection, and negative selection of 4 forest types in northeastern Minnesota. Confidence intervals used to determine selection were conservative estimates using ± 2 *SE* and were based on model-averaged coefficents and unconditional variance estimates for candidate models with Δ_i AIC values < 10.

Comparison[a]	Selection	Mixed	Lowland conifer	Upland conifer	Successional
CA-CA	Neutrality	73	45	82	64
	Positive	9	0	9	36
	Negative	18	55	9	0
CA-PZ	Neutrality	55	27	73	9
	Positive	27	0	18	82
	Negative	18	73	9	9
CA-OUT	Neutrality	64	27	55	0
	Positive	18	0	36	91
	Negative	18	73	9	9

[a] CA= core area, PZ = peripheral zone, OUT = outside territory

Table 5. Mean (± *SE*) importance ranks, $w_+(j)$, for 11 individual-level Canada lynx habitat selection models evaluated for 3 interterritorial spatial comparisons.

Comparison[a]	Mixed	Lowland Conifer	Upland Conifer	Successional
CA-CA	0.49 ± 0.04	0.64 ± 0.07	0.51 ± 0.05	0.55 ± 0.05
CA-PZ	0.61 ± 0.08	0.72 ± 0.08	0.56 ± 0.08	0.83 ± 0.07
CA-OUT	0.52 ± 0.07	0.70 ± 0.07	0.65 ± 0.08	0.80 ± 0.07

[a] CA= core area, PZ = peripheral zone, OUT = outside territory

Table 6. Pooled candidate models with Δ_iAIC values < 2, indicating strong support as best approximating model. Models are based on data collected from 11 lynx monitored with GPS telemetry in northeastern Minnesota from 2003-2006.

	Comparison[a]		
Model rank	CA-CA	CA-PZ	CA-OUT
1[b]	L*R	L*U*R	L*U*R
2[b]	L*U*R	M*L*U*R	M*L*U*R
3[b]	M*L*R	L*R	

[a] CA= core area, PZ = peripheral zone, OUT = outside territory

[b] M=mixed forest, L = lowland conifer forest, U = upland conifer forest, R = successional forest

Table 7. Predictive ability of lynx habitat models based on validation. Values represent percentage of both individual and pooled models that have unacceptable, acceptable, or good predictive ability based on criteria in Howlin et al. (2003).

	Comparison[a]		
Predictive ability	CA-CA	CA-PZ	CA-OUT
Unacceptable	22	0	11
Acceptable	44	33	33
Good	33	67	56

[a] CA= core area, PZ = peripheral zone, OUT = outside territory

Table 8. *P*-values indicating statistically significant differences in forest edge use within Canada lynx territories for 4 primary forest types occurring in northeastern Minnesota study area. Significance indicated by * ($P < 0.05$), ** ($P < 0.01$), and *** ($P < 0.001$). Direction of trend shown in parentheses where – indicates negative selection and + indicates positive selection. Non-significant results (NS) indicate that lynx use these edge types in proportion to their availability.

	USED PATCH							
	Mixed		Lowland Conifer		Mature conifer		Successional	
ADJACENT PATCH	CA-CA[a]	CA-PZ[a]	CA-CA[a]	CA-PZ[a]	CA-CA[a]	CA-PZ[a]	CA-CA[a]	CA-PZ[a]
Mixed	-	-	NS	NS	* (-)	*** (-)	NS	NS
Lowland conifer	NS	NS	-	-	* (-)	* (-)	NS	NS
Mature conifer	NS	NS	NS	NS	-	-	* (+)	NS
Successional	NS	** (+)	NS	NS	*** (+)	*** (+)	-	-

[a] CA= core area, PZ = peripheral zone, OUT = outside territory

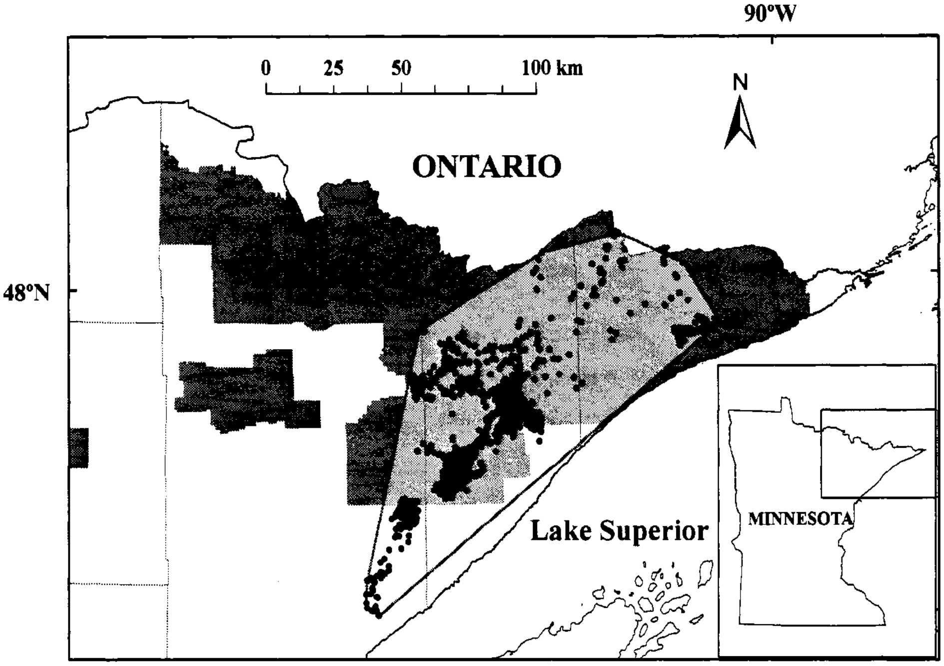


Figure 1. Northeastern Minnesota Canada lynx study area defined by minimum convex polygon around all Minnesota GPS collar locations. The locations of lynx that traveled into Ontario, Canada are not shown. The shaded area is the Superior National Forest.

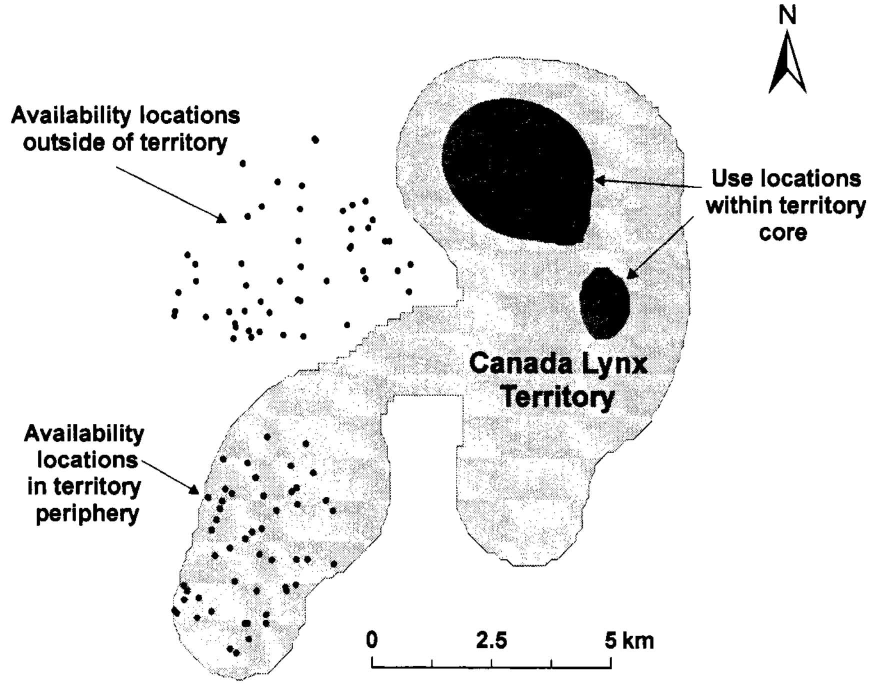


Figure 2. Diagram of sampling strategy used to evaluate lynx habitat selection within 95% fixed-kernel territory. Use locations are daily locations from GPS collars that occurred within core area. Availability locations are random locations sampled along a hierarchal gradient of decreasing use (within core area, within territory periphery, outside of territory). Availability locations within the core area and additional availability sample sets from other portions of the territory periphery and outside the territory are not shown for clarity.

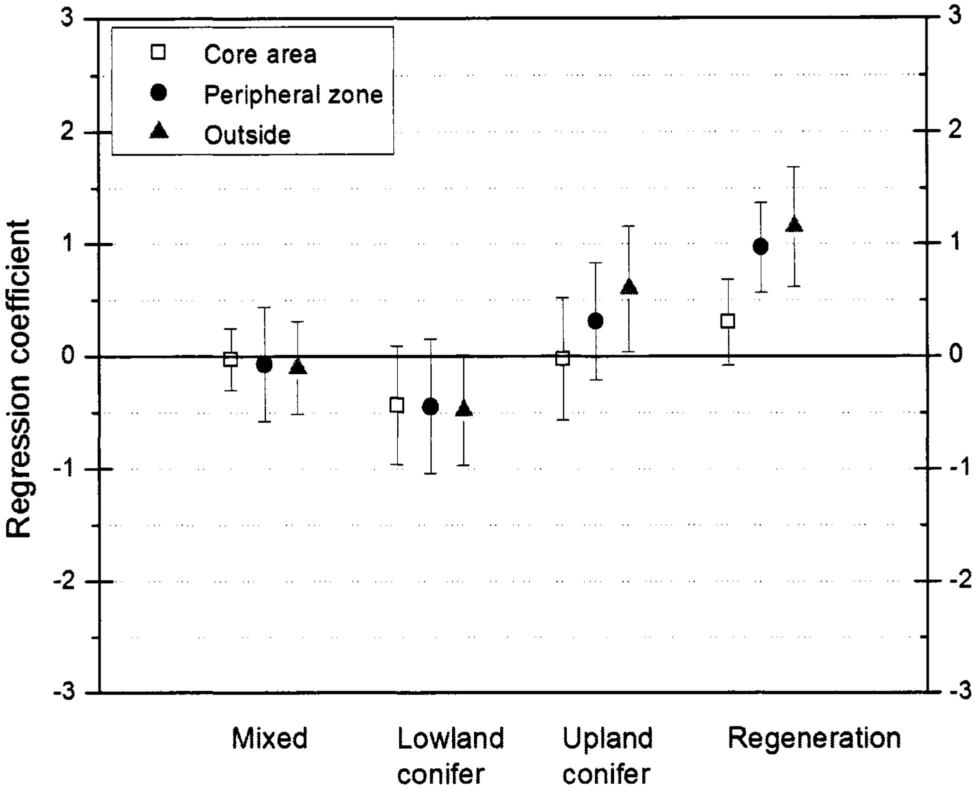


Figure 3. Regression coefficients showing direction of selection for four most abundant forest types in northeastern Minnesota. Plots represent mean ± 2 *SE* of model-averaged coefficients from logistic regression. If lower error bar is above zero, that forest type is preferred whereas if upper error bar is below zero that forest type is avoided. Forest types used in proportion to availability have error bars that overlap zero.

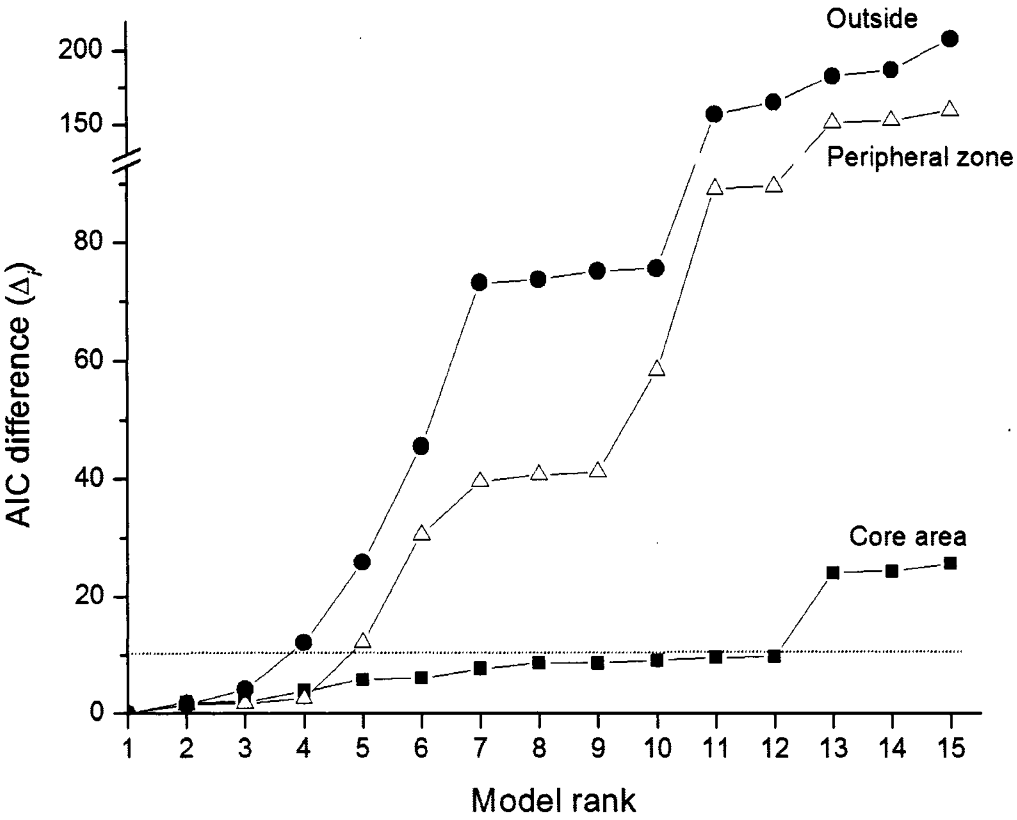
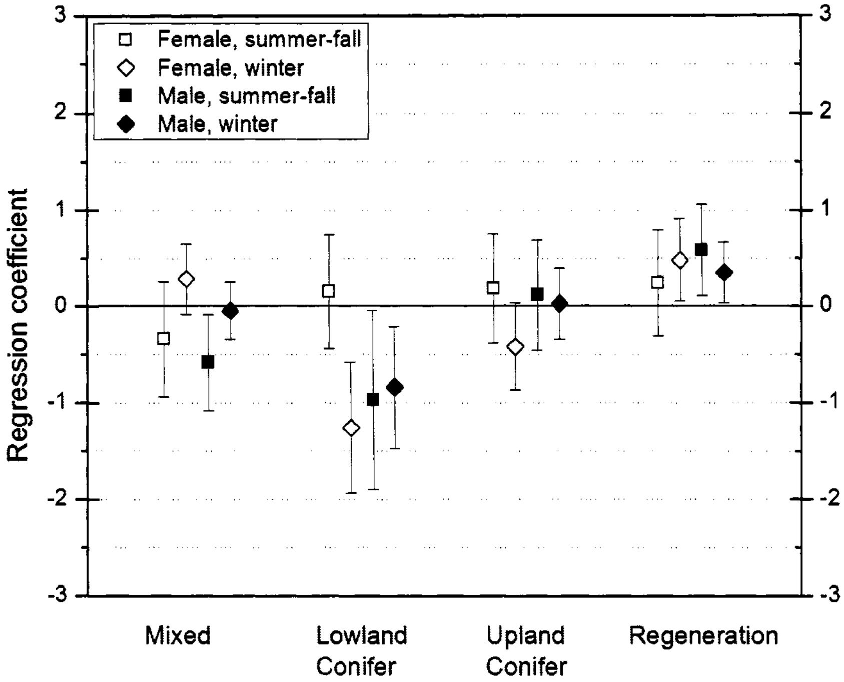
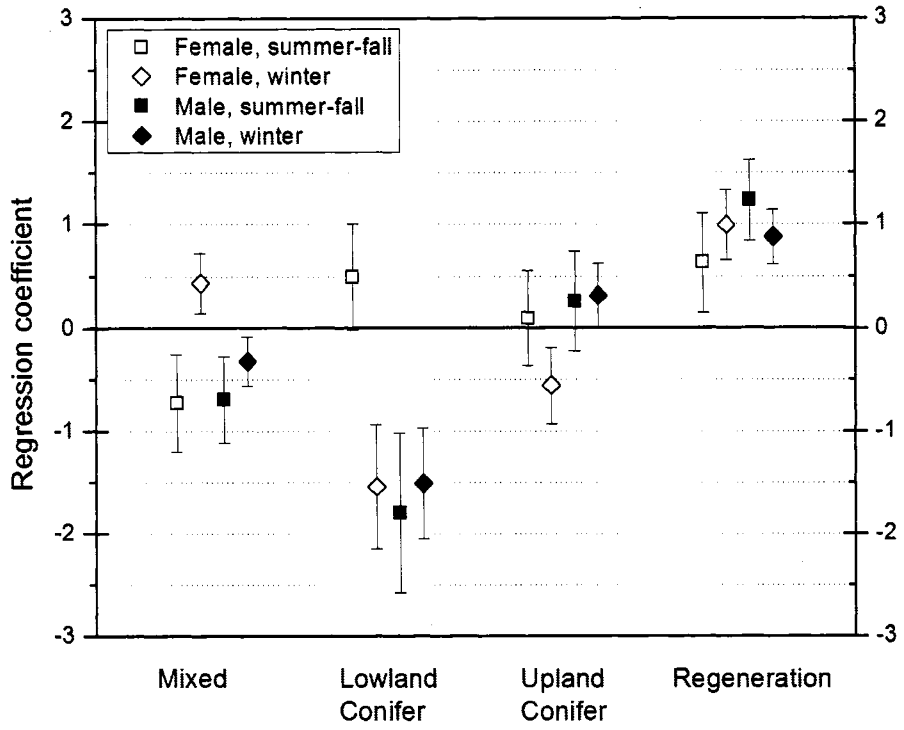


Figure 4. AIC difference (Δ_i) for all 15 candidate models evaluated for each spatial comparison when individuals were pooled. Models with a Δ_iAIC > 10, which is the value represented by the dashed horizontal line, have no support as the best model (Burnham and Anderson 2002).



A

Figure 5. Continued on next page.



B

Figure 5. Regression coefficients from stratified analysis showing direction of forest- type selection for male and female lynx in summer-fall and winter. Plots represent mean ± 2 *SE* of coefficients from logistic regression. If lower error bar is above zero, that forest type is preferred whereas if upper error bar if below zero that forest type is avoided. Forest types used in proportion to availability have error bars that overlap zero. Shown are results from (A) the CA-CA comparison, and (B) the CA-PZ comparison.