Spatial Ecology of a Canada Lynx Population in Northern Maine

JENNIFER H. VASHON,[1] *Maine Department of Inland Fisheries and Wildlife, 650 State Street, Bangor, ME 04401, USA*

AMY L. MEEHAN, *Maine Department of Inland Fisheries and Wildlife, 650 State Street, Bangor, ME 04401, USA*

WALTER J. JAKUBAS, *Maine Department of Inland Fisheries and Wildlife, 650 State Street, Bangor, ME 04401, USA*

JOHN F. ORGAN, *United States Fish and Wildlife Service, 300 Westgate Center Drive, Hadley, MA 01035, USA*

ADAM D. VASHON, *United States Department of Agriculture, Wildlife Services, 79 Leighton Road, Suite 12, Augusta, ME 04330, USA*

CRAIG R. MCLAUGHLIN, *Utah Division of Wildlife, 1594 W North Temple, Suite 2110, Salt Lake City, UT 84114, USA*

GEORGE J. MATULA, JR., *Maine Department of Inland Fisheries and Wildlife, 650 State Street, Bangor, ME 04401, USA*

SHANNON M. CROWLEY, *University of Northern British Columbia, International Center, 3333 University Way, Prince George, BC V2N 429, Canada*

ABSTRACT Canada lynx (*Lynx canadensis*) were listed as a federally threatened species in 14 states at the southern extent of their geographic range in March 2000, with Maine being the only state in the northeastern United States known to support a resident population. Relatively little information is known about the ecology of lynx living at the southern edge of their range, including range requirements, movements, and spatial organization. Basic knowledge of lynx ecology is needed for federal recovery planning efforts. Between 1999 and 2004, we trapped and radiocollared 43 lynx (21 M, 22 F) in northern Maine in an intensively managed and predominantly early successional forested landscape. We estimated diurnal annual and seasonal home-range size for male and female lynx using the 85% fixed-kernel home-range estimator. Annual home ranges of adult male lynx ($\bar{x} = 53.6$ km^2) were more than twice the size of adult female home ranges ($\bar{x} = 25.7$ km^2). Home ranges of adult females during snow periods ($\bar{x} = 38.3$ km^2) were nearly 3 times larger than their snow-free-period ranges ($\bar{x} = 14.3$ km^2), whereas, snow-free ranges of adult males ($\bar{x} = 58.8$ km^2) were slightly larger than their snow-period ranges ($\bar{x} = 45.2$ km^2). We observed a limited amount of home-range overlap among lynx of the same sex (F: $\bar{x} = 17.2\%$; M: $\bar{x} = 11.8\%$). Lynx of opposite sex showed more extensive overlap ($\bar{x} = 24.3\%$). Most home-range shifts of resident lynx were typically not extensive. Based on territory mapping, we estimated a minimum lynx density of 9.2–13.0 lynx/100 km^2. We observed lynx spatial ecology and densities that were more similar to northern lynx populations when hares were abundant than to other southern lynx populations, suggesting that region-specific studies under varying habitat conditions and hare densities are needed to ensure realistic recovery goals and effective management of lynx at the southern extent of their range. (JOURNAL OF WILDLIFE MANAGEMENT 72(7):1479–1487; 2008)

Canada lynx (*Lynx canadensis*) were listed as a federally threatened species in 14 of the conterminous United States in March of 2000 (U.S. Department of Interior 2000). Once listed, the United States Endangered Species Act (ESA; 1973) requires that areas critical to the species recovery be identified (i.e., Critical Habitat Designation—Section 4[C] of ESA) and conservation efforts established and implemented to lead to the recovery of the species. At the time of federal listing, lynx had been studied at only a few locales, despite the occurrence of lynx across a broad geographic range (Buskirk et al. 2000). Much of our knowledge of lynx ecology had come from the core of lynx range (i.e., the boreal forests of Canada and Alaska, USA [e.g., Ward and Krebs 1985, Bailey et al. 1986, Poole 1994, Slough and Mowat 1996, O'Donoghue et al. 2001]). Only 7 studies of short duration and with low sample size had been conducted at the edge of the species' geographic range, mostly in the western United States (i.e., Koehler et al. 1979, Mech 1980, Parker et al. 1983, Brittell et al. 1989, Koehler 1990, Apps 2000, Squires and Laurion 2000).

Lynx prey mostly on snowshoe hare (*Lepus americanus*); consequently, lynx populations exhibit dramatic population cycles in delayed synchrony (1–2 yr) in areas where snowshoe hare cycle (Elton and Nicholson 1942, Keith 1963). During periods of highest hare abundance, lynx exhibit high productivity and recruitment, low mortality, and small home ranges. However, when hare numbers decline lynx productivity declines, and mortality, movements, and home-range sizes increase (Ward and Krebs 1985, O'Donoghue et al. 1997). Koehler and Aubry (1994) hypothesized that lynx population demographics at the southern extent of their geographic range were similar to lynx populations in the core of their range during cyclic hare lows. Lynx in the western United States and southwestern Canada had large home ranges and low densities, productivity, and survival, supporting this hypothesis (Koehler 1990, Apps 2000, Squires and Laurion 2000). Murray (2000) summarized information on hare demographics in the contiguous United States, finding hare populations to be either weakly cyclic, irruptive, or largely stable providing additional support for this hypothesis. McKelvey et al. (2000) and Ruggiero et al. (2000) suggested that southern lynx populations are sustained by functioning as parts of metapopulations that include the more stable lynx populations of Canada.

[1] *E-mail: Jennifer.Vashon@maine.gov*

To date, radiotelemetry studies in Washington, USA, provide the most comprehensive information on lynx home-range requirements and potential lynx densities at the southern edge of their range (Brittell et al. 1989, Koehler 1990). Koehler (1990) reported density estimates that did not incorporate home-range overlap among lynx; thus, densities were potentially underestimated. When lynx were listed as threatened, almost no information on the status of lynx in Maine, USA, was available and information specific to the northeast was limited to a single study with a small sample size on Cape Breton Island, Nova Scotia, Canada (Parker et al. 1983). We studied lynx in Maine to address concerns raised by Buskirk et al. (2000) about extrapolating information from one region to another and to provide information needed for lynx recovery efforts. Our objectives were to describe the annual and seasonal home-range size and spatial relationships of a radiocollared sample of an unexploited lynx population in northern Maine. We evaluated the hypothesis that southern lynx populations exhibit demographics similar to lynx in Canadian boreal forests during hare lows and its applicability to the conservation of Maine's lynx population.

STUDY AREA

The study area encompassed 4 townships (386 km^2) in the Musquacook lakes region of northwestern Maine; our capture effort focused in the 2 southern townships (Fig. 1). The area ranged in elevation from 250 m to 550 m and was characterized by rolling hills and wide valleys. Regenerating white (*Picea glauca*) and red spruce (*P. rubens*) and balsam fir (*Abies balsamea*) stands dominated the area. This spruce–fir forest was interspersed with lowlands comprised of black spruce (*P. mariana*), tamarack (*Larix laricina*), and northern white cedar (*Thuja occidentalis*) and ridges dominated by sugar maple (*Acer saccharum*) and birch (*Betula* spp.). Much of the area (approx. 46% or 17,562 ha) was clear-cut in the 1980s to salvage trees impacted by the spruce-budworm (*Choristoneura fumiferana*) epizootic and to prevent further expansion of the spruce-budworm.

Nearly half of Maine's 6.8 million ha of forest, including our entire study area, were owned by large timber companies and were intensively managed for forest products (Seymour and Hunter 1992). Land-management activities included timber harvesting, herbicide applications to promote conifer regeneration, precommercial thinning to enhance stand growth, and road construction. Human settlements were limited to seasonal camps and logging operations, and most roads were unimproved dirt roads used primarily for wood harvest and transportation. Public access was allowed and regulated by the North Maine Woods Association, a non-profit organization of landowners established to manage access on 1.4 million ha of private forestland in northern Maine.

METHODS

From March 1999 to December 2004, we captured lynx using number 3 Soft Catch® foothold traps (Woodstream
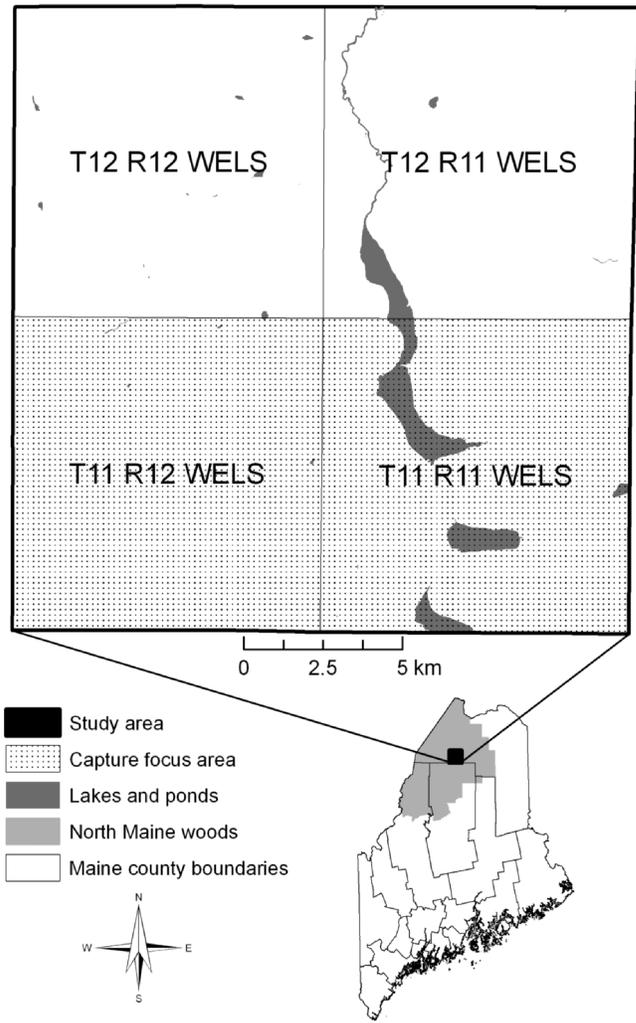

Figure 1. Map of the Musquacook Lake lynx study area in northern Maine, USA, 1999–2004, showing the 2 townships where we focused our capture effort. The entire study area encompassed 4 townships (386 km^2) in the North Maine Woods, which encompassed approximately 1.4 million ha of commercial forestland.

Corporation, Lititz, PA), cage traps (Model no. 50590, 122-cm front-release box trap; Safeguard Products, Inc., New Holland, PA, and hand-made traps), and hounds trained to pursue bobcats (*Lynx rufus*). We immobilized lynx with a mixture of ketamine hydrochloride (10 mg/kg) and xylazine hydrochloride (2 mg/kg) administered intramuscularly with a syringe pole (91.4-cm 3-cm^3 Pole Syringe; Tomahawk Live Trap, Tomahawk, WI) or dart gun (Vario IV Blowpipe Rifle; Telinject USA, Inc., Saugus, CA). We equipped lynx ≥1 year of age with very high frequency (VHF) radiocollars from Lotek Wireless Inc. (New Market, Ontario, Canada [SMRC1]) and lynx >6 months and <1 year of age with VHF radiocollars from Advanced Telemetry Systems (Isanti, MN [RPT]) and marked all lynx with uniquely numbered ear tags (Standard Rototags; Nasco Farm and Ranch, Ft. Atkinson, WI) in each ear. We collected genetic samples (tissue, blood, and hair) and morphological measurements from each lynx. We examined each lynx to estimate age (i.e., kitten <1 yr, subad 1–2 yr, or ad >2 yr)

and determine its sex. We estimated age based on body mass and tooth wear. For each lynx that died and was recovered, we pulled a canine tooth and submitted it to Matson Laboratory LLC (Milltown, MT) for age determination by cementum annuli. Animal capture and handling procedures conformed to guidelines established by the American Society of Mammalogists (American Society of Mammalogists 1998).

From March 1999 to December 2004, we located radiocollared lynx 2–3 times/week from fixed-wing aircraft (Piper Super Cub [Piper Aircraft Inc., Vero Beach, FL] Apr 1999–May 2003 and Cessna 172 [Cessna Aircraft Company, Wichita, KS] May 2003–Nov 2004) and we recorded their coordinates (Universal Transverse Mercator [UTM]) with a Global Positioning System unit. We obtained telemetry locations between 0500 hours and 1900 hours (Eastern Standard Time). From 2000 to 2002, 69% of telemetry locations occurred between 1000 hours and 1500 hours. In 2003 and 2004, 60% of telemetry locations occurred between 0800 hours and 1100 hours. We estimated telemetry error by comparing the aerial UTM coordinates for each collar on mortality mode to each mortality site UTM coordinates ($n = 18$ of 21 lynx mortalities). Other mesocarnivores were monitored in the study area during this study period, providing additional error estimates (10 mesocarnivore mortalities).

We estimated diurnal annual and seasonal home-range size for adult lynx using the Animal Movements Extension (Hooge and Eichenlaub 2000) for ArcView 3.2. We classified lynx that maintained established home ranges as residents ($n = 42$) and those that displayed wide-ranging movements as transients ($n = 1$). We did not calculate home-range size for lynx monitored for <9 months ($n = 6$) or with <50 locations ($n = 14$) following the recommendation of Seaman et al. (1999), or for transient lynx, because we were unable to track lynx that made extensive movements.

We estimated home-range size for the remaining 22 resident lynx using the fixed-kernel density method (Worton 1989). We used the least-squares cross-validation procedure to determine the appropriate bandwidth value (i.e., the width of individual kernels that determines the amount of smoothing of the data) for kernel estimates because it minimizes errors between the estimated and true density. We calculated the 95%, 90%, and 85% fixed-kernel contours to determine which estimate was most biologically meaningful and the 75% and 50% fixed-kernel contours to assess the importance of core areas for lynx, because the bounds of the 75% contour for females and 50% contour for males were the first contour that resembled a core area. We report the 85% fixed-kernel contour as a biologically meaningful approximation of home-range area, because we observed few locations in the outer contours for most lynx (17 of 22) and felt that the 95% or 90% contours would overestimate lynx range requirements. We monitored most lynx during multiple years; thus, we calculated an average annual home range for each individual lynx. We

evaluated gender-specific differences in home-range sizes for lynx using the Wilcoxon rank-sum test.

For diurnal seasonal home-range estimates, we defined 2 seasons based on snow climatological data from National Oceanic and Atmospheric Administration weather stations at Clayton Lake, Maine (approx. 15 km W of the western boundary of our study area): snow-free period (16 Apr–14 Nov) and snow period (15 Nov–15 Apr). We estimated seasonal home-range sizes for lynx that were monitored for 2 entire seasons and had ≥ 30 locations/season following recommendations by Seaman et al. (1999). We calculated an average seasonal home range for each lynx monitored during multiple years. We evaluated gender-specific differences in seasonal home-range size for lynx using paired-difference t-tests. We used SAS software (SAS Institute, Cary, NC) to conduct all statistical analyses and set $\alpha = 0.05$.

Of the 22 resident lynx monitored sufficiently to calculate annual home-range estimates, 16 were monitored during the third year of our study, representing the largest sample of lynx in a given year. Therefore, we evaluated spatial interactions during year 3 (15 Nov 2001–14 Nov 2002).

We evaluated spatial interaction among the annual home ranges of both intra- and inter-sexual pairs of lynx. We classified each pair of home ranges as either nonadjacent, adjacent nonoverlapping, or adjacent overlapping. Similar to Schenk et al. (1998), we defined home ranges as being adjacent if the minimum distance between home ranges was less than the average home-range diameter (M = 7.6 km, F = 5.0 km). We also determined the number of lynx with whom an individual shared a portion of its home range, both between sexes and among individuals of the same sex.

A few individual lynx home ranges were outside our capture focus area; thus, we were not monitoring all resident lynx in those areas. To minimize this bias, we excluded those individuals ($n = 3$) from our analyses. We estimated the amount of spatial overlap in the entire annual range (85% fixed kernel) and within core areas (M: 50% fixed kernel and F: 75% fixed kernel) of space-sharing (i.e., adjacent overlapping ranges) lynx using the methodology described by Atwood and Weeks (2003).

To evaluate change in an individual lynx home range (e.g., expansions, contractions, or shifts) from year to year, we used the multiresponse permutation procedure (MRPP) as described by Mielke and Berry (1982) with Blossom statistical software (Cade and Richards 2001). The MRPP determines if ≥ 2 sets of locations come from a common distribution. This test is independent of assumptions regarding underlying distributions and homogeneity of variances and has the power to detect small differences (Kernohan et al. 2001). If a lynx home range was not stable from year to year, according to MRPP, we examined the reason behind the instability (i.e., a shift in home-range centroid, expansion or contraction of home range).

In year 3, we estimated a minimum lynx density based on the home-range boundaries of radiocollared lynx in the portion of the study area where we focused our capture effort (Fig. 1). We defined a polygon based on the 85%

Table 1. Annual kernel home-range estimates (km^2) for resident radiocollared lynx in northern Maine, USA, averaged across years from November 1999 to November 2004.

	85% kernel			75% kernel			50% kernel				
Sex	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	N[a]	n[b]
F	25.7	4.0	13.8–56.0	15.3	3.4	6.8–43.1	5.3	1.8	1.8–20.5	11	58–132
M	53.6	4.7	33.3–83.9	39.9	3.5	26.8–62.9	17.3	1.5	9.6–28.3	11	51–130

[a] N = no. of radiocollared lynx in sample.
[b] n = min. and max. no. of telemetry locations/lynx used to estimate home-range size.

fixed kernels of 13 resident adult lynx (6 M, 7 F), excluding lynx outside the capture focus area. We used the demographic information from this study to estimate density of kittens in our study area (J. H. Vashon, Maine Department of Inland Fisheries and Wildlife, unpublished report). We provided the minimum and maximum number of kittens in our study area based on the number of kittens at the den site and the number of kittens traveling with females the next winter (estimated by backtracking collared ad F).

RESULTS

We captured and radiocollared 43 lynx (21 M, 22 F) from March 1999 to December 2004. Four of these lynx were captured incidentally by fur-trappers in or near our study site during the open coyote- and fox-trapping season and we radiocollared the 4 lynx before their release. At time of initial capture, we considered 26 lynx adults (11 M, 15 F; >2 yr), 14 subadults (8 M, 6 F; 1–2 yr), and 3 kittens (2 M, 1 F; <1 yr). We equipped all 3 kittens with radiocollars at 10 months of age. We observed no mortalities and only one injury related to capture.

Aerial radiotelemetry error varied with aircraft pilots but in all cases was <80 m ($n = 28$). From March 1999 to April 2003, we used one pilot and his telemetry error averaged 44.3 m (SE = 5.5 m, $n = 22$).

Although we radiocollared 43 lynx (21 M, 22 F), only 22 (11 M, 11 F) were residents and monitored sufficiently to produce annual estimates of home-range sizes. All 22 residents were adults. We monitored individual lynx an average of 3.4 years (range = 1–5 yr) for males and 2.3 years (range = 1–4 yr) for females, and we averaged home-range size across years for lynx monitored >1 year. The number of telemetry points/animal/year ranged from 51 to 132 ($\bar{x} = 85$, SE = 2.1).

Adult female annual home ranges averaged 25.7 km^2 (range = 13.8–56.0, SE = 4.0, $n = 11$). Adult male annual home ranges were twice the size of adult female home ranges ($W = 177$, $P = 0.004$; Table 1).

The average 50% fixed-kernel home ranges for female lynx ($\bar{x} = 5.3$ km^2) were associated with den sites; as a result, these areas were 3.3 times smaller than the average 50% fixed-kernel home ranges for males ($W = 177$, $P = 0.004$). The average 75% fixed-kernel contours for females ($\bar{x} = 15.3$ km^2) were 2.6 times smaller than for males ($W = 179$, $P = 0.003$) but did not differ in size from males' average 50% fixed-kernel contour ($W = 150$, $P = 0.146$; Table 1).

We monitored 18 resident lynx (9 M, 9 F) for both a snow and snow-free period allowing pairwise comparisons. Average snow-period home ranges for adult females ($\bar{x} = 38.3$ km^2) were 2.7 times larger than their snow-free-period ranges ($t_8 = 4.70$, $P = 0.002$) and most females (91%) were accompanied by kittens during both periods. Mean snow-free-period ranges for adult males ($\bar{x} = 58.8$ km^2) were 1.3 times larger than their snow-period ranges ($t_8 = -5.00$, $P = 0.001$; Table 2).

Spatial Interactions

Of the male pairs, 93% ($n = 14$) had annual home ranges that were adjacent, with 57% ($n = 8$ pairs) of the adjacent male home ranges overlapping (Table 3). On average, a space-sharing male home range overlapped with 2.7 other male home ranges (range = 2–4, $n = 6$ lynx). The average amount of home-range overlap each year was about 12%, but the amount of overlap varied by lynx pair (SE = 3.2; Table 4; Fig. 2). Of male core areas (50% kernel), 73% ($n = 11$ pairs) were adjacent, with 27% ($n = 3$ pairs) of adjacent male core areas overlapping (Table 3). Percent core area overlap was low ($\bar{x} = 3.0\%$, SE = 1.7; Table 4).

Of the female pairs, 67% ($n = 14$) had annual home ranges that were adjacent, with 21% ($n = 3$ pairs) of adjacent female home ranges overlapping (Table 3). On average, a space-sharing female home range overlapped with 1.2 other female home ranges (range = 1–2, $n = 5$ lynx); the average amount of home-range overlap was low ($\bar{x} = 17.2\%$ SE = 14.6, $n = 3$ pairs). Only 2 female pairs (15%) had overlapping core areas (75% fixed kernel; Table 3).

Table 2. Mean seasonal home-range (85% fixed kernel) sizes with associated standard errors for resident male and female lynx in northern Maine, USA, averaged across years from November 1999 to November 2004.

	Snow-free period				Snow period			
Sex	$\bar{x}$	SE	Range	n	$\bar{x}$	SE	Range	n
F	14.3	2.7	6.4–28.6	9	38.3	6.3	18.6–82.1	9
M	58.8	4.1	36.4–73.6	9	45.2	3.1	35.5–59.6	9

Table 3. Percent of lynx pairs with adjacent home ranges (defined as those with a min. distance between home ranges that was less than the average home-range diam [M = 7.6 km, F = 5.0 km]) and percent of adjacent pairs with overlapping annual home ranges in northern Maine, USA, during the third year of study (15 Nov 2001–14 Nov 2002).

	Fixed-kernel contour									
	85%					Core areas (M 50%, F 75%)				
Lynx pairs	N^a	A^b	n	AO^c	n	N^a	A^b	n	AO^c	n
M:M	15	93%	14	57%	8	15	73%	11	27%	3
F:F	21	67%	14	21%	3	21	62%	13	15%	2
M:F	42	74%	31	65%	20	42	71%	30	27%	8

[a] N = no. of pairs.
[b] A = % of lynx pairs with adjacent home ranges (n = no. of pairs with adjacent home ranges).
[c] AO = % of lynx pairs where adjacent home ranges overlapped (n = no. of adjacent pairs whose home ranges overlapped).

Although overlap in both the outer and inner contours was low (Table 4), one female pair had a high degree of overlap (46% in the 85% contour and 39% in the core area; Fig. 2).

Most (74%) male annual home ranges were adjacent to a female annual home range (n = 31 of 42 pairs), with 65% (n = 20 pairs) of adjacent male:female home ranges overlapping (Table 3; Fig. 2). On average, a male's home range overlapped with 3.3 female home ranges (range = 2–5, n = 6 lynx), whereas a female's home range overlapped with 2.9 male home ranges (range = 2–5, n = 7 lynx). The amount of home-range overlap between male and female space-sharing pairs was greater ($\bar{x}$ = 24.3%, SE = 6.2) than that observed between male:male and female:female space-sharing pairs (Table 4). Of male:female pairs, 27% showed an overlap ($\bar{x}$ = 41.0%, SE = 6.5; Table 4) of their core areas.

We monitored 9 resident adult males and 8 resident adult females for ≥2 years. Most (64%) home ranges were not stable from year to year, although between years 3 and 4 we observed a higher degree of stability among both male and female home ranges (Table 5). Among males, lack of stability was primarily due to home-range shifts but among females, home-range instability was a result of both shift and expansion or contraction of home-range areas. Although statistically lynx appear to lack fidelity to an area, a visual examination of home-range polygons indicates that this may be an artifact of the sensitivity of MRPP (Fig. 3), as also demonstrated by the average distance between home-range centroids (Table 5). The average distance between home-range centroids was greater for non-stable ranges; however, the differences were minor (M: $\bar{x}$ = 1,851.97 m, SE = 139.6, n = 13 for non-stable ranges vs. $\bar{x}$ = 516.5 m,

SE = 77.5, n = 9 for stable ranges; F: $\bar{x}$ = 1,057.0 m, SE = 108.1, n = 10 for non-stable ranges vs. $\bar{x}$ = 323.1 m, SE = 93.2, n = 5 for stable ranges) with the exception of one female (L40), who moved her home range (>11,000 m) due to suspected social factors.

We estimated an adult resident lynx density of 4.5 lynx/100 km^2 based on telemetry locations for 13 lynx (6 M, 7 F) in a 292.3-km^2 polygon. Our sex ratio of adult lynx was 54% female and 43% male, thus supporting 2.4 adult female lynx/100 km^2. Based on unpublished demographic data from this study, we estimated a density of 4.8–8.6 kittens/100 km^2 (J. H. Vashon, unpublished data), resulting in a total density of 9.2–13.0 lynx/100 km^2. This total density estimate is a minimum density, because we suspect that we did not radiocollar all resident lynx, and while snow-tracking we may not have detected all kittens that were present.

DISCUSSION

Our data on lynx spatial ecology do not support the hypothesis that southern populations of lynx exhibit home-range characteristics similar to lynx in northern populations during cyclic hare lows. This hypothesis was derived from lynx studies in the western United States and southwestern Canada, where lynx had large home ranges, low densities, and low productivity and survival (Koehler 1990, Koehler and Aubry 1994, Apps 2000, Squires and Laurion 2000). Conversely, Aubry et al. (2000) suggested that based on lynx densities, frequency of hares in the diet and home-range sizes, lynx demographics in Nova Scotia were probably more similar to northern lynx populations during periods of hare

Table 4. Percent of home-range overlap in annual 85% fixed-kernel and core-area home ranges of resident male and female lynx with overlapping ranges in northern Maine, USA, during the third year of study (15 Nov 2001–14 Nov 2002).

	85% fixed kernel				Core areas (M 50%, F 75%)			
Lynx pairs	$\bar{x}$	SE	Range	n^a	$\bar{x}$	SE	Range	n^a
M:M	11.8	3.2	0.7–26.6	8	3.0	1.7	0.1–5.8	3
F:F	17.2	14.6	0.6–46.4[b]	3	19.4	19.3	0.1–38.8[b]	2
M:F	24.3	6.2	0.1–77.6	20	41.0	6.5	2.7–55.5	8

[a] n = no. of pairs of lynx with overlapping home ranges.
[b] Note: One pair of F with a high degree of overlap inflated the average. Without this pair, the average F:F overlap would be 2.3%, with a range of 0.6–4.7. F:F core-area overlap would be 0.1%.
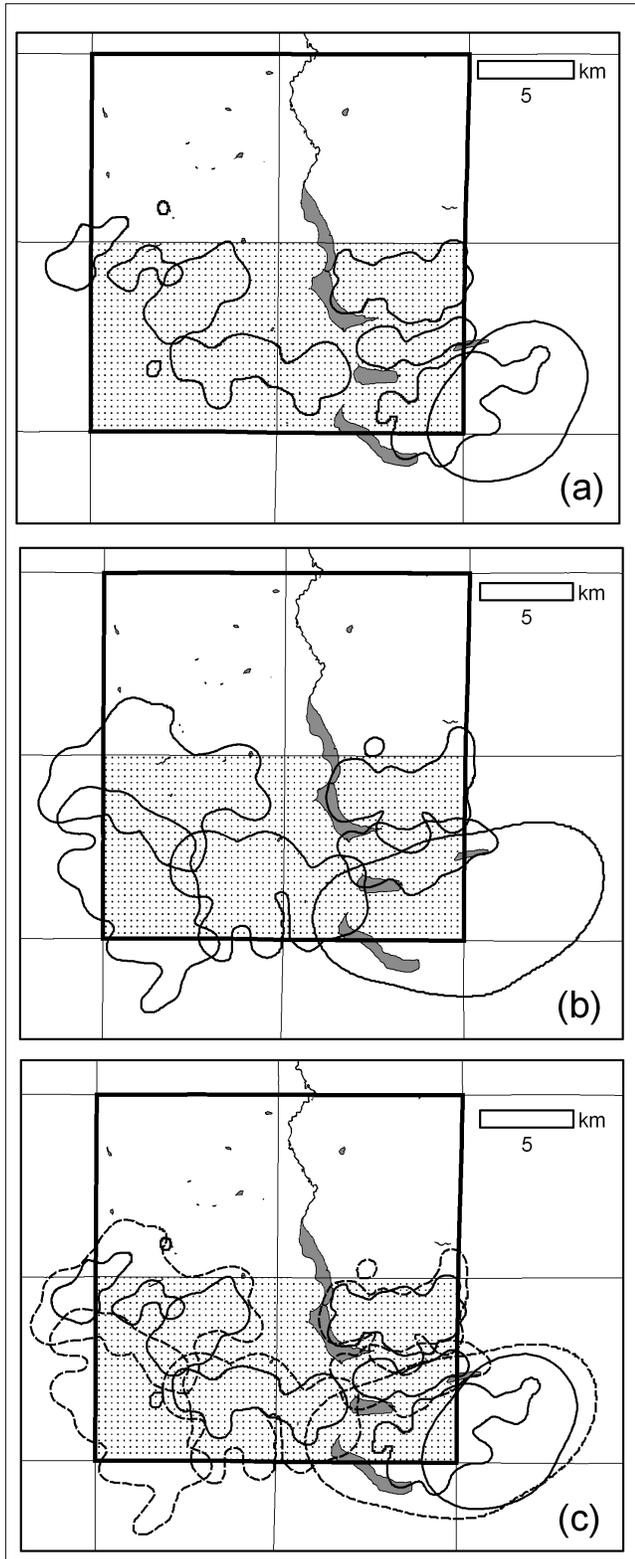
Figure 2. Configuration of (a) female, (b) male, and (c) both female (solid lines) and male (dashed lines) lynx home ranges in the Musquacook Lake study area in northern Maine, USA, from 15 November 2001 to 14 November 2002, the year with the highest sample size (13 individuals, 20 M–F overlapping pairs). The study area (dark outline) is overlaid on the township lines and the capture focus area is shaded. Major lakes and ponds are also shown.

abundance than to lynx populations in western montane regions. Demographic parameters we observed suggest that lynx populations in Maine are more similar to those in neighboring Nova Scotia, rather than to other southern lynx populations in the western United States. In our study, lynx home-range sizes were similar to those in Nova Scotia, and lynx densities approached estimates reported for that region (18.0/100 km^2; Parker et al. 1983). Our lynx density estimate (9.2–13.0/100 km^2) was between the low (2.3–3.0/100km^2) and high (17.0–44.9/100km^2) of the lynx population cycle to the north (Poole 1994, Slough and Mowat 1996, and O'Donoghue et al. 1997), and was >3 times the density reported in Washington (2.6/100 km^2; Koehler 1990).

In the western United States, dense regenerating coniferous habitats, which support high hare densities, are more disjunct than in the east (Buskirk et al. 2000). In our study area, dense regenerating conifers were well distributed and 46% of the forested habitat was estimated to have supported >1 hare/ha (Vashon et al. 2008). A hare density of 1/ha has been suggested as a threshold density for supporting lynx, because a collapse of home ranges and increases in home-range overlap and lynx movements have been observed when hare densities declined below this level (Ward and Krebs 1985, Poole 1994, Mowat et al. 2000, O'Donoghue et al. 2001).

Although no studies have examined home-range overlap of lynx at the geographic core of their range during hare highs, home ranges were exclusive in the Yukon (O'Donoghue et al. 2001) during declining hare densities, until hare densities dropped below 1/ha (F: 11% vs. 28% overlap; M: 7% vs. 75%). We observed little overlap among intra-sexual pairs of lynx and even less in their core areas, suggesting that both male and female home ranges were exclusive. Sandell (1989) suggested that an overlap of <10% measured on minimum convex polygon (MCP) ranges was a strong indicator of exclusivity; however, MCP ranges include areas not used by the animal, leading to more inflated estimates than the 85% fixed-kernel method we used. We believe that a low amount of overlap measured on the 85% fixed kernel would not only be more biologically meaningful, but also a stronger indication of exclusivity.

Female home-range size has been used as an indicator of habitat quality (Bailey 1974, Sandell 1989, Conner et al. 1999) and is principally determined by the distribution and availability of food during critical times of the year (MacDonald 1983, Sandell 1989, Gehrt and Fritzell 1998, Apps 2000). However, time in residence may also influence home-range size, with older females expected to have smaller home ranges (Conner et al. 1999). In our study, all radiocollared females were adults and nearly all were accompanied by young-of-the-year (J. H. Vashon, unpublished report). Incorporating measures of population fitness (e.g., recruitment rates) improves inferences from home-range sizes on habitat quality. The high kitten survival we observed ($\bar{x} = 73\%$; J. H. Vashon, unpublished report) suggests the small size of female home ranges reflects not

Table 5. Distance (m) between home-range centroids in consecutive years and indication of site fidelity[a] (from multiresponse permutation procedure) for lynx home ranges in northern Maine, USA, from November 1999 to April 2004.

| | M | | | | | | | | | F | | | | | | | | |
| | Yr 1–2 | | Yr 2–3 | | Yr 3–4 | | Yr 4–5 | | | Yr 1–2 | | Yr 2–3 | | Yr 3–4 | | Yr 4–5 | |
ID[b]	Distance	SF	Distance	SF	Distance	SF	Distance	SF	ID[b]	Distance	SF	Distance	SF	Distance	SF	Distance	SF
L18			1,685.7	NS	764.4	S	2,468.9	NS	L1	328.6	S	1,541.7	NS				
L2	1,625.9	NS	1,968.8	NS	1,628.4	NS	565.1	S	L24			1,311.0	NS	186.8	S	782.7	NS
L22			2,547.3	NS	394.6	S			L25			1,051.9	NS	66.1	S	875.8	NS
L23			425.4	S	1,598.4	NS			L35					1,213.7	NS	749.2	NS
L26			1,196.1	NS	571.2	S	2,423.9	NS	L37					600.8	S	1,561.9	NS
L28			853.6	S	1,439.7	NS	1,201.3	NS	L40					20,973.1	NS	11,641.1	NS
L29					552.7	S	1,674.3	NS	L43					433.1	S	928.1	NS
L4			2617.1	NS					L67							553.7	NS
L42					480.7	S	40.8	S									

[a] Site Fidelity (SF) is defined as not stable (NS) or stable (S).
[b] ID = lynx identification no.
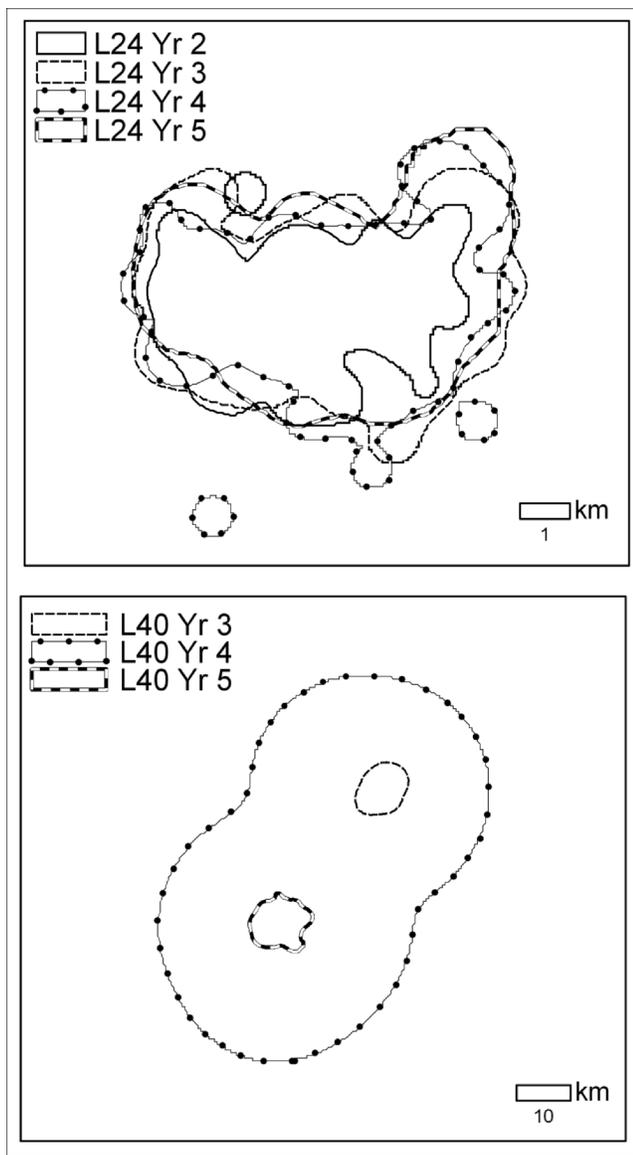
Figure 3. The 85% annual fixed-kernel home ranges of L24 and L40 (both F lynx) in northern Maine, USA, 2001–2004. Multiresponse permutation procedure results showed both home ranges as unstable from year to year.

only the age structure of our sample, but also the habitat quality and abundant prey in our study area.

Male spatial organization and home-range size are influenced by both food acquisition and the availability of receptive females (Sandell 1989). Because the snow period included the breeding season when males increase their movements in search of mates, we expected male home-range sizes to be largest during winter; however, that was not the case. Our sampling intensity (2 locations/week) may not have been sufficient to detect increased movements by males during the breeding season; nonetheless, typical male annual ranges overlapped the home ranges of ≥3 females, indicating that males did not need to increase their home ranges during the breeding season to acquire mates.

In most years of our study, lynx home ranges were not statistically stable. However, we observed minimal shifts in lynx home-range centroids, suggesting that although detectable statistically, the shift was not important biologically. Strong site fidelity has also been observed in other lynx studies, even during periods of hare decline (Poole 1994, 1995).

We would argue that the home-range exclusivity, small home-range sizes, and biological fidelity we observed reflects the habitat quality and abundant prey at the time of this study, and suggest that habitat quality plays a role in the differing spatial ecology of southern lynx populations. This region-specific information should help to improve lynx conservation efforts (e.g., recovery planning).

MANAGEMENT IMPLICATIONS

Our data may have been gathered at a lynx population peak; thus, the home-range sizes, lynx densities, and productivity that we observed may be impractical to use as parameter estimates for anything but high-end projections. Further, changes in forest harvest regulations may make it difficult to perpetuate the current levels of dense, early successional conifer forest in northern Maine. Thus, we recommend additional studies of lynx under varying habitat conditions and hare densities to document the variability in parameter

estimates to ensure realistic recovery goals and effective management of lynx in the northeastern United States.

ACKNOWLEDGMENTS

LITERATURE CITED

American Society of Mammalogists. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 19:1416–1431.

Apps, C. D. 2000. Space-use, diet, demographics, and topographic associations of lynx in the southern Canadian Rocky Mountains. Pages 351–372 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

Atwood, T. C., and H. P. Weeks, Jr. 2003. Spatial home-range overlap and temporal interaction in eastern coyotes: the influence of pair types and fragmentation. Canadian Journal of Zoology 81:1589–1597.

Aubry, K. B., G. M. Koehler, and J. R. Squires. 2000. Ecology of Canada lynx in southern boreal forests. Pages 373–396 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

Bailey, T. N. 1974. Social organization in a bobcat population. Journal of Wildlife Management 38:435–446.

Bailey, T. N., E. E. Bangs, M. F. Portner, J. C. Malloy, and R. J. McAvinchey. 1986. An apparent overexploited lynx population on the Kenai Peninsula, Alaska. Journal of Wildlife Management 50:279–290.

Brittell, J. D., R. J. Poelker, S. J. Sweeney, and G. M. Koehler. 1989. Native cats of Washington. Section III: lynx. Washington Department of Wildlife, Olympia, USA.

Buskirk, S. W., L. F. Ruggiero, K. B. Aubry, D. E. Pearson, J. R. Squires, and K. S. McKelvey. 2000. Comparative ecology of lynx in North America. Pages 397–418 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

Cade, B. S., and J. D. Richards. 2001. User manual for BLOSSOM statistical software. U.S. Ecological Survey Midcontinent Ecological Science Center, Fort Collins, Colorado, USA.

Conner, M., B. Plowman, B. D. Leopold, and C. Lovell. 1999. Influence of time-in-residence on home range and habitat use of bobcats. Journal of Wildlife Management 63:261–269.

Elton, C., and M. Nicholson. 1942. The ten-year cycle in numbers of lynx in Canada. Journal of Animal Ecology 11:215–244.

Gehrt, S. D., and E. Fritzell. 1998. Resource distribution, female home range dispersion, and male spatial interactions: group structure in a solitary carnivore. Animal Behaviour 55:1211–1227.

Hooge, P. N., and B. Eichenlaub. 2000. Animal movement extension to Arcview version 2.0. U.S. Geological Survey, Alaska Science Center–Biological Science Office, Anchorage, USA.

Keith, L .B. 1963. Wildlife's ten-year cycle. University of Wisconsin Press, Madison, USA.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166 in J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking animal populations. Academic Press, San Diego, California, USA.

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

Koehler, G. M., and K. B. Aubry. 1994. Lynx. Pages 74–98 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinkski, editors. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. U.S. Forest Service General Technical Report RM-254, Fort Collins, Colorado, USA.

Koehler, G. M., M. G. Hornocker, and H. S. Hash. 1979. Lynx movements and habitat use in Montana. Canadian Field-Naturalist 93: 441–442.

MacDonald, D. W. 1983. The ecology of carnivore social behaviour. Nature 301:379–384.

McKelvey, K. S., Y. K. Ortega, G. M. Koehler, K. B. Aubry, and J. D. Brittell. 2000. Canada lynx habitat and topographic use patterns in north central Washington: a reanalysis. Pages 307–336 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

Mech, L. D. 1980. Age, sex, reproduction, and spatial organization of lynxes colonizing northeastern Minnesota. Journal of Mammalogy 61: 261–267.

Mielke, P. V., and K. J. Berry. 1982. An extended class of permutation techniques for matched pairs. Communications in Statistics: Theory and Methods 11:1197–1207.

Mowat, G. K., G. Poole, and M. O'Donoghue. 2000. Ecology of lynx in northern Canada and Alaska. Pages 265–306 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

Murray, D. L. 2000. A geographic analysis of snowshoe hare population demography. Canadian Journal of Zoology 78:1207–1217.

O'Donoghue, M., S. Boutin, C. J. Krebs, and E. J. Hofer. 1997. Numerical responses of coyotes and lynx to the snowshoe hare cycle. Oikos 80:150–162.

O'Donoghue, M., S. Boutin, D. L. Murray, C. J. Krebs, E. J. Hofer, U. Breitenmoser, C. Breitenmoser-Wuersten, G. Zuleta, C. Doyle, and V. O. Nams. 2001. Coyotes and lynx. Pages 276–323 in C. J. Krebs, S. Boutin, and R. Boonstra, editors. Ecosystem dynamics of the boreal forest: the Kluane project. Oxford University Press, New York, New York, USA.

Parker, G. R., J. W. Maxwell, and L. D. Morton. 1983. The ecology of lynx

(*Lynx canadensis*) on Cape Breton Island. Canadian Journal of Zoology 61:770–786.

Poole, K. G. 1994. Characteristics of an unharvested lynx population during a snowshoe hare decline. Journal of Wildlife Management 58:608–618.

Poole, K. G. 1995. Spatial organization of a lynx population. Canadian Journal of Zoology 73:632–641.

Ruggiero, L. F., K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires. 2000. The scientific basis for lynx conservation: qualified insights. Pages 443–454 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pages 164–182 *in* J. L. Gittleman, editor. Carnivore behavior, ecology and evolution. Volume 1. Cornell University Press, Ithaca, New York, USA.

Schenk, A., M. E. Obbard, and K. M. Kovacs. 1998. Genetic relatedness and home-range overlap among female black bears (*Ursus americanus*) in northern Ontario, Canada. Canadian Journal of Zoology 76:1511–1519.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Taedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home-range estimates. Journal of Wildlife Management 63:739–747.

Seymour, R. S., and M. L. Hunter, Jr. 1992. New forestry in eastern spruce-fir forests: principals and applications to Maine. Maine Agricultural Experiment Station Miscellaneous Publication 716, Orono, USA.

Slough, B. G., and G. Mowat. 1996. Population dynamics of lynx in a refuge and interactions between harvested and unharvested populations. Journal of Wildlife Management 60:946–961.

Squires, J. R., and T. Laurion. 2000. Lynx home range and movements in Montana and Wyoming: preliminary results. Pages 337–350 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

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

Vashon, J. H., A. L. Meehan, J. F. Organ, W. J. Jakubas, C. R. McLaughlin, A. D. Vashon, and S. M. Crowley. 2008. Diurnal habitat relationships of Canada lynx in an intensively managed private forest landscape in northern Maine. Journal of Wildlife Management 72:1488–1496.

Ward, R. M. P., and C. J. Krebs. 1985. Behavioural responses of lynx to declining snowshoe hare abundance. Canadian Journal of Zoology 63:2817–2824.

Worton, B. J. 1989. Optimal smoothing parameters for multivariate fixed and adaptive kernel methods. Journal of Statistical Computation and Simulation 32:45–57.

Associate Editor: McDonald.