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Christopher Burdett

Ron Moen

Gerald J. Niemi

L. David Mech
USGS Northern Prairie Wildlife Research Center, david_mech@usgs.gov

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DEFINING SPACE USE AND MOVEMENTS OF CANADA LYNX WITH GLOBAL POSITIONING SYSTEM TELEMETRY

CHRISTOPHER L. BURDETT,* RON A. MOEN, GERALD J. NIEMI, AND L. DAVID MECH

Natural Resources Research Institute, University of Minnesota, 5013 Miller Trunk Highway, Duluth, MN 55811-1442, USA (CLB, RAM, GJN)
United States Geological Survey, Gabbert Raptor Center, University of Minnesota, 1920 Fitch Avenue, St. Paul, MN 55108, USA (LDM)

Space use and movements of Canada lynx (*Lynx canadensis*) are difficult to study with very-high-frequency radiocollars. We deployed global positioning system (GPS) collars on 11 lynx in Minnesota to study their seasonal space-use patterns. We estimated home ranges with minimum-convex-polygon and fixed-kernel methods and estimated core areas with area/probability curves. Fixed-kernel home ranges of males (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 that the home-range sizes of breeding females are less sensitive to sample size than those of 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 space use and movements by lynx 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.

Key words: Canada lynx, core area, global positioning system, home range, *Lynx canadensis*, movements, telemetry

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 very-high-frequency (VHF) radiotransmitters. Consequently, many estimates of annual home-range size have been based on fewer than 60 locations per animal (Koehler 1990; Mech 1980; Poole 1994; Slough and Mowat 1996; Ward and Krebs 1985). Global positioning system (GPS) collars have previously been restricted to use on large mammals (e.g., Arthur and Schwartz 1999; Merrill et al. 1998; Moen et al. 1996), 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.

Global positioning system collars also make it possible to use probability-based home-range methods, such as the fixed-kernel estimator, which require large samples (Seaman et al. 1999; Seaman and Powell 1996; Worton 1989). Kernel estimators offer advantages over traditional methods for determining home ranges 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 (Bingham and Noon 1997; Seaman et al. 1999; Seaman and Powell 1990). Also,

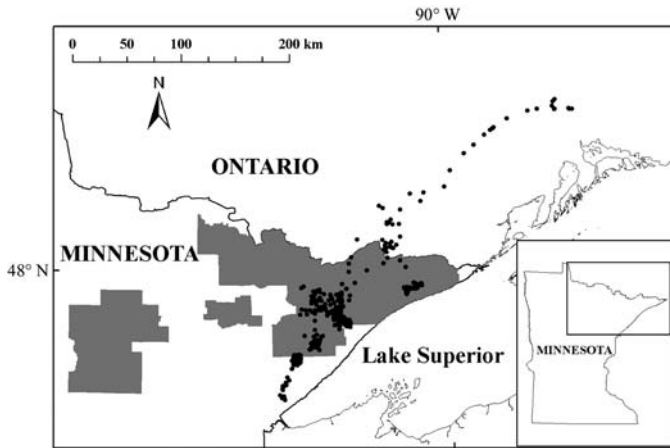* Correspondent: cburdett@nrri.umn.edu

Fig. 1.—Canada lynx study area in Superior National Forest, Minnesota, United States. Points represent the GPS locations of 11 Canada lynx wearing GPS collars in 2004–2005. The Superior National Forest is the shaded portion of the figure.

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; Mowat et al. 2000; Poole 1997; Squires and Laurion 2000).

Lynx range throughout much of Canada, with southern range extensions into the United States. Minnesota is one of only 4 or 5 states in the conterminous United States with a consistent history of lynx presence (Hoving et al. 2003; McKelvey et al. 2000). 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, 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.

We deployed GPS collars on Canada lynx in Minnesota. Our 1st 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. We investigated the effect of sampling frequency on estimates of lynx home-range size by sex and season. We also compared overlap among kernel home-range isopleths estimated from different sampling intervals. Our 2nd objective was to estimate sizes of annual and seasonal home ranges and core areas for lynx and relate these results to previous Minnesota

home-range estimates (Mech 1980). Finally, we evaluated monthly home-range sizes when lynx movements would have been strongly influenced by breeding activity.

MATERIALS AND METHODS

Study area.—Our 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 nonforested wetlands of alder (*Alnus*), willow (*Salix*), black spruce (*Picea mariana*), and cedar (*Thuja occidentalis*). Northern hardwoods are common along ridges because of milder climate resulting from topography and proximity to Lake Superior (Flaccus and Ohmann 1964). Historically, most forest types in northeastern Minnesota experienced a 50- to 200-year disturbance regime with upland-conifer–dominated stands typically having a shorter rotation period than upland-mixed or lowland-conifer forests (Heinselman 1996). Human activities have 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.

Capture of Canada lynx and data collection.—We captured lynx from February 2003 through March 2006 in custom-made cage traps (0.6 × 0.6 × 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). We monitored temperature, heart rate, and respiration rate of anesthetized animals at 10-min intervals, determined sex, weighed and measured the animals, and fitted them with a radiocollar. We reversed the xylazine with yohimbine (0.11 mg/kg) after an injection of Dualcillin (9,500 units/kg; G. C. Hanford Mfg. Co., Syracuse, New York). We 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 American Society of Mammalogists (Animal Care and Use Committee 1998) 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, Minnesota) or 1 of 3 models of GPS collars (GPS_3300; Lotek Wireless, Inc., Newmarket, Ontario, Canada; and C200 or C300; Telemetry Solutions, Inc., Concord, California). Lotek collars were programmed to attempt 4–12 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. We 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, whereas Lotek collars provided the number of satellites used for location estimates, search time, and the horizontal dilution of precision of each location (Moen et al. 1997). We screened our data for collars with extremely low fix rates that may indicate collar malfunction, the presence of improbable locations, and did not delete 2-dimensional fixes to avoid potential bias and because little topographic relief occurs in our study area (D'Eon et al. 2002).

Home-range and core-area estimation.—We used the Animal Movement Analyst extension (Hooge and Eichenlaub 2000) for ArcView 3.3 (ESRI, Redlands, California) 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 et al. 1999; Seaman and Powell 1996). We considered 3 seasons relevant to lynx biology: winter, when snow is typically present in the study area (1 December–30 April); denning (1 May–30 June); and summer–fall (1 July–31 November), when snow is typically absent. We 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. We 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 h. We 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). We 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.

We also investigated how breeding behavior affected lynx movements. We estimated fixed-kernel home ranges for March, the month with the most breeding activity in our 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, we did not exclude lynx with home ranges >1,600 km^2 in the

monthly breeding-season analysis because we were specifically interested in the presence and extent of long-distance movements associated with breeding behavior. We used a 2-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). We simulated this location frequency by randomly sampling locations from our 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, we created 100% MCP home ranges for all GPS-collared lynx with ≥18 locations, the minimum sample size used in the previous study (Mech 1980). We tested for differences between home-range sizes of males and females in these simulated home ranges with a *t*-test on log-transformed values.

We estimated the core areas of the annual and seasonal fixed-kernel home ranges with area/probability curves (Bingham and Noon 1997; Powell 2000; Seaman and Powell 1990). 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 (Bingham and Noon 1997; Seaman and Powell 1990). We used daily locations from individual lynx to calculate fixed-kernel home ranges with isopleths at 5% increments from 5% to 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. We created area/probability curves by plotting the percentage of the total home-range area within each isopleth as a function of the isopleths. We 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. We used the resulting regression coefficients (b_i) to determine the point (x) where the slope of the exponential regression curve was 1 by solving $x = [\ln(1/b_i)]/bi$ for each lynx (Bingham and Noon 1997).

We summarized the isopleths predicting core area and the core-area size by sex and period. We 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, we also estimated core areas for ten 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 nondenning

TABLE 1.—Summary statistics for 95% minimum convex polygon (MCP) and fixed-kernel home ranges (km²) of resident male and female Canada lynx estimated with GPS telemetry in Minnesota, 2003–2005.[a]

	n		$\bar{X} \pm SE$		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 > 1,600 km² were excluded from this analysis.
[b] Home-range sizes are significantly different between sexes ($P < 0.05$).

intervals. Five bimonthly nondenning season estimates were evaluated for each sex.

Effect of location interval on home-range area.—We calculated seasonal MCP and fixed-kernel home ranges using locations obtained daily, on alternate days, twice weekly, weekly, biweekly, 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 data sets 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.—We examined the extent of overlap among fixed-kernel home-range isopleths estimated from our simulated sampling frequencies to determine how the kernel estimate of internal home-range structure would change with less-intensive sampling. We estimated lynx home ranges with 5% isopleth increments using the daily, alternate day, twice weekly, and weekly locations. We restricted the overlap analysis to the 10-month winter and summer–fall seasons and excluded the biweekly and monthly home ranges to maintain sufficient sample sizes for kernel-based home-range estimation (Seaman et al. 1999). We used ArcGIS 9.1 (ESRI) 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 (C%—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 ∩ 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% to 95% in 5% increments and results compared between sexes. Unless otherwise noted, all mean values are presented as mean $\pm$ SE.

RESULTS

Global positioning system collar diagnostics.—Global positioning system 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, we have yet to recover the last 3 Lotek collars. The drop-off mechanism on 1 TS collar was successful and we recaptured 3 lynx wearing TS collars for collar replacement before drop-off occurred. The drop-off mechanism failed in 1 TS collar and we 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 because of 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-dimensional locations, 24% 2-dimensional locations, and 18% failed attempts. The horizontal dilution of precision ($\pm SD$) from the Lotek collars was 5.0 ± 4.0 for 2-dimensional fixes and 5.7 ± 4.1 for 3-dimensional fixes. Of the 1,995 location attempts by the C200 and C300 collars, 69% were successful, with 52% 3-dimensional locations, 16% 2-dimensional locations, and 32% failed attempts. None of the collars had fix rates < 20% indicative of collar malfunction and <0.1% of our locations were excluded as improbable.

Home-range and core-area estimation.—We used data from every GPS collar that we recovered although some lynx could not be included in an analysis because of limited monitoring time within a season or because the lynx made long-distance movements. Ten (6 males and 4 females) 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. We 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). We 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,

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]

Season	n		Isopleth (%)		Core area (km^2)	
	♂	♀	♂	♀	♂	♀
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 > 1,600 km^2 were excluded from this analysis.

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

2 of 5 winter and 3 of 5 denning season ranges included extraterritorial movements ≥ 30 km. Except for 1 winter home range, all females we monitored were either pregnant or raising kittens. Consequently, the denning and summer–fall seasonal results for females represent the ranges of females with maternal dens or traveling with kittens ≤ 5 months old. The summer–fall kernel home range for females was 3.4 times larger, and the winter kernel home range for females was 7.0 times larger than the denning season kernel home range. For females, the summer–fall MCP home range was 1.5 times larger, and the winter MCP home range was 3.6 times larger, than the denning MCP home range.

Random sampling of our GPS data with a similar location frequency as that of Mech (1980) created 42 (12 females and 30 males) home ranges from 8 (3 females and 5 males) individual lynx. Three lynx wearing GPS collars were not represented in our simulation results because they were monitored for insufficient time to meet our sampling criteria. Similarly, we did not create home ranges for the remaining 68 simulated location data sets because they had ≤18 locations. The 100% MCP annual home-range sizes were 27–355 km^2 for males ($\bar{X} = 134 \pm 13$ km^2) and 7–193 km^2 for females ($\bar{X} = 56 \pm 23$ km^2). 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 to 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 $65\% \pm 2\%$ 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 $60\% \pm 1\%$ (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
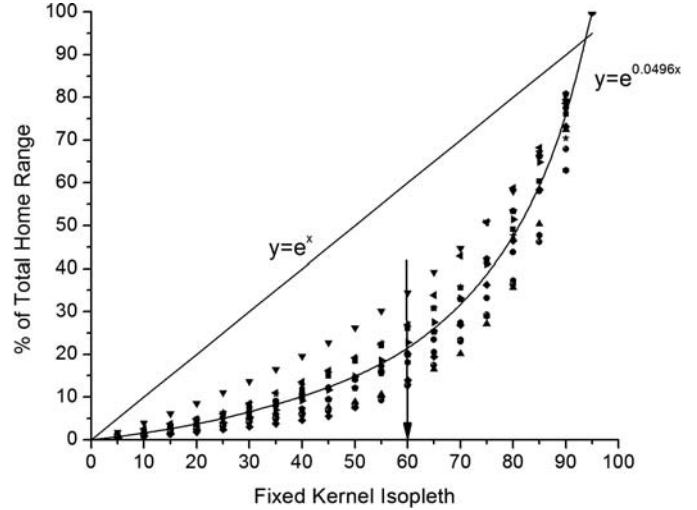

FIG. 2.—Area/probability curve estimating mean winter and summer–fall core areas of 8 Canada lynx wearing GPS collars in Minnesota, 2004–2005. Arrow depicts inflection point of exponential regression curve where slope of tangent line was equal to 1, predicting mean core area (60% isopleth) as area of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

seasons did not show similar increases to those during the denning season, with mean core-area isopleths of $59\% \pm 1\%$ for males ($n = 5$) and $60\% \pm 2\%$ for females ($n = 5$). We therefore used the 60% isopleth for statistical tests.
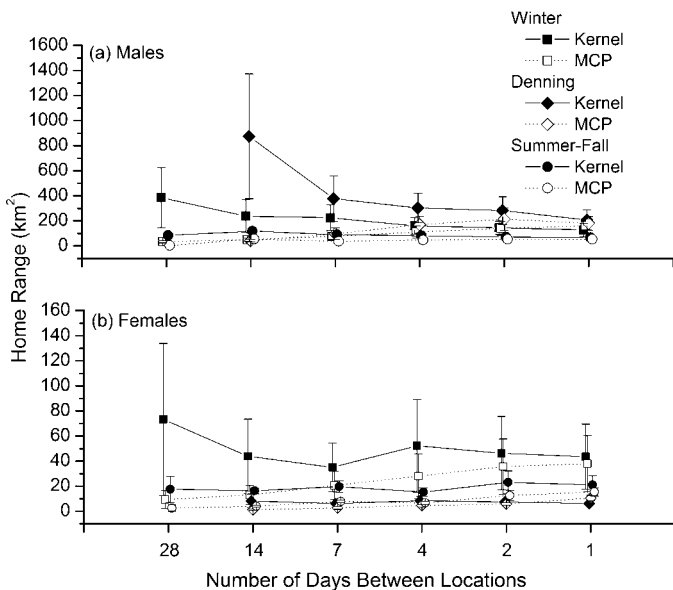
Similar to home ranges, the log-transformed core-area size was larger for males than for females annually ($t = 3.57$, $d.f. = 4$, $P < 0.02$) and during denning ($t = 6.98$, $d.f. = 6$, $P < 0.001$) but not during winter ($t = 1.63$, $d.f. = 6$, $P < 0.15$; Table 2). During winter the only nonbreeding female used a 19-km^2 core area, which was similar in size to most core areas of males. In comparison, the mean winter core-area size for 3 breeding females was 4 ± 1 km^2 (range = 3–6 km^2). Seasonal core areas of males averaged $24\% \pm 1\%$ and seasonal core areas of females averaged $23\% \pm 3\%$ of the 95% fixed-kernel home ranges.

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 to March. The monthly home-range size of adult female lynx changed little during the 3 breeding months but the home range of a subadult female decreased from 104 km^2 in February to 54 km^2 in March. Evidence along the snow trail of this subadult female indicated that she mated during late March 2004 (C. L. Burdett, in litt.). Although the mean home-range size for males in March was larger than in the other breeding months, the nonsignificant results were due to variability in home-range sizes of males 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 4,140 km^2 in 2 of the 5 males used in the breeding-season analysis.
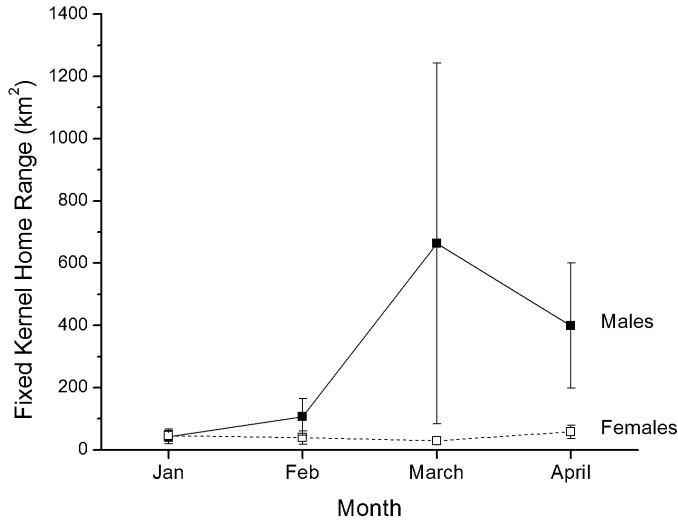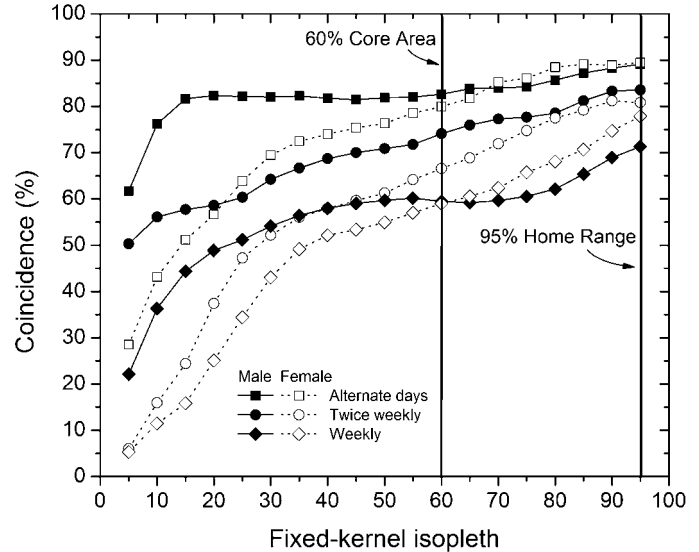
FIG. 3.—Monthly breeding season 95% fixed-kernel home ranges for January, February, and March. April also was included for comparison to preceding months with greater breeding activity. Mean values developed from 10 (5 males and 5 females) of 11 lynx monitored with GPS telemetry in Minnesota. Two males and 1 female were monitored over multiple winters.

FIG. 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.

Sensitivity analysis on location frequency.—Mean home-range size of males was overestimated with the fixed kernel and underestimated with the MCP as time between locations increased (Fig. 4). Home ranges of females showed little effect

FIG. 4.—Home-range area (km^2) for Canada lynx in Minnesota by home-range estimator (95% minimum convex polygon [MCP] and 95% fixed kernel [Kernel]), season, and number of days between locations for a) males and b) females. 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 ($\pm SE$).

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 fixed-kernel estimates for males.

Spatial analyses of home-range overlap.—Coincidence among fixed-kernel isopleths decreased with decreasing location frequency (Fig. 5). Our 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.—Shapes of the home-range area by number of observations curve varied between sexes. For males during the winter and denning seasons, the MCP home-range size increased with sample size, whereas the kernel estimator decreased, similar to other mammals (Arthur and Schwartz 1999; Bekoff and Mech 1984; Belant and Follmann 2002; Fritts and Mech 1981; Girard et al. 2002). The large variability associated with reduced sampling frequency for kernel home ranges of males likely resulted from the large sample requirements of kernel methods (Seaman et al. 1999). The home-range area by number of observations curves for females showed far

less sensitivity to location frequency. The home-range size of female lynx was affected by our use of reproductive animals. Although home ranges of females were consistently smaller than home ranges of males, 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 home-range estimates for females 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 (Slough and Mowat 1996; Ward and Krebs 1985). 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. Although female lynx also often required a similar location frequency to obtain home-range estimates within 20% of the maximum, the much smaller size of home ranges of females 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 < 30 km^2.

The sampling frequencies typical of VHF studies seem more problematic when kernel methods are used to depict the internal structure of a home range. 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. 2004).

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 (Seaman et al. 1999; Seaman and Powell 1996; Silverman 1986; Worton 1989). Least-squares cross validation is commonly used to calculate bandwidth for fixed-kernel home ranges (Seaman et al. 1999; Seaman and Powell 1996). However, the least-squares cross-validation algorithm can fail for GPS data sets 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 (Blundell et al. 2001; Silverman 1986). We found that least-squares cross validation applied an appropriate level of smoothing to our data because most of the lynx home ranges in this study consisted of ≤ 2 disjunct segments. We did not adjust bandwidth for 2 reasons. First, we did not experience failures in bandwidth calculation like Hemson et al. (2005) because we used daily locations and estimated home ranges on a seasonal basis. We 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, we did not encounter serious prob-

lems with linear movements because we excluded wide-ranging lynx from our 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. Although our use of daily locations for maximum estimates minimized the potential drawbacks of least-squares cross validation in this study, we agree that bandwidth calculation methods currently available in most home-range software may be problematic for GPS data sets 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 (Bingham and Noon 1997; Seaman et al. 1999). Currently, much of the conterminous United States lynx population lives on land managed by the United States Forest Service. The United States Forest Service evaluates the effects of forest management on lynx populations with lynx analysis units, which approximate the size of lynx home ranges (Ruediger et al. 2000). Current conservation strategies for lynx analysis units on United States Forest Service lands suggest that approximately 48 km^2 of quality lynx habitat should be present within a lynx analysis unit (Ruediger et al. 2000). Although we did not evaluate habitat use, the core areas we defined for male and female lynx with GPS telemetry are generally within the spatial extent suggested by these lynx analysis unit guidelines. Further validation of these conservation measures requires a better understanding of habitat selection by lynx, 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 core areas of lynx in northeastern Minnesota. The core areas of male (62.7%) and female (62.5%) Eurasian lynx (*Lynx 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 we 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.

Examination of our data supports earlier descriptions of lynx having large home ranges in Minnesota (Mech 1980). However, the mean home-range sizes of the male and female

TABLE 3.—Home-range sizes (km^2) for northern (>50°N) and southern (<50°N) populations of lynx, summarizing mean annual minimum convex polygon home-range sizes from individual studies.

Location	Latitude (°N)	$\bar{X}$ (range) ♂	$\bar{X}$ (range) ♀	n ♂	n ♀	Reference
Northern						
Alaska	65	20 (14−25)	13	2	1	Berrie 1973
Yukon	61	32 (14−255)	29 (7−33)	6	4	Ward and Krebs 1985
Northwest Territories	61	31 (3−68)	32 (7−91)	30	24	Poole 1994
Yukon	60	76 (12−498)	79 (3−775)	46	51	Slough and Mowat 1996
Alaska	60	424 (64−783)	70 (25−70)	2	2	Bailey et al. 1986
Nova Scotia	59	19	26	1	1	Parker et al. 1983
Manitoba	51	221	158 (138−177)	1	2	Carbyn and Patriquin 1983
Alberta/British Columbia	51	277 (224−357)	135 (44−276)	3	3	Apps 2000
Southern						
Washington	49	69 (56−99)	39 (38−41)	5	2	Koehler 1990
Minnesota[a]	48	194 (145−243)	87 (51−122)	3	4	Mech 1980
Minnesota[a,b]	48	267 (146−439)	21 (19−23)	4	2	This study
Montana	47	238 (20−534)	115 (15−164)	6	4	Squires and Laurion 2000
Wyoming	42	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.

lynx we 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 our study (Heinselman 1996; Mech 1973, 1980). In contrast, the lynx we 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, 1980). However, some lynx having home ranges within Minnesota during our study also moved north into Ontario. As expected, this trend was more common among males.

The use of GPS collars improved our 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 our primary reason to exclude these animals from our 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 our 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). We found that animals making these long movements maintained a constant body mass after long movements, although we only examined them 1–5 times. The male lynx we 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 (Liberg et al. 2000; Sandell 1989). Although we 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 we studied may be a response to the distribution of resident females. Home ranges of males are often larger in southern populations whereas home ranges of females 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 ($\pm SD$) home-range size of males in northern populations ($\bar{X} = 74 \pm 78$ km^2) is less than that of males in southern populations ($\bar{X} = 175 \pm 91$ km^2). Conversely, weighted mean ($\pm SD$) home-range sizes of females are similar between northern ($\bar{X} = 67 \pm 32$ km^2) and southern ($\bar{X} = 74 \pm 43$ km^2) 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 in northern populations because of 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 distribution of females (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 (*Lynx pardinus*) did not increase their home ranges in response to breeding activity, likely because of the lack of a well-defined breeding season for Iberian lynx (Ferreras et al. 1997). Although 5 of our 7 comparisons showed larger home-range sizes in March than in other breeding

months, these results were not significantly different because of limited sample size and the long-distance movements of 2 male lynx. One male made a movement of >70 km from Minnesota to Ontario, resulting in a fixed-kernel home range in March of 4,140 km². Although we cannot be certain this male bred with females in both Minnesota and Ontario, a male lynx with a home range > 700 km² 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 our 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, we found some male lynx traveling widely throughout January–March. However, the extraterritorial movements of the male lynx we 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.

Although some males moved long distances during the breeding months, others reduced their movements in March. Lynx likely reduce their breeding-season movements when population density permits access to multiple females in small areas (Breitenmoser et al. 1993). We suspect 1 male had a home range of <10 km² in March because of access to ≥2 females in this area. Examination of our data suggests that male lynx may increase their movements during the peak of the breeding season but also may adjust their movements based on density of females.

During our study, lynx in Minnesota appeared to have a social organization similar to that of 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; Liberg et al. 2000; Poole 1995). The frequent locations from our GPS collars allowed us to relate this pattern of social organization to lynx movements associated with reproduction. Although males had a tendency to increase their home ranges during breeding months, movements of females 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- to 2-km² core area. Understanding the space use of breeding females is clearly important for the conservation of lynx populations in the United States and GPS collars have allowed us 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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