

Space-Use, Diet, Demographics, and Topographic Associations of Lynx in the Southern Canadian Rocky Mountains: A Study

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Abstract—Snowshoe hares are considered the primary prey of Canada lynx throughout their range. Relative to northern populations, hares occurring in mountainous regions at southern latitudes are thought to remain at low and stable densities through time. Hence, the ecology of associated southern lynx populations is expected to resemble that of northern populations during the low phase of the hare population cycle. The space use, diet, and demographics of lynx in the Rocky Mountains of southeastern British Columbia and southwestern Alberta are consistent with this hypothesis, based on data collected from 10 lynx, including six (three males, three females) resident adults, during two years of an assumed increase phase of a hare cycle. Mean hare densities were low, ranging from 0.01 to 0.47/ha among cover types and landscapes. Lynx winter diet ($n = 137$ kills) was diverse and included hares (52%), red squirrels (30%), northern flying squirrels (5%), grouse (3%), martens (3%), and voles (3%). Kitten recruitment to winter was zero among adult females for four lynx-years. Family groups that did occur in the study area during winter were associated with small litters of two. Survival among resident

adults was 100%, but three of four subadults monitored during winter did not survive to mid-May. Home ranges were large, with annual 95% adaptive kernel utilization distributions averaging 381 and 239 km² for resident males and females respectively. Minimum daily movements averaged 3.8 and 3.0 km respectively. Two juvenile dispersals were short (44 and 17 km) and ended in starvation.

Space use by lynx may also relate to physiography, the influence of which may vary seasonally in mountainous landscapes. Most lynx selected mid elevations (1,550-1,850 m) and moderate to gentle slopes (<40%) within home ranges. Residents used higher elevations, and some used steeper slopes during summer than during winter. Highways were crossed less than random expectation within home ranges, suggesting that they influenced lynx movements. Sexual differences in home range size were not significant, but daily movements of males were greater than those of females, indicating that they used space more extensively.

Introduction

The ecology of northern Canada lynx populations varies temporally with snowshoe hare densities, as demonstrated with respect to population characteristics (Brand et al. 1976; Brand and Keith 1979; Poole 1994; Mowat et al. 1996; Slough and Mowat 1996; O'Donoghue et al. 1997), food habits and foraging behavior (Brand et al. 1976; O'Donoghue et al. 1998a; O'Donoghue et al. 1998b), space-use and movements (Ward and Krebs 1985; Poole 1994; Slough and Mowat 1996), and dispersal (Poole 1997). However, it appears that hare populations of southern latitudes and mountainous regions remain at relatively low and stable densities through time, possibly a result of a more patchy habitat distribution, greater competition, and a greater suite of predators (Dolbeer and Clark 1975; Wolff 1980). Hence, Koehler (1990) theorized that the ecology of southern lynx populations resembles that of northern populations during cyclic hare lows. Assuming that any variation of hare density will be synchronous throughout their range (Smith and Davis 1981), it follows that several hypotheses would hold true during the increase and high phase of the cycle. Relative to results reported for northern populations during hare lows, southern lynx populations should be associated with: (1) hare densities that are as low, (2) diet of as much alternate prey, (3) resident home ranges that are as large, (4) daily foraging movements that are as long, (5) reproduction and survival that are as low, and (6) dispersal rates that are as great.

Space use by lynx may also relate to physiography (Koehler and Aubry 1994), the influence of which may vary seasonally in mountainous landscapes. For example, open habitats that occur in conjunction with higher elevations and rugged topography are associated with several prey species that would be available only during snow-free months (Scotter and Ulrich 1995). Snow conditions that may restrict lynx movements and/or increase expended energy (Murray and Boutin 1991) are also more likely at higher elevations. Thus, individuals occurring in mountainous terrain can be expected to use lower elevations and gentler slopes, make shorter daily movements, and use smaller home ranges when snow is present. Near southern range extents, lynx can also be expected to use cooler, north and east aspects more often during snow-free months. This assumes that they are more susceptible to heat stress during summer because the species is better adapted physiologically to northern regions more central to its geographic range. Finally, just as physiography may affect space use of resident lynx, landscape features may also influence dispersal, and in highly mountainous terrain, movements can be expected to align with major valleys. Lynx movements may also be negatively influenced by highways due to habitat fragmentation and direct avoidance, an important consideration for their conservation (B. Ruediger 1996, unpublished). If highways restrict lynx movements, they should be crossed less than random expectation where they occur within home ranges.

Among solitary carnivores, it is assumed that female spacing patterns will reflect the distribution of resources, whereas space use by males also will conform to the distribution of females (Sandell 1989). Accordingly, home ranges of female lynx are generally smaller than those of males, and spatial overlap between sexes is extensive (Koehler and Aubry 1994; Poole 1995; Slough and Mowat 1996). Because social tolerance is expected among solitary foragers where resources are dispersed (Carr and McDonald 1986), these relationships should also hold true among southern lynx populations persisting in mountainous regions, where habitat is patchy and female home ranges are not necessarily contiguous. The more extensive space use expected from males also should be reflected in daily movements greater than those of females.

In this paper, I examine the hypotheses outlined above with research conducted in the southern Canadian Rocky Mountains between November 1996 and October 1998. Results are of an unexploited, southern lynx population, occurring in a highly mountainous region, during the increase phase of a snowshoe hare cycle in other regions (C. J. Krebs, personal communication).

Study Area

The study area ($>3,000 \text{ km}^2$) is centrally located within the Shining Mountains ecoprovince (Demarchi 1994), and most of it lies within the East Kootenay Wildlife Management Sub-region of southeastern British Columbia. It is defined by the Beaverfoot and upper Kootenay drainages on provincial land and straddles the Continental Divide of British Columbia and Alberta to include the Vermilion, Middle Bow, and Kicking Horse valleys within Kootenay, Banff, and Yoho National Parks.

Characteristic of the Canadian Rockies, much of the area is rock, ice, and other inherently unsuitable lynx habitat, and high peaks separate broad valleys incised by narrow tributary valleys. Elevations (1,200 to over 3,000 m) span three biogeoclimatic zones (Meidinger and Pojar 1991). Below 1,500 m, the Montane Spruce Zone is characterized by a climax overstory of hybrid Engelmann/white spruce and subalpine fir. The Engelmann Spruce-Subalpine Fir Zone occurs at higher elevations but below 2,300 m, where Engelmann spruce and subalpine fir dominate the climax overstory up to the Alpine Tundra Zone at highest elevations. Sub-climax stands throughout the study area are dominated by lodgepole pine. The macroclimate is continental, with mean temperatures ranging from -18°C (January) to 23°C (July) and 42-63% of the 51-81 cm mean annual precipitation falling as snow (Achuff et al. 1984). Natural and human conditions vary throughout the study area, and linear features include two- to four-lane paved highways with annual (1994) average daily traffic volumes of 1,119-8,322 vehicles per day (A. Clevenger, personal communication, Banff, AB), as well as industrial road networks, a twin-tracked railway, and trail systems.

Other predators and potential competitors with lynx include coyote, wolf, black bear, grizzly bear, marten, wolverine, cougar, at least three hawk species, golden eagle, and the great-horned owl. Fishers and red fox are rare, and bobcats are not resident (Poll et al. 1984). Potential lynx prey include snowshoe hares, red squirrels, northern flying squirrels, gallinaceous birds, microtine rodents, hoary marmots, ground squirrels, bushy-tailed woodrats, and beavers. Potential ungulate prey include moose, elk, bighorn sheep, mountain goat, mule deer, and white-tailed deer.

Despite a limited season in British Columbia, lynx have not been legally harvested on the provincial section of the study area for at least 15 years. Based on this, and the 68 years of protection that lynx have received in the national parks (Poll et al. 1984), I consider the resident population in the study area to be unexploited.

Methods

Hare Densities

I determined a range of snowshoe hare densities by counting fecal pellets during September 1998 in established 305 x 5.1 cm quadrats (Krebs et al. 1987). Ten quadrats were spaced at 30.5 m intervals along each of 61 transects. Transects were placed randomly among early- (20-60 years), mid- (60-120 years), and late- (>120 years) successional stands but were spaced by ≥ 500 m. Sampling was further stratified among three landscapes within the study area, representing geographically distinct areas where I consider terrain conditions conducive to supporting lynx. Hare densities were calculated with a modified version of the Krebs et al. (1987) regression equation, using the HARETURD program (C. J. Krebs, personal communication).

Lynx Capture

Study animals were captured during the winters of 1996-1997 and 1997-1998, with efforts focused in landscapes where lynx signs had been reported in recent years. Hounds trained to pursue felids were used to tree lynx, following methods described for cougars and bobcats (Hornocker 1970; Apps 1996). Live trapping was also carried out using Soft Catch® (Woodstream Corp., Litiz, PA.) #3 padded foot-hold traps in cubby sets (Hawbaker 1974) with modifications (Mowat et al. 1994). Captured lynx were immobilized with ketamine hydrochloride and xylazine hydrochloride at 10.0 and 2.5 mg/kg estimated body mass (Woodbury 1996), administered intramuscularly with an extendable pole-syringe or a *Cap-chur*® (Palmer Chemical and Equipment Co. Inc., Douglasville, GA.) Powder Projector dart gun. Anesthesia was occasionally maintained with an additional ketamine injection of 6.0 mg/kg. Immobilized lynx were sexed, and age was subjectively classed (adult: >2 years; juvenile: 1-2 years; kitten: <1 year) based on skeletal measurements and tooth wear. Study animals were fitted with motion/mortality sensing whip antennae radiocollars (Lotek Eng. Inc., Newmarket, ON.) and allowed to recover before release. Recovery was expedited on three occasions using atipamezole hydrochloride to reverse xylazine at twice the dosage of the latter (Woodbury 1996).

Radiotelemetry

Radiolocations were obtained throughout the year, at least weekly for all animals, and at least four days per week for most animals. Radiotelemetry was conducted from the ground and fixed-wing aircraft using standard

techniques (Samuel and Fuller 1996). Ground locations were estimated from three bearings taken within 1.5 hours, with origins located using hand-held Eagle Explorer® GPS receivers (Eagle Electronics, Catoosa, OK). Bearings were taken <2 km from the animal's estimated location 69% of the time. Two azimuths intersected at 70-110° for 88% of error polygons, and 89% of error polygons were <25 ha. Lynx were mostly inactive during 71% of ground locations, and I expect that time delays between bearings had a negligible effect on accuracy. Universal Transverse Mercator coordinates of radiolocations were referenced to ± 50 m from 1:20,000 orthophoto or 1:50,000 National Topographic System (NTS) maps. Positional error associated with 95% of aircraft radiolocations was considered to be ± 150 m (M. Gibeau, personal communication).

Food Habits

Study animals were snow-tracked during both years when possible, and kills and scavenging were documented over 759 km of trails. Prey remains were sufficient for positive species identification in most cases, although some kills may have been missed due to recent snow or for small prey. Tracks were directly observed wherever possible to minimize missed kills.

Population Attributes

Lynx carcasses and/or radiocollars were retrieved as soon as possible after mortality. Probable cause of death was determined from necropsies (Shury Veterinary Services, Canmore, AB) and field evidence. Female study animals were snow-tracked pre- and post-capture to determine whether kittens were present. When encountered, family groups of uncollared lynx were also snow-tracked to count kittens. The movements of females exhibiting strong site fidelity during May through July were radiotracked daily.

Space Use and Movements

I defined resident lynx as those associated with one activity center subjectively determined over at least three months. Home ranges of resident adults were estimated seasonally and annually over both years using the program CALHOME (Kie et al. 1996). I defined summer and winter seasons by the typical six-month snow and snow-free periods beginning and ending 1 November and 1 May. The late-February to early-April breeding period (Koehler and Aubry 1994) occurred in winter. To facilitate comparison with other research, I calculated the 100% and 95% minimum convex polygon (MCP) (Hayne 1949) and 95%, 75%, and 55% adaptive kernel utilization

distributions (UD) using optimal smoothing parameters (Worton 1989). Lynx movements indicated that home ranges could be traversed within 24 hours, thus only radiolocations that were temporally independent by this interval were used (*sensu* Swihart and Slade 1985). Among all animals, the 95% UD area appeared to asymptote at 43 to 55 radiolocations (Apps, unpublished). I compared UD levels between sexes and seasons using multivariate analysis of variance (MANOVA; $\alpha = 0.05$). Static interaction between lynx known to have neighboring or contiguous home ranges was inferred from spatial home range overlap (Macdonald et al. 1980).

I defined minimum daily movements (MDM) as the distance between sequential radiolocations separated by 18-36 hours ($\bar{x} = 24$ hours). Mean MDM were compared among resident lynx of each sex using analysis of variance (ANOVA; $\alpha = 0.05$), and between seasons and sexes using unpaired Student's *t*-tests ($\alpha = 0.025$). I assumed that lynx exhibiting consistent, linear movements were transient or dispersing animals. Where possible, I summarized the movements of these animals with respect to timing of dispersal, direction, distance, MDM, and proximate outcome.

Topographic Selection and Highway Influence

For each resident lynx, I assessed seasonal selection for elevation, slope, and aspect within respective annual home ranges. This corresponds to Johnson's (1980) third-order resource selection and Thomas and Taylor's (1990) Study Design 3, with inferences relevant at the individual level. Digital elevation, slope, and aspect models were derived in a GIS from 1:50,000 NTS elevation contours. Aspect was described by two ratio-scale (0→1) variables depicting south→north and west→east aspects. The raster resolution of each variable was set to 25 ha, roughly corresponding to the maximum spatial error of lynx radiolocations. Topographic attributes used by each animal were estimated from radiolocations temporally independent by at least 24 hours, following rationale described for home range analysis. Available attributes were estimated from an equivalent sample of systematic random locations within each animal's 95% UD. Variables were screened for multicollinearity using Pearson correlation coefficients (Tabachnick and Fidell 1989), and non-redundant ($r < 0.8$) variables were entered into multiple logistic regression to derive probabilistic resource selection functions (Manly et al. 1993). Box-Tidwell transformations (Box and Tidwell 1962) of elevation and slope were significant in some initial models, indicating that lynx selection for these attributes was non-linear (Hosmer and Lemeshow 1989). To facilitate comparisons among animals, I grouped elevation and slope data into three classes for each variable, roughly

corresponding to average 0.33 percentile groupings of available habitat among all animals. I tested the improvement of fitted models over null models by evaluating the reduction in (-2) log-likelihood ratios against a Chi-square distribution (Hosmer and Lemeshow 1989; $\alpha = 0.05$), and I assessed the explanatory power of each model by regressing actual use against predicted use probabilities to derive coefficients of determination (r^2). The significance of variable coefficients was evaluated using Chi-square tests of Wald statistics ($\alpha = 0.05$), and the contributions of each variable were assessed from the sign and strength of their partial correlations (r) with each model (Hosmer and Lemeshow 1989; Norusis 1994). From r statistics, I inferred preference where positive, and avoidance where negative. I evaluated differences in seasonal use of each variable using unpaired Student's t -tests ($\alpha = 0.0125$). I used SPSS 7.0 (SPSS Inc., Chicago, IL) software for statistical analyses.

Paved highways dissected all lynx home ranges relatively linearly. I therefore assumed that a crossing occurred if sequential radiolocations were obtained on opposite sides of a highway (Chapter 10). This facilitated tests of the null hypothesis that lynx movements within home ranges were random with respect to highways. Movements of resident lynx were defined as the minimum distance between sequential radiolocations, and for each, a movement vector of the same length but random location and azimuth was generated within respective 95% UD isopleths. Lynx and random movements were then coded according to their intersection with highways, and differences in lynx vs. random crossing frequencies were evaluated using Chi-square tests ($\alpha = 0.05$).

Results

Hare Densities

For early-, mid-, and late-successional stands respectively, mean hare densities by landscape were 0.16/ha (95% CI = 0.11-0.24), 0.08/ha (95% CI = 0.05-0.11), and 0.01/ha (95% CI = 0-0.02) in the upper Kootenay Valley; 0.25/ha (95% CI = 0.19-0.35), 0.06/ha (95% CI = 0.04-0.10), and 0.10/ha (95% CI = 0.07-0.15) in the Beaverfoot Valley; and 0.47/ha (95% CI = 0.36-0.62), 0.39/ha (95% CI = 0.26-0.57), and 0.32/ha (95% CI = 0.22-0.46) in the Vermilion Pass.

Food Habits and Population Attributes

Ten lynx, comprising three adult males, three adult females, one juvenile male, two kitten/juvenile females, and one kitten male, were radiocollared,

monitored and snow-tracked for 1-23 months between November 1996 and October 1998. Lynx kills ($n = 137$) documented over both years were composed of snowshoe hares (52%), red squirrels (30%), northern flying squirrels (5%), grouse (3%), martens (3%), voles (3%), a northern flicker (<1%), and unknown species (3%). One case of scavenging on an intact mule deer, presumed to have died from a vehicle collision, occurred for 2-4 days before it was usurped by wolves.

None of the three adult females in the study sample were traveling with kittens at the time of their capture in November 1997 or 1998. One uncollared family group was detected in the study area during March 1997, and three uncollared family groups were detected during November and December 1997. I assumed the latter groups were different individuals because each group was separated by a linear distance >30 km, beyond the maximum exploratory movement of radiocollared females (personal observations). Each group contained an adult and two kittens. Both kittens (M/04, F/03) from one family group were subsequently radiocollared, but neither survived to May. Two females that were monitored through March of 1997 (F/01) and 1998 (F/02) were snow-tracked while traveling with males, and F/02 was also directly observed during copulation with an uncollared male on 13 March. Daily radiolocations of F/01 were within 250 m of an activity center between 20 May and 1 June 1997, after which she resumed normal movements and did not revisit the presumed den site. From this, I inferred that she lost or abandoned her litter at or just after parturition. Kittens were also not detected with her during snow-tracking early in the following winter. Radiolocations of F/02 were within 500 m of an activity center on 82% of days between 22 May and 14 July 1998, and she was observed with one kitten in August of that year.

Known survival of resident adults was 100% over both years. A dispersing female kitten (F/03) and a transient, juvenile male (M/05) died of starvation on 15 April and 3 May 1998 respectively. A male kitten (M/04) likely was killed by an uncollared adult male lynx in December 1997 while traveling with his family group and within his natal range. A female kitten (F/05) released to her natal area in April 1998 after four months in captivity due to a capture injury survived at least the following six months.

Space Use and Movements

The mean number of radiolocations used for summer and winter home range estimates was 96 (range = 63-183) and 149 (range = 72-265) respectively. Mean 95, 75, and 55% UD estimates did not significantly differ between seasons for males ($F = 3.66$, 3 df, $p = 0.222$) or females ($F = 1.34$, 3 df, $p = 0.548$). Mean annual UD estimates (Table 12.1) also did not significantly

Table 12.1—Annual minimum convex polygon (MCP) and adaptive kernel utilization distribution (UD) home range estimates (km²) for resident lynx in the southern Canadian Rocky Mountains, British Columbia and Alberta, 1996-1998.

Lynx sex/ID	Period monitored (m/y)	n	100% MCP	95% MCP	95% UD	75% UD	55% UD
M/01	11/96 – 10/98	448	559	357	337	117	45
M/02	03/97 – 10/98	189	346	224	330	49	24
M/03	03/97 – 06/98	141	388	249	477	150	51
Male mean		3	431	277	381	105	40
Male SD			113	71	83	52	14
F/01	11/96 – 09/97	200	408	276	505	85	31
F/02	11/97 – 10/98	254	133	85	94	25	11
F/04	04/98 – 10/98	103	77	44	87	30	13
Female mean		3	206	135	229	47	18
Female SD			177	124	239	33	11

differ between sex ($F = 2.92$, 3 df, $p = 0.266$). Spatial overlap between the annual 95, 75, and 55% UD areas of M/01 and F/01 was 36, 63, and 60%, respectively. Of their 183 concurrent daily radiolocations, 78% were separated by >3 km. A second adult female was known to occur also within the 50% UD area of these two lynx, as inferred from snow-tracking and radiolocations of her dependent kitten (M/04). In addition, unmarked adult lynx were detected within the 70% UD of all other study animals between 1 November and 15 February 1998.

Minimum daily movement (MDM) (Table 12.2) differed among resident females during summer ($F = 9.81$; 2, 163 df; $p < 0.001$) but not winter ($F = 0.43$; 2, 235 df; $p = 0.65$). MDM differed among resident males during both summer ($F = 3.67$; 2, 182 df; $p = 0.027$) and winter ($F = 4.62$; 2, 349 df; $p = 0.010$). Movements were greater during summer for M/01 ($t = 3.48$, 278 df, $p < 0.001$) and were greater during winter for F/02 ($t = 2.72$, 125 df, $p = 0.007$), while seasonal differences were not significant among other residents ($t < 1.77$, 26-110 df, $p > 0.082$). Male movements were greater than those of females during both summer ($t = 5.01$, 347 df, $p < 0.001$) and winter ($t = 3.05$, 584 df, $p = 0.002$).

Dispersal

Dispersal movements were documented for three subadult lynx. After he was radiocollared on 19 March 1998, a juvenile male (M/05) made a 44 km southeast movement over 11 days (MDM: $\bar{x} = 3.7$ km, SD = 1.9). He then used one meadow complex intensively (MDM: $\bar{x} = 1.3$ km, SD = 0.9) for the next 31 days before his death on 3 May. After she was radiocollared within her natal range, a female kitten (F/03) rejoined her mother for three days, then moved independently for three days before 28 March when she initiated a

Table 12.2—Minimum daily movements (MDM; km) for resident lynx during summer (1 May–31 October), winter (1 November–30 April), and annually in the southern Canadian Rocky Mountains, British Columbia and Alberta, 1996-1998.

Lynx sex/ID	n	Summer			n	Winter			Annual	
		Range	Mean	SD		Range	Mean	SD	Mean	SD
M/01	124	0.1 – 14.3	4.8	3.2	212	0.5 – 19.3	3.5	3.5	3.9	3.5
M/02	27	0.4 – 13.7	3.3	3.1	45	0.8 – 23.2	5.0	5.2	4.3	4.6
M/03	34	0.4 – 10.9	3.7	2.3	95	0.1 – 19.8	3.0	2.9	3.2	2.7
Males	3		3.9	0.8	3		3.8	1.1	3.8	0.6
F/01	53	0.0 – 10.3	3.0	2.4	101	0.1 – 12.0	2.7	2.5	2.9	2.5
F/02	64	0.0 – 10.9	1.9	2.2	125	0.1 – 10.4	2.8	2.1	2.5	2.2
F/04	49	0.5 – 13.7	3.9	2.8	12	0.8 – 6.1	3.4	1.8	3.9	2.6
Females	3		2.9	1.0	3		3.0	0.4	3.0	0.7

southeast linear movement of 17 km over three days (MDM: $\bar{x}$ = 5.6 km, SD = 0.4). She then used one area intensively (MDM: $\bar{x}$ = 0.9 km, SD = 0.5) for the next 15 days before her death. The movements of both animals followed the major valley in which they occurred and paralleled but did not cross the Trans-Canada Highway. After her 30 April release, a kitten/juvenile female (F/05) used a 75% UD home range of 53 km² for five months, after which she made two separate exploratory movements of a minimum 74 km and 55 km over 24 and 11 days respectively. The second movement continued in a southward dispersal.

Topographic Selection and Highway Influence

Topographic selection within home ranges was apparent among all six resident lynx during summer ($\chi^2 > 21.6$, 5-6 df, $p < 0.002$), and among five during winter ($\chi^2 > 35.6$, 5-6 df, $p < 0.001$). Among animals, models explained variation (r^2) ranging from 12 to 36% during summer and 19 to 36% during winter. Lynx either avoided or did not select highest (>1,850 m) elevations, preferred or did not avoid mid (1,550-1,850 m) elevations, and although lowest (<1,550 m) elevations were not avoided during winter, two animals did avoid them during summer (Table 12.3). All males and one female used mean elevations 90-133 m higher during summer than during winter ($t > 2.72$, 131-434 df, $p < 0.008$). However, seasonal use of elevations did not differ for two females ($t < 1.19$, 97-237 df, $p > 0.240$). Most lynx avoided or did not select steeper (>40%) slopes, and preferred or did not avoid moderate (20-40%) or gentle (<20%) slopes (Table 12.3). Mean slopes used were 4-9% steeper during summer than during winter for two males and two females ($t > 2.65$, 131-237 df, $p < 0.009$), whereas slope use did not differ between seasons for one male and one female ($t < 0.95$, 97-434 df, $p > 0.344$). Selection for aspect varied among animals (Table 12.3). Among all six lynx, there were

Table 12.3—Significance (*p*) and partial correlations (*r*) of variables considered within multiple logistic regression models of topographic selection within home ranges. Results are given for summer (1 May–31 October) and winter (1 November–30 April) for resident lynx in the southern Canadian Rocky Mountains, British Columbia and Alberta, 1996–1998. Preference (+) or avoidance (–) is inferred from *r* statistics where $p < 0.05$.

Variable		Lynx sex/D: summer						Lynx sex/D: winter					
		M/01	M/02	M/03	F/01	F/02	F/04	M/01	M/02	M/03	F/01	F/02	F/04
Elevation (m)	<i>p</i>	<0.001	0.006	0.049	<0.001	0.511	0.196	<0.001	0.071	<0.001	<0.001	0.773	0.547
<1,550	<i>r</i>	–0.20	+0.11	+0.13	–0.20	—	0.00	0.00	+0.12	+0.22	0.00	—	0.0
1,550 – 1,850	<i>r</i>	+0.30	+0.10	0.00	+0.29	0.00	+0.06	+0.26	0.00	0.00	+0.27	0.00	0.00
>1,850	<i>r</i>	0.00	–0.21	–0.11	0.00	0.00	0.00	–0.21	–0.13	–0.20	–0.21	0.00	0.00
Slope (%)	<i>p</i>	<0.001	0.163	0.025	0.038	0.890	0.859	0.018	0.465	0.192	0.015	0.008	0.931
<20	<i>r</i>	+0.07	0.00	–0.18	+0.15	0.00	0.00	+0.09	0.00	0.00	+0.12	0.00	0.00
20 – 40	<i>r</i>	+0.12	+0.09	+0.04	0.00	0.00	0.00	0.00	0.00	0.00	+0.05	+0.13	0.00
>40	<i>r</i>	–0.19	0.00	+0.07	–0.07	0.00	0.00	–0.07	0.00	+0.06	–0.14	–0.11	0.00
S→N aspect	<i>p</i>	0.358	0.002	0.100	0.513	0.333	0.024	0.050	0.345	0.711	0.914	0.057	0.723
	<i>r</i>	0.00	–0.19	–0.06	0.00	0.00	–0.12	–0.051	0.00	0.00	0.00	–0.06	0.00
W→E aspect	<i>p</i>	0.001	0.071	<0.001	0.323	<0.001	0.020	0.973	0.265	<0.001	0.119	<0.001	0.466
	<i>r</i>	+0.13	–0.08	+0.30	0.00	–0.29	–0.123	0.00	0.00	+0.27	+0.04	–0.22	0.00

no significant seasonal differences in the use of northward aspects ($t < 2.26$, 97–434 df, $p > 0.025$), and although one male used eastward aspects greater during summer than during winter ($t = 2.56$, 434 df, $p = 0.011$), seasonal differences were not significant among the other five lynx ($t < 1.93$, 97–237 df, $p > 0.055$). All six resident lynx crossed highways less than random expectation within their home ranges ($\chi^2 > 139.9$, 1 df, $p < 0.001$).

Discussion

Hare Densities

Hare densities (range = 0.01–0.47/ha) observed in the southern Canadian Rockies during 1996–1998 are comparable to those reported in northern lynx study areas during cyclic hare population lows. Hare densities in the southwest Yukon declined from 8.0 to 10.7/ha to 0.2 to 0.5/ha during one cycle (Ward and Krebs 1985), and another population fell from 7.5/ha to 1.3/ha during the next cycle (Slough and Mowat 1996). Similarly, a population in the Northwest Territories fell from 7 to 9/ha to 0.4 to 1.0/ha during the early 1990s (Poole 1994), and a northern Alberta population declined drastically from about 17/ha to 0.34/ha during the early 1970s (Brand et al. 1976). Because my study period coincided with the increase phase of a hare cycle (C. J. Krebs, personal communication), assuming geographic synchrony, my results are consistent with suggestions that hare densities remain relatively

low in southern British Columbia and the northwestern United States (Chitty 1950; Dolbeer and Clark 1975; Wolff 1980).

Food Habits

The large proportion (47%) of prey other than snowshoe hares documented during winter in this study to date generally is consistent with observations of opportunistic lynx food habits during hare lows (Koehler and Aubry 1994; Staples 1995; O'Donoghue et al. 1998b). The 35% combined proportion of red squirrel and flying squirrel kills also is roughly consistent with Koehler's (1990) reported 24% occurrence of tree squirrels in lynx scats collected year-round in Washington. Lynx predation on marten has not been previously reported and likely is opportunistic. Despite the substantial numeric quantity of alternate prey in the diet of lynx in this study, hares clearly represent the most important food source when biomass ratios are considered (e.g., 1:5 squirrel:hare; Nellis and Keith 1968), as is consistent with other lynx populations (Koehler and Aubry 1994; Staples 1995; O'Donoghue et al. 1998b). My results, however, may underestimate the diversity of prey used due to missed kills of small species during snow-tracking, as was found by O'Donoghue et al. (1998b) in a comparison of kill-site with scat data. Although lynx in the Yukon cached partially consumed hares (O'Donoghue et al. 1998b), this behavior was not observed in the southern Canadian Rockies.

Reproduction and Recruitment

Kitten production and survival were low during the study period. The apparent lack of recruitment to early winter among study animals is consistent with northern populations after a hare decline, when winter litter sizes were zero (Brand et al. 1976; Poole 1994; Mowat et al. 1996). O'Donoghue et al. (1997) also did not detect family groups in their Yukon study area after the hare decline. Among the four uncollared family groups, litter sizes also were low in comparison to northern populations in the year preceding the hare decline, when mean winter litter sizes were 3.0 ($n = 3$; Poole 1994) and 3.3 ($n = 12$; Mowat et al. 1996). However, the occurrence of some kittens suggests that habitat quality varied among female home ranges within the study area. Among southern populations, Koehler (1990) also reported low (12%) kitten survival to winter from three litters in north-central Washington, and three adult females monitored in Montana from 1982 through 1984 did not produce kittens (Brainerd 1985). Evidence of breeding and den site abandonment of F/01 is consistent with the suggestion by Mowat et al. (1996) that breeding and implantation continues to occur regardless of prey densities.

Survival

Survival of resident adults was high over both years, as was found in another population refugium (Slough and Mowat 1996). During hare lows in northern populations, most natural mortality is due to starvation and is preceded by nomadic movements (Ward and Krebs 1985; Poole 1994; Slough and Mowat 1996), as observed for two lynx in this study. These two deaths occurred during spring, in contrast to Poole's (1994) observation that most natural mortality in his Northwest Territories study area occurred during mid-winter. Evidence of cannibalism that I report has been documented before (Elsey 1954; Nellis et al. 1972; Brittell et al. 1989; Poole 1994; O'Donoghue et al. 1995; Slough and Mowat 1996).

Space Use and Movements

Annual home ranges of resident lynx in the southern Canadian Rockies were considerably larger than those reported for most other studies employing the same estimators, regardless of prey density or geographic locale (Koehler and Aubry 1994; Poole 1994; Slough and Mowat 1996). Minimum convex polygon (MCP) home ranges in my study area were roughly 5-10 times larger than previously reported (Ibid.), although the influence of sample size on this estimator may confound comparisons (White and Garrot 1990). An exception to this was reported for the year after a hare decline in the Yukon, when four female and two male resident lynx maintained larger mean home ranges with high variability (Slough and Mowat 1996). Similarly, MDM mostly were higher than in other studies of comparable methods (Ward and Krebs 1985; Poole 1994), implying greater foraging effort. One exception to this was documented by Ward and Krebs (1985) during a hare decline in the Yukon, when lynx increased their daily movements from 2.4 to 3.3 to 5.4 km/day as hares declined from 1.0 to 0.5 to 0.2/ha, respectively. However, another Yukon study did not find that lynx increased their active time in response to declining hare numbers (O'Donoghue et al. 1998b). Differences between 100 and 95% MCP home ranges reflect exploratory movements that were made throughout the year by all resident study animals. Physiography and the distribution of potential habitat may partially account for lynx home range size differences between geographic areas (Koehler and Aubry 1994). In comparison to other study areas, space use and movements by lynx in the southern Canadian Rocky Mountains therefore may be disproportionately greater relative to prey densities.

Few studies have examined seasonal variation in space-use by lynx. Although I found no significant seasonal differences in UD areas for either sex, tests were based on a low sample size. More extensive space-use during

summer was apparent for only one male; however, inclusion of the breeding period within the winter season may have masked seasonal differences among other lynx. Although not statistically tested, in Nova Scotia, individuals of both sexes used areas during summer that were larger than those used during winter (Parker et al. 1983), and two females with young used smaller areas during summer in Alaska (Bailey et al. 1986). In accordance with the latter observation, the only lynx that made smaller daily movements during summer was a female with kittens.

Relative to other study animals, the noticeably smaller UD areas that I report for two females (F/02, F/04) may reflect the distribution and configuration of potential habitat in the landscape where they occur. Still, although samples were small, home range comparisons between sex did not reveal more intensive space use by females as has generally been observed (Koehler and Aubry 1994), perhaps because females were mostly without kittens during the monitoring period. Smaller female home ranges were reported in the Yukon only during years of high kitten survival to 1 March (Slough and Mowat 1996). Poole (1994), however, did not detect home range differences between sexes over four years of variable kitten survival in the Northwest Territories. Regardless of home range comparisons, differences in daily movements suggest that females used space more intensively than males during both seasons.

Differential space use within home ranges may be influenced by habitat features and social interactions (Samuel et al. 1985). Obvious differences between annual UD levels indicate that lynx home ranges were not used homogeneously but were associated with distinct core use areas. Poole (1994) also reported the use of obvious core home ranges by lynx (50% vs. 95% MCP). Evidence of intersexual spatial overlap that I report is consistent with most other populations (Koehler and Aubry 1994; Poole 1995). Sharing of home ranges between sexes or related females observed elsewhere also would be expected in the southern Canadian Rockies, considering the heterogeneous distribution of potential lynx habitat (Sandell 1989).

Topographic Selection

Lynx exhibited variable selection for topographic attributes, which may relate to differing associations of topography with habitat, human, and snow conditions; however, there was some consistency in pattern. Avoidance of highest elevations and steepest slopes by lynx in this study area likely is due to unsuitable habitat associations and energetic costs of accessing any habitat that is suitable. Lynx may also use topography to help partition themselves from competing species. Although they used higher mean elevations than coyotes during winter in the Yukon (Murray and Boutin

1991), lynx may not avoid lowest elevations within home ranges if habitat and terrain conditions are otherwise unsuitable for canids. During summer, they may further minimize interference competition with canids by using higher elevations and steeper slopes. The seasonal shift in elevation use that I found is similar to that reported by Koehler (1990) among lynx in the mountains of north-central Washington. Within their home ranges, bobcats occurring sympatric with coyotes in southeast British Columbia preferred mid elevations, avoided slopes $<10^\circ$, and selected distances <0.75 km from slopes associated with rock outcrops (Apps 1996). Terrain was also a factor in habitat partitioning between bobcats and coyotes in Idaho (Koehler and Hornocker 1991). Regardless of interspecific relationships, the open habitats associated with higher elevations in my study area contain additional prey species not available during winter (Scotter and Ulrich 1995), and snow conditions may increase the energetic cost of travel at higher elevations during much of the winter.

I found no obvious pattern of aspect selection by lynx within home ranges, and use did not differ seasonally among most animals. However, McKelvey et al. (Chapter 10) detected preference for northeast aspects at the scale of their Washington study area. If lynx exhibit aspect preferences in the southern Canadian Rockies, they may occur at broader or finer spatial scales than I considered. Moreover, finer-scale selection for this variable may relate to solar insolation, which will vary greatly within and among days. The individual selection for aspect that did occur may be an artifact of covariation with other habitat and human conditions.

Highway Influence

The likelihood of highway crossings by resident lynx can be expected to vary among home ranges according to proximal habitat conditions, width of road allowance and traffic volume, and perhaps by the animal's sex and reproductive status. Although my analysis did not account for these factors, all lynx crossed highways less than random expectation within their 95% UD home ranges, suggesting that highways influenced lynx movements. Although my analysis only considered the influence of highways within home ranges, they may also influence home range selection just as dominant natural features can (Koehler and Aubry 1994), and this would decrease the substantive influence apparent within home ranges. Although there have been no other reports to date of lynx space use and movements relative to human linear disturbance, four lynx in Washington did not cross logging roads differently from random within home ranges (Chapter 10). However, bobcats in Wisconsin selected home ranges with lower densities of secondary roads and crossed paved highways less than expected, a function of

vehicle traffic levels and juxtaposition of preferred habitat to roads (Lovallo and Anderson 1996).

Dispersal

The timing of F/03's dispersal is within the March-June emigration peak observed by Slough and Mowat (1996) in the Yukon but occurred nine days before their earliest female kitten dispersal. The linear movements by this lynx and M/05 are in the lower extremes of those reported for lynx emigrating from northern populations (Slough and Mowat 1996; Poole 1997); however most reported lynx dispersals have been of adults. The orientation of movements relative to terrain and the Trans-Canada Highway suggests that dominant natural and human features may constrain dispersal options in the southern Canadian Rockies. The intensive use of one area exhibited by both lynx before their deaths does not imply residency because dispersing felids have exhibited short-term use of temporary home ranges (Beier 1995; Apps 1996).

Conclusions

Although results are based on limited data, several conclusions specific to the southern Canadian Rocky Mountains can be made. Hare densities, and the diet, space-use and movements, reproduction, subadult survival, and dispersal of lynx were consistent with those of northern populations during hare lows. However, assuming geographic synchrony, the study period coincided with the increase phase of a snowshoe hare cycle, suggesting that lynx populations in the southern Canadian Rocky Mountains are not subject to the dramatic, cyclic pulses in productivity reported for northern populations. The following are also apparent: lynx spacing patterns suggest that resource distribution is patchy; males use space more extensively than females; topography influences habitat potential, with seasonal differences; and highways may negatively influence lynx movements.

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