Lynx Ecology in the Southern Canadian Rocky Mountains: Preliminary Results and Conservation Implications

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ABSTRACT

Throughout the range of the Canada lynx, snowshoe hares are considered their primary prey. Relative to northern populations, hares occurring in mountainous regions at southern latitudes are thought to remain at low and stable densities. Hence, the ecology of 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 southern British Columbia and Alberta are consistent with this hypothesis, based on data collected from 10 lynx, including 6 (3M, 3F) resident adults, during 2 years of an assumed increase phase of a hare cycle. Mean hare densities were low, ranging from 0.01–0.47/ha among cover types and landscapes. Lynx 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 0 among adult females for 4 lynx-years. Family groups that did occur in the study area during winter were associated with small litters of 2. Survival among resident adults was 100%, but 3 of 4 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 km^2 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. Results suggest that lynx populations in the southern Canadian Rocky Mountains are not subject to the dramatic cyclic pulses in productivity reported for northern populations. Coupled with evidence that resident animals are patchy in distribution, this implies that lynx are vulnerable to mismanagement of habitat and populations within this region.

Key words: Canada lynx, demographics, diet, dispersal, home range, *Lepus americanus, Lynx canadensis*, movement, recruitment, Rocky Mountains, survival, snowshoe hare.

There is concern for the conservation of Canada lynx (*Lynx canadensis*) populations occurring near the species' southern range extents, as has recently been highlighted by a proposal for listing under the federal Endangered Species Act within the conterminous United States (Fish and Wildlife Service 1998). However, the status of southern lynx populations, and associated threats, are clouded by a lack of information regarding their local ecology, demographic trends, and habitat associations. Most research has occurred within northern boreal forests more central to the species' geographic range. In comparison, regional landscapes with which lynx are associated in southern British Columbia and Alberta and the northwestern Unites States are typically mountainous and vary greatly in their inherent potential to support lynx. Capable habitat is therefore limited in area and naturally fragmented relative to northern landscapes, and is subject to multiple demands of a growing human population.

Ecotypic differences may also occur between northern and southern lynx populations, important considerations for population and habitat management. Lynx ecology is closely tied to the density and distribution of snowshoe hares (*Lepus americanus*), their primary prey. In the north, hare densities vary dramatically over an approximate 10-year cycle, influencing lynx demographics (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 behaviour (Brand et al. 1976, O'Donoghue et al.1998*a*,*b*), space

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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 as 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) a 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 make shorter daily movements and use smaller home ranges when snow is present.

We examine the above hypotheses with preliminary results from an ongoing study in the southern Canadian Rocky Mountains. Data were collected between November 1996 and October 1998, and 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. Krebs, University of British Columbia, pers. comm.).

STUDY AREA

The study area (>3000 km2) is centrally located within the Shining Mountains ecoprovince (Demarchi 1994), and most of it lies within the East Kootenay Wildlife Management Subregion of southeastern British Columbia (Fig. 1). 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–>3,000 m) span 3 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 (*Picea engelmannii* x *glauca*) and subalpine fir (*Abies lasiocarpa*). The Engelmann Spruce–Subalpine Fir zone occurs at higher elevations but below 2,300 m, and the Alpine Tundra zone occurs at the highest elevations. Subclimax stands throughout the study area are dominated by lodgepole pine (*Pinus contorta*). 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).

Several other predators and potential competitors with lynx occur in the study area (Scotter and Ulrich 1995). Potential lynx prey include snowshoe hares, red squirrels (*Tamiasciurus hudsonicus*), northern flying squirrels (*Glaucomys sabrinus*), gallinaceous birds, microtine rodents, hoary marmots (*Marmota caligata*), ground squirrels (*Spermophilus* spp.), bushy-tailed woodrats (*Neotoma cinerea*), beavers (*Castor canadensis*), and several ungulate species.

METHODS

We determined a range of snowshoe hare densities by count-

Figure 1. Study area location in the southern Canadian Rocky Mountains of southeast British Columbia and southwest Alberta.

ing 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-successional (20–60 yr old), mid-successional (60–120 yr old), and late-successional (>120 yr old) stands, but were spaced by 500 m. Sampling was further stratified among 3 landscapes within the study area, representing geographically distinct areas where we consider terrain conditions conducive to supporting lynx. Hare densities were calculated with a modified version of Krebs et al.'s (1987) regression equation, using the HARETURD program (C. Krebs, University of British Columbia, 27 Oct 1998, pers. comm.).

Study animals were captured during the winters of 1996–97 and 1997–98, with efforts focused in landscapes where lynx sign had been reported in recent years. Capture, handling, and radiotelemetry methods are detailed by Apps (1999). Upon capture, lynx were sexed, and age was subjectively classed (adult: >2 yr; juvenile: 1–2 yr; kitten: <1 yr) based on skeletal measurements and tooth wear. They were then fitted with motion/mortality-sensing whip antennae radio-collars (Lotek Eng. Inc., Newmarket, ON) before release. Radio-locations were obtained throughout the year, at least weekly for all animals, and at least 4 days per week for most animals.

Study animals were snow-tracked during both years when possible, and kills and scavenging were documented over 759 km. 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.

Lynx carcasses and/or radio-collars were retrieved as soon as possible after mortality was detected. 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 radio-tracked daily.

We defined resident lynx as those associated with 1 activity centre subjectively determined over at least 3 months. Home ranges of resident adults were estimated seasonally and annually over both years using the program CALHOME (Kie et al. 1996). We defined summer and winter seasons by the typical 6-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, we 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 hr, thus only radio-locations that were temporally independent by this interval were used (Swihart and Slade 1985). Among all animals, the 95% UD area appeared to asymptote at 43–55 radio-locations (Apps unpubl. data). We compared UD levels between seasons using multivariate analysis of variance (MANOVA; $\alpha = 0.05$). Static interaction between lynx known to have neighbouring or contiguous home ranges was inferred from spatial home range overlap (Macdonald et al. 1980).

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

RESULTS

HARE DENSITIES

For early-, mid-, and late-successional stands respectively, mean hare densities by landscape were 0.16/ha, 0.08/ha, and 0.01/ha in the upper Kootenay Valley; 0.25/ha, 0.06/ha, and 0.10/ha in the Beaverfoot Valley; and 0.47/ha, 0.39/ha, and 0.32/ha in the Vermilion Pass.

FOOD HABITS AND POPULATION ATTRIBUTES

Ten lynx, comprising 3 adult males, 3 adult females, 1 juvenile male, 2 kitten/juvenile females, and 1 kitten male, were radio-collared, monitored, and snow-tracked for 1–23 months between November 1996 and October 1998. Lynx kills (n = 137) documented over both years consisted of snowshoe hares (52%), red squirrels (30%), northern flying squirrels (5%), grouse (*Dendragapus* spp.; 3%), martens (3%), voles (3%), a northern flicker (*Colaptes auratus*; <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 the lynx (M/01) was forced out by wolves and did not return.

None of the 3 adult females in the study sample were travelling 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 3 uncollared family groups were detected during November and December 1997. We assumed the latter groups were different individuals because each group was separated by a linear distance of >30 km, beyond the maximum exploratory movement of radio-collared females (Apps unpubl. data). Each group contained an adult and 2 kittens. Both kittens (M/04, F/03) from 1 family group were subsequently radio-collared, but neither

Table 1. Annual minimum convex polygon (MCP) and adaptive kernel utilization distribution (UD) home range estimates (km^2) for resident lynx in the southern Canadian Rocky Mountains, British Columbia and Alberta, 1996–98.

Lynx (sex/identity #)	Period monitored	n	MCP		UD		
			100%	95%	95%	75%	55%
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

survived to May. Two females that were monitored through March of 1997 (F/01) and 1998 (F/02) were snow-tracked while travelling with males, and F/02 was also directly observed during copulation with an uncollared male on 13 March. Daily radio-locations of F/01 were within 250 m of an activity centre between 20 May and 1 June 1997, after which she resumed normal movements and did not revisit the presumed den site. From this, we 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. Radio-locations of F/02 were within 500 m of an activity centre on 82% of days between 22 May and 14 July 1998, and she was observed with 1 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 travelling with his family group and within his natal range. A female kitten (F/05) released to her natal area in April 1998 after 4 months in captivity due to a capture injury survived at least the following 6 months.

SPACE USE AND MOVEMENTS

The mean number of radio-locations 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 (Table 1) did not significantly differ between seasons for males ($F = 3.66$, 3 df, $P = 0.222$) or females ($F = 1.34$, 3 df, $P = 0.548$). Spatial overlaps between the annual 95%, 75%, and 55% UD areas of M/01 and F/01 were 36%, 63%, and 60%, respectively. Of their 183 concurrent daily radio-locations, 78% were separated by >3 km. A second adult female was known to occur also within the 50% UD area of these 2 lynx, as inferred from snow-tracking and radio-locations 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 movements were 3.8 km ($n = 537$, SD = 3.5) and 3.0 km ($n = 404$, SD = 2.4) for males and females respectively. MDMs 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, $P > 0.082$).

DISPERSAL

Dispersal movements were documented for 3 subadult lynx. After he was radio-collared on 19 March 1998, a juvenile male (M/05) made a 44-km southeast movement over 11 days (MDM: $\bar{\chi}$ = 3.7 km, SD = 1.9). He then used 1 meadow complex intensively (MDM: $\bar{\chi}$ = 1.3 km, SD = 0.9) for the next 31 days before his death on 3 May. After she was radio-collared within her natal range, a female kitten (F/03) rejoined her mother for 3 days, then moved independently for 3 days before 28 March, when she initiated a southeast linear movement of 17 km over 3 days (MDM: $\bar{\chi}$ = 5.6 km, SD = 0.4). She then used 1 area intensively (MDM: $\bar{\chi}$ = 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 km^2 for 5 months, after which she made 2 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.

DISCUSSION

HARE DENSITIES

Hare densities (range = 0.01–0.47/ha) observed in the southern Canadian Rockies during 1996–98 are comparable to those reported in northern lynx study areas during cyclic hare population lows. Hare densities in the southwest Yukon declined from 8.0–10.7/ha to 0.2–0.5/ha during 1 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 7–9/ha to 0.4–1.0/ha during the early 1990s (Poole 1994), and a northern Alberta population crashed from about 17/ha to 0.34/ha during the early 1970s (Brand et al. 1976). Because our study period coincided with the increase phase of a hare cycle (C. Krebs, University of British Columbia, pers. comm.), our 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 is generally consistent with observations of opportunistic lynx food habits during hare lows (Koehler and Aubry 1994, Staples 1995, O'Donoghue et al. 1998*b*). 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. 1998*b*). Although lynx in the Yukon cached partially consumed hares (O'Donoghue et al. 1998*b*), this behaviour 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 0 (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 crash. Among the 4 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. Koehler (1990) also reported low (12%) kitten survival to winter from 3 litters in north-central Washington. 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.

MORTALITY

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 2 lynx in this study. These 2 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 we 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). MCP home ranges in our study area were roughly 5–10 times larger than previously reported (Koehler and Aubry 1994, Poole 1994, Slough and Mowat 1996), 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 crash in the Yukon, when 4 female and 2 male resident lynx maintained larger mean home ranges with high variability (Slough and Mowat 1996). Similarly, MDMs 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. 1998*b*). 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 we 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 1 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 2 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.

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 we 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 (compare Carr and MacDonald 1986, Sandell 1989).

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 9 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 of these were of adults. The orientation of movements relative to terrain and the Trans-Canada Highway suggest that dominant natural and human features may constrain dispersal options in the southern Canadian Rockies. The intensive use of 1 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*a*).

CONSERVATION IMPLICATIONS

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. Because the study period coincided with the increase phase of a snowshoe hare cycle, this suggests that lynx populations in the southern Canadian Rocky Mountains are not subject to the dramatic, cyclic pulses in productivity reported for northern populations. Further, our results suggest that the regional population presently exists at low densities, is of low productivity, and is patchy in distribution, as was also reflected by a regional trapper survey (Apps 1996*b*). Hence, we expect that lynx in the southern Canadian Rockies will be more vulnerable to mismanagement of habitat and populations than would otherwise be expected within northern ecosystems.

Conventional harvest management strategies allow for a more liberal take during the increase and high phase of the hare-lynx population cycle (Quinn and Parker 1987). However, where populations may not exhibit pronounced variation in productivity, conservative management should be adopted throughout the cycle. Moreover, the implications of localized overharvest may be severe where regional populations are patchy, and the spatial distribution of any harvest must be carefully managed. Localized populations are susceptible to extirpation, given the low densities and low recruitment with which they appear to be associated, and accelerated fragmentation at the regional level may inhibit the recolonization of suitable landscapes.

Productive and appropriately distributed population refugia are crucial to the regional conservation of wide-ranging carnivores, yet their existence for lynx in the southern Canadian Rockies is questionable. Across the regional landscape, human access levels and multiple resource demands (CORE 1994) on a limited land base with potential to support lynx suggest that de facto population refugia for this species do not presently exist in this region. The effectiveness of refugia requires land management that is consistent with lynx habitat, and it cannot be assumed that the management of "protected" areas has necessarily reflected such biodiversity values (e.g., Page et al. 1996). Resource development in our study area is focused within valley bottoms, or in broad, forested mountain passes, both of which have high potential to support resident lynx and to facilitate dispersal. Within such landscapes, forest management that promotes the attributes and distributions of stands preferred by lynx is required to sustain or enhance habitat effectiveness and connectivity, and it is important that options for such be maintained into the future. For example, to minimize risk from wildfire, facilities such as resorts, backcountry lodges, and campgrounds require permanent buffers of stands with little structural diversity and of limited value to communities with which lynx are associated. Hence, it is preferred that such developments be clustered rather than dispersed. In addition to forest management considerations, research into mitigation options is required where highways dissect lynx habitat, as they constrain lynx movements within our study area (Apps 1999).

Continued research will provide insight into lynx-habitat associations across spatial scales. Such information needs to be integrated with land-use planning at ecologically relevant scales, requiring coordination among agencies and management jurisdictions. Although we do not advocate single-species management, lynx tend to be associated with forest mosaics of stand and landscape structure that may resemble conditions under a natural disturbance regime. Therefore, they may represent an ideal "focal-species" for assessing the efficacy of biodiversity management strategies, at multiple spatial and temporal scales, within montane and subalpine ecosystems of the southern Canadian Rockies.

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LITERATURE CITED

Achuff, P. L., W. D. Holland, G. M. Coen, and K. Van Tighem. 1984. Ecological land classification of Kootenay National Park, British Columbia. Vol I: Integrated resource description. Alberta Inst. of Pedology, Univ. Alberta, Edmonton, AB. 373 pp.

Apps, C. D. 1996*a*. Bobcat (*Lynx rufus*) habitat selection and suitability assessment in southeast British Columbia. Thesis. Faculty of Environmental Design, Univ. Calgary, Calgary, AB. 145pp.

_____. 1996*b*. East Kootenay trapper survey: lynx, bobcat, fisher, wolverine. Summary of results. B.C. Environ., Wildl. Branch, Cranbrook, BC, and Kootenay Natl. Park, Warden Serv., Radium Hot Springs, BC. Unpubl. rep. 5pp.

_____. 1999. Space use, diet, demographics, and topographic associations of lynx in the southern Canadian Rocky Mountains. Chap. 12 *in* L. F. Ruggiero, K. Aubry, S. W. Buskirk, G. Koehler, C. J. Krebs, and K. S. McKelvey, eds. The scientific basis for lynx conservation. U.S. Dep. Agric. For. Serv., Rocky Mountain Res. Stn., Fort Collins, CO. Gen. Tech. Rep. 30.

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. J. Wildl. Manage. 50:279–289.

Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. J. Wildl. Manage. 59:228–237.

Brand, C. J., and L. B. Keith. 1979. Lynx demography during a snowshoe hare decline in Alberta. J. Wildl. Manage. 43:827–849.

_____, _____, and C. A. Fischer. 1976. Lynx responses to changing snowshoe hare densities in central Alberta. J. Wildl. Manage. 40:416–428.

Brittell, J. D., R. J. Poelker, S. J. Sweeney, and G. M. Koehler. 1989. Native cats of Washington. Section III: Lynx. Washington Dep. Wildl., Olympia, WA. 169pp.

Carr, G., and D. W. MacDonald. 1986. The sociality of solitary foragers: a model based on resource dispersion. Anim. Behav. 34:1540–1549.

Chitty, H. 1950. The snowshoe rabbit enquiry, 1946–48. J. Anim. Ecol. 19:15–20.

CORE. 1994. East Kootenay land use plan. B.C. Comm. on Resour. and Environ., Victoria, BC. 176pp + appendices.

Demarchi, D. A. 1994. Ecoprovinces of the central North American Cordillera and adjacent plains. Pp. 153–167 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, eds. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. U.S. Dep. Agric. For. Serv., Fort Collins, CO. Gen. Tech. Rep. RN-254. 184pp.

Dolbeer, R. A., and W. R. Clark. 1975. Population ecology of snowshoe hares in the central Rocky Mountains. J. Wildl. Manage. 24:52–60.

Elsey, C. A. 1954. A case of cannibalism in Canada lynx (*Lynx canadensis*). J. Mammal. 35:129.

Fish and Wildlife Service. 1998. Endangered and threatened wildlife and plants: proposal to list the contiguous United States distinct population segment of the Canada lynx; proposed rule. Federal Register 50 CFR Part 17.

Hayne, D. W. 1949. Calculation of home range size. J. Mammal. 30:1–18.

Kie, J. G., J. A. Baldwin, and C. J. Evans. 1996. CALHOME: a program for estimating animal home ranges. Wildl. Soc. Bull. 24:342–344.

Koehler, G. M. 1990. Population and habitat characteristics of lynx and snowshoe hares in North Central Washington. Can. J. Zool. 68:845–851.

_____, and K. B. Aubry. 1994. Lynx. Pp. 74–98 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, eds. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. U.S. Dep. Agric. For. Serv., Fort Collins, CO. Gen. Tech. Rep. RN-254. 184pp.

Krebs, C. J., B. S. Gilbert, S. Boutin, and R. Boonstra. 1987. Estimation of snowshoe hare population density from turd transects. Can. J. Zool. 65:565–567.

Macdonald, D. W., F. G. Ball, and N. G. Hough. 1980. The evaluation of home range size and configuration using radiotracking data. Pp. 405–424 *in* C. J. Amlaner Jr., and D. W. Macdonald, eds. A handbook on biotelemetry and radiotracking. Pergamon Press, Oxford, England.

Meidinger, D. V., and J. Pojar. 1991. Ecosystems of British Columbia. B.C. Minist. For., Victoria, BC. Spec. Rep. Ser. Number 4. 330pp.

Mowat, G., B. G. Slough, and S. Boutin. 1996. Lynx recruitment during a snowshoe hare population peak and decline in southwest Yukon. J. Wildl. Manage. 60: 441–452.

Murray, D. L., and S. Boutin. 1991. The influence of snow on lynx and coyote movements: does morphology affect behaviour? Oecologia 88:463–469.

Nellis, C. H., and L. B. Keith. 1968. Hunting activities and successes of lynxes in Alberta. J. Wildl. Manage. 32:718–722.

_____, S. P. Whetmore, and L. B. Keith. 1972. Lynx-prey interactions in central Alberta. J. Wildl. Manage. 36:320–329.

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.

_____, _____, _____, D. L. Murray, and E. J. Hofer. 1998*a*. Behavioural responses of coyotes and lynx to the snowshoe hare cycle. Oikos 82:169–183.

_____, _____, _____, G. Zuleta, D. L. Murray, and E. J. Hofer. 1998*b*. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecol. 79:1193–1208.

_____, E. Hofer, and F. I. Doyle. 1995. Predator versus predator. Nat. Hist. 10:6–9.

Page, R., S. Bayley, J. D. Cook, J. Green, and J. R. Ritchie, eds. 1996. Banff Bow Valley: at the crossroads. Prep. by Banff Bow Valley Task Force for Minister of Canadian Heritage, Ottawa, ON.

Parker, G. R., J. W. Maxwell, and L. D. Morton. 1983. The ecology of lynx (*Lynx canadensis*) on Cape Breton Island. Can. J. Zool. 61:770–786.

Poole, K. G. 1994. Characteristics of an unharvested lynx population during a snowshoe hare decline. J. Wildl. Manage. 58:608–618.

_____. 1995. Spatial organization of a lynx population. Can. J. Zool. 73:632–641.

_____. 1997. Dispersal patterns of lynx in the Northwest Territories. J. Wildl. Manage. 61:497–505.

Quinn, N. W., and G. Parker. 1987. Lynx. Pp. 683–694 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, eds. Wild furbearer management and conservation in North America. Ontario Minist. of Nat. Resour., Toronto, ON. 1150pp.

Samuel, M. D., D. J. Pierce, and E. O. Garton. 1985. Identifying areas of concentrated use within the home range. J. Appli. Ecol. 54:11–719.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pp. 164–182 *in* J. L. Gittleman, ed. Carnivore behavior, ecology, and evolution. Cornell University Press, Ithaca, NY. 620pp.

Scotter, G. W., and T. J. Ulrich. 1995. Mammals of the Canadian Rockies. Fifth House, Saskatoon, SK. 185pp.

Slough, B. G., and G. Mowat. 1996. Lynx population dynamics in an untrapped refugium. J. Wildl. Manage. 60:946–961.

Smith, C. H., and J. M. Davis. 1981. A spatial analysis of wildlife's ten-year cycle. J. Biogeogr. 8:27–35.

Staples, W. R. 1995. Lynx and coyote diet and habitat relationships during a low hare population on the Kenai Peninsula, Alaska. Thesis. Univ. Alaska, Fairbanks, AK. 150pp.

Swihart, R. K., and N. A. Slade. 1985. Influence of sampling interval on estimates of home range size. J. Wildl. Manage. 49:1019–1025.

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

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, Toronto, ON. 383pp.

Wolff, J. O. 1980. Role of habitat patchiness in the population dynamics of snowshoe hares. Ecol. Monogr. 50:111–130.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecol. 70:164–168.