Habitat Selection by Lynx in the North Cascades

Final Report

Seattle City Light, Skagit Wildlife Research Grant Program

Gary M. Koehler, Ph.D.
Washington Department of Fish and Wildlife

and

Keith B. Aubry, Ph.D.
USDA Forest Service, Pacific Northwest Research Station

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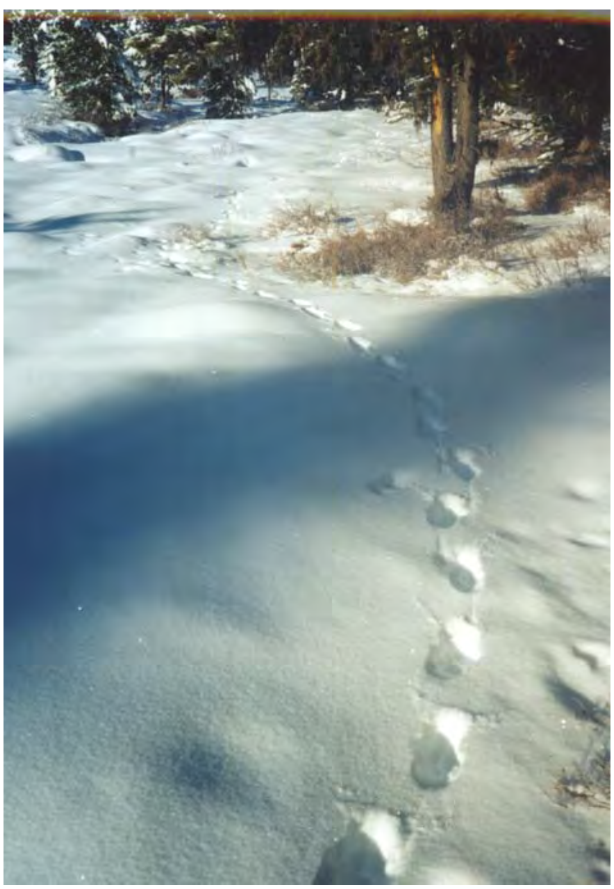

Winter Habitat Selection and Food Habits of Lynx on the

Okanogan Plateau, Washington

Jeff A. von Kienast

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This is to certify that I have examined this copy of a masters' thesis by

Jeff A. von Kienast

and have found that it is complete and satisfactory in all respects,
And that any and all revisions required by the final
Examining committee have been made.

Committee Members:

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Stephen D. West

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Keith B. Aubry

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James K. Agee

Date: ________________

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CHAPTER I: FINE-SCALE HABITAT SELECTION

INTRODUCTION

The conservation of Canada lynx (*Lynx canadensis*) in the U.S. is an extremely emotional issue that has generated a level of public interest comparable to that which surrounded the federal listing decision for the northern spotted owl (*Strix occidentalis caurina*) in the late 1980's. Lynx interest groups have recently purchased timber rights in a portion of the Loomis State Forest in Washington at a cost of over $16 million, and activists reportedly burned a ski lodge in Colorado to protest inadequate protection of lynx habitat. Some have argued that logging, road construction, and ski and snowmobile areas may destroy lynx habitat and provide human access that disrupts hunting activities, kitten rearing, and increases the likelihood that lynx will be killed illegally or incidentally (Ruediger et al. 2000). However, reliable information from lynx populations in southern boreal forests that could be used to evaluate the validity of these claims is lacking. Numerous petitions have been submitted to list the lynx under the federal Endangered Species Act, and several lawsuits were filed against the U.S. Fish and Wildlife Service during the 1990's (Ruggiero and McKelvey 2000). These actions eventually led to federal listing of the lynx as "threatened" in the contiguous U.S. due to the inadequacy of existing regulatory mechanisms (USFWS 2000).

In the western states, lynx are known to select areas where lodgepole pine, (*Pinus contorta*) is predominant. In Montana, Koehler et al. (1979) reported 23 of 29 relocations of lynx were in densely stocked lodgepole pine stands. Lynx used lodgepole pine and Engelmann spruce (*Picea engelmannii)*-subalpine fir (*Abies lasiocarpa*) forest cover types more than expected in the northern Cascade Range of Washington (Koehler 1990). In Washington, lynx primarily occupy mid- and late-successional (>40 yr old) subalpine fir/lodgepole pine forests (Koehler 1990, McKelvey et al. 2000*a*), and in Montana (Koehler et al. 1979) and Nova Scotia (Parker 1981, Parker et al. 1983) lynx select mid-successional (20-40 yr old) conifer forests. Mid-successional forests that result from wildfires (Koehler 1990, Poole et al. 1996) and timber harvesting (Parker 1981, Thompson et al. 1989) are believed to be preferred by lynx because they support abundant snowshoe hare (*Lepus americanus*) populations on which lynx depend for both survival and reproduction (Parker 1981, Koehler 1990, Koehler and Aubry 1994, Hodges 2000*a*, McKelvey et al. 2000*a*).

Koehler and Brittell (1990) provided lynx management guidelines for forest managers. These findings provided the foundation for lynx habitat management plans for the Okanogan National Forest, Washington Department of Natural Resources Loomis State Forest, Plum Creek Timber Company, and Boise Cascade Corporation timberlands. Because of the recommendations made by Koehler and Brittell (1990), management plans developed for the Loomis State Forest and private timberlands in Washington primarily address snowshoe hare habitat requirements; other than considerations for denning habitat, these plans do not directly address lynx habitat relations. However, the timber management guidelines presented by Koehler and Brittell (1990) were based on informed hypotheses about the habitat relations of lynx and snowshoe hares that have never been rigorously tested. Good hare habitat may not always be good lynx habitat, because lynx hunting success may be determined, in part, by stand structure (Murray et al. 1995) and prey vulnerability (Murray and Boutin 1991, Haglund 1966), as well as snowshoe hare density (Murray et al. 1994, O' Donoghue et al. 1998*a*).

The age or structural conditions of forests that are selected by lynx for hunting in western montane regions are not well understood, yet are likely to be important determinants of habitat quality for lynx. Knowledge of lynx habitat relations in the U.S. at any spatial scale is limited (Aubry et al. 2000*b*), and studies of lynx habitat use in the western mountains of the contiguous U.S. are urgently needed (Koehler and Aubry, 1994). New research on lynx in the U.S. should address multiple spatial scales and multiple levels of biological organization (Aubry et al., 2000*b*). Radiotelemetry studies of lynx that documented habitat use in the U.S. (Smith 1984, Brainard 1985, Koehler et al. 1979, Koehler 1990) have monitored relatively few animals, and such studies do not provide reliable information on fine-scale habitat selection (i.e., within forest stands; Aubry et al. 2000*a*). Intensive snow-tracking studies comparing habitat use with availability may provide insights into fine-scale habitat selection by lynx that could be used to design silvicultural treatments and forest management strategies that will be beneficial to this listed species.

Beginning in the 1980's, extensive timber harvesting (both clearcuts and pre-commercial thinning) has occurred on the Loomis State Forest, whereas none has occurred on the adjacent portion of the Okanogan National Forest. In addition, a stand-replacement fire (the Thunder Mountain fire) occurred on the Okanogan National Forest in 1994. Both of these areas were included in the study area where Brittell et al. (1989) and Koehler (1990) conducted lynx research in the 1980's. These stand and landscape-scale differences in both natural and anthropogenic disturbances, and the continued presence of a resident population of lynx in that area, provide a unique opportunity to investigate fine-scale habitat selection by lynx.

STUDY AREA

The study was conducted on the Okanogan Plateau in the north-central Cascade Range of Washington, approximately 25 km northwest of Conconully, Washington (Figure 1). The study area is 200 km^2, is within the Okanogan Highlands physiographic province (Franklin and Dyrness 1973), and was delineated primarily from telemetry locations (Figure 2) obtained by Koehler (1990) and Brittell et al. (1989). Thus, lynx were known to occur throughout the study area.

The study area is characterized by moderate slopes and broad, rounded summits with elevations ranging from 1,400 to 2,260 m. Borders of the study area are defined by the Chewuck River on the west and the headwaters of the Middle Fork Toats Coulee Creek and Sinlehekin Creek drainages on the east. Lands are managed by the Okanogan National Forest and Washington Department of Natural Resources, Loomis State Forest (Figure 3). Forests occur on 85 percent of the area; burned areas on 9 percent; herbaceous plant communities on 3 percent; shrub communities on 3 percent; and rock, snow, and other cover categories on 1 percent (Bio/West, Inc., Figure 4). Major forest associations within the study area are Engelmann spruce and subalpine fir, with lodgepole pine being the dominant early seral species. Aspen (*Populus tremuloides*) occurs occasionally on mid-slope and riparian areas. Douglas-fir (*Pseudotsuga*

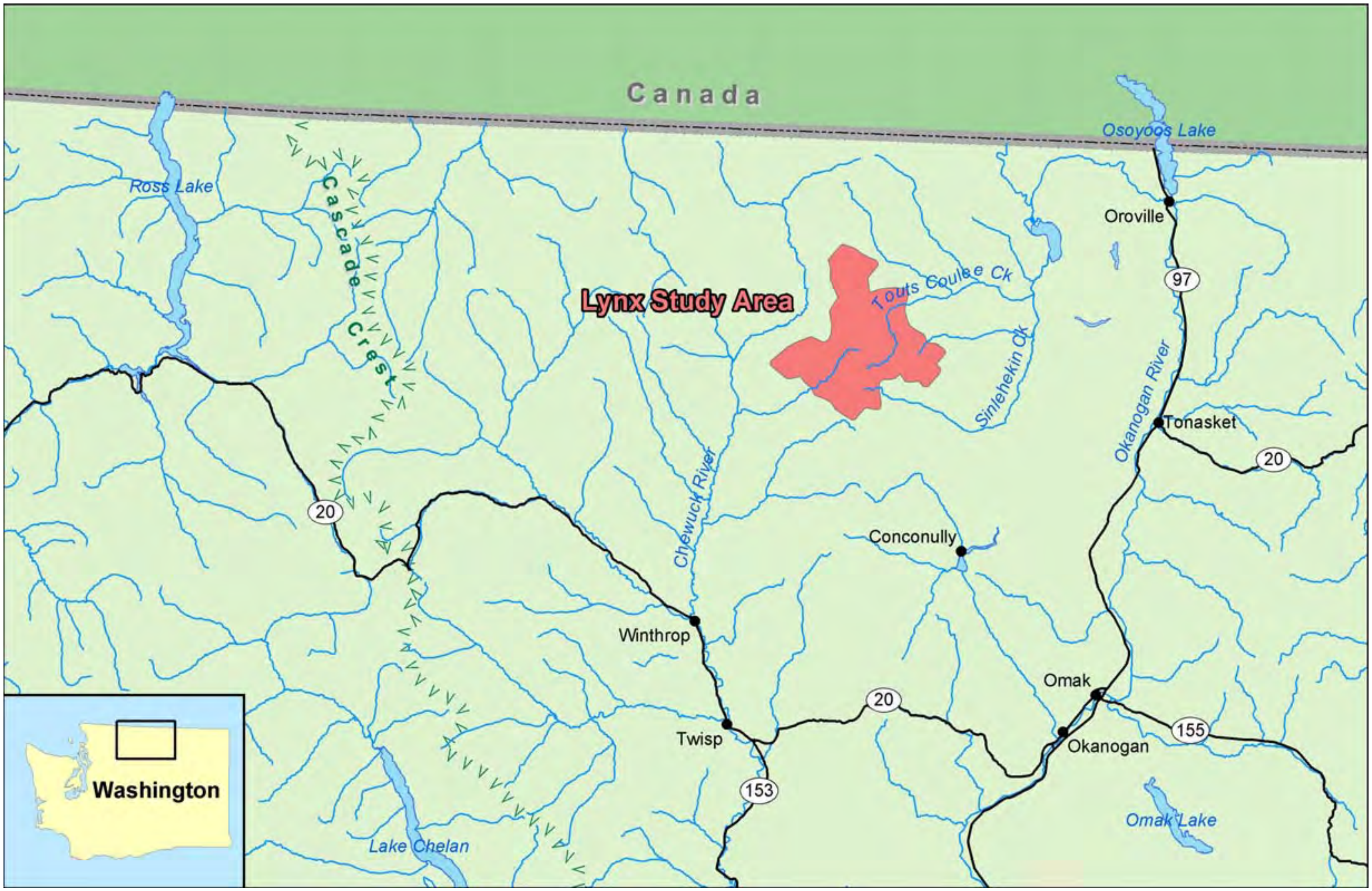

Figure 1. Location of lynx study area on the Okanogan Plateau, Washington.

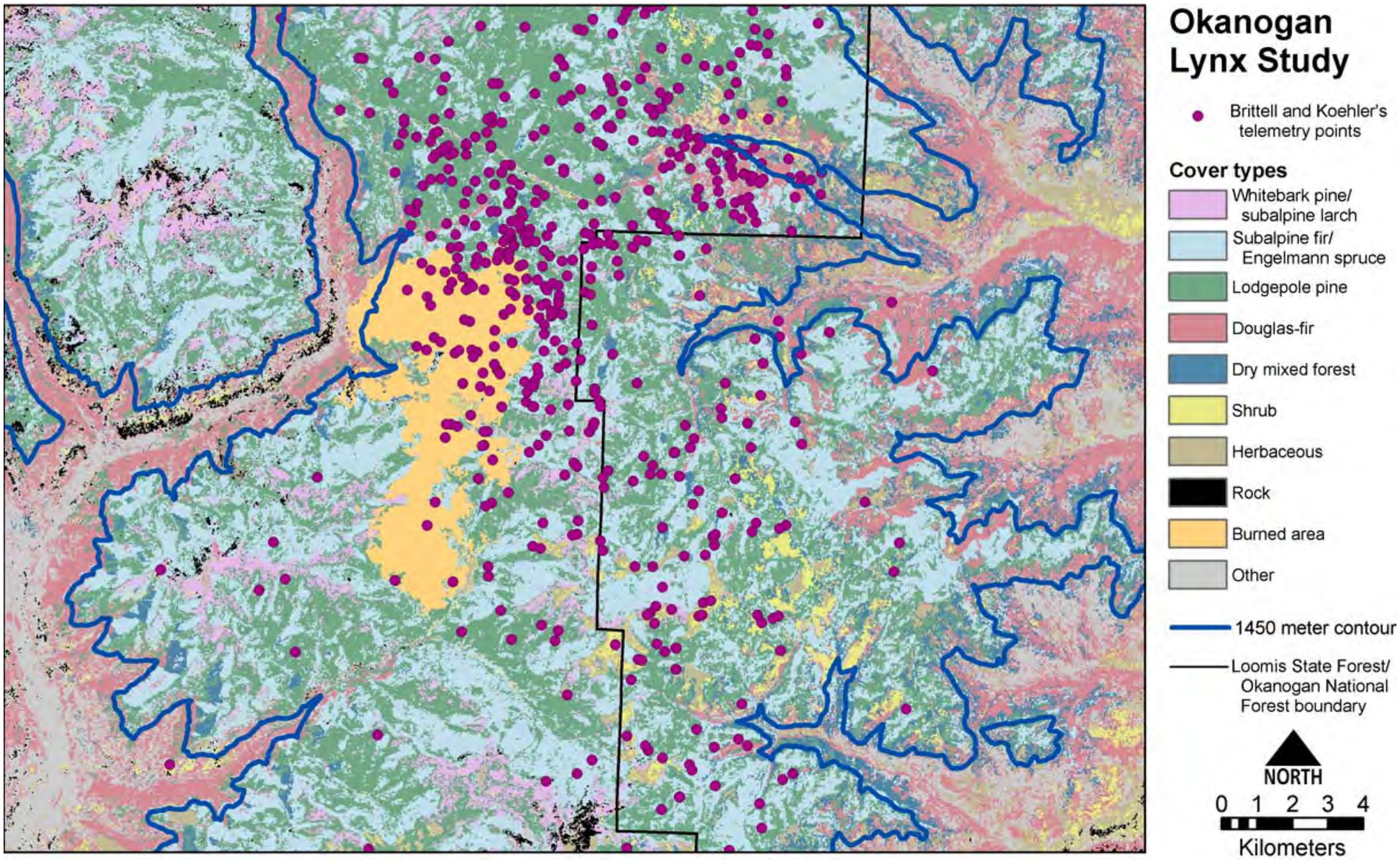

Figure 2. Forest cover types on the Okanogan Plateau, Washington (data from Utah State Veg Grids). Point locations from radiotelemetry studies of lynx conducted by J. David Brittell and Gary M. Koehler during the 1980s are shown as burgundy circles. The Thunder Mountain fire (shown in orange) occurred after these studies took place.

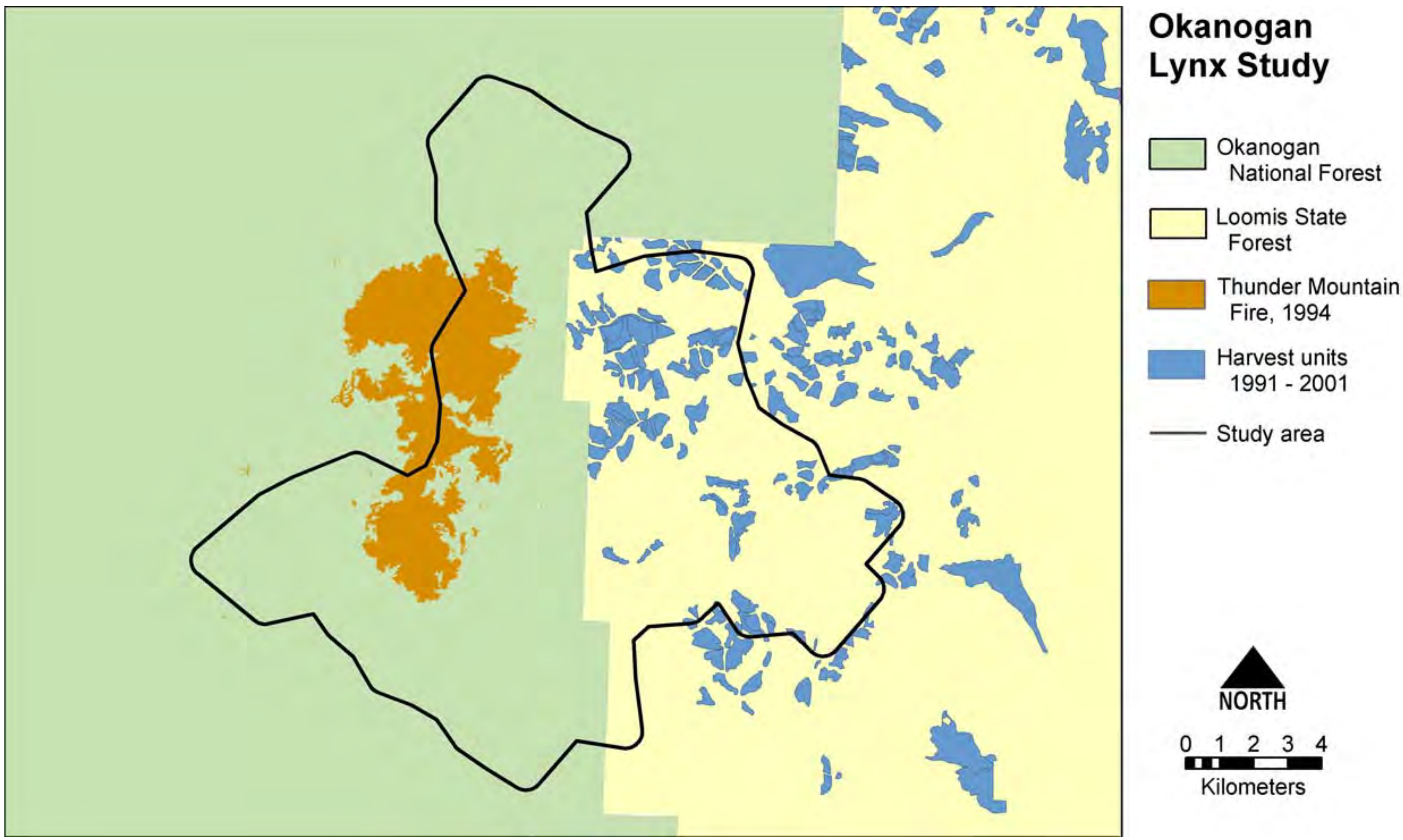

Figure 3. Land ownership and major patterns of disturbance on the Okanogan Plateau, Washington. The Okanogan National Forest is shown in green and the Loomis State Forest is shown in yellow. The 1994 Thunder Mountain fire is shown in orange and harvest units since 1991 are shown in blue.

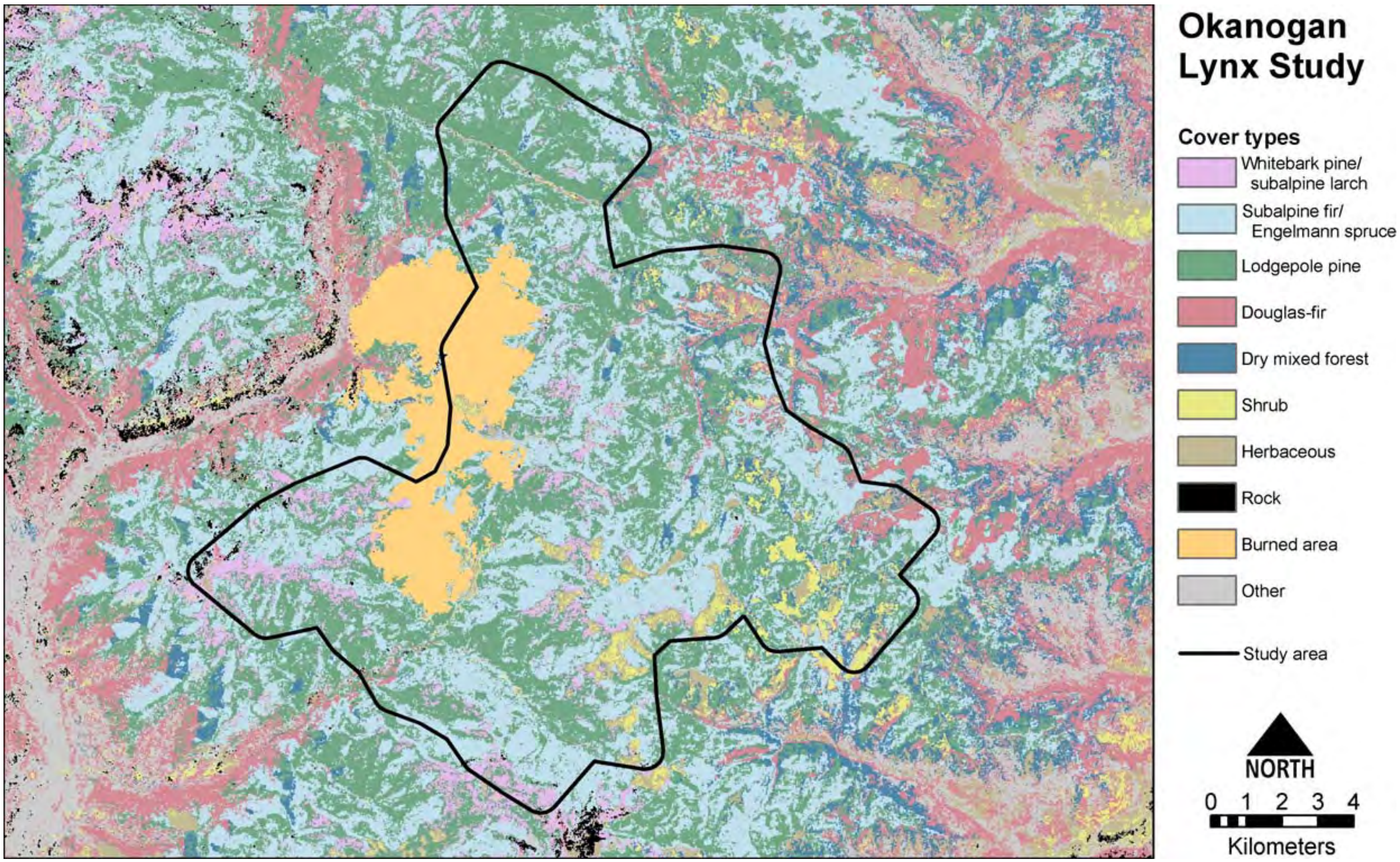

Figure 4. Forest cover types and outer boundary of lynx snowtracking study area on the Okanogan Plateau, Washington.

menziesii) dominates on south-facing aspects at lower elevations. Whitebark pine (*Pinus albicaulis*) and subalpine larch (*Larix lyalli*) are found near timberline. Small to moderate-sized openings frequently occur near ridgelines, and vegetation within these non-forested habitats are generally composed of herbaceous plants with sagebrush types (*Artemisia* spp.) interspersed. Several wet meadows are located within the central portion of the study area.

Snow covers the area from November through April, but snowpacks may persist on north-facing slopes until June (Brittell et al. 1989). Snow depths at the Mutton Creek snow course station (Natural Resources Conservation Service 2003*a*), located approximately 4 km south of the study area boundary at 1,730 m, averaged 60 cm during winter 2000/01 (year 1) and 99 cm during winter 2001/02 (year 2). Snow depth was not measured at higher elevations within the study area, but based on our field observations, did not appear to exceed 2 m. The average minimum and maximum temperatures in the central portion of the study area for February are –9.3º C and –2.5º C, respectively (Daly and Taylor 2000).

Wildfires are an important determinant of forest composition within the study area. The majority of fires result from lightning strikes. The Thunder Mountain fire burned approximately 18 km^2 within the study area in 1994. Fire-return intervals have been estimated at 250 yr (Fahnestock 1976) in the Pasayten Wilderness, located north and west of the study area, and 109-137 yr in the North Cascades (Agee 2000), however, large fires have burned more frequently within the study area in recent years (Thunder Mountain fire in 1994 and Thirtymile fire in 2001). Subalpine fir and Engelmann spruce are both considered to be intolerant of fire, possessing thin bark, a low crown with persistent branches, and shallow root systems, which generally results in tree mortality when exposed to fire (Agee 1993). Because of the lack of fire resistance among dominant tree species, most large fires in this area tend to be stand-replacement events (Agee 1993).

Potential prey of lynx in the study area include the snowshoe hare, red squirrel (*Tamiasciurus hudsonicus*), Columbian ground squirrel (*Spermophilus columbianus*), porcupine (*Erethizon dorsatum*), beaver (*Castor canadensis*), voles (*Clethrionomys* spp, *Microtus* spp, *Phenacomys intermedius*, *Synaptomys borealis*), blue grouse (*Dendragapus obscurus*), and spruce grouse (*Falcipennis canadensis*). Moose (*Alces alces*), and mule deer (*Odocoileus hemionus*) may be available as carrion. Other carnivores that inhabit the study area and may compete with lynx include the mountain lion (*Felis concolor*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), American marten (*Martes americana*), long-tailed weasel (*Mustela frenata*), and short-tailed weasel (*Mustela erminea*). Avian predators that are present in winter and may compete with lynx include goshawks (*Accipiter gentilis*) and, possibly, great-horned owls (*Bubo virginianus*).

The area was historically and is currently grazed by domestic cattle during the summer months. There are a few gravel roads within the Okanogan National Forest portion of the study area, but logging roads are numerous on the Loomis State Forest, due to intensive clear-cutting and partial cutting in the last 2 decades. Snowmobiling is a popular winter activity in the study area, and several groomed trails are available in the

Okanogan National Forest. Snowmobile access within the Loomis State Forest is not confined to groomed routes. Snowmobile activity is heavy during the weekends, but generally few snowmobiles are seen during the week.

Trapping for lynx occurred in the study area until 1981 when the season was suspended to facilitate Brittell and Koehler's field studies (Brittell et al. 1989). The history of trapping and lynx management in this area are discussed in Brittell et al. (1989) and McKelvey et al. (2000*b*).

METHODS

Field Methods

Field work was conducted from December 27, 2000 to March 7, 2001 and again from December 12, 2001 to March 11, 2002. Snowmobiles provided all access to and within the study area.

Investigation of habitat selection by lynx was accomplished by comparing habitat conditions on systematically arrayed transects (availability) to those along lynx trails (use). Surveys along transects were used to quantify available forest conditions and relative prey abundances throughout the study area. Snow tracking of lynx was used to describe fine-scale habitat use. Sampling on transects and tracking of lynx were conducted on snowshoes. A systematic survey grid covering the entire study area was generated using a Geographic Information System (GIS). Seventy-eight 2-km transects were placed 1 km apart within the study area, which was divided into six comparably sized zones (Figure 5), each of which approximated the average size of a female lynx

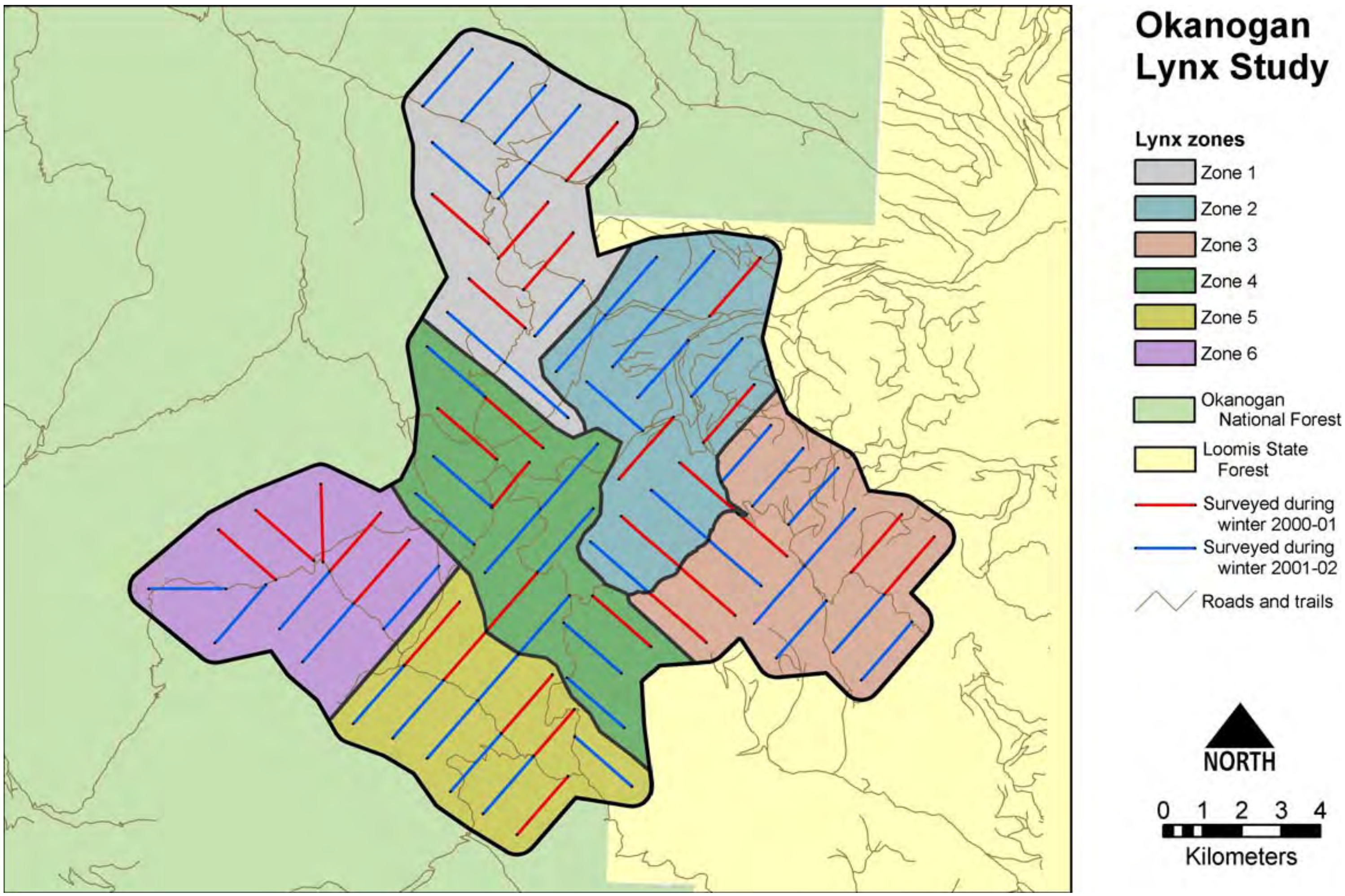

Figure 5. Lynx zones and availability transects sampled on the Okanogan Plateau, Washington. Transects sampled during the winter of 2000/01 are shown in red; transects sampled during the winter of 2001/02 are shown in blue.

home range (39 km^2) as determined by Koehler (1990). Zones were numbered 1-6, and there were 10-14 transects within each zone. All plots along each transect were located with Universal Transverse Mercator (UTM) coordinates. To obtain a representative sample of use and availability, both temporally and spatially, a zone was randomly selected at the beginning of the season, and the next sequential zone was searched each working day after that. Transects sampled within each zone were selected randomly. Lynx tracks were located by searching all available roads and trails by snowmobile within the zone selected until a lynx track was found. If a lynx track was not located in the selected zone, the next sequential zone(s) was searched until a track was located or available fuel or time was expended. If more than one lynx track was located, the freshest track was selected.

Data on habitat characteristics (physiographic conditions, forest structure, and relative prey abundance) were collected within 5-m radius plots at 200-m intervals along both availability transects and lynx trails. Starting points for all transects and lynx trails began at the snowmobile trail, with the first sample plot located 200 m from the starting point. For availability transects, locations of sample plots (UTM waypoints) were entered in Rockwell Precision Lightweight GPS Receivers (PLGRs) global positioning system (GPS) units. To locate sample plots, we used a compass to follow the bearing of each transect line. We then used the PLGR unit to navigate to the exact waypoint. A hip chain was used to measure 200-m intervals along lynx trails. Trimble ProXL GPS units were used to digitize lynx trails. Trimble units were set to record locations at two-second intervals while traveling along lynx trails. When we negotiated around or over obstructions along the lynx trails such as windfall patches, we used the pause function of the Trimble unit to avoid taking repeated locations from the same place, which created “noise” in the trail feature. To record a point along a lynx trail, the Trimble units were set to receive and average five locations at one-second intervals.

Physiographic Conditions

Relative snow firmness was measured by dropping a 100-g balance weight (penetrometer) attached to a nylon cord three times each from heights of 20 cm, 50 cm, and 100 cm above the snow surface. All penetrometer drops were conducted within 1 m of plot center on undisturbed snow. On lynx trails, penetrometer drops were placed between two consecutive lynx tracks. The depth penetrated into the snow was measured in cm by pulling the string taught without disturbing the weight, grasping the string with the thumb and forefinger at the top of the snow surface, pulling the weight from the snow, and measuring the distance between the thumb and the bottom of the weight. The average of the three drops from each height was recorded.

The average slope (%) of each plot was estimated using a clinometer. Aspect was measured to the nearest degree using a compass, then converted to degrees from southwest (0º - 180º). Thus, higher values were representative of wetter and cooler environmental conditions. Elevation for each plot was generated from UTM coordinates and digital elevation models using ArcInfo.

Forest Structure

All trees ≥1 m in height above the snow surface within the plot were identified to species and assigned to one of five diameter-at-breast-height (dbh) classes: ≤10.1 cm;

10.2–17.8 cm; 17.9-27.9 cm; 28.0–50.8 cm; and >50.8 cm. Canopy cover was visually estimated at two levels, >2.5 m above the snow surface, and ≤2.5 m above the snow surface, then placed into one of 4 cover classes: <10%; 10-39%; 40-69%; >70%. For data analyses, each dbh, understory, and overstory class was converted to the midpoint of the interval encompassed.

Relative Prey Abundance

The relative abundance of snowshoe hare, red squirrel, and grouse was estimated by counting all tracks intercepted in the snow along a 20-m transect at each plot beginning at plot center and extending toward the next sequential plot. For intensively used snowshoe hare runways, interpretation of use becomes somewhat subjective. Depending on interpretation of intensity of use, a tally of 3, 6, 9, or 12 tracks was recorded (Koehler 1990). Analysis of prey abundances was restricted to plots sampled 12-96 hr after the last snowfall. Prey counts within 12 hr of the last snowfall typically resulted in very few or no tracks encountered because prey species either became inactive during and shortly after storm events, or not enough time had elapsed for tracks to accumulate. I considered prey counts >96 hr since the last snowfall to be unreliable due to the effects of solar radiation, which obliterated tracks of both lynx and prey in open areas. For data analyses, track counts were standardized to the number of track intercepts per day by dividing the number of tracks by the number of hours since last snowfall, then multiplying by 24.

Data Analyses

Variables included in my analyses were based primarily on those that were identified as important to lynx in previous studies (Brittell et al. 1989, Koehler 1990). In part, this variable selection process was designed to reduce the number of variables included, given my relatively small sample sizes. Several subsets of the complete set of data were used for model building (Table 1). These included: (1) Physiographic variables. Selection of physiographic conditions such as slope, aspect, and elevation are not expected to be influenced by the presence or absence of forest vegetation, so I retained all plots in analyses of these physiographic variables. (2) Forest structure variables. Because the primary objective of this study is to investigate fine-scale habitat selection by lynx, all plots (both use and availability), which did not contain live trees, were removed from the forest structure analysis. One of the physiographic variables, snow firmness, may be influenced by forest structure due to the effects of shading by the forest canopy and melting/sloughing of snow from the canopy during warm periods, therefore I also analyzed snow firmness using the forest structure data subset. (3) Prey variables. Analysis of prey data was further reduced from the forest structure data set by including only those transects and trails which were sampled within 12-96 hr after the last snowfall.

Individual plots along a lynx trail are not independent of each other because the lynx is likely to choose how it moves through the landscape based on previous experience, energetic or competitive constraints placed upon the individual, or other factors that can’t be measured or even identified by the researcher. In addition, the

Table 1. Descriptive statistics for datasets used in logistic regression analyses of habitat selection by lynx on the Okanogan Plateau, Washington during the winters of 2000/01 and 2001/02.

	Lynx trails			Availability transects		
Dataset	No. of trails	Mean (range) no. of plots/trail	Total no. of plots	No. of transects	Mean (range) no. of plots/transect	Total no. of plots
Winter 2000/01						
Physiographic	23	8.7 (5 - 13)	200	30	9.4 (6 - 10)	283
Vegetation	20	8.8 (5 - 13)	175	29	8.5 (5 - 10)	247
Prey	19	8.7 (5 - 13)	165	24	8.5 (5 - 10)	204
Winter 2001/02						
Physiographic	17	15.2 (7 - 23)	259	46	9.8 (6 - 11)	450
Vegetation	17	14.4 (7 - 22)	244	41	9.0 (6 - 11)	367
Prey	14	14.9 (7 - 22)	209	33	9.1 (6 - 11)	300

location of a plot is dependent on the location of the previous plot for both lynx trails and availability transects. Consequently, I analyzed habitat selection by lynx using each trail or availability transect as the unit of analysis. Some transects were not sampled completely due to concerns about potential avalanche danger and, occasionally, due to complete loss of satellite coverage by the GPS unit. Lynx trails were followed as far as possible, given time constraints and tracking conditions. For all subsets of the data, availability transects and lynx trails were included in statistical analyses only if they contained ≥5 plots.

Final selection of variables included in logistic regression analyses was based on results of contingency table analyses for categorical variables and Mann-Whitney U tests and cumulative percent curves for continuous variables (Zar 1999). I conducted the majority of univariate data exploration using SPSS 10.0 for windows. To test the hypothesis that habitat characteristics used by lynx did not differ from availability, I conducted stepwise logistic regression analyses (GenMod, SAS version 8e) incorporating a hierarchical design (i.e., plots within transects). This is analogous to repeated-measures analysis, but with repeated measures being made spatially, rather than temporally. Because my analyses were exploratory in nature, I used $\alpha < 0.1$ for statistical significance.

RESULTS

One hundred and four kilometers of lynx trails were followed on snowshoes during the 2 years of the study, 43 km in year 1 and 61 km in year 2 (Figure 6). Two hundred and one habitat use plots were sampled in year 1 and 269 in year 2. Seventy-

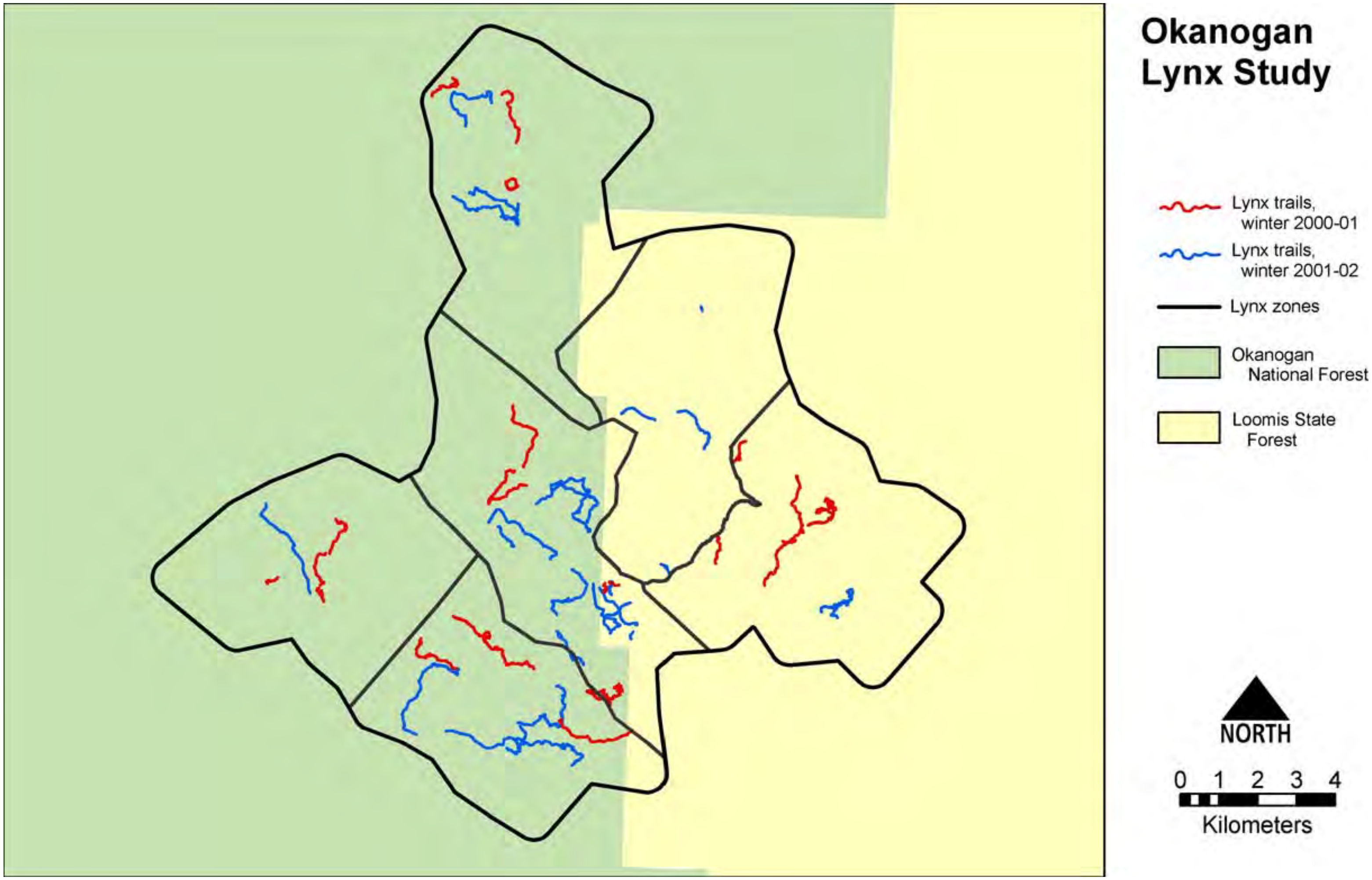

Figure 6. Lynx zones and trails sampled on the Okanogan Plateau, Washington. Trails sampled during the winter of 2000/01 are shown in red; trails sampled during the winter of 2001/02 are shown in blue.

eight availability transects were either fully or partially sampled during the study, 30 in year 1 and 48 in year 2 (Figure 5). Two hundred and eighty-six availability plots were sampled in year 1 and 454 in year 2.

Lynx tracks were never found within the boundaries of the Thunder Mountain fire either during snow-tracking sessions or while sampling plots on availability transects. Additionally, we did not record lynx crossing openings greater than 150 m in size.

Physiographic Conditions

Snow conditions varied substantially between the two winters of the study. In year 1, the snow pack remained powdery throughout the entire depth of the snow pack and for nearly the entire study period. No discernable ice crusts were present within the snow profile. Temperatures generally remained below freezing until March when they increased and the snow pack began to firm up. In year 2, the snow pack was much more firm, and had multiple ice layers within the snow profile. Snow density is a quantitative measure of water content in the snow pack that provides an indication of bearing strength of the snow between the two winters. Snow density is derived by dividing the snow water equivalent (SWE) by the snow depth. Snow density at Mutton Creek Snow Course station for February 2001 was 0.21 and increased to 0.32 for February 2002 (Natural Resources Conservation Service 2003*a*). Average snow density for the month of February at this station over the past 35 yrs is 0.27. These differences in snow density resulted in dramatic differences in the bearing strength of snow on the study area between the two winters. Because habitat selection by lynx may be influenced by differences in snow conditions, data from each winter was analyzed separately. During the second field season, the 100-g weight when dropped from heights of 20 cm and 50 cm did not contain enough energy to penetrate ice layers within the upper snow profile. Consequently, analyses of snow firmness was limited to data from 100-cm drops.

Lynx were highly selective for firmer snow in year 1 (Table 2) but did not select for snow firmness in year 2. Mean elevation for lynx trails was slightly higher than availability transects during both winters (Table 2), but differences between lynx trails and availability transects were not significant in either year. Mean slope on lynx trails was slightly greater than availability transects in year 1 (Table 2), though not significant. Selection for flatter slopes by lynx was significant in year 2 (Table 2). Probability of lynx use was not significantly influenced by aspect in either year. However, overall mean aspects were more southerly for lynx trails than availability transects in year 1 (Table 2).

Forest Structure

Lynx selected for greater understory cover in year 1 but not in year 2 (Table 3). Overstory cover was not selected for by lynx in either year. Lynx selected for stands with higher densities of live trees <10.1 cm dbh in year 1, but not in year 2 (Table 3). Few stands of small-diameter (<10 cm dbh) trees occurred within the study area, though small-diameter trees occurred in higher densities than any other size class (Figure 7). Generally, small-diameter trees occurred in small groups or singly in gaps within the older forest matrix. Stands with higher percentages of lodgepole pine <10.1 cm dbh were not selected by lynx in either year (Table 3). Lynx selected against stands with higher

Table 2. Physiographic variables used in stepwise logistic regression analyses of habitat selection by lynx on the Okanogan Plateau, Washington during the winters of 2000/01 and 2001/02. Descriptive statistics are calculated at the level of trails and transects. *P*-values represent the results of univariate logistic regression analyses.

	Lynx trails			Availability transects			
Variable	Mean	SE	Range	Mean	SE	Range	*P*-value[1]
Winter 2000/01[2]							
Snow firmness[3] (cm)	23.8	1.36	11.5 - 32.1	29.1	0.87	16.5 - 39.1	0.003 (+)
Elevation (m)	1861.6	1.82	1690.3 - 2034.6	1853.4	2.24	1512.7 - 2034.7	0.773
Slope (%)	30.0	1.94	13.0 - 49.2	27.0	1.38	14.3 - 41.6	0.214
Aspect[4]	83.9	6.44	27.2 - 145.6	92.2	4.57	46.8 - 136.6	0.291
Winter 2001/02[5]							
Snow firmness[3] (cm)	21.7	0.80	14.4 - 25.8	21.7	1.00	2.5 - 31.7	0.999
Elevation (m)	1867.8	2.81	1645.5 - 2123.1	1833.3	1.68	1619.7 - 2108.4	0.289
Slope (%)	23.7	1.62	14.3 - 39.4	27.4	1.03	12.4 - 42.0	0.062 (-)
Aspect	90.3	6.70	32.3 - 141.0	9208	4.21	32.5 - 147.4	0.753

[1]The direction of significant relationships are shown in parentheses.
[2]Sample sizes for all variables except snow firmness for the winter of 2000/01 were N=23 for lynx trails and N=30 for availability transects.
[3]Expressed as the mean depth a 100-g weight penetrates the snow when dropped three times from 100 cm above the snow surface; lower values indicate firmer snow. Sample sizes for snow firmness in winter 2000/01 were N=20 for lynx trails and N=29 for availability transects; sample sizes for snow firmness in winter 2001/02 were N=17 for lynx trails and N=41 for availability transects.
[4]Expressed as the angular distance from southwest (0-180°); higher values indicate cooler and wetter aspects.
[5]Sample sizes for all variables except snow firmness for the winter of 2001/02 were N=17 for lynx trails and N=46 for availability transects.

Table 3. Forest structure variables used in stepwise logistic regression analyses of habitat selection by lynx on the Okanogan Plateau, Washington during the winters of 2000/01 and 2001/02. Descriptive statistics are calculated at the level of trails and transects. *P*-values represent the results of univariate logistic regression analyses.

	Lynx trails			Availability transects			
Variable	Mean	SE	Range	Mean	SE	Range	*P*-value[1]
Winter 2000/01[2]							
Understory cover (%)	35.0	1.90	18.3 - 55.0	29.0	1.41	13.0 - 49.0	0.017 (+)
Overstory cover (%)	42.6	2.63	26.1 - 70.0	38.6	1.82	21.7 - 61.0	0.215
Density of live trees <4” dbh[3]	21.6	3.61	4.0 - 58.8	13.8	1.89	1.0 - 42.9	0.061 (+)
% lodgepole pine <4” dbh	37.8	6.13	0 - 92.5	31.5	3.75	0 - 81.3	0.372
Density of live trees >7” dbh	4.3	0.56	1.9 - 10.8	3.9	0.29	1.4 - 9.4	0.482
% lodgepole pine >7” dbh	44.3	4.71	2.9 - 100.0	42.4	4.25	0 - 85.2	0.752
Winter 2001/02[4]							
Understory cover (%)	24.8	2.53	6.2 - 44.3	25.1	1.41	5.0 - 42.0	0.912
Overstory cover (%)	37.9	3.33	14.4 - 76.4	37.1	1.65	18.0 - 60.0	0.815
Density of live trees <4” dbh	8.3	1.77	2.1 - 32.7	7.6	1.01	1.4 - 37.1	0.720
% lodgepole pine <4” dbh	27.4	3.93	8.9 - 68.2	26.8	3.15	0 - 76.3	0.903
Density of live trees >7” dbh	2.6	0.24	1.0 - 4.7	3.2	0.19	1.3 - 5.7	0.025 (-)
% lodgepole pine >7” dbh	43.5	3.63	20.8 - 87.4	38.5	3.04	0 - 90.5	0.292

[1]The direction of significant relationships are shown in parentheses.
[2]Sample sizes for the winter of 2000/01 were N=20 for lynx trails and N=29 for availability transects.
[3]Expressed as the mean density of stems per plot (78.5 m^2) within each trail or transect.
[4]Sample sizes for the winter of 2001/02 were N=17 for lynx trails and N=41 for availability transects.

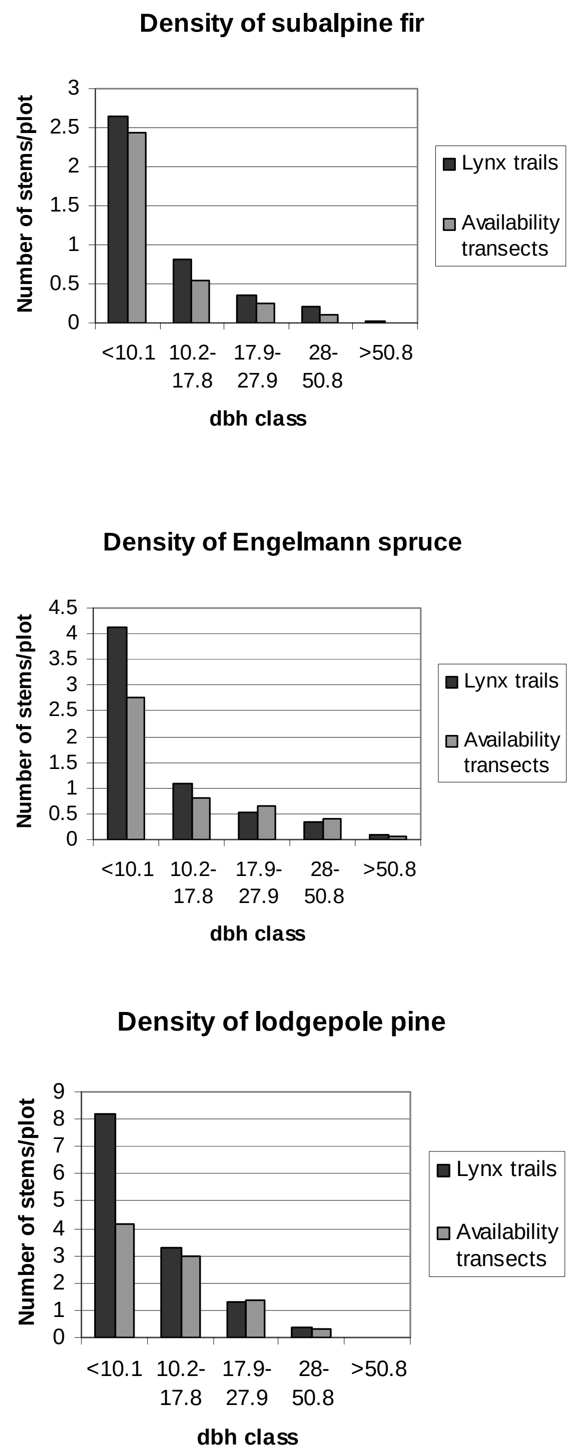

Figure 7. Size class and number of stems per plot on lynx trails and availability transects on the Okanogan Plateau, Washington.

densities of live trees >17.9 cm dbh during year 2, but no selection for these stands was apparent in year 1 (Table 3). Selection did not occur for stands with higher percentages of lodgepole pine >17.9 cm dbh in either year.

Relative Prey Abundance

Lynx selected for higher relative abundance of snowshoe hares in year 1, but hare indices between lynx trails and availability plots were similar in year 2 (Table 4). Relative abundance of red squirrels was similar between use and expected in year 1, but lynx selected against higher relative abundance of red squirrels in year 2 (Table 4).

Stepwise Logistic Regression Analyses

During the stepwise logistic regression analyses, I selected the univariate model with the lowest *P*-value for each data subset, then built all possible 2-variable models. However, none of the multivariate models resulted in significance for more than one variable at $\alpha < 0.1$. Therefore, final habitat selection models are the univariate models shown in Tables 2-4.

DISCUSSION

Physiographic Conditions

Lynx selected for small differences in bearing strength of snow during year 1 (Table 2). These results support the findings of Murray and Boutin (1991) in southwest Yukon. They demonstrated that snow was significantly firmer on lynx trails than it was 1 m off the trail, and that the use of hard-snow travel routes by lynx was not entirely due to travel on trails hardened by other animals. On the Okanogan Plateau, I believe that lynx used

Table 4. Prey variables used in stepwise logistic regression analyses of habitat selection by lynx on the Okanogan Plateau, Washington during the winters of 2000/01 and 2001/02. Descriptive statistics are calculated at the level of trails and transects. *P*-values represent the results of the univariate logistic regression analyses.

	Lynx trails			Availability transects			
Variable	Mean	SE	Range	Mean	SE	Range	*P*-value[1]
Winter 2000/01[2]							
Snowshoe hares[3]	2.3	0.31	0.9 - 6.2	1.1	0.21	0.2 - 4.0	0.006 (+)
Red squirrels[3]	0.4	0.12	0 - 2.0	0.3	0.08	0 - 1.3	0.430
Winter 2001/02[4]							
Snowshoe hares	1.5	0.29	0.5 - 4.5	1.4	0.22	0 - 5.9	0.889
Red squirrels	0.3	0.05	0 - 0.6	0.9	0.18	0 - 4.9	0.007 (-)

[1]The direction of significant relationships are shown in parentheses.
[2]Sample sizes for winter of 2000/01 were N=19 for lynx trails and N=24 for availability transects.
[3]Expressed as the mean number of track crossings along 20-m segments at each sample plot (5-m radius plus 15 m beyond plot) within each trail or transect.
[4]Sample sizes for winter of 2001/02 were N=14 for lynx trails and N=33 for availability transects.

multiple behavioral strategies to remain on firmer snow during year 1, whenever possible. At the landscape scale, lynx typically traveled in forested stands where snow was firmer, due to intermittent warm spells which caused the snow load in the canopy to slough and compact the snow profile. Snowshoe hare trails were used by lynx, as well as trails of conspecifics. Groups of lynx walked in each other's tracks while traveling through the landscape. Often, the lynx following placed their feet so perfectly in the previous cat's track that it was not possible to determine whether there were multiple animals until they diverged. Single lynx also followed previous lynx tracks in the same manner. Lynx were frequently found walking on both groomed and un-groomed snowmobile trails, which compacted snow and provided for ease of movement. Occasionally, we found lynx traveling on our snowshoe trails along transect lines. Although lynx used firmer snow surfaces whenever possible, I am not suggesting that travel by lynx was limited to these conditions. Lynx trails were often found crossing roads within 100 m or less of where we found them previously, and were found in many of the same places they were found during the late 1980's (G. Koehler, personal communication). We also followed two trails, approximately 1 month apart, that were almost exactly on top of one another. Therefore, my observations are that, with the exception of intensive hunting behavior within a habitat patch, lynx generally maintained what appeared to be pre-determined travel routes. Use of compacted surfaces by lynx described above was limited to situations where it provided a more energetically efficient means of moving in the chosen direction of travel. If a compacted surface diverged from the direction of travel, lynx continued without hesitation on undisturbed snow.

During year 2, maximum daily temperatures were generally higher than in year 1 (Natural Resources Conservation Service 2003*b*), which resulted in more periods of melting, and multiple ice crusts in the snow profile. Consequently, snow firmness increased throughout the study area in year 2, resulting in no difference detected in snow firmness between used and available habitat conditions (Table 2).

Koehler (1990) reported that lynx in north-central Washington used higher elevations in summer than in winter. A reanalysis of Koehler's data (McKelvey et al. 2000*a*) found that the majority of telemetry locations from 1985 to 1987 were at elevations between 1,700 and 2,000 m during all seasons. My data were consistent with these findings; mean elevations for lynx trails were 1,862 m and 1,868 m for year 1 and 2, respectively (Table 2). Only ten percent of plots along lynx trails were above 2,000 m (45/456), and only two of 40 lynx trails (5%) were entirely above 2,000 m. Mean elevations for lynx trails were slightly higher than for availability transects (Table 2), but were not significantly different. Within my study area, forest composition changes abruptly from subalpine fir/Engelmann spruce at higher elevations to Douglas-fir types below approximately 1,450 m, depending on aspect. Due to the fact that my study area was delineated, in part, based on Koehler's (1990) finding that lynx occurrence was primarily within the high-elevation subalpine fir/Engelmann spruce zone, it is not surprising that lynx use of elevation was not different than availability.

Lynx have been reported to use flatter slopes than available in both north-central Washington (McKelvey et al. 2000*a*) and in the southern Canadian Rockies (Apps 2000). Selection for flatter slopes is likely related to energetic demands if prey and vegetative composition and density remain similar throughout the range of available habitats. Lynx on my study area did not select for flatter slopes during year 1, but did in year 2 (Table 2). During the first winter of study, I believe that habitat selection by lynx was driven primarily by snow firmness; thus lynx were limited by snow conditions and energetic constraints in their ability to select for flatter slopes. During year 2, lynx were able to select for significant, though small, differences in slope, which further suggests that they attempt to reduce energetic costs whenever possible.

Lynx use of aspects was not significantly different than expected during either year of the study, although lynx used more southerly aspects in year 1 compared to availability (Table 2). Snow firmness on north-facing aspects (≥315º and ≤45º) was extremely low in year 1. During that year, plot-level data confirm that lynx were selecting routes on north-facing aspects where snow firmness was substantially greater than available (use: mean = 21.9 cm, availability: mean = 31.3 cm) compared to averages along availability transects and lynx trails within the entire study area (Table 2).

Forest Structure

Numerous studies have shown that lynx and snowshoe hares select mid-successional (20-40 yr old) forest stands that have regenerated from stand-replacement disturbances. Throughout the taiga, lynx select such stands at all phases in the hare cycle (Mowat 2000). Habitat selection by lynx in interior Alaska was nearly exclusive for a 25-yr-old burn, and lynx trails were rarely seen in an early seral burn (9 yr old) or mature forest greater than 100 yr old (Paragi et al. 1997). Very few lynx studies have been conducted in areas where 20-40 yr old stands were not available for lynx. Some studies have shown that lynx will select for mature coniferous forests as well as mid-successional stands. However, most of the researchers have not defined ‘mature’. Therefore, based on the age range of other forest types, which were defined, I assume that ‘mature’ stands described in these studies were >60 yrs old. Kesterson (1988) and Staples (1995) demonstrated strong selection by lynx for a mid-successional burn (approx. 40 yr old) and mature forest patches within the burned area in the Kenai National Wildlife Refuge. In Nova Scotia, Parker (1981) found that the habitats most preferred by lynx were early (14 yr old) and mid (22-28 yr old) successional stages followed closely by open mature conifer and open bog types. Koehler (1990) reported that pellet plot counts of snowshoe hares were highest in 20-yr-old lodgepole pine stands during the late 1980’s, and that these stands made up <10% of the area above 1,460 m where lynx occurred. In addition, these stand types rarely exceeded 1 ha in size. Only a few lynx studies have been conducted in areas where the majority of forest was mature (Murray et al. 1994, O’Donoghue et al. 1998*a*). In southwest Yukon, when hare numbers were higher in dense white spruce (*Picea glauca*) stands compared to open white spruce stands, lynx selected those habitats where hare numbers were higher. When hare numbers were similar among dense and open spruce habitats, lynx selected habitats according to their availability (Murray et al. 1994).

Currently, I would consider the forested portion of the Okanogan Plateau study area to consist primarily of older mid- and late- (>40 yr old) successional forest. Early seral stands (<15 yr old) on my study area, both natural and human-caused, have not grown tall enough for vegetation to protrude above the snow during winter. Dense stands of small-diameter lodgepole pine are extremely rare 15 yr after Brittell and Koehler's research. It appears that the young lodgepole pine stands with dense hare populations Koehler (1990) identified during his study have now reached the stem-exclusion stage and are no longer providing high-quality habitat for hares.

Lynx selected areas for hunting that had higher understory cover than available during year 1 (Table 3). Habitat patches that were used by lynx for hunting had the highest densities of small-diameter stems and/or included areas where subalpine fir and Engelmann spruce canopies extended to the ground. In year 2, relative abundance of hares was slightly lower overall and hares were more evenly dispersed between lynx trails and availability transects (Table 4). Lynx did not select for higher understory cover in year 2, but used stands with higher densities of mature trees less than expected (Table 3). Because I measured understory cover as any cover below 2.5 m above the snow surface, a large proportion of this variable was influenced by the branches of large trees near the snow surface. I believe that the canopies of large trees had an important influence on snow firmness in year 1, due to the sloughing of snow from the canopy. Therefore, I hypothesize that lynx used these stands during year 1 both to find hares and to gain the advantage of firm snow for chasing hares. Major (1989) found that the distance of a hare from escape cover was an important factor in determining the hunting success of lynx during a chase, and that longer distances from escape cover resulted in more successful kills by lynx. He also found that visibility was considerably higher in areas where lynx chased hares compared to visibility in available habitat types. During my study, snow was firmer in year 2 compared to year 1 and hares were more evenly dispersed, so lynx may have been concentrating their movements in more open areas where escape cover for hares was reduced and where visibility was higher.

Relative Prey Abundance

Hares generally avoid clearcuts, young stands (<10-15 yr old), and open areas (Hodges 2000*b*). Snowshoe hares did not use habitats where understory cover was absent. Hares were found in only 2 of 54 plots within the Thunder Mountain burn, and each contained only one hare track/transect. One of the plots was 130 m from the unburned edge, and the other was 14 m from the edge; both plots had some cover in the form of standing dead trees. Recent clearcuts (<10 yrs old) and natural openings did not contain hares, and lynx either traveled around the edge of these habitat types or made straight-line movements across them, usually at the narrowest point.

Late-seral coniferous forests generally do not contain dense populations of hares, but they produce red squirrels and are temporally stable (Ruggiero et al. 2000). The abundance of hares appeared to be relatively stable on the Okanogan Plateau during both years of the study, although their overall abundance appeared to be slightly less in year 2 (Table 4). In year 1, hare tracks were twice as numerous on lynx trails than on availability transects. During year 2, hares tracks were equally abundant on use trails and availability transects (Table 4). Relative abundance counts are not a reliable estimate of snowshoe hare densities. However, they may provide some insights into overall changes in hare numbers between years. Observations by myself, my crew, and others during the study period suggested that hare tracks were not as abundant in my study area in year 2 as they were in year 1. It may be that deep, powdery snow conditions in year 1 had a negative effect on the hare population, either through reduction in food availability, decreased reproduction, or increased vulnerability to predation.

Relative abundance of red squirrels decreased slightly on use trails from year 1 to year 2, but increased on availability transects (Table 4). Red squirrels are dependent on cone-producing trees. During year 2, lynx selected against the largest size classes of trees, and habitats with red squirrels were used significantly less than expected. Based on behaviors interpreted from snow-tracking, lynx concentrated their hunting efforts on hares during both years and squirrels were preyed upon opportunistically. The fact that lynx did not select within-stand characteristics that provide high-quality habitat for squirrels supports our observations that lynx were not concentrating their hunting efforts on locating squirrels, at least during year 2 of the study.

CHAPTER II: FOOD HABITS

INTRODUCTION

Throughout North America, the distribution of lynx is virtually coincident with the distribution of snowshoe hares (Aubry et al. 2000*a*). Ruggiero et al. (2000) concluded that snowshoe hares are the dominant prey of lynx throughout their range. Within their home ranges, lynx select stands where snowshoe hares are most abundant (Parker 1981, Koehler 1990, Murray et al. 1994). With the exception of two studies conducted in the taiga during low hare densities (Brand and Keith 1979, O'Donoghue et al. 1998), food habits studies of lynx have shown that snowshoe hares are present in 52-100% of all samples analyzed (Aubry et al. 2000*a*).

Hodges (2000*b*) concluded that habitat use by snowshoe hares is linked to dense understory cover rather than canopy closure, and that hares appear to select habitats for cover rather than for food, though cover and food often co-vary. Based on pellet counts, Koehler (1990) found that the density of snowshoe hares in Washington was four to five times greater in 20-year-old lodgepole pine stands than it was in lodgepole stands >43 years old, and nine times greater than in Engelmann spruce/subalpine fir stands. Koehler (1990) suggested that hares used densely stocked young lodgepole pine stands because they provided the forage, escape, and thermal cover required by snowshoe hares for survival. Koehler found that small-diameter (<2.5 cm) lodgepole pine stems comprised 96% of his observations of snowshoe hare browse. Ferron et al. (1998) and Hodges (2000a) both concluded that snowshoe hares do not use newly clear-cut areas. During Ferron's study, hares had not re-colonized clearcuts 4 years after harvest. In Maine, Litvaitis et al. (1985) found that hares began to colonize harvest units 6-7 years after cutting, and increased to peak population levels 20-25 years after harvest.

Red squirrels are considered to be an important alternative prey of lynx, particularly in southern boreal forests where hare densities are thought to be similar to hare population lows in the taiga (Aubry 2000*a*). Food habits studies of lynx have shown that red squirrels are the second most numerous prey species, after snowshoe hares. In Washington, Koehler (1990) found red squirrel remains in 24% of lynx scats collected in both summer and winter. Apps (2000) reported red squirrels were the prey item in 30% of 137 kills located while snow-tracking lynx in the southern Canadian Rockies. In the taiga, behavioral data showed that lynx actively hunted for red squirrels and may have switched from preying on hares to preying on red squirrels during a hare population low (O'Donoghue et al. 1998*b*).

Frequency of occurrence of prey species other than snowshoe hares and red squirrels have been as high as 39% in food habits studies of lynx during summer. However, during the winter, many small mammal species hibernate or spend the majority of their time in subnivean habitats, which make them unavailable as prey for lynx. Voles are occasionally found on the snow surface, and have been identified as prey items during winter food habits studies (Apps 2000, Kesterson 1988, O'Donoghue et al. 1998*b*, Staples 1995). Grouse and carrion are also found to occur in lynx scats during winter (Major 1989, Brand et al. 1976, Staples 1995).

The second objective of this study is to investigate winter food habits of lynx on the Okanogan Plateau.

METHODS

Scat Analyses

Scats were collected along lynx trails only if they were associated with fresh, identifiable lynx tracks. Each individual scat was placed into a small paper bag, and marked with the date, collector, location (UTM), and sample number. Scats were kept as snow-free as possible by either scraping the snow off the scat, or shaking the snow out of the bag once the scat was collected. Scats were dried at the field quarters by opening the top of the paper bag and placing them in a makeshift dryer (plywood box with an incandescent bulb). When they had dried thoroughly, the paper bags were closed and stored in a cool, dry environment. The scats were never removed from the original paper bags, nor were they touched during the entire process. All scats were sent to the Wildlife Conservation Genetics Laboratory in Missoula, Montana for DNA identification, and all were confirmed to be from lynx.

Scats were weighed and prepared for analysis by placing them in individual nylon mesh bags and soaking them in a mild soap and water solution for 24-48 hr. Each scat was hand-agitated in a clean soap and water solution to remove lipid content, then placed in a 500-micrometer sieve and rinsed with water. Remaining materials were placed into a petri dish and separated with forceps into bone, hair, skin, feather, and plant categories using a 10X dissecting microscope. Remains were identified using reference collections and standard mammal and hair identification manuals (Verts and Carraway 1998, Moore et al. 1974).

Prey Chases and Hunting Behaviors

Segments of lynx trails exhibiting a bounding gait were recorded as chases. Behaviors that indicated lynx had sighted prey, such as crouches, body drags or abbreviated strides prior to a bounding pattern were also included in the chase segment. Chase and kill-site data recorded included species chased, outcome, and total chase distance. If lynx were able to pounce on a prey item without a chase, we recorded the behavior as an ambush. Scats and urine stains were recorded as scent markings. Lynx frequently sat in the snow leaving an impression of their hindquarters; this kind of impression was described by Major (1989) as a “lookout site”. Lynx beds were recorded as either resting beds or ambush beds. Resting beds were usually ice-encrusted, presumably from body heat generated by the lynx from extended use. Typically, some portion of resting beds appeared to have an impression of the lynx in a curled-up position. Ambush beds were impressions of a lynx lying in the snow with it’s forefeet stretched out in front of it. Generally, ambush beds were not ice-encrusted, indicating short-duration use, but there were some exceptions. Lynx frequently deviated, sometimes only slightly, from their direction of travel to investigate snow-covered brush piles, logs, thickets, etc. This behavior was recorded as a structure investigation.

RESULTS

Scats Analyses

Forty-six scats were analyzed for food contents, 20 from year 1 and 26 from year 2. In year 1, remains of snowshoe hare were found in 18 scats (90%) and red squirrels in

9 (45%) scats (Table 5). Two scats contained remains of unknown sciurids (10%), and remains of an unknown bird and a porcupine were each found in a single scat (5%). Vegetation was found in 10 (50%) of scats in year 1 and consisted of one to a few conifer needles or fragments of herbaceous vegetation that were probably ingested incidentally during a meal.

In year 2, snowshoe hare remains were found in 22 (85%), red squirrels in 4 (15%), and southern red-backed voles (*Clethrionomys gapperi*) in 3 (12%) of the 26 scats. Grouse and unknown bird remains were each found in 1 scat (4%). Nine (35%) of the scats contained vegetation (Table 5).

Prey Chases and Hunting Behaviors

Four prey items were located along lynx trails in year 1 (Table 6). Snowshoe hares were identified as prey on three occasions and 1 was a blue grouse. Chase trails were recorded prior to locating two of the hare kills. At the site of the third hare kill, all evidence of a chase was obliterated by the lynx, which had spent considerable time at the feeding site. At this kill, there were two lynx beds within 5 m of the carcass, and several lynx trails radiating out from the carcass remains. An attempt was made to follow all lynx trails originating at the feeding site for approximately 50 m. However, a bounding pattern could not be found in the general area of the kill site. Therefore, it appeared that the lynx had ambushed the hare from above, which was a hunting technique we identified from tracks in the snow during year 2. An additional bed was located approximately 100 m uphill from the feeding site indicating that the lynx had spent a considerable amount of time around this hare carcass. The grouse kill was located in an open sagebrush area. It

Table 5. Food items found in 46 lynx scats collected on the Okanogan Plateau, Washington during the winters of 2000/01 and 2001/02.

	Frequency of occurrence (%)		
Food item	Winter 2000/01 (N=20)	Winter 2001/02 (N=26)	Both winters (N=46)
Mammals			
Snowshoe hare	90	85	87
Red squirrel	45	15	28
Southern red-backed vole	0	12	7
Porcupine	5	0	2
Unidentified squirrel	10	0	4
Unidentified mammal	0	8	4
Birds			
Unidentified grouse	0	4	2
Unidentified bird	5	4	4
Vegetation[1]	55	35	43

[1]Includes conifer needles and fragments of herbaceous vegetation.

Table 6. Results of prey chases by lynx on the Okanogan Plateau, Washington during the winters of 2000/01 and 2001/02.

Species chased	Number of successful chases	Mean (SE, range) ground distance (m) of successful chases	Number of unsuccessful chases	Mean (SE, range) ground distance (m) of unsuccessful chases
Winter 2000/01				
Snowshoe hare	3	6.33 (3.3, 0 - 11)	8	45.93 (11.0, 6 - 104)
Red squirrel	0	NA	3	16.67 (4.9, 7 - 23)
Grouse	1	0[1] (0, 0)	0	NA
Winter 2001/02				
Snowshoe hare	3	31.52 (25.0, 1 - 81)	20	46.06 (8.2, 6 - 133)
Red squirrel	4	6.17 (4.0, 0 - 18)	10	8.85 (1.6, 2 - 17)
Grouse	2	18.53 (9.5, 9 - 28)	2	8.00 (5.0, 3 - 13)
Both winters				
Snowshoe hare	6	18.93 (12.6, 0 - 81)	28	45.94 (6.6, 6 - 133)
Red squirrel	4	6.17 (4.0, 0 - 18)	13	10.65 (1.8, 2 - 23)
Grouse	3	12.35 (8.3, 0 - 28)	2	8.00 (5.0, 3 - 13)

[1]Grouse was ‘ambushed’; no chase segment was recorded.

appeared that two lynx traveling together located the grouse under the snow and dug it out. It was determined that the grouse was alive when the lynx located it because wing impressions were made in the snow while it was being carried by the lynx.

We recorded 13 prey chases by lynx in which the prey species was identified. As mentioned previously, one hare and one grouse did not have chases associated with them. Bounding patterns were observed on three occasions in which a prey item could not be identified. Overall hunting success for trails in which a known species was chased or ambushed was 27%. Success for hare chases was 27%, red squirrels 0%, and grouse 100%. Mean distances for successful and unsuccessful chases varied by species (Table 6). The mean distance for successful chases of all species combined was 4.8 m, unsuccessful chases for all species combined averaged 37.7 m.

In year 2, 41 chases were recorded in which the species chased could be identified (Table 6). Nine kills were recorded along lynx trails. Snowshoe hares were identified as prey items on three occasions, red squirrels on four, and spruce grouse on two (Table 6). Prey species could not be identified on 15 chase trails. Overall hunting success for trails in which a known species was chased was 22%. Success for hare chases was 13%, red squirrels 29%, and grouse 50%. Distances for successful chases for all species combined averaged 17.4 m, unsuccessful chases for all species combined averaged 32.1 m.

DISCUSSION

Scat Analyses

Because my sample sizes of kill data are small for both years, scat analyses provide a much more complete description of food habits by lynx during this study. Based on these analyses (Table 5), snowshoe hares were clearly the most important prey of lynx during both winters of study on the Okanogan Plateau, as they have been in virtually all studies conducted on Canada lynx during winter. These data further support our observations that lynx concentrated their hunting efforts on capturing snowshoe hares.

Red squirrels were the second most important food item in both years. Year 1 scats had a high frequency of red squirrel compared to year 2. This may reflect the fact that lynx concentrated their hunting efforts during year 1 in areas that had significantly higher understory cover (Table 4), much of which was the lower canopy of large trees, and also higher overstory cover classes (Table 4). These data indicate that lynx were hunting in areas where squirrels were more likely to occur because of the presence of larger cone-bearing trees. During year 2, lynx selected against large trees and, as a result, red squirrels. This behavior is further reflected in the fact that only 15% of scats contained red squirrels in year 2 (Table 5).

Grouse were positively identified in only 1 scat from year 2. However, 2 additional scats (one from each year) contained an unknown bird. Both of these scats contained large quills, which I could not identify to species because no feather was left on the quills. Based on the size of the quills, I suspect that both of these food items were grouse. The only other bird species observed on the study area with quills that large was the common raven (*Corvus corax*). Based on snow tracking and sightings, grouse did not appear to be abundant on the study. However, snow-tracking is not a reliable method of indexing grouse populations during winter because both species of grouse that occurred in the study area (blue and spruce) are likely to spend the vast majority of their time in the canopy where their forage is located. Because neither of these species flushes unless approached closely, our observations of grouse may have been biased in that we simply did not see them in the canopy unless they flushed.

Voles were found in 3 (12%) of the 26 scats from year 2 (Table 5). Although we saw vole tracks occasionally during snow-tracking, the tracks of these small animals are likely to melt out quickly and can be covered over by even a trace of new snow. We did not locate any chases by lynx involving voles, but for reasons stated above and the fact that they would be eaten whole, we probably would not be able to identify a vole kill in the snow. We found several bounding patterns by lynx in which we could not identify a prey species, and it is possible that some of these chases did involve voles or other small prey. Other items found in scats included 1 porcupine quill, and 2 scats in which I could not identify hairs either because they were broken and too short to positively identify or they were underfur, which have no characteristics that can be used to make a positive identification.

Caution must be taken when making inferences about the relative importance of prey based on scat analyses. Clearly, there are differential rates of passage of prey items through the digestive tract of a lynx. Even for voles, which are almost certainly eaten entirely in one meal, I found both hair and identifiable teeth in one scat and only hair in the next scat from the same lynx trail. This problem is probably compounded with larger prey, such as hares or squirrels, of which portions may remain in the GI tract for several consecutive scat deposits.

Prey Chases and Hunting Behaviors

Parker (1981) reported an unusual hunting behavior by an immature lynx in which it rushed blindly under snow-laden fir boughs, then walked out the other side. This behavior may explain the lack of an identified prey species on bounding trails during this study. Other possibilities are that the lynx obliterated the tracks of the prey species during the chase, or ran toward a squirrel or bird that was perched low in a tree, so no prey tracks were available to identify. Juveniles traveling with females often exhibited bounding patterns even though there was no prey item present.

Haglund (1966) reported that the most common reason for unsuccessful prey chases by European lynx (*Lynx lynx*) seemed to be the consistency (low bearing strength) of the snow. In Alberta, Nellis and Keith (1968) hypothesized that the reason for reduced success of chases by lynx on snowshoe hares during one year of their study was due to the low bearing strength of the snow. Murray and Boutin (1991) found that snow hardness had an effect on sinking depth of lynx, and that snow depth was less and snow hardness greater at successful chases of prey by lynx and coyotes compared to unsuccessful chases. During this study, snow was firmer on lynx trails than availability transects throughout the study area during year 1 (Table 2), and successful chases for both years were shorter than unsuccessful chases (Table 6) for all species (except grouse, which flushed). Although my sample sizes are small, I believe that areas with firm snow in year 1 did provide an advantage to lynx during prey chases because firm snow provides better footing and allowed lynx to close the distance between them and the prey item more quickly, which is evident in the mean distance for successful vs. unsuccessful chases between years. In year 1, if hares were not captured by the lynx in very few bounds, they escaped. Successful chases of hares in year 2 were much longer than year 1 (Table 6). Based on my observations, it appeared that hares relied heavily on breaking the line-of-sight between themselves and the lynx in order to escape. Hares nearly always changed direction during escape attempts once they put an obstruction, such as a suspended log, between themselves and the lynx. During unsuccessful chases of hares by lynx, the hare generally used several obstructions and direction changes during which the lynx obviously lost sight of the hare, because the lynx would immediately change from a bounding pattern to a walking pattern. Conroy et al. (1979) showed that snow compaction was negatively correlated to hare activity, and hypothesized that it was due to the fact that crusted snow was more prevalent in open areas which had less hare activity. However, hares may have an advantage while trying to escape from predators in soft snow due to their relatively lower foot-loading.

Lynx are morphologically adapted to hunt snowshoe hares (Murray and Boutin 1991). Accordingly, their foraging behavior is characterized by hunting tactics and movement patterns appropriate for hunting hares (Mowat et al. 2000). Lynx trails became more sinuous in areas with dense understory structure, indicating an increase in hunting behavior. Typically, habitat patches that contained high densities of small-diameter stems and downed logs, as well as areas where the canopy of mature trees extended to the ground, were searched intensively by lynx. This behavior indicated that lynx were primarily focused on actively seeking out snowshoe hares rather than red squirrels as prey. Lynx trails often zig-zagged through patches of dense understory cover. Structures that might contain hares were nearly always investigated. Even when traveling through habitats with little understory structure, lynx would deviate from the direction of travel to investigate any downed logs or snow-covered brush or small trees which may contain a hare.

Red squirrels are generally considered to be the most important alternative prey of lynx in southern boreal forests (Aubry et al. 2000*a*). In year 1, red squirrel remains were found in 45% of lynx scats (Table 5). The high percentage of red squirrel in the diet in that year is likely due to the fact that lynx were selecting habitats with higher understory cover, much of which was lower branches of large trees. Since red squirrels are dependent on larger, cone-producing trees, lynx likely encountered red squirrels more regularly in year 1 than in year 2. Also, red squirrels are inefficient at negotiating deep, powdery snow and therefore, were probably easier for lynx to capture in these conditions.

During a hare decline and low phase in southwest Yukon Territory, O'Donoghue et al. (1998*a*) found that 20-30% of all chases of red squirrels by lynx were initiated from lynx beds. Although lynx in the Okanogan did use ambush beds and lookout sites, this behavior was not common either on hare trails or near squirrel middens. We did not record any prey chases initiated from either resting or ambush beds. On one occasion, I recorded a chase of a red squirrel by a lynx in which the squirrel ran into a midden. The lynx dug into the midden in several places in an attempt to capture the squirrel, but was unsuccessful. Observed lynx behaviors did not indicate that they actively hunted squirrels or grouse, rather, these species appeared to be taken opportunistically. On one occasion, we tracked a lynx that happened upon a covey of spruce grouse. In this instance, the lynx made a concerted effort to capture a grouse by hunting intensively throughout the immediate area.

Caching behavior by lynx has been documented in several studies (Parker 1981, O'Donoghue et al. 1998*b*, Nellis and Keith 1968). Presumably, caching behavior indicates a lynx's ability to obtain excess food. Parker (1981) reported that the hindquarters of a hare appeared to be the last part of the carcass eaten and that it was often left untouched. He also claimed that the incisors and feet were also left untouched due to possible injury from ingestion. Caching behavior was not observed during this study. Snowshoe hare prey remains generally consisted only of the hide, the caecum and its contents, and occasionally a foot or two; numerous hare teeth, including incisors, and claws were found in scats. Red squirrel prey remains consisted of the caecum and the tail. Grouse were generally plucked, but eaten entirely.

Hare densities in the contiguous U.S. are generally considered to be similar to those in the taiga during hare population lows. Hodges (2000*a*) summarized the results of hare surveys in the contiguous U.S. and found peak hare densities of 1-2 hares/ha compared to 4-6 hares/ha or more in northern areas. Hare densities on the Okanogan Plateau were estimated from Koehler's (1990) pellet plot data at 0.09-1.79 hares/ha during the period 1986-1989, depending on habitat type (Hodges 2000*a*). Hares were clearly the most important prey item for lynx on the Okanogan Plateau. Because an individual snowshoe hare provides five times the biomass of a red squirrel (Nellis and Keith 1968), it is clear why lynx spent nearly all of their foraging time in search of them. Although red squirrels were found in 45% of lynx scats from year 1, only 15% of scats in year 2, which was about average in terms of snow density, contained red squirrels (Table 5). Lynx reproduction and survival is closely tied to their ability to kill sufficient numbers of snowshoe hares. Koehler (1990) hypothesized that a diet of squirrels may not be adequate for lynx reproduction and survival of kittens. Apps (2000) reported low kitten production and survival in the southern Canadian Rockies during a period when 47% of prey were species other than hares. The lack of caching behavior, consumption of entire prey, and documentation of low kitten production and survival indicate that lynx in southern populations may always be near the energetic lower limit for population persistence.

Summary and Conclusions

Our goal during tracking sessions was to follow lynx for a minimum of 2 km, so that data from lynx trails were comparable to those from availability transects. During year 1, snow conditions made tracking extremely difficult because of dry and powdery snow conditions, which caused us to sink deep into the snow even on snowshoes. In addition, there were safety concerns because of avalanche conditions that had formed early in the season and persisted through February due to a layer of hoar frost at the soil surface. Because the snow pack would frequently crack and slump around us even on moderate slopes, we did not follow lynx trails or transect lines through open areas on steep slopes. Therefore, we rarely tracked lynx more than 2 km during the first field season and had to abandon tracks and transects occasionally. During year 2, snow conditions were much easier to negotiate and crews nearly always completed 2 km along lynx trails and, in many cases, were able to follow lynx much further. Many times we went back on successive days and continued on a lynx track or backtracked the same lynx because I felt that it would help to better understand how lynx used the study area. For example, when we followed lynx further, we were able to collect more scats, document more chases, and find more prey remains for food habits analyses. Also, we were able to start a track earlier because we did not have to take the time to locate one, enabling us to go further on lynx tracks. However, this strategy reduced my sample size of lynx trails in year 2, because it resulted in longer but fewer trail segments. In retrospect, I probably should have tried to increase my sample size of trails, rather than distance tracked.

The Okanogan Plateau study area was composed primarily of mid- and late-successional forests; early seral conditions consisted of a stand-replacement burn and harvest units, all of which were essentially clearcuts. Lynx did not use early seral habitats probably because they had not regenerated to the point where vegetation was protruding above the snow. Mid-successional stands (20-40 yr old) which previous studies have shown to be selected by hares were generally not available. Therefore, lynx habitat use was confined to older mid- and late-successional stands where they sought out areas where small-diameter stems occurred in forest gaps. Vegetative characteristics within the forest matrix did not differ widely between lynx trails and availability transects. Some possible reasons for not finding more significant differences in use vs.

availability among the vegetation and prey variables we measured are: (1) Habitat use by lynx was averaged among plots over the entire length of the trail. Lynx must travel through a variety of habitats which may not be suitable or desirable for hunting, to get to those that are. Therefore, we measured habitat use on plots that may not have been representative of high-quality lynx habitat, and combined them with those that were. However, to conduct statistically valid analyses of habitat selection, I could not consider individual plots along trails to be independent. (2) Because this study was conducted over only 2 winter seasons, our sample sizes of lynx trails were relatively small, and may not represent the full range of habitats that lynx use on the study area. This, combined with the probability that many of the availability plots we measured may be used by lynx, further reduces our ability to differentiate use trails from availability transects. (3) Throughout their range, lynx select early to mid-successional stands (15-30 yr old) for hunting because they are more productive for snowshoe hares. Stands of this type were not available on the Okanogan Plateau during the study period. (4) We may not have identified and measured some of the habitat characteristics that are important to lynx and therefore, would better differentiate use from availability.

Many of the habitat variables included in logistic regression models had a narrow range of available conditions. Thus, even though differences between use and availability for these variables were small, they were important to lynx. An increase in plot size may have improved our characterization of within-stand characteristics. I believe that if I had split the smallest diameter class of trees measured (<10 cm dbh) into two classes, it would have better explained use vs. availability. In many cases, trees approaching 10 cm dbh were in the stem exclusion phase of forest regeneration. This phase of forest regeneration does not provide abundant food for hares because small-diameter stems are generally not available. This phase also provides only marginal cover for hares because there is little structure in such stands near the snow surface. The smaller trees associated with this size class (<5 cm dbh) appeared to be the most useful to hares for both forage and cover.

Future research on this population of lynx should include telemetry studies that include a tracking component. Snow-tracking does not provide information on demographic characteristics of the population. However, I believe it does provide a much more accurate measure of habitat use than telemetry because habitat characteristics are identified at frequent intervals and the entire travel route of the lynx can be digitized. In my opinion, research on lynx habitat relations should focus on regenerating stands within the study area. The Thunder Mountain and Thirty-Mile fires, along with harvest units on the Loomis State Forest, would provide excellent opportunities for future research on both hare and lynx habitat relations. An understanding of how lynx and hares respond to regeneration in terms of age, stocking-levels, species composition, and juxtaposition (both within the stand and across the landscape) would provide managers with useful information on both species. Future research should also be aimed at further elucidating the effects of snow firmness on both lynx and hares, including effects of vegetative cover on snow firmness.

Because the Okanogan Plateau lynx population is at the southern extent of lynx range, this population may be at the threshold of persistence. This population occupies a relatively small area just south of the Canadian border. Large stand-replacement fires have been numerous within the range of this population in recent years. In addition, an accelerated rate of timber harvest is now taking place on the Loomis State Forest portion of the study area. Because lynx did not use non-forested areas during winter, these large-scale habitat disturbances may be detrimental to this population until the disturbed areas become re-vegetated and capable of supporting snowshoe hares.

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