Canada Lynx Habitat and Topographic Use Patterns in North Central Washington: A Reanalysis

Kevin S. McKelvey, USDA Forest Service, Rocky Mountain Research Station, Forestry Science Lab, 800 E. Beckwith, Missoula, MT 59807

Yvette K. Ortega, USDA Forest Service, Rocky Mountain Research Station, Forestry Science Lab, 800 E. Beckwith, Missoula, MT 59807

Gary M. Koehler, Washington Department of Fish and Wildlife, 600 Capitol Way N., Olympia, WA 98501

Keith B. Aubry, USDA Forest Service, Pacific Northwest Research Station, 3625 93rd Ave. SW, Olympia, WA 98512

J. David Brittell, Washington Department of Fish and Wildlife, 600 Capitol Way N., Olympia, WA 98501

Abstract—We examined habitat selection by 22 lynx on the Okanogan National Forest in Washington, analyzing radiotelemetry data collected during two previous studies, 1981 through 1988. At a coarse scale, lynx showed little use of areas below 1,400 m or above 2,150 m. Within the zone between 1,400 and 2,150 m, lynx used areas with slopes <10% and moderate stream densities in winter. Selection for combinations of physical variables and vegetation types was stronger in winter versus summer, and lynx showed strong selection for lodgepole pine cover

types in winter. Relative abundance of snowshoe hares measured from pellet counts on plots within the study area were highest within lodgepole pine and lowest within Douglas-fir cover types, and winter selectivity may have been influenced by abundance and distribution of hares. In summer, lynx avoided Douglas-fir cover types and selected northeast aspects; Douglas-fir tended to occur on southwest aspects, especially at higher elevations. Road densities in the study area did not have a significant effect on habitat selection, and lynx crossed roads at frequencies that did not differ from random expectation.

Introduction

Little is known about habitat use patterns of Canada lynx at the southern periphery of their range, and relevant telemetry studies are particularly limited. Koehler et al. (1979) found that two radio-tracked lynx in Montana used densely stocked stands of lodgepole pine almost exclusively, but results were based on only 29 telemetry locations. Smith (1984) found that approximately 80% of locations obtained from four lynx radio-tracked for two years in Montana were within areas classified in the subalpine fir series (Pfister et al. 1977). Neither Koehler et al. (1979) nor Smith (1984) compared use patterns to the distribution of available forest types. Other telemetry-based studies in the contiguous United States include Mech (1980), who monitored 14 lynx in Minnesota, and Brainerd (1985), who tracked seven lynx in Montana, but neither reported habitat use. Three telemetry-based studies of lynx are in progress in the western United States and Southwest Canada (see Chapters 11, 12).

Most information on habitat relationships of lynx in the contiguous United States has been derived from two telemetry studies conducted on the Okanogan National Forest, Washington. Brittell et al. (1989) obtained 540 locations for 17 lynx between 1981 and 1983, and Koehler (1990) recorded 302 locations for seven lynx between 1984 and 1988 (Table 10.1). Koehler (1990) reported that home ranges contained a higher proportion of lodgepole pine and a lower proportion of Douglas-fir cover types than the overall study area (a zone surrounding the lynx locations and confined to elevations above 750 m). He also found more pellets of snowshoe hares within lodgepole pine forests than within other cover types used by lynx and concluded that lynx selected habitat based on hare densities. Additionally, Koehler (1990) found that cover types associated with low-elevation grass-lands or alpine areas were rare within home ranges and that the average elevation of telemetry locations in winter was lower than that in summer. In contrast, Brittell et al. (1989) reported that lynx home ranges did not differ

Table 10.1 — Telemetry data for the 22 lynx sampled by Brittell et al. (1989) and Koehler (1990). Two lynx were monitored during both studies.

Lynx ID	Sex	n	Start (mo/yr)	Stop (mo/yr)	Duration (days)	Avg. days between locations	J	F	M	A	M	J	J	A	S	O	N	D	Study[a]	Sampled[b]
1	M	23	10/81	7/82	274	12	4	2	3	3	2	5	2	0	0	1	1	0	B	B
3	F	31	10/81	8/82	298	10	5	2	4	3	3	5	4	2	0	1	1	1	B	B
4	M	19	8/82	3/83	227	12	2	2	4	0	0	0	0	4	0	3	2	2	B	W
6	M	64	4/82	9/83	534	8	2	2	4	7	7	10	6	8	9	4	2	3	B	B
7	M	47	11/81	3/83	483	10	4	4	7	2	4	5	4	4	3	3	3	4	B	B
11	M	60	4/82	9/83	534	9	2	2	4	7	5	10	5	8	9	3	2	3	B	B
14	F	47	5/82	9/83	506	11	1	2	3	1	4	8	4	6	9	4	2	3	B	B
16	M	49	7/82	9/83	431	9	2	2	4	4	4	5	4	9	9	3	0	3	B	B
17	F	18	7/82	1/83	177	10	2	0	0	0	0	0	2	2	3	4	2	3	B	B
18	F	18	7/82	1/83	169	9	2	0	0	0	0	0	1	4	3	3	2	3	B	B
20	F	41	10/82	9/83	338	8	2	2	4	4	4	5	3	4	6	2	2	3	B	B
21	M	25	4/83	9/83	169	7	0	0	0	2	4	5	3	5	6	0	0	0	B	S
24	F	12	7/83	9/83	65	5	0	0	0	0	0	0	1	5	6	0	0	0	B	S
31	M	11	7/83	9/83	65	6	0	0	0	0	0	0	0	5	6	0	0	0	B	S
33	F	16	5/82	6/82	53	3	0	0	0	0	6	10	0	0	0	0	0	0	B	S
55087	M	28	2/87	2/88	345	12	0	5	4	1	3	6	1	2	0	0	0	0	K	B
59011	M	28	6/85	6/86	384	14	4	5	5	0	3	9	2	2	1	1	0	1	K	B
104090	M	88	7/82;6/86	9/83;9/87	883	10	7	8	9	4	4	15	8	10	12	3	4	4	B,K	B
109062	M	37	2/86	10/87	721	19	1	8	7	2	1	6	3	1	4	1	2	1	K	B
111167	F	103	8/83;6/85	9/83;10/87	927	9	6	1	4	2	9	21	13	12	17	3	5	1	B,K	B
112071	F	33	3/86	10/87	595	18	0	3	2	2	3	7	6	0	3	1	4	1	K	B
195058	M	44	11/84	7/86	606	14	0	1	4	2	3	3	7	8	9	2	3	2	K	B
Total		842					46	51	72	46	65	130	79	102	115	42	37	38		

[a] B = Brittell et al.; K = Koehler.
[b] Sampled in both (B) seasons, or exclusively in winter (W) or summer (S).

significantly from the study area in terms of slope, aspect, elevation, and vegetation type.

Considering the scarcity of information on habitat use by lynx and the conflicting results described above, we reexamined data from Brittell et al. (1989) and Koehler (1990). Because these two studies occurred in the same area and used the same methods, they represent a continuum of data collection amounting to 842 locations for 22 lynx (Table 10.1). By combining these data, and by taking advantage of current GIS and statistical technologies, we were able to evaluate habitat relationships in greater detail than had been possible in the past.

Using the combined telemetry locations of Brittell et al. (1989) and Koehler (1990) as well as spatial data describing vegetation, topography, roads and streams, we evaluated habitat selection by lynx in the study area considering multiple spatial scales. Additionally, we considered location data from road-based track and camera surveys recently conducted by the State of Washington and the Okanogan National Forest. Because lynx locations derived from such surveys are sometimes used to infer lynx habitat relationships, we assessed the concordance between these locations and the telemetry data. We also used hare data from Koehler (1990) to examine the relationship between habitat use by lynx and hare densities.

Methods

Study Area

Lynx studies were conducted by Brittell et al. (1989) and Koehler (1990) in a 1,800-km^2 area of Okanogan County in the northeastern Cascade Range of Washington (48° 15' to 49° N., 119° 45' to 120° 15' W.) where elevations range from 750 to 2,540 m. Road densities averaged 800 m/km^2 (±STD of 870 m/km^2; range 0-3,400 m/km^2), and >90% of the length consisted of narrow, unpaved roads. Annual precipitation averaged 51 cm at 660 m, and snow depth exceeded 1 m above 1,980 m during November through March (Koehler 1990). Douglas-fir and ponderosa pine dominated forests below 1,370 m and southern aspects at higher elevations. High elevation forests above 1,370 m were dominated by Engelmann spruce, subalpine fir, and lodgepole pine (Koehler 1990).

Available Data

Telemetry locations were obtained by Brittell et al. (1989) and Koehler (1990) for 13 adult male and nine adult female lynx from 1982 to 1988 (Table 10.1). Lynx were captured in leg-hold and box-type live traps.

Under ketamine hydrochloride anesthesia, lynx were marked with ear tags, and fitted with activity-sensitive transmitter collars (Telonics, Mesa, AZ). Movements of radio-collared animals were monitored from aircraft at seven to 15 day intervals, depending on weather, and at one to five day intervals from the ground. Lynx were approached to within 200 m for ground monitoring and attempts were made to obtain ≥2 locations at ~90° direction from the animal. Locations were plotted on 1:62,500 U.S. Geological Survey topographic maps to the nearest 50 m. Telemetry error averaged 200 m for data collected 1982 through 1986 (Koehler 1990) but was not estimated for other years.

For examination of habitat selection by lynx, we obtained three GIS vegetation layers: one used by Koehler (1990) that was designed to model areas of equivalent fuel loading (Fuels), another generated for the Okanogan National Forest by Pacific Meridian Resources, Inc. (PMR), and a third resulting from the North Cascades Grizzly Bear Ecosystem Evaluation (NCGBEE) (Almack et al. 1993). The maps were derived from various LANDSAT images dating from the early to mid-1980s and had similar resolution (pixel size ~50 m). Because the maps were classified with differing methods into different vegetation classes (Table 10.2), their depiction of vegetation in the study area also varied. Labeling of vegetation classes must be considered primarily nominal: it is unknown to what extent class label reflects actual vegetation in a given area. For these reasons, we considered each vegetation coverage separately in examinations of habitat selection, describing our results in terms of the classes in each coverage. In the discussion, we look for common patterns among these analyses, making inferences about the types of vegetation selected by lynx (Table 10.2).

Our analyses of habitat selection by lynx also incorporated physical variables including road and stream densities, elevation, slope, and aspect. Coverages of roads and streams developed from 1:24,000-scale data were converted to density maps by rasterizing the lines and using Arc/INFO's FOCALSUM function (ESRI 1997) to index densities. Densities were computed within a fixed neighborhood extending 2.3 km, equivalent to the average radius of the 50% adaptive kernel home range estimate for lynx with >50 locations (Table 10.1). Used in this way, FOCALSUM produces a raster-map in which the value of each raster is the sum of the number of "road" or "stream" rasters within 2.3 km.

One problem with using this approach to calculate densities is that all roads or streams within the 2.3 km neighborhood contribute equally regardless of distance from the "focal" raster. Not only is it likely that roads or streams close to a location influence habitat use more than distant ones, but the area within the neighborhood is concentrated at the edge, away from the focal raster. Unless this is corrected, the road or stream densities

Table 10.2— Vegetation classes within the study area as defined by the Fuels (A), PMR (B), and NCGBEE (C) layers (see text for explanation). Also listed are labels for vegetation types used in the text Discussion section to refer to important classes. Species names are: subalpine fir (Abies lasiocarpa), subalpine larch (Larix lyallii), lodgepole pine (Pinus contorta), whitebark pine (Pinus albicaulis), Engelmann spruce (Picea engelmannii), ponderosa pine (Pinus ponderosa), Douglas-fir (Psuedotsuga menziesii), western larch (Larix occidentalis), PUTR (Purshia tridentata), VACA (Vaccinium caespitosum), VADE (Vaccinium deliciosum), VASC (Vaccinium scoparium).

Original class label	Class definitions for meso-scale analyses	Vegetation type	Area (%)	Mean elevation (meters)	STD elevation (meters)
A					
Lodgepole pine	Lodgepole pine	Lodegepole pine	32.6	1,705	209.8
Engelmann spruce	Engelmann spruce	Spruce-fir	8.9	1,840	151.1
Engelmann spruce/subalpine fir/other	Engelmann spruce/subalpine fir/other		9.6	1,780	161.5
Ponderosa pine/Douglas-fir/western larch	Ponderosa pine/Douglas-fir/western larch	Douglas-fir	13.0	1,388	199.6
Lodgepole pine/other	Lodgepole pine/other		7.4	1,780	221.8
Douglas-fir/ponderosa pine	Douglas-fir/ponderosa pine		6.9	1,307	205.6
Grass, rock	Grass, rock		8.0	1,835	368.7
Hardwood/hardwood conifer	Other		1.9	1,294	257.3
Subalpine larch	Other		4.7	2,085	100.5
Mountain hemlock/silver fir	Other		1.2	1,934	132.7
Whitebark pine	Other		1.3	2,125	140.8
Ponderosa pine	Other		2.7	1,047	252.7
Shrub, grass/conifer	Other		1.8	1,453	332.0
B					
Douglas-fir	Douglas-fir	Douglas-fir	6.1	1,382	307.8
Douglas-fir/mix conifer	Douglas-fir/mix conifer		9.5	1,504	243.7
Lodgepole pine	Lodgepole pine	Lodgepole pine	20.4	1,776	230.1
Mix-various conifer species	Mix-various conifer species		10.8	1,503	310.7
Subalpine fir	Subalpine fir		17.7	1,782	220.1
Subalpine fir/Engelmann spruce	Subalpine fir/Engelmann spruce		5.1	1,668	219.1
Subalpine fir/Douglas-fir	Subalpine fir/other		0.7	1,558	231.7
Subalpine fir/lodgepole pine	Subalpine fir/other		2.6	1,854	248.8
Subalpine fir/mix conifer	Subalpine fir/other		1.8	1,835	177.4
Grass	Grass		9.0	1,662	435.6
Douglas-fir/lodgepole pine	Other		0.5	1,557	305.3
Engelmann spruce/mix conifer	Other		1.0	1,775	227.6
Less than 25% any species	Other		6.2	1,508	391.5
Lodgepole pine/mix conifer	Other		0.8	1,788	196.9
Pacific silver fir	Other		1.2	1,865	195.6
Pacific silver fir/mix conifer	Other		0.1	1,949	66.2
Ponderosa pine	Other		1.5	1,325	274.6
Shrub	Other		3.9	1,684	418.6

(con.)

Table 10.2 (Con.)

Original class label	Class definitions for meso-scale analyses	Vegetation type	Area (%)	Mean elevation (meters)	STD elevation (meters)
B (con.)					
Subalpine larch/mix conifer	Other		0.0	2,115	0.0
Various hardwood species	Other		0.1	1,480	96.9
Western larch/mix conifer	Other		0.6	1,472	148.1
Whitebark pine/mix conifer	Other		0.3	1,853	183.6
Agriculture and developed	Absent		<0.1	380	0.0
Ponderosa pine/Douglas-fir	Absent		0.2	967	192.1
C					
Subalpine fir-Engelmann spruce-lodgepole pine—east	Subalpine fir-Engelmann spruce-lodgepole pine	Lodgepole pine	60.3	1,751	172.9
Douglas-fir-mixed conifer—east	Douglas-fir-mixed conifer		14.7	1,396	252.5
Subalpine larch	Other forest		2.3	2,128	65.5
Non-riparian deciduous—east	Other forest		0.8	1,730	179.9
Whitebark pine	Other forest		1.5	2,130	57.3
Engelmann spruce riparian	Other forest		1.8	1,540	361.5
Riparian deciduous forest—east	Other forest		0.2	1,273	406.6
Subalpine - alpine VASC - VACA meadow	Subalpine meadow		2.8	2,028	177.2
Subalpine heather-VADE meadow	Subalpine meadow		0.4	2,192	200.8
Subalpine lush meadow—southwest	Subalpine meadow		0.5	2,102	138.0
Subalpine meadow -messic to dry—east	Subalpine meadow		1.2	1,708	143.9
Subalpine mosaic—east	Subalpine meadow		0.9	1,653	98.9
Alpine meadow—east	Other open		0.7	2,244	89.0
Bare and rock	Other open		0.5	1,964	365.7
Montane herbaceous—east	Other open		2.7	1,315	149.9
Montane mosaic—east	Other open		1.6	1,263	151.8
Montane shrub—east	Other open		0.2	1,708	372.3
Agriculture - fallow and dry pasture	Absent		0.1	433	73.3
Lush shrub elev. herbaceous—east	Absent		0.1	813	281.0
Ponderosa pine	Absent		0.5	756	111.4
Ponderosa pine-Douglas-fir	Absent		5.1	1,046	139.0
Shrub steppe - herbaceous	Absent		0.7	987	163.5
Shrub steppe - PUTR	Absent		0.5	888	175.5
Wet soil and gravel	Absent		0.0	2,152	0.0

computed for a location using FOCALSUM will be dominated by land conditions 2 km away and will be relatively insensitive to adjacent roads or streams. We therefore applied a linear distance-weighting function to the neighborhood: adjacent road or stream rasters contributed 3.0 to the FOCALSUM, and roads or streams at distances of 1.15 and 2.3 km contributed 1.5 and 0.0, respectively.

The digital elevation model (pixel size ~32 m) that we obtained contained systematic errors, or bands, which produced ridges and trenches along the cardinal directions. We removed the bands using Arc/INFO's FOCALMEAN function (Brown and Barra 1994) and used the resultant grid to obtain elevation, slope, and aspect data (ESRI 1997). Because aspect may be most relevant to the biology of the lynx through its influence on temperature and moisture gradients, we transformed aspect from a circular statistic into a measure of angular distance from northeast. Redefined aspect values ranged from 0 on the coldest, wettest slopes (due northeast) to 180 on the warmest, driest slopes (due southwest). We also assigned flat areas a value of 180 because they receive high radiant energy loads.

Evaluating Habitat Use

Methods developed to evaluate habitat selection for populations compare the distribution of animal locations relative to that of available habitat types. When a habitat type is used at a proportion significantly greater than its availability, we state that it is selected, while we infer that the opposite inequality indicates avoidance of the type (White and Garrott 1990). However, the definition of available habitat is problematic: whether or not analysis indicates that a particular type is selected depends, in part, on the degree to which underused types are included in the definition of available habitat, and results are therefore somewhat arbitrary (Johnson 1980; White and Garrott 1990; Rosenberg and McKelvey 1999).

Established methods for evaluating population-level habitat selection include two approaches that view the population and available universe differently (Manly et al. 1993). In one approach, data from all individuals are pooled, and available habitat is generally defined as the study area (e.g., Neu et al. 1974). However, given that lynx in our data set were sampled unevenly, with the number of locations per individual ranging from 11 to 103 (Table 10.1), simple pooling would give unsatisfactory results because depiction of habitat selection for the population would be skewed toward those heavily sampled individuals. Pooling may also suppress habitat selection patterns of individuals or classes of individuals (White and Garrott 1990). An alternate approach is to compute resource use functions for individuals and then combine these into a population-level statistic.

In this case, available habitat is defined by the home range (Manly et al. 1993; White and Garrott 1990). However, these methods are only meaningful when applied to well-sampled individuals. Of the 22 lynx for which we had data, most had too few points for meaningful calculation of individual use patterns, and only four had >50 locations (Table 10.1).

Given the nature of our sample and the problems associated with established methods, we developed an approach for evaluating habitat selection that combined principles of the approaches described above. Because habitat use may vary by season, we first split the location data into winter (October-March) and summer (April-September) periods for which we conducted separate analyses. We chose these six-month seasons because of convenience and because they distinguished the period of significant snow cover (winter) from that of breeding activity (summer). For each season, we pooled data across individuals, but used sub-sampling to obtain an equivalent number of points per animal so that habitat choices of each could be equally represented. A subset of points was generated by randomly picking five points per animal. By picking a relatively small number of points per individual, we could incorporate lynx with few points and minimize sequential autocorrelation and potential pseudo-replication (Swihardt and Slade 1985). We generated multiple subsets ($n = 20$) of points for which we conducted separate analyses of habitat selection, allowing us to consider the robustness of derived habitat relationships among potential subsamples.

Rather than limiting the analysis to one definition of availability, we evaluated habitat selection at multiple spatial scales, clearly defining available habitat at each scale such that statements concerning selection could be qualified. We began analyses at a coarse scale to consider patterns within the study area that we defined as the 100% minimum convex polygon for all the locations buffered by the diameter (4.8 km) of the average 50% adaptive kernel home range (Fig. 10.1). Because most habitat variables were highly correlated with elevation, we limited analysis at this scale to evaluation of selection among broad elevation classes. We used resultant understandings to delineate a more restricted zone of available habitat that excluded those elevation classes with little or no use, allowing us to examine meso-scale habitat selection.

For categorical data describing elevation and vegetation, we compared use to availability for each subset by computing χ^2 goodness-of-fit statistics and Bonferroni confidence intervals (Neu et al. 1974). We assessed the overall significance of results as follows: if χ^2 tests for at least 75% of subsets showed that use of a class significantly exceeded availability ($p < 0.05$), then we inferred strong selection for that class; if analysis showed that at least 50% of subsets demonstrated use that was significantly greater than
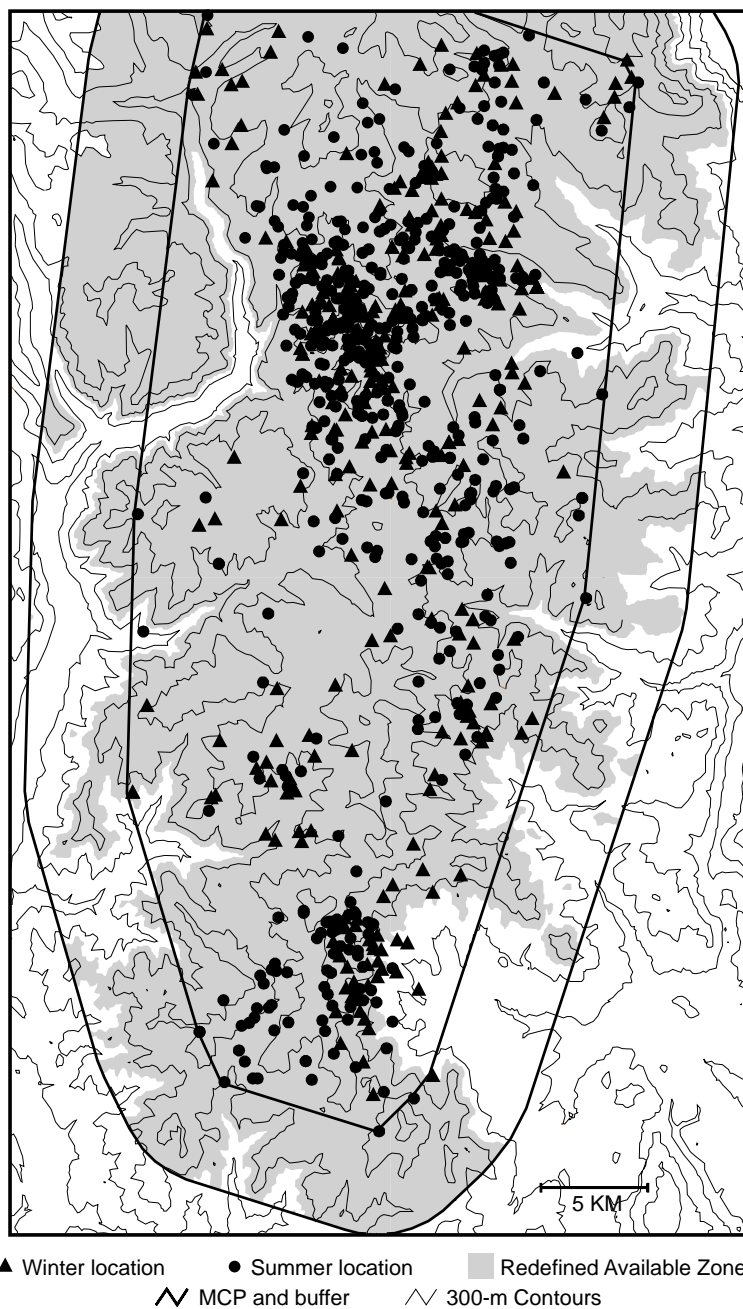
Figure 10.1—The study area on the Okanogan National Forest in north-central Washington showing the distribution of 836 lynx telemetry locations collected 1981 through 1988. Also pictured are zones of availability used for coarse and meso-scale analyses of habitat selection.

availability, we inferred marginal selection for the class. Avoidance was assessed in the same manner.

To incorporate continuous physical variables into analyses of meso-scale selection, we developed logistic regression models for each subset that compared lynx locations to random points within the available zone. Vegetation patterns are correlated to physical variables: drier forests are typically located on lower, south-facing slopes. To assess the degree to which lynx selection patterns indicated by the physical models reflected selection for vegetation types, we developed combined models that included vegetation class as a design variable to consider whether vegetation was an important indicator of use when physical features were accounted for.

Overall significance of regression results was assessed as follows: if a variable was statistically significant (Wald χ^2 test, $p <0.05$) in logistic regression models derived for at least 75% of the subsets, then we described the variable as either strongly selected or strongly avoided, depending on the sign of its coefficient. Statistical significance of models was evaluated with the Score test ($p <0.05$), and models were compared using Akiake's Information Criterion (AIC), with lower AIC scores indicating better models (SAS 1990).

To consider patterns that may have been masked by pooling the data, we used χ^2 tests of homogeneity to compare use of vegetation classes between sexes. Similarly, we tested for differences in use of vegetation classes between the two time periods of study, 1981 through 1983 (Brittell et al. 1989) and 1984 through 1988 (Koehler 1990), and descriptive statistics were used to assess similarity of use patterns among the 22 lynx. When we found significant differences between sexes or time periods, we repeated the χ^2 analyses (above) on these subsets.

For evaluation of fine-scale habitat selection, we examined use within home ranges of lynx with >50 locations. For each of these lynx, the distribution of available types was defined by a 100% minimum convex polygon that surrounded its locations. We evaluated selection of vegetation classes using χ^2- goodness-of-fit statistics and Bonferroni confidence intervals.

To examine whether roads may have had direct affects on fine-scale habitat use, we considered the degree to which lynx crossed roads. Sequential telemetry locations on opposite sides of a road should indicate that the road was crossed unless the road ended within the home range, thereby enabling the animal to move between the points without crossing the road. Most roads in the study area passed through lynx home ranges rather than ending within them (Fig. 10.2). For each individual with >50 locations, we tested whether line segments defined by sequential telemetry

A

▲ Winter location   ● Summer location   ╱⌄ Home Range

⌒ Potential Movement ⋀ Road
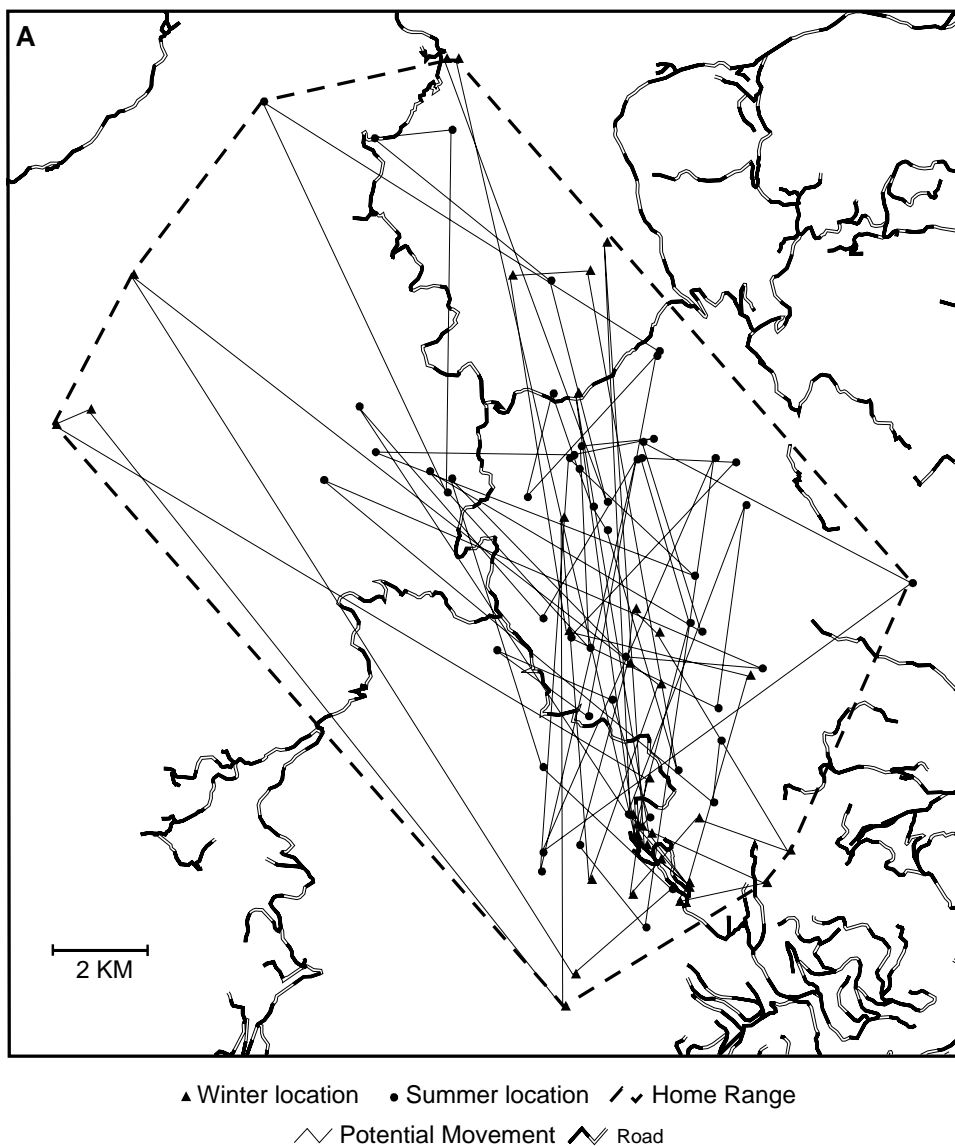
Figure 10.2—Methodology used to evaluate rates at which lynx crossed roads. The frequency of road intersections for lines between sequential telemetry locations (A) was compared to that for randomly generated lines (B, page 319).

Home Range   Potential Movement   Road
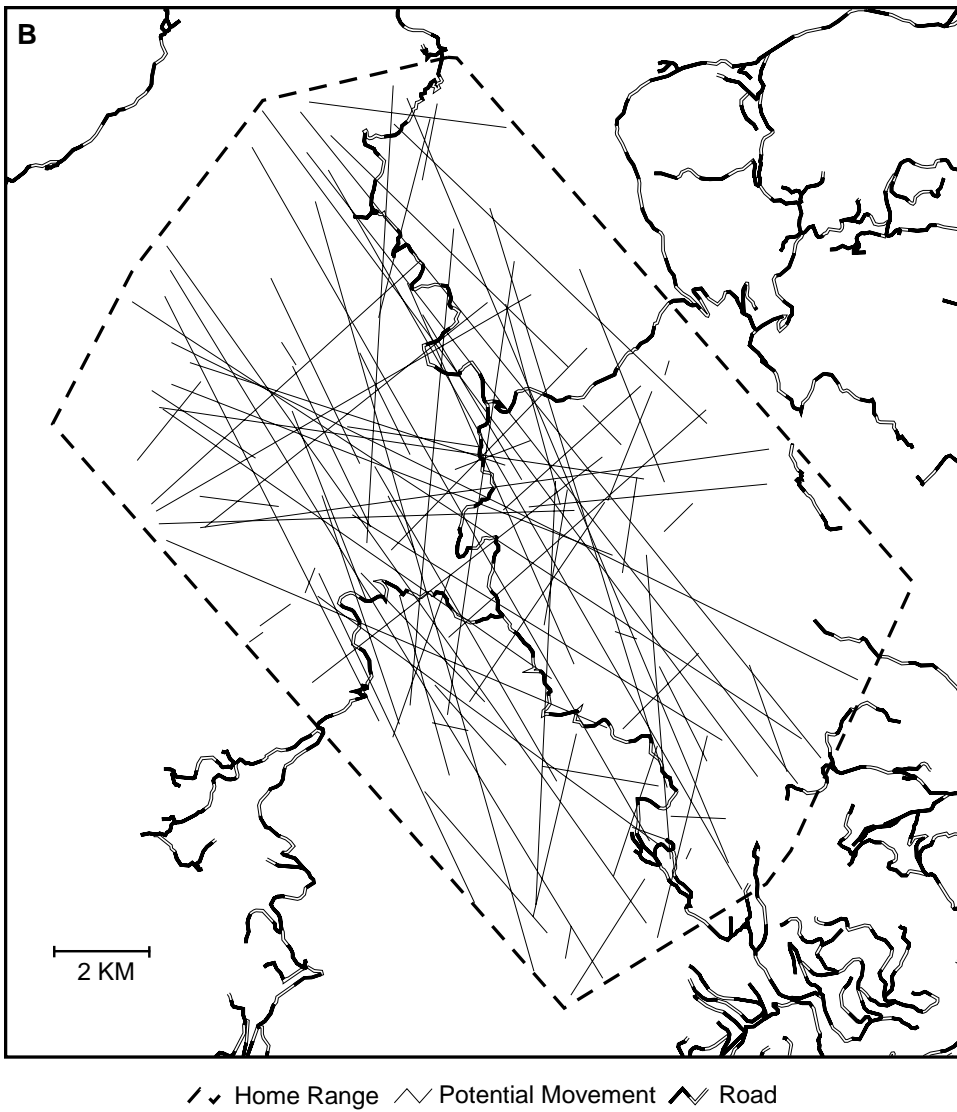
locations intersected roads more or less than expected. To generate the null expectation for each lynx, we first computed the distances between successive telemetry locations. Line segments of length chosen randomly from this set of distances were placed at random locations and azimuths within the home range so that they fit entirely within its boundary (Fig. 10.2). Because we generated a large number of random lines per lynx ($n = 8,000$), we treated the proportion that intersected roads as a known expectation (no variance) and used χ^2-goodness-of-fit statistics for comparison to the proportion of road intersections indicated by telemetry locations.

Okanogan National Forest Road Surveys

For comparison to telemetry-based findings, we considered the types of habitat where lynx were detected by remote camera and track surveys conducted on the Okanogan National Forest 1994-1998 (J. Rohrer, unpublished). These detections were obtained at baited stations located at non-random points along roads. Still, because lynx are not thought to be drawn long distances to baits (Robert Naney personal communication; John Weaver personal communication), we reasoned that lynx may have been detected in habitat types similar to those used by radio-tracked lynx. We therefore examined the distribution of detections among elevation and vegetation classes, but limited our analyses to descriptive statistics.

Hares

Koehler (1990) sampled pellets of snowshoe hares within the study area to consider the distribution of hares among habitat types used by lynx. Transects ($n = 68$) were partitioned among cover types in proportion to their abundance within the study area (Koehler 1990). However, because transects were placed perpendicular to roads, they did not constitute a representative sample of the study area. To allow data to be independent among transects, transects were spaced ≥325 m apart based on the assumption that home range sizes for hares were <8.8 ha (Wolff 1980; Chapters 6 and 7). Pellets were counted within 10, 1-m-radius circular plots spaced at 10 m intervals along each transect, and counts were summed per transect. Pellets were counted and cleared from plots during September 1986 and counted again on cleared plots in May and June 1987. Habitat measurements were also taken on the sample plots (Koehler 1990), allowing us to examine relative abundance of hares among forest cover types and elevation classes. Because pellet samples were non-representative, we confined analyses to descriptive statistics.

Results

For the combined data set, most lynx were sampled across several seasons, and in some cases several years (Table 10.1). Locations were distributed through time such that the average interval between sampling was >2 days for all 22 lynx, but more locations were recorded in summer than winter.

Coarse-Scale Habitat Selection

Six telemetry locations fell beyond our maps of habitat features, leaving 836 telemetry locations ($n = 305$ and 531 for winter and summer, respectively) for analyses of habitat selection. When buffered, the minimum convex polygon formed by these points defined an area of available habitat of 166,620 ha (Fig. 10.1). The majority of telemetry locations fell at elevations between 1,700 and 2,000 m (Fig. 10.3). Lynx strongly avoided (100% of subsets) areas <1,100 m, 1,100-1,250 m, and 1,250-1,400 m in both seasons (Fig. 10.3). Seasonal differences in habitat selection were apparent for
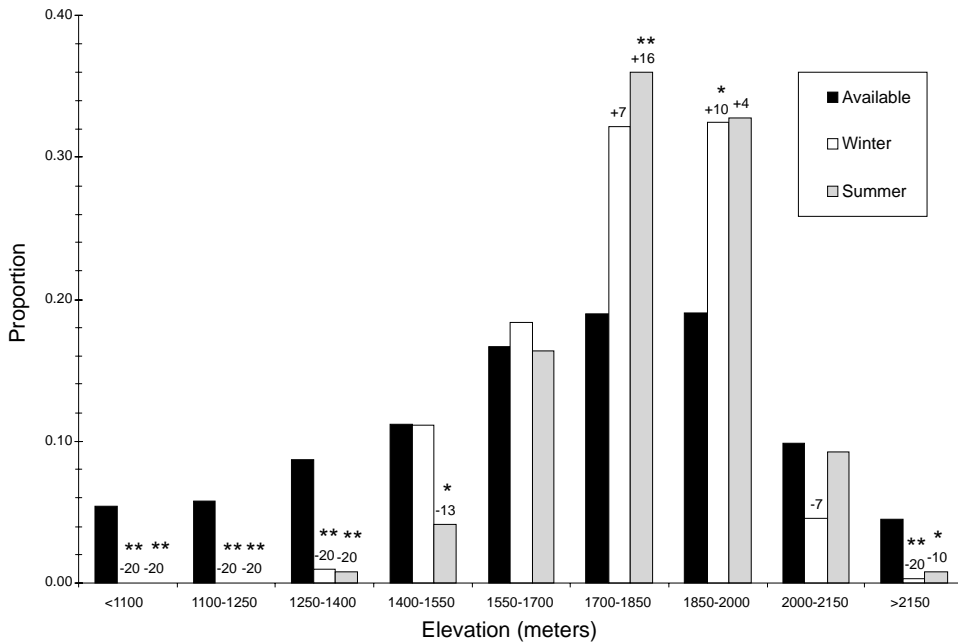
Figure 10.3—Coarse-scale use of elevation classes summarized across locations for 22 lynx. Above each bar is the number of subsets for which use was greater (+) or less (−) than availability (p <0.05). Classes with marginal (*) or strong (**) selection patterns (see text) are marked accordingly.

higher elevations: use of the 1,400-1,550-m class did not differ from availability in winter, but lynx showed marginal avoidance of this zone in summer (65% of subsets; Fig. 10.3). Similarly, avoidance of the >2,150-m class was strong in the winter (100% of subsets), but marginal in the summer (50% of subsets; Fig. 10.3).

Meso-Scale Habitat Selection

Based on coarse-scale patterns of habitat use, we redefined available habitat to exclude elevation classes that were avoided in both seasons (Fig. 10.3). Removal of zones <1,400 m and >2,150 m reduced the available area by 25% (Fig. 10.1), eliminated several vegetation classes (Table 10.2), and left 98.6% of the locations (301 and 523 for winter and summer, respectively).

Vegetation classes—Selection of vegetation classes within the redefined area was similar for the three vegetation layers. Using the Fuels map, the majority of telemetry locations fell within the lodgepole pine class: 53% in winter and 48% in summer, compared to 39% of the available area (Fig. 10.4A). Each of seven remaining classes had ≤15% of locations. Lynx showed strong selection for the lodgepole pine class in winter (85% of subsets), and strong avoidance of the ponderosa pine/Douglas-fir/western larch class in summer (85% of subsets; Fig. 10.4A).

Using the PMR classification, the majority of lynx points fell into the lodgepole pine class: 39% in winter and 33% in summer, compared to an availability of 24% (Fig. 10.4B). The subalpine fir class contained 25% of locations, and each of the remaining seven classes had <15%. Lynx showed marginal selection for the lodgepole pine class in winter (55% of subsets), avoidance of the Douglas-fir class in both winter (100% of subsets) and summer (50% of subsets), and strong avoidance of the Douglas-fir/mixed conifer class in both seasons (≥95% of subsets; Fig. 10.4B).

More than 80% of lynx locations fell into the subalpine fir-Engelmann spruce-lodgepole pine class of the NCGBEE map, with <10% in each of the four remaining classes (Douglas-fir-mixed conifer, other forest, subalpine meadow, other open). Lynx showed marginal selection for the subalpine fir-Engelmann spruce-lodgepole pine class in summer (65% of subsets). However, the NCGBEE map was coarse at this scale, with 78% of the available area falling into this class, and we did not include this map in subsequent analyses.

Physical variables—Correlation among pairs of physical variables (road and stream densities, elevation, aspect, and slope) was low (Pearson r <0.5). Logistic regression models that included all five variables were significant

A

B
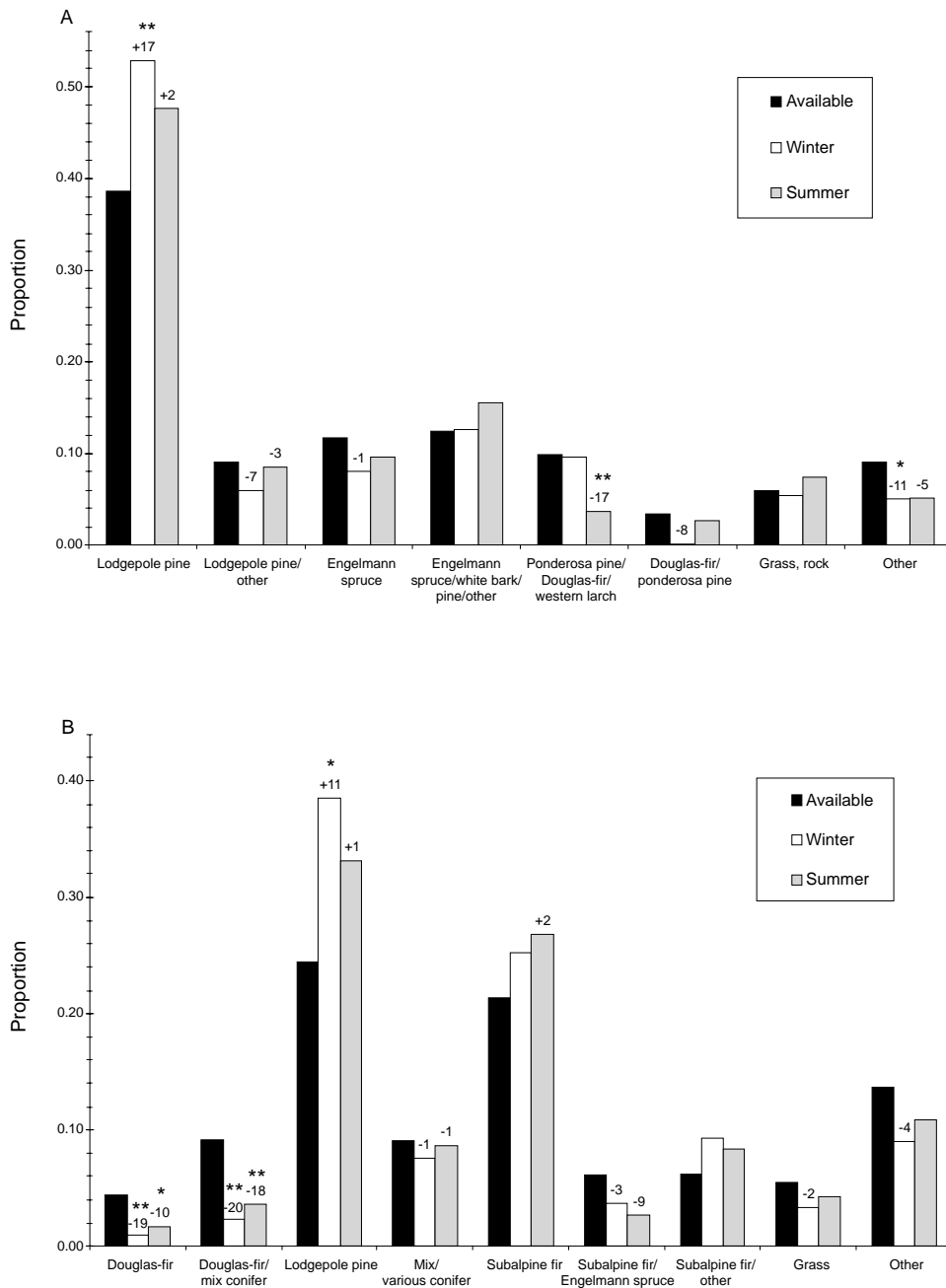
Figures 10.4—Meso-scale use of vegetation classes summarized across locations for 22 lynx using the Fuels (A) and PMR (B) vegetation layers (see Table 10.2 and text for explanation). Above each bar is the number of subsets for which use was greater (+) or less (-) than availability (p <0.05). Classes with marginal (*) or strong (**) selection patterns (see text) are marked accordingly.

for all subsets (χ^2 >11.5, df = 5, p <0.05), with better models in winter (AIC = 766-792) compared to summer (AIC = 848-876). In winter, selection patterns were strong for slope and stream density: probability of lynx use increased significantly with decreasing slope (χ^2 >4.2, df = 1, p <0.04 for 80% of subsets; Fig. 10.5A) and increasing stream density (χ^2 >4.2, df = 1, p <0.04 for 80% of subsets; Fig. 10.5B). In summer, selection patterns were strong for elevation and aspect: probability of lynx use increased significantly with increasing elevation (χ^2 >4.4, df = 1, p <0.04 for 70% of subsets; Fig. 10.5C) and decreasing aspect (χ^2 >5.1, df = 1, p <0.025 for 85% of subsets; Fig. 10.5D). However, for stream density and elevation, selection did not follow a linear pattern: use deviated most from availability at intermediate values of these variables (Fig. 10.5B, C). Use also deviated from availability at low to intermediate road densities (Fig. 10.5E), although selection patterns were weak (winter: χ^2 <3.4, df = 1, p >0.06 for 100% of subsets; summer: χ^2 <3.8, df = 1, p >0.05 for 55% of subsets).

Combined models of vegetation and physical variables—Vegetation class was a significant predictor of probability of lynx use, even when physical variables were accounted for within logistic regression models. Using the Fuels map, models that included vegetation class were better (χ^2 >21.8, df = 12, p <0.05) than models with only physical variables for 80% of winter subsets (AIC = 764-790) and 60% of summer subsets (AIC = 837-877). The lodgepole pine class was strongly selected in the winter (χ^2 >4.3, df = 1, p <0.04 for 80% of subsets) and marginally selected in the summer (χ^2 >5.3, df = 1, p<0.03 for 50% of subsets). The addition of vegetation to the model did not significantly change relationships between habitat use and the physical variables described above: in winter, flatter slopes were strongly selected (χ^2 >4.7, df = 1, p <0.04 for 80% of subsets), as were areas with higher stream densities (χ^2 >5.0, df = 1, p <0.03 for 90% of subsets). In summer, northern aspects were strongly selected (χ^2 >4.1, df = 1, p <0.05 for 85% of subsets), but elevation was significant for only 40% of subsets (χ^2 >4.0, df = 1, p <0.05).

Logistic regression models that included vegetation classes from the PMR layer (χ^2 >23.0, df = 13, p <0.04) were better (χ^2 >23.0, df = 13, p <0.04) than models with only physical variables for 100% of winter subsets (AIC = 741-786) and 10% of summer subsets (AIC = 850-873). Selection for the lodgepole pine class was strong in the winter (χ^2 >4.0, df = 1, p <0.05 for 100% of subsets) and marginal in the summer (χ^2 >4.0, df = 1, p <0.05 for 60% of subsets). As with the Fuels map, relationships between habitat use and physical variables generally did not change with the addition of vegetation class to the model: in winter, flatter slopes were marginally selected (χ^2 >4.5, df = 1, p <0.04 for 50% of subsets), and selection was
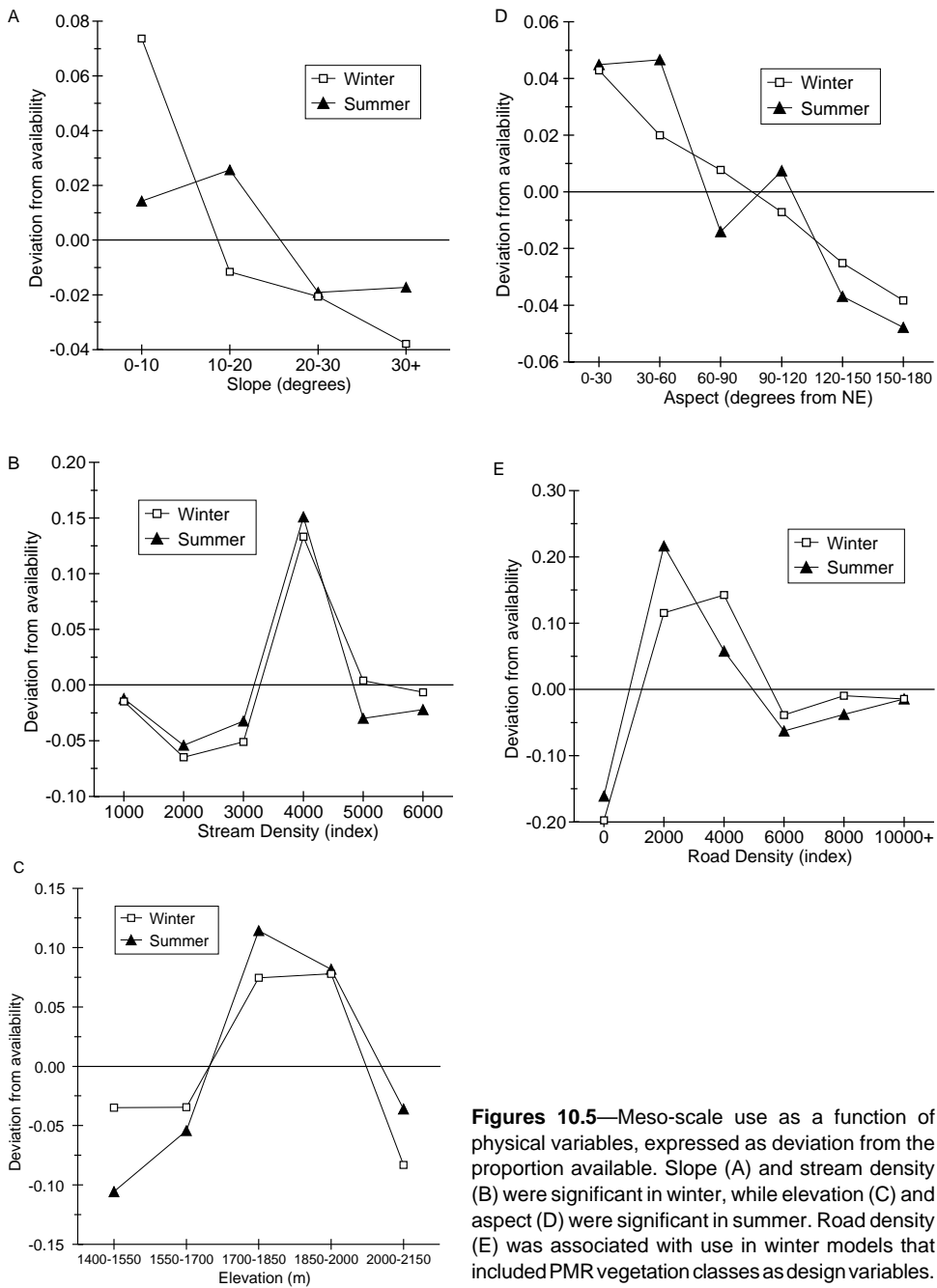
Figures 10.5—Meso-scale use as a function of physical variables, expressed as deviation from the proportion available. Slope (A) and stream density (B) were significant in winter, while elevation (C) and aspect (D) were significant in summer. Road density (E) was associated with use in winter models that included PMR vegetation classes as design variables.

strong ($\chi^2 > 5.0$, df = 1, $p < 0.03$ for 80% of subsets) for areas with higher stream densities. Road density also showed a strong association ($\chi^2 > 4.1$, df = 1, $p < 0.05$ for 80% of subsets) with lynx use in winter. In summer, northern aspects were strongly selected ($\chi^2 > 5.5$, df = 1, $p < 0.02$ for 80% of subsets), but elevation was significant for only 30% of subsets ($\chi^2 > 3.9$, df = 1, $p < 0.05$).

To examine the degree to which selection for physical variables by lynx was associated with specific vegetation classes, we built logistic regression models that used physical variables to predict the occurrence of vegetation classes that were strongly selected or avoided. Because selection patterns were similar for the two vegetation layers, we limited these analyses to the Fuels map. Occurrence of the lodgepole pine type decreased along slope and aspect gradients, and increased with stream density ($\chi^2 > 4.1$, df = 1, $p < 0.05$ for each parameter; model $\chi^2 = 35.0$, df = 5, $p = 0.0001$, AIC = 3485). Therefore, this class tended to occur in flatter areas with northeast aspects and higher stream densities. Occurrence of the ponderosa pine/Douglas-fir/western larch class increased with aspect and decreased with elevation and road density ($\chi^2 > 6.4$, df = 1, $p < 0.02$ for each parameter; model $\chi^2 = 475.0$, df = 5, $p = 0.0001$, AIC = 1262). Therefore, this class tended to occur within lower elevation areas with southwest aspects and lower road densities.

Additional factors—To examine whether patterns in habitat use for the combined population were consistent within various subgroups, we compared the distribution of locations among vegetation classes defined by the Fuels map for the two time periods of study, 1981 through 1983 and 1984 through 1988. Annual and summer use patterns between time periods were significantly different ($\chi^2 = 14.6$, df = 7, $p = 0.04$ and $\chi^2 = 18.5$, df = 7, $p = 0.01$, respectively), but winter patterns did not differ ($\chi^2 = 9.6$, df = 7, $p = 0.21$; Fig. 10.6).

Because use of vegetation classes differed significantly between time periods, we split the locations by time period and repeated tests for meso-scale selection for each period separately. Tests for winter selection showed stronger patterns in 1984 through 1988 compared to 1981 through 1983. Lynx selected the lodgepole pine class marginally (65% of subsets) in 1984 through 1988 but did not show selection (10% of the subsets) in 1981 through 1983. Similarly, avoidance of Douglas-fir classes in winter was stronger in 1984 through 1988 versus 1981 through 1983 (ponderosa pine/Douglas-fir/western larch: 25% versus 0%; Douglas-fir/ponderosa pine: 100% versus 45%). Results for summer were comparable between time periods with selection for lodgepole pine shown for 5% (1981 through 1983) and 0% (1984 through 1988) of subsets, and avoidance of ponderosa pine/Douglas-fir/western larch shown for 60% and 50% of subsets.
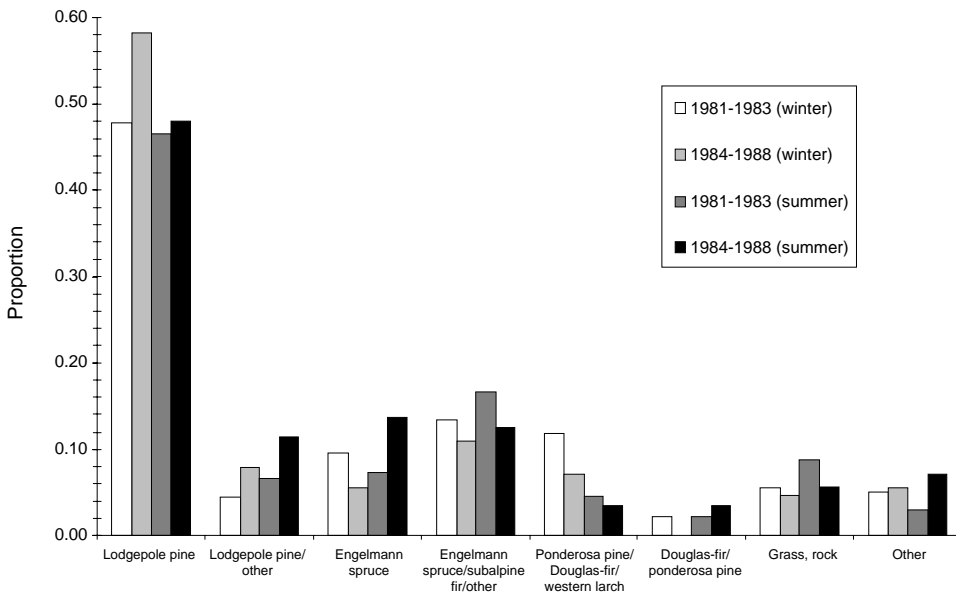
Figure 10.6—Use of vegetation classes of the Fuels layer for each time period of study and season.

Distribution of locations among vegetation classes also differed by sex ($\chi^2 = 19.8$, df = 7, $p = 0.006$), and this difference applied to winter ($\chi^2 = 19.7$, df = 7, $p = 0.006$) but not summer ($\chi^2 = 8.2$, df = 7, $p = 0.31$; Fig. 10.7). To assess whether these differences in use between sexes indicated differences in habitat selection, we split the subsets by sex and repeated tests for meso-scale selection. Selection by season for each sex followed results obtained for the combined population (Fig. 10.4A). Both sexes showed selection for the lodgepole pine class and avoidance of the ponderosa pine/Douglas-fir/western larch class: in winter, selection for lodgepole pine was shown for 50% of subsets for females compared to 10% for males; avoidance of ponderosa pine/Douglas-fir/western larch was shown for 10% of subsets for females versus 0% for males and avoidance of Douglas-fir/ponderosa pine for 45% versus 100%. In summer, selection for lodgepole pine was shown for 5% of subsets for females compared to 10% for males; avoidance of ponderosa pine/Douglas-fir/western larch was shown for 85% of subsets for females versus 40% for males.

Proportions of locations in each vegetation class defined by the Fuels map were similar across the 22 lynx (Fig. 10.8). Use of lodgepole pine by the group was relatively high (49 ± STD of 13.0%), and 19 lynx had a higher proportion of locations in this class than the proportion available. Use of
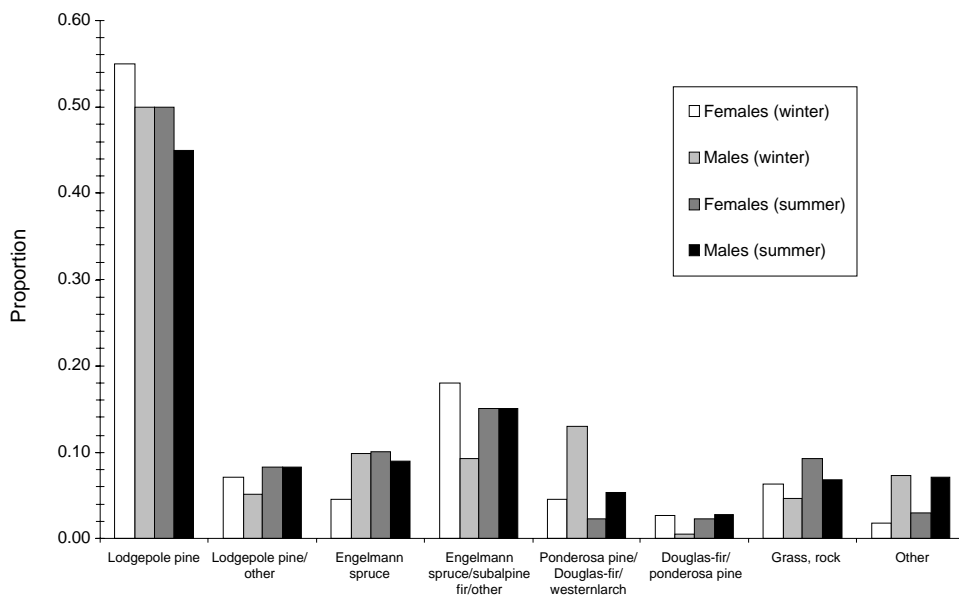
Figure 10.7—Use of vegetation classes of the Fuels layer for each sex and season.
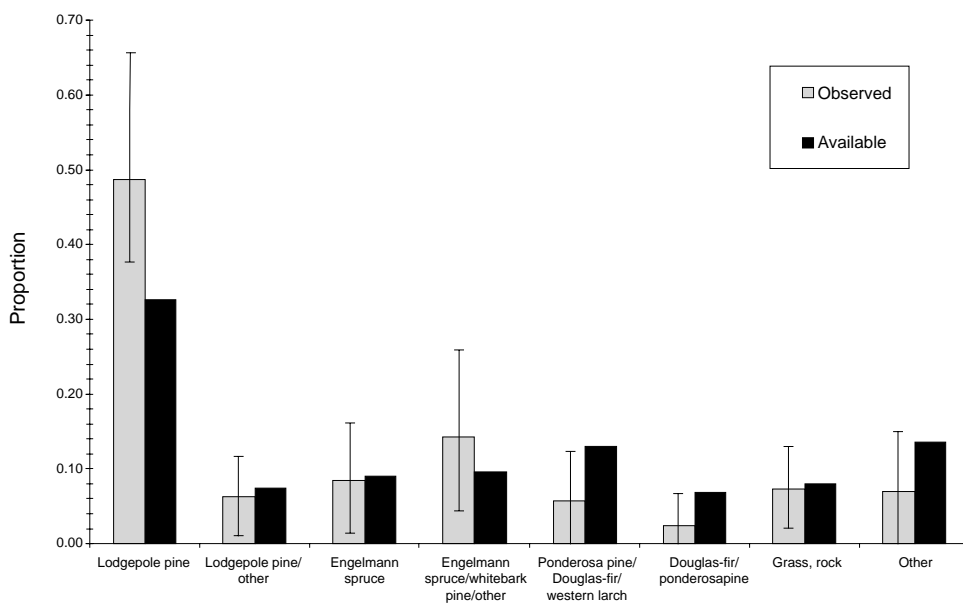
Figure 10.8—The average (± STD) proportion of locations in each vegetation class defined by the Fuels layer for 22 lynx. Availability of each class is shown for comparison.

ponderosa pine/Douglas-fir/western larch was relatively low (6 ± STD of 3.9%), and 18 lynx had a lower proportion of locations in this class than the proportion available.

Fine-Scale Selection Patterns

Four lynx had >50 locations distributed across seasons and covering >500 days (Table 10.1). Only one of these lynx showed use of vegetation classes that differed significantly from availability within its home range: lynx 104090 selected the lodgepole pine class (Fuels map) in winter ($\chi^2 = 6.0$, df = 1, p <0.02) and avoided the subalpine fir class (PMR map) in summer ($\chi^2 = 4.5$, df = 1, p <0.04). However, relatively few classes (2-6 and 2-7 classes for the Fuels and PMR maps, respectively) could be tested for selection because of their low representation within home ranges of individual lynx. For each of the four lynx, frequency of road crossings did not differ from random expectation ($\chi^2 = 0.4, 0.7, 1.6$, and 3.2; df = 1; $p = 0.08, 0.21$, 0.39, and 0.55).

Okanogan National Forest Road Surveys

Lynx detections from road surveys were in different habitat types than predicted by telemetry data. The majority (48%) of detections occurred at lower elevations (1,400 to 1,700 m). Although 28% of detections were within the lodgepole pine class, 34% fell into the ponderosa pine/Douglas-fir/western larch and Douglas-fir/ponderosa pine classes of the Fuels layer. Similarly, 43% of detections occurred in Douglas-fir classes of the PMR layer with 10% in the lodgepole pine class. To further examine these patterns, we compared the vegetation classes occurring along survey roads to those of the surrounding landscape. Roads tended to pass through Douglas-fir classes while the landscape was dominated by lodgepole pine classes. For example, in the southwest portion of the Okanogan National Forest (Fig. 10.9), the lodgepole pine class of the Fuels layer covered 41% of the area and the ponderosa pine/Douglas-fir/western larch and Douglas-fir/ponderosa pine classes covered 21%. In contrast, only 20% of the road's length passed through the lodgepole class and 21% passed through Douglas-fir classes. Similarly, 21% of lynx detections in this area fell within lodgepole pine and 36% within the Douglas-fir classes. However, those detections that fell within non-lodgepole pine classes were generally adjacent and proximal to patches of the lodgepole pine class (Fig. 10.9).

▲ Lynx detection   ▦ Lodgepole pine   ⋀⋀ Road   ⋀⋀ 30-m Contours
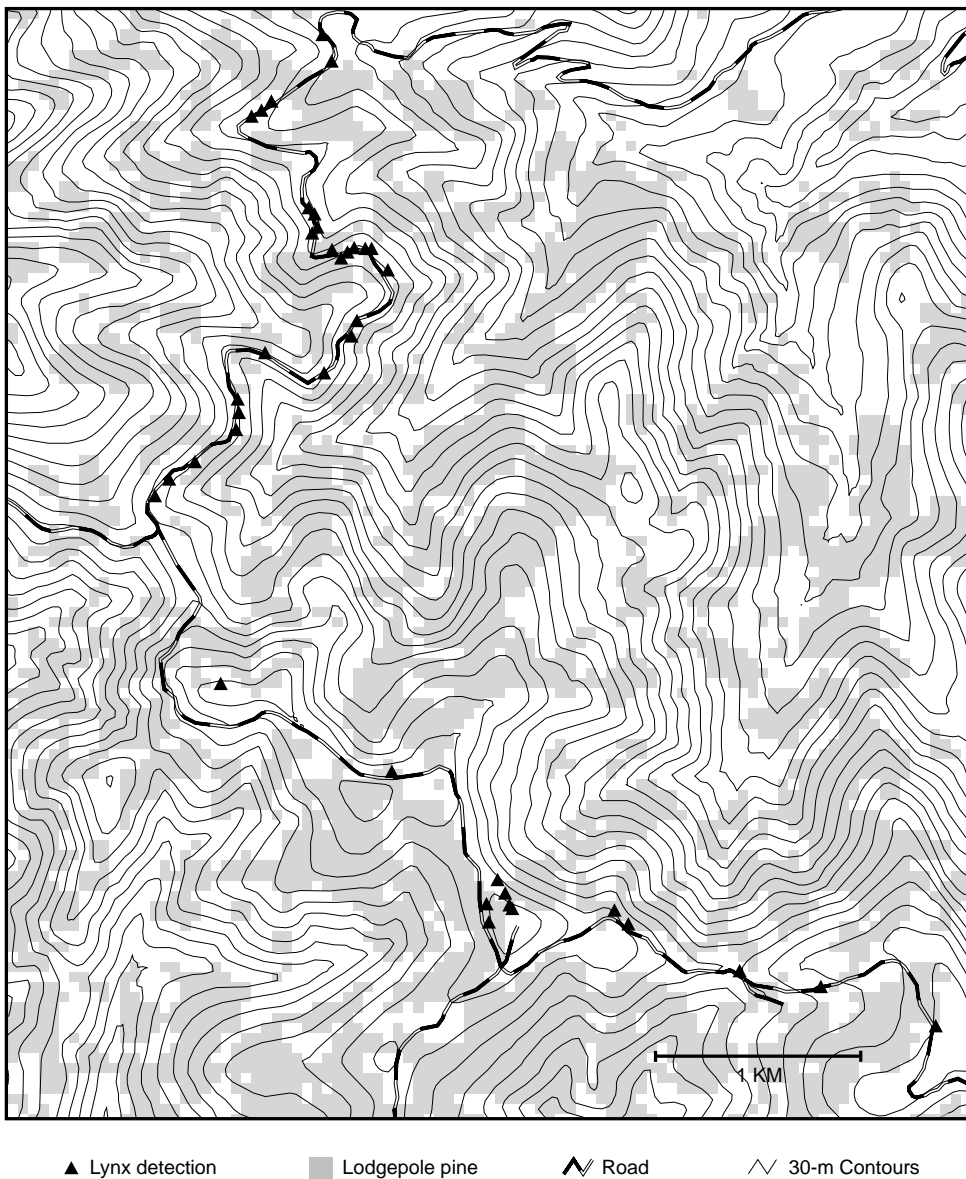
Figure 10.9—Locations within the southwestern portion of the Okanogan National Forest where lynx were detected during road surveys. Lynx locations are not distributed uniformly along the road, but conform more to the habitat characteristics of the road than of the surrounding landscape.

Hares

Hare abundance broadly followed patterns of selection by lynx. Forest types and elevation zones with the highest densities of hares corresponded to those classes strongly selected by lynx (Fig. 10.10A,B). However, only
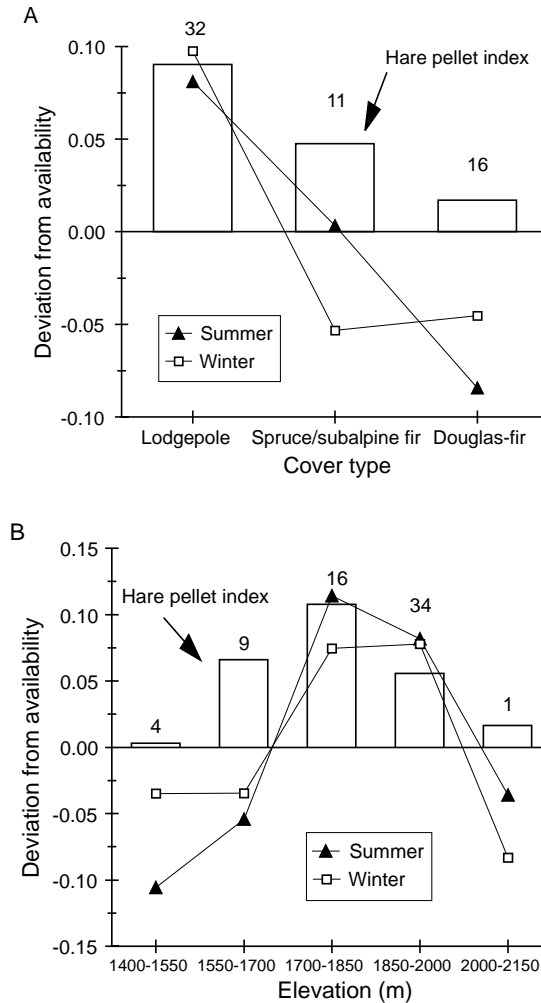
Figure 10.10—Standardized abundance of hare pellets (bars) and use by lynx (lines) as a function of cover type (A) and elevation (B). Pellet counts from the first (unswept) sample were averaged across the number of transects shown above each bar. Use of cover types by lynx, expressed as deviation from the proportion available, was defined by the distribution of locations across corresponding vegetation classes of the Fuels layer.

four hare samples were taken between 1,250 and 1,550 m, and they were all within Douglas-fir cover types that had lower hare densities across elevation zones. In addition, only 36% of the available area between 1,400 and 1,550 m consisted of Douglas-fir classes (Fuels map), whereas lodgepole pine classes composed 26% of the area. Douglas-fir was similarly over-represented in pellet samples taken in the 1,550 to 1,800-m zone.

Discussion

Our multi-scale analyses of habitat selection provide strong support for Koehler's (1990) original findings that lynx use lodgepole pine more than expected and Douglas-fir less than expected. Even when our models were limited to the elevation zone used by lynx, and we accounted for the physical attributes of the landscape, selection for lodgepole pine was still statistically significant. Vegetation classes defined by lodgepole pine were important in meso-scale comparisons of use to availability using all three vegetation layers (Table 10.2), and the inclusion of lodgepole classes as design variables significantly improved models of habitat use derived from physical variables. Lynx avoided areas defined by Douglas-fir (Table 10.2), although Douglas-fir classes were not important in models of habitat use that included other habitat variables. Physical features associated with occurrence of lodgepole pine and Douglas-fir were the same features associated with habitat selection by lynx, suggesting that these physical features were primarily indicators of selection for vegetation types.

Selection of northeast aspects in the summer, however, may have been independent of selection for vegetation. In winter, the proportional use of northeast aspects was greater than availability (Fig. 10.5D), but aspect was not significant when considered along with the other habitat variables. However, in summer, models combining physical and vegetation variables indicated that northeast aspects were strongly selected. Douglas-fir was associated with southwest aspects in a logistic regression model, and avoidance of Douglas-fir in summer was the most strong and consistent pattern among analyses of selection for the combined population, and for sex and time periods separately, with at least 45% of subsets demonstrating avoidance in each case. Therefore, avoidance of Douglas-fir in summer may have been associated with the tendency of lynx to select areas with northeast aspects. Preliminary summer telemetry data for lynx in the Seeley Lake area in Montana also suggest selection of north-facing aspects where 80% of locations fell (John Squires personal communication). Lynx habitat in the Seeley Lake area differs significantly from that on the Okanogan National Forest, and it is unlikely that topographic correlates to vegetation would be

the same for the two areas. Thermoregulation provides a plausible explanation for the apparent selection of aspects with wetter, cooler conditions in the summer.

Use of lower elevations in the winter described by Koehler (1990) was also apparent for the broader population of 22 lynx. We detected a seasonal elevation shift: decreased use of the 2,000 to 2,150-m zone and increased use of areas 1,400 to 1,550 m in winter. Selection for vegetation types also varied with season. Lynx showed stronger selection for lodgepole pine in winter compared to summer for the combined population, and for both sexes and time periods. These shifts also translated into an increased proportion of locations on flatter slopes with higher road densities (Figs. 10.5A, E). Use of Douglas-fir also increased in winter, although only according to the Fuels map. This pattern may have related to increased adjacency of lodgepole and Douglas-fir classes at lower elevations where the latter type becomes more prevalent and less associated with southwest aspects. Overall, comparisons of logistic regression models indicated that selection for combinations of physical and vegetation variables was stronger in winter than in summer.

Patterns in habitat use by lynx also corresponded to relative abundance of snowshoe hares as measured by pellet counts. The elevation zones and cover type with the highest hare indices were those selected by lynx. This association was evident despite the high variability in the hare data (Table 3 in Koehler 1990) and that cover types representing hare habitat were based on ground-based assessments (Koehler 1990) whereas lynx habitat was represented by broad vegetation classes defined from LANDSAT imagery. Because the hare data were derived from non-representative samples, caution must be exercised when interpreting the apparent relationship between elevation and hare density. However, given the strong use patterns that Koehler (1979) observed in Montana, we suspect that the observed correlation between lynx and hare patterns indicates a strong causal relationship. A review of studies of lynx at northern latitudes (Chapter 10.9) shows similar patterns of lynx selecting habitats where hares are more plentiful. From snow tracking studies of lynx among white spruce forests in the Yukon, Murray et al. (1994) found that lynx selected densely stocked stands of white spruce where hares were most abundant during one year, but used spruce stands according to the availability the next year, when hare numbers were similar among habitats.

Given the variability of hare densities in time and space and the apparent sensitivity of lynx to these fluctuations, the overall difference in habitat use observed between the periods of study is not surprising. Lynx showed relatively high use of lodgepole pine and low use of Douglas-fir in both 1981

through 1983 and 1984 through 1988. However, use was more skewed toward lodgepole pine and away from Douglas-fir in winter 1984 through 1988 versus winter 1981 through 1983 (Fig. 10.6). Similarly, comparisons of use to availability indicated that selection for lodgepole pine was much stronger for winter 1984 through 1988 versus winter 1981 through 1983, as was avoidance of Douglas-fir classes. Selection patterns for summer were similar between time periods.

Koehler (1990) characterized hare densities measured during his study as low, and these data also indicated that hares were concentrated within areas of lodgepole pine. Lower hare densities may lead to a more patchy distribution of hares and subsequent stronger habitat selection by lynx (Murray et al. 1994), particularly in winter when lynx have fewer opportunities to use alternate prey (Chapter 13).

Our analyses also indicated a neutral relationship between habitat selection and roads. A significant positive association between road density and habitat use was observed for winter locations, but only when the vegetation classes of the PMR layer were combined in models with physical variables. We suspect that this statistical relationship reflects a correlation between the classification of vegetation and the prevalence of roads. Therefore, road density, as computed within home-range-sized areas, did not appear to have significant effects on habitat selection for the combined population. Our analysis of habitat use at a finer scale indicated that frequency of road crossing for each of four lynx did not differ from expected. We acknowledge that our results are based on a small number of lynx within a limited geographic area, but can state that we found no evidence that habitat use by lynx was affected by narrow, forest roads at the relatively low densities that characterized the study area. However, we caution that our analyses did not address potential indirect effects of roads on habitat quality for lynx (Chapter 4).

Road-based surveys did not provide a representative sample of the surrounding landscape, and patterns of use appear to have been influenced by composition of adjacent habitat types (i.e., prevalence of lodgepole). We therefore believe simple examination of the distribution of the resulting detections—including comparisons to the surrounding landscape, to areas along survey roads, or to surveyed locations where lynx were not detected—should not be used to make inferences about habitat use.

Overall, our results suggest that habitat selection by lynx may be driven by differing mechanisms in summer compared to winter. In summer, lynx showed more general use of cover types but consistently avoided warm, dry slopes: behavior that may have been associated with thermoregulation. Although habitat selection was stronger in winter for all sets of analyses, use

of vegetation in this season was not constant across time periods. Habitat selection in winter may be more influenced by hares and therefore more sensitive to variability in hare distribution and abundance. To develop understandings of mechanisms that underlie habitat requirements for lynx in the contiguous United States, further examination of habitat selection that includes consideration of fluctuations in availability of snowshoe hares is needed.

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