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Source: Journal of Wildlife Management, 74(8):1648-1660. 2010.
Published By: The Wildlife Society
DOI: 10.2193/2009-184
URL: http://www.bioone.org/doi/full/10.2193/2009-184

Journal of Wildlife Management 74(8):1648–1660; 2010; DOI: 10.2193/2009-184

Management and Conservation Article

Seasonal Resource Selection of Canada Lynx in Managed Forests of the Northern Rocky Mountains

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ABSTRACT We investigated seasonal patterns in resource selection of Canada lynx (*Lynx canadensis*) in the northern Rockies (western MT, USA) from 1998 to 2002 based on backtracking in winter (577 km; 10 M, 7 F) and radiotelemetry (630 locations; 16 M, 11 F) in summer. During winter, lynx preferentially foraged in mature, multilayer forests with Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in the overstory and midstory. Forests used during winter were composed of larger diameter trees with higher horizontal cover, more abundant snowshoe hares (*Lepus americanus*), and deeper snow compared to random availability; multilayer, spruce–fir forests provided high horizontal cover with tree branching that touched the snow surface. During winter, lynx killed prey at sites with higher horizontal cover than that along foraging paths. Lynx were insensitive to snow depth or penetrability in determining where they killed prey. During summer, lynx broadened their resource use to select younger forests with high horizontal cover, abundant total shrubs, abundant small-diameter trees, and dense saplings, especially spruce–fir saplings. Based on multivariate logistic-regression models, resource selection occurred primarily at a fine spatial scale as was consistent with a sight-hunting predator in dense forests. However, univariate comparisons of patch-level metrics indicated that lynx selected homogenous spruce–fir patches, and avoided recent clear-cuts or other open patches. Given that lynx in Montana exhibit seasonal differences in resource selection, we encourage managers to maintain habitat mosaics. Because winter habitat may be most limiting for lynx, these mosaics should include abundant multistory, mature spruce–fir forests with high horizontal cover that are spatially well-distributed.

KEY WORDS Canada lynx, ecological scale, forest management, habitat selection, logistic regression, *Lynx canadensis*, Montana, resource selection.

The Canada lynx (*Lynx canadensis*) was federally listed in the contiguous United States as a threatened species under the Endangered Species Act in 2000 (U.S. Fish and Wildlife Service 2000). Although inadequate regulatory protection was cited as the primary reason for federal listing, human alteration of forest abundance, composition, and connectivity was identified as the most influential factor affecting lynx habitat. Configuring landscapes to maintain persistent lynx populations at the southern extent of the species' range is difficult due to our limited knowledge of lynx resource selection and the natural patchiness of southern boreal forests (Agee 2000, Aubry et al. 2000*b*, Ruggiero et al. 2000*b*).

Conserving lynx requires that we consider the regional population rather than the species as the appropriate taxonomic level for resource planning (Ruggiero et al. 2000*b*). Changes in carnivore habitat quality can be driven at the regional scale by gradients of human disturbance (Mladenoff et al. 1995, Kerley et al. 2002, Beckmann and Berger 2003), forest management and changes in vegetation structure (Nielsen et al. 2004*a*, *b*; Fuller et al. 2007), reduced metapopulation connectivity (Coulon et al. 2004), and prey density (Sullivan and Sullivan 1988, Bull et al. 2005, Griffin and Mills 2007). Given these diverse environmental factors, resource selection by carnivores may vary considerably across a species' distribution (Ruggiero et al. 2000*b*). Emphasizing populations reduces mismatches in ecological scale while preserving ecotypic variation and is consistent with the statutory requirements of the National Forest Management Act of 1976 and the Endangered Species Act of 1973 (Ruggiero et al. 1994, McKelvey et al. 2000*c*). Moreover, because lynx exhibit broad differences in resource selection across their range, analyzing population-level information across a species' range can provide a stronger basis for conservation planning.

Most understandings of lynx ecology are based on northern populations in Canada and Alaska, USA (Buskirk et al. 2000*b*, Mowat et al. 2000). Northern lynx habitat consists of a homogenous landscape dominated by boreal forest, whereas elevation gradients in the habitat of southern lynx populations create naturally heterogeneous forest types and more fragmented habitat patches (Aubry et al. 2000*a*). Lynx in the contiguous United States also confront greater human disturbance (Aubry et al. 2000*a*, Murray et al. 2008*a*). Lynx populations in the contiguous United States occur in western subalpine forests in Washington, Wyoming, and Montana, mixed conifer forests in Minnesota, eastern mixed conifer forests in Maine, and include a reintroduced population in Colorado.

Results from northern studies (see Mowat et al. 2000) led Ruggiero (2000) to describe suitable lynx habitat as mixed forests dominated by early successional stages, though at the time he acknowledged that few studies in southern populations were available for comparison. Lynx from

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northern populations selected regenerating forests (>20 yr old) with limited use of mature forests (Kesterson 1988, Murray et al. 1994, Staples 1995, Mowat et al. 2000). Under this paradigm, forest management that creates early succession forests would not directly degrade southern lynx habitat, though alterations to landscape configuration or community dynamics may pose indirect threats to persistence (Buskirk et al. 2000*a*, McGarigal et al. 2002, Kolbe et al. 2007). Boreal forests that support lynx in the Rocky Mountains are heterogeneous due to elevation and moisture gradients (Agee 2000). Management within boreal forests often creates early successional mosaics that may or may not provide adequate habitat for lynx and snowshoe hares (*Lepus americanus*), their primary prey. Selection patterns, like avoidance of open areas and selection for moderate to dense understory cover (Hoving et al. 2004, Fuller et al. 2007, Koehler et al. 2008, Maletzke et al. 2008, Vashon et al. 2008*b*) remain consistent across southern populations, but whether there are important differences in the age or successional stage of forests preferred by lynx across regions of the contiguous United States is still debated (Murray et al. 2008*a*).

Few studies have assessed seasonal changes of resource selection for lynx (Parker et al. 1983, Koehler 1990, Mowat and Slough 2003) even though annual variation in vegetation structure and composition induces changes in resource selection of prey populations (Hodges 2000 *a*, *b*; Griffin 2004; Griffin and Mills 2009). Snowshoe hares exhibit seasonal shifts in foraging between herbaceous shrub habitats in summer and dense conifer habitats in winter (Wolff 1980, Griffin 2004, Griffin and Mills 2009). However, studies of lynx resource selection are often based on winter snow-tracking (Brand et al. 1976, Fuller et al. 2007, Squires and Ruggiero 2007, Koehler et al. 2008, Maletzke et al. 2008) or annual data pooled across seasons (Vashon et al. 2008*b*). Buskirk et al. (2000*b*) speculated that lynx from southern populations may depend on mature forests as foraging habitat for both snowshoe hares and alternate prey, red squirrels (*Tamiasciurus hudsonicus*). Understanding seasonal changes in how lynx use resources is necessary for managers to better evaluate the potential impacts of their proposed actions.

Empirical and theoretical evidence increasingly indicate that resource selection is scale-dependent for a variety of organisms (Mitchell et al. 2001, McLoughlin et al. 2002), including carnivores (Chamberlain et al. 2003, Apps et al. 2004), and specifically Canada lynx (Squires et al. 2008). We assume that carnivores select resources in a multilevel, hierarchical process that scales from landscape to microhabitat features (Johnson 1980, Senft et al. 1987). Lynx are sight-hunting predators that hunt snowshoe hares in dense cover across seasons. Thus, it is plausible that selection of resources within lynx home ranges occurs at fine spatial scales regardless of seasonal changes in resource availability. However, patch- and landscape-level metrics could also affect within-home-range resource selection for lynx as prey abundance, movement patterns, or security change at broader spatial scales. Determining how lynx respond to habitat features at both fine and broad scales is needed to develop management strategies for southern boreal forests that are heterogeneous and support multiple uses (Buskirk et al. 2000*a*, McKelvey et al. 2000*a*, Murray et al. 2008*a*).

Our goal was to identify key habitat components selected by lynx in western Montana as they may change seasonally relative to forest structure, composition, prey abundance, topography, and patch-level pattern. We hypothesized that lynx in western Montana would select for high prey abundance and structurally dense habitats, but that the specific vegetation characteristics associated with these qualities would vary seasonally. We also hypothesized that lynx would select habitat at both fine- and patch-level scales; we expected a stronger selection signature at finer scales given that lynx are sight-predators that ambush and stalk prey in dense boreal forests (Murray et al. 1995, O'Donoghue et al. 1998*b*, Squires and Ruggiero 2007).

STUDY AREA

Our study area was centered in the Clearwater River drainage, near the town of Seeley Lake, Montana. This 900-km^2 area extended east to west from the Swan Range to the Mission Mountains and north to south from Lindbergh Lake to Salmon Lake. The Bob Marshall Wilderness complex and the Mission Mountain Wilderness flanked the east and west sides of the study area, respectively. We expanded the study area during summer to include animals captured in wilderness areas and additional front-country areas to the east and north (Fig. 1). Past lynx fur harvest (1977–1994) and track surveys suggest our study area may have historically supported the highest density of lynx in Montana (B. Giddings, Montana Fish, Wildlife and Parks, personal communication).

Lands in the Seeley Lake area were primarily owned by the United States Forest Service (48%) and Plum Creek Timber Company (37%) with smaller parcels of private, state, tribal, and Bureau of Land Management holdings. Commercial forest lands received more intense management in the form of large clear-cuts and thinning units than did the interspersed public lands. Forest management created an extensive road system and a fragmented mosaic of forest types, ages, and densities across the study area. Two-lane Highway 83 bisected the study area along the Clearwater River. Density of gravel forest roads averaged 3.2 km/km^2 and 2.6 km/km^2 on roaded portions of the winter and summer study areas, respectively. Winter recreation supported 243 km of groomed snowmobile roads at a density of 0.3 km/km^2.

Elevations ranged from 1,200 m to 2,500 m. Average annual low and high temperatures were $-2°$ C and $11°$ C, respectively, and annual precipitation averaged roughly 0.8 m/year. Warm and dry forests at lower elevations were dominated by Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*P. ponderosa*), usually as mixed forests (S. Tomson, United States Forest Service, unpublished report). Low-elevation forests were historically open or park-like, but dense stands became common due to timber harvest and

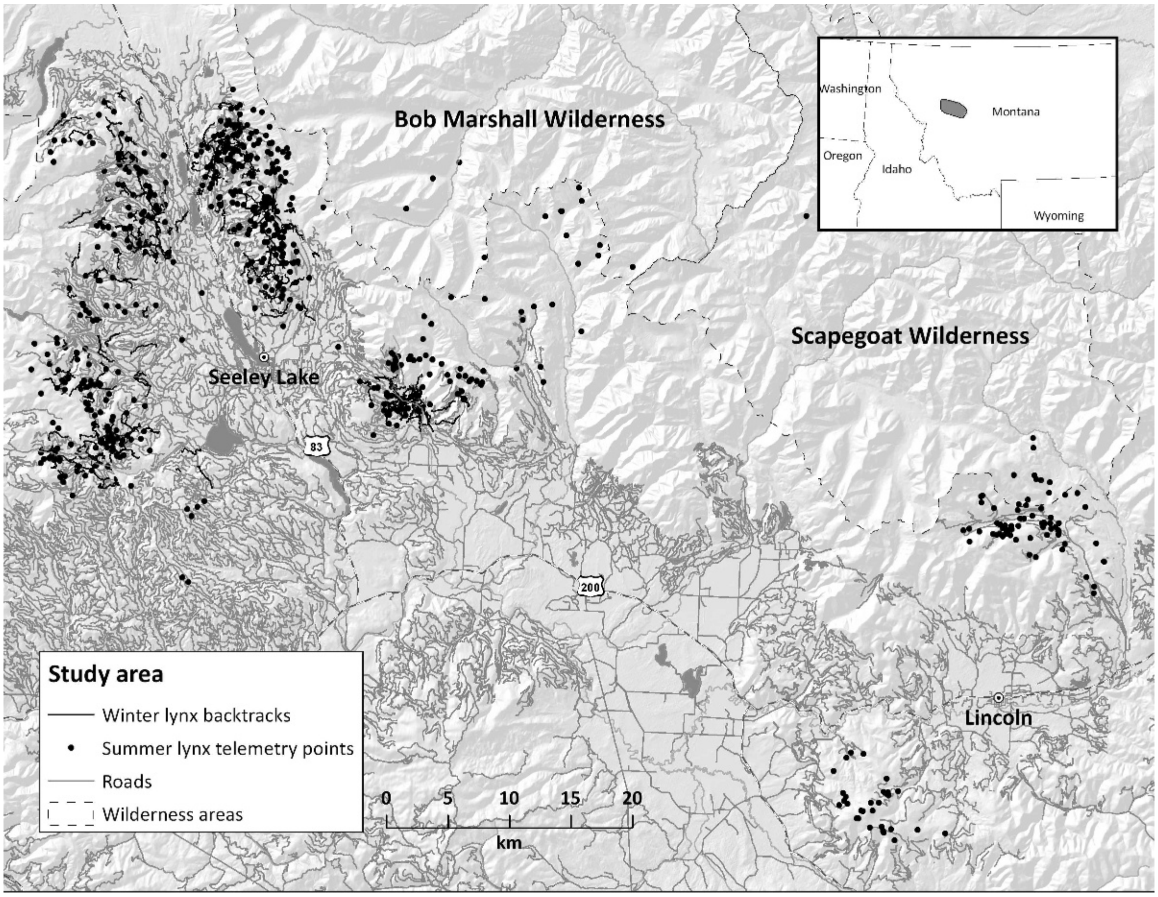

Figure 1. Canada lynx study area located near Seeley Lake, Montana, USA, 1998–2002.

fire suppression. Upper-elevation forests were composed primarily of subalpine fir, Engelmann spruce, and whitebark pine (*P. albicaulis*), with lesser components of lodgepole pine, Douglas-fir, and western larch. Subalpine forests were multistoried and multiaged, often with a dense shrub understory. Shrub communities in this zone were predominantly alder (*Alnus* spp.), huckleberry (*Vaccinium* spp.), and false huckleberry (*Menziesia ferruginea*). Forested riparian areas were primarily subalpine fir, Engelmann spruce, Douglas-fir, and black cottonwood (*Populus balsamifera trichocarpa*).

METHODS

From December to April, 1998–2002, we trapped lynx in activity areas as indicated by snow tracks and in situations where topographic features such as forested corridors and converging valleys may have acted as travel conduits. Although we set traps selectively, the extensive road system allowed representative access across the entire study area. We trapped and handled lynx according to Squires et al. (2008) using methods approved by the Institutional Animal Care and Use Committee (permit IACUC no. 4-2008).

Study Design and Seasonal Monitoring

We used radiocollared lynx to study resource selection within home ranges (Johnson's third-order selection; Johnson 1980) during winter and summer. Additionally, we documented resource characteristics at kill-sites relative to travel paths (Johnson's fourth-order selection; Johnson 1980) during winter only. We used radiotelemetry to sample individual lynx representatively across both seasons. However, we varied monitoring strategy by season; during summer we used telemetry locations, and during winter we backtracked radiocollared lynx. Summer data consisted of telemetry point locations, whereas winter backtracks were linear paths (tracks) extending from telemetry point locations. Winter backtracks provided additional data not available during summer, including kill-sites. There was little seasonal bias in our ability to locate lynx, and systematic sampling of radiotelemetered animals during both seasons prevented biases of more opportunistic detection methods.

During 3 winters (1999–2000, 2000–2001, and 2001–2002) we quantified the winter resource-use patterns of 17 radiocollared lynx (10 M, 7 F) by snowshoeing along snowtracks for 577 km. We used radiotelemetry to locate collared individuals sequentially to systematically sample animals throughout winter. Once we located a track, we backtracked the individual up to 3 km and digitized the travel path using data-logging Global Positioning System (GPS) units; we backtracked away from lynx when they were nearby to avoid altering their movements. On the same day we recorded each lynx track, we sampled resource availability on a random track beginning at a random start point within 2–3 km of the lynx-use track start point. We generated random tracks using the geometry of actual lynx tracks recorded during previous tracking sessions, and we oriented them in a random bearing from each start point. We then navigated this track geometry from the random start location using waypoints entered in Trimble GeoExplorer III® GPS units. Thus, random tracks had the same general shape as actual lynx tracks to control for potential internal correlations due to track geometry, and by sampling both tracks the same day we controlled for weather and snow effects. Global Positioning System track lengths can be biased across habitat types due to differential position accuracy across forest types (DeCesare et al. 2005). Thus, we used a Bezier smoothing algorithm available in the ET Geowizards® (ET GeoWizards version 9.3; <http://www.ian-ko.com>, accessed 1 Jun 2005) extension for ArcGIS® Desktop 9.x to smooth all tracks in accordance with DeCesare et al. (2005). We identified winter kill-sites on use backtracks, based on track patterns and prey remains as described by Squires and Ruggiero (2007).

During summer, 2 technicians used telemetry to approach within 100 m of radiocollared lynx to triangulate the animal's location. We took simultaneous bearings from tracking locations that we plotted using differentially correctable GPS units. We used handheld radios to ensure that locations were simultaneous and that bearings crossed at approximately 90° (Schmutz and White 1990). We located lynx between 1 hour before sunrise to 1 hour after sunset twice weekly throughout the summer to evenly distribute the sample (Otis and White 1999). We estimated our ground-point relocation error by having 2 technicians triangulate transmitters held by a third technician whose location was unknown to trackers. We also located all lynx weekly using fixed-wing aircraft and plotted locations using a GPS. We estimated our aerial-telemetry error by asking the pilot and observer to locate collars without knowing if they were hidden test collars or lynx. For ground and aerial telemetry, we calculated location error by comparing the collar's true location (as determined by averaging 180 differentially corrected GPS points) to the estimated position.

Quantifying Fine- and Patch-Scale Resources

We measured fine-scale habitat resources during summer using vegetation plots at all locations and during winter using a combination of systematic plots and continuous recording of forest species and size categories along tracks (Table 1). To understand seasonal changes in resource selection, we needed different methods to quantify resource characteristics as they changed seasonally (e.g., snow characteristics, shrub availability, forest herbaceous cover). Thus, our statistical comparisons of resource selection were confined within season to account for any potential biases associated with different field methods; we did not compare resource use across seasons.

During summer, we navigated to lynx-use and random points using a military GPS (real time field error <6 m). We established a 22.4-m tape transect at a random azimuth that bisected the plot, and we defined 11.2-m (0.04-ha) and 5.6-m (0.01-ha) fixed-radius plots centered on the point. Within the large (11.2-m-radii) fixed plot, we identified all tree (>8 cm dbh) species and measured diameter at breast height of trees and snags >8 cm diameter at breast height. We calculated tree basal area by summing the area of each stem. We also estimated tree basal area using a variable plot (20-factor prism) centered at the point. On the 5.6-m-radius plot, we tallied all conifer saplings (<8 cm dbh and >0.5 m in ht), and deciduous trees and tree-like shrubs

Table 1. Fine- and broad-scale resource measurements collected at summer lynx locations and along winter backtracks. Winter measurements were a combination of continuous recordings along the full length of tracks (T) and averaged measurements taken at both kill-sites and a systematic sample of 5 plots (P) during the first 1,000 m of track (P), Seeley Lake, Montana, USA, 1998–2002.

Variable	Summer locations	Winter backtracks and kill-sites
Fine-scale variables		
Overstory species composition	Fixed-radius plot	(T) Track segmentation by species
Overstory size class	Fixed-radius plot	(T) Track segmentation by size class
Midstory species composition	Fixed-radius plot	(T) Track segmentation by species
Tree basal area	Variable plot (20-factor prism)	(P) Variable plot (20-factor prism)
Canopy closure	Densiometer plot	(P) Visual classification from plot center
Slope	Clinometer from plot center	(P) Clinometer from plot center
Aspect	Compass from plot center	(P) Compass from plot center
Saplings	Fixed-radius plot	(P) Fixed-radius plot
Horizontal cover	Cover board (4 directions)	(P) Cover board (4 directions)
Woody debris	Line-intersect sample	NA
Shrub species composition	Line-intersect sample	NA
Shrub cover	Densiometer plot	NA
Grass cover	Densiometer plot	NA
Relative prey density	Pellet count plot	(T) Track crossings
Snow depth	NA	(P) Probe measurement at plot center
Snow compaction	NA	(P) Weight penetration at plot center
Broad-scale variables[a]		
% species composition	GIS	GIS
% canopy closure class	GIS	GIS
Mean patch area	GIS	GIS
Patch richness	GIS	GIS
Mean distance to openings	GIS	GIS
Roughness	GIS	GIS
Solar insolation	GIS	GIS
Curvature	GIS	GIS

[a] We used a Geographic Information System (GIS) to quantify broad-scale variables.

(e.g., alder) with stems 1.4–8 cm diameter at breast height. We used line-intercept sampling (Krebs 1989) along the 22.4-m transect to estimate percentage of shrub cover (woody, nontree vegetation between 0.5 m and 2 m tall) by genus; we estimated volume of logs intersecting the tape by measuring log lengths and diameters. We used a vertical sighting tube (e.g., moosehorn densiometer) held at head height to assess presence–absence of canopy cover on a 11.2-m × 11.2-m grid of 25 evenly spaced points centered on the plot. We then inverted the sighting tube and used it to assess presence–absence of grasses, forbs, shrubs, and conifer seedlings on the same grid.

We estimated slope (%) and aspect (°) at plot center using a clinometer and compass. Also at plot center, we counted fecal pellets of snowshoe hares on a 1-m circular plot as a noncalibrated index of prey abundance (McKelvey et al. 2002). We estimated horizontal cover in 4 directions (along and perpendicular to the random transect) using canvas cover board (2 m × 0.5 m; Nudds 1977) erected 10 m from plot center. The cover board was divided into 4 0.5-m blocks and each block was further divided into quarters. Observers estimated horizontal cover from plot center, recording cover at 10% intervals at each of the 4 heights. We then averaged all levels and directions to derive an overall plot estimate of horizontal cover.

Along winter tracks, we quantified vegetation structure and composition on 5 plots spaced at 200-m intervals within the first kilometer of the track, and we recorded forest overstory, midstory, and size classes continuously during backtracking (Table 1). We also measured vegetation plots at all kill-sites along lynx-use tracks using the same plot procedures. Similar to summer plots, we estimated tree basal area (using a 20-factor prism), density of woody stems (<2.5 cm diam and >0.5 m tall), slope, aspect, and horizontal cover (in 4 directions along and perpendicular to the track). Shrub, forb, and grass measurements were not applicable during winter, but instead we measured snow depth using an avalanche probe and snow penetrability by measuring how far a 100-g weight dropped from 1 m penetrated the snow pack. We visually estimated canopy closure at plot center into 1 of 4 classes: 0–10%, 11–40%, 41–70%, and 71–100%.

Along backtracks, we also mapped changes in dominant forest overstory (Douglas-fir, Douglas-fir mixed, larch mixed, lodgepole pine, lodgepole pine mixed, Engelmann spruce–subalpine fir mixed [hereafter, spruce–fir], and open [clear-cuts, meadows, rock]), midstory (Douglas-fir mixed, larch mixed, lodgepole pine mixed), and size class (sapling: 2.5–8 cm, pole: >8–18 cm, mature: >18–28 cm, and large: >28 cm) using data-logging GPS units. We considered a forest stand mixed when the dominant tree species made up <50% of species composition based on visual observation. We tallied track crossings of snowshoe hares and red squirrels as noncalibrated indices of prey abundance according to Squires and Ruggiero (2007; Nichols 1986, Slade and Blair 2000, McKelvey and Pearson 2001).

During winter, we evaluated the proportional travel distance of lynx in clear-cuts and natural openings by overlaying digitized winter lynx tracks over 1-m-resolution imagery from the U.S Department of Agriculture 2005 National Agricultural Imagery Program. We categorized movements approximately parallel to and within 20 m of a forested edge as edge-associated movements, and we estimated an average distance to forest edge for each track segment in clear-cuts. We followed the same procedure on random tracks to compare the proportion of edge-associated track and average distances to edge of lynx-use tracks to random expectation using *T*-tests (Zar 1999).

We also assessed resource selection at broader spatial scales by creating nested sets of buffered polygons around winter backtracks and summer relocation points. Given that we did not know a priori the ecological scales that lynx perceive when making resource choices within home range (third-order selection; Johnson 1980), we tested patch characteristics at multiple scales (50 m, 100 m, 150 m, 250 m, 500 m, 750 m, and 1,000 m; Grand et al. 2004) with our smallest scale corresponding roughly to the distance that lynx chased prey (33 m) on our winter study area (Squires and Ruggiero 2007). We generated nested buffers using ArcView 3.2a and overlaid buffers on raster-based habitat layers to derive proportionate areas of categorical variables within each buffer and mean and standard deviation values of continuous variables. Patch variables addressed vegetative composition, patch configuration, and topography. We characterized vegetation by simplifying cover types and canopy-closure grids derived from the United States Forest Service's Region 1 VMAP v. 05 layers into 6 categories: 1) open (clear-cuts, grasslands, or rock), 2) shrub, 3) dry forest (ponderosa pine, Douglas-fir, western larch mix), 4) lodgepole pine, 5) spruce–fir (Engelmann spruce, subalpine fir mix), and 6) other (water or developed areas). We used Fragstats (Fragstats 3.3; <www.umass.edu>, accessed 1 Jun 2005) and ArcGIS 9.x to quantify the percent composition of each cover type class, mean distance to openings, mean patch area, and patch richness within all nested buffers (McGarigal et al. 2002).

Donahue and Jensen (2001) found that surface roughness, skyward angle (or surface curvature), and aspect collectively accounted for most of the variation in topographic information. Thus, we used 30 × 30-m digital elevation models (DEMs) from the United States Geological Survey National Elevation Dataset to derive 3 metrics that captured these sources of variability (Gesch et al. 2002, Gesch 2007). We used ArcView 3.2a and the Surface Areas and Ratios from Elevation Grid extensions (Jenness Enterprises v. 1.2; <http://www.jennessent.com/arcgis/arcgis_extensions.htm>, accessed 1 Jun 2005) to estimate surface roughness using a ratio of 3-dimensional surface area to 2-dimensional surface area (Jenness 2004). We used the Solar Analyst extension (Fu and Rich 1999) to estimate solar insolation as a continuous surrogate to aspect, and the CURVATURE command in the Spatial Analyst and ArcInfo Workstation to derive surface curvature (Pellegrini 1995, Apps et al. 2004). We also used DEMs to calculate elevation and slope.

During summer, we compared the distance from lynx-use and random points to forest roads, distinguishing gated roads from those open to public access in analysis. During winter, wheeled vehicular traffic was largely absent from forest roads due to deep snow, but snowmobiles were present. Road density was 3.19 km/km^2 (2,843 km total length), of which 243 km (0.27 km/km^2) of roads and trails were machine-groomed to encourage snowmobile use. Although we were unable to quantify the number of snowmobiles using forest roads in lynx home ranges, one primary groomed trail was used by approximately 130 snowmobiles/day ($n = 67$ days; S. Tomson, United States Department of Agriculture Seeley Lake Ranger District, unpublished data). We segmented tracks at 200-m intervals and measured the distance from the centroids of each track segment to the nearest forest road and to the nearest road groomed for snowmobile traffic.

Hierarchical Resource Selection Modeling

We used logistic regression to model selection within home ranges (third-order selection; Johnson 1980) and selection specific to winter kill-sites (fourth-order; Johnson 1980). We modeled seasonal resource selection in home ranges using winter backtracks and summer relocation data, including buffers to investigate the patch context (Table 1; Hosmer and Lemeshow 2000, Manly et al. 2002, Keating and Cherry 2004). We used logistic regression to estimate habitat rankings and calculate coefficients related to relative odds of habitat use (Keating and Cherry 2004, Johnson et al. 2006). We used SAS GENMOD to account for repeated measures within individuals, and the multivariable Wald test to test the significance of overall models (SAS Institute, Cary, NC). We reported generalized estimating equation coefficients given potential correlation within individuals (Hosmer and Lemeshow 2000).

We built multivariate logistic models of resource selection beginning with important ($P < 0.25$) variables as identified using univariate logistic regression according to Hosmer and Lemeshow (2000). We evaluated the variables included in multivariate models in terms of their stability, collinearity, biological meaningfulness and interpretability, and contribution to the model log-likelihood. We used a manual forward-stepping procedure, adding variables according to strength of univariate relationships as measured by Wald statistics. We retained variables in the multivariate models if the model log-likelihood was improved enough to generate significant ($P < 0.05$) likelihood ratio tests (Hosmer and Lemeshow 2000). We evaluated stability of multivariate models including potentially collinear predictor variables by selectively adding and removing variables and observing changes in the sign or standard errors of variable coefficients (Hosmer and Lemeshow 2000). We recognized that complex cross-correlations among variables can occur across spatial scales (Kie et al. 2002, Battin and Lawler 2006). When testing whether patch-level variables should be included in multivariate models, we included only the single scale for each variable with the most predictive power to avoid issues of collinearity among scales. Correlations among patch-metrics were low ($r < 0.25$), so we did not formally evaluate cross-scale correlations according to Battin and Lawler (2006). Although we acknowledge that forward stepwise regression may be conservative in including variables (Pearce and Ferrier 2000), our goal was to provide multivariate models of lynx resource selection that were parsimonious, descriptive, and biologically meaningful.

To compare resource characteristics at winter kill-sites to those along foraging paths, we defined use points as the actual kill-sites and availability as the systematic sample of vegetation plots quantified along the animal's respective backtrack. We used SAS GENMOD to estimate the exchangeable working correlation within individual lynx and to identify important ($P < 0.25$) variables for potential inclusion into the multivariate model (Hosmer and Lemeshow 2000); exchangeable working correlation specification allows for constant correlations among measurements within a subject. This exploratory analysis indicated there was a low exchangeable working correlation (0.016) within lynx. Therefore, we then used SAS LOGISTIC to compare kill-sites to vegetation plots (no within-animal correlation correction was needed), which allowed a weighting parameter (1/5) that set vegetation points equal to kill-sites in our final analysis (Fielding and Bell 1997).

Seasonal Components of Horizontal Cover

Given the association of lynx use (Maletzke et al. 2008, Squires et al. 2008, Vashon et al. 2008*b*) and hare abundance (Hodges 2000*a*, *b*) with horizontal cover, we used vegetation plots along random winter snow-tracks and at randomly located summer vegetation plots to identify habitat components that best predicted horizontal cover. We used a forward stepwise multiple regression to identify the relationship between seasonally measured habitat variables and associated horizontal cover values (Zar 1999). Candidate variables included in the analysis were the proportion of overstory trees by species, tree basal area by species, total number of trees and saplings, and snow penetrability. Although we originally measured snow penetrability to relate how lynx responded to snow supportiveness, this variable also related to horizontal cover because penetrability was highest when snow had just fallen and contributed most to horizontal cover (present on tree limbs). All variables included in multiple regression analyses had low ($r < 0.3$) correlation.

RESULTS

Winter Resource Selection Within Forest Stands

During winter, lynx foraged primarily within a narrow elevation band (range = 1,270–1,995 m, $\bar{x} = 1,606$ m, SD = 147, $N = 234$ backtracks) of mid- to high-elevation forest composed of mature, large-diameter trees with higher horizontal cover, more abundant hares, and deeper snow than available based on multivariate logistic regression (Table 2). These preferred forests included spruce–fir in the overstory and midstory forming a multistory structure with high horizontal cover (45%, SD = 14) from conifer boughs touching the snow surface (Fig. 2). During winter, the primary component of horizontal cover based on multiple regression was subalpine fir (standardized coeff.

Table 2. Lynx selection of winter resources based on multivariate logistic regression,[a] Seeley Lake, Montana, USA, 1998–2002.

Variable	Coeff. ($\hat{\beta}_i$)	SE	Z	P
Horizontal cover	0.039	0.006	7.12	<0.001
Hare tracks	0.073	0.020	3.68	<0.001
Overstory size (28–51 cm dbh)	1.351	0.457	2.96	0.003
Spruce–fir midstory	1.707	0.605	2.82	0.005
Snow depth	0.680	0.242	2.81	0.005
Canopy (11–39%)	0.862	0.447	1.93	0.058
Spruce–fir overstory	0.744	0.440	1.69	0.091
Overstory size (2.5–10 cm)	−1.984	1.120	−1.77	0.076
Open overstory	−2.674	1.247	−2.15	0.032

[a] Global Likelihood Ratio Test $\beta = 0$: $\chi^2 = 98.13$, $P \leq 0.001$.

= 0.31, Adjusted $R^2 = 0.338$, $n = 417$, $F = 31.313$, df = 7, $P < 0.001$) followed by sapling density (dbh < 7 cm; 0.27), snow penetrability (0.26), and tree density (dbh > 7.62 cm; 0.24); snow penetrability likely related to horizontal cover as an indirect measure of snow clinging to conifer boughs. Although Englemann spruce and subalpine fir were the dominant tree species, forests used by lynx were typically composed of mixed conifers including Douglas-fir (proportion = 0.22), larch (0.13), and lodgepole pine (0.17). Tree (>10 cm dbh) and sapling (<10 cm dbh) densities in forests used by lynx during winter were 0.07 (SD = 0.04) and 0.25 (SD = 0.14) stems/m^2, respectively; tree basal area was 20.93 m^2/ha (SD = 11.65). During winter, the proportion overstory size classes of trees in forests used by lynx were 0.05 saplings (SD = 0.10), 0.19 pole (SD = 0.20), 0.42 mature (SD = 0.23), and 0.29 large (SD = 0.23). Forests composed of small diameter saplings (<10 cm dbh) were generally avoided (Table 2).

Snow pack in areas used by lynx was deeper ($\bar{x} = 86$ cm, SD = 34) than generally available ($\bar{x} = 80$ cm, SD = 32) within home ranges, but we found no evidence that snow penetrability affected lynx travel routes. Average snow depth on the study area was variable ($F = 16.63$, df = 3, $P < 0.001$) with more ($P < 0.05$) snow falling in the winter of 1998–1999 compared to winters of 2000 through 2002, but snow penetrability was similar ($F = 1.24$, df = 3, $P = 0.295$) across years.

Figure 2. Example of multilayer, spruce–fir forests providing high horizontal cover, an important habitat attribute for Canada lynx in western Montana, USA, 1998–2002.

Lynx rarely crossed clear-cuts or natural openings during winter. Lynx crossing open habitat accounted for only 3% of total travel distance compared to 7% on random tracks. When they did cross openings, lynx remained closer ($\bar{x} = 37$ m) to forest edges compared to random tracks with 62.8% of lynx-use tracks near (<20 m) forest edges versus 39% of random tracks ($T = 3.874$, $P < 0.001$). Lynx traveled away (>20 m) from forest edges and into openings on 40 occasions during 577 km of backtracking with an average crossing distance of 117 m (range = 40–379 m, $N = 26$).

Average distance lynx traveled from snow-covered roads that excluded vehicular traffic was 99 m (SD = 80); lynx traveled 1,049 m (SD = 1,440) from groomed snowmobile trails. We found no evidence that lynx selected areas away from forest roads ($\beta = <-0.01$, $Z = -0.50$, $P = 0.619$) or groomed snowmobile trails ($\beta = < -0.01$, $Z = -0.89$, $P = 0.375$) during winter.

Lynx killed prey ($N = 71$), mostly snowshoe hares (96% biomass of winter diet; Squires and Ruggiero 2007), at sites with higher horizontal cover compared to general foraging paths based on a multivariate model of important ($P < 0.25$) resource variables (lodgepole pine, snags, spruce–fir, and horizontal cover; Table 3). Horizontal cover at kill-sites averaged 52% (SD = 24%), which was significantly higher than along travel paths. Univariate comparisons indicated that lynx kill-sites had higher proportions of spruce–fir overstory (0.49, SD = 0.36 vs. 0.39, SD = 0.32) and lower proportion of lodgepole pine (0.08, SD = 0.18 vs. 0.12, SD = 0.22); we found no evidence that snow attributes such as depth (0.86 m, SD = 0.37 vs. 0.86 m, SD = 0.34) or penetrability (20.05 cm, SD = 8.85 vs. 20.47, SD = 9.05) were factors in determining where lynx killed prey. We selected our final model, which contained only horizontal cover, over the full model based on parsimony and similar log-likelihoods (Likelihood Ratio Test; $\chi^2 = -2.72$, df = 3, $P = 0.437$; Table 3).

Summer Resource Use Within Forest Stands

We documented summer use of resources based on 630 lynx relocation points from 27 lynx (16 M, 11 F; $\bar{x} = 23$ locations/animal, SD = 13). Our location error associated with ground-based telemetry averaged 27 m (SD = 22, $N = 120$ test points) compared to 45 m (SD = 30, $N = 11$) using aircraft; we assumed a maximum tracking error of 63 m (mean error using aircraft = 45 m, 95% CI = 27–63 m) for habitat-use analyses.

During summer, lynx selected habitats with high horizontal cover, abundant total shrubs, abundant small-diameter, pole-sized trees (8–18 cm dbh), dense saplings, and spruce–fir species composition based on multivariate logistic regression (Table 4). These resources were found in the same mid- to high-elevation forests (range = 1,260–2,355 m, $\bar{x} = 1,742$ m, SD = 191) as lynx used during

Table 3. Multivariate analysis of resource selection of lynx at winter kill-sites compared to travel routes in northwestern Montana, USA, 1998–2002. The full model[a] included all important ($P < 0.25$) variables identified based on univariate logistic regression compared to preferred, statistically similar[b] reduced model.

Variable	Coeff. ($\hat{\beta}_i$)	SE	Z	P
Full model				
Lodgepole pine	−0.805	0.961	0.701	0.402
Spruce–fir	0.469	0.593	0.625	0.429
Snag	−1.332	1.906	0.488	0.485
Horizontal cover	0.015	0.008	3.290	0.070
Reduced model				
Horizontal cover	0.018	0.008	5.495	0.019

[a] Global Likelihood Ratio Test $\beta = 0$: $\chi^2 = 5.743$, $P = 0.017$.

[b] Likelihood Ratio Test between full vs. reduced models $= -2[-94.191 - (-95.55)] = -2.72$, df = 3, $P = 0.437$.

winter, but at slightly higher elevations (summer use 136 ± 24 m higher compared to winter, $P < 0.05$). These forests, like in winter, were located below the alpine zone and above low-elevation, dry forest types dominated by ponderosa pine. High horizontal cover ($\bar{x} = 65\%$, SD = 23.3) was the most important resource that lynx selected during summer with primary components of horizontal cover including total sapling density (standardized coeff. = 0.343), proportion of subalpine fir (<8 cm dbh; 0.185) and pole-sized trees (8–18 cm dbh; 0.162) in the overstory, and proportion of false huckleberry (0.14), alder (0.13), and logs (0.13) in the understory; these variables collectively accounted for 41% of variation in horizontal cover (adjusted $R^2 = 0.413$, n = 1,178, $F = 70.144$, df = 12, $P < 0.001$). Lynx generally avoided conifer forests containing a high proportion of Douglas-fir trees, grass in the understory, or snags (Table 4). Tree (>10 cm dbh) density in forests used by lynx during summer was 0.07 stems/m^2 (SD = 0.05). Density of saplings (stems 2.5–7.6 cm dbh) averaged 0.44/m^2 (SD = 0.51); 82% of saplings were conifers and 18% were deciduous trees or shrubs. Total tree basal area was 20.02 m^2/ha (SD = 16.66). During summer, the proportion overstory size classes of trees in forests used by lynx were 0.66 pole (SD = 0.26), 0.21 mature (SD = 0.17), and 0.06 large (SD = 0.12).

Univariate logistic comparisons indicated that lynx selected stands with abundant spruce–fir in the overstory ($\bar{x}$ = 0.46, SD = 0.34; $\beta = 1.00$, $Z = -5.23$, $P < 0.001$) and mid-story ($\bar{x}$ = 0.56, SD = 0.39; $\beta = 0.57$, $Z = 4.48$, $P < 0.001$) during summer, but these variables contributed little to the overall model log-likelihood so were not included in the multivariate model. Consistent with lynx using young forests during summer, diameter of trees in selected stands averaged 17.3 cm diameter at breast height (SD = 6.1), which was smaller ($\beta = -0.09$, $Z = -4.54$, $P < 0.001$) than diameter of trees in random plots ($\bar{x}$ = 19.0, SD = 6.9) within lynx home ranges. Lynx tended to avoid forests composed of mature (18–28 cm dbh; $\beta = -0.49$, $Z = -2.04$, $P = 0.041$) and large diameter trees (>28 cm dbh; $\beta = -0.74$, $Z = -2.40$, $P = 0.016$) during summer. Lynx did not select ($\beta = -0.00$, $Z = -1.13$, $P = 0.257$) habitats according to their proximity to dirt–gravel forest roads that were gated or the subset of roads open to vehicular traffic ($\beta = -0.00$, $Z = -1.05$, $P = 0.295$).

Table 4. Lynx selection of summer resources based on multivariate logistic regression, Seeley Lake, Montana, USA, 1998–2002.[a]

Variable	Coeff. ($\hat{\beta}_i$)	SE	Z	P
Horizontal cover	0.011	0.003	3.35	0.001
Douglas fir (%)	−0.685	0.224	−3.06	0.002
Grass (%)	−0.655	0.234	−2.80	0.005
Spruce–fir saplings	0.481	0.183	2.63	0.009
Total shrubs	0.031	0.012	2.61	0.009
Sapling density (m^2)	0.562	0.233	2.41	0.016
Snags	−0.955	0.464	−2.06	0.040
Trees 8–18 cm dbh	0.345	0.187	1.85	0.065

[a] Global Likelihood Ratio Test $\beta = 0$: $\chi^2_8 = 180.336$, $P \leq 0.001$.

Resource Selection at Hierarchical Scales

Selection for patch metrics was insufficient to justify their inclusion into our multivariate resource-use models based on their low contribution to model log-likelihoods. However, lynx did exhibit some selection for patch characteristics based on univariate tests. Lynx selected ($P < 0.05$) forest patches of spruce–fir forests at most spatial scales during winter (50 m = logistic coeff. = 0.15; 150 m = 0.13; 250 m = 0.12; 500 m = 0.10; 750 m = 0.09) and summer (50 m = 0.38; 150 m = 0.63; 250 m = 0.80; 500 m = 0.79; 750 m = 0.71; 1,000 m = 0.67). Lynx also tended to select basin-like patches such as drainages. Lynx exhibited seasonal differences in their response to patch-level metrics describing open habitat (primarily clear-cuts), patch richness, and dry forests. During winter, lynx avoided clear-cuts and openings across spatial scales (50 m = −0.54; 150 m = −0.36; 250 m −0.29; 500 m = −0.26; 750 m = −0.26; 1,000 m = −0.25), whereas in summer there was no evidence of avoidance. During winter, lynx selected habitats with low patch richness (50 m = −0.07; 150 m = −0.03; 250 m −0.04; 500 m = −0.05; 750 m = −0.05; 1,000 m = −0.05) compared to summer when patch richness (i.e., habitat heterogeneity) was not a factor in selection. During summer, lynx also strongly avoided dry-forest patches across scales (50 m = −0.25; 150 m = −0.29; 250 m −0.33; 500 m = −0.32; 750 m = −0.33; 1,000 m = −0.32) compared to winter when this patch metric was not a factor. At winter kill-sites, lynx were insensitive to patch size ($\beta = -0.609$, $Z = -0.85$, $P = 0.394$) or distance to patch edges ($\beta = 0.001$, $Z = 0.33$, $P = 0.745$) in determining where they successfully captured prey.

DISCUSSION

Lynx exhibit substantial regional differences in resource selection across the contiguous United States (Koehler 1990, Fuller et al. 2007, Moen et al. 2008, Vashon et al. 2008*b*). Appreciating these differences is fundamental to management and conservation of southern lynx populations. In contrast to populations in Canada (O'Donoghue et al. 1998*a*, Mowat et al. 2000) and other southern populations in the contiguous United States (Parker et al. 1983, Fuller et al. 2007, Vashon et al. 2008*b*), lynx in the Rocky Mountains of Montana selected mature, multistoried forests composed of large-diameter trees with high horizontal cover during winter. These forests were composed of mixed conifers that included lodgepole pine, Douglas-fir, and western larch, but predominately consisted of Englemann spruce and subalpine fir in the overstory and midstory. Forest structures used by lynx in Montana differed markedly from those used by lynx in Alaska and Canada where mature forests were used in proportion to availability and selection was for regenerating (>20 yr) forests (Murray et al. 1994, Staples 1995, Mowat et al. 2000). Regenerating forests used by lynx in Montana during winter were old enough to have developed a multistoried structure with high horizontal cover that supported hares.

During summer, however, lynx broadened their resource use to include early succession forest with high horizontal cover from abundant shrubs, abundant small-diameter trees, and dense spruce–fir saplings. Lynx use of early succession forests during summer in Montana was similar to habitat structures used by other southern populations during winter (Parker et al. 1983, Koehler 1990, Fuller et al. 2007, Vashon et al. 2008*b*). Seasonal differences in resource selection was not absolute in that lynx in summer still used mature forest, but the gestalt of selection shifted to an earlier successional stage of forest development compared to winter. We collected summer relocation data during daylight hours compared to winter backtracks that also included use of habitat during the night. We do not believe this strongly biased our sample of habitat use, but we could not statistically evaluate the issue. We did not observe seasonal movements to new spatial use areas. Thus, lynx selected a mosaic of forest stages to meet their seasonal resource needs within home ranges (Koehler and Aubry 1994, Aubry et al. 2000*a*, Buskirk et al. 2000*b*, Vashon et al. 2008*a*).

How should managers prioritize their management actions given that lynx use a mosaic of forest structures composed primarily of mature multistory forests during winter and earlier succession forests during summer? We believe the answer to this question rests in the recognition that winter is the most constraining season for lynx in terms of resource use. Starvation mortality was most common during winter and early spring on our study area (J. R. Squires, Rocky Mountain Research Station, unpublished data) and lynx in winter used a narrow subset of available habitat compared to summer. Winter is also a time in the northern Rockies when lynx return to home ranges from exploratory movements elsewhere (Squires and Laurion 2000, Squires and Oakleaf 2005). Contrary to Murray et al. (2008*a*), spruce–fir forests in mature and old-growth age classes can support high hare densities in the northern and southern Rocky Mountains during winter (Wolfe et al. 1982, Griffin 2004, Malaney and Frey 2006, Zahratka and Shenk 2008). Thus, within heavily managed landscapes of the northern Rockies, we believe that managers should prioritize retention and recruitment of abundant and spatially well-distributed patches of mature, multilayer spruce–fir forests.

Lynx in the northern Rockies, like those in other southern populations (see Vashon et al. 2008*b* for an exception), depend on low-density hare populations ($\bar{x}$ = 0.6 hares/ha; Griffin 2004, Mills et al. 2005, Zahratka and Shenk 2008). These low hare densities are similar to the cyclic lows of northern populations (Hodges 2000*a*, *b*), during which lynx populations in Alaska and Canada experience low recruitment, expanded spatial-use areas, and increased mortality (Poole 1994, Mowat et al. 1996, Slough and Mowat 1996, O'Donoghue et al. 1997); Ruggiero et al. (2000*a*) recommended that a density of 0.5–1.0 hares/ha was necessary for lynx populations to persist, which is similar to hare densities at Seeley Lake (Griffin 2004, Griffin and Mills 2009). Thus, lynx in Montana depend on a winter prey base at or slightly above the threshold required for persistence; minor reductions in hare density could disproportionately impact lynx.

We hypothesized that lynx would select dense habitats that support high hare densities given this population's almost complete reliance on snowshoe hares during winter (Squires and Ruggiero 2007) and the patterns of resource selection observed for other populations (O'Donoghue et al. 1998*a*, Mowat and Slough 2003, Vashon et al. 2008*b*). An alternative hypothesis was that lynx selected habitat based primarily on prey vulnerability rather than abundance. We believed that lynx selected mature, spruce–fir forest during winter in response to high hare abundance rather than to meet other ecological needs (e.g., predator avoidance, thermoregulation). Snowshoe hares at Seeley Lake exhibited source–sink dynamics among forest-structure classes (Griffin 2004, Griffin and Mills 2009). During winter and concurrent with our study, Griffin (2004) found in Seeley Lake that mature-dense forests supported the highest hare densities ($\bar{x}$ = 0.53 hares/ha, SD = 0.53) compared to other forest-structure classes. However, during summer, Griffin (2004) found that young-dense forests supported the highest hare densities ($\bar{x}$ = 0.64 hares/ha, SD = 0.44) compared to mature-dense forests (0.34 hares/ha, SD = 0.41). Thus, seasonal changes in resource use we observed for lynx in Montana mirrored patterns of hare abundance.

Consistent with the seasonal changes in hare density reported by Griffin (2004, Griffin and Mills 2009), lynx exhibited the strongest selection for dense horizontal cover compared to other resource metrics, regardless of season or scale. During winter, multilayer spruce–fir forests with branching that descended to the snow surface provided the dense horizontal cover necessary to support hares (Hodges 2000*a*, *b*). During summer, lynx selected young mixed-conifer forests with high horizontal cover composed primarily of spruce–fir and larch. Commercial foresters at Seeley promoted larch recruitment, which likely reduced winter hare density in regenerating clear-cuts, because larch is a deciduous conifer. Forests that were thinned as a silvicultural treatment were generally avoided by lynx. High horizontal cover from dense lateral foliage coupled with high stem density in high-elevation spruce–fir forests (especially subalpine fir) was similarly found to support the highest hare densities in New Mexico (Malaney and Frey 2006). The highest horizontal cover that lynx used in the northern Rockies of Montana was at spring–summer den sites (Squires et al. 2008).

Both vegetative structure and prey density affect lynx foraging behavior, which can vary across spatial scales (Murray et al. 1994, 1995; O'Donoghue et al. 1998*a*; Hopcraft et al. 2005). Our finding that lynx in winter killed prey in areas with greater horizontal cover than was present on their general foraging paths suggests that prey abundance, rather than vulnerability, may drive predation patterns. In contrast, lynx in Maine selected forests with intermediate to high hare density and intermediate cover values (Fuller et al. 2007); lynx avoided dense stands (>14,000 confer stems/ha) that supported the highest hare density. Stem density at Montana kill-sites (3,200 stems/ha) was considerably below the level (>14,000 stems/ha) that provided refugia for hares in Maine (Fuller et al. 2007). The predation strategy of lynx in Montana was also consistent with a low vegetation density, in that chasing prey (55% of kills) was more prevalent than ambushing (45%; Squires and Ruggiero 2007). In southwest Yukon Territory, Canada, lynx chased hares more frequently in sparse stands and ambushed prey in dense stands (Murray et al. 1995).

Ecological theory suggests that wildlife relate to their environment at hierarchical scales ranging from sites (<1 ha) and patches (1 ha to hundreds of hectares) to landscapes (hundreds to thousands of hectares) and regions (>10,000 km^2; Johnson 1980, Bissonette 1997, Murray et al. 2008*b*). Given that the relationship between organisms (Mitchell et al. 2001, McLoughlin et al. 2002), including carnivores (Chamberlain et al. 2003, Apps et al. 2004, Squires et al. 2008), and their environment is scale-dependent, identifying the appropriate scales at which resources are perceived is fundamental to understanding ecological processes and species distributions (Morris 1987, Carlile et al. 1989). Lynx are similar to other organisms in selecting resources at both fine and coarse spatial scales (Murray et al. 2008*b*, Squires et al. 2008, Vashon et al. 2008*a*). However, patch-level metrics provided insignificant improvements in our multivariate resource models to warrant inclusion. The importance of fine-scale metrics suggests that lynx primarily selected resources at fine spatial scales, which is consistent with a sight-hunting predator evolved to capture prey in deep snow and dense cover. However, lynx did exhibit some sensitivity to patch-level metrics based on univariate relationships. For example, lynx selected patches of spruce–fir forest across all scales and seasons. Lynx also selected basin-like patches, such as drainages, regardless of season. However, lynx use of drainages may be attributed to statute or agency policy for establishing streamside management zones to protect riparian areas on federal, state, and private lands, which required managers to retain mature forest patches in buffers along the streams that lynx used to navigate the larger matrix of less suitable habitat, especially in winter (Natural Resource Conservation Service 2007).

Lynx exhibited seasonal differences in patterns of selection for other patch-metrics, including open patches (primarily created by clear-cutting), patch richness, and dry-forest patches. During winter, lynx strongly avoided clear-cuts and open patches across all spatial scales, whereas in summer there was no evidence of avoidance. Clear-cuts and openings in winter are covered with deep snow and provide little horizontal cover for hares compared to summer, when dense deciduous shrubs and saplings support hares (Griffin 2004). Lynx also exhibited seasonal differences in selection for patch richness by foraging in homogeneous patches of mature forests dominated by spruce–fir (low patch richness) in winter, compared to summer, when lynx were insensitive to this metric. During winter, lynx were also insensitive to patch size or distance to patch edges in determining where they successfully captured prey. Such insensitivity to patch edges contrasted with studies in Alaska where lynx preferentially hunted in edge habitat (Kesterson 1988, Staples 1995).

Seeley Lake had an extensive road network associated with commercial timber harvest that may substantially impact wildlife (Forman and Alexander 1998). Dirt or gravel roads received little traffic, except for a paved, 2-lane highway that bisected the study area. S. Tomson (unpublished data) estimated that 8 vehicles/day traveled low-volume roads (98% of road length) and approximately 55 vehicles/day traveled the remaining (2%) high-volume forest roads. Spur roads that extended off primary timber haul roads were mostly gated and may have received <20 vehicle trips/year. Similar to McKelvey et al. (2000*b*), we found no evidence that lynx were sensitive to forest roads, including roads used by snowmobiles during winter. Dense forest vegetation at Seeley Lake concentrated snowmobile use on roads and trails, with some dispersed use occurring in clear-cuts already avoided by lynx. We concluded that seasonal resource-selection patterns of lynx were little affected by forest roads with low vehicular or snowmobile traffic.

MANAGEMENT IMPLICATIONS

Lynx in the northern Rockies exhibited a strong selection for spruce–fir forests. Managers should prioritize retention of a habitat mosaic of abundant and spatially well-distributed patches of mature, multilayer spruce–fir forests and younger forest stands. Given the positive correlation between hare abundance and horizontal cover (Keith et al. 1984; Hodges 2000*a*, *b*), management actions that reduce horizontal cover, such as precommercial thinning, degrade lynx habitat. Recovery of high-elevation, spruce–fir forests following harvest or thinning tends to be slow due to short growing seasons, cold temperatures, high winds, and deep snow (Fiedler et al. 1985, Long 1995). Therefore, reducing horizontal cover within multistory spruce–fir forests through thinning or harvest may degrade lynx habitat for many decades.

ACKNOWLEDGMENTS

We acknowledge the many excellent technicians that assisted with field data collection. Research was funded by the Rocky Mountain Research Station, Forestry Sciences Laboratory, Missoula, Montana. We thank Plum Creek Timber Company and the Bureau of Land Management for additional financial support; we also thank Montana Fish, Wildlife, and Parks and the Seeley Lake District, United States Forest Service for their cooperation and logistical support. We thank R. King for providing statistical advice and review. We also thank J. Ganey, M. Rumble, and 2 anonymous reviewers for their helpful suggestions.

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Associate Editor: Clark.