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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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

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.

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.

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 (β = < −0.01, $Z = -0.50$, $P = 0.619$) or groomed snowmobile trails (β = < −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