Habitat Conditions Associated With Lynx Hunting Behavior During Winter in Northern Washington

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ABSTRACT Effectively managing habitat for threatened populations of Canada lynx (Lynx canadensis) requires knowledge of habitat conditions that provide for the ecological needs of lynx. We snow-tracked lynx to identify habitat conditions associated with hunting behavior and predation during winters of 2002–2003 and 2003–2004 in the northern Cascade Range in Washington state, USA. We recorded number and success of predation attempts, prey species killed, and trail sinuosity on 149 km of lynx trails. Lynx killed snowshoe hares (Lepus americanus), red squirrels (Tamiasciurus hudsonicus), and cricetids more than expected in Englemann spruce (Picea engelmannii) and subalpine fir (Abies lasiocarpa) forests, where snowshoe hare densities were highest. Lynx killed prey less than expected in Douglas-fir (Pseudotsuga menziesii) and ponderosa pine (Pinus ponderosa) forests and forest openings. We used the sinuosity of lynx trails as an index of quality of habitat hunted. Lynx trails that included predation attempts were more sinuous than trail segments without predation attempts. Lynx trails had greater sinuosity in forest stands with high hare densities dominated by Engelmann spruce and subalpine fir than in stands with low hare densities dominated by Douglas-fir and ponderosa pine or in forest openings. We encourage forest managers to maintain or create sufficient understory cover to support high densities of snowshoe hares as foraging habitat for lynx. (JOURNAL OF WILDLIFE MANAGEMENT 72(7):1473–1478; 2008)

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Canada lynx (*Lynx canadensis*) is listed as a threatened species in both Washington state and throughout its range in the contiguous United States (U.S. Fish and Wildlife Service 2000, Stinson 2001). Northern Washington represents the southern periphery of lynx range on the Pacific coast of North America, where both timber harvesting and natural fires have temporarily contributed to the fragmentation of lynx habitat (Koehler and Aubry 1994; Buskirk et al. 2000; K. B. Aubry, United States Forest Service, unpublished data). To ensure persistence of lynx populations in Washington, habitat management must be based on a clear understanding of the prey species and habitat conditions selected by lynx.

Snowshoe hares (*Lepus americanus*) are the primary prey of lynx throughout their range in North America (Nellis et al. 1972, Aubry et al. 2000, Mowat et al. 2000). Low-density hare populations appear to be characteristic of populations at the southern extent of their range, which may contribute to low productivity of lynx in northern Washington (Koehler 1990, Aubry et al. 2000). Understanding lynx habitat-selection patterns and hunting strategies in areas with consistently lower hare densities than in the core lynx range is critical information needed for lynx conservation and habitat management.

In Washington, lynx preferred Engelmann spruce (Picea engelmannii) and subalpine fir (Abies lasiocarpa) forests and

avoided Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) forests and natural and human-caused forest openings (Koehler et al. 2008). We hypothesized that lynx select Engelmann spruce and subalpine fir forests because snowshoe hares are both abundant and vulnerable to lynx predation in these forests. Lynx avoided Douglas-fir and ponderosa pine forests and forest openings because potential prey is scarce (Koehler 1990, Koehler et al. 2008).

Quantifying movement patterns of an animal may help determine the relative quality of different habitats (Nams and Bourgeois 2004). Our objective was to quantify habitat quality by relating lynx movement patterns. We tested whether trail sinuosity could be a valid index to lynx hunting behavior in different habitat conditions. We hypothesized that lynx moving through low-quality habitats traveled in a more or less straight line to conserve energy while searching for more suitable foraging habitats. For lynx hunting snowshoe hares in high-quality habitats, their trails became increasingly nonlinear or sinuous as they searched potential cover to locate or flush hares.

STUDY AREA

We conducted our study in a 211-km² study area in the Black Pine Basin (see map in Koehler et al. 2008) on the Okanogan–Wenatchee National Forest in northern Washington, USA (48°N, 120°W). Habitat conditions in the Black Pine Basin were typical of those occupied by lynx in northern Washington, where Engelmann spruce and

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subalpine fir forests, Douglas-fir and ponderosa pine forests, natural burns, and human-caused forest openings dominated the landscape. Average road density in our study area was 1.8 km/km², which enabled us to access most areas by snowmobile during the winter. Elevations ranged from 643 m to 2,134 m; 22% of the study area occurred at low elevations (850-1,219 m), 43% at moderate elevations (1,220-1,524 m), 28% at high elevations (1,525-1,829 m), and 7% at very high elevations (>1,829 m). Average daily temperatures ranged from -26° C to 38° C and average annual snowfall was 315 cm at an elevation of 655 m (Western Regional Climate Center, Reno, NV, USA). Forests were dominated by Engelmann spruce and subalpine fir at higher elevations and on steep, narrow drainages and north-facing aspects at lower elevations. Douglas-fir and ponderosa pine forests dominated wide drainage bottoms and south-facing slopes <1,066 m in elevation. Engelmann spruce and subalpine fir forests comprised 55% of the study area; Douglas-fir and ponderosa pine forests, 37%; burned areas <10 years old, 6 %; and forest openings, 2%. Timberharvest records were incomplete, but about 19% of the area was harvested since 1950.

METHODS

We snow-tracked lynx from December through March during winters of 2002-2003 and 2003-2004 to investigate habitat selection at the landscape scale (i.e., among habitat polygons; Koehler et al. 2008) and hunting behavior at the stand scale (i.e., within habitat polygons; this study). We divided the study area into 6 39-km² search zones, each about the average size of a female lynx home range (Koehler 1990). We used these zones to disperse our search effort and maximize opportunities for locating tracks of different individuals and to obtain a representative sample in both time and space during each winter. We established 4 9-km² search units in each zone from which we randomly selected to begin systematic searches for lynx tracks. We began searches on snowmobiles >12 hours after snowfall to ensure that lynx had sufficient time to leave tracks throughout the study area. If we detected no tracks in the first unit, we searched the adjacent unit and continued in that fashion until we located a track. Once we located lynx tracks, we followed them on snowshoes for as long as possible each

To avoid influencing lynx behavior, we back-tracked lynx trails if they were <24 hours old and forward-tracked them if they were >24 hours old. We used submeter precision Trimble Pathfinder ProXL and ProXR Global Positioning System (GPS) receivers to spatially reference lynx trails and behavioral attributes. The GPS connected line segments along trails at 2-second intervals, collecting locations every 3.0 ± 2.3 m. We paused the GPS between paces if snow travel was difficult or to record lynx behaviors. We used the datalogger to assign attributes for lynx behaviors associated with trail and point features, including bounding gaits and species chased, which we interpreted as predation attempts that resulted in either kills or unsuccessful attempts. We

differentially corrected data downloaded from the GPS and used ArcGIS 9.2 to analyze the data. We collected scats along lynx trails for genetic profiling and gender determination by the Wildlife Genetics Laboratory in Missoula, Montana, USA, and used the results to determine the minimum number of lynx tracked (McKelvey et al. 2006).

We recorded vegetation type, canopy cover, and understory cover at 200-m intervals along each lynx trail following procedures used by von Kienast (2003). Within a 5-m radius of plot centers, we counted stem densities 1 m above snow level by tree species and categorized them into the following size (dbh, cm) classes: <10, 10-18, 19-28, and >28. We visually estimated lateral and overhead canopy cover using the following cover (%) classes for trees >2.5 m above snow level and for understory vegetation <2.5 m above snow level: <10, 10-39, and 40-100. For data analysis, we developed a Geographic Information System (GIS) coverage of forest-stand boundaries, vegetation types, stem densities, and canopy and understory-cover classes that included 330 habitat polygons averaging 12.1 ± 19.1 ha in size (Koehler et al. 2008). Habitat polygons were generally broad in length and width with few narrow strips of habitat. We classified each polygon as Engelmann spruce and subalpine fir forest, Douglas-fir and ponderosa pine forest, burn, or forest opening. We ground-truthed all polygons with ≥ 1 plot during summer, and we evaluated some classifications using data collected along lynx trails. We did not include stand age as a polygon attribute because age data were not available in all portions of the study area.

We used results from Walker's (2005) concurrent study of snowshoe hare distribution, densities, and habitat-use patterns in the Black Pine Basin to estimate hare density in each polygon. Walker (2005) estimated snowshoe hare abundance from pellet counts in 3.05-m × 5.08-cm plots (Krebs et al. 2001) in 78 polygons and used methods comparable to ours to collect vegetation data. Low hare densities (0.0-0.5 hare/ha) were associated with sapling (<10-cm dbh) densities of 1,039 \pm 210 (SE) stems/ha and medium-sized tree (10-28-cm dbh) densities of 356 \pm 39 stems/ha. Medium hare densities (0.5-1.0 hare/ha) were associated with sapling densities of 1,555 ± 227 stems/ha and medium-sized trees with 526 ± 38 stem/ha. High hare densities (>1.0 hares/ha) were associated with sapling densities of 2,784 ± 381 stems/ha and medium-sized tree densities of 712 \pm 80 stems/ha (Walker 2005).

We estimated sinuosity of lynx trails in each habitat polygon by calculating in ArcGIS 9.2 the ratio of the distance traveled by the lynx to the straight-line distance from the point where the lynx trail entered the polygon to the point where it left the polygon. We considered the trail segment in each polygon as our experimental unit. We used only lynx trails >600 m in our analyses to ensure that each lynx trail transected ≥ 1 polygon, and we excluded trails that contained missing segments due to poor snow-tracking conditions. When we encountered multiple lynx trails traveling along the same route (presumably F accompanied by kittens), we only collected data on the trail that appeared

Table 1. Nonparametric univariate analyses of variance comparing sinuosity values for original lynx trail data and smoothed trail data with habitat variables in each habitat polygon in the Black Pine Basin in northern Washington, USA, from 2002 to 2004.

Variable	N	Segment length (m)		Sinuosity			df		
		\bar{x}	SE	\bar{x}	SE	F-statistic	Model	Error	P-value
Hare density									
High (>1 hares/ha)	291	233.8	18.5	1.99A	0.15				
Medium (0.5-1 hare/ha)	110	229.8	26.8	1.70A	0.11				
Low (<0.5 hares/ha)	306	189.7	14.1	1.46B	0.04				
Original						15.15	2	704	< 0.01
Smoothed ^b						11.26	2	704	< 0.01
Forest type									
Engelmann spruce and	564	216.2	12.4	1.80A	0.09				
subalpine fir ^c									
Douglas-fir and	101	198.0	20.7	1.43A	0.05				
Ponderosa pine ^c									
Forest openings	42	224.3	40.9	1.26B	0.09				
Original						13.04	2	704	< 0.01
Smoothed						12.33	2	704	< 0.01
Canopy cover ^d									
40-100%	113	246.5	30.8	1.89A	0.12				
11-39%	419	231.7	14.3	1.76A	0.10				
0-10%	175	151.0	15.7	1.49B	0.13				
Original						32.62	2	704	< 0.01
Smoothed						28.59	2	704	< 0.01
Understory cover ^e									
40–100%	65	297.5	54.6	1.76AB	0.10				
11-39%	517	216.3	11.9	1.82A	0.09				
0-10%	125	161.5	18.8	1.27B	0.04				
Original						28.25	2	704	< 0.01
Smoothed						25.00	2	704	< 0.01

^a Different letters indicate least significant differences (P < 0.05).

to belong to the mother (i.e., the track that followed the most direct route and lacked indications of play behavior). To investigate potential bias in GPS locations resulting from differences in canopy cover (DeCesare et al. 2005), we analyzed sinuosity values for the original trail data and for smoothed trails using a polynomial approximation with exponential kernel interpolation smoothing algorithm with an 8-m tolerance in ArcGIS 9.2.

We used chi-square goodness-of-fit tests to evaluate whether the observed distribution of kills in areas of high, medium, and low hare-density classes fit the expected distribution (Zar 1996). We determined expected numbers of kills by the percentage of habitat available in each category multiplied by total number of kills. We identified prey species from their tracks or remains of carcasses.

To test the validity of our sinuosity value as an index of lynx hunting behavior, we used 2-sample *t*-tests for unequal variances to compare average measures of sinuosity for trail segments associated with predation attempts to those without predation attempts (Zar 1996). The data had a nonnormal distribution so we used a series of nonparametric univariate analyses of variance (ANOVAs) with least significant difference pairwise comparisons to test for differences in sinuosity among hare density classes, forest types, canopy-cover classes, and understory-cover classes (Zar 1996).

RESULTS

We snow-tracked lynx for 149 km along 51 trails during both winters (19 trails in 2002–2003 and 32 in 2003–2004). Mean distance (\pm SD) of lynx trails was 2,591 \pm 1,495 m during 2002–2003 and 3,138 \pm 1,296 m during 2003–2004. We excluded 17 trails (3 associated with kill sites) from data analyses due to poor tracking conditions or trail lengths \leq 600 m. Of 51 lynx trails 11 represented family groups. Based on 57 scats collected along lynx trails, we tracked \geq 9 individual lynx, 6 males and 3 females (B. T. Maletzke, Washington State University, unpublished data). Some of these individuals may have been kittens, because we located putative tracks of females with kittens during both winters.

We observed remains of prey at 21 locations along lynx trails (17 with snowshoe hares, 3 red squirrels [Tamiasciurus hudsonicus], and 1 unidentified cricetid). Lynx killed all species more frequently in stands where hare densities were high (n = 21, $\chi^2_2 = 7.49$, P = 0.02). Observed kills:expected kills were 13:7.1, 2:2.7, and 6:11.2 in stands with high, medium, and low hare densities, respectively. Lynx killed all species more than expected in Engelmann spruce and subalpine fir forests and less than expected in Douglas-fir and ponderosa pine forests and forest openings (n = 21, $\chi^2_2 = 6.03$, P = 0.05). Ratios of observed:expected kills in these forest types were 17:11.6, 4:7.7, and 0:1.7, respectively.

^b Polynomial approximation with exponential kernel interpolation smoothing algorithm using 8-m tolerance F-statistic and P-value.

^c Dominant overstory species.

^d Visually estimated lateral and overstory canopy cover >2.5 m above snow level.

^e Visually estimated lateral cover <2.5 m above snow level.

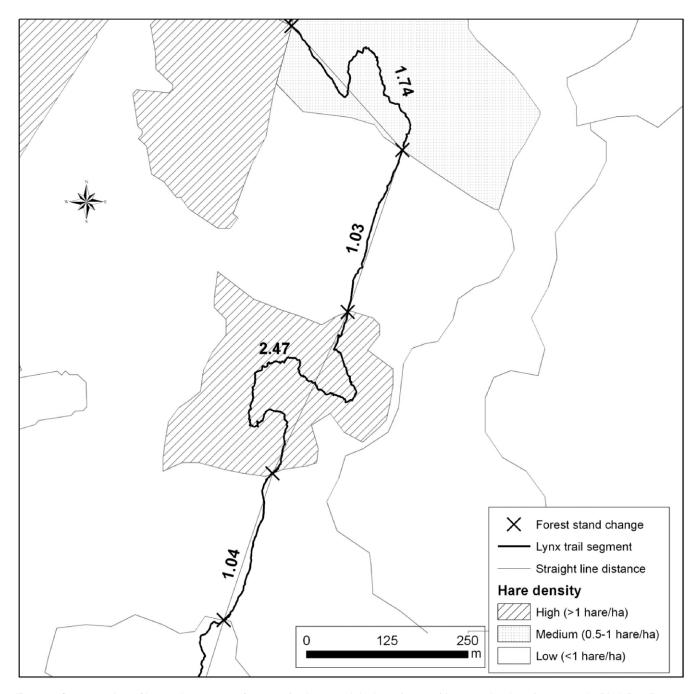


Figure 1. Sinuosity values of lynx trail segments in forest stand polygons with high, medium, and low snowshoe hare densities in the Black Pine Basin in northern Washington, USA, during winter from 2002 to 2004.

Sinuosity values were greater for trail segments containing predation attempts (2.65 \pm 0.38, n = 59, $t_{61.4}$ = -2.63, P = 0.01) than for those without predation attempts (1.63 \pm 0.07, n = 648). Sinuosity values for lynx trails were different (P < 0.01) among hare density classes, vegetation types, overstory canopy cover, and understory-cover classes (Table 1). Sinuosity values were greater in stands with high hare densities (S = 1.99) than in stands with low hare densities (S = 1.46; Fig. 1). Lynx trails associated with Engelmann spruce and subalpine fir forests had a higher sinuosity (S = 1.80) than did forest openings (S = 1.26). We found trail sinuosity for overstory canopy cover 11-39% (S = 1.76) and 40-100% (S = 1.89) was higher (P < 0.01) than in cover 0-

10% (S = 1.49). Understory cover of 11–39% had higher sinuosity (S = 1.82) than stands with <10% cover (S = 1.27; P = 0.01). The effect of canopy cover on GPS location error did not affect results of the univariate ANOVAs (Table 1; DeCesare et al. 2005).

DISCUSSION

Our results demonstrated that the sinuosity value provided a useful index to lynx hunting behavior in the Black Pine Basin. We followed lynx trails collecting locations, on average, every 3 m; at this scale, the landscape patch size and configuration provided ample opportunity for lynx to move unrestricted and the sinuosity value to be unbiased.

Snowshoe hare densities were generally higher where understory cover was greater (Hodges 2000, Walker 2005). We found an understory cover of 11-39% had a higher sinuosity value than 40-100% or 0-10% understory, perhaps due to the ability of lynx to effectively locate, chase, and kill prey in these habitat types. Fuller et al. (2007) found lynx selected stands that provided intermediate to high hare densities and intermediate cover for hares, but lynx exhibited lower selection for stand types with highest hare densities where coniferous saplings exceeded 14,000 stems/ha. In the southwestern Yukon, lynx pursued hares more frequently in habitats with an open spruce (Picea spp.) overstory and a dense understory, where hare numbers were presumably high (Murray et al. 1995). Lynx selected for habitats where hares were most abundant (Squires and Ruggiero 2007). Mowat and Slough (2003) found that understory stem density, hare density, and lynx habitat use were positively correlated, whereas overstory canopy cover was not necessarily related to use by lynx. It is likely that overstory canopy cover did not influence lynx hunting behavior much in our study because regeneration stands (open canopy) and mature multistoried stands (closed canopy) had similar understory structures, and each provided sufficient cover to support high densities of hares.

Habitat conditions selected by lynx in the Black Pine Basin included Engelmann spruce and subalpine fir forests, slopes <30°, elevations ranging from 1,525 m to 1,828 m, and moderate (11–39%) canopy cover (Koehler et al. 2008). These habitat conditions were used more frequently for hunting and had higher trail sinuosity values than the vegetation types lynx used less than expected. Our findings regarding the influence of habitat conditions and hare densities on lynx hunting behavior at the stand scale provide an important behavioral link to the results of habitat-selection studies conducted at the landscape scale (Koehler et al. 2008).

MANAGEMENT IMPLICATIONS

Selection of suitable habitat conditions favors successful reproduction and survival (Bolen and Robinson 1999). To maximize the habitat value of forest stands as foraging habitat for lynx, we encourage forest managers to maintain or create sufficient understory cover to support high densities of snowshoe hares, which can be accomplished in a variety of ways, including deferring or avoiding precommercial thinning, precommercial thinning with reserves (Griffen and Mills 2007), curtailing brush and other understory removal, and planting regeneration stock at high densities. Our focus was on habitat conditions lynx selected for hunting; however, such conditions may not provide habitat requirements for other important needs such as denning or resting areas.

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