

# Winter Habitat Selection by Canada Lynx in Maine: Prey Abundance or Accessibility?

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**ABSTRACT** We related winter habitat selection by Canada lynx (*Lynx canadensis*), relative abundance of snowshoe hares (*Lepus americanus*), and understory stem densities to evaluate whether lynx select stands with the greatest snowshoe hare densities or the greatest prey accessibility. Lynx (3 F, 3 M) selected tall (4.4–7.3 m) regenerating clear-cuts (11–26 yr postharvest) and established partially harvested stands (11–21 yr postharvest) and selected against short (3.4–4.3 m) regenerating clear-cuts, recent partially harvested stands (1–10 yr), mature second-growth stands (>40 yr), and roads and their edges (30 m on either side of roads). Lynx selected stands that provided intermediate to high hare density and intermediate cover for hares (i.e., prey access) but exhibited lower relative preference for stand types with highest hare densities where coniferous saplings exceeded 14,000 stems/ha. (JOURNAL OF WILDLIFE MANAGEMENT 71(6):1980–1986; 2007)

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The Canada lynx (*Lynx canadensis*) is designated as federally threatened in the contiguous United States (United States Fish and Wildlife Service 2000) and is listed as provincially threatened or endangered in some provinces of eastern Canada (NB and NS, respectively); however, little is known about habitat relationships of lynx in eastern North America (Ruggiero et al. 2000). Buskirk et al. (2000) suggest that results of the few habitat studies conducted in other portions of the lynx range, primarily in the western United States and Canada (but see Parker et al. 1983; Hoving et al. 2004, 2005), have been incorrectly extrapolated to areas with potentially unique ecologies, including differences in climate, prey abundance, predator–prey communities, tree species composition, and rates of forest succession. Because of these potential differences, region-specific data are needed to help elucidate habitat selection patterns of lynx in eastern North America.

The primary prey of lynx is snowshoe hare (*Lepus americanus*; Koehler 1990, O'Donoghue et al. 2001), and stand types that receive the strongest habitat selection by lynx are closely associated with density of hares (Parker et al. 1983, Koehler 1990, O'Donoghue et al. 1998, Mowat et al. 2000). However, habitat choices by lynx may be affected by factors other than high densities of snowshoe hares (Ruggiero et al. 2000), such as visibility and mobility needed to successfully capture hares (Parker et al. 1983, Murray et al. 1995, Mowat et al. 2000). Snowshoe hares are associated with stands that have dense understories (Keith et al. 1984, Litvaitis et al. 1985) that provide hares cover from predation (Sievert and Keith 1985), thermal protection, and a source of browse (Litvaitis et al. 1985). Despite the apparent link between understory cover and hare density, it is unknown how the structure of vegetation affects the vulnerability of hares to be captured by lynx (Aubry et al. 2000, Ruggiero et al. 2000). Habitat quality and foraging

success by lynx is likely determined by the interaction of prey accessibility and prey density (Parker et al. 1983, Murray et al. 1995). Thus, we related stand-scale habitat selection by lynx, relative hare abundance, and understory stem densities to evaluate whether lynx select stands with the greatest snowshoe hare densities or the greatest prey accessibility.

Lynx often forage in stands with the highest density of snowshoe hares (O'Donoghue et al. 1998, Aubry et al. 2000, Mowat et al. 2000, O'Donoghue et al. 2001). There was a strong relationship between hare density and stem cover units ( $3 \times$  coniferous saplings + deciduous saplings) in northern, eastern, and western Maine, USA, suggesting that conifer saplings were the most important determinant of hare density (Litvaitis et al. 1985, Fuller 2006) and that differences in density of conifer saplings may be a primary contributor to lower hare densities in mature stands and partial harvests relative to regenerating conifer clear-cuts in eastern forests (Robinson 2006). Similar to snowshoe hares (Hodges 2000), lynx are also influenced by vegetation structure when selecting habitat; the most preferred vegetation types in the Yukon Territory, Canada, had high understory stem densities (Mowat and Slough 2003), which presumably supported high densities of snowshoe hares.

Hares use crypsis and escape through dense cover to avoid predators; therefore, dense understories provide hares with visual obstruction from predation (Litvaitis et al. 1985, Wirsing et al. 2002). Visual obstruction is particularly important for snowshoe hares to avoid predation because lynx are visual foragers that hunt by stalking or ambushing (Murray et al. 1995, O'Donoghue et al. 1998). Hunting success by lynx in Nova Scotia was related more to cover that provided close encounters with hares than with density of hares (Parker et al. 1983). Similarly, lynx in the Yukon were most successful in capturing prey in stands with low stem density and high visibility (Murray et al. 1995). Mowat et al. (2000) support these findings and suggest that some stands are too dense for lynx to be successful in capturing hares.

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**Table 1.** Stand-type classification used in Canada lynx habitat selection analyses, northern Maine, USA, 2002–2003.

Stand type	Code	Description	% of study area <sup>a</sup>	$\bar{x}$ stand area (ha)
Mature forest	Mature	Mature, >40 yr postharvest, 62% coniferous, 27% deciduous, and 11% mixed coniferous–deciduous forest, dense to closed canopy (>50%), dominant trees >12-m ht, regenerating understory	8	9.0
Recent partial harvest	RecentPH	1–10 yr postharvest, 74% deciduous, 18% mixed coniferous–deciduous, 8% coniferous overstory; composed of 62% selection harvesting, 26% overstory removal, 12% shelterwood	8	17.6
Established partial harvest	EstablishedPH	11–21 yr postharvest, 56% deciduous, 36% mixed coniferous–deciduous, and 8% coniferous overstory; composed of 89% selection harvesting, 11% overstory removal, <1% shelterwood	6	10.2
Short regenerating clear-cut	RegenShort	3.4–4.3 m tall, 11–26 yr postharvest, 71% coniferous, 29% mixed coniferous–deciduous, and <1% deciduous regeneration	20	14.5
Tall regenerating clear-cut	RegenTall	4.4–7.3 m tall, 11–26 yr postharvest, 58% mixed coniferous–deciduous, 22% deciduous, and 20% coniferous regeneration	25	13.0
Road and road edge	RoadEdge	30-m buffer on both sides of roads (unpaved and unplowed logging roads with no vehicle access during winter)	11	

<sup>a</sup> The remaining 22% of the study area was composed of water, precommercially thinned stands, early successional (<10 yr) clear-cuts, older regenerating clear-cuts (>7.3 m tall), and non-forested areas.

Despite the apparent protection provided to hares in stands with high woody stem densities, there is little empirical insight into how vegetation structure affects the vulnerability and accessibility of hares and, likewise, the mobility and visibility to hares by lynx (Aubry et al. 2000, Ruggiero et al. 2000).

The only population of Canada lynx east of Minnesota in the contiguous United States occurs in Maine. Contrary to lynx habitat in the western United States, which occurs primarily on federal lands, the lynx range in Maine (Hoving et al. 2005) comprises primarily privately owned forestlands where fiber extraction is the principal economic incentive for ownership. Little is known about lynx use of human-altered habitats in the southeastern portion of its range; thus, one of our goals was to increase understanding of the relationships between lynx habitat selection, foraging success, and dominant silvicultural treatments in the region, which will be essential to future habitat conservation and recovery of lynx. Our second goal was to increase understanding of the mechanisms that determine habitat quality for lynx by relating habitat selection by lynx to differences in understory structure among stand types and to relative snowshoe hare abundance.

## STUDY AREA

Our study area included parts of 9 townships in northwestern Maine (T 10, R 10–11 west of the easterly line of the state [WELS]; T 11, R 10–13 WELS; T 12, R 11–13 WELS) with elevations 244–536 m. Intensive management for pulpwood and saw timber resulted in 81% of our study area receiving a harvest treatment within the past 26 years.

Stand types (Table 1) included mature forests (Mature), which had stumps indicating a history of high-grading for large spruce (*Picea* spp.) and white pines (*Pinus strobus*) since the 19th century. There were essentially no old-growth forest stands occurring on our study area; however, Mature stands were characterized by dominant trees >12 m in height that were typically >60 years of age and had not been

substantially altered from harvesting during the 40 years prior to our study. Other stand types included short regenerating clear-cuts (RegenShort), tall regenerating clear-cuts (RegenTall), recent partially harvested stands (RecentPH), and established partially harvested stands (EstablishedPH). We also included road edge (RoadEdge; 30-m buffer on both sides of roads), defined as a transition zone between adjacent habitats where vegetation structure is affected (Murcia 1995). Previous studies have quantified that edge effects persist  $\leq 50$  m from openings into the forest for vertebrates and plants (Paton 1994, Murcia 1995) and 25–35 m for amphibians in Maine (DeMaynadier and Hunter 1998). Thus, we were conservative and set a 30-m buffer surrounding each side of roads to account for an edge effect.

Dominant species in mature deciduous stands included red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), paper birch (*Betula papyrifera*), and yellow birch (*B. alleghaniensis*). Mature coniferous forests were composed of balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), and white pine. Forests regenerating from clear-cutting were primarily composed of balsam fir, red spruce, red maple, paper birch, and raspberries (*Rubus* sp.).

## METHODS

We located radiocollared lynx, intersected their tracks, and backtracked them on snow. We spatially verified all prey kills and resting beds (defined as an area where a lynx bedded long enough for an ice crust to form; Parker 1981, O'Donoghue et al. 2001) that we encountered on the lynx track. We chose 3 adult male and 3 adult female lynx with kittens from a sample of 17 lynx. We chose the lynx based on their proximity, with the constraint that females produced kittens the previous spring. We followed 2 females and 1 male in 2002 and 1 female and 2 males in 2003. All tracking occurred <48 hours, usually (88%) <24 hours, after snowfall.

**Table 2.** An index of snowshoe hare abundance and mean values for 9 structural variables measured on random transects within 6 Canada lynx home ranges across 6 stand types, winters 2002–2003, in northern Maine, USA.

Variable	Stand type <sup>a</sup>											
	RegenShort		RegenTall		RecentPH		EstablishedPH		Mature		RoadEdge	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Hare abundance <sup>b</sup>	5.0	1.2	5.1	1.3	3.7	1.4	4.4	1.5	2.4	1.0	0.6	0.3
Canopy closure (%)	33	3.0	59	3.0	41	3.0	57	6.0	65	5.0	9.7	2.5
Coniferous basal area (m <sup>2</sup> /ha)	7.3	1.0	10.3	1.3	3.7	0.7	9.0	2.4	18.5	3.4	0.7	0.3
Deciduous basal area (m <sup>2</sup> /ha)	1.6	0.5	7.3	1.0	10.8	1.2	12.1	2.0	9.3	1.9	2.4	0.7
Snag basal area (m <sup>2</sup> /ha)	1.4	0.3	1.6	0.2	2.6	0.5	2.0	0.7	3.5	0.5	0.5	0.2
Live-tree basal area (m <sup>2</sup> /ha)	8.9	1.1	17.6	1.4	14.5	1.1	21.0	2.5	27.9	2.6	3.1	0.8
SCU <sup>c</sup>	52,249	5,623	48,054	3,528	33,253	3,665	39,674	7,487	44,984	7,522	25,383	5,236
Coniferous saplings <sup>d</sup>	14,304	2,003	10,923	1,277	4,476	1,451	7,676	2,311	11,084	2,484	1,569	537
Deciduous saplings <sup>e</sup>	9,335	1,249	15,283	1,468	19,825	2,386	16,646	2,474	11,733	2,059	20,675	4,781
Dead saplings <sup>f</sup>	1,613	300	4,324	586	1,799	238	4,237	777	3,783	631	806	307

<sup>a</sup> Stand type: RegenShort = regenerating (11–26 yr postharvest) short (3.4–4.3 m tall) clear-cut, RegenTall = tall (4.4–7.3 m) regenerating (11–26 yr postharvest) clear-cut, RecentPH = recent (1–10 yr postharvest) partial harvest, EstablishedPH = established (11–21 yr postharvest) partial harvest, Mature = >40 yr postharvest stands with a regenerating understory, RoadEdge = 30-m buffer on both sides of roads.

<sup>b</sup> Hare abundance = index of relative abundance of snowshoe hares based on the no. of snowshoe hare intersections encountered per 100 m of random transects within lynx home ranges.

<sup>c</sup> SCU = density (no./ha) of stem cover units (3 × coniferous saplings + deciduous saplings; Litvaitis et al. 1985) <7.6 cm, protruding from snowpack.

<sup>d</sup> Coniferous saplings = density (no./ha) of coniferous saplings <7.6 cm, protruding from snow pack.

<sup>e</sup> Deciduous saplings = density (no./ha) of deciduous saplings <7.6 cm, protruding from snow pack.

<sup>f</sup> Dead saplings = density (no./ha) of dead saplings <7.6 cm, protruding from snow pack.

We indexed relative hare abundance by recording all snowshoe hare intersections on random transects that we surveyed within lynx home ranges and calculated an index of hare abundance in each stand type as the number of intersections of hare tracks per 100 m of transect. We adjusted the index for the number of 12-hour periods since last snowfall, and we did not include data >96 hours after snowfall. We were unable to calibrate our hare-track index with a mark–recapture study; therefore, the index has an unknown relationship to actual hare densities but provides a relative rank in abundance among habitat types.

We used forest-type coverages to define areas used and available to lynx based on stereoscopic interpretation of 1:15,840 color infrared aerial photographs we obtained from landowners. We incorporated overstory types and snow-track data from lynx into a Geographic Information System. Habitat types we used in the analyses included RegenShort and RegenTall clear-cuts, RecentPH, EstablishedPH, Mature stands, and RoadEdge (Table 1). Partial harvesting is defined as a timber harvest operation >2.02 ha that results in a residual stand of trees ≥11.4 cm diameter at breast height with a residual basal area >6.9 m<sup>2</sup>/ha (Maine Forest Service 1990), and includes shelterwood, selection harvests, and overstory removal. Clear-cutting is defined by an overstory removal resulting in a residual basal area <6.9 m<sup>2</sup>/ha (Maine Forest Service 1990). We included regenerating clear-cuts of 2 different height classes (3.4–4.3 m and 4.4–7.3 m); the short and tall regenerating clear-cuts were the same age but differed in maturity as indexed by tree height, likely because of differences in site quality. Differences in site quality also likely affected stand composition; short regenerating stands were composed largely of coniferous regeneration and tall regenerating stands were composed primarily of mixed coniferous–deciduous regen-

eration (Table 1). The Mature stands had a past history of forest harvesting (selective removal of large saw timber since the 19th century) and had a regenerating understory with dense overhead canopy (Table 2). The RecentPH had very low densities of understory saplings; in contrast, density of saplings was greater in the older EstablishedPH (Table 2). Road edges were characterized by the lowest values of canopy closure, basal area, and density of coniferous and dead saplings relative to all other stand types but also had the greatest density of deciduous saplings (Table 2). We omitted land cover categories from statistical analyses if they were considered non-habitat for lynx (water and non-forest) or if there was not enough of the type (<5% within home ranges) to statistically evaluate habitat selection (i.e., precommercially thinned stands, early successional clear-cuts, older clear-cuts).

We captured lynx using foothold traps (Victor no. 3 soft catch traps; Woodstream Corp., Litiz, PA) or cage traps (model 50590; Safeguard Products, Inc., New Holland, PA) and fitted them with radiocollars (SMRC-1; Lotek Wireless, Inc., Newmarket, ON, Canada). We immobilized lynx with a 5:1 mixture of ketamine hydrochloride (100 mg/ml) and xylazine hydrochloride (100 mg/ml) administered intramuscularly with a syringe pole or dart gun. We determined the locations of lynx approximately every 3–4 days from fixed-wing aircraft and recorded the locations of lynx with a Global Positioning System. We estimated error associated with aerial telemetry at 44.3 m (SE = 5.5 m) based on the mean difference between actual and estimated locations for 22 transmitters. We calculated yearly (1 Nov–31 Oct) 90% fixed-kernel home ranges (Worton 1989) of adult lynx using the Animal Movements Extension (Hooge and Eichenlaub 2000) for ArcView. We did not obtain a sufficient number of relocations to calculate seasonal ranges;

however, home ranges have been documented to be larger during winter than during summer (Bailey et al. 1986, Squires and Laurion 2000). Thus, our estimates of annual home range included both seasons and likely incorporated winter availability. Field observations suggested that lynx did not exhibit seasonal shifts in home ranges (i.e., 97% of lynx foraging paths on snow occurred within the annual home-range areas based on prior radiolocations). We evaluated stand-scale habitat selection (third-order selection; sensu Johnson 1980) for overstory types within home ranges using individual lynx as the sampling unit. We calculated selection indices as  $[\ln(\text{use}/\text{availability})]$ ; Aebischer et al. 1993], where use was defined as the proportional distance traveled by an individual lynx in each stand type and availability was defined as the total percentage of that stand type within the home range; it is centered on zero (i.e., use in proportion to availability). Based on the small sample size ( $n = 3$  of each sex), we were unable to statistically evaluate whether there was a difference in habitat selection between males and females, so we pooled data across sexes. Mowat and Slough (2003) and Poole et al. (1996) reported that habitat selection did not differ between sexes in the Yukon ( $n = 45$  F, 58 M) and Northwest Territories, Canada ( $n = 12$  F, 15 M), respectively.

Sample size of animals was limited by logistical constraints and the number of days with fresh snow; therefore, we did not test statistical hypotheses or conduct multiple statistical comparisons using selection ratios because of limitations in our statistical power. Alternatively, we inferred differences in habitat selection across stand types by examination of nonoverlapping standard errors around the mean selection indices (Gosselink et al. 2003), and we used them to infer differences in relative preference by lynx among our 6 stand types.

To help explain the habitat selection results by lynx, we measured habitat characteristics using a stratified random design on transects that we placed within verified home ranges of our 6 lynx. We randomly chose the starting point and direction of each 1-km-long transect, with the constraints that the transect was completely inside the home range and that all stand types were proportionally sampled relative to the composition of stand types within home ranges. We measured vegetation in  $6 \times 2$ -m plots spaced every 100 m. We sampled 514 vegetation plots and we averaged the values across plots within each stand: 125 plots occurred in RegenShort, representing 36 stands; 155 plots in RegenTall, representing 52 stands; 95 plots in RecentPH, representing 24 stands; 52 plots in EstablishedPH, representing 15 stands; 44 plots within 23 Mature stands; and 43 plots in RoadEdge, representing 30 stands. We measured canopy closure at the center of the plot with a spherical densiometer and averaged readings from the 4 cardinal compass directions. We calculated basal area of live coniferous and deciduous trees ( $\text{m}^2/\text{ha}$ ) with a 2-factor wedge prism and counted deciduous, coniferous, and dead saplings ( $<7.6$  cm diam, stems protruding through snowpack) within the 12- $\text{m}^2$  plots.

We used a multivariate Hotelling's  $T^2$  to test for differences in structural variables between stand types that represented different successional stages and whether selected for or against by lynx. Specifically, we compared RegenShort versus RegenTall clear-cuts, RecentPH versus EstablishedPH stands, and EstablishedPH versus Mature stands to determine which structural variables differed as stands matured. We assessed normality of each variable with a Lilliefors test and homogeneity of error variances with Levene's test. We transformed non-normal variables or those exhibiting heteroscedasticity to meet parametric assumptions. If the Hotelling's  $T^2$  test suggested differences in habitat variables between stand types, we used univariate  $F$ -tests with a Bonferroni-adjusted critical value of  $\alpha/k$  to determine which habitat variables differed significantly between stand types.

## RESULTS

We snow-tracked radiocollared adult lynx during January–March 2002 and 2003 for 65.5 km (median = 10.77 km/lynx, range = 9.64–12.34), representing 74 individual snow-tracking days (median = 12 snow-tracks/lynx, range = 11–14). All adult females were accompanied by kittens (1, 2, and 3 kittens) that remained with them during the January–March period when snow-tracking occurred. We recorded 592 radiolocations and used them to calculate home ranges for the 6 lynx ( $\bar{x} = 99$  radiolocations/lynx, range = 85–113). One lynx had 1% EstablishedPH stands within the home range and no use, so we did not use the selection index for that lynx when evaluating selection of that stand type. Home ranges of the 6 lynx comprised an average of 19% RegenShort, 24% RegenTall, 10% Mature, 10% RecentPH ( $n = 5$  lynx), 6% EstablishedPH stands, 11% RoadEdge, and 20% other (i.e., water, unforested areas; land cover types that we did not analyze).

Stand-scale habitat selection by lynx was strongest for RegenTall and EstablishedPH stands (Fig. 1). Lynx selected against RegenShort, RoadEdge, RecentPH, and Mature stands (Fig. 1). Despite small sample sizes of lynx ( $n = 5$ –6) analyzed for each of the 6 stand types, none of the standard errors associated with mean selection indices overlapped zero. Thus, power was adequate given the strong selection patterns exhibited by lynx.

We observed 16 snowshoe hare kills; lynx killed 81% (13 of 16) of the hares in regenerating clear-cuts (RegenShort:  $n = 5$ ; RegenTall:  $n = 8$ ). We observed the remaining kills in a recent (6 yr old) PH ( $n = 1$ ), in an established (12 yr old) PH stand ( $n = 1$ ), and in an early successional ( $<3.4$  m tall) clear-cut ( $n = 1$ ). Conifer sapling density averaged 7,833/ha at kill sites in RegenShort and was 6,111/ha at kill sites in RegenTall compared to a mean of 14,304/ha and 10,923/ha, respectively, on random transects within home ranges (Table 2).

We observed most resting beds in RegenTall ( $n = 11$ ) and fewer beds in RegenShort ( $n = 6$ ), EstablishedPH ( $n = 3$ ), Mature ( $n = 3$ ), RoadEdge ( $n = 2$ ), and RecentPH stands ( $n = 1$ ).

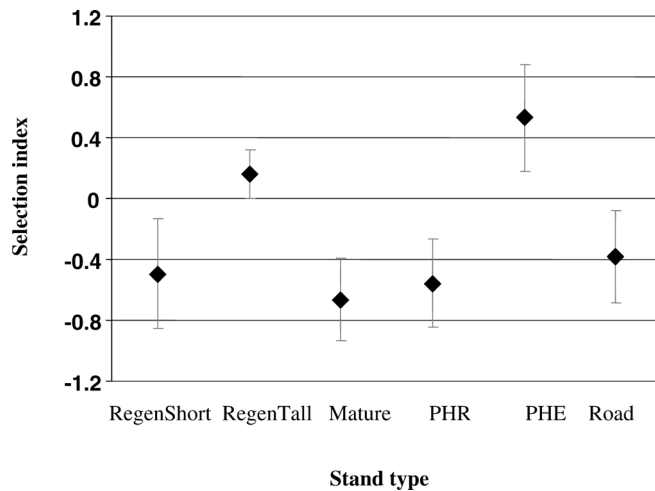
The prey encounter rate (Table 2) was greatest in RegenTall clear-cuts (7,187 m surveyed in 23 stands), RegenShort clear-cuts, (6,406 m surveyed in 17 stands), and in EstablishedPH stands (1,850 m surveyed in 8 stands). We observed relatively lower rates of hare encounters (Table 2) in RecentPH (5,657 m surveyed in 16 stands), Mature stands (1,936 m surveyed in 12 stands), and in RoadEdge (2,758 m surveyed in 36 stands).

At least one of the structural variables differed between RegenShort and RegenTall clear-cuts (Wilks'  $\lambda = 0.62$ ,  $F_{5,82} = 10.03$ ,  $P \leq 0.001$ ). Post hoc univariate  $F$ -tests indicated that canopy closure ( $P \leq 0.001$ ), density of deciduous saplings ( $P \leq 0.001$ ), and density of dead saplings ( $P \leq 0.001$ ) were greater (Bonferroni-adjusted  $\alpha = 0.02$ ) in RegenTall than in RegenShort clear-cuts (Table 2). Structural variables also differed (Wilks'  $\lambda = 0.68$ ,  $F_{5,33} = 3.14$ ,  $P = 0.02$ ) between RecentPH and EstablishedPH stands. EstablishedPH stands had greater (Bonferroni-adjusted  $\alpha = 0.02$ ) live-tree basal area ( $P = 0.01$ ), density of dead saplings ( $P \leq 0.001$ ), and canopy closure ( $P = 0.02$ ) than RecentPH stands (Table 2). There were no significant differences (Wilks'  $\lambda = 0.88$ ,  $F_{5,32} = 0.89$ ,  $P = 0.50$ ) in structural variables between EstablishedPH stands and Mature stands (Table 2).

## DISCUSSION

Lynx selected RegenTall and EstablishedPH stands that had high to intermediate encounter rates of hares, intermediate canopy closure (57–59%), live-tree basal area (18–21 m<sup>2</sup>/ha), and stem cover units (40,000–48,000/ha) relative to the other 4 (RegenShort, RecentPH, Mature, RoadEdge) stand types. These stand types maintained a moderate level of protection provided by overhead canopy closure and basal area of live trees, as well as intermediate understory density and easier access to hares. Lynx avoided stands where encounter rates of hares were <3.7 track intersections/100 m, with densities of conifer saplings <5,000 stems/ha, dead saplings <4,000/ha, or stands with canopy closure >60%. Lynx also avoided stands (RegenShort) with relatively high (5.0 intersections/100 m) hare encounter rates where coniferous saplings exceed 14,000 stems/ha, which presumably created less favorable conditions for hunting or capturing hares. Lynx were not always associated with stands with the highest hare encounter rates, which suggests the importance of an interaction between prey density and prey access in determining lynx foraging success and habitat selection.

Consistent with research that concluded that lynx are typically associated with less dense stands than hares (O'Donoghue et al. 1998), greater densities of dead saplings and lower densities of conifer saplings in RegenTall (positive selection by lynx) versus RegenShort (negative selection by lynx) indicate that the taller regenerating clear-cuts were undergoing self-thinning, which likely increased the visibility and vulnerability of hares to lynx. Lower than optimal cover for hares may be more important than hare abundance in determining hunting success because lynx



**Figure 1.** Mean ( $\pm$  SE) selection indices [ $\ln(\text{use}/\text{availability})$ ] for 6 stand types used to evaluate stand-scale habitat selection by Canada lynx in northern Maine, USA, winters 2002–2003. RegenShort = short (3.4–4.3 m tall) regenerating (11–26 yr postharvest) clear-cut; RegenTall = tall (4.4–7.3 m) regenerating clear-cut; Mature = >40-yr-old stands with a regenerating understory; PHR = recent partial harvest, 1–10 yr postharvest; PHE = established partial harvest, 11–21 yr postharvest; Road = 30-m buffer on both sides of roads.

require a close approach to their prey (Parker et al. 1983). Correspondingly, conifer sapling density was 44–45% lower at kill sites within RegenTall and RegenShort stands, respectively, compared to mean values we observed within those stand types. We also observed the greatest number of resting beds in RegenTall stands, suggesting that lynx were selecting the same stand types for both resting and foraging. Consistent with previous research (e.g., Parker et al. 1983, O'Donoghue et al. 1998), where densities of hares are high (RegenShort and RegenTall) it may be more energetically efficient for lynx to hunt in stands that afford greater relative visibility to hares (e.g., RegenTall) and greater mobility (i.e., lower conifer sapling densities) for lynx. Further, a companion study documented higher fractal dimension of foraging paths in RegenTall stands over RegenShort stands (Fuller 2006), which suggests that lynx increased their foraging activity in stands that had lower relative densities of conifer saplings.

EstablishedPH stands were selected positively by lynx and also provided lynx the opportunity to hunt and rest in areas with intermediate hare encounter rates and conifer sapling density; companion studies suggested that EstablishedPH stands commonly support hare densities >0.8 hares/ha (Robinson 2006). In contrast, RecentPH stands were selected against by lynx during winter, likely because of their low relative abundance of snowshoe hares as indicated by the second-lowest ranking in prey encounters and low relative abundances as indicated via pellet densities (Fuller and Harrison 2005). Additionally, modeling work reported that RecentPH stands were negatively associated with the landscape-scale presence of lynx (Hoving et al. 2004) and snowshoe hares (Hoving 2001) in Maine. Thus, we infer that the reduced density of understory stems in RecentPH stands creates easy access and mobility for lynx, but low

densities of hares in these stands suggest that they may be unsuitable for foraging. Further, the greater density of dead stems in EstablishedPH stands relative to RecentPH suggests that lynx select for dense regenerating stands after they enter the stage of self-thinning.

Our conclusions are derived from third-order (sensu Johnson 1980) habitat selection by 6 lynx whose home ranges were composed largely of 11-year-old to 26-year-old regenerating clear-cuts ( $\bar{x} = 43\%$ ). Lynx may be exhibiting strong second-order selection for home ranges dominated by regenerating clear-cuts where hare densities are  $>1.5$  hares/ha (Robinson 2006, Homyack et al. 2007); therefore, use of EstablishedPH within those home ranges may be dependent on higher-order habitat choices. Despite the positive selection of EstablishedPH by lynx at the stand scale, only 6% of our study area was composed of this type, only 6% composed lynx home ranges, and only 11% of foraging paths occurred in this type. Thus, we urge caution when inferring the suitability of EstablishedPH for supporting lynx across substantial portions of their home ranges.

Following clear-cutting or partial harvesting, there appears to be a period of approximately 10 years when understory conditions are suboptimal for hares. After densities of conifer saplings increase to  $>7,000$  stems/ha in harvested stands, hares increase substantially (Robinson 2006); however, selection of regenerating stands by lynx represents a trade-off between density of hares and optimal understory conditions for prey cover and escapement from predators.

Mature stands had low relative abundance of hares in our study and elsewhere in north-central Maine (Fuller and Harrison 2005) and were selected negatively by lynx. Mature forests are often used by lynx but rarely receive positive selection (Mowat et al. 2000); we speculate that those stands studied elsewhere may have had more older-growth characteristics (i.e., tree-fall gaps with advanced regeneration) than occurred in our study area where Mature stands had a history of high-grading for large saw-timber. Consistent with our findings, other studies have generally reported negative selection by lynx for mature forests (Parker et al. 1983, Mowat and Slough 2003).

We documented lynx traveling on roads (unplowed during winter), but roads and their associated edges were selected against within home ranges. Contrary to our study, lynx followed road edges in Nova Scotia for "considerable" distances (Parker 1981:229) and there was no relationship between habitat selection by lynx and roads in Washington, USA (McKelvey et al. 2000). The roads on our study area were snow covered during winter and recreational snowmobiling was uncommon; therefore, disturbance by vehicles was probably not a factor in the negative selection for roads. Lynx may have exhibited negative selection for road edges because of increased potential for interactions with generalist competitors such as coyotes (*Canis latrans*; Aubry et al. 2000) or, more likely, because the removal of large trees and light penetration following road construction were associated with the lowest density of conifer saplings and the lowest index of hare abundance relative to all other stand

types. Negative selection for habitat conditions associated with road edges has important implications for forestry operations where road building is required for access; road edges composed 11% of the total land and water surface on our study area.

## MANAGEMENT IMPLICATIONS

In intensively managed forests, habitat for lynx is provided by areas with few overstory trees dominated by a mixture of conifer and deciduous saplings that are in the stage of stem exclusion and self-thinning. We recommend maintaining conifer sapling density of 7,000–11,000 stems/ha and canopy closure  $<60\%$  within stands where use by hares and lynx is a priority. In the forests of northern Maine, these stand conditions typically occur 10–35 years following partial or complete overstory removal; however, site quality may be an interacting factor influencing the onset and maturation of hare habitat, the process of self-thinning, and lynx selection of stands with densities  $>1$  hare/ha. Forest harvesting has the potential to create favorable conditions for hares and lynx, but the landscape-scale effects of partial harvesting and extensive road edges require additional study.

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