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# Fine-scale disturbances shape space-use patterns of a boreal forest herbivore

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Natural disturbance is a key determinant of ecosystem structure and function. Disturbances can create novel resource patches and modify habitat structure, thereby inducing spatial heterogeneity in the trade-off between food acquisition and predator avoidance by prey. We evaluated how canopy gap dynamics in eastern Canadian old-growth boreal forest alter the spatial distribution of food and cover for snowshoe hares (*Lepus americanus*) and how hares responded to these spatial patterns. We 1st compared browse availability within canopy gaps and the surrounding forest. We then examined fine-scale habitat selection, movement patterns, and foraging decisions by hares during winter. Perception of risk within canopy gaps was assessed using foraging experiments. We found that browse availability was 4 times higher within gaps than under forest cover. Although hares acquired most of their browse from gaps, their use of space during winter was influenced by a greater perception of predation risk within gaps. Hares selectively used areas of higher canopy closure suggesting that they restricted their use of gaps to foraging activities. Furthermore, hares biased their movements away from gaps or increased their speed of travel in areas of relatively low cover. Hares consumed experimental browse stems more intensively under forest cover than in canopy gaps, indicating a trade-off between food and safety. When foraging within canopy gaps, hares also were less likely to use both experimental and natural food patches located far away from cover. Our study demonstrates how gap dynamics in old-growth stands can structure the fine-scale spatial organization of a key prey species of the boreal forest by creating spatial heterogeneity in their landscapes of fear and food. Spatial variation in browse use in response to predation risk may in turn influence patterns of sapling growth and survival within canopy gaps. Gap dynamics therefore may be a fundamental process structuring predator–prey interactions in old-growth boreal forests. DOI: 10.1644/09-MAMM-A-289.1.

Key words: foraging, giving-up density, habitat heterogeneity, movement, predation risk, resource selection functions, snowshoe hare, step-selection functions

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Natural disturbances that vary in size, severity, and frequency play a fundamental role in structuring aquatic and terrestrial ecosystems by creating heterogeneity at multiple spatial and temporal scales (Pickett and White 1985; Sousa 1984). Habitat disturbance can affect animal distribution by altering the composition and structure of vegetation that provide food and cover, and many animals benefit from disturbances that create productive conditions associated with areas undergoing regeneration (Sousa 1984). Although infrequent broadscale disturbances such as forest fires and tropical storms can influence patterns of species occurrence at the landscape scale (Fisher and Wilkinson 2005; Willig et al. 2007), frequent microhabitat disturbances such as tree-fall gaps, blowouts, and wave action create fine-scale heterogeneity that also plays an important role in determining species distribution (Bouget and Duelli 2004; Cramer and Willig 2005; Paine and Levin 1981).

Habitat heterogeneity can have a profound influence on trophic interactions. For example, heterogeneity can promote the persistence of predator–prey populations by reducing predator foraging efficiency, by creating spatial refuges for prey, or by creating locally asynchronous population dynamics (Hastings 1977; Holt and Hassell 1993; Huffaker 1958). Recent investigations have shown that the functional response of both herbivores and carnivores to food availability can



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depend on the spatial distribution of these resources (Hobbs et al. 2003; Pitt and Ritchie 2002). Resource heterogeneity therefore can influence the functional link among trophic levels. For herbivores, variation in the spatial arrangement of plants can affect the rate at which they encounter food patches, thereby influencing their rate of energy intake and dietary choice (Fortin et al. 2002; Hobbs et al. 2003). To increase their intake rate in heterogeneous environments herbivores should concentrate on aggregations of food patches to reduce travel time between patches (Nonaka and Holme 2007), but the most profitable food patches often are also the most risky (Brown and Kotler 2004).

Fear of predation is a major force influencing movement and foraging decisions of prey (Lima and Dill 1990), and disturbances that increase food resources also can remove habitat structure that provides protection against predators. Given that predators may be more efficient at detecting and capturing prey in certain habitats (Rohner and Krebs 1996), prey often rely on habitat structure as a cue for risk (Brown and Kotler 2004). For example, they may trade off food for safety by foraging less intensively in open habitats or with increasing distance from protective cover (Hochman and Kotler 2007). During locomotion prey also may attempt to mitigate risk by moving in areas of greater cover (Fortin et al. 2005; Lagos et al. 1995), or by adjusting their speed to quickly traverse areas where they would be more conspicuous to predators (Vasquez et al. 2002). Slight variations in habitat structure can result in relatively large changes in the perception of risk (van der Merwe and Brown 2008). Therefore, microhabitat disturbances should shape prey distribution by continually changing the landscapes of food and fear (Laundré et al. 2001) around which prey species structure their home ranges.

Canopy gap dynamics in old-growth forests provide an interesting system in which to evaluate how fine-scale disturbances influence the distribution of resources, prey, and their interaction in the presence of predation risk. Old-growth boreal forests are characterized by high structural heterogeneity due to fine-scale canopy disturbances such as windthrow, insect outbreaks, disease, and tree senescence (McCarthy 2001). Because canopy closure in mature boreal forest generally limits the availability of food resources for browsing herbivores (Fisher and Wilkinson 2005), the establishment of early successional plants and the release of advanced regeneration within canopy gaps could create resource-rich patches within a matrix of low food availability. Gap disturbances also decrease the cover on which such herbivores rely for protection from predators. Predation risk should influence how far and intensively herbivores are willing to forage within canopy gaps. Foraging and movement behaviors of herbivores can reveal how balancing food acquisition and predator avoidance lead to their spatial distribution in forests structured by gap dynamics.

Our objective was to evaluate how canopy gaps in mature and old-growth boreal forests influenced the fine-scale distribution of snowshoe hares (*Lepus americanus*). Snowshoe hares are a key species of the boreal forest for multiple predators (Boutin et al. 1995). Hares rely mainly on deciduous browse during winter (Pease et al. 1979), and they are known to move and forage in proximity to cover as a response to predation risk (Hodges and Sinclair 2005; Morris 2005). Snowshoe hares should be sensitive to variations in the interspersion of food and cover created by canopy gaps, but little is known about their response to fine-scale disturbances ($<0.1$ ha) that characterize old-growth boreal forest.

We 1st assessed whether browse availability was higher within gaps than under surrounding forest cover, thereby creating a potential conflict between the search for food and cover. We then tested whether heterogeneity in food and cover created by gap dynamics influenced snowshoe hare habitat selection at the stand level, whether the presence of gaps influenced movement decisions, and whether foraging behavior was influenced by a relatively high perception of risk within canopy gaps. Perception of risk was evaluated through giving-up density (GUD) experiments (Brown 1988) and surveys of natural browse use within canopy gaps. GUD experiments are based on optimal foraging theory, which predicts that foragers should leave a food patch when foraging gains no longer exceed the sum of metabolic, missed-opportunity, and predation costs associated with exploiting the patch (Brown 1988). Everything else being equal, prey should allocate greater foraging effort to safe than risky patches, and the density of food left in different patches can reveal their perception of risk (Brown 1988). We used GUD experiments to test the predictions that, if hares trade off food for safety, consumption of experimental food patches should be lower within canopy gaps than under forest cover, foraging effort should decrease with distance from cover (i.e., from the forest edge toward the center of gaps), and the probability of using experimental food patches should decline toward the center of gaps.

## Materials and Methods

*Study area*.—The study was conducted in the boreal forest of the Côte-Nord region (49°50′–51°30′N, 68°30′–69°30′W) of Quebec, Canada. The study area lies in the eastern black spruce–moss bioclimatic region and has forest fire cycles between 270 and >500 years (Bouchard et al. 2008). The region's long fire cycles have led to a forest landscape composed of 70% irregularly structured old-growth stands dominated by black spruce (*Picea mariana*) or mixed stands of balsam fir (*Abies balsamea*) and black spruce (Boucher et al. 2003). Other common tree species include jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), and eastern larch (*Larix laricina*). The regional climate is subhumid and subpolar, with a mean annual temperature of −2.5°C and abundant annual precipitation (1,000–1,300 mm), 35% of which is snow (Robitaille and Saucier 1998).

*Cover and browse availability within canopy gaps and under forest cover*.—We sampled 4 gaps from each of 28 sites

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in spruce and spruce–fir stands during the summer of 2007 to determine whether browse and availability of lateral cover within canopy gaps differed from the surrounding forest. We used fire maps created by Bouchard et al. (2008) to identify stands ranging from 80 years, the age at which canopy gap formation and transition to irregular stand structure begins (Bouchard et al. 2008), to >200 years. Gaps were classified as being either of primarily edaphic origin or originating from mortality of canopy trees. At each site we selected 1 canopy gap in each of 4 size classes (50–100 $m^2$, 100–200 $m^2$, 200–300 $m^2$, and >300 $m^2$) based on gaps typical of eastern boreal forests (Pham et al. 2004). We measured the length and width of each gap to estimate gap area as an ellipse (Runkle 1981). We sampled the 1st gap encountered of each size class along a 300-m transect starting and finishing within the stand. Additional transects were walked if we did not encounter all gap size classes on the 1st transect. If we were unable to find gaps >300 $m^2$ ($n = 5$ sites), we sampled a 2nd gap from either the 100–200 $m^2$ or 200–300 $m^2$ size class to obtain 4 gaps per site.

Near-ground lateral cover is provided mainly by coniferous saplings, and the terminal twigs of deciduous saplings and shrubs constitute the main source of browse for hares during winter (Litvaitis et al. 1985; Pease et al. 1979). To measure cover and browse availability within gaps we counted the number of coniferous saplings (>50 cm in height and <9 cm diameter at breast height) and the number of deciduous twigs (terminal shoots > 5 cm long) between 0 and 2 m above ground level within a 1-m buffer on either side of the long axis of each gap. Each stem was identified to species and classified according to its height: 0.5–1 m, 1–2 m, 2–3 m, or >3 m. We also measured the distance of each sapling (conifer and deciduous) to the gap edge in 1-m intervals. The main deciduous browse species included white birch, willow (*Salix* spp.), speckled alder (*Alnus incana rugosa*), green alder (*Alnus viridis crispa*), serviceberry (*Amelanchier* spp.), and mountain ash (*Sorbus* spp.). We did not count the number of black spruce and balsam fir twigs (these 2 species represented 99% of conifer stems in our gap regeneration surveys), because these species are rarely browsed by hares (Newbury and Simon 2005; St-Laurent et al. 2008).

To compare browse and cover availability within gaps to surrounding forests we extended the gap's transect by 5 m into the forest at either end of the gap ($n = 57$ gaps). In some cases canopy gaps were too frequent to sample 5 m of intact forest adjacent to each gap so we either moved 1 of the 5-m plots to 1 of the ends of the wide axis ($n = 35$ gaps), extended the long axis by 10 m in 1 direction ($n = 15$ gaps), or sampled the next first 10 m of intact forest following the gap along our gap inventory transect ($n = 5$ gaps). We used Wilcoxon signed-rank tests to compare browse and cover availability within gaps and adjacent forests (Lehmann 1998).

*Stand-level habitat selection*.—To evaluate how snowshoe hares respond to heterogeneity in the distribution of browse and cover created by canopy gaps we compared habitat characteristics at points along single winter snowshoe hare trails to randomly located points within 4 conifer stands (>90 years) during March and April of 2007. This information was used to estimate resource selection functions (Boyce et al. 2002; Manly et al. 2002). We focused on winter habitat use because tracks left in the snow permitted a fine-scale assessment of habitat selection. Single winter trails represented tracks left in the snow by the passage of a single hare moving in 1 direction. Fifty random points were generated within each stand using ArcView GIS software (version 3.2; ESRI Inc., Redlands, California). Random points were ≥20 m from each other and from the edge of stand boundaries. To obtain a random sample of snowshoe hare trails we followed a path linking the random points within each stand and sampled snowshoe hare trails that intersected this random trajectory as we encountered them. We sampled points at 20-m intervals along each encountered trail, following the hare's direction of travel, up to a maximum of 5 points per trail. The coordinates of each observed point were recorded with a global positioning system (Garmin, Olathe, Kansas) to make sure that all sampled trails were at least 20 m apart, as for random points. Sampled trail segments were sufficiently long (80 m) to occur both within gaps and under canopy cover. We sampled a total of 125 points from 25 single trails ($n = 7, 7, 5$, and 6 trails within each of the 4 sampled stands, respectively) and 184 random points before access to sites was limited by road closure for the spring thaw.

To quantify habitat structure at observed and random points we measured cover and browse availability within circular plots around each point. Canopy closure was estimated visually in 10% classes at each point and 5 m away in 4 opposite directions, and we used the mean of the 5 readings in subsequent analyses. We estimated lateral visual obstruction at each point in 10% classes by observing a 0.5 × 2-m (width × height) cover board (Nudds 1977) from 5 m away in 4 opposite directions and used the average of the 4 readings in subsequent analyses. To further quantify cover availability we counted the number of conifer stems within a 4-m-radius circle (50-$m^2$ plots), and each stem was classified into 1 of 2 cover classes based on its lateral visual obstruction between 0 and 1 m from the snow surface. Class 1 stems included bare trunks and trunks with dead lateral branches (mainly mature stems and snags), whereas Class 2 stems included trees with live green branches, saplings completely covered with snow, and recently fallen trees with green branches that would completely obstruct vision. Browse availability was measured as the number of deciduous stems within each plot that had twigs available between 0 and 1 m of the snow surface.

Resource selection function models were estimated using mixed-effects logistic regressions, with sites included as a random effect. A set of candidate models was produced based on combinations of canopy closure, lateral visual obstruction, conifer stem density by cover class, and browse availability. Candidate models were compared based on Akaike's information criterion (AIC), differences in AIC (ΔAIC), and Akaike weights ($w_i$s—Burnham and Anderson 2002). Because none of our candidate models had $w_i > 0.90$, we used

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multimodel inference based on average coefficients, and associated unconditional *SE*s and 95% confidence intervals (95% *CI*s—Burnham and Anderson 2002). Multicollinearity was absent from candidate resource selection functions, because variance inflation factors were always <2 (Graham 2003). Evaluation of candidate models with similarly strong empirical support (those with $\Delta AIC \leq 2.0$—Burnham and Anderson 2002) was performed using *k*-fold cross-validation (Boyce et al. 2002). Models were built by randomly selecting 70% of observed locations as a training set and withholding 30% of the data for model evaluation (test set). Random locations were ranked according to resource selection function scores calculated from the models and were binned into 10 approximately equal-sized groups. The number of observed locations from the evaluation set within each bin was tallied, and we calculated a Spearman-rank correlation ($r_s$) between the frequency of test-set observed locations within each bin and bin number to evaluate the predictive success of each model. This process was repeated 100 times for each model, and the averages ($\overline{r_s}$) are reported. Mixed-effects logistic regressions were performed with R 2.6.2 software (R Development Core Team 2006) using the lme4 package (Bates and Sarkar 2006), and *k*-fold cross-validation was run using SAS 9.1 (SAS Institute Inc. 2003).

*Fine-scale movements*.—Snowshoe hares could use 2 movement tactics to minimize risk associated with the reduced protective cover characterizing canopy gaps: they could bias movements away from openings toward greater cover, or increase movement speed to reduce time spent in openings. To assess whether snowshoe hares adjust their movements to fine-scale habitat structure we used step-selection functions (Fortin et al. 2005). A step was defined as a 10-bound segment along single winter snowshoe hare trails based on fresh tracks left in the snow. Predator tracks following the observed trails were absent, meaning that observed movements did not reflect responses to active pursuit by predators. Each observed step was paired with 2 random segments originating from the same point of departure. Lengths and turning angles of random steps were drawn from the distributions of observed steps. An initial sample of observed step lengths and turning angles was necessary before we could start measuring habitat attributes along observed and associated random steps. Each new observed step length and turning angle was added to the pooled distribution from which random steps were drawn. Kolmogorov–Smirnov 2-sample tests (Sokal and Rohlf 1995) confirmed that the distribution of observed and random step lengths and turning angles were similar (step lengths: $P = 0.23$; turning angles: $P = 0.27$), thereby reducing potential risk of bias (Fortin et al. 2005).

Along observed and random steps we made a visual assessment of canopy closure in 10% classes at the start, middle, and end of each step segment. The proportion of the step that occurred within a canopy gap was estimated in 10% classes. Lateral cover was estimated from the number of coniferous tree stems by cover class (Class 1 or 2, as described previously) within 1 m on either side of the step. Browse availability was estimated by counting all deciduous twigs by species located <1 m above the snow surface within 1 m on either side of the step. A total of 105 steps were surveyed along 16 snowshoe hare trails. Observed and associated random steps were compared using conditional logistic regression (Fortin et al. 2005). Pairs of observed and random steps were included as individual strata. To account for nonindependence of multiple steps along a given trail, series of successive steps were included as individual clusters in the model, and robust variance was calculated on the basis of independent clusters (Fortin et al. 2005). We used model comparison based on the quasi-likelihood under independence criterion (QIC—Craiu et al. 2008) to compare candidate models with different combinations of canopy closure, conifer stem density, and browse availability. Model averaging was then used to calculate parameter estimates, unconditional *SE*s, and 90% and 95% *CI*s. Conditional logistic regressions were run using the PHREG procedure in SAS 9.1 (SAS Institute Inc. 2003).

To evaluate whether snowshoe hares responded to variations in cover availability by changing their speed we used general linear mixed models with the distance traveled in 10 bounds, an index of movement speed, as the dependent variable and combinations of canopy closure, conifer stem density, and browse availability as independent variables. We did not include the proportion of segments within gaps as a variable (''proportion in gap'') in candidate models because almost half of the observed trail segments (47 [45%] of 105) were completely under canopy cover (i.e., 0% of the trail segment was within a gap). This variable also did not capture variation in canopy cover that was due to changes in interstitial spacing between trees (average canopy closure along segments without canopy gaps varied between 27% and 77%, but average closure along segments with gaps varied between 3% and 73%). Individual trails nested within sites were considered as random effects, and we used an autoregressive (order 1) correlation structure to account for autocorrelation between successive trail segments. We used AIC corrected for small sample size ($AIC_c$) to rank candidate models and multimodel inference to calculate coefficients for variables with 90% and 95% *CI*s. To evaluate the accuracy of top ranking models ($\Delta AIC_c \leq 2.0$) we calculated marginal $R^2$-values for each model (Orelien and Edwards 2008). General linear mixed models were run using the MIXED procedure in SAS 9.1 (SAS Institute Inc. 2003).

*Giving-up densities*.—We selected 88 gaps distributed within 20 different sites (1–11 gaps/site) in spruce- and spruce–fir–dominated stands (>90 years old). Gaps were sampled during the winters of 2006 (65 gaps) and 2007 (23 gaps). Selected gaps were free of coniferous regeneration that could provide cover and of deciduous regeneration that could provide alternative foraging opportunities. Length and width of gaps were used to estimate gap size as the area of an ellipse, and sizes ranged from 20 $m^2$ to 942 $m^2$. Within the gaps, GUDs were measured using jack pine boughs as experimental food patches, consistent with methods developed by Morris

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(2005). Jack pine is a preferred browse species for snowshoe hares (Bergeron and Tardif 1988) and was absent in the understory of stands in which we conducted gap surveys and GUD experiments. Jack pine boughs thus represented attractive food patches for hares within these stands. Furthermore, we had access to a 30-year-old fire-origin stand of regenerating jack pine that gave us a vast source of boughs from trees of similar age and height, helping to reduce sources of variability in the quality of boughs used in the experiment. Changes in protein and fiber content are such that the digestibility and energetic value of boughs should decrease as stems get thicker toward their bases (Palo et al. 1992). Therefore the rate of energy gain should decrease as hares clip progressively larger diameter segments. The diameter at point of browse thus provides an estimate of GUD, with smaller browse diameters indicating higher GUDs (Morris 2005). We cut terminal jack pine boughs to a length of 50 cm and removed all cones and lateral branches. The basal diameter of each bough was measured to the nearest 0.02 mm with calipers to account for variations in branch morphology. Then boughs were inserted 10 cm into the snow in pairs at 1-m intervals, starting at the center of the gap and extending 4 m into the adjacent forest along the wide axis, with a pair positioned at the gap edge. We placed between 2 and 11 branch pairs within gaps according to gap width. Boughs were left in place between 4 and 26 days to allow sufficient time for hares to encounter the gaps and revisit branches over several nights. At the end of each sampling period we removed boughs and measured the diameter at point of browse and the residual length of all browsed stems. Motion-sensitive digital cameras (Reconyx Silent Image, La Crosse, Wisconsin) were installed at some gaps to observe foraging behavior.

Diameter at point of browse was compared between canopy gaps and continuous forests where foraging had occurred in both the gap and the adjacent forest. To test whether GUDs differed by habitat (Gap versus Forest) and increased with distance from the gap edge within gaps we used a linear mixed-effects model with habitat (Gap = 1, Forest = 0) and a Habitat × Distance interaction as fixed effects. The basal diameter of jack pine stems (ln-transformed) was included as a covariate to account for variation in branch morphology. Because the amount of time branches were left in place varied from gap to gap, the natural log of the number of nights (''no_nights'') also was included in the model, both as a simple effect to test whether diameter at point of browse increased with time that branches were left in place and in a triple interaction with habitat and distance (Habitat × Distance × ln(no_nights)) to test whether branches farther from cover within gaps were browsed to larger diameters the longer they were left in place. We included sites and gaps nested within sites as random effects to account for our hierarchical sampling design of branches grouped within gaps, and gaps grouped within sites. Random site effects also accounted for potential site-level differences in snowshoe hare abundance. We used the Kenward–Roger method (Kenward and Roger 1997) to calculate denominator degrees of freedom for the fixed effects because the number of branch pairs within gaps varied according to gap size, thereby creating an unbalanced design. Linear mixed-effects models were run using the MIXED procedure in SAS 9.1 (SAS Institute Inc. 2003), and type III contrasts were used to test the significance of fixed effects.

All gaps with at least 1 clipped bough in either the forest or gap were used to test the probability of bough use in forests versus gaps and, once in gaps, the effect of distance of branches to the gap edge. To model the probability of branch use (Browsed = 1, Nonbrowsed = 0) we used a mixed-model logistic regression with habitat (Gap = 1, Forest = 0) and a Habitat × Distance interaction as fixed effects and sites and gaps nested within sites as random effects. We also included the natural log of the number of nights branches were left in place as a simple effect to test whether branches were more likely to be browsed the longer they were left in place, and in a triple interaction with habitat and distance (Habitat × Distance × log(no_nights)) to determine if branches that were farther from cover within gaps were more likely to be used the longer they were left in place. The mixed-model logistic regression was run using the GLIMMIX procedure in SAS 9.1 (SAS Institute Inc. 2003).

*Use of natural browse within canopy gaps.*—Signs of browsing by snowshoe hares were recorded during surveys of browse availability within canopy gaps. We counted the number of twigs browsed by snowshoe hares during the winter (2007) previous to our survey (summer 2007) to estimate browsing intensity as a proportion of used versus available twigs. Each stem (including conifers) was also classified as browsed or nonbrowsed based on the presence of any twigs clipped by snowshoe hares. Because hares mainly consume woody browse during winter, browse surveys reflected patterns of winter habitat use. Based on areas where deciduous stems were present in both the gap and adjacent forest, we modeled the probability of stem use as a function of habitat (Gap versus Forest) and, once in gaps, the distance of stems to the gap edge. We used a mixed-model logistic regression with habitat (Gap = 1, Forest = 0) and a Habitat × Distance interaction as fixed effects, and sites and gaps nested within sites as random effects. The Kenward–Roger degrees of freedom correction was applied to account for spatial variations in numbers of stems at different distances from the gap edge. Because conifer regeneration within gaps may provide cover for hares, we tested a 2nd model that also included the density of conifer regeneration within gaps. This model included a Habitat × Conifer sapling density interaction and the 3-way interaction Habitat × Conifer density × Distance of browse stems to the gap edge. Mixed-model logistic regressions were run using the GLIMMIX procedure in SAS 9.1 (SAS Institute Inc. 2003).

## Results

*Browse within canopy gaps.*—Of the 112 canopy gaps sampled 99 had browse available within the gap, including 61

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**Table 1.**—Mean (± 1 *SE*) deciduous browse density and conifer sapling density within canopy gaps of edaphic and mortality origin in eastern Canadian boreal conifer stands (80–>200 years), and Wilcoxon signed-rank tests (*S*) of paired differences between browse and conifer density between gaps and adjacent forest cover. Positive differences indicate a higher browse or conifer sapling density within canopy gaps than adjacent forest.

| Gap origin | Browse and cover | Gap | Forest | Gap − Forest | *S* | *P* |
|---|---|---|---|---|---|---|
| Edaphic ($n = 41$) | Deciduous browse (twigs/m$^2$) | 4.93 ± 0.98 | 1.17 ± 0.29 | 3.76 ± 0.95 | 298 | <0.001 |
| | Conifer saplings (stems/m$^2$) | 0.30 ± 0.05 | 0.82 ± 0.09 | −0.52 ± 0.11 | −319 | <0.001 |
| Mortality ($n = 71$) | Deciduous browse (twigs/m$^2$) | 4.09 ± 0.72 | 1.14 ± 0.35 | 2.95 ± 0.71 | 736 | <0.001 |
| | Conifer saplings (stems/m$^2$) | 0.75 ± 0.06 | 0.70 ± 0.06 | 0.05 ± 0.06 | 157 | 0.36 |

gaps with browse found in both the gap and the adjacent forest. Gaps originated more frequently from the mortality of canopy trees ($n = 71$; 63%) than from edaphic conditions ($n = 41$; 37%). The density of deciduous browse was greater within gaps of both edaphic and mortality origin than under adjacent forest cover (Table 1). The density of coniferous saplings was lower within edaphic-origin gaps than adjacent forest, whereas no difference was detected between mortality-origin gaps and adjacent forest.

*Winter habitat selection at the stand level*.—Among the competing models explaining snowshoe hare selection for winter trail location, 3 resource selection functions received similarly strong empirical support ($\Delta AIC \leq 2$; Table 2). The *k*-fold cross-validation indicated that all 3 models had good predictive success, with $\overline{r_s}$ ranging between 0.86 and 0.91. Model averaging of parameter estimates revealed that canopy closure and browse availability had the strongest influence on selection for winter trail locations, because these 2 habitat attributes were the only ones with 95% *CI*s that excluded 0 (Table 3). Snowshoe hares selected areas with greater canopy closure ($\overline{\beta}_{\text{Canopy closure}} = 0.064$, 95% *CI* = 0.043–0.085) and browse availability ($\overline{\beta}_{\text{Browse availability}} = 0.085$, 95% *CI* = 0.002–0.169) compared to random locations within stands (Table 4).

*Fine-scale movements*.—Model comparison of step-selection functions did not provide overwhelming support for a particular model ($\Delta QIC < 2$ for 5 models; Table 5). Model averaging of the parameter estimates revealed that the proportion of steps made within canopy gaps was lower than expected by chance alone ($\overline{\beta}_{\text{Proportion in gap}} = -0.005$, 95% *CI* = −0.009–−0.001; Table 3). Unconditional 90% *CI*s also indicated that hares tended to move selectively in areas with higher canopy closure ($\overline{\beta}_{\text{Canopy closure}} = 0.022$, 90% *CI* = 0.000–0004). However, little evidence was found that hares selectively moved along areas with higher conifer stem density or greater browse availability (Tables 3 and 6).

The distance traveled by hares in 10 bounds, an index of movement speed, varied from 3.4 m to 16.9 m. Several competing models received similarly high support, with $\Delta AIC_c \leq 2$ (Table 7). Model averaging (Table 3) revealed that snowshoe hares reduced their speed in areas with greater canopy closure ($\overline{\beta}_{\text{Canopy closure}} = -0.044$, 95% *CI* = −0.081–−0.008) and greater densities of Class 1 conifer stems ($\overline{\beta}_{\text{Class 1 conifer stem density}} = -1.545$, 95% *CI* = −2.618–−0.472). Hares also tended to reduce speed in areas with greater densities of Class 2 conifer stems ($\overline{\beta}_{\text{Class 2 conifer stem density}} = -1.161$, 90% *CI* = −2.217–−0.105). Although these habitat features explained a statistically significant portion of the variation in the distance hares covered in 10 bounds, this portion remained rather low for all candidate models ($R^2 < 0.15$ for all regressions used in model averaging).

*Giving-up densities*.—Snowshoe hares visited (i.e., ≥1 branch clipped) 45 of the 88 canopy gaps used for GUD experiments. Visited gaps were 4–16 m in width (i.e., between 2 and 8 branch pairs placed within the gap) and 22–440 m$^2$ in area. Of those, 36 gaps had branches clipped by hares in both the gap and the adjacent forest. The diameter at which hares clipped boughs within gaps did not vary as a function of distance from cover (Habitat × Distance; $F_{1,598} = 1.02$, $P = 0.31$) or as a function of distance to cover and time (Habitat ×

**Table 2.**—Competing models of resource selection by snowshoe hares using logistic regression to compare points observed ($n = 125$) along winter snowshoe hare trails to randomly located points ($n = 184$) within eastern Canadian boreal conifer stands (>90 years). *K* = number of parameters; AIC = Akaike's information criterion; $w_i$ = Akaike weight.

| Model | K | AIC | ΔAIC | $w_i$ |
|---|---|---|---|---|
| Canopy closure + Browse availability | 3 | 364.8 | 0.0 | 0.42 |
| Canopy closure + Lateral visual obstruction 0–2 m + Browse availability | 4 | 366.1 | 1.3 | 0.22 |
| Canopy closure + Class 1 conifer stem density + Class 2 conifer stem density + Browse availability | 5 | 366.8 | 2.0 | 0.15 |
| Canopy closure | 2 | 367.3 | 2.5 | 0.12 |
| Canopy closure + Lateral visual obstruction 0–2 m | 3 | 368.6 | 3.8 | 0.06 |
| Canopy closure + Class 1 conifer stem density + Class 2 conifer stem density | 4 | 369.9 | 5.1 | 0.03 |
| Class 1 conifer stem density + Class 2 conifer stem density + Browse availability | 4 | 390.5 | 25.7 | 0.00 |
| Class 1 conifer stem density + Class 2 conifer stem density | 3 | 397.7 | 32.9 | 0.00 |
| Browse availability | 2 | 414.1 | 49.3 | 0.00 |
| Lateral visual obstruction 0–2 m + Browse availability | 3 | 416.0 | 51.2 | 0.00 |
| Lateral visual obstruction 0–2 m | 2 | 422.9 | 58.1 | 0.00 |

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**Table 3.**—Model-averaged coefficients ($\overline{\beta}$) and unconditional standard errors ($SE(\overline{\beta})$) for habitat variables used in resource selection functions (RSFs) comparing points observed ($n = 125$) along winter snowshoe hare trails to randomly located points ($n = 184$), step-selection functions (SSFs) for winter snowshoe hare trails ($n = 105$ observed step segments), and analysis of movement speed by snowshoe hares along 10-bound segments of winter trails in eastern Canadian boreal conifer stands (>90 years). Coefficients are in boldface type when their 95% (*) or 90% confidence intervals excluded 0. NA = not available.

| Variable | RSFs ($\overline{\beta} \pm SE(\overline{\beta})$) | SSFs ($\overline{\beta} \pm SE(\overline{\beta})$) | Movement speed ($\overline{\beta} \pm SE(\overline{\beta})$) |
|---|---|---|---|
| Canopy closure (%) | **0.064* ± 0.011** | **0.022 ± 0.013** | **−0.044* ± 0.019** |
| Proportion in gap (%) | NA | **−0.005* ± 0.003** | NA |
| Browse availability[a] | **0.085* ± 0.043** | −0.028 ± 0.059 | 0.110 ± 0.154 |
| Class 1 conifer stem density[b] | 0.015 ± 0.012 | 0.078 ± 0.305 | **−1.545* ± 0.547** |
| Class 2 conifer stem density[b] | −0.003 ± 0.028 | −0.476 ± 0.780 | **−1.161 ± 0.642** |
| Lateral visual obstruction 0–2 m (%) | −0.008 ± 0.010 | NA | NA |

[a] Measured as the density of deciduous stems per 50 $m^2$ for RSFs and as the density of deciduous twigs between 0 and 1 m above the snow per 1 $m^2$ for SSFs and movement speed.
[b] Measured as the number of conifer stems per 50 $m^2$ for RSFs and as the number of stems per 1 $m^2$ for SSFs and movement speed.

Distance × ln(no_nights); $F_{1,598} = 0.42$, $P = 0.52$). Inferences were thus based on a model investigating whether the diameter at point of browse varied between gaps and the adjacent forest (variable: Habitat) while controlling for basal stem diameter and time; that is, Diameter at point of browse = Habitat + ln(Basal stem diameter) + ln(no_nights), where habitat was a class variable. Variations in branch morphology had a strong influence on diameter at point of browse ($\beta_{\text{ln basal diameter}} = 2.50$; $F_{1,609} = 74.54$, $P < 0.0001$), and diameter at point of browse also increased with the time that boughs were left in place ($\beta_{\text{ln no_nights}} = 0.82$; $F_{1,41.1} = 11.56$, $P = 0.002$). This model further revealed that hares clipped boughs to larger diameters under forest cover than within gaps (Habitat: $F_{1,587} = 12.67$, $P = 0.0004$, $n = 36$ gaps). Based on the least-squared means of the mixed model (based on a mean basal branch diameter of 8.08 mm and a mean time of 13 nights), hares clipped boughs to a mean diameter of 5.08 ± 0.24 mm under forest cover, whereas those within gaps were clipped to 4.84 ± 0.24 mm.

We also found that hares were less likely to clip experimental branches within gaps as the distance from the forest edge increased ($\beta_{\text{Habitat} \times \text{Distance}} = -1.11$; $F_{1,841} = 9.38$, $P = 0.002$, $n = 45$ gaps with ≥1 branch clipped). However, boughs located farther within gaps were more likely to be browsed the longer they were left in place ($\beta_{\text{Habitat} \times \text{Distance} \times \ln(\text{no_nights})} = 0.33$; $F_{1,841} = 6.08$, $P = 0.014$; Fig. 1). To determine whether a threshold distance could be identified where the probability of branch use became significantly lower within gaps than in adjacent forests, we used a mixed-effects model with distance as a class variable (Forest = 0, Gap = 1–>6 m; distances 6–8 m were pooled due to low number of replicates) and time as a covariate and compared the probability of use at each distance with that of the forest. At distances of ≥4 m, the probability of branch use was systematically lower within gaps than under forest cover ($P < 0.05$ for all cases).

**Table 4.**—Mean (± 1 *SE*) values of habitat variables measured at points along single winter snowshoe hare trails ($n = 125$) and randomly located points ($n = 184$) used in resource selection functions within eastern Canadian boreal conifer stands (>90 years).

| Variable | Observed | Random |
|---|---|---|
| Canopy closure (%) | 54.10 ± 1.09 | 41.76 ± 1.07 |
| Lateral visual obstruction 0–2 m (%) | 18.41 ± 1.10 | 18.98 ± 0.97 |
| Class 1 conifer stem density (stems/50 $m^2$) | 22.71 ± 1.35 | 15.40 ± 0.82 |
| Class 2 conifer stem density (stems/50 $m^2$) | 4.14 ± 0.43 | 5.48 ± 0.39 |
| Browse availability (stems/50 $m^2$) | 2.20 ± 0.38 | 1.08 ± 0.17 |

*Natural browse use*.—Similar proportions of deciduous stems had signs of browsing by snowshoe hares (current or previous years) within gaps (42%, $n = 1{,}337$ stems) and forest adjacent to gaps (37%, $n = 251$ stems). We did not observe any signs of browsing by snowshoe hares on coniferous saplings within either gaps ($n = 1{,}233$ stems) or under adjacent forest cover ($n = 634$ stems). The proportion of available terminal twigs that were browsed during the last winter season (2007) was low in both habitats (Forest = 1.8%, Gap = 2.3%). Consistent with GUD experiments, we found a decreasing probability of use by hares of natural browse stems located farther within gaps (Habitat × Distance: $F_{1,1257} = 7.98$, $P = 0.005$, $n = 61$ gaps; Fig. 2). Using distance as a class variable, we also found that browsing in gaps was significantly less likely than under adjacent forests at distances ≥7 m from cover within gaps ($P < 0.005$). Including the density of conifer regeneration within gaps in logistic regressions did not change the probability of browse stem use within gaps, because neither the 3-way interaction of Habitat × Conifer density × Distance nor the 2-way interaction Habitat × Conifer density were significant ($P > 0.40$). However, when we included only the density of conifer regeneration > 2 m in height, we found that it had a positive effect on the probability that deciduous stems within gaps would be browsed ($\beta_{\text{Habitat} \times \text{Conifer sapling density} > \text{2-m height}} = 2.609$; $F_{1,130.8} = 4.63$, $P = 0.03$), but it did not change the pattern that stems at greater distances from the forest edge within gaps remained less likely to be browsed ($\beta_{\text{Habitat} \times \text{Distance}} = -0.1381$; $F_{1,1265} = 7.90$, $P = 0.005$, after removing the nonsignificant 3-way interaction of Habitat × Distance × Conifer sapling density >2-m height).

## Discussion

Movement and foraging behaviors revealed that fine-scale disturbances in old-growth boreal forest shape space-use

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**TABLE 5.**—Competing models for step-selection functions along single winter snowshoe hare trails ($n$ = 105 observed step segments) in eastern Canadian boreal conifer stands (>90 years). $K$ = number of parameters; QIC = quasi-likelihood under independence criterion; $w_i$ = Akaike weight.

| Models | K | QIC | ΔQIC | $w_i$ |
|---|---|---|---|---|
| Canopy closure | 1 | 230.1 | 0.0 | 0.21 |
| Proportion in gap | 1 | 230.3 | 0.2 | 0.19 |
| Canopy closure + Browse availability | 2 | 230.7 | 0.6 | 0.15 |
| Proportion in gap + Browse availability | 2 | 230.9 | 0.8 | 0.14 |
| Browse availability | 1 | 231.2 | 1.1 | 0.12 |
| Canopy closure + Class 1 conifer stem density + Class 2 conifer stem density | 3 | 233.4 | 3.3 | 0.04 |
| Proportion in gap + Class 1 conifer stem density + Class 2 conifer stem density | 3 | 233.7 | 3.6 | 0.03 |
| Class 1 conifer stem density + Class 2 conifer stem density | 2 | 233.9 | 3.8 | 0.03 |
| Canopy closure + Class 1 conifer stem density + Class 2 conifer stem density + Browse availability | 4 | 234.0 | 3.9 | 0.03 |
| Class 1 conifer stem density + Class 2 conifer stem density + Browse availability | 3 | 234.3 | 4.2 | 0.03 |
| Proportion in gap + Class 1 conifer stem density + Class 2 conifer stem density + Browse availability | 4 | 234.3 | 4.2 | 0.03 |

patterns of snowshoe hares by creating heterogeneity in their landscapes of fear and food. Canopy gaps created areas of higher browse density compared to closed-canopy conditions, but hares perceived these openings as relatively risky. Hares responded to spatial variation in food and safety by selecting areas within stands that had both higher canopy closure and higher browse availability than random locations. Furthermore, hares adjusted their movements and foraging behavior to minimize time spent in openings. To our knowledge this is the 1st study linking snowshoe hare distribution to habitat heterogeneity induced by fine-scale canopy gap dynamics. The process of gap formation, regeneration, and closure should create a shifting mosaic of food and cover for hares, which in turn should shape their interactions with predators in old-growth boreal forests.

Gap dynamics induced by fine-scale disturbances create a ''foodscape'' (Searle et al. 2007) for snowshoe hares that is constantly changing over time and space. We observed that hares acquire most of their winter food within canopy gaps. Although hares harvested similar proportions of twigs available within gaps and under forest cover, they consumed considerably more twigs from gaps because these openings offered nearly 4 times more browse ($\bar{X}$ = 4.5 twigs/m$^2$ in all gaps; $\bar{X}$ = 1.15 twigs/m$^2$ under canopy cover). Therefore, gap dynamics should increase browse supply for hares as forest stands undergo a transition from mature to old-growth structure. The spatial and temporal distribution of food resources for hares in these stands should depend largely on the rate of gap formation and gap closure. New gaps in old-growth boreal forests form at a rate of approximately 1% of stand area per year (McCarthy 2001), and these gaps can take between 50 and 200 years to close (Lertzman and Krebs 1991). Gaps thus accumulate and expand faster than they close, such that the gap fraction within old-growth stands increases with time (Harper et al. 2006) until the next major stand-replacing disturbance occurs. The process of gap closure also appears to depend on the origin of canopy gaps. Compared to gaps originating from tree mortality, edaphic gaps were characterized by little to no coniferous regeneration. These gaps likely persist from the previous stand-initiating disturbance and should remain open for long time periods because poor germination beds and competition by shrubs do not generally facilitate tree establishment (Harper et al. 2006; Mallik 2003). Consequently, the spatial and temporal distribution of gaps within old-growth stands should remain fairly constant when edaphic gaps predominate, whereas stands dominated by gaps from tree mortality should have a spatial distribution of food that varies dynamically over shorter time scales. These processes also determine the snowshoe hare's landscape of fear (Laundré et al. 2001).

Prey need to balance resource acquisition with safety to realize their potential fitness (Brown and Kotler 2004). When prey are more vulnerable to predation in areas of reduced vegetation cover they may structure their movements to reduce time spent in openings. For example, in the presence of predators degus (*Octodon degus*) select travel routes that follow the distribution of shrub cover and increase their speed when crossing openings. In the absence of predators, however, they increase their use of open habitats (Lagos et al. 1995; Vasquez et al. 2002). Hares appear to be more vulnerable to

**TABLE 6.**—Mean (± 1 *SE*) values of habitat variables measured along 10-bound segments ($n$ = 105) and paired random segments from 16 single winter snowshoe hare trails, and mean paired differences between values along observed and random segments used in step-selection functions within eastern Canadian boreal conifer stands (>90 years).

| Variables | Observed | Random | Paired difference |
|---|---|---|---|
| Proportion in gap (%) | 28.76 ± 3.20 | 31.24 ± 2.41 | −2.48 ± 2.41 |
| Canopy closure (%) | 47.62 ± 1.63 | 46.41 ± 1.17 | 1.21 ± 0.76 |
| Class 1 conifer stem density (stems/m$^2$) | 0.63 ± 0.05 | 0.62 ± 0.03 | 0.01 ± 0.03 |
| Class 2 conifer stem density (stems/m$^2$) | 0.36 ± 0.03 | 0.38 ± 0.03 | −0.02 ± 0.02 |
| Browse availability (twigs/m$^2$) | 0.26 ± 0.13 | 0.31 ± 0.11 | −0.05 ± 0.05 |

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**Table 7.**—Competing models of the influence of cover availability on movement speed, estimated as the distance travelled in 10-bound segments ($n = 105$), along single winter snowshoe hare trails ($n = 16$) in eastern Canadian boreal conifer stands (>90 years old). $K$ = number of parameters; $AIC_c$ = Akaike's information criterion corrected for small sample size; $w_i$ = Akaike weight.

| Model | K | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| Canopy closure + Class 1 conifer stem density + Class 2 conifer stem density | 5 | 428.8 | 0.0 | 0.33 |
| Class 1 conifer stem density + Class 2 conifer stem density | 3 | 428.8 | 0.0 | 0.33 |
| Canopy closure + Class 1 conifer stem density + Class 2 conifer stem density + Browse availability | 6 | 430.1 | 1.3 | 0.17 |
| Class 1 conifer stem density + Class 2 conifer stem density + Browse availability | 5 | 430.3 | 1.5 | 0.16 |
| Canopy closure | 3 | 441.1 | 12.3 | 0.00 |
| Canopy closure + Browse availability | 4 | 441.8 | 13.0 | 0.00 |
| Intercept only | 2 | 450.4 | 21.6 | 0.00 |
| Browse availability | 3 | 450.7 | 21.9 | 0.00 |

predation in open habitats than in closed habitats (Rohner and Krebs 1996), and we found that hares selected areas within mature and old-growth stands that had higher than average canopy closure. They also made fine-scale adjustments to reduce the proportion of their trajectory that occurred within gaps and sped up in areas of reduced canopy closure. These behavioral adjustments suggest that snowshoe hares spend most of their time under closed canopy cover and that the use of gaps is largely restricted to foraging activities. Their fear of predators also appears to constrain their foraging behavior in gaps.

In the presence of predators prey may forego foraging in resource-rich habitats in return for greater safety (Wirsing et al. 2007). Numerous studies, where patches of vegetation cover are embedded in an open matrix, have demonstrated that small mammals accept reduced rates of energy intake for the greater safety of exploiting food patches under cover (Brown and Kotler 2004). In our system canopy gaps represented open patches embedded in a matrix of vegetative cover. We observed that snowshoe hares clipped experimental jack pine boughs to larger diameters (lower GUDs) under forest cover than within gaps, presumably accepting a lower rate of energy intake by foraging more intensively under the safety of canopy cover. Although prey often display higher GUDs (i.e., lower foraging efforts) as distance from cover increases (Hochman and Kotler 2007; Hughes and Ward 1993), snowshoe hares did not appear to diminish their foraging effort toward the center of gaps. These findings are consistent with Hodges and Sinclair (2005), but contrary to Morris (2005), who observed that hares clipped jack pine boughs to smaller diameters at greater distances from cover along sharp ecotones between shrub habitat and abandoned agricultural fields. The lack of change in browse diameter with distance from cover in gaps could be the result of weak diminishing returns for hares browsing jack pine boughs. If hares experienced a relatively flat harvest rate curve while consuming boughs, meaning little decrease in the rate of energy gain with increasing diameter, this would have limited our capacity to detect fine-scale variation in perception of risk. Accordingly, information on

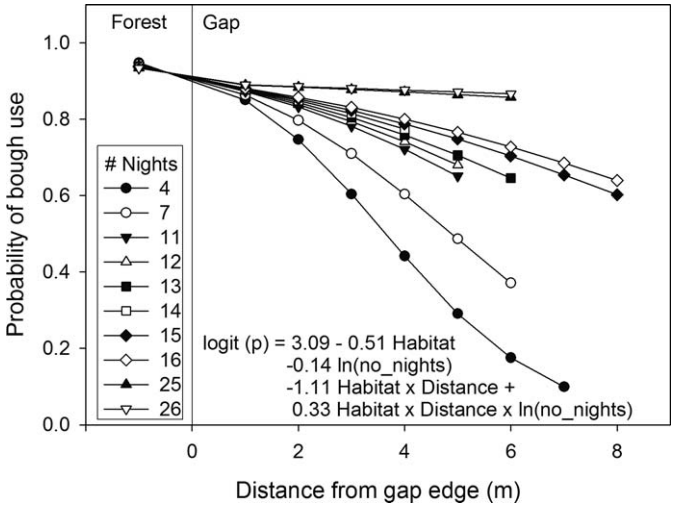



**Fig. 1.**—Predicted probability of jack pine bough use by snowshoe hares as a function of habitat (Gap versus Forest), the number of nights boughs were left within gaps and adjacent forest, and the distance of boughs ($n = 846$ boughs) placed within canopy gaps ($n = 45$ gaps) to the gap edge, in eastern Canadian boreal conifer stands (>90 years).

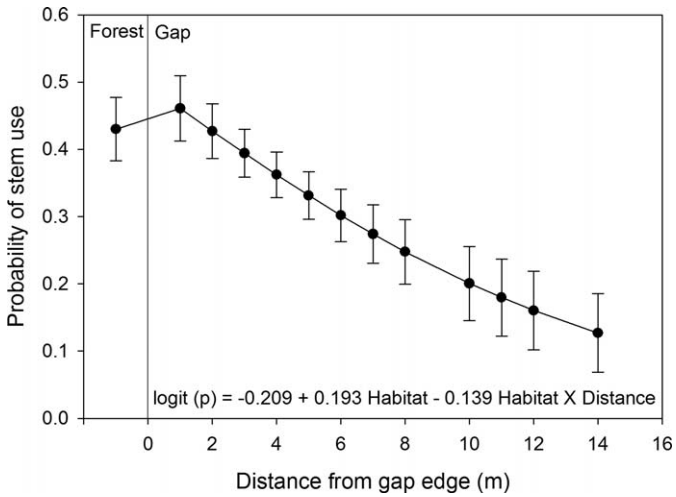



**Fig. 2.**—Predicted probability (± 1 *SE*) of natural browse use by snowshoe hares as a function of habitat (Gap versus Forest) and distance of stems ($n = 1,269$ stems) to the gap edge, within edaphic- and mortality-origin canopy gaps ($n = 61$ gaps) in eastern Canadian boreal conifer stands (80–>200 years).

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protein and fiber content of jack pine boughs at increasing stem diameters would be necessary to quantify harvest rate curves, which in turn would facilitate the interpretation of GUD experiments on hare foraging behavior. Our results also could be explained by a foraging tactic displayed by snowshoe hares. When foraging away from cover, prey must balance exposure time against foraging efficiency, and they often choose to carry items back to protective cover rather than consume them in the open (Hughes and Ward 1993; Lima 1985). Our motion-sensitive cameras revealed that hares can clip large segments of branches and carry them back to the forest cover (Fig. 3). In such cases hares would have been consuming boughs in the same place with the same risk, regardless of where the bough was initially placed. The diameter at point of browse would then no longer reflect time spent in the open harvesting a series of successively larger diameter segments of diminishing energetic value.

Although distance to cover might not influence the diameter at point of browse when harvesting a branch, herbivores may remain reluctant to venture far from cover to browse. Foragers should accept greater risk only for greater rewards (Kotler and Blaustein 1995). When presented with similar food patches, foragers should select the safest patches first. Consistently, we found that hares were less likely to use experimental food patches as their distance from the safety of canopy cover increased. Moreover, the probability of natural browse use also declined as stems were located farther within gaps. Overall, hares were significantly less likely to use natural browse stems that were >7 m from cover (i.e., near the center of gaps of >14 m in diameter). The landscape of fear is therefore shaped by variations in the size of canopy openings. Although gap formation can improve habitat quality for hares by increasing food availability, browse in the center of large gaps essentially could be unavailable to hares. Although most gaps in old-growth boreal stands are <100 $m^2$ in area (<12-m diameter), gaps may cover >80% of stands (Pham et al. 2004). The accumulation and expansion of many small gaps therefore could have important stand-level implications for habitat quality as the matrix of continuous canopy cover offering safe travel corridors becomes increasingly fragmented. Hares were more likely to use browse within gaps with greater densities of coniferous regeneration tall enough (>2 m) to provide cover above the snow during winter. Succession within gaps should contribute to spatiotemporal heterogeneity in the distribution of risk for hares.

Trade-offs between food and safety also can vary according to population density (China et al. 2008). Snowshoe hares display cyclical population dynamics (Krebs et al. 2001a), with up to 182-fold changes in density in some regions (Krebs et al. 1986). Wolff (1980) observed that snowshoe hares increased their use of open food-rich habitats and clipped deciduous twigs to larger diameters (>1 cm) toward the peak phase of their cycle. The patterns of browse use observed in our study could vary according to the phase of the snowshoe hare cycle. Examination of furbearer harvest data suggests that snowshoe hare populations are cyclical in our study region (Bourbonnais 1999; Godbout 1998), but cycles are of much lower amplitude (9- to 10-fold changes in density) than those reported in western Canada (Keith and Windberg 1978; Krebs et al. 1986). Previous population peaks in the study region occurred in 1980–1981 and 1988–1989 (Bourbonnais 1999), and St-Laurent et al. (2008) reported that hares were at their




**FIG. 3.**—Snowshoe hare foraging behavior captured from motion-sensitive cameras installed at canopy gaps with giving-up density (GUD) experiments in eastern Canadian boreal conifer stands (>90 years). Photographs show a hare clipping a large jack pine bough segment (indicated by arrows) in the gap and returning with it to forest cover.

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peak in 1998–1999 in an adjacent region. Our study should have occurred during the peak phase of the cycle, assuming an 8- to 9-year periodicity. Pellet count data from 18 stands >80 years old, each sampled over 3 consecutive years (2006–2008), seem to confirm this. We recorded mean pellet densities of 0.31 pellets/$m^2$ in 2006, 0.50 pellets/$m^2$ in 2007, and 0.39 pellets/$m^2$ in 2008, suggesting that the peak occurred in 2007 (J. Hodson, pers. obs.). These pellet densities would correspond to hare densities of roughly 0.03–0.05 hares/ha based on regression equations developed by Krebs et al. (2001b). These estimates are lower than most hare densities recorded during the low phase of population cycles in other regions (range = 0.03–1.70 hares/ha, $\bar{X}$ = 0.62 hares/ha—Murray 2003). The low proportion of terminal twigs consumed by hares (1.8–2.3%) suggests that they were not faced with a food shortage, whereas other hare populations can consume 80–100% of available browse during population peaks (Smith et al. 1988; Wolff 1980). This suggests that fine-scale spatial patterns of browse use might not change considerably over the course of low-amplitude population cycles in eastern old-growth boreal forests.

*Multitrophic implications of habitat heterogeneity resulting from gap dynamics.*—Despite increasing emphasis on the maintenance of old-growth stands in managed boreal landscapes (Mosseler et al. 2003), we still understand little about how gap dynamics in these forests influence the fine-scale distribution of boreal wildlife. Our study indicates that gap dynamics could have multitrophic-level consequences by creating spatial heterogeneity in the landscapes of fear and food for the snowshoe hare, a key prey species of boreal ecosystems. Nonlethal effects of predators on their prey can have major repercussions on ecosystems. For example, the evasive games played between herbivores and their predators can have cascading effects on vegetation growth triggered by spatial variations in browsing intensity (Beyer et al. 2007; Schmitz et al. 1997). Traditionally, models of vegetation succession following disturbance have not considered the roles of herbivores (Wisdom et al. 2006), but studies suggest that forest herbivores can shape competitive vegetation interactions by preferentially browsing certain tree species (Schmitz 2005). These interactions may be further modified by spatial variation in predation risk. For example, moose (*Alces americanus*) preferentially browse deciduous vegetation that competes with regenerating conifers in clear-cuts, but their use of browse declines from the forest edge toward the center of clear-cuts because of increased predation risk (Schmitz 2005). Spatial heterogeneity in risk-sensitive foraging by hares similarly could influence patterns of vegetation succession within canopy gaps. Furthermore, fine-scale disturbances such as canopy gap dynamics may shape predator–prey ''shell games'' by determining where food occurs for prey that must balance patch use with remaining elusive to predators, and by shaping the movement of predators that may focus their search for prey in areas where their prey's resources are most concentrated (Andruskiw et al. 2008; Mitchell and Lima 2002). Gap dynamics therefore may be a fundamental process structuring predator–prey interactions in old-growth boreal forests, with cascading implications across several trophic levels.

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