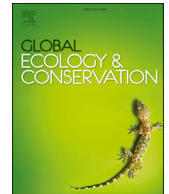




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Salvage logging after an insect outbreak reduces occupancy by snowshoe hares (*Lepus americanus*) and their primary predatorsJulie P. Thomas^{a, b, *}, Mary L. Reid^a, Robert M.R. Barclay^a, Thomas S. Jung^{b, c}^a Department of Biological Sciences, University of Calgary, Calgary, Alberta, T2N 1N4, Canada^b Department of Environment, Government of Yukon, Whitehorse, Yukon, Y1A 2C6, Canada^c Department of Renewable Resources, University of Alberta, Edmonton, Alberta, T6G 2H1, Canada

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ABSTRACT

Salvage logging after a natural disturbance is controversial because it may disrupt forest succession and reduce the value of wildlife habitat, but few studies have examined consequences on predator-prey systems. For herbivores that consume early-seral vegetation, salvage logging may simultaneously improve food abundance and reduce protective cover, imposing trade-offs that influence their habitat selection and that of their predators. We examined habitat use by snowshoe hares (*Lepus americanus*)—a keystone prey species in the boreal forest—and their primary predators, Canada lynx (*Lynx canadensis*) and coyotes (*Canis latrans*), in response to salvage logging following a bark beetle outbreak in Yukon, Canada. We monitored hare, lynx, and coyote presence in beetle-affected forests and salvage-logged stands of different tree retention levels and ages (up to 25 years post-logging) using wildlife cameras, and modelled species occupancy as a function of forest structure at local and landscape scales. Snowshoe hares occupied stands with dense canopies and avoided salvage-logged stands regardless of retention class or age, selecting habitat with the most cover from aerial and terrestrial predators. Lynx and coyote generally used the same habitat as hares, selecting unsalvaged stands with high snowshoe hare occupancy. Habitat use by coyote and hare was more strongly linked than that of lynx and hare, perhaps because coyotes are versatile predators that can adjust their hunting tactics in dense habitat. Our study demonstrates that salvage-logged stands have lower value than beetle-affected forest for snowshoe hares and their predators in the short-term—regardless of retention levels—which may have localized impacts on boreal forest food webs. Higher tree retention, long harvest intervals, and small cut areas interspersed with large unlogged forest patches are recommended to mitigate negative impacts of salvage logging on these species.

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1. Introduction

Natural disturbances such as forest fires and insect outbreaks shape the composition, structure, and function of boreal forests (Attiwil, 1994). These disturbances are natural ecological processes that have shaped the evolution of resident species; yet they typically invoke management responses, including attempts to control the extent and severity of the disturbance or

* Corresponding author. Department of Environment, Government of Yukon, Whitehorse, Yukon, Y1A 2C6, Canada.

E-mail address: julie.thomas@gov.yk.ca (J.P. Thomas).

manage the aftermath (Fettig et al., 2007; Noss et al., 2006). One such response is post-disturbance logging (i.e., “salvage logging”), which is the harvesting of disturbance-killed trees to minimize economic losses and reduce wildfire risk (Mansuy et al., 2015; Shore et al., 2003). Salvage logging has been claimed to aid forest recovery (Sessions et al., 2004) and improve wildlife habitat (Beguín et al., 2015), and is used as a management tool in protected areas (Heil and Burkle, 2018; Thorn et al., 2018). Alternatively, evidence suggests that salvage logging may disrupt post-disturbance succession, remove biological legacies (e.g., snags), and reduce the value of disturbed areas as wildlife habitat (Lindenmayer and Noss, 2006; Schmiegelow et al., 2006; Lindenmayer et al., 2017; Thorn et al., 2018). The ecological effects of natural disturbances and logging may interact, such that ecological responses to salvage logging are difficult to predict and are not comparable to green-tree harvest (Leverkus et al., 2018). Public discourse regarding salvage logging may become increasingly relevant, as climate warming is predicted to increase the frequency and severity of natural disturbances in forested landscapes (Fettig et al., 2013).

Fire has historically been the predominant disturbance agent in the boreal forest, but insect outbreaks are increasingly influential agents of tree mortality (Raffa et al., 2008). Forests affected by bark beetles (Coleoptera: Curculionidae, Scolytinae) have different successional trajectories than burned forests (Stevens-Rumann et al., 2015), and the impacts of post-infestation logging on wildlife may differ from those of post-fire logging for the same species (Kroll et al., 2012). Post-infestation salvage logging has received relatively little attention compared to that of fire (Saab et al., 2014; Thorn et al., 2018). Moreover, the impact of salvage logging on ecological processes such as predation or food web dynamics is largely unknown.

In this study, we examine responses of snowshoe hare (*Lepus americanus*) and its mammalian predators to small-scale salvage-logging after an insect outbreak in the boreal forest. Snowshoe hare are prey to a host of predators, and are considered a keystone species in North American boreal forests (Boutin et al., 1995). Hare abundance fluctuates in 8–10 year cycles, and these cycles have a substantial influence on local food webs (Boonstra et al., 2018; Boutin et al., 1995; Krebs, 2011). Anthropogenic disturbances that alter habitat conditions for snowshoe hare, such as salvage logging, may have deleterious impacts on localized trophic dynamics. Understanding the effects of salvage logging on hare habitat selection, and mitigating any negative impacts from anthropogenic changes to forest structure, may be important for preserving ecological processes in boreal forests.

Wildlife responses to post-infestation salvage logging are expected to vary, with potential benefits for early-seral species and negative consequences for species that require mature forests (Saab et al., 2014). For herbivores such as snowshoe hares that consume early-successional shrub vegetation (Fisher and Wilkinson, 2005; Hodges, 2000), canopy gaps created by beetle infestations may improve food resources by increasing light penetration and promoting understory growth (Klenner and Arsenault, 2009). This effect could be enhanced by salvage logging, particularly in boreal forests where ground disturbance from harvest machinery may be necessary to stimulate an understory response (Jonášová and Prach, 2008). Selective salvage logging may have relatively minor impacts on understory vegetation, but clear-cut salvage logging substantially alters early-successional communities (Fornwalt et al., 2018) and favours deciduous re-growth (Goodman and Hungate, 2006; Timoney et al., 1997).

Salvage logging also removes concealment and escape cover provided by beetle-killed trees, which can otherwise remain standing for decades after an infestation (Garbutt et al., 2006). For snowshoe hares, the loss of cover provided by the forest canopy and understory may significantly increase the risk of predation by aerial or terrestrial predators (Hodges, 2000; Feierabend and Kielland, 2015). This is particularly true in recently-logged stands where understory shrubs and trees have not yet recovered (Hodges, 2000). Selective salvage logging practices that retain residual trees or coarse woody debris could mitigate some of these negative impacts (Hodson et al., 2010b; Ruel et al., 2013). Woody debris from windthrow or felled unmerchantable timber provides valuable cover for snowshoe hares (Strong and Jung, 2012).

For Canada lynx (*Lynx canadensis*) and coyotes (*Canis latrans*)—the primary predators of snowshoe hare—habitat selection is closely linked to prey abundance (Mowat and Slough, 2003; O'Donoghue et al., 2001). Habitat selection may also depend on the ability to detect and access prey (Boisjoly et al., 2010). Lynx may avoid stands with dense saplings, despite the abundance of hares, because hares are difficult to locate and capture in these habitats (Fuller et al., 2007). If hare abundance is reduced in salvage logged stands, then predator use of these stands should also be reduced. However, logging may improve success rates for stalking and capturing snowshoe hares (Thibault and Ouellet, 2005), resulting in lynx and coyote using logged habitats at relatively higher rates than their prey (Boisjoly et al., 2010; O'Donoghue et al., 2001). This advantage may decline as understory cover increases with stand age (Fisher and Wilkinson, 2005).

Habitat choices for prey species are often influenced by trade-offs between food availability and predation risk (Verdolin, 2006). During post-harvest succession in the boreal forest, forage abundance may peak at a different successional stage than vertical or lateral cover, thus imposing trade-offs for herbivores (Hodson et al., 2011). Similarly, predators experience trade-offs between prey density and accessibility (Fuller et al., 2007), and the balance between these competing factors will likely shift through successional time (Fisher and Wilkinson, 2005). These mechanisms are likely to influence habitat use by predators and prey in response to salvage logging.

Our objective was to determine the patterns and processes by which post-infestation salvage logging, in response to an outbreak of spruce beetles (*Dendroctonus rufipennis*), affects habitat use by snowshoe hares and their primary predators, lynx and coyote. Few studies have examined the simultaneous responses of predators and prey to salvage logging. We used stands with different intensities of salvage logging (low tree retention, high tree retention, and unsalvaged) and different times since logging (0–10, 11–25 years) to elucidate the relative importance of food and cover in determining occupancy by hares and their predators.

We hypothesized that hares select habitats that minimize predation risk. Predation is likely the limiting factor that drives the snowshoe hare cycle (Krebs, 2011), with most hares in the boreal forest dying from predation rather than starvation (Hodges, 2000). Thus, we predicted that hares would favour unsalvaged stands, and among logged stands they would prefer high-retention over low-retention, because these stands would provide more concealment cover. An alternative hypothesis is that hares select habitat based on food availability, in which case they would preferentially use low-retention salvage-logged stands. Finally, if food and cover are both important, then high-retention stands would be an optimal balance of these conflicting requirements. If food availability and concealment cover increase over time in salvage-logged stands, we predicted that hares would use older logged stands more than recently logged stands. For predators, we hypothesized that habitat selection would be influenced by both the presence and accessibility of snowshoe hares. We predicted that lynx and coyote would use the same stands as hares, but they would show higher relative use of logged stands if prey were more accessible. With respect to stand age, habitat use by lynx and coyote should parallel that of hares (i.e., they should avoid recently logged stands); however, we expected predators would use older logged stands less than hares, if high shrub and sapling densities impede access to prey.

2. Methods

2.1. Study area

Our study was conducted in a boreal forest landscape near the village of Haines Junction, Yukon, Canada (60.7522°N, -137.5108°W). Forests were characterized by homogenous white spruce (*Picea glauca*) overstories with willow (*Salix* spp.) understories and a groundcover of moss and ground shrubs. Trembling aspen (*Populus tremuloides*) stands were rare but present in previously logged or burned areas. The average age of overstory spruce in the study area was 170 years (Garbutt et al., 2006). From 1990 to 2005, a severe infestation of spruce bark beetles affected nearly all mature spruce forest in this region, cumulatively impacting >360,000 ha (Berg et al., 2006; Garbutt et al., 2006). On average, forest stands had 32% ± 21.1 (SD) tree mortality caused by spruce beetles (Randall et al., 2011). Salvage logging began in the 1990's and is ongoing, with most of the wood used for fuel or building materials. Stands with the highest beetle mortality were generally selected for logging, although existing road access, community fire risk, recreational value, and fish and wildlife habitat were also considered (Alesk Renewable Resource Council, 2004). An average of 25% stand retention was recommended in designated High Wildlife Value Areas, which comprised over 86% of the region (Resource Assessment Technical Working Group, 2006), but clear-cut logging was practiced in areas where wildfire fuel reduction was the higher priority. Most logging occurred on a relatively small scale (<30 ha). Aside from post-infestation logging and associated roads, there were few anthropogenic disturbances on the landscape.

Snowshoe hare are a dominant component of the boreal forest food web in Yukon, and they were at the peak of their 10-year cycle during our study in 2016, with a mean density of close to 1 hare per ha (Boonstra et al., 2018). In addition to lynx and coyote, other predators of snowshoe hare in our study area included wolverine (*Gulo gulo*), red fox (*Vulpes vulpes*), red squirrel (*Tamiasciurus hudsonicus*), northern goshawk (*Accipiter gentilis*), and great horned owl (*Bubo virginianus*; Boonstra et al., 2018). Lynx largely specialize on hare as prey, whereas coyote are generalists that may include hare in their diet. Alternate prey for lynx and coyote included red squirrel, arctic ground squirrel (*Urocyon parryii*), various small rodents, and spruce grouse (*Falcapennis canadensis*; Boonstra et al., 2018). During our study, however, lynx and coyote were likely focused on hare because they were at a cyclic high (Boutin et al., 1995; O'Donoghue et al., 1998).

2.2. Study design

We collected data at 90 study sites, including high-retention salvage-logged (n = 38), low-retention salvage-logged (n = 22), and unsalvaged stands (n = 30; Fig. 1). We categorized salvage-logged stands as high retention if post-harvest overstory tree densities were ≥250 trees/ha, and low retention if densities were <250 trees/ha. Salvage-logged stands were also classified as recently logged (0–10 years old; n = 40) or older (11–25 years old; n = 20); these age classes likely reflect meaningful stages of vegetation change for snowshoe hare in the boreal forest, in terms of food and cover (Fisher and Wilkinson, 2005). Sample sizes for retention and age combinations reflected the availability of these stands on the landscape (high retention stands: 30 recently logged and 8 older logged stands; low retention stands: 10 recently logged and 12 older logged stands). Unsalvaged sites were randomly selected from areas within 1 km of logging roads, and salvage logged sites were selected to achieve adequate samples for each retention and age class. Sampling sites were separated by ≥ 300 m, with an average of 741 m ± 484 SD between neighbouring sites.

2.3. Occupancy surveys

From May to October 2016, we recorded hare, lynx, and coyote presence using 50 wildlife cameras (Hyperfire PC800, Reconyx Inc., Holmen, Wisconsin, USA). Cameras were rotated through 90 sites during two phases, with half surveyed prior to 27 July, and the remainder surveyed thereafter. Sites of each stand type were randomly assigned to either the first or second sampling phase. To reduce bias, we selected camera locations randomly within each stand, and directed cameras towards forest openings to improve detection. We positioned cameras on trees approximately 50 cm above ground level to maximize

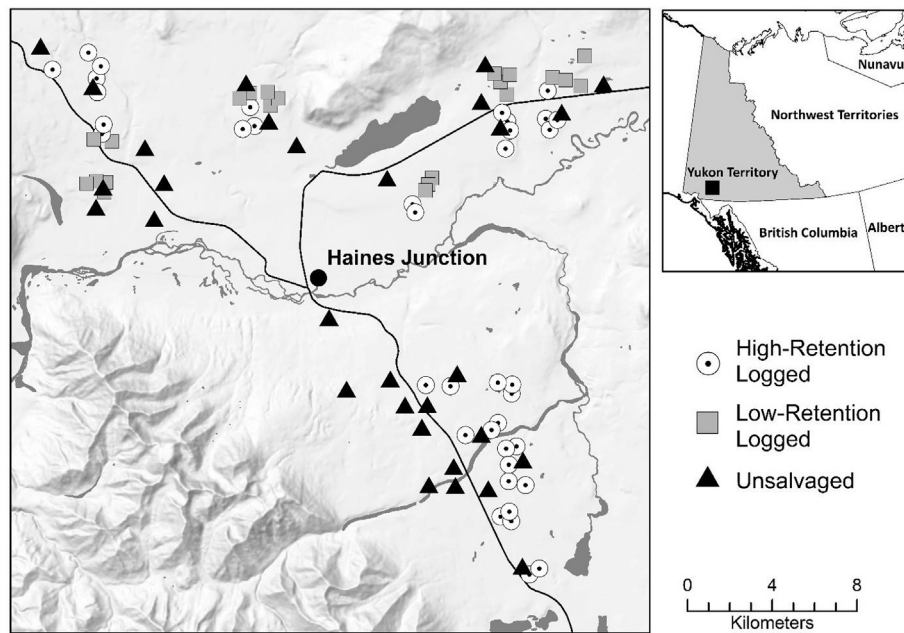


Fig. 1. Study area and wildlife camera locations in the boreal forest of southwestern Yukon, Canada. Cameras were placed in high-retention salvage logged ($n = 38$), low-retention salvage logged ($n = 22$), and unsalvaged spruce beetle stands ($n = 30$). Black lines represent major roads, and areas shaded in dark grey are water bodies.

the detection of snowshoe hare, lynx, and coyote. Camera images were processed using Timelapse 2 software (Greenberg Consulting Inc., Calgary, Alberta, Canada). We defined individual wildlife capture events as either a) consecutive photos of different species, b) consecutive photos of the same species, separated by > 30 min, or c) non-consecutive photos of the same species. A 30-min lag between capture events provided a close approximation of estimated hare density in our study area (Villette et al., 2017).

2.4. Vegetation, forest, and landscape structure

We measured understory vegetation and forest structure at each site to characterize habitat value in terms of food and escape or concealment cover (Table 1). We used habitat characteristics as a proxy for predation risk, as prey often have a stronger response to habitat features than to actual predator abundance (Verdolin, 2006). We collected vegetation data along three 40-m transects originating at the wildlife camera; one transect was in the centre of the camera detection zone, and the other two were perpendicular to the first. We determined tree density (trees/ha) and basal area (m^2/ha) using the point-centred quarter method (Cottam and Curtis, 1956), taking measurements at the camera location and at the 20-m and 40-m locations on each transect (seven locations total). Trees were classified as overstorey trees if the diameter at 1.3 m (DBH) was ≥ 5 cm, and understory trees if DBH was < 5 cm. At each of the seven locations, we used a convex spherical densiometer to record canopy cover (%), and we measured lateral cover (%) with a 2-m tall cover pole at 5-m distances from the sampling point in each cardinal direction (Griffith and Youtie, 1988). To quantify available food for hare, we estimated percent cover of shrubs, herbaceous plants, and grasses in seven $0.5 m^2$ circular plots at each sampling location. We also counted the number of deciduous stems within three $1 \times 10 m$ rectangular plots ($stems/10 m^2$). Stem counts included shrubs and deciduous trees with at least one twig $\leq 0.5 m$ from the ground (to reflect summer food for hares).

Mammals may respond to habitat characteristics at the landscape-scale (Fisher et al., 2011). Land cover data with adequate resolution were not available for the study area, so we developed a land cover product through classification of Sentinel-2 satellite images (European Space Agency Copernicus Program). We used supervised maximum-likelihood classification in ArcGIS version 10.4.1 (ESRI, Redlands, California, USA) to distinguish three classes: forest, open, and water. Classification accuracy was 90%, verified with ground truthing and aerial imagery at 100 locations. Because hares and predators may associate with forest edges (Gigliotti et al., 2018; Oehler and Litvaitis, 1996), we calculated total forest edge (m) and forest cover (%) within a 500-m radius of each site using Fragstats version 4.2.1 (University of Massachusetts, Amherst, Massachusetts, USA). We also measured the distance to the nearest forest edge (i.e., logged stand or linear feature) with the Point Distance tool in ArcGIS.

Table 1

Variable names, descriptions, hypotheses, and predictions (in parentheses) for site- and landscape-level habitat variables used in occupancy models for snowshoe hare and their predators (lynx and coyote) in beetle-affected and salvage-logged forests in Yukon, Canada.

Variable	Description	Species, Hypothesis, and Prediction
<i>Site-level Covariates</i>		
Stand Type	Low-retention logged, high-retention logged, un-salvaged	Hares: Logging reduces cover (–) Predators: Follow prey (–)
Stand Age	Early-seral (0–10 years) and mid-seral (11–20 years), un-salvaged (>100 years)	Hares: Cover and food improve over time (+) Predators: Follow prey (+)
Overstory Trees	Stand density (trees/ha) of overstory trees (DBH >3 cm), measured along 40 m transects	Hares: Provides cover from terrestrial/aerial predators (+) Predators: Follow prey but avoid dense stands where hunting success is reduced (+ asymptote)
Understory Trees	Stand density (trees/ha) of understory trees (DBH <3 cm), measured along 40 m transects	Hares: Provides cover and food (+) Predators: Follow prey but avoid dense stands where hunting success is reduced (+ asymptote)
Canopy	Canopy cover (%) of stand, measured along three 40 m transects	Hares: Provides overhead cover (+)
Deciduous Stems	Number of deciduous stems (stems/10m ²), including shrubs and trees <2 m tall	Hares: Increases food (+)
Lateral Cover	Percent cover (%), measured with a 2 m tall cover pole	Hares: Provides cover (+) Predators: Follow prey but avoid dense stands where hunting success is reduced (+ asymptote)
Shrub Herb Grass Cover	Percent cover (%) of herbaceous plants, grasses, and shrubs in 0.5m ² circular plots	Hares: Increases food (+)
CWD	Total number of downed trees with diameter >4 cm, intersecting three 40 m transects	Hares: Provides cover (+)
<i>Landscape Covariates</i>		
Edge	Distance (m) from camera to nearest forest edge (e.g., edge of logged stand, road, pipeline)	Hares: Edges have high food, close to cover (–) Predators: Follow prey (–)
Total Edge	Total forest edge distance (m) within a 500 m radius of camera	Hares: Edges have high food, close to cover (+) Predators: Follow prey (+)
Forest Cover	Percent cover (%) of forest within a 500 m radius of camera	Predators: Prey prefer forest, predators respond to prey abundance on a landscape scale (+)

2.5. Analyses

We conducted a multi-staged analysis. First, we determined the effects of salvage logging on food and cover to provide context for hare, lynx, and coyote occupancy analyses. Next, we ran species occupancy models, first developing the detection component, then directly testing the effects of stand type and age on hare, lynx, and coyote occupancy. Lastly, we developed a set of candidate occupancy models and used model selection procedures to determine the underlying mechanisms of salvage logging effects.

We compared food and cover (i.e. vegetation and forest structure) metrics among stand-types (low retention, high retention, and un-salvaged) with ANOVAs and post-hoc Tukey's HSD tests. Basal area, overstory tree density, and understory tree density were log₁₀ transformed to meet model assumptions. We compared understory tree density, lateral cover, deciduous stem density, and shrub + herb + grass cover between stand ages (0–10 years and 11–25 years) using independent sample t-tests. Analyses were completed in R version 3.4.3 (www.r-project.org).

We analyzed wildlife camera data using single-season occupancy models with the R package *RPresence* (version 2.12.6, [Mackenzie and Hines, 2017](#)). Occupancy models allow the use of presence/absence data to assess landscape-level patterns in habitat use while accounting for imperfect species detection ([Mackenzie et al., 2006, 2002](#)). Models incorporated the effects of site-specific covariates on occupancy (ψ), as well as site- and survey-specific covariates that could influence detection rates (p). Although data were analyzed using an occupancy modelling framework, results for lynx and coyote should be interpreted as relative habitat use rather than patch occupancy because home ranges were larger than the spacing between camera units ([Efford and Dawson, 2012; Mackenzie et al., 2006](#)). We assumed that occupancy rates would reflect the relative importance of these habitats to each species.

Camera data are continuous and must be divided into discrete sampling periods for occupancy models. We defined a sampling period as 7 days for hare and 15 days for lynx and coyote; this yielded detection probabilities that were adequate (>0.2) for models to converge on precise occupancy estimates ([Mackenzie and Royle, 2005](#)). Before occupancy analysis, we determined the most plausible detection model for each species by fitting different combinations of site- and survey-specific covariates suspected to influence detection. Vegetation structure may alter the size of the camera detection zone, or influence animal behaviour in a way that affects detection ([Burton et al., 2015](#)), resulting in habitat-specific detection rates. Phenological changes in species behaviour and abundance may cause detection rates to vary. We considered tree density, lateral cover, basal area, and sampling date as potential detection covariates. We incorporated the best detection model into all subsequent occupancy models for each species.

To test the effects of salvage logging on hare, lynx, and coyote occupancy, we ran the models ψ (stand type) and ψ (stand age). In both cases, “unsalvaged” was the reference category to which logged stands of different retention categories or ages were compared. We used regression coefficients and odds ratios to interpret effect sizes. We then developed a set of models to test *a priori* hypotheses about the influences of forest structure and landscape composition on hare, lynx, and coyote occupancy (Table 1), thus evaluating the mechanisms by which salvage logging affects these species. The candidate set of occupancy models included single-variable models as well as additive and interactive combinations of variables when biologically relevant (i.e. when interactive or additive effects were anticipated based on species' ecology). For example, lynx may select sites with high snowshoe hare occupancy, but this effect may be reduced in very dense habitats where hunting efficiency is lower (Fuller et al., 2007); therefore, we included the interaction between hare occupancy and understory tree density in our lynx models. All continuous covariates were standardized by converting to z-scores (overall mean of 0 and standard deviation of 1), and correlated covariates ($r > 0.6$) were not included in the same model to avoid multicollinearity (Dormann et al., 2013). To test for trends in occupancy along longitudinal or latitudinal gradients, and to account for potential spatial autocorrelation, we ran models with first- and second-order polynomials of spatial coordinates (Legendre and Legendre, 2012). If spatial terms improved model performance, they were retained in candidate models.

We compared candidate models to each other, and to the null and global models, using Akaike's Information Criterion (AIC) or Quasi-AIC (QAIC). We removed models with uninformative parameters from the candidate set (i.e. complex models that received lower AIC than the simpler nested model; Arnold, 2010), as well as models that did not converge. AIC weights were used to evaluate the relative strength of each candidate model. If no single model received a weight $> 90\%$, we calculated parameter estimates and unconditional standard errors by averaging across a set of confidence models (the “confidence set”) where Akaike weights summed to approximately 0.95 (Burnham and Anderson, 2003).

We calculated occupancy model residuals (Warton et al., 2017) from the best-fitting (lowest AIC) model and tested for spatial autocorrelation using Moran's I correlograms of residuals (Dormann et al., 2007). We evaluated the fit of the most saturated model with 10,000 bootstrapping events and a chi-square goodness-of-fit test (MacKenzie and Bailey, 2004), and QAIC values were used to compare models when overdispersion and a lack of fit were indicated ($\hat{c} > 1$). When QAIC was used for model selection, we inflated unconditional standard errors by the square root of the \hat{c} value (MacKenzie and Bailey, 2004).

3. Results

Salvage logging resulted in habitat changes (i.e., food and cover) that were dependent on retention level and stand age. Unsalvaged stands had significantly higher basal area, canopy cover, and overstory tree density than high-retention-logged stands, which in turn had higher values than low-retention-logged stands (Fig. A1). Understory tree density and lateral cover were highest in unsalvaged stands, whereas deciduous stem density was highest in low-retention logged stands (Fig. A1). Unsalvaged stands also had the least amount of coarse woody debris and the lowest shrub + herb + grass cover (Fig. A1). Understory tree density, lateral cover, and shrub + herb + grass cover did not differ between low and high retention stands, but they did increase with stand age (Fig. A1, A2). In contrast, deciduous stem density did not differ between recently logged (0–10 year) and older (11–25 year) logged stands (Fig. A2).

Camera monitoring was successful at 89 of 90 sites (one camera malfunctioned at an unsalvaged site), resulting in a total of 5,905 camera-trap days. Hare, lynx, and coyote were detected at 63%, 34%, and 22% of sites, respectively. We recorded 1298 capture events for snowshoe hare across all sites. Lynx and coyote were captured on camera a total of 50 and 51 times, respectively.

3.1. Snowshoe hare

The best-fitting detection model for snowshoe hare contained tree basal area, which was positively related to probability of detection (Tables 2 and 3).

Hare occupancy was significantly higher in unsalvaged stands ($\beta = 3.51$ [95% confidence interval (CI) = 0.39, 6.64]) than in high-retention ($\beta = -3.60$, 95% CI = -6.79, -0.41) or low-retention logged stands ($\beta = -3.48$, 95% CI = -6.72, -0.25; Fig. 2). Unsalvaged stands also had higher occupancy than salvage-logged stands of either age category (0–10 years: $\beta = -3.49$, 95% CI = -6.67, -0.31; 11–25 years: $\beta = -3.69$, 95% CI = -6.93, -0.44; Fig. 2). However, among the logged stands there was no difference in occupancy between low-retention and high-retention logged stands, or between recently logged and older stands (Fig. 2; Table A1; Table A2).

For models that included covariates related to food and cover, our model selection procedures resulted in seven occupancy models in the confidence set, with models including single variables and additive combinations of overstory tree density, canopy cover, lateral cover, shrub + herb + grass cover, stand age, and stand type (Table 2). The top model (overstory trees + lateral cover) received 1.5 times more support than the second-best model, and 15.5 times more support than the last model in the confidence set. Both overstory tree density and canopy cover had a significant positive relationship with hare occupancy (Table 3), approaching asymptotes at approximately 2000 trees/ha and 70% canopy cover, respectively (Fig. 3A and B). Hare occupancy tended to increase with lateral cover but confidence intervals overlapped zero (Table 3, Fig. 3C). In contrast, hare occupancy declined with increasing food availability, measured as percent cover of shrubs, herbs, and grasses (Table 3, Fig. 3D). Deciduous stem density, another metric of food, was not included in any models in the confidence set.

Table 2

Confidence set of occupancy (ψ) and detection (ρ) models (QAIC or AIC weights sum to ~0.95) for snowshoe hare, lynx, and coyote in beetle-affected and salvage-logged forest in Yukon, Canada. Quasi-Akaike's Information Criterion (QAIC), delta QAIC, QAIC weight, and number of parameters (K) are shown for each candidate model (lynx values are in AIC units). Occupancy covariates are defined in Table 1. Null models are indicated with (.).

Species/Model	QAIC	Δ QAIC	QAIC weight	K
<i>Snowshoe Hare</i>				
ψ (Overstory Trees + Lateral Cover), ρ (Basal Area)	533.09	0	0.3169	5
ψ (Canopy + Lateral Cover), ρ (Basal Area)	533.98	0.89	0.2146	5
ψ (Canopy), ρ (Basal Area)	534.17	1.08	0.2001	4
ψ (Overstory Trees), ρ (Basal Area)	534.40	1.31	0.1671	4
ψ (Stand Age), ρ (Basal Area)	537.51	4.42	0.0326	4
ψ (Lateral Cover + Shrub Herb Grass), ρ (Basal Area)	537.51	4.90	0.0222	5
ψ (Stand Type), ρ (Basal Area)	538.49	5.40	0.0205	4
<i>Lynx</i>				
ψ (Stand Type + Easting), ρ (.)	256.98	0	0.3705	4
ψ (Hare Occupancy + Easting), ρ (.)	257.55	0.57	0.2786	4
ψ (Easting), ρ (.)	258.07	1.09	0.2149	3
ψ (Stand Age), ρ (.)	261.45	4.47	0.0396	3
ψ (Hare Occupancy), ρ (.)	262.93	5.95	0.0189	3
ψ (.), ρ (.)	263.48	6.5	0.0144	2
ψ (Stand Type + Total Edge), ρ (.)	263.53	6.55	0.014	4
<i>Coyote</i>				
ψ (Hare Occupancy + Northing), ρ (.)	165.04	0	0.5451	4
ψ (Stand Type + Northing), ρ (.)	166.73	1.69	0.2341	4
ψ (Stand Age + Northing), ρ (.)	167.78	2.74	0.1385	4
ψ (Overstory Trees + Northing), ρ (.)	170.04	5	0.0447	4

Results of the goodness-of-fit test for the global model suggested an adequate fit ($\chi^2 = 4724.12$, $P = 0.05$), but data were overdispersed ($\hat{c} = 1.41$). Weak but significant spatial autocorrelation was detected up to a lag distance of 1 km; however, the Moran's I statistic was <0.3 within this distance range (Fig. A3). Given that spatial autocorrelation was weak, and that sites were spaced at greater distances than snowshoe hare summer home range sizes (Feierabend and Kielland, 2014), we did not adjust models for spatial autocorrelation.

Table 3

Model averaged parameter estimates, unconditional standard errors (SE), and 95% confidence intervals (CI) for detection (ρ) and occupancy (ψ) of snowshoe hare, lynx, and coyote in beetle-affected and salvage-logged forest in Yukon, Canada. Covariates following ρ and ψ intercepts are detection and occupancy parameters, respectively. Estimates were calculated by averaging across the set of confidence models where QAIC or AIC weights summed to 0.95. Occupancy covariates are defined in Table 1. Significant coefficient estimates (CI's do not overlap zero) are denoted with an asterisk (*).

Species/Parameter	Estimate	SE	95% Lower CI	95% Upper CI
<i>Snowshoe Hare</i>				
ρ intercept	0.04	0.11	-0.18	0.26
Basal Area*	0.65	0.12	0.42	0.88
Ψ intercept	0.84	0.51	-0.15	1.84
Overstory Tree Density*	1.6	0.73	0.17	3.04
Canopy*	1.19	0.44	0.33	2.04
Lateral Cover	0.55	0.35	-0.13	1.23
Shrub Herb Grass Cover*	-0.68	0.33	-1.3268	-0.0332
Stand Type ^{a, *}	1.13	0.42	0.3068	1.9532
Stand Age ^{a, *}	1.07	0.39	0.3056	1.8344
<i>Lynx</i>				
ρ intercept	-1.27	0.24	-1.73	-0.8
Ψ intercept	-0.68	1.09	-2.82	1.45
Stand Type	0.99	0.58	-0.14	2.12
Hare Occupancy	2.96	2.01	-0.99	6.91
Easting*	-0.0014	0.00067	-0.0027	-0.000087
Stand Age	0.83	0.51	-0.17	1.83
Total Edge	0.51	0.37	-0.22	1.24
<i>Coyote</i>				
ρ intercept	-1.04	0.30	-1.62	-0.46
Ψ intercept	-4.00	1.84	-7.61	-0.38
Hare Occupancy*	6.16	2.04	2.16	10.16
Stand Type*	1.38	0.47	0.46	2.30
Stand Age*	1.14	0.43	0.30	1.98
Overstory Tree Density	0.91	0.50	-0.07	1.89
Northing*	0.002	0.0008	0.00043	0.0036

^a Stand type and stand age were treated as ordinal variables in model selection procedures to facilitate model convergence.

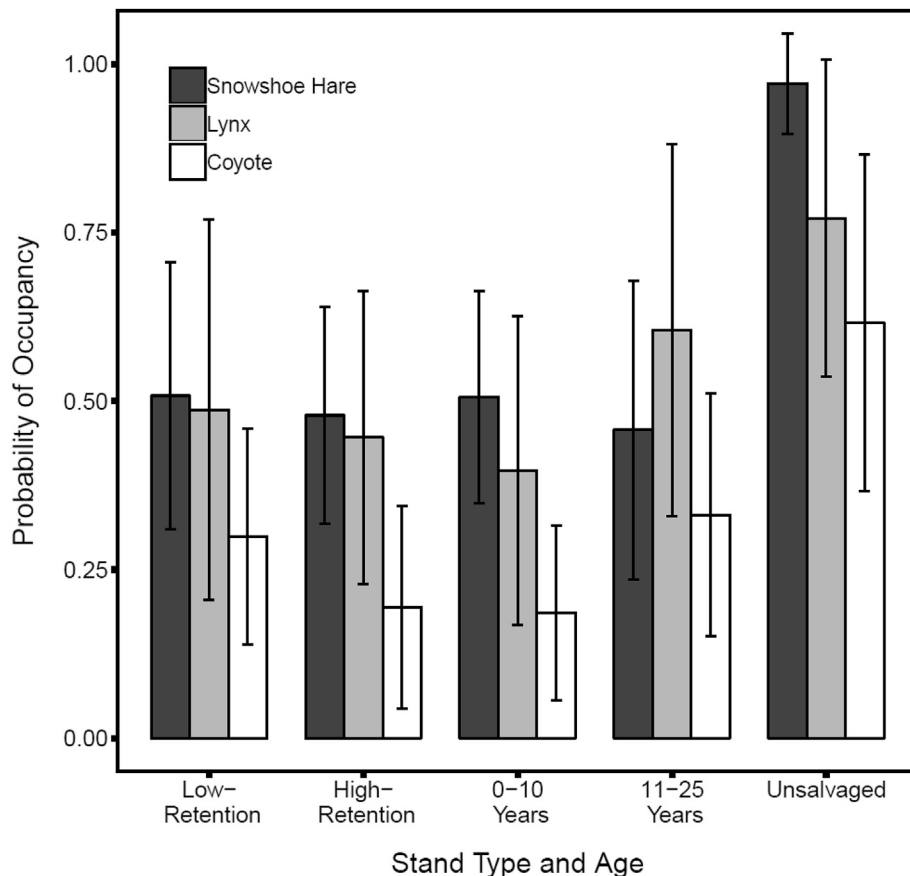


Fig. 2. Estimates of snowshoe hare, lynx, and coyote occupancy in salvage logged stands of different retention levels (low/high) and ages (0–10 years and 11–25 years post-harvest), and in un-salvaged forest stands in southwest Yukon, Canada. Results shown are from models testing the effects of stand type and age on species occupancy while accounting for imperfect detection, i.e., snowshoe hare: $\psi(\text{stand type})$, $\rho(\text{basal area})$ and $\psi(\text{stand age})$, $\rho(\text{basal area})$; lynx and coyote: $\psi(\text{stand type})$, $\rho(\cdot)$ and $\psi(\text{stand age})$, $\rho(\cdot)$. Error bars represent 95% confidence intervals.

3.2. Lynx and coyote

Lynx and coyote detection did not vary with any of our measured covariates.

Logging treatments alone did not predict occupancy by lynx as well as they did for hare. Lynx occupancy declined in salvage-logged stands, but differences between stand types were not significant (low retention: $\beta = -1.27$, 95% CI = $-3.52, 0.99$; high retention: $\beta = 1.43$, 95% CI = $3.50, 0.64$; Fig. 2; Table A1). Compared to un-salvaged stands, lynx occupancy was lower in the older logged stands (i.e., 11–25 year stands; $\beta = -0.80$, 95% CI = $-3.13, 1.53$), and even more so in recently logged stands (i.e., 0–10 year stands; $\beta = -1.64$, 95% CI = $-3.74, 0.45$), but confidence intervals overlapped (Fig. 2, Table A2). Patterns of lynx and hare occupancy were generally similar with respect to stand type and age, although lynx may have used un-salvaged stands less than hare, and 11–25-year-old logged stands more than hare (Fig. 2). Compared to hare, occupancy rates for lynx were more variable.

When covariates were included, the confidence set of occupancy models for lynx included models with stand type, hare occupancy, stand age, and total edge, as well as the null model (Table 2). The best-fitting lynx model (stand type + easting) had similar support to the alternative model (hare occupancy + easting; Table 2). Easting was present in all three top models and was the only parameter with significant effects (Table 3). Although lynx occupancy was positively related to hare occupancy, confidence intervals overlapped zero (Table 3, Fig. 4A). No models with interactive effects were included in the confidence set. Occupancy models were a good fit to the data ($\chi^2 = 58.59$, $P = 0.43$), and there was no overdispersion ($\hat{c} = 0.95$) or spatial autocorrelation (Fig. A3).

Coyote occupancy was higher in un-salvaged stands than in high-retention logged stands ($\beta = -1.90$, 95% CI = $-3.52, -0.27$), while use of low-retention and high-retention stands was similar (Fig. 2, Table A1). Occupancy was lower in recently logged stands compared to un-salvaged stands ($\beta = -1.96$, 95% CI = $-3.58, -0.33$), but coyotes did not select older logged stands more than recently logged stands (Fig. 2, Table A2). Coyote occupancy was more variable than hare occupancy in different stand types and ages.

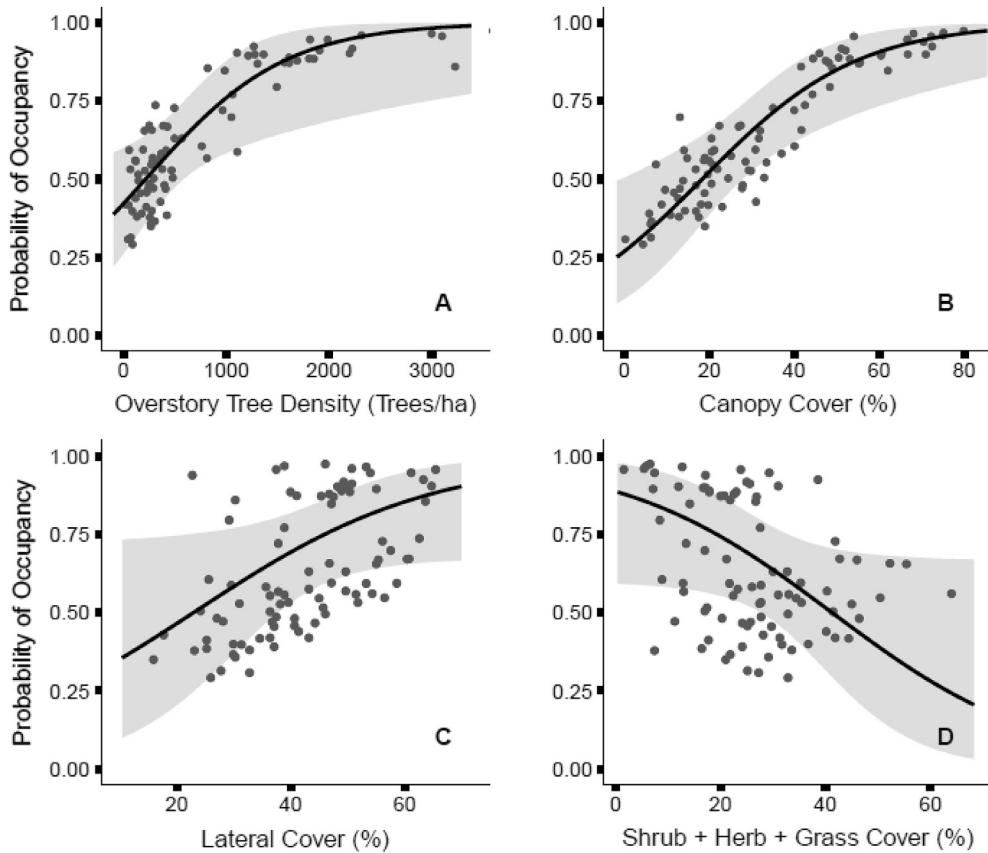


Fig. 3. Model-averaged estimates of snowshoe hare occupancy as a function of overstory tree density (A), canopy cover (B), lateral cover (C), and shrub + herb + grass cover (D) in beetle-affected and salvage-logged forests in southwest Yukon, Canada. Occupancy estimates (points) and predicted relationships (lines) were obtained by model-averaging across the confidence set of models where QAIC weights summed to 0.95. Lines show predicted covariate effects, when all other covariates are held constant at their mean. Shaded regions are unconditional 95% confidence intervals.

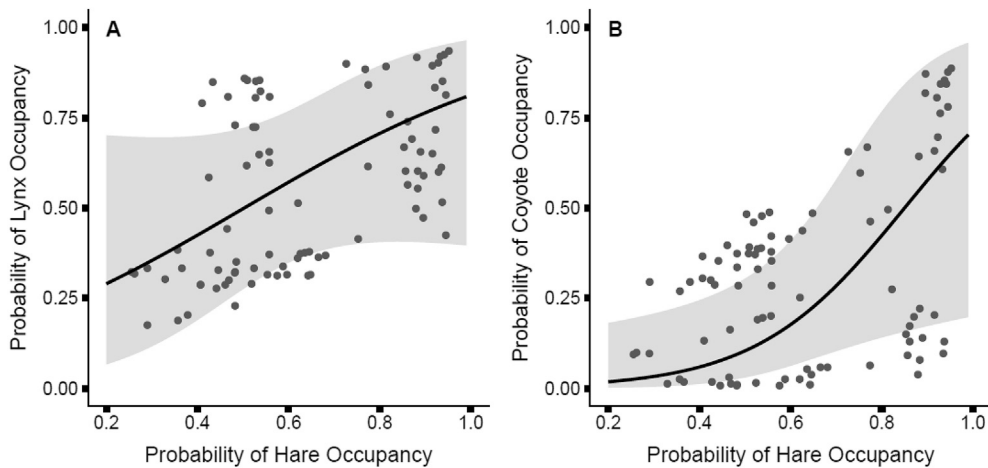


Fig. 4. Model-averaged estimates of lynx (A) and coyote (B) occupancy versus predicted snowshoe hare occupancy in beetle-affected and salvage-logged stands in southwest Yukon, Canada. Occupancy estimates (points) and predicted relationships (lines) were obtained by model-averaging across the confidence set of models where QAIC weights summed to 0.95. Lines show the predicted effects of snowshoe hare occupancy, while accounting for effects of all other covariates. Shaded regions represent unconditional 95% confidence intervals.

Model selection, with covariates included, resulted in four occupancy models with additive effects in the confidence set (Table 2). The top model (hare occupancy + northing) for coyotes received > 2.3 times more support than any other model. Hare occupancy had a significant positive effect on coyote occupancy (Table 3, Fig. 4B). All models in the confidence set included northing as a covariate (Table 3). Overstory tree density had a positive effect but confidence intervals were large, suggesting that effects were inconsistent (Table 2). Models were a good fit for the data ($\chi^2 = 61.69$, $P = 0.23$) and there was minor overdispersion ($\hat{c} = 1.09$). Spatial autocorrelation was not detected (Fig. A3).

4. Discussion

Our main finding was that salvage logging reduced occupancy by snowshoe hare, lynx, and coyote via changes to forest structure. As predicted by our predation hypothesis, salvage logging had a negative impact on hares, although high stand retention did not mitigate these effects, and occupancy did not improve with time since logging. Lynx and coyote generally used the same habitat as hares, but this relationship was weaker for lynx. Habitat use by lynx and coyote tended to increase with stand age.

4.1. Snowshoe hare

Vegetation characteristics only influenced the probability of camera detection for snowshoe hare. We expected dense vegetation to reduce detection rates, but detection increased with basal area. Hares may experience lower predation rates in densely-treed forests, so they are more active and abundant in these habitats (Ewacha et al., 2014; Hodson et al., 2010a), potentially causing an increase in detection rates.

Our predictions about hare response to salvage logging were supported. Hares showed strong selection for unsalvaged stands with high overstory tree density, canopy cover and, to a lesser extent, lateral cover. Negative impacts of logging on snowshoe hares have been documented previously, but in a relatively restricted area of eastern Canada (de Bellefeuille et al., 2001; Hodson et al., 2010b; Potvin et al., 2005). The value of intact forest and logged stands were expected to converge with increasing stand retention (Hodson et al., 2010b; Ruel et al., 2013), yet hares in our study area did not use logged stands of one retention class more than the other. Residual trees in high-retention stands may have provided inadequate protection from aerial predators.

Unsalvaged stands had the highest canopy cover and tree densities but the lowest deciduous stem densities and shrub + herb + grass cover, likely imposing a trade-off between food and cover for hares. Hares occupied stands with apparently low predation risk (i.e., unsalvaged stands) rather than high food (i.e., logged stands). Predation is the most significant constraint on snowshoe hare populations in the boreal forest (Hodges, 2000; Krebs, 2011). Hare occupancy approached its asymptotic maximum in stands with high overstory tree density and canopy cover, perhaps because food became limiting in very dense forests.

The positive relationship between hare occupancy and cover was consistent with previous studies (Hodson et al., 2010a, 2011; Ewacha et al., 2014, but see Fuller and Harrison, 2013). More surprising was that habitat selection was driven by overhead cover more than understory cover; covariates relating to overhead cover (canopy and overstory tree density) ranked higher in model selection and had stronger relationships with hare occupancy. This suggests that evading avian predators (e.g., northern goshawks and great horned owls) may be more important than avoiding terrestrial predators during spring and summer. Aerial predators may be more difficult for hares to detect and avoid. Conversely, during winter, mammalian predation rates are higher than avian predation rates (Feierabend and Kielland, 2015), perhaps explaining the elevated importance of understory cover found by studies conducted in winter (Ewacha et al., 2014; Fuller and Harrison, 2013).

Amongst salvage-logged stands, hares exhibited no preference for older (11–25 years) or recently-logged (0–10 years) stands, contrary to our predictions. Logged stands of all ages had significantly lower occupancy than unsalvaged stands which were all >100 years old (Garbutt et al., 2006). This is contrary to findings from studies at lower latitudes, where early- and mid-successional stands (10–40 years old) supported more hares than mature coniferous forests (Allard-Duchène et al., 2014; Fisher and Wilkinson, 2005; Newbury and Simon, 2005). Forest succession may progress slowly at high latitudes, suggesting that salvage-logged stands will take a comparatively long time to recover their value for hares.

Snowshoe hare habitat preferences are density-dependent (Hodson et al., 2010b) and may vary throughout the 10-year population cycle, which is largely driven by predation rather than food (Krebs, 2011). Hares are more likely to use open habitat with minimal canopy cover during high phases of the cycle when competition for food is highest and predation risk lowest. Conversely, they use denser cover during decline and early low phases of the cycle because competition for food decreases and predation risk intensifies (O'Donoghue et al., 2001). Hares also use more open habitat in summer compared to winter (Hodges, 2000). Despite our study being conducted largely in summer during the peak phase of the hare cycle (Boonstra et al., 2018), hares strongly avoided logged stands and selected densely-treed areas. This suggests that these habitat preferences could be even more pronounced in winter and during the decline and low phases of the cycle, when predation risk is highest. However, there is evidence that hares may not alter their habitat preferences under different levels of predation pressure (Hodges and Sinclair, 2005). Additional study during the low phase of the hare cycle would help clarify whether their response to salvage logging is density-dependent.

4.2. Lynx and coyote

As predicted, the patterns of habitat use by lynx and coyote were similar to those of snowshoe hare: all three species tended to use unsalvaged stands more than salvage-logged stands. Among logged stands, the level of tree retention had no effect on predator occupancy, likely because hares were similarly unaffected. Lynx are a specialist predator of hare and are thought to select habitat based on hare availability more so than land cover (Mowat and Slough, 2003; O'Donoghue et al., 2001). Coyote are more of a generalist predator than lynx, but they too prefer habitats with abundant hares in Yukon, and this may result in the use of dense forest (O'Donoghue et al., 2001). This contrasts with their behaviour in eastern North America where coyotes do not rely on hares to the same extent, and where they benefit from anthropogenic disturbance and favour clear-cuts over intact forest (Boisjoly et al., 2010; Crimmins et al., 2012).

Habitat characteristics that affect prey encounter rates and hunting success can also be important for predators (Gorini et al., 2012). Lynx and coyote are thought to use more open habitat than hares (Fuller et al., 2007; O'Donoghue et al., 2001), as these predators may seek habitat where hares are more vulnerable (Arias-Del Razo et al., 2011; Fuller et al., 2007). Lynx may have reduced hunting success in habitats where conifer trees exceed a density threshold (Fuller et al., 2007). Thus, we predicted that lynx and coyote would exhibit stronger selection for salvage-logged stands relative to hares, but our data did not support this prediction. We found no evidence that the strength of the relationship between lynx, coyote, and hare occupancy was influenced by understory cover. Predator occupancy was more closely tied to hare occupancy than any habitat characteristic. Coyotes had a particularly strong relationship to hare occupancy, perhaps because coyotes are highly versatile predators that can switch their hunting techniques in dense habitats, potentially out-competing lynx (Buskirk et al., 2000). Snowshoe hare were likely the main prey for coyote during our study because hare populations were at a cyclic high (O'Donoghue et al., 1998, 2001).

We predicted that lynx and coyote would select older logged stands compared to recently logged stands. Although highly variable, lynx did have higher occupancy in older logged stands, consistent with previous findings that lynx prefer mid-successional stands over newly harvested areas (Fisher and Wilkinson, 2005; Fuller et al., 2007; Parker et al., 1983). As predicted, coyote also avoided recently logged stands. Coyotes in eastern Canada may have higher hunting success in open habitats (Thibault and Ouellet, 2005); however, coyotes in the western boreal forest may improve their success by using dense vegetation as concealment cover when hare are a main prey item (Murray et al., 1995). Such dense vegetation was lacking in recently logged stands.

4.3. Conclusions

Climate change is predicted to heighten the potential for large scale bark beetle outbreaks and wildfires (Fettig et al., 2013), and salvage logging may become increasingly prevalent. As post-infestation salvage logging of boreal and sub-boreal forests is a relatively new practice, guidelines are being developed and research is needed to inform forest management policies. The results of our study suggest that salvage-logged stands have lower value than beetle-affected forest for snowshoe hares and their terrestrial predators. Logging practices that maintain residual trees—even at relatively high retention levels—do not provide adequate cover for hares. Higher retention may be required to mitigate negative impacts at the stand scale. Retaining patches of residual trees rather than individual trees may be beneficial to hares, as intact patches could provide refugia from predators.

Salvage logging in the northern boreal forest is occurring at a small scale (i.e., < 30 ha per cut) and our results are not necessarily transferrable to regions where salvaged areas are larger and more widespread on the landscape. Extensive salvage logging could ultimately cause hare population declines, as open habitats are population sinks for hares (Griffin and Mills, 2009), causing potential impacts to boreal forest food webs (Boonstra et al., 2018; Boutin et al., 1995; Krebs, 2011). Further study on the impacts of salvage logging during the low phase of the hare cycle would help clarify the potential for density-dependent population-level responses. Salvage logging practices that maintain small cut-sizes interspersed with large patches of boreal forest are least likely to effect hares and their predators. If salvage operations continue to expand in the boreal forest, it will be important to consider the timing of logging cycles, as well as the scale of logging. Forest succession proceeds slowly in northern climates, and it will likely be well over 25 years before logged stands recover to the point where they provide high quality habitat for snowshoe hare and their predators.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00562>.

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