

Can retention harvests help conserve wildlife? Evidence for vertebrates in the boreal forest

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Abstract. Retention harvesting, or the approach of leaving live mature trees behind during forest harvest, is used in natural disturbance-based management to mitigate the effects of logging on biodiversity. However, responses of many boreal vertebrates to variable retention harvesting are unknown. We investigated the influence of different retention levels in forest harvests on stand use by wildlife 15–18 yr post-harvest using a combination of surveys of wildlife signs (scats, middens) and camera trapping. Site-level measures of forest structure, including canopy cover, horizontal cover, tree height, tree diameter, basal area, cover of downed coarse woody material, and understory plant cover, were used to describe post-harvest differences in habitats used by common wildlife species in northwest Alberta's boreal forest. Stand use of six species (black bear, coyote, fisher, red squirrel, wolverine, woodland caribou) increased with level of retention, while stand use of two species (grouse, snowshoe hare) declined with retention level. Retention level did not significantly affect stand use of five species (American marten, Canada lynx, deer, gray wolf, moose). Higher levels of retention characterized by greater canopy cover, basal area, and abundance of deadwood were associated with use of forest habitats by late-seral species. Woodland caribou, a species of conservation concern, was detected only in harvested stands with at least 20% retention. Greater understory and horizontal cover characterized lower levels of retention being attractive for early-seral species. These findings demonstrate the value of retention harvesting for conservation of wildlife species in boreal forest, while highlighting the challenge of managing forests for multiple species with different habitat preferences.

Key words: anthropogenic disturbance; boreal forest; logging; mammals; natural disturbance-based management; partial harvesting; sustainable forestry; tree retention harvesting; vertebrates; wildlife; woodland caribou.

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INTRODUCTION

The traditional method of harvesting forests by clear-cutting leads to changes in wildlife activity (Telfer 1974, Thompson 1988, Fisher and Wilkinson 2005). The recent alternative of retention harvesting, whereby live mature trees are retained in cutblocks at time of harvest, is now widely and increasingly used in sustainable forestry for biodiversity conservation (Work et al. 2003, Gustafsson et al. 2012). Retention harvests are thought to reduce the impacts of logging by

increasing habitat connectivity, enhancing structural complexity, and facilitating recovery of forest species within harvested areas (Franklin et al. 1997). Retention harvesting could, therefore, mitigate the effects of forestry on wildlife by retaining habitat structure associated with late-successional forests used by vertebrates.

Wildlife responses to retention harvesting are, however, species-specific reflecting their individual habitat requirements (Rosenvald and Löhman 2008, Vanderwel et al. 2009). While populations of early-seral species benefit from open

areas created by harvesting, populations of those species dependent on closed-canopy forest are negatively affected by the removal of overstory trees (Fedrowitz et al. 2014). Species responses vary by retention level (percent of original basal area retained), as the amount of residual trees will influence post-harvest habitat characteristics, including forage/prey availability and protective cover (Vanderwel et al. 2009). Habitat quality can vary by season (Wolff 1980, Allan 1985); hence, the influence of retention harvesting on vertebrate activity could be further affected by seasonal differences in forest structure.

In addition to level of harvesting in a stand, time since logging is another important factor that affects responses of some wildlife to harvesting (Fisher and Wilkinson 2005). Residual live trees left as retention may not only provide greater canopy cover than clear-cut stands, but also improve overall structural heterogeneity since such standing trees eventually contribute to deadwood abundance (Hämäläinen et al. 2016). Retention level also affects forest regeneration (Gradowski et al. 2008, 2010), which further influences habitat quality (Thompson et al. 1989). While recent clear-cuts may not provide habitat for some species, retention harvests provide important structural elements that may enable populations of forest species to persist during forest regeneration or promote more rapid post-harvest recovery of populations. However, previous studies on retention harvesting and biodiversity have spanned fewer than six years post-harvest (Fedrowitz et al. 2014), and thus, longer-term studies are needed to detect lag effects in wildlife responses to forest regeneration.

Furthermore, the majority of previous studies on retention harvesting and vertebrates have focused on small forest-floor mammals (mice, voles, shrews; e.g., Gitzen et al. 2007), arboreal rodents (Fisher and Bradbury 2006), bats (Patriquin and Barclay 2003), and passerine birds (Le Blanc et al. 2010). Although some studies investigated the influence of silvicultural treatments on larger mammals (e.g., lynx in Holbrook et al. 2018), the effects of different levels of retention harvesting on many mammals and game birds are poorly understood (Vanderwel et al. 2009) despite their ecological, economic, and cultural values (Muth et al. 1996). A better understanding of responses to different levels of retention

harvesting is needed to assess whether these alternative timber harvesting practices mitigate the negative effects of harvesting on these species.

The objective of this research was to test the influence of retention harvesting on vertebrate wildlife by (1) comparing wildlife use (activity) among different levels of retention harvesting 15–18 yr post-harvest and (2) identifying forest structural attributes most associated with the presence of individual species. We classified species as late-seral, early-seral, or generalist according to the literature (Table 1 and *Methods*). We hypothesized that retention harvesting would provide habitat that was intermediate between unharvested mature forest and that arising from clear-cut harvesting and that species would respond to this gradient according to their habitat preferences (Hypothesis 1). Supporting evidence for Hypothesis 1 would be (1) increased use of areas with higher levels of retention (characterized by greater canopy cover, basal area, and deadwood abundance) by late-seral species, (2) increased use of areas with lower levels of retention (characterized by lower canopy cover and greater understory cover) by early-seral species, and (3) neutral use of harvested areas by habitat generalist species. Season was included as a factor in the analyses to detect possible seasonal differences in wildlife use of retention levels. We also hypothesized that canopy cover, tree height, tree diameter, basal area (live and dead), and downed coarse woody material cover would increase with increasing retention level, while horizontal cover and understory cover would decrease with increasing retention level because stands with higher levels of retention would contain more retained trees and be characterized by greater structural diversity (Hypothesis 2).

METHODS

Study site

The study area comprised the large-scale Ecosystem Management Emulating Natural Disturbance (EMEND) experiment located in northwest Alberta, Canada ($56^{\circ}46'13''$ N, $-118^{\circ}22'28''$ W; Fig. 1). Climate data from nearby Eureka River ($56^{\circ}29'00''$ N, $-118^{\circ}44'00''$ W) collected from 1981 to 2010 indicated mean temperatures of -16.9°C and 15.0°C for January and July, respectively (Environment Canada 2017). Mean

Table 1. Predicted responses of species habitat use to increasing retention levels (0–100%) 15–18 yr post-harvest indicated as positive (habitat use increases with increasing retention level), negative (habitat use declines with increasing retention level), or neutral (habitat use is not affected by retention level) with the rationale for predictions and supporting references.

Species	Prediction	Rationale	References
American marten	Positive	Late-seral specialist	Hargis and McCullough (1984), Buskirk et al. (1989), Ruggiero et al. (1998), Bull and Heater (2000), Payer and Harrison (2003), Bull et al. (2005), Proulx (2006)
Black bear	Neutral	Habitat generalist	Jonkel and Cowan (1971), Lindzey and Meslow (1977), Young and Beecham (1986), Boileau et al. (1994), Mitchell and Powell (2003)
Canada lynx	Neutral	Habitat generalist	Koehler and Brittell (1990), Slough (1999), Gilbert and Pierce (2005), Fuller et al. (2007), Simons-Legaard et al. (2013), Holbrook et al. (2017)
Coyote	Neutral	Habitat generalist	Bekoff and Gese (2003), Thibault and Ouellet (2005), Boisjoly et al. (2010)
Fisher	Positive	Late-seral specialist	Carroll et al. (1999), Aubry and Raley (2006), Purcell et al. (2009), Raley et al. (2012), Aubry et al. (2013), Schwartz et al. (2013)
Gray wolf	Neutral	Habitat generalist	Mladenoff et al. (1995), Kuzyk et al. (2004), Houle et al. (2010), Lesmerises et al. (2012), Ehlers et al. (2016)
Grouse	Negative	Early-seral specialist	Boag and Sumanik (1969), Stauffer and Peterson (1985a, b)
Moose	Negative	Early-seral specialist	Peek et al. (1976), Timmermann and McNicol (1988), Forbes and Theberge (1993), Fisher and Burton (2018)
Mule deer	Positive	Late-seral specialist	Armleder et al. (1994), Sullivan et al. (2008)
Red squirrel	Positive	Late-seral specialist	Kemp and Keith (1970), Rusch and Reeder (1978), Fancy (1980), Thompson et al. (1989), Holloway and Malcolm (2006)
Snowshoe hare	Negative	Early-seral specialist	Montney (1986), Ferron and Ouellet (1992), Hodson et al. (2011)
White-tailed deer	Negative	Early-seral specialist	Beier and McCullough (1990), Fisher and Burton (2018)
Wolverine	Positive	Late-seral specialist	Krebs et al. (2007), Bowman et al. (2010), Dawson et al. (2010), Fisher et al. (2013)
Woodland caribou	Positive	Late-seral specialist	Chubbs et al. (1993), Rettie and Messier (2000), Smith et al. (2000), Courtois et al. (2004), Bowman et al. (2010)

annual snowfall and rainfall were 128.8 cm and 307.4 mm, respectively (Environment Canada 2017). The area is representative of the boreal mixedwood plains, and the landscape is a mosaic of upland mesic mixedwood forests of varying compositions interspersed with lower-lying, wetter areas occupied by forested peatlands dominated by black spruce (*Picea mariana*) or larch (*Larix laricina*). The EMEND site, which is embedded in an area managed for forestry, includes 1000 ha of forest characterized by four tree cover types (deciduous, deciduous with conifer understory, mixedwood, and coniferous). Data were collected in stands dominated by conifers, predominantly white spruce (*Picea glauca*), prior to harvest, and post-harvest regeneration mainly consisted of aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*; Gradowski et al. 2008, 2010). The stands were ~120–180 yr old at the time of sampling as they experienced fires in 1895, 1877, and/or 1837 (Bergeron et al. 2017).

Harvest treatments were randomly assigned to compartments (~10 ha each) within blocks (i.e., within an area; although we never treat these as statistical blocks because they are imperfect) that were distributed across the study area whereby a minimum distance of 1.6-km separated compartments characterized by the same treatment (Fig. 1). Each compartment was harvested in the winter of 1998–1999 according to one of five harvest retention levels (treatments): 0% (clear-cut), 10%, 20%, 50%, and 75% retention. Harvesting equipment operated on 5 m wide corridors that were separated by 15 m wide strips, which were distributed across the 10-ha compartment, and from which a portion of randomly selected trees was removed by feller-bunchers according to the target retention level. The only trees harvested in the 75% retention treatment were those removed in the 5 m wide corridors. The retention pattern was predominantly dispersed green-tree retention but each compartment contained two small (<0.50 ha each) embedded retention patches. All

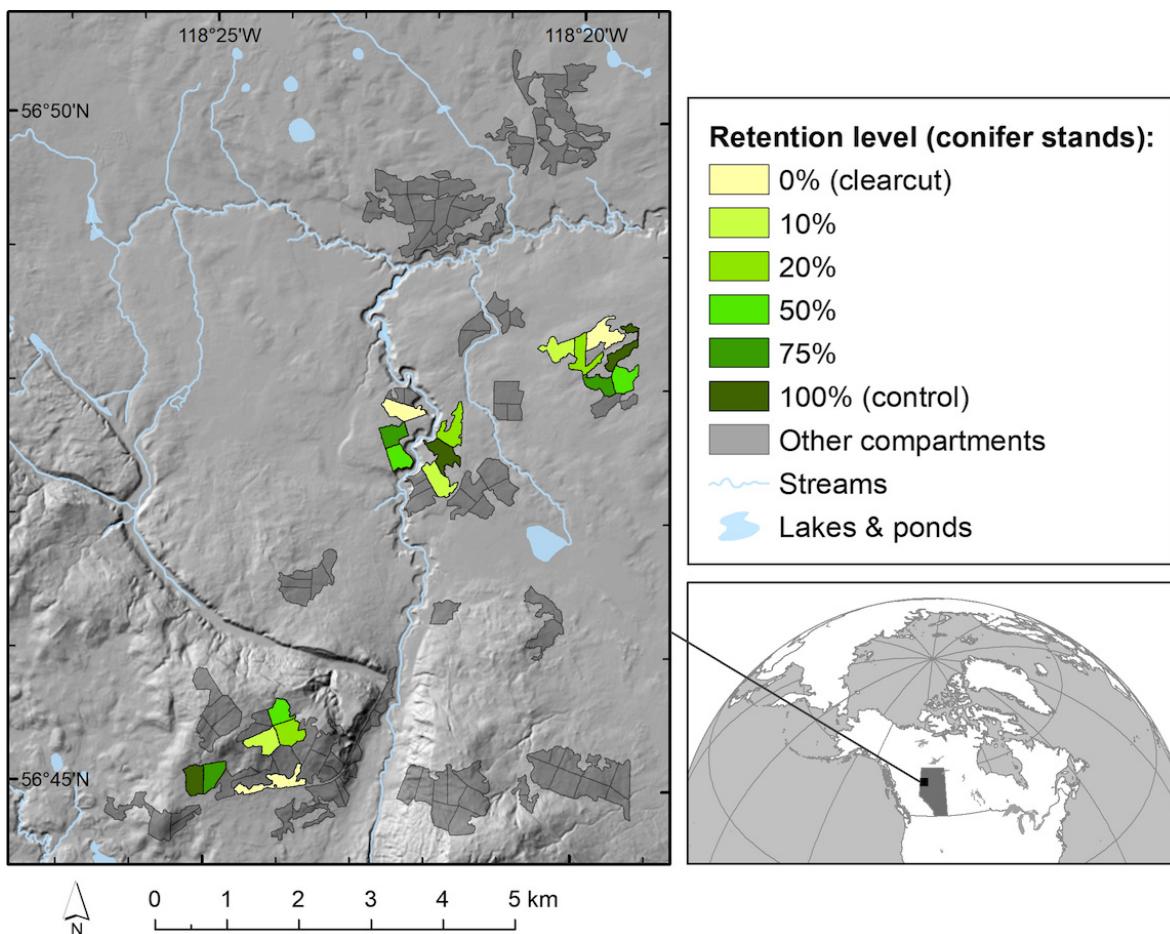


Fig. 1. Map of study area with colored compartments representing different levels of retention harvests (left). Other compartments include compartments in different forest types that are part of the Ecosystem Management Emulating Natural Disturbance experiment but that were not examined in this study. Alberta shaded in gray with study area location (right). Data were collected 15–18 yr after the application of harvesting treatments.

sampling occurred in the dispersed retention areas. Unharvested compartments (~10 ha each) were used as controls (100% retention). There was a total of 18 compartments as each treatment, including control stands without harvest, had three replicates. Sampling was conducted 15–18 yr following application of the harvest treatments.

Data collection

Transect surveys of animal sign.—Belt transects (east–west orientation) comprising a search area of 1200 m² were randomly established in each 10-ha compartment in June 2015. The width of

each transect was 4 m and the length varied depending on the shape of the compartment but the length of all transects in a compartment totaled 300 m. All transects were located >40 m from each other and >30 m from compartment edges. Within each belt transect, the number of red squirrel (*Tamiasciurus hudsonicus*) middens and cone shell piles, which are considered suitable indicators of red squirrel feeding activity (Gurnell et al. 2009), was counted in June 2015. Along these transects, all fecal pellets were removed in June 2015. To obtain estimates of animal use, we subsequently counted and cleared all fecal pellets along transects; this was done prior to leaf fall in 2015 and 2016 and prior to leaf

out in 2016 and 2017 for spring/summer and fall/winter use, respectively. Fecal pellets of black bear (*Ursus americanus*), coyote (*Canis latrans*), deer (*Odocoileus* spp.), gray wolf (*Canis lupus*), grouse (*Bonasa umbellus/Canachites canadensis*), moose (*Alces alces*), and snowshoe hare (*Lepus americanus*) were identified. Coyote and gray wolf were excluded from analyses of these data due to insufficient observations.

Camera traps.—We used 35 motion-triggered wildlife cameras (25 Reconyx Hyperfire HC500 and 10 Reconyx Hyperfire PC900, Holmen, Wisconsin, USA) to capture use of compartments (treatments) by wildlife species from 31 October 2014 to 30 May 2017. During the sampling time period, 1–2 cameras were randomly moved within each compartment at least once every year so that each compartment had a total of 4–6 different camera locations (Appendix S1). Cameras were programmed on the normal setting with trigger speed set to high sensitivity and five pictures per trigger with one-second delay between each photograph and no delay between consecutive triggers (Burton et al. 2015). The cameras were set facing north to avoid sun glare and mounted to trees approximately 1 m from the ground in spring/summer or 1.5 m from the ground in winter/fall to account for snow accumulation. Light vegetation was removed from the area to avoid triggers from wind-induced vegetation movement. In the zone of detection, which was approximately 3–5 m from the camera lens, we applied 10 mL of a scented lure (O'Gorman's Long Distance Call, Broadus, Montana, USA) to a tree in full view of the camera (Burton 2014). The University of Alberta Research Ethics Office (Study ID: AUP00001231) as well as the Government of Alberta Environment and Sustainable Resource Development Fish and Wildlife Division (Permit #54605 and Collection Licence #54606) approved the research.

A total of 18 species, excluding passerine birds, were detected and identified throughout the sampling period (American marten [*Martes americana*], black bear, Canada lynx [*Lynx canadensis*], coyote, fisher [*Martes pennanti*], gray wolf, moose, mule deer [*Odocoileus hemionus*], red squirrel, river otter [*Lutra canadensis*], ruffed grouse [*B. umbellus*], short-tailed weasel [*Mustela erminea*], snowshoe hare, spruce grouse [*C. canadensis*], white-tailed deer [*Odocoileus virginianus*],

wolverine [*Gulo gulo*], woodchuck [*Marmota monax*], woodland caribou [*Rangifer tarandus*]). River otter, short-tailed weasel, and woodchuck were excluded from analyses because total detections were low. Ruffed grouse and spruce grouse were combined (hereafter referred to as grouse) for the purpose of analysis. Based on scientific literature related to habitat associations, we made predictions for responses of individual species to increased levels of retention (Table 1). Briefly, we predicted negative, neutral, or positive responses to retention based on whether the species was considered to be late-seral specialist, early-seral specialist, or a habitat generalist. Predictions were based on considerations of resource (e.g., prey) availability in our study area and therefore could differ for other study locations or forest types.

At each camera station, we measured the following variables of forest structure: canopy cover, horizontal vegetation cover, tree height, tree diameter at breast height (dbh), basal area of live trees, basal area of snags, downed coarse woody material cover, and understory vegetation cover. Canopy cover and horizontal cover were measured in both spring and fall to account for seasonal changes in leaf cover. Average canopy cover was determined using a convex spherical densiometer, averaging four measurements, one in each cardinal direction. Horizontal vegetation cover was measured by an observer at each camera that estimated the percentage of a Robel pole that was concealed by vegetation. The Robel pole was placed 10 and 20 m from the camera lens, and average horizontal vegetation cover was calculated from estimates of vegetation cover in the 0–1 m and 1–2 m height from ground strata. Basal area of live trees and snags was measured using a prism with a basal area factor of 3. Average tree height was calculated by measuring height of the three tallest trees considered in by the prism using a clinometer. Maximum tree dbh was determined for the largest trees considered in by the prism as measured by diameter at breast height (1.37 m from the ground). Cover of downed coarse woody material was determined along a transect that extended 10 m in front of the camera and 10 m behind the camera and calculated by measuring the diameter at the point of intersection with the transect for each log (diameter ≥ 5 cm at largest point). Understory vegetation cover (total of all

vascular plants and by group: saplings, shrubs, forbs, graminoids) was visually estimated in a 10-m² circular plot (camera in center) and placed in a cover class with the following percent cover midpoints: 1 (0.5%), 2 (2%), 3 (7%), 4 (18%), 5 (38%), 6 (63%), and 7 (87.5%).

Data analysis

We fitted a series of generalized linear models to counts of animal sign, number of detections from cameras, or forest structural variables using the R statistics programming environment version 3.4.1 (R Development Core Team 2017). We tested nonlinear effects by adding the quadratic term of retention level, and the most supported model was determined by a lower Akaike information criterion (AIC) value. When the models with and without the quadratic term had a difference in AIC of <2, they were considered equally supported, in which case results are presented for the simpler linear models. The most supported model (linear or nonlinear) was used for hypothesis testing. Grouse was an exception because the linear model resulted in predicted values below zero; we thus chose to present results for the nonlinear model which was the one with the lowest AIC. Diagnostic plots were used to assess normality and homoscedasticity of the residuals for all models.

To examine the influence of retention harvesting on red squirrel stand use (Hypothesis 1) as measured by number of feeding sites, transect data for red squirrel sign were number of feeding sites/1200 m² (count data) and were analyzed using a negative binomial generalized linear model with the `glm.nb` function in the MASS package (Ripley et al. 2018). Number of feeding sites and retention level (0%, 10%, 20%, 50%, 75%, 100%) were the response and continuous predictor variables, respectively.

To investigate the influence of retention harvesting on black bear, deer, grouse, moose, and snowshoe hare stand use (Hypothesis 1) as measured by pellet counts, transect data for pellet counts were analyzed using the `lmer` function in the lme4 package (Bates et al. 2018). Unlike the red squirrel feeding sites, which were only counted once, pellet groups were counted four times; hence, the number of pellet groups was standardized for the number of accumulation days. Models included retention level (0%, 10%,

20%, 50%, 75%, 100%) and season (spring/summer, fall/winter) as continuous and categorical fixed independent variables, respectively. Compartment and year were random variables. The interaction between retention level and season (retention level × season) was not significant in any model, so we included only retention level and season as main effects (retention level + season). Mule deer and white-tailed deer were combined (hereafter referred to as deer) because fecal pellets were not differentiated between species. Fall/winter season was excluded for black bear due to hibernation.

For examining the influence of retention harvesting on stand use of all species (Hypothesis 1) based on photographic detections, photographs from the motion-triggered cameras were examined to determine number of detections for individual species standardized by number of trapping nights. Detections for a given species were considered independent after a 30-min time period or if individuals were distinctly different (i.e., multiple individuals of the same species captured in a single photograph). Photographs taken April–September and October–March were classified as spring/summer and fall/winter, respectively. Data were zero-inflated (Appendix S2) and analyzed using zero-inflated negative binomial models using the glmmTMB package (Magnusson et al. 2019). Number of detections for individual species was the response, number of trap nights was an offset, retention level (0%, 10%, 20%, 50%, 75%, 100%) was a continuous variable, and season (spring/summer, fall/winter) was a categorical variable. Compartment and year were, again, included as random variables. Because the interaction between retention level and season (retention level × season) was not significant in any model, we fit retention level and season as main effects (retention level + season). As above, fall/winter season was excluded for black bear due to hibernation. Retention level did not significantly affect mule deer or white-tailed deer when analyzed individually so these species were combined and hereafter referred to as deer.

We acknowledge that we did not account for imperfect detection in our analyses and thus indices of animal use reported here are underestimates (minimum values) of true use. However, accurate inferences from models that adjust for non-detections are known to be challenging

(Welsh et al. 2013). To partly address this point, we used two different methods to quantify relative use of treatments: transect surveys and camera traps. We also attempted to minimize detectability issues in transect surveys by using a narrow width (2 m on each side of transect) and ensuring the same observer participated in all surveys. To minimize temporal detectability issues, 1–2 cameras were deployed in each replicate of all treatments during the entire study period (893 calendar days). A single person was responsible for the identification and count of individuals in all photographs. Our analyses therefore provide minimum estimates of stand use for comparisons among treatments with the assumption that detectability did not vary substantially between treatments. We believe that confirmatory results between techniques (cameras vs. transects) would support the conclusion that detection bias across treatment levels of individual techniques is unlikely.

To investigate the influence of retention harvesting on measures of forest structure (Hypothesis 2), forest structure variables were analyzed using the lmer function in the lme4 package (Bates et al. 2018). Mixed-effects models for canopy cover and horizontal cover included retention level (0%, 10%, 20%, 50%, 75%, 100%) and season (spring/summer, fall/winter) as continuous and categorical fixed independent variables, respectively, plus the interaction between retention level and season. Models for the remaining forest structure variables (tree height, tree dbh, basal area of live trees, basal area of

snags, downed woody material cover, total understory cover, sapling cover, shrub cover, forb cover, and graminoid cover) included only retention level as a main effect. Compartment and year were included as random variables in all models.

RESULTS

Wildlife responses to retention harvesting

The number of red squirrel feeding sites totaled 206 while the total number of scat/pellet groups was 30 for black bear, 92 for deer, 760 for grouse, 370 for moose, and 8062 for snowshoe hare. The total number of photographic detections was 43 for American marten, 311 for black bear, 75 for Canada lynx, 33 for coyote, 177 for deer, 38 for fisher, 85 for gray wolf, 31 for grouse, 323 for moose, 550 for red squirrel, 478 for snowshoe hare, 10 for wolverine, and 102 for woodland caribou. The average number of camera trap nights for each compartment was 1319 ± 49 (Appendix S2).

Activity of red squirrel, fisher, coyote, wolverine, black bear, and caribou in the study area 15–18 yr after application of the harvesting treatments increased with retention level of harvested stands (Tables 2, 3). Red squirrel use especially increased with retention level as the median number of red squirrel feeding sites was 0/1200 m² in the clear-cut increasing to 18/1200 m² in both 75% and 100% retention harvests (Fig. 2a). This trend was supported by the camera data, which also revealed a notable increase in red squirrel activity from 10% to 20% retention

Table 2. Results of regression models (beta coefficient with standard error, β [SE] and P values, P) examining the influence of retention level (0%, 10%, 20%, 50%, 75%, 100%) and season (spring/summer, fall/winter) on wildlife activity as examined by the number of pellet groups and red squirrel middens.

Species	Retention		Retention ²		Season	
	β (SE)	P	β (SE)	P	β (SE)	P
Black bear†	0.010 (0.004)	0.036	—	—	—	—
Deer	−0.009 (0.009)	0.342	—	—	−0.948 (0.319)	0.004
Grouse	−0.265 (0.102)	0.020	0.002 (0.001)	0.149	2.712 (1.195)	0.027
Moose	−0.014 (0.012)	0.250	—	—	−1.187 (0.436)	0.009
Red squirrel	0.080 (0.022)	<0.001	−0.0004 (0.0002)	0.036	—	—
Snowshoe hare	−3.771 (1.036)	0.002	0.025 (0.010)	0.028	20.405 (8.016)	0.014

Notes: Data for all species, except red squirrel, were from counts of pellet groups (no. of pellet groups/100 d) and analyzed using Gaussian distribution. Data for red squirrel were based on number of feeding sites/1200 m² and were analyzed using negative binomial distribution. Reference category for season was spring/summer. P values in bold were considered significant at $\alpha = 0.05$. En dash indicates that the predictor variable was not included in the model.

† Winter excluded from analysis due to hibernation.

Table 3. Results of regression models (beta coefficient with standard error, β [SE] and P values, P) examining the influence of retention level (0%, 10%, 20%, 50%, 75%, 100%) and season (spring/summer, fall/winter) on wildlife activity as examined by photographic (camera trap) detections.

Species	Retention		Season	
	β (SE)	P	β (SE)	P
American marten	0.008 (0.008)	0.283	0.090 (0.493)	0.856
Black bear†‡	-0.003 (0.003)	0.285	—	—
Canada lynx	-0.005 (0.005)	0.322	-0.188 (0.324)	0.562
Coyote‡	0.021 (0.009)	0.022	0.606 (0.310)	0.051
Deer	-0.006 (0.005)	0.267	-4.574 (1.016)	<0.001
Fisher	0.029 (0.010)	0.003	0.320 (0.568)	0.572
Gray wolf‡	0.004 (0.006)	0.470	0.361 (0.392)	0.357
Grouse	-0.043 (0.014)	0.002	-1.643 (0.620)	0.008
Moose	-0.005 (0.003)	0.127	0.156 (0.187)	0.405
Red squirrel	0.011 (0.006)	0.041	0.219 (0.257)	0.395
Snowshoe hare	-0.021 (0.006)	<0.001	-0.671 (0.206)	0.001
Wolverine‡	0.022 (0.011)	0.047	1.835 (1.103)	0.096
Woodland caribou§	0.073 (0.010)	<0.001	—	—

Notes: Data were analyzed using zero-inflated negative binomial models. Reference category for season was spring/summer. P values in bold were considered significant at $\alpha = 0.05$.

† Winter excluded from analysis due to hibernation.

‡ Comparison of Akaike information criterion values suggested that nonlinear model was better; however, inability to test significance was caused by too few non-zero values so results from linear models are presented.

§ Insufficient data to present values for season.

(Fig. 3a). Although camera data did not reveal a significant effect of retention level on stand use of black bear (Table 3), the number of black bear scats increased with retention level and no black bear scat was found in clear-cuts (Table 2, Fig. 2b). The maximum number of coyote detections was highest in the 75% retention harvest and unharvested control (Fig. 3b). Stand use of fisher increased with retention level and was notably higher at 50% retention and above (Fig. 3c). Retention level had a significant positive effect on stand use of wolverine (Fig. 3d). Woodland caribou were never detected in harvested stands with <20% retention and the number of detections increased with retention levels above 20% (Fig. 3e).

Snowshoe hare and grouse use declined with increasing retention level reaching quite low values at retention levels of $\geq 50\%$ 15–18 yr post-harvest (Tables 2, 3, Fig. 4a, b). The median number of snowshoe hare pellet groups was more than one-third as high in clear-cuts than in retention harvested stands, and was higher in fall/winter compared to spring/summer (Fig. 4a). Number of snowshoe hare detections, as captured by the motion-triggered cameras, also declined with increasing retention level; however, detections were higher in spring/summer compared to fall/winter (Fig. 4f). Similar to snowshoe hare, grouse activity was higher in spring/summer according to photographs but in fall/winter according to pellet counts (Figs. 3g, 4b).

American marten, Canada lynx, gray wolf, deer, and moose showed no significant differences related to retention level 15–18 yr post-harvest (Tables 2, 3). Deer activity was higher in all compartments in spring/summer than in fall/winter based on both pellet counts and photographs (Tables 2, 3). Pellet group counts also revealed greater use of compartments by moose in spring/summer compared to fall/winter (Table 2).

Forest structure responses to retention harvesting

There was a significant interaction between retention level and season with respect to canopy cover (Table 4). While canopy cover was higher in spring/summer compared to fall/winter, the increase in canopy cover with retention level was more drastic in fall/winter so differences in canopy cover between seasons attenuated as retention level increased (Fig. 5a). Field observations revealed that differences in canopy cover between low and high retention levels in fall/winter resulted from differences in canopy composition as canopy trees were predominantly early-successional deciduous species in low retention treatments but conifer species in higher retention levels. Horizontal cover was also significantly lower in fall/winter compared to spring/summer, but in both seasons it declined with increasing retention level (Table 4, Fig. 5b). Average tree height, maximum live tree dbh, live tree basal area, dead tree basal area, and downed coarse woody material cover all increased with retention level (Table 4, Fig. 5c–g). Conversely, total understory cover, sapling cover, and graminoid cover declined with

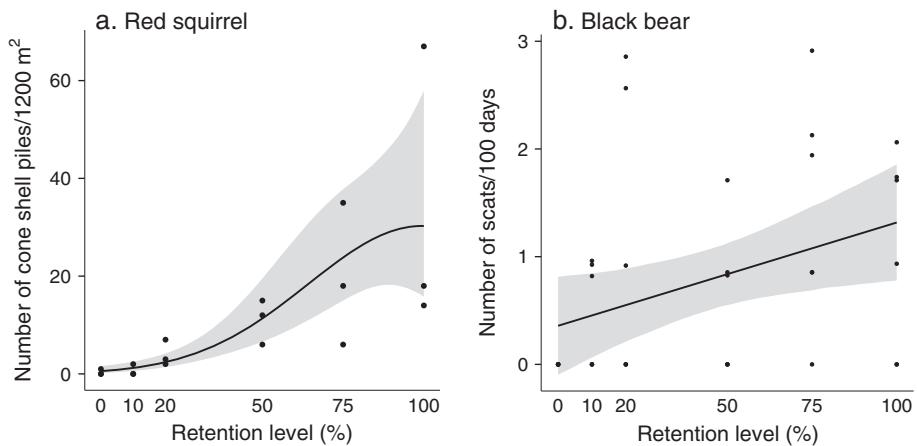


Fig. 2. Scatterplots and regression lines with bootstrapped 95% confidence intervals for (a) red squirrel and (b) black bear activity 15–18 yr post-harvest based on number of feeding sites (a) and number of pellet groups (b) from surveys along transects in 0%, 10%, 20%, 50%, 75%, and 100% retention.

increasing retention level (Table 4, Fig. 5h–j). Shrub cover and forb cover were not significantly affected by retention level (Table 4).

DISCUSSION

These findings reveal different responses of multiple wildlife species to varying retention levels 15–18 yr post-harvest. The responses of stand use to retention level were as predicted for all vertebrates except for American marten, black bear, coyote, deer, and moose. Six species (red squirrel, fisher, coyote, black bear, wolverine, woodland caribou) showed increased activity with increasing retention level, for two species (snowshoe hare, grouse) activity declined with increasing retention level, and activity of five species (American marten, Canada lynx, gray wolf, moose, deer) did not significantly vary with retention level. These wildlife responses likely reflect structural attributes that characterized stands harvested to different retention levels.

Positive responses of stand use to increasing retention harvest levels

As predicted, red squirrel activity increased with retention level and this corresponded to higher canopy cover, greater basal area, and larger trees that could better support both feeding and nesting sites for red squirrels. The median maximum live tree dbh in stands harvested to ≥20% retention was over 30 cm, which is a

preferred tree size for nesting (Fancy 1980). Mature seed-producing conifers also provide a reliable food source for red squirrels (Kemp and Keith 1970, Rusch and Reeder 1978). Our findings conform to other studies that revealed that red squirrels preferred unharvested stands with high densities of large spruce trees and snags, as compared to stands that had been more recently partially harvested (<10 yr post-harvest; Holloway and Malcolm 2006, Herbers and Klenner 2007). The complete lack of red squirrel activity in clear-cut stands more than 15 yr post-harvest highlights the importance of retention harvesting for these arboreal rodents. Moreover, the presence of red squirrel middens benefits other species, including martens (Ruggiero et al. 1998) and toads (Browne and Paszkowski 2010).

Fishers select habitats with complex vertical forest structure that includes large trees, deadwood, and high canopy cover (Carroll et al. 1999, Raley et al. 2012, Schwartz et al. 2013, Lewis et al. 2016). These structural attributes, which were associated with high retention levels, are important for fisher denning and resting sites (Aubry and Raley 2006, Aubry et al. 2013). Activity of fishers was lowest in stands harvested to 0% and 10% retention, where canopy cover was lower than the minimum threshold (56%) for fisher habitat (Purcell et al. 2009). Fishers were previously shown to avoid recently logged stands (<10 yr post-harvest; Weir and Corbould 2010). Our results suggest that residual trees in

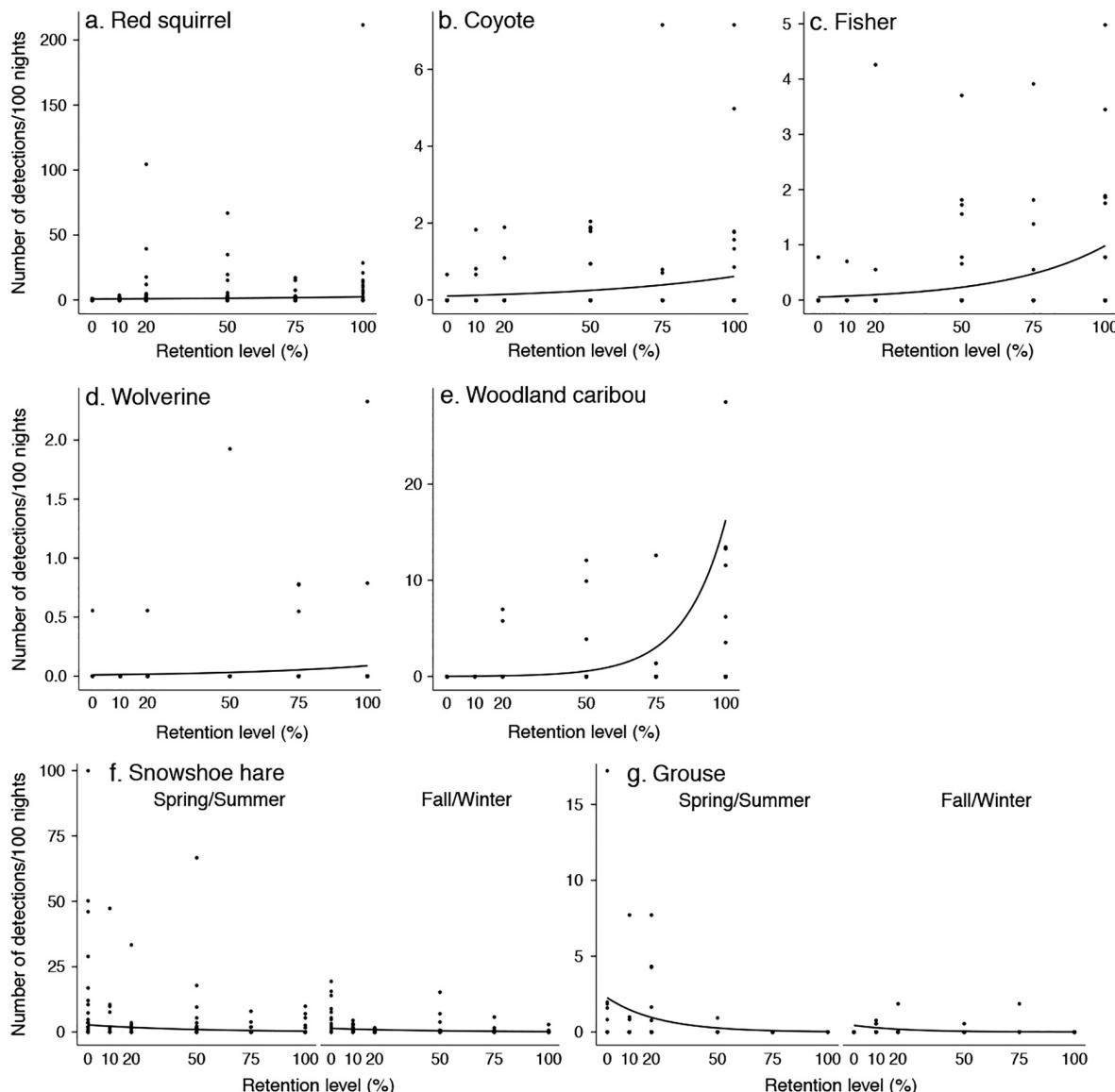


Fig. 3. Scatterplots and regression lines for number of detections/100 nights for (a) red squirrel, (b) coyote, (c) fisher, (d) wolverine, (e) woodland caribou, (f) snowshoe hare, and (g) grouse based on photographs captured by motion-triggered cameras deployed in 0%, 10%, 20%, 50%, 75%, and 100% retention harvest treatments 15–18 yr post-harvest.

retention harvests $\geq 20\%$ could promote structural heterogeneity and therefore offer better habitat than do clear-cut areas (Sauder and Rachlow 2015).

Coyotes were predicted to be neutral to retention harvesting because they are generalist predators (Thurber et al. 1992, Bekoff and Gese 2003), but our results showed that their activity increased with increasing retention. Although

coyotes have been found to select clear-cuts 5–20 yr old due to availability of moose carcasses and berries (Boisjoly et al. 2010), they also use mature conifer forest to avoid deep snow that hampers mobility (Parker and Maxwell 1989, Thibault and Ouellet 2005). We found no evidence that moose activity or shrub cover was greater in areas with higher levels of retention; thus, the observation of apparent preferred stand

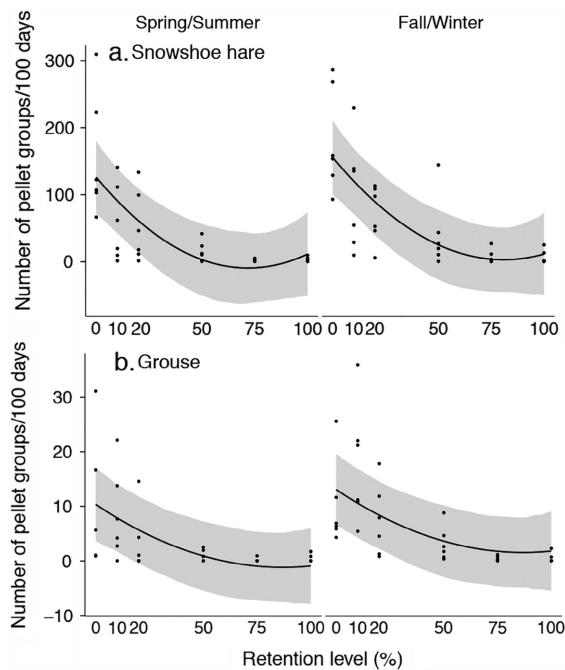


Fig. 4. Scatterplots and regression lines with bootstrapped 95% confidence intervals for (a) snowshoe hare and (b) grouse activity 15–18 yr post-harvest based on number of pellet groups from surveys along transects in 0%, 10%, 20%, 50%, 75%, and 100% retention.

use of higher retention levels by coyotes could correspond to other factors, such as snow depth.

Black bears were also predicted to exhibit a neutral response to retention harvesting; however, we found that stand use increased with retention level. Several studies have provided evidence that recent clear-cuts are a preferred habitat for black bears due to forage availability (Lindzey and Meslow 1977, Mitchell and Powell 2003, Brodeur et al. 2008, Mosnier et al. 2008). In our study, shrub and forb cover did not vary significantly with retention level, which suggests that food availability was not greater at lower (vs. higher) retention levels 15 yr post-harvest. High levels of retention could provide both forage and cover, two important factors in habitat selection of black bears (Young and Beecham 1986). Other studies revealed that mature forests are valuable for black bear denning sites (Tietje and Ruff 1980, Boileau et al. 1994). Mature residual trees with large diameters, such as are found in retention harvested areas, may also be

important for climbing (Herrero 1972) and rubbing (Green and Mattson 2003).

As predicted, wolverine stand use increased with increasing retention level. Wolverines have been shown to avoid logged areas in British Columbia (Krebs et al. 2007), Ontario (Bowman et al. 2010), and in the Rocky Mountains of Alberta (Fisher et al. 2013). Scrafford et al. (2017) considered wolverine occurrence in post-harvest forest successional stages and demonstrated that wolverines avoided the interior of cutblocks at 11–25 yr. Greater downed coarse woody material cover in high levels of retention compared to lower retention levels could benefit wolverines by providing den sites (Dawson et al. 2010).

Our results corroborate previous studies that revealed caribou preference for mature coniferous forest and avoidance of clear-cuts and low retention harvested stands at least up to 12 yr post-harvest (Chubbs et al. 1993, Rettie and Messier 2000, Smith et al. 2000, Bowman et al. 2010). Logging not only alters caribou distribution, but has also been associated with chronic stress, as measured by cortisol concentrations (Ewacha et al. 2017). Servheen and Lyon (1989) stated that canopy cover >50% and tree diameter >20 cm were important for caribou habitat. We found that these thresholds were observed in harvested stands with at least 20% retention, below which caribou were not detected. Caribou may prefer the low horizontal cover in stands with high retention levels because it better enables them to visually detect predators (Pinard et al. 2012). Furthermore, retention trees and snags may support arboreal lichens, an important winter food source for caribou.

Negative responses of stand use to increasing retention harvest levels

As expected, snowshoe hare preferred low levels of retention, especially clear-cuts. Higher levels of activity in low retention levels than in retention of 50% or above could be attributed to greater habitat quality as determined by availability of food and cover (Wolff 1980, Pietz and Tester 1983). Areas harvested to low retention levels were characterized by high sapling cover, total understory cover, and horizontal cover, which provide snowshoe hares with food resources and protection from predators (Dodds 1960, Wolfe et al. 1982, Litvaitis et al. 1985,

Table 4. Results of regression models (beta coefficient and standard error, β [SE], and P values, P) examining the influence of retention level (0%, 10%, 20%, 50%, 75%, 100%), season (spring/summer, fall/winter), and their interaction (when relevant) on measures of forest structure (DCWM = downed coarse woody material).

Forest structure	Retention		Retention ²		Season		Retention × Season	
	β (SE)	P	β (SE)	P	β (SE)	P	β (SE)	P
Canopy cover	0.077 (0.064)	<0.001	—	—	-58.441 (3.573)	<0.001	0.580 (0.064)	<0.001
Horizontal cover	-0.211 (0.072)	0.005	—	—	-10.398 (4.289)	0.017	0.046 (0.075)	0.538
Tree height	0.200 (0.026)	<0.001	—	—	—	—	—	—
Tree diameter	0.835 (0.170)	<0.001	-0.005 (0.002)	0.013	—	—	—	—
Live basal area	-0.100 (0.162)	0.549	0.004 (0.002)	0.021	—	—	—	—
Dead basal area	0.065 (0.011)	<0.001	—	—	—	—	—	—
DCWM cover	0.055 (0.022)	0.021	—	—	—	—	—	—
Understory cover	-0.630 (0.147)	0.001	—	—	—	—	—	—
Sapling cover	-0.196 (0.055)	0.003	—	—	—	—	—	—
Shrub cover	-0.093 (0.071)	0.208	—	—	—	—	—	—
Forb cover	0.026 (0.065)	0.698	—	—	—	—	—	—
Graminoid cover	-0.363 (0.087)	0.001	—	—	—	—	—	—

Notes: Data were analyzed using Gaussian distribution, and the reference for season was spring/summer. Season and the interaction between retention and season were included to account for seasonal differences in deciduous foliage. P values in bold were considered significant at $\alpha = 0.05$. En dash indicates the exclusion of the predictor variable or the interaction between predictor variables from the model.

Ferron and Ouellet 1992, Holbrook et al. 2017). Previous studies demonstrated that regeneration in clear-cut stands <10 yr post-harvest failed to provide adequate protective cover (Thompson et al. 1989, de Bellefeuille et al. 2001, Potvin et al. 2005). Retention harvests could be beneficial for snowshoe hare in sites younger than the ones investigated in this study because retention harvest areas would provide structural elements important for cover as well as food (Ferron et al. 1998).

As predicted, stand use by grouse was greatest in stands harvested with low levels of retention where understory vegetation cover was high and the canopy was dominated by trembling aspen, which is a prevalent tree species characterizing preferred habitat by grouse (Stauffer and Peterson 1985a, b). The higher levels of horizontal cover that were associated with low retention levels may provide protective cover from predators (Boag and Sumanik 1969). Throughout the post-harvest regeneration period, retention harvests may be important as they provide downed logs, which are used by drumming males (Rusch and Keith 1971).

The rationale for opposite findings in seasonal differences for grouse and snowshoe hare activity between pellet counts and photographic detections is unclear. Denser habitats with greater canopy cover are used more in winter

than summer for both grouse (Allan 1985) and snowshoe hare (Wolff 1980). Increased habitat use in fall/winter as compared to spring/summer according to pellet counts corroborates a speculation by Adams (1959), who stated that individual hares might produce more pellets in winter than in summer because of a woodier diet in colder months with less herbaceous plant material. Nevertheless, our results revealed that season did not influence wildlife use of different retention levels so we refrain from an extensive discussion on seasonal differences in habitat use.

Neutral responses of stand use to retention harvesting

Contrary to expectation, American marten stand use did not exhibit a significant positive response to retention level. We predicted that stand use of American marten would increase with increasing retention level because this species has been associated with high abundance of downed coarse woody material, high basal area, and mature forests (Hargis and McCullough 1984, Sturtevant et al. 1996, Proulx 2006, Andruskiw et al. 2008). While previous research considered clear-cuts up to 15 yr old as poor marten habitat (Soutiere 1979), regenerating stands of aspen that are 15 yr post-harvest may provide adequate habitat (Poole et al. 2004). Habitat for marten includes canopy cover of at least 50%,

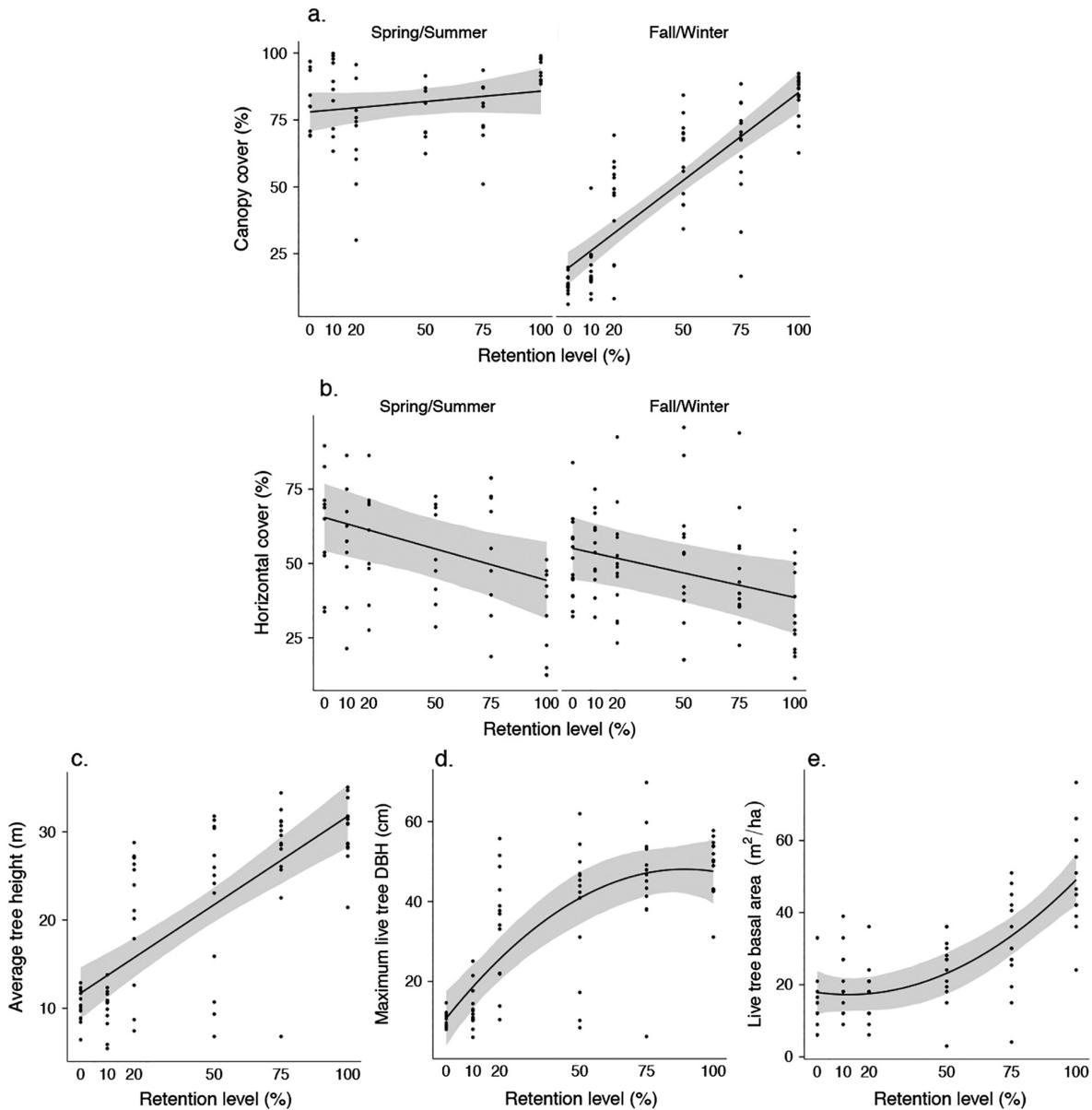
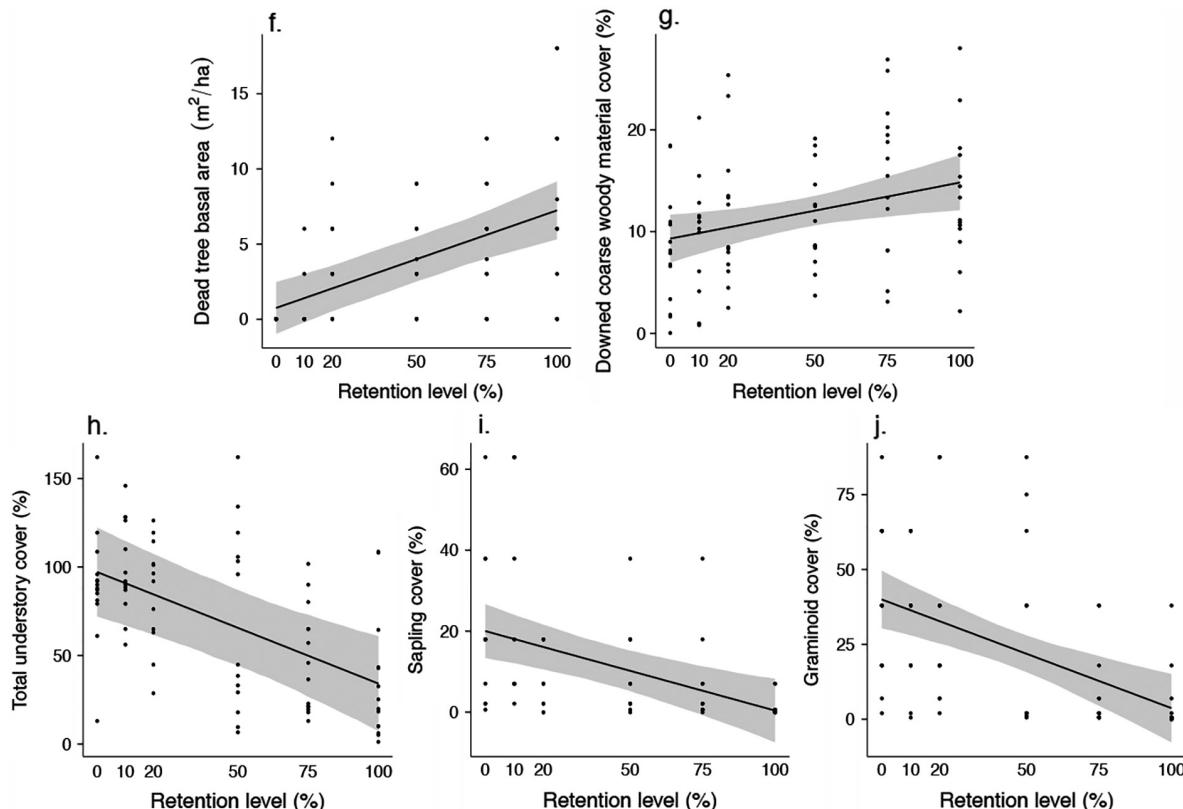


Fig. 5. Scatterplots and regression lines with bootstrapped 95% confidence intervals of (a) canopy cover, (b) horizontal cover, (c) average tree height, (d) maximum live tree dbh, (e) live tree basal area, (f) dead tree basal area, (g) downed coarse woody material cover, (h) total understory cover, (i) sapling cover, and (j) graminoid cover in 0%, 10%, 20%, 50%, 75%, and 100% retention 15–18 yr post-harvest.

average tree height over 6 m, tree diameter over 7.6 cm, and live tree basal area over 18 m^2/ha (Chapin et al. 1998, Payer and Harrison 2003, Bull et al. 2005). More than 15 yr post-harvest, the regenerating stands for all levels of retention in this study supported these minimum requirements. Marten use partially harvested stands in

Quebec (Godbout and Ouellet 2008) and Maine (Soutiere 1979, Steventon and Major 1982, Fuller and Harrison 2005). In Newfoundland, marten used a variety of habitat types, including recent clear-cuts, mature forest, and regenerating stands (Hearn et al. 2010). Forest structural attributes may be a more important factor than

(Fig. 5. *Continued*)

successional stage in determining marten habitat (Chapin et al. 1997). More than 15 yr post-harvest, original retention level may no longer influence American marten activity because after some site regeneration all retention levels could potentially provide adequate structural complexity for marten habitat (Payer and Harrison 2000, Godbout and Ouellet 2010).

The neutral response of Canada lynx to retention harvesting was as predicted and reflects the use of various structural attributes for different habitat needs. Lynx have been reported to use both regenerating post-disturbance forest and mature conifer forest (Vashon et al. 2008, Simons-Legard et al. 2013). Regenerating harvested areas supported abundant snowshoe hares that would have served as prey (Mowat and Slough 2003, Holbrook et al. 2017); however, stands with higher levels of retention had reduced understory cover and that could improve prey accessibility (Fuller et al. 2007, Fuller and Harrison 2010, Ivan and Shenk 2016). Furthermore, retention

harvesting, as compared to clear-cutting, provides greater basal area and abundance of downed wood, which provide den sites for lynx (Slough 1999, Gilbert and Pierce 2005). Thus, all levels of retention harvesting, as well as unharvested forest, could be useful habitat for lynx.

As a generalist predator, wolves occupy various habitats (Mladenoff et al. 1995, Houle et al. 2010). Our findings concur with those of Kuzyk et al. (2004), who found that wolf stand use did not significantly vary between cutblocks and unharvested forests in west-central Alberta (Kuzyk et al. 2004). Wolf prey, such as moose, also exhibited a neutral response to retention harvesting, which may partly explain the lack of response in wolves as they select areas based on prey availability (Lesmerises et al. 2012).

Both moose and deer benefit from the higher forage availability in early-seral stands and the greater hiding and thermal cover in late-seral stands; this could explain the lack of response to different levels of retention harvest 15–18 yr

post-harvest. Moose habitat is characterized by closed-canopy forest for shelter from extreme temperatures and predators, as well as more recently disturbed areas for food availability (Timmermann and McNicol 1988, Forbes and Theberge 1993). Browse availability for moose has been reported to be greater in regenerating stands more than 10 yr old post-harvest (Potvin et al. 2005, Newbury et al. 2007). Retention harvests could, therefore, be more valuable moose habitat, as compared to clear-cuts, in the shorter-term, when moose habitat quality is reduced immediately post-harvest (Dodds 1960, Potvin et al. 1999). Large mature trees in retention harvests could provide thermal cover as well as cover from predators (Mastenbrook and Cumming 1989, Kunkel and Pletscher 2000). Similar to moose, deer could benefit from greater forage availability in stands harvested to lower retention levels (Lyon and Jensen 1980). Nevertheless, deer could select stands harvested to high retention levels with greater canopy cover to facilitate movement in snow (Armleder et al. 1994), or to avoid temperature extremes (Schmitz 1991).

Management implications

We recognize the limitations in this study related to both transect surveys (Keiter et al. 2016) and camera trapping (Burton et al. 2015). Our estimates of stand use do not represent absolute abundance and we assumed that there was no interaction between detectability and treatment level. We acknowledge that (1) treatment areas were not necessarily devoid of a particular species when not detected (MacKenzie et al. 2002, 2005), and (2) detectability was likely unequal between species because detection rates may vary by animal behavior (MacKenzie et al. 2004). Our findings should therefore be interpreted with caution; especially since treated compartment sizes (~10 ha) were smaller than the home ranges for several of the species examined. We recognize that the scent lure may have affected the responses of stand use to retention level by attracting animals from outside compartments. Although scent lure is frequently used in camera trap studies (Burton et al. 2015), additional research should consider the relationship between lure amount, lure type, and distance of attraction for individual species. Despite these study limitations, our research exemplifies the

use of pellet counts and camera trapping as complementary methods for multi-species detections (Pfeffer et al. 2018).

This study highlights the benefits of retention harvesting for conserving faunal biodiversity while revealing challenges associated with managing forest landscapes for multiple species. Over half of the species investigated exhibited a significant response to retention harvesting more than 15 yr post-harvest. Many late-seral species revealed notable differences in activity between 20% and 50% retention, and use of stands harvested to at least 50% retention was comparable to use of unharvested stands. While responses of individual species could have differed immediately post-harvest, our findings suggest that retention harvesting could enable closed-canopy species to use cutblocks earlier than if they had been clear-cut (Fisher and Wilkinson 2005). Our results corroborate previous studies that reveal variation in species' responses to anthropogenic disturbances (Fisher and Burton 2018).

Our study demonstrates the value of retention harvests for sensitive species such as woodland caribou, which was not detected in stands harvested to <20% retention and is a species of conservation concern with rapid population declines (Hervieux et al. 2013). Canada has been criticized for neglect of habitat protection for caribou (Hebblewhite and Fortin 2017), and industrial activities, such as forestry, are implicated as a dominant cause of caribou habitat degradation (Festa-Bianchet et al. 2011). Courtois et al. (2008) suggested amalgamating forest harvesting in localized areas to preserve large areas of intact habitat in the landscape; retention harvests could facilitate habitat connectivity between areas of intact forest (Courtois et al. 2004). Knowing that woodland caribou use retention harvest cut-blocks, forestry companies could consider other management strategies to enhance habitat quality, such as terrestrial lichen transplants or seeding (Government of Alberta 2017).

Stands harvested to varying levels of retention could represent multiple successional stages and thereby provide a range of wildlife habitats across a landscape. Nevertheless, additional research is required to determine whether or not harvesting multiple small areas using a wide range of retention levels is more advantageous than harvesting a single large area to low

retention while preserving a large area of unharvested forest (St-Laurent et al. 2007, Lindenmayer et al. 2015). When comparing these different harvesting designs, the amount of edge creation and consequent effects of fragmentation on vertebrates should also be considered to better accommodate habitat preferences of numerous species and ultimately maintain vertebrate diversity in harvested landscapes.

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