

# Stand-level Attributes of Snowshoe Hare (*Lepus americanus*) Habitat in a Post-Fire Trembling Aspen (*Populus tremuloides*) Chronosequence in Central Yukon

WAYNE L STRONG<sup>1,3,4</sup> and THOMAS S. JUNG<sup>2</sup>

<sup>1</sup>Arctic Institute of North America, 2500 University Drive NW, Calgary, Alberta T2N 1N4 Canada

<sup>2</sup>Yukon Department of Environment, P.O. Box 2703, Whitehorse, Yukon Y1A 2C6 Canada

<sup>3</sup>Corresponding author (email: strong@ucalgary.ca)

<sup>4</sup>Present address: P.O. Box 40186 Station Main, Whitehorse, Yukon Y1A 6M9 Canada

Strong, Wayne L, and Thomas S. Jung. 2012. Stand-level attributes of Snowshoe Hare (*Lepus americanus*) habitat in a post-fire Trembling Aspen (*Populus tremuloides*) chronosequence in central Yukon. *Canadian Field-Naturalist* 126(4): 295–305.

Large-scale fires are anticipated to increase in frequency in the boreal forest under global climate warming scenarios. To understand concomitant responses by wildlife to fire-induced habitat changes, fecal pellet counts were used to assess Snowshoe Hare (*Lepus americanus*) use of four age-classes of boreal forest after fire in central Yukon, Canada. Use of stands across a chronosequence of 8–177 years was bimodal. Post-fire Trembling Aspen (*Populus tremuloides*) stands  $\leq 20$  years old had greater densities of Snowshoe Hare pellets (median 156 pellets/dam<sup>2</sup>) than Trembling Aspen stands 21–70 years old, mixedwood stands 71–120 years old ( $< 17$  pellets/dam<sup>2</sup>), or Western White Spruce (*Picea albertiana*)-dominated stands 121–170 years old (71 pellets/dam<sup>2</sup>). Forty stand-level compositional and structural variables were assessed as possible predictors of Snowshoe Hare pellet densities. Multidimensional scaling was used to identify variables ( $n = 10$ ) that were most strongly related to pellet densities and was followed by multiple regression. Canopy cover of Trembling Aspen  $< 50$  cm tall and Western White Spruce  $\leq 1$  m tall, and deadfall depth, in combination, were the best estimators of Snowshoe Hare pellet densities among stands in the chronosequence ( $P < 0.001$ , 64.5% variance explained). Although Trembling Aspen  $< 50$  cm tall explained the most variance, its canopy cover did not exceed 10%. More Trembling Aspen cover  $< 50$  cm tall and greater deadfall depths within the chronosequence were associated with stands  $\leq 20$  years old. Peak Snowshoe Hare use occurred in early ( $\leq 20$  years old) rather than mid-successional (21–120 years old) stands, contrary to use patterns reported elsewhere. The lack of tall understory shrubs likely limited the use of mid-successional stands.

**Key Words:** Trembling Aspen, *Populus tremuloides*, Western White Spruce, *Picea albertiana*, Snowshoe Hare, *Lepus americanus*, chronosequence, coarse woody debris, deadfall, forest fire, post-fire succession.

Large-scale fires are anticipated to increase in frequency in the boreal forest under global climate warming scenarios (McCoy and Burn 2005). If increasingly larger portions of the landscape are affected by fire, then it is important to understand concomitant responses by wildlife to those changes. The focus of studies that aim to explore how landscape-level disturbances, such as climate change, may affect wildlife should initially be on keystone species, because changes in their abundance and distribution may result in major shifts in ecosystem dynamics (*sensu* Krebs et al. 2001a).

The Snowshoe Hare (*Lepus americanus*) is a keystone species in Nearctic boreal forests (Boutin et al. 1995). Snowshoe Hare are important as prey of commercially-valued furbearers such as the Canada Lynx (*Lynx canadensis*) and as a harvested food (Jacqmain et al. 2007; Nelson et al. 2008). Various studies have been conducted to identify important habitat attributes of the Snowshoe Hare. From these studies, it is clear that Snowshoe Hare prefer tall dense shrubby vegetation, with or without a tree overstory (e.g., Litvatis et al. 1985; St-Georges et al. 1995; Hodges 2000). Greater site use occurs when the shrub stratum is 1–4 m tall with  $> 4000$  stems/ha (Wolfe et al. 1982; Pietz and

Tester 1983; de Bellefeuille et al. 2001; Jacqmain et al. 2007) and forage is within 3 m of the ground surface, when overhead and lateral vegetation cover  $\leq 2.5$  m tall exceeds 60–70% in summer (Litvatis et al. 1985; Ferron and Ouellet 1992; de Bellefeuille et al. 2001), and when overhead cover is  $> 40\%$  in winter (Wolfe et al. 1982). Stand structure and adequate cover are often more important than either the species composition or an immediately available food supply (Litvatis et al. 1985; Ferron and Ouellet 1992).

When habitats that are favoured by Snowshoe Hare (i.e., greater relative use) develop and how long they persist in a forest landscape can vary with the type of vegetation and the associated rate of ecological succession. For example, de Bellefeuille et al. (2001) suggested that peak use of clearcuts in southern Quebec forest was expected when Balsam Fir (*Abies balsamea*) and Black Spruce (*Picea mariana*) regeneration was 15–22 and 18–30 years old, respectively. Forest stands  $> 15$  years old were more intensively used than younger post-disturbance areas in Quebec (Jacqmain et al. 2007; Hodson et al. 2011), Labrador (Newbury and Simon 2005), Ontario (Thompson et al. 1989), Maine (Monthey 1986), and central Alaska (Paragi et al.

1997). Nevertheless, Keith and Surrndi (1971) reported Snowshoe Hare use of 1-year-old burns in central Alberta.

Few studies have investigated the longer term (>50 years) response by the Snowshoe Hare to botanical and structural changes that occur within stands during secondary succession (Fisher and Wilkinson 2005), particularly in high-latitude boreal forests. Most comparative habitat studies have evaluated stand re-establishment during the first 20–30 years after disturbance (e.g., Jacqmain et al. 2007), focused on concurrent differences in composition and structure among vegetation types that were not necessarily part of the same chronosequence (e.g., Poole et al. 1996), or assessed only selected segments of a chronosequence (e.g., Paragi et al. 1997). Unfortunately, changes in Snowshoe Hare abundance in northwestern Canada successional sequences can probably not be extrapolated from studies conducted in southern or eastern boreal forests, except at a very general level, because of regional variability in successional patterns and differences in understory vegetation composition and stand structure (e.g., Chen and Popadiouk 2002; Redburn and Strong 2008; Strong 2009).

The objective of this study was to examine Snowshoe Hare use of forest vegetation after stand-devastating fires in the boreal forest of northwestern Canada. Using fecal pellet counts, we compare Snowshoe Hare use of different age classes of forest after fire, within a 169-year Trembling Aspen (*Populus tremuloides*) chronosequence. To better understand Snowshoe Hare response to forest succession, we identified stand-level botanical and structural variables that were associated with Snowshoe Hare habitat use. These data may be useful in better understanding the response of the Snowshoe Hare (a keystone species) to an increased frequency in forest fires (a predicted result of climate change) and an associated increase in juvenile vegetation.

## Methods

### Study area

The study was conducted along a 223 km north-south transect running from Little Fox Lake (61.368°N, 135.675°W) to north of Pelly Crossing (63.024°N, 136.448°W) in central Yukon, Canada (see Figure 1 in Strong 2009). The area occurs in the Northern Cordilleran Boreal (NCb) ecoclimatic region, which is characterized by early seral Trembling Aspen and successional more mature Trembling Aspen and Trembling Aspen–Western White Spruce (*Picea albertiana* ssp. *albertiana*, Strong and Hills 2006) forests on zonal sites, as opposed to spruce (*Picea* spp.) or Lodgepole Pine (*Pinus contorta* var. *latifolia*) forests that predominate in the surrounding regions (Strong 2013). Western White Spruce is the predominant late-successional species on upland sites in the Northern Cordilleran Boreal ecoclimatic region, which occurs below ~1200 m elevation; open Spruce/Willow-Birch (*Picea*

*Salix-Betula*) vegetation occurs above. Sampled sites are between 470 and 875 m in elevation.

The median May–September temperature is 10.8°C, and in the November–March period it is –18.8°C, based on 1984–2007 monthly data from three meteorological stations within the region (Strong 2013). Most precipitation (177 of 279 mm) occurs in summer, but ~72 cm of snow falls on average during November–March. Wildfires have been a common disturbance agent in the study area, with extensive burns in 1958, 1995, and 1998 (Englefield 2003). The location and distribution of sampled sites as well as the extent of more recent wildfires in the study area were reported by Strong (2009). Hunting, gathering, furbearer trapping, firewood harvesting, and a small amount of agriculture are the principal land uses in the area.

### Field sampling

Vegetation sampling included post-fire Trembling Aspen, mixedwood, and late-successional Western White Spruce stands. Late-successional stands were sampled if they contained live, standing dead, or remnant downed Trembling Aspen trees. Only sites with ≤3% slope gradients and well to moderately well drained soils, without atypical levels of disease or insect infestation and without notable recent or historical tree cutting were sampled. Sites (mostly <15 years old) were excluded if post-fire snags and deadfall had been harvested. Stands were arbitrarily selected for sampling, and an attempt was made to distribute sites across as broad an age range as possible.

Vegetation composition and species abundance sampling of individual stands was based on a 20 m × 30 m plot that included a centrally located transect 30-m in length with five 2.5 m × 2.5 m quadrats for assessing the canopy cover of plants 1–2.5 m tall. Each quadrat included a 1 m × 1 m nested quadrat for sampling vascular plants ≤1 m tall, bryophytes, and terrestrial lichens. The lower left-hand corner of each quadrat was placed at 5-m intervals along the transect beginning at the 5-m mark. The 20 m × 30 m plot was used to assess the canopy cover of trees and shrubs >2.5 m tall. Ocular percent canopy cover estimates were used to gauge plant species abundance. Plant nomenclature follows ITIS Partners (2013\*), unless otherwise indicated.

Point-centered quarter sampling (Mueller-Dombois and Ellenberg 1974) was used to estimate tree (>1 m tall) stem densities, with sampling points located at 10-m intervals (at the –5-, 5-, 15-, and 25-m marks) along the vegetation composition sampling transect. Tree ages were determined for the two tallest Trembling Aspen (or Western White Spruce if Aspen were absent); remnant pre-fire trees were excluded. Stand aging was based on annual growth-ring counts that were obtained from immediately above the tree root collar. The older of the two cored trees, regardless of species, was considered to represent the stand age.

The length, median diameter, and maximum depth of woody stems  $\geq 5$  cm in diameter were measured in each 2.5 m  $\times$  2.5 m vegetation sampling quadrat to determine coarse woody debris or deadfall volume and the number of stems. All stems within 2.5 m of the forest floor and at an incline of  $<45^\circ$  were included. The latter criterion was used to differentiate between downed and standing dead trees. Any substantial portion of a woody stem that was in contact with the ground surface was excluded from assessment.

Snowshoe Hare fecal pellets were counted along a transect 1.5 m in width and 30 m in length (90 m<sup>2</sup>) located on each side of, and 5 m from, the vegetation sampling transect. This sampling design allowed 15% of the study plot to be efficiently sampled, and the large proportion of sampled area increased the likelihood of encountering pellets on sites where few occurred (Hodges and Mills 2008) while potentially avoiding some of the technical issues related to the use of small plots (e.g.,  $\leq 1$  m<sup>2</sup>) with higher edge-to-area ratios (McKelvey et al. 2002). All observed intact pellets were counted regardless of age due to the difficulty of reliable aging (Prugh and Krebs 2004).

In the absence of a specific equation to determine Snowshoe Hare density through the use of pellet counts for the study area, densities were estimated using an algorithm developed by Krebs et al. (2001b). However, these estimates may be inflated because pellets were not cleared from each site a year prior to sampling (Hodges and Mills 2008). Pellet and tree stem densities, and deadfall volumes were summarized by decameter<sup>2</sup> (dam<sup>2</sup>, i.e., 100 m<sup>2</sup>). Field sampling was limited to late June and July 2008. This was a period when the Snowshoe Hare population was in decline (Sheriff et al. 2011).

#### Data analysis

In addition to analyzing individual forest stand variables and plant taxa by stratum, composite variables (e.g., total herb, forb, species cover) and selected botanical diversity measures (e.g., richness and dominance concentration – Strong 2002) were also assessed. Composite variables were created by summing species percent cover values within individual relevés. The cover values of bryum moss (*Bryum caespiticium*) and Fire Moss (*Ceratodon purpureus*) were combined to represent early seral or pioneer mosses.

A total of 40 stand variables were considered in the analysis. Forest stands ( $n = 96$ ) were segregated into four age classes:  $\leq 20$  ( $n = 24$ ), 21–70 ( $n = 29$ ), 71–120 ( $n = 33$ ), and 121–177 ( $n = 10$ ) years old. These age classes generally corresponded to major physiognomy and overstory composition differences within the chronosequence: juvenile post-fire (early seral); Trembling Aspen- (mid-seral); Trembling Aspen-Western White Spruce (late seral); and Western White Spruce (late-successional) vegetation, respectively. Kruskal-Wallis tests were used to determine whether there

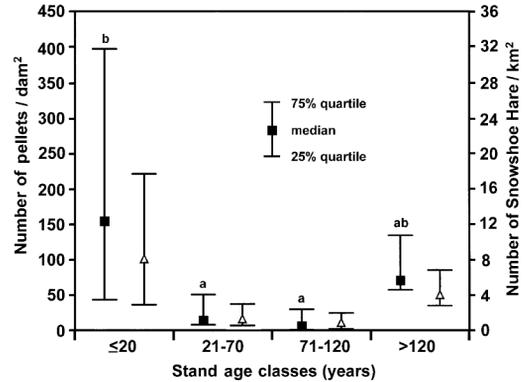


FIGURE 1. Snowshoe Hare (*Lepus americanus*) fecal pellet densities (■) and corresponding population densities (△) by age class within a Trembling Aspen (*Populus tremuloides*) chronosequence from central Yukon. Comparison of pellet densities among stand age classes was based on a Kruskal-Wallis test ( $P < 0.001$ ). Age classes with the same letter above the quartile range bars do not differ at the  $\alpha 0.05$  level based on Scheffé rank test results. Snowshoe Hare population densities were estimated using an algorithm developed by Krebs et al. (2001b), but may be overestimated because vegetation stands were not cleared of pellets the year prior to sampling.

were differences in stand variables among age classes. Post-hoc nonparametric Scheffé rank tests (Miller 1966) were used to identify pair-wise differences at the  $\alpha 0.05$  level.

Multidimensional scaling (an ordination technique) was used to determine the relative numerical relationship among stand variables and Snowshoe Hare pellet densities, based on a two-dimensional solution using the standard Guttman-Lingoes procedure (Statsoft 1995). The purpose of the ordination was to identify candidate variables that had the best potential for estimating pellet densities. Variables that occurred in closer proximity to the pellet density loci were most strongly associated, but it was unknown which combination of variables could be used to optimize the estimation of Snowshoe Hare pellet densities. As an objective criterion, only stand variables with the shortest Euclidean distances to the pellet density loci ( $<25\%$  of longest distance) were included in the regression analyses (see below). This criterion approximated the first quartile value among Euclidean distance measurements and a natural break in the distribution of variables within the ordination. The percentage of variance explained by the ordination was equal to  $100 - \text{coefficient of alienation}^2 \times 100$  (Schiffman et al. 1981, page 92).

Multiple regression analysis was used to simultaneously compare the relative importance of candidate variables (independent variables) selected from the mul-

TABLE 1. Median (1st–3rd quartile in parentheses) botanical characteristics of different age classes in a Trembling Aspen (*Populus tremuloides*) chronosequence from central Yukon.

Variable	Stand age classes (years)				P value <sup>1</sup>
	≤20 (n = 24)	21–70 (n = 29)	71–120 (n = 33)	121–177 (n = 10)	
Tree stratum (>2.5 m tall, percent cover)					
Trembling Aspen (POTR5)	10(2–28)ab <sup>1</sup>	60(40–65)c	45(15–60)bc	+(0–2)a <sup>†</sup>	<0.001
Western White Spruce (PIAL3)	0a	10(4–30)b	25(15–35)bc	40(35–40)c	<0.001
Willow (SX3)	0(0–1)a	+(0–1)a	0(0–+a)	0a	0.143
Tall shrub stratum (1–2.5 m tall, percent cover)					
Trembling Aspen (POTR4)	9(6–13)b	0(0–1)a	0(0–+a)	0a	<0.001
Western White Spruce (PIAL2)	0a	0(0–2)a	0a	+(0–1)a	0.005
Willow (SX2)	3(1–8)b	0(0–+a)	0(0–1)a	0a	<0.001
Low shrub stratum (≤1 m tall, percent cover)					
Trembling Arctic Lupine (LUAR)	0a	0(0–2)a	0(0–2)a	0a	0.208
Trembling Aspen ≤1 m tall (POTR3)	5(2–9)b	+(0–1)a	0(0–1)a	0a	<0.001
Trembling Aspen 50–100 cm tall (POTR2)	2(1–8)b	0a	0(0–+a)	0a	<0.001
Trembling Aspen <50 cm tall (POTR1)	1(0–1)a	+(0–1)a	0a	0a	0.006
Common Bearberry (ARUV)	0(0–+a)	10(2–22)b	0(0–7)a	0a	<0.001
Bog Cranberry (SAVI)	0a	0(0–2)a	0(0–2)a	+(0–+a)	0.118
Buffalobery (SHCA)	0(0–1)a	0(0–1)ab	3(0–16)b	0(0–1)ab	0.004
Fireweed (CHAN)	6(2–11)c	3(1–5)bc	1(+–3)ab	0a	<0.001
Purple Reedgrass (CAPU)	3(0–14)b	17(6–21)c	8(2–12)bc	+(0–+a)	<0.001
Twinflower (LIBO)	0(0–1)a	0(0–1)a	+(0–3)a	+(0–+a)	0.225
Western White Spruce (PIAL1)	+(0–2)a	0(0–1)a	+(0–1)a	0a	0.106
Wild Rose (ROAC)	0a	0(0–+a)ab	0(0–5)a	0ab	0.001
Willow (SX1)	3(2–9)b	0(0–1)a	0a	0a	<0.001
Ground stratum (percent cover)					
Dog tongue lichens (PELT)	1(+–3)ab	+(0–1)a	+(0–3)a	4(3–6)b	<0.001
Mature stand mosses (Mm)	+(0–3)a	+(0–1)a	3(1–31)b	71(55–87)b	<0.001
Pioneer mosses (Mp)	44(24–60)b	0a	0a	0a	<0.001

<sup>1</sup> Comparisons based on Kruskal-Wallis tests. Values in rows with the same letter(s) do not differ at the  $\alpha$  0.05 level according to post-hoc Scheffé rank tests.

<sup>†</sup> “+” indicates a cover value ≤0.55%.

tidimensional scaling ordination. Variables that substantially overlapped in botanical composition with better estimators were excluded from the analysis. The stepwise backwards procedure was used to identify the combination of independent variables that best explained the variation in Snowshoe Hare pellet densities (dependent variable). Both composite and stepwise regression analyses were based on a correlation matrix. Variable normalization and standardization were not done because both procedures substantially reduced the degree of dependent variables explanation. Neither procedure is a necessity when multiple regression analysis is based on a correlation matrix, although they can sometimes improve the degree of explanation (Tabachnick and Fidell 1989).

The fit of sample distributions to a normal curve was assessed using Kolmogorov-Smirnov one-sample tests. Statistical comparisons were performed using STATISTICA software (Statsoft 1995); except for Scheffé rank tests, which were manually determined.

## Results

### Vegetation

Stands ranged from 8 to 177 years old. Post-fire stands ≤20 years old had an open canopy tree stratum

of Trembling Aspen that ranged up to 4–5 m in height (Tables 1 and 2). The tree and tall shrub strata had a similar amount of Trembling Aspen cover, but willows (*Salix* spp.) were more abundant in the tall shrub stratum. Stands typically contained 42–168 live tree stems/dam<sup>2</sup>, but ranged up to 677 stems/dam<sup>2</sup>. The low shrub stratum included willows, Fireweed (*Chamerion angustifolium*), Purple Reedgrass (*Calamagrostis purpurascens*), and small amounts of Trembling Aspen in the <50 and 50–100 cm height ranges, with a discontinuous ground layer of post-fire pioneer mosses on mineral soil (Table 1). Western White Spruce often occurred in the low shrub stratum. Half of the stands (1st–3rd quartiles, Table 2) in this age class contained 0.1–0.9 m<sup>3</sup>/dam<sup>2</sup> of downed and criss-crossed deadfall, mostly coniferous trees from the pre-fire forest. Deadfall reached a depth of 1 m, with an upper quartile value of 46 cm. Typically, 8–23 downed trees ≥5 cm in diameter occurred in each 2.5 m × 2.5 m quadrat.

Stands 21–70 years old were dominated by Trembling Aspen 7–10 m tall with some Western White Spruce in the tree stratum. Stands typically contained 29 to 52 live tree stems/dam<sup>2</sup> (Table 2). Purple Reedgrass and Common Bearberry (*Arctostaphylos uva-ursi*) with Fireweed dominated the low shrub stratum

TABLE 2. Median (1st–3rd quartile in parentheses) stand and structural characteristics of different age classes in a Trembling Aspen (*Populus tremuloides*) chronosequence from central Yukon.

Variable	Stand age classes (years)				P value <sup>1</sup>
	≤20 (n = 24)	21–70 (n = 29)	71–120 (n = 33)	121–177 (n = 10)	
Growth form (percent cover)					
Trees (STt)	10(3–30)a	74(67–81)b	70(56–80)b	41(37–51)a	<0.001
Shrubs (SH2)	13(5–19)b <sup>1</sup>	21(8–30)ab	13(1–35)b	+ (0–2)a <sup>†</sup>	0.002
Shrubs ≤1 m tall (SH1)	8(3–13)b	1(0–3)a	6(+–22)ab	0(0–2)a	0.001
Forbs (FORBS)	11(5–15)ab	11(5–21)b	8(3–14)ab	2(1–7)a	0.033
Trees <2.5 m tall (TRun)	18(10–25)b	2(1–3)a	1(+–2)a	+ (0–1)a	<0.001
Tall shrub stratum (STts)	13(10–22)b	1(+–3)a	+ (0–1)a	+ (0–1)a	<0.001
Low shrub stratum (STls)	36(23–45)b	58(40–67)b	44(18–52)b	82(58–96)a	<0.001
Ground stratum (STg)	52(38–69)c	1(+–2)a	55(45–74)b	82(58–96)c	<0.001
Understory plants (UNDER)	88(79–100)c	60(40–69)bc	55(45–74)ab	92(65–98)a	<0.001
Total species (TOTc)	125(111–131)	133(115–144)	123(113–142)	127(122–136)	0.411
Stand characteristics					
Age (years, AGE)	10(10–14)	55(47–59)	99(87–110)	142(136–156)	–
Tree stems >1 m tall/dam <sup>2</sup> (STEMS)	87(42–168)b	41(29–52)b	16(12–26)a	19(11–21)a	<0.001
Deadfall depth (cm; DFd)	0(0–46)a	8(0–15)a	0(0–11)a	<1(0–30)a	0.658
Deadfall stems (per 6.25m <sup>2</sup> , DFn)	14(8–23)c	2(1–4)ab	3(1–7)b	4(0–6)a	<0.001
Deadfall volume (m <sup>3</sup> /dam <sup>2</sup> , DFv)	0.4(0.1–0.9)b	0.1(+–0.1)a	0.1(+–0.2)a	0.1(0–0.3)ab	0.002
Richness of vascular taxa (Rv)	9(8–11)ab	12(10–14)b	10(8–13)ab	5(3–8)a	<0.001
Richness of nonvascular taxa (Rn)	4(3–4)a	3(2–5)a	4(2–9)a	12(9–13)b	<0.001
Dominance concentration (× 100, Dw)	53(50–59)a	63(58–67)b	64(56–67)b	71(65–74)b	<0.001

<sup>1</sup>Comparisons based on Kruskal-Wallis tests. Age-classes by variable with the same letters do not differ at the  $\alpha$  0.05 level according to post-hoc Scheffé rank tests.

<sup>†</sup>“+” indicates a cover value ≤0.55%.

(Table 1). Bryophytes and lichens were essentially absent. The abundance of deadfall was less than in stands ≤20 years old stands, but depths between the age classes were statistically the same (Table 2). Two downed trees typically occurred in each 2.5 m × 2.5 m quadrat. Trembling Aspen >2.5 m tall, Purple Reedgrass, and Common Bearberry canopy cover peaked in this age class (Table 1).

Trembling Aspen <15 m tall dominated the tree stratum of stands 71–120 years old, but Western White Spruce composed one-third of the overstory cover. Purple Reedgrass was the dominant understory species, with a median cover of 8%. Buffaloberry (*Shepherdia canadensis*), Wild Rose (*Rosa acicularis*), and Common Bearberry (all ≤3% cover), with various herbaceous species (e.g., Twinflower, *Linnaea borealis*, Arctic Lupine, *Lupinus arcticus*, and Bog Cranberry–*Vaccinium vitis-idaea*) had low cover and constancy in the low shrub stratum (Table 1). The abundance of most understory plants was less than in stands 21–70 years old, except for Stairstep Moss (*Hylocomium splendens*), which increased (Table 1). Deadfall was typically less than 0.2 m<sup>3</sup>/dam<sup>2</sup> in stands of this age class, with three downed trees per 2.5 m × 2.5 m quadrat (Table 2).

Stands 121–177 years old were dominated by Western White Spruce. Stands typically contained 11–21 stems/dam<sup>2</sup> (Table 1 and 2) and maximum heights were 19–22 m. Tall and low shrub strata were absent,

but a relatively continuous Stairstep Moss carpet occurred that included dog tongue lichens (*Peltigera aphthosa* and *P. malacea*).

The median abundance of deadfall decreased with increasing stand age, although a slight increase occurred in the 121–177 year age class based on the upper quartile value (Table 2). The abundance of Trembling Aspen declined as Western White Spruce cover increased. Total tree stratum cover peaked when stands were 21–120 years old (Table 2). In contrast, nonvascular species richness and dominance concentration showed a pattern of increase with stand age, but total species cover was similar among age classes (Table 2).

#### Pellet densities

A median density of 31 (quartile range 5–119) Snowshoe Hare fecal pellets/dam<sup>2</sup> was found among sampled stands, with significant differences among age classes (Figure 1). The quartile limits for stands ≤20 years old were 48 to 399 pellets/dam<sup>2</sup>, with a median of 156 pellets/dam<sup>2</sup>. Peak densities occurred in stands 8–15 years old (Figure 2a). Few pellets were found in the 21–70 and 71–120 year age classes (median 16 and 8 pellets/dam<sup>2</sup>, respectively), whereas the oldest age class had slightly less than half as many pellets as ≤20 year-old stands. Stands ≤20 years old had Snowshoe Hare densities above the dataset median, whereas older age classes were below the median, especially the stands 21–120 years old, with the equivalent of <1 Snowshoe Hare/km<sup>2</sup> (Figure 1).

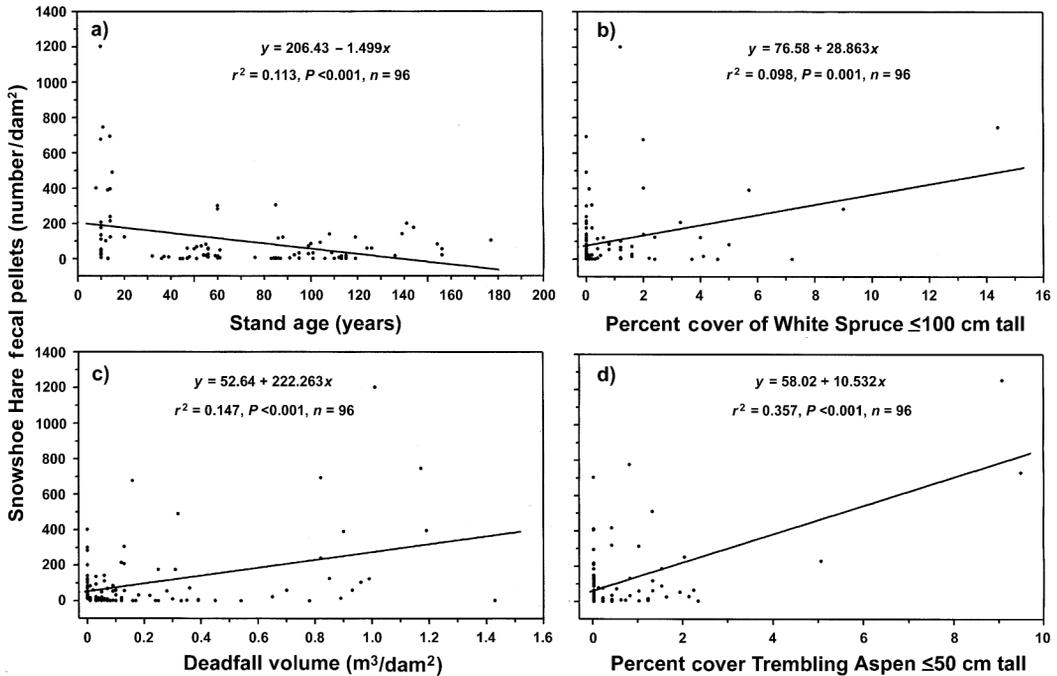


FIGURE 2. Scatter diagrams and associated linear regression models of independent variables that formed model 2b (Table 3), with Snowshoe Hare (*Lepus americanus*) pellet densities as the dependent variable.

#### Ordination and regression

Ordination produced a distinct cluster of variables, which included Snowshoe Hare pellet densities (PD), with other variables generally at a similar distance from and to the right of the pellet density loci in a crescent-shaped pattern (Figure 3). Most understory taxa; overstory tree, forb, shrub, pioneer moss, and sometimes tall shrub cover variables; species richness; dominance concentration; and stand age occurred outside the 25% Euclidean distance limit. Dog tongue lichens (PELT) and ground stratum cover (STg) occurred halfway between the two groupings. The clustered variables were related to understory vegetation composition, stem densities, deadfall, pioneer mosses, and trees and shrub cover in the low and tall shrub strata. The ordination explained ~96% of the variance among variables.

Eleven stand variables occurred within the established distance limit from the pellet density loci (Figure 3). However, Trembling Aspen cover  $\leq 1$  m tall (POTR3) was removed from consideration, because its composition overlapped with Trembling Aspen  $< 50$  cm tall (POTR1) and 50–100 cm tall (POTR2). Subsequent testing by regression analyses also showed that Trembling Aspen cover  $\leq 1$  tall was a less useful variable for explaining pellet density variation than the two other variables.

Regression analysis of the remaining 10 variables, as a group, explained 53.8% of the variance in Snowshoe Hare pellet densities (Model 1a in Table 3). Among these variables, however, only two had a significant  $P$  values ( $P < 0.05$ ): Trembling Aspen cover  $< 50$  cm tall and Western White Spruce cover  $\leq 1$  m tall (PIAL1). Based on the standardized beta coefficient, the cover of Trembling Aspen  $< 50$  cm tall explained most of the variance (Table 3). Stepwise regression analysis (model 1b in Table 3) identified the two former variables and deadfall depth (DFd) as the most useful for predicting Snowshoe hare pellet densities. In combination, these variables explained 53.9% of the variance. All three variables were positively correlated with pellet densities. None of the other stand variables had significant  $P$  values (i.e.,  $P < 0.05$ ) in the stepwise regression analysis. In addition, the  $y$ -intercept did not contribute significantly to the estimation of pellet densities in either model 1a or model 1b (Table 3), i.e., the  $y$ -intercept was not significantly different from zero.

Re-analysis of the data with the  $y$ -intercept set to zero yielded similar regression results between models 1a and 2a based on a comparison of standardized beta coefficients (Table 3). The exceptions were the additional recognition of pioneer moss cover (Mp) as

a significant variable in model 2a and a greater proportion of explained variance (i.e., 64% versus 54%). The same independent variables were identified as significant in models 1b and 2b. Stepwise regression model 2b explained more variance than model 1b (Table 3). Model 2b explained almost twice the variance of any of the individual independent variables in the model (Figure 2b, 2c, and 2d).

Model 2b was the most efficient of the four models for predicting Snowshoe Hare pellet densities in the chronosequence. It had the highest proportion of explained variance and included of the fewest independent variables. Differences between observed and model 2b predicted pellet densities (residuals) did not conform to a normal distribution ( $P > 0.05$ ). However, the standard deviation of the residuals was 42 pellets for two-thirds of the stands that did fit a normal distribution. All stands not conforming to a normal distribution had under-predicted pellet densities, and most of these stands were <20 years old. No particular trend was identified among the independent variables that could be used to explain the under-predictions.

In the absence of Trembling Aspen canopy cover variables in the understory vegetation, stepwise regression identified the density of tree stems >1 m tall as the strongest variable for estimating pellet densities. However, the associated regression model explained only 50% of the variation in the data.

## Discussion

Among chronosequence stands, the greatest cover of Trembling Aspen  $\leq 50$  cm tall and greatest deadfall depths were associated with post-fire stands  $\leq 20$  years old. Low-growing Trembling Aspen might be ecologically-important because of the cover and food that it can provide Snowshoe Hares (Wolff 1978) during the snow-free season. The 50–100 cm height class might be more important in winter, when snow buries the shorter plants (Bider 1961). Successionally, both height classes diminish in abundance as stands age because of height growth, overstory suppression, and tree stem exclusion.

Stand characteristics, such as shrub cover and tree stem density, have been traditionally recognized as important habitat variables for the Snowshoe Hare (e.g., Wolfe et al. 1982; Pietz and Tester 1983; Litvatis et al. 1985; Ferron and Ouellet 1992; de Bellefeuille et al. 2001; Jacqmain et al. 2007), but the depth of deadfall less so. Deadfall above the forest floor likely serves as hiding cover (Hodges 1998; Andruskiw 2003; Berg et al. 2012), possibly as thermal cover in winter (Conroy et al. 1979; Roy et al. 1995), and likely facilitates safer movement by Snowshoe Hares through the local vegetation. Not all young forest stands contained deadfall, possibly due to the pre-fire characteristics of a stand or the intensity of local burning, nor were older stands devoid of the material. The greater availability of elevated deadfall in the stands 121–177

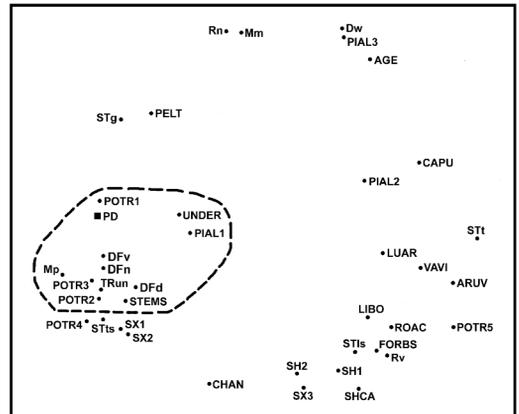


FIGURE 3. Relative numerical relationships among stand variables and Snowshoe Hare (*Lepus americanus*) fecal pellet densities within a Trembling Aspen (*Populus tremuloides*) chronosequence from central Yukon based on ordination by multidimensional scaling ( $n = 96$  stands). Variables in the delineated group occurred nearest the Snowshoe Hare pellet density loci (i.e.,  $\leq 25\%$  of the distance to the most distal stand variable). DFD – Deadfall depth, DFn – Deadfall stems, DFv – Deadfall volume, Mp – pioneer moss cover, PD – Snowshoe Hare pellet densities, PIAL1 – Western White Spruce  $\leq 1$  m tall cover, POTR1 – Trembling Aspen  $< 50$  cm tall cover, POTR2 – Trembling Aspen 50–100 cm tall cover, POTR3 – Trembling Aspen  $\leq 1$  m tall, POTR4 – Trembling Aspen 1–2.5 m tall, STEMS – Tree stems >1 m tall, TRun – Trees  $< 2.5$  m tall cover, and UNDER – understory plant cover. See Table 1 or 2 for additional acronyms.

years old and dominated by Western White Spruce may explain the associated greater pellet densities (as opposed to the prolonged persistence or greater visibility of pellets on feathermoss carpets in these stands) than in the Trembling Aspen or mixedwood forest stands 21–120 years old.

The small sample size for stands in the oldest age class ( $n = 10$ ) may have limited our ability to detect a statistically significant difference in pellet densities and deadfall levels between stands 121–177 years old and 21–120 years old. However, a similar bimodal pattern of pellet densities was reported in eastern Quebec by Hodson et al. (2011). Although Hudson et al. (2011) did not measure deadfall, its association with more intensively used canopy gaps in older growth stands seems likely (J. Hodson, personal communication, 2011; cf. Lowe et al. 2011). Greater pellet densities in Western White Spruce stands dominated by a ground cover of feathermosses indicates possible use in winter as cover, when young Trembling Aspen stands lack foliar cover and deep snow has buried other cover (Wolff 1980; Keith and Bloomer 1993; Hodges and Sinclair 2005). The occurrence of deadfall in conjunc-

TABLE 3. Results of standard and stepwise backward multiple regression analyses of selected stand variables based on an estimated  $\gamma$ -intercept (models 1a and 1b) and  $\gamma$ -intercept set to zero (model 2a and 2b) models for predicting Snowshoe Hare (*Lepus americanus*) fecal pellet densities in an Trembling Aspen (*Populus tremuloides*) chronosequence from central Yukon, Canada.

Variable	Beta coefficients	Standardized beta coefficients	P value	Beta coefficients	Standardized beta coefficients	P value
<b>Composite multiple regression models</b>						
$\gamma$ -intercept	-57.201	-	0.184	0	-	-
Trembling Aspen cover <50 cm tall (POTR1)	66.930	0.523	<0.001	66.799	0.493	<0.001
Trembling Aspen cover 50-100 cm tall (POTR2)	-0.069	-0.001	0.993	1.481	0.115	0.840
Western White Spruce cover $\leq$ 1 m tall (PIAL1)	24.899	0.283	0.003	24.901	0.271	0.003
Tree cover <2.5 m tall (TRun)	-2.841	-0.143	0.339	-3.268	-0.173	0.272
Tree stems >1 m tall (STEMS)	0.356	0.161	0.174	0.342	0.161	0.193
Understory cover $\leq$ 1 m tall (UNDER)	0.625	0.082	0.314	-0.096	-0.032	0.752
Pioneer moss cover (Mp)	1.332	0.155	0.143	1.722	0.196	0.048
Deadfall depth (DFd)	2.119	0.210	0.116	1.925	0.251	0.152
Deadfall volume (DFv)	-7.304	-0.013	0.931	3.486	0.007	0.967
Number of deadfall stems (DFn)	-0.551	-0.023	0.892	-1.125	-0.057	0.774
Adjusted coefficient of determination ( $R^2 \times 100$ )		53.8%	<0.001		64.1%	<0.001
<b>Best stepwise multiple regression model</b>						
$\gamma$ -intercept	-18.714	-	0.354	0	-	-
Trembling Aspen cover <50 cm tall (POTR1)	70.714	0.552	<0.001	9.301	0.516	<0.001
Western White Spruce cover $\leq$ 1 m tall (PIAL1)	27.937	0.317	<0.001	6.159	0.293	<0.001
Deadfall depth (DFd)	2.553	0.252	<0.001	0.576	0.275	<0.001
Adjusted coefficient of determination ( $R^2 \times 100$ )		53.9%	<0.001		64.5%	<0.001

tion with low-growing Trembling Aspen may enhance Snowshoe Hare use of young stands compared with only one or the other habitat characteristics being present (Hodges and Sinclair 2005; de Chantal and Granström 2007).

The statistically significant relationship between pellet density and Western White Spruce  $\leq 1$  m tall (Table 3) might be due to the hiding cover that small, dense-canopied trees might provide. The low abundance of such stems in stands 21–120 years of age might explain the lower relative abundance of Snowshoe Hare within this age range. The potential importance of Trembling Aspen  $< 50$  cm tall and Western White Spruce  $\leq 1$  m tall to Snowshoe Hare in this chronosequence must be great, based on their limited abundance in these stands (Table 1). The occurrence of pioneer mosses as an important attribute in the composite regression analyses likely represents a proxy variable for post-fire ecological conditions, because these mosses provide no cover and have little if any known forage value for the Snowshoe Hare.

The finding that tree stem density was not an important Snowshoe Hare habitat variable in the studied vegetation chronosequence is contrary to other studies (Wolfe et al. 1982; Pietz and Tester 1983; de Bellefeuille et al. 2001; Jacqmain et al. 2007). This result occurred with or without regression variables normalized and/or standardized. Therefore, Trembling Aspen cover in summer might be more critical than the number of tree stems needed to form the canopy, although the two factors are not unrelated.

The stands 21–120 year-old in the chronosequence had essentially no deadfall and little shrubbery to provide hiding cover or browse for Snowshoe Hares. The lack of deadfall was probably due to the settling and decomposition of post-fire debris and the fact that healthy stands of this age range do not typically generate large quantities of deadfall. Minimal shrub content occurs because of forest overstory suppression as part of the ecological succession process, and the general lack of medium-height and tall shrubs such as Beaked Hazelnut (*Corylus cornuta*), Saskatoon (*Ame-lanchier alnifolia*), or Low-bush Cranberry (*Viburnum edule*) in the vegetation of central Yukon. As a result, stands 21–120 years old were largely unused by Snowshoe Hares in the chronosequence, even though they are important habitats elsewhere (e.g., Monthey 1986; Thompson et al. 1989; Paragi et al. 1997; Newbury and Simon 2005; Jacqmain et al. 2007; Hodson et al. 2011).

Burns  $< 9$  years old were uncommon in the study area. Therefore, it cannot be directly determined when relatively intense or peak post-fire use of young Trembling Aspen stands began by Snowshoe Hare. Data compiled by Oswald and Brown (1990) suggest that sufficient stem densities (148 stems/dam<sup>2</sup> with 89% cover) and heights of  $< 1$  m develop within 5 years after a wildfire in southwestern Yukon. The presence

of deadfall, however, might encourage early use of post-fire stands if vegetation does not provide sufficient cover (Conroy et al. 1979). The fact that a high pellet density occurred in the youngest stand in the chronosequence (402 pellets/dam<sup>2</sup>, stand 8 years old) suggests that peak Snowshoe Hare abundance may occur within a few years after a fire; this is earlier than reported in other studies ( $> 15$  years – e.g., Monthey 1986; Thompson et al. 1989; Paragi et al. 1997; Newbury and Simon 2005; Jacqmain et al. 2007; Hodson et al. 2011). In cutblocks with only spruce and Balsam Fir tree regeneration, the delay in Snowshoe Hare reoccupation may be related to the conical physiognomy of the trees, which provide limited horizontal and lateral cover until the trees reach a sufficient height and density (i.e., 15–30 years – Paragi et al. 1997; de Bellefeuille et al. 2001; Jacqmain et al. 2007). In contrast, regenerating Trembling Aspen tend to increase in height quicker and have bushy stems that often establish at higher densities than planted or naturally regenerating conifer stands and, as a result, produce greater canopy cover at a much lower height in less time.

The habitat most intensively used by Snowshoe Hares within the studied chronosequence conformed to vegetation characteristics generally recognized as important in other studies, i.e., shrubby vegetation. Among the studied forest stands, the strongest predictors of Snowshoe Hare habitat use were common attributes of young post-fire stands. Forest stands  $> 20$  years old that have been documented as being important habitat elsewhere were largely unused in central Yukon. Therefore, the general abundance of Snowshoe Hares in central Yukon is in part dependent upon the extent and frequency of wildfires (cf. Fox 1978), which may increase with future global warming (McCoy and Burn 2005). A shortening of the fire-return interval in the study area might initially increase the abundance of juvenile forest stands because of the mature nature of most of the current vegetation and thereby increase the availability of better quality Snowshoe Hare habitat. In the long-term, however, more frequent fires will reduce the average age of stands at the landscape-level. A warmer climate might also cause a shift towards forest understories with a greater shrub content and possibly cause a reduction in the availability of trees that form persistent coarse-woody debris, such as Western White Spruce. Such changes could alter the current Snowshoe Hare habitat use relationship. Unfortunately, the potential effects of future climatic warming on vegetation in this high-latitude environment are not fully known.

### Acknowledgements

Field data collection was in part funded by the Yukon Department of Environment. Karen Clyde provided comments on an initial project design and Val Loewen provided an unpublished manuscript (Yukon Department of Environment), and Yukon Energy, Mines and

Resources Library staff provided helpful assistance. Dr. James Hodson (formerly at Université Laval) provided background commentary on a related paper that he published. Comments that improved the clarity of the manuscript were provided by an associate journal editor and two anonymous reviewers.

### Documents Cited (marked \* in text)

**ITIS Partners.** 2013\*. Integrated taxonomic information system. <http://www.itis.gov/index.html> (accessed 8 February 2013).

### Literature Cited

- Andruskiw, M.** 2003. Prey abundance, availability, and anxiety in structured environments. M.Sc. thesis, University of Guelph, Guelph, Ontario. 46 pages.
- Berg, N. D., E. M. Gese, J. R. Squires, and L. A. Aubry.** 2012. Influence of forest structure on the abundance of snowshoe hares in western Wyoming. *Journal of Wildlife Management* 76: 1480–1488.
- Bider, J. R.** 1961. An ecological study of the hare *Lepus americanus*. *Canadian Journal of Zoology* 39: 81–103.
- Boutin, S., C. J. Krebs, R. Boonstra, M. R. T. Dale, S. J. Hannon, K. Martin, A. R. E. Sinclair, J. N. M. Smith, R. Turkington, M. Blower, A. Byrom, F. I. Doyle, C. Doyle, D. Hik, L. Hofer, A. Hubbs, T. Karels, D. L. Murray, V. Nams, M. O'Donoghue, C. Rohner, and S. Schweiger.** 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos* 74: 69–80.
- Chen, H. Y. H., and R. V. Popadiouk.** 2002. Dynamics of North American boreal mixedwoods. *Environmental Review* 10: 137–166.
- Conroy, M. J., L. W. Gysel, and G. R. Dudderar.** 1979. Habitat components of clear-cut areas for snowshoe hares in Michigan. *Journal of Wildlife Management* 43: 680–690.
- de Bellefeuille, S., L. Bélanger, J. Huot, and A. Cimon.** 2001. Clear-cutting and regeneration practices in Quebec boreal balsam fir forest: effects on snowshoe hare. *Canadian Journal of Forest Research* 31: 41–51.
- de Chantal, M., and A. Granström.** 2007. Aggregations of dead wood after wildfire act as browsing refugia for seedlings of *Populus tremula* and *Salix caprea*. *Forest Ecology and Management* 250: 3–8.
- Englefield, A. (compiler).** 2003. Yukon fire history atlas: 1946–2001 (CD-ROM). Yukon Fire Centre, Whitehorse, Yukon, and Northern Forestry Research Centre, Edmonton, Alberta.
- Ferron, J., and J-P. Ouellet.** 1992. Daily partitioning of summer habitat and use of space by the snowshoe hare in southern boreal forests. *Canadian Journal of Zoology* 70: 2179–2183.
- Fisher, J. T., and L. Wilkinson.** 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Review* 35: 51–81.
- Fox, J. F.** 1978. Forest fires and the snowshoe hare–Canada lynx cycle. *Oecologia* 31: 349–374.
- Hodges, K. E.** 1998. Snowshoe hare demography and behaviour during a cyclic population low phase. Ph.D. thesis, University of British Columbia, Vancouver, British Columbia. 230 pages.
- Hodges, K. E.** 2000. The ecology of snowshoe hares in northern boreal forests. Pages 163–206 in *Ecology and Conservation of Lynx in the United States*. Edited by L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires. University of Colorado Press, Boulder, Colorado.
- Hodges, K. E., and L. S. Mills.** 2008. Designing fecal pellet surveys for snowshoe hares. *Forest Ecology and Management* 256: 1918–1926.
- Hodges, K. E., and A. R. E. Sinclair.** 2005. Browse site selection by snowshoe hares: effects of food supply and predation risk. *Canadian Journal of Zoology* 83: 280–292.
- Hodson, J., D. Fortin, and L. Bélanger.** 2011. Changes in relative abundance of snowshoe hare (*Lepus americanus*) across a 265-year gradient of boreal forest succession. *Canadian Journal of Zoology* 89: 908–920.
- Jacqmain, H., L. Bélanger, S. Hilton, and L. Bouthillier.** 2007. Bridging native and scientific observations of snowshoe hare habitat restoration after clearcutting to set wildlife habitat management guidelines on Waswanipi Cree land. *Canadian Journal of Forest Research* 37: 530–539.
- Keith, L. B., and S. E. M. Bloomer.** 1993. Differential mortality of sympatric snowshoe hares and cottontail rabbits in central Wisconsin. *Canadian Journal of Zoology* 71: 1694–1697.
- Keith, L. B., and D. C. Surrendi.** 1971. Effects of fire on a snowshoe hare population. *Journal of Wildlife Management* 35: 16–26.
- Krebs, C. J., R. Boonstra, S. Boutin, and A. R. E. Sinclair.** 2001a. Conclusions and future directions. Pages 491–502 in *Ecosystem Dynamics of the Boreal Forest: the Kluane Project*. Edited by C. J. Krebs, S. Boutin, and R. Boonstra. University of Oxford Press, New York City, New York.
- Krebs, C. J., R. Boonstra, V. Nams, M. O'Donoghue, K. E. Hodges, and S. Boutin.** 2001b. Estimating snowshoe hare population density from pellet plots: a further evaluation. *Canadian Journal of Zoology* 79: 1–4.
- Litvatis, J. A., J. A. Sherburne, and J. A. Bissonette.** 1985. Influence of understory characteristics on snowshoe hare habitat use and density. *Journal of Wildlife Management* 49: 866–873.
- Lowe, J., D. Pothier, J-P. L. Savard, G. Rompré, and M. Bouchard.** 2011. Snag characteristics and cavity-nesting birds in the unmanaged post-fire northeastern Canadian boreal forest. *Silva Fennica* 45: 55–67.
- McCoy, V. M., and C. R. Burn.** 2005. Potential alteration by climate change of the forest-fire regime in the boreal forest of central Yukon Territory. *Arctic* 58: 276–285.
- McKelvey, K. S., G. W. McDaniel, L. S. Mills, and P. C. Griffin.** 2002. Effects of plot size and shape on pellet density estimates for snowshoe hares. *Wildlife Society Bulletin* 30: 751–755.
- Miller Jr., R. G.** 1966. *Simultaneous Statistical Inferences*. McGraw-Hill Book Company, New York, New York. 299 pages.
- Monthey, R. W.** 1986. Responses of snowshoe hare, *Lepus americanus*, to timber harvesting in northern Maine. *Canadian Field-Naturalist* 100: 568–570.
- Mueller-Dombois, D., and H. Ellenberg.** 1974. *Aims and Methods of Vegetation Ecology*. John Wiley & Sons, New York, New York. 547 pages.
- Nelson, J. L., E. S. Zavaleta, and F. S. Chapin III.** 2008. Boreal fire effects on subsistence resources in Alaska and adjacent Canada. *Ecosystems* 11: 156–171.
- Newbury, T. L., and N. P. P. Simon.** 2005. The effects of clearcutting on snowshoe hare (*Lepus americanus*) relative

- abundance in central Labrador. *Forest Ecology and Management* 210: 131–142.
- Oswald, E. T., and B. N. Brown.** 1990. Vegetation establishment during 5 years following wildfire in northern British Columbia and southern Yukon Territory. Information Report BC-X-320. Forestry Canada, Victoria, British Columbia. 46 pages.
- Paragi, T. F., W. N. Johnson, D. D. Katnik, and A. J. Magoun.** 1997. Selection of post-fire seres by lynx and snowshoe hares in the Alaskan Taiga. *Northwestern Naturalist* 78: 77–86.
- Pietz, P. J., and J. R. Tester.** 1983. Habitat selection by snowshoe hares in north central Minnesota. *Journal of Wildlife Management* 47: 686–696.
- Poole, K. G., L. A. Wakelyn, and P. N. Nicklen.** 1996. Habitat selection by lynx in the Northwest Territories. *Canadian Journal of Zoology* 74: 845–850.
- Prugh, L. R., and C. J. Krebs.** 2004. Snowshoe hare pellet-decay rates and aging in different habitats. *Wildlife Society Bulletin* 32: 386–393.
- Redburn, M. J., and W. L. Strong.** 2008. Successional development of silviculturally treated and untreated high-latitude *Populus tremuloides* clearcuts in northern Alberta, Canada. *Forest Ecology and Management* 255: 2937–2949.
- Roy, L. D., J. B. Stelfox, and J. W. Nolan.** 1995. Relationship between mammal biodiversity and stand age and structure in aspen mixedwood forests in Alberta. Pages 159–189 in *Relationships Between Stand Age, Stand Structure, and Biodiversity in Aspen Mixedwood Forests in Alberta*. Edited by J. B. Stelfox. Alberta Environmental Centre, Vegreville, and Canadian Forest Service, Edmonton, Alberta.
- Schiffman, S. S., M. L. Reynolds, and F. W. Young.** 1981. Introduction to multidimensional scaling: theory, methods, and application. Academic Press, New York, New York. 413 pages.
- Sheriff, M. J., C. J. Krebs, and R. Boonstra.** 2011. From process to pattern: how fluctuating prediction risk impacts the stress of snowshoe hares during the 10-year cycle. *Oecologia* 166: 593–605.
- Statsoft.** 1995. STATISTICA for Windows. Statsoft Inc., Tulsa, Oklahoma.
- St-Georges, M., S. Nadeau, D. Lambert, and R. Décarie.** 1995. Winter habitat use by ptarmigan, snowshoe hares, red foxes, and river otters in the boreal forest–tundra transition zone of western Quebec. *Canadian Journal of Zoology* 73: 755–764.
- Strong, W. L.** 2002. Assessing species abundance unevenness within and between plant communities. *Community Ecology* 3: 237–246.
- Strong, W. L.** 2009. *Populus tremuloides* Michx. postfire stand dynamics in the northern boreal-cordilleran ecoclimatic region of central Yukon Territory, Canada. *Forest Ecology and Management* 258: 1110–1120.
- Strong, W. L.** 2013. Ecoclimatic zonation of Yukon (Canada) and ecoclimatic variation of vegetation. *Arctic* 66: 52–67.
- Strong, W. L., and L. V. Hills.** 2006. Taxonomy and origin of present-day morphometric variation in *Picea glauca* (*xengelmannii*) seed-cone scales in North America. *Canadian Journal of Botany* 84: 1129–1141.
- Tabachnick, B. G., and L. S. Fidell.** 1989. Use of multivariate statistics. Harper & Row Publishers, New York, New York. 746 pages.
- Thompson, I. D., I. J. Davidson, S. O'Donnell, and F. Brazeau.** 1989. Use of track transects to measure the relative occurrence of some boreal mammals in uncut forest and regenerating stands. *Canadian Journal of Zoology* 67: 1816–1823.
- Wolfe, M. L., N. V. Debyle, C. S. Winchell, and T. M. McCabe.** 1982. Snowshoe hare cover relationships in northern Utah. *Journal of Wildlife Management* 46: 662–670.
- Wolff, J. O.** 1978. Food habits of snowshoe hare in interior Alaska. *Journal of Wildlife Management* 42: 148–153.
- Wolff, J. O.** 1980. The role of habitat patchiness in population dynamics of snowshoe hares. *Ecological Monographs* 50: 111–130.

Received 13 May 2012

Accepted 26 September 2012