



Mammalian responses to windrows of woody debris on clearcuts: Abundance and diversity of forest-floor small mammals and presence of small mustelids



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ARTICLE INFO

Article history:

Received 16 March 2017

Accepted 15 May 2017

Keywords:

Abundance

Habitat structure

Small mammals

Mustelids

Populations

Windrows

Woody debris

ABSTRACT

Forest harvesting often leaves excess woody debris on the forest floor that could provide habitat for small mammals and mustelid predators. A windrow or series of piles constructed from woody debris may connect patches of mature forest and riparian areas to allow small mammals and some of their predators to use clearcut openings. We tested two hypotheses (H) that woody debris arranged in windrows connecting reserves of uncut forest, on newly clearcut sites, would increase (H₁) abundance of the major vole species and total abundance, species richness, and species diversity of the forest-floor small mammal community, and (H₂) presence of small mustelids in response to abundance of small mammal prey; compared with sites of dispersed woody debris or uncut forest. We measured abundance and diversity of small mammals and the presence of small mustelids (American marten, *Martes americana*; short-tailed weasel, *Mustela erminea*; long-tailed weasel, *M. frenata*) from 2012 to 2016 in replicated treatments of woody debris in windrow and dispersed sites compared with uncut forest sites at two study areas near Elkhart and Golden in south-central British Columbia, Canada.

At Elkhart, mean abundance of total voles and total small mammals per index-line were higher in the windrow than dispersed sites, and higher or similar to forest sites. At Golden, mean abundance of total voles was similar, but the dispersed and windrow sites had higher numbers of total small mammals than the forest sites. Mean species richness and diversity were highest in the windrow sites at both study areas. Thus, the predictions of H₁ were supported, except for total voles at Golden. Mean abundance of the southern red-backed vole (*Myodes gapperi*), a principal prey species for mustelids, was higher in windrow than dispersed sites, and similar or lower than forest sites. *M. gapperi*, along with the long-tailed vole (*Microtus longicaudus*) dominated the overall vole population in windrows at Elkhart. *M. longicaudus* dominated the windrows and dispersed sites at Golden. Deer mice (*Peromyscus maniculatus*) and northwestern chipmunks (*Neotamias amoenus*) were at similar numbers in dispersed and windrow sites, but shrews (*Sorex* spp.) showed a positive response to windrows. Overall mean presence by marten and small weasels were, on average, 3.3–4.8 times higher in windrow than dispersed sites, and higher or similar to forest sites, which supported H₂. Our study is the first to connect windrows to patches and larger units of uncut forest and to cover a 5-year period since harvest. Responses in mean total abundance, species richness, and diversity of small mammals in windrows were maintained throughout the 5-year period. This consistent result was likely related to the connectivity between windrows and uncut forests. Strategic management of post-harvest woody debris in a network of windrows or piles will help to maintain abundance and diversity of forest mammals, both predator and prey species, on clearcuts.

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1. Introduction

Harvesting of forests in temperate and boreal ecological zones of North America and Europe continues to be dominated by

clearcutting, with and without some form of green-tree retention for conservation of biodiversity (Lindenmayer and Franklin, 2002; Rosenvald and Lohmus, 2008). Coarse woody debris (dead or down wood) on the forest floor also contributes to biodiversity by providing many important functions that are essential for long-term ecosystem productivity such as nutrient cycling, contribution of organic matter to soil structure, and modification of micro-

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climate (Harmon et al., 1986; McComb and Lindenmayer, 1999; Laiho and Prescott, 2004). Retention of some post-harvest woody debris on newly harvested forest sites may provide critical habitat for wildlife (McComb, 2003; Bunnell and Houde, 2010; Fauteux et al., 2012; Sullivan et al., 2012). Although management of woody debris in forest ecosystems is crucial to conservation of biodiversity, it suffers from a dearth of experimental studies in both Europe and North America (Seibold et al., 2015). Woody debris structures (e.g., piles and windrows) may be built at the time of forest harvesting and log processing, and are composed of tops, branches, and bole ends of harvested trees, as well as trees knocked down during harvest, low-quality commercial trees, dead wood, and non-commercial trees left at the harvest site. A windrow or series of piles may connect patches of mature forest and riparian areas to allow small mammals and some of their predators to access and traverse clearcut openings. This practice is particularly relevant on large openings (e.g., >10 ha) in standard, but also larger (e.g., >100 ha) salvage harvesting operations (Lindenmayer et al., 2008), where many mammal species have declined in abundance (Fisher and Wilkinson, 2005).

Piles and windrows, not connected to uncut forest reserves, have consistently provided habitat on new clearcuts for southern red-backed voles (*Myodes gapperi*) and *Microtus* voles, as well as a host of other forest-floor small mammal species, at least up to three years post-construction (Sullivan et al., 2012; Sullivan and Sullivan, 2014). However, relative abundance levels of voles have declined in the third year in all studies, to date. In addition, the variable sizes and locations of constructed piles and windrows has been a confounding factor and at least partly responsible for the variable results with respect to abundance, species richness, and diversity of small mammal populations (Sullivan et al., 2012).

M. gapperi is a closed canopy specialist in old-growth and mature coniferous forests of western North America (Merritt, 1981) and may be considered an indicator species of “old-forest conditions” (Nordyke and Buskirk, 1991; Pearce and Venier, 2005; Boonstra and Krebs, 2012), but may also occur in younger managed forests (Gitzen et al., 2007). In addition, *M. gapperi* is a major mycophagist consuming hypogeous ectomycorrhizal fungi and disseminating their spores in the forest environment (Maser et al., 2008). This microtine may also be considered a “keystone species” (Thompson and Angelstam, 1999) because of its linkages in the various food webs found in old forests. When comparing habitats in managed forests, the presence of *M. gapperi* populations at mature or old-growth forest levels of abundance suggests that networks of food sources and predators may also be present as components of biodiversity. As is the case with mammalian carnivores, *M. gapperi* disappears from clearcuts within a year of harvest, presumably because of a loss of food, cover (both thermal and security), and other attributes of forest stand structure (Fisher and Wilkinson, 2005; Zwolak, 2009). Responses of other small mammal species to clearcutting in North America are species-specific with generalists that occupy a variety of habitats such as the deer mouse (*Peromyscus maniculatus*), northwestern chipmunk (*Neotamias amoenus*), and *Microtus* voles and *Sorex* shrews persisting on clearcuts, although some for variable periods (Fisher and Wilkinson, 2005).

The linear configuration of constructed windrows of woody debris may provide connectivity across forest openings and assist small- and medium-sized mustelids in using and crossing these sites in both summer and winter (Buskirk et al., 1989; Buskirk and Zielinski, 2003; Moriarty et al., 2015). American marten (*Martes americana*), short-tailed (*Mustela erminea*) and long-tailed weasels (*Mustela frenata*) may seek out such corridors since these mustelids may be prey species for other carnivores (Buskirk and Zielinski, 2003). This particular group of three mustelids readily used culverts (i.e., tunnels) as travel corridors to pass under road-

ways (Clevenger et al., 2001). Marten and weasels forage and select paths near or in downed wood (Buskirk and Zielinski, 2003; Andruskiw et al., 2008; Bunnell and Houde, 2010). Marten prefer habitats with dense canopy cover and complex understory conditions provided by coniferous trees and downed wood on the forest floor (Buskirk and Powell, 1994; Thompson et al., 2012). The small weasels (*Mustela* spp.) rely on a hunting strategy that takes them through the burrows and runway systems of various small mammal prey species and through all types of cover into which the prey could escape (King, 1989). Thus, the small mammal prey base available within woody debris structures is likely a critical source of food for mammalian carnivores on forest openings (Sullivan et al., 2012). Voles (*Myodes* and *Microtus* spp.) are major prey species for several mammalian carnivores such as marten (Martin, 1994), short-tailed weasels, and long-tailed weasels (Simms, 1979; Buskirk and Zielinski, 2003).

To date, large-scale field experiments have assessed various arrays and scales of piles and windrows of debris as habitat for mammals on clearcuts (Sullivan et al., 2012; Sullivan and Sullivan, 2014), but an evaluation of strategic management of windrows connecting forest reserves and patches has not been done. Thus, we tested two hypotheses (H) that woody debris arranged in windrows connecting patches and reserves of uncut forest, on newly clearcut sites, would increase the (H₁) abundance of the major vole species and total abundance, species richness, and species diversity of the forest-floor small mammal community, and (H₂) presence of small mustelids in response to abundance of small mammal prey; compared with sites of dispersed woody debris or uncut forest.

2. Methods

2.1. Study areas

Two study areas were located in south-central British Columbia (BC), Canada: (i) Elkhart (49°51'15"N; 120°18'23"W) 65 km west of Peachland; and (ii) Golden (51°14'39"N; 116°41'27"W) 30 km east of Golden. The Elkhart area is in the Montane Spruce (MS_{dm}) biogeoclimatic subzone with topography of rolling hills at 1558–1638 m elevation on the Okanagan plateau. The MS landscape has extensive young and maturing seral stages of lodgepole pine, which have regenerated after wildfire. Hybrid interior spruce (*Picea glauca* × *P. engelmannii*) and subalpine fir (*Abies lasiocarpa*) are the dominant shade-tolerant climax trees. Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) is an important seral species in zonal ecosystems and is a climax species on warm south-facing slopes in the driest ecosystems (Meidinger and Pojar, 1991).

The Golden area is in the Interior Cedar-Hemlock (ICH_{mk}) biogeoclimatic subzone with topography ranging from hilly to steep terrain at 1090–1280 m elevation in the lower ranges of the Rocky Mountains. Upland coniferous forests dominate the ICH landscape and comprise the highest diversity of tree species of any zone in BC. Western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) dominate mature climax forests with Douglas-fir, lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), Engelmann spruce (*Picea engelmannii*), their hybrids, and subalpine fir common in these stands (Meidinger and Pojar, 1991).

Study stands, prior to harvesting, at Elkhart had a mixture of lodgepole pine with variable amounts of subalpine fir and interior spruce, and at Golden were composed of a mixture of Douglas-fir, spruce, subalpine fir, western red-cedar, and western hemlock. Average ages of lodgepole pine ranged from 80 to 120 years and for Douglas-fir and other conifers ranged from 120 to 220 years. Overstory mean tree heights ranged from 22 to 26 m at Elkhart and from 25 to 32 m at Golden over all conifer species. There were

no site preparation treatments on any of these harvested sites, prior to planting.

2.2. Experimental design and landscape context

The Elkhart study area was located in an intensively managed commercial forest landscape where much of the original forest has been removed by clearcutting over the past 15–20 years. Patches and reserves of uncut forest are typically situated along, or near, riparian areas such as streams, ponds and lakes. There are few large unbroken patches of uncut forest. This study area had 87.7 ha of clearcut openings that provided relatively independent sites for installation of windrow and dispersed woody debris treatments. Windrow treatments were established where logistically feasible to build between patches of uncut forest (areas ranging from 1 to 20 ha). Dispersed treatments were located to maximize distance among independent treatment sites as noted below.

The Golden study area was located in a less-intensive commercial forest landscape than at Elkhart, with much larger expanses of unbroken forest (100–1000 s of ha). This study area had 30.3 ha of clearcut openings where the windrow and dispersed treatments were established, again directed by logistical feasibility for building windrows and distance among treatment sites. At both study areas, sites of uncut forest were established in reasonable proximity to the dispersed and windrow treatments.

Each study area had a completely randomized design with 3 replicates each of: (i) woody debris dispersed uniformly over each clearcut site (Fig. 1a); (ii) woody debris distributed into a windrow on each clearcut site (Fig. 1b), connecting stands of uncut forest (Fig. 1c); and (iii) uncut forest (Fig. 1d). The 18 sites (3 treatments \times 3 replicates at each study area) were selected on the basis of operational scale, harvest sites that were the size of typical forestry operations, and proximity of sites to one another within a study area. All treatment sites within a study area were reasonably separated to enhance statistical independence (Hurlbert, 1984): Elkhart an average (\pm SE) of 0.37 ± 0.04 km (range 0.2–0.6 km) and Golden an average (\pm SE) of 1.00 ± 0.13 km (range 0.2–1.9 km). A measure of this independence was that no *M. gapperi* or *Microtus* spp. were captured on more than one site. Treat-

ment sites were not considered independent for marten or small weasels.

2.3. Woody debris treatments

Timber harvesting was targeted at lodgepole pine and spruce at Elkhart and Douglas-fir and spruce at Golden. Clearcut harvesting and construction of windrows of woody debris occurred in autumn 2011 at both study areas. Windrows were created by post-harvest site preparation work with an excavator. Windrows were variable in length with mean (\pm SE) values ranging from 166.3 ± 9.5 m (Golden) to 181.5 ± 47.0 m (Elkhart) depending on availability of woody debris. These structures provided connectivity between stands of uncut forest reserves and forest patches (Fig. 1c). Volumes of downed wood in the windrow treatments were determined by the method of Hardy (1996).

2.4. Forest stand structure

Sampling of coniferous tree species in layers in 0–1, 1–2, 2–3, and >3 m height classes was done in a 5.64-m radius circular plot (100 m^2) located systematically at alternate trap stations along lines in the forest sites (see below) at each study area. In each plot, we counted trees in each height class by species, and measured dbh (diameter at breast height, 1.3 m above soil surface) and total height (digital hypsometer – Forestor Vertex) of selected overstory trees in the dominant and suppressed height classes. Percentage canopy closure was measured by four readings of a spherical densiometer (Englund et al., 2000) at each plot for a total of 20 measurements per stand.

2.5. Forest-floor small mammals

Forest-floor small mammal populations were sampled at 4-week (Elkhart) or 4- to 8-week (Golden) intervals from early summer to autumn in 2012, 2013, 2014, 2015, and 2016: June to October at Elkhart, and May to September at Golden. Each of the 18 sites had a 143-m line for efficient sampling of community composition of forest-floor small mammals (Pearson and



Fig. 1. Photographs of post-harvest woody debris and uncut forest sites at the study areas in south-central British Columbia, Canada: (a) dispersed, (b) windrow, (c) windrow connected to forest patch, and (d) uncut forest.

Ruggiero, 2003). Each line had 10 trap stations at 14.3-m intervals with three Longworth live-traps at each station. Traps were supplied with whole oats and carrot, with cotton as bedding. Each trap had a 30-cm × 30-cm plywood cover for protection from sunlight (heat) and precipitation. Traps were set on the afternoon of day 1, checked on the morning and afternoon of day 2 and morning of day 3, and then locked open between trapping periods. All small mammals captured were ear-tagged with serially numbered tags and point of capture recorded (Krebs et al., 1969). Animals were released on the grids immediately after processing. Unfortunately, the overnight trapping technique resulted in a high mortality rate for shrews. Therefore, shrews were collected, frozen, and later identified according to Nagorsen (1996). All handling of animals was in accordance with the principles of the Animal Care Committee, University of British Columbia.

Abundance estimates of animals were derived from the Jolly-Seber (J-S) stochastic model for open populations with small sample size corrections (Seber, 1982; Krebs, 1999). We consider this estimate to be an index of population size (Krebs et al., 2011). Jolly trappability was calculated according to the estimate discussed by Krebs and Boonstra (1984). Species richness was the total number of species sampled for the mammal communities in each site (Krebs, 1999). Species diversity was based on the Shannon-Wiener index which is well represented in the ecological literature (Burton et al., 1992; Magurran, 2004). Mean annual measurements of abundance, species richness, and species diversity of small mammals were calculated using the estimated parameter for each species or community for a given sampling period and then averaged over the number of sampling periods for each year.

2.6. Presence of mustelids

The presence of mustelids was measured along the small mammal sampling line at each site by (a) live-trapping and release (marten and small weasels), (b) fecal scats on three 30 × 30 cm plywood boards used as covers at trap stations (Fig. 2a + b), and (c) predation disturbance of small mammals at trap sites (Zielinski and Kucera, 1995; BC Ministry of Environment, 1998). Fecal scats were identified to marten or weasel according to Murie (1954) and Rezendes (1999). One Tomahawk live-trap (Model 201, Tomahawk Live trap Company, Tomahawk, Wisconsin) equipped with a nest box (1-L plastic bottle with coarse brown cotton) was located at each station. Traps were baited with sunflower seeds (*Helianthus annuus*) and strawberry jam. Traps were set in the evening on day 1 and checked in the morning and afternoon of day 2 and morning of day 3. Sampling periods and intervals were identical to those described below for small mammal species. Mustelid live captures (marten and weasels in Tomahawk traps and weasels in Longworth traps), fecal scats, and disturbance of live-traps were recorded during the last three trapping periods (mid-summer to autumn) each year. Thus, there were nine cells for possible data entries each year: 3 trapping periods × 3 indicators of mustelid presence that yielded a proportional value/9 for each treatment site. Fecal scats may have been deposited at any time during the intervals between these trapping periods. All captured mustelids were identified to species and released.

2.7. Statistical analysis

A one-way analysis of variance (ANOVA) was used to detect differences in stand structure and dimensions of windrows of woody debris between the two study areas (Zar, 1999). A repeated-measures analysis of variance (RM-ANOVA) (IBM Corp., 2016) was used to determine the effect of the three treatments on mean values for abundance of total voles (*M. gapperi*, *Microtus* spp., *P. intermedius*), total small mammals, individual species of small



Fig. 2. Photographs of (a) marten fecal scat on sampling board (1-cm increments), and (b) marten fecal scat on sampling board on live-trap at a trap station along the 143-m transect.

mammals, species richness, species diversity, and overall mean presence of mustelids, as well as time and treatment × time interactions. The mustelid presence measurement was a combination of captures, fecal scats, and predation disturbance by marten or small weasels for each replicate site and year. In this case, we combined the two study areas to improve the sample size of this measurement of mustelid presence with $n = 6$ replicate sites. Homogeneity of variance was measured by the Levene statistic. Mauchly's W -test statistic was used to test for sphericity (independence of data among repeated measures) (Littel, 1989; Kuehl, 1994). For data found to be correlated among years, the Huynh-Feldt (H-F) correction was used to adjust the degrees of freedom of the within-subjects F -ratio (Huynh and Feldt, 1976). Proportional data were transformed by arcsin square root (Fowler et al., 1998). Overall mean values ($n = 15$; 3 replicate sites × 5 years) ± 95% confidence intervals (CIs) at each study area were calculated for incidence of mustelid presence. Duncan's multiple range test (DMRT), adjusted for multiple contrasts, was used to compare mean values based on RM-ANOVA results (Saville, 1990). In all analyses, the level of significance was at least $P = 0.05$.

3. Results

3.1. Forest stand structure and woody debris treatments

Mean diameters and heights of overstory coniferous trees ranged from 28 to 33 cm and 22 to 26 m at Elkhart and 29 to 41 cm

and 25 to 32 m at Golden, respectively (Table 1). Mean canopy closure (91–92%) and stand density of overstory trees (513–540/ha) were similar ($P > 0.05$) among the forest sites at the two study areas. In addition, mean overall densities of understory conifers were similar ($P > 0.05$) in all height classes and in total (Table 1). Mean total volume (m^3) and volume per m of windrow length of woody debris were similar ($P > 0.05$) between the two study areas (Table 1). Mean area (m^2) covered by the debris in these windrows was also similar. Windrows averaged 1.3–1.6 m in height and 4.1–4.9 m in diameter or width.

3.2. Forest-floor small mammals

A total of 11 species of forest-floor small mammals, composed of 3512 individuals, were captured at the two study areas. The red-backed vole was the most common species captured with 1188 individuals followed by the long-tailed vole (*Microtus longicaudus*) (766), deer mouse (541), montane shrew (*Sorex monticolus*) (433), northwestern chipmunk (358), meadow vole (*Microtus pennsylvanicus*) (85), heather vole (*Phenacomys intermedius*) (74), masked shrew (*S. cinereus*) (60), American shrew-mole (*Neurotrichus gibbsii*) (5), western jumping mouse (*Zapus princeps*) (1), and northern bog-lemming (*Synaptomys borealis*) (1). For the major vole species, mean (\pm SE) Jolly trappability for *M. gapperi* ranged from $63.9 \pm 3.1\%$ to $91.4 \pm 3.4\%$ in windrows and from $70.9 \pm 4.7\%$ to $77.5 \pm 3.4\%$ in forest sites; for *M. longicaudus* ranged from $76.6 \pm 10.8\%$ to $81.1 \pm 2.8\%$ in windrows.

At Elkhart, mean abundance of total voles ($F_{2,6} = 31.06$; $P < 0.01$) and small mammals ($F_{2,6} = 6.70$; $P = 0.03$) per index-line were significantly different among treatment sites (Table 2). The windrow sites had higher (DMRT; $P = 0.05$) total vole numbers than the dispersed sites; but similar to the forest sites (Fig. 3). Total voles

in the dispersed sites reached an annual peak of 18 animals per line in 2012 before declining to <5 voles per line for the duration of the study. Mean abundance of total voles in the windrow sites was 33 animals per line in October 2012 and remained relatively high with annual peaks ranging from 11 to 20 voles per line in 2013 to 2016 (Fig. 3). Population changes for total voles showed a similar pattern over time for both windrow and forest sites. The windrow sites had higher (DMRT; $P = 0.05$) mean abundance of total small mammals than both the dispersed and forest sites (Table 2; Fig. 4). Total small mammals reached an annual peak of 38 animals per windrow line in 2012 and maintained a range of 22–32 animals as annual peak numbers in 2013–2016. Total small mammals in the windrow sites were, on average, 1.5 times higher in mean abundance than in the dispersed and forest sites (Fig. 4).

At Golden, mean abundance of total voles was similar ($F_{2,6} = 1.37$; $P = 0.32$), but mean total abundance of small mammals was significantly ($F_{2,6} = 7.35$; $P = 0.02$) different among treatment sites (Table 2). The dispersed sites were dominated by long-tailed voles in 2012–2014, before this microtine declined in abundance in the overwinter period 2014–15 (Fig. 5). At least to some degree, red-backed voles also followed this pattern in dispersed and windrow sites declining to ≤ 6 voles per line in the last two years of the study. Mean annual peaks in abundance of total voles, primarily *M. gapperi*, in the forest sites ranged from 12 to 18 voles per line over the 5-year study (Fig. 5). The dispersed and windrow sites had higher (DMRT; $P = 0.05$) numbers of total small mammals than the forest sites. Despite the lower numbers of total voles in 2015–2016 in the dispersed and windrow sites, mean abundance of total small mammals was maintained at 1.8 to 2.3 times higher, on average, than in the forest sites (Fig. 6).

Both study areas had significant ($P < 0.05$) changes in mean abundance measurements with time (Table 2) owing to declining

Table 1

Mean ($n = 3$ replicate sites) \pm SE diameter (cm), height (m), and stand density of overstory (>3 m height) coniferous trees, abundance of understory (<3 m height) conifers, dimensions of windrow treatments, and results of analyses for uncut forest sites at each study area.

Parameter and species ^a	Elkhart	Golden	Analysis	
Overstory conifers				
Mean diameter				
DF	–	41.3 \pm 8.0	–	–
Pl	31.1 \pm 0.9	–	–	–
Sal	28.2 \pm 4.4	29.0 \pm 1.6	–	–
Sp	32.5 \pm 1.8	39.0 \pm 6.0	–	–
Cw	–	40.7 \pm 4.2	–	–
Hw	–	37.6 \pm 4.1	–	–
Mean height				
DF	–	31.8 \pm 3.0	–	–
Pl	26.2 \pm 0.6	–	–	–
Sal	22.3 \pm 0.6	29.1 \pm 1.1	–	–
Sp	25.5 \pm 1.1	29.1 \pm 1.3	–	–
Cw	–	24.5 \pm 1.2	–	–
Hw	–	27.3 \pm 0.2	–	–
Stand structure				
% Canopy closure	91.4 \pm 0.9	92.2 \pm 1.7	$F_{1,4}$ 0.17	P 0.70
Overstory density (stems/ha)	513 \pm 127	540 \pm 80	0.03	0.87
Understory conifers				
0–1 m height class	7660 \pm 4162	5713 \pm 1049	0.21	0.67
1–2 m height class	760 \pm 335	1367 \pm 127	2.87	0.17
2–3 m height class	193 \pm 110	427 \pm 164	1.40	0.30
>3 m height class	640 \pm 197	953 \pm 302	0.75	0.43
Total conifers	9767 \pm 4641	9000 \pm 537	0.03	0.87
Woody debris				
Total volume (m^3)	707.0 \pm 209.8	497.8 \pm 113.4	$F_{1,4}$ 0.77	P 0.43
Length (m)	170.8 \pm 52.0	166.3 \pm 9.5	0.01	0.94
Volume (m^3) per m of windrow	4.2 \pm 0.1	3.0 \pm 0.6	3.58	0.13
Area covered by windrow (m^2)	778.4 \pm 188.6	683.3 \pm 96.0	0.20	0.68
Height (m)	1.60 \pm 0.00	1.33 \pm 0.14	3.86	0.12
Width (m)	4.90 \pm 0.57	4.10 \pm 0.52	1.00	0.38

^a DF Douglas-fir; Pl lodgepole pine; Sal subalpine fir; Sp spruce; Cw western red-cedar; Hw western hemlock.

Table 2

Overall mean ($n = 15$; 3 replicate sites \times 5 years) \pm SE abundance per line of total voles, total small mammals, species richness, and species diversity within the prey base of small mammals by year at the Elkhart and Golden study areas, and results of RM-ANOVA for 2012 to 2016. F -values identified by * were calculated using an H-F correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures. Within a row, columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts.

Study area and parameter	Treatment			RM-ANOVA					
				Treatment		Time		Treatment \times time	
	Dispersed	Windrow	Forest	$F_{2,6}$	P	$F_{4,24}$	P	$F_{8,24}$	P
Elkhart									
Abundance of total voles	4.03b \pm 1.30	12.25a \pm 1.52	12.28a \pm 1.20	31.06	<0.01	8.66	<0.01	1.94	0.09
Abundance of total small mammals	14.35b \pm 1.29	21.21a \pm 1.37	14.81b \pm 1.28	6.70	0.03	2.88	0.04	0.68	0.71
Species richness	2.73b \pm 0.26	3.92a \pm 0.15	2.36b \pm 0.16	42.74	<0.01	8.04	<0.01	3.00	0.02
Species diversity	0.92b \pm 0.11	1.59a \pm 0.07	0.74b \pm 0.09	40.04	<0.01	8.31	<0.01	10.09	<0.01
Golden									
Abundance of total voles	10.62 \pm 2.51	10.26 \pm 1.75	6.50 \pm 1.08	1.37	0.32	32.31*	<0.01	2.34*	0.08
Abundance of total small mammals	19.37a \pm 1.96	21.30a \pm 1.80	9.05b \pm 0.93	7.35	0.02	8.04*	<0.01	1.54*	0.20
Species richness	3.20a \pm 0.19	3.98a \pm 0.21	2.15b \pm 0.17	11.70	<0.01	2.52	0.07	1.64	0.17
Species diversity	1.04b \pm 0.08	1.44a \pm 0.08	0.76b \pm 0.10	14.48	<0.01	0.76	0.56	0.93	0.51

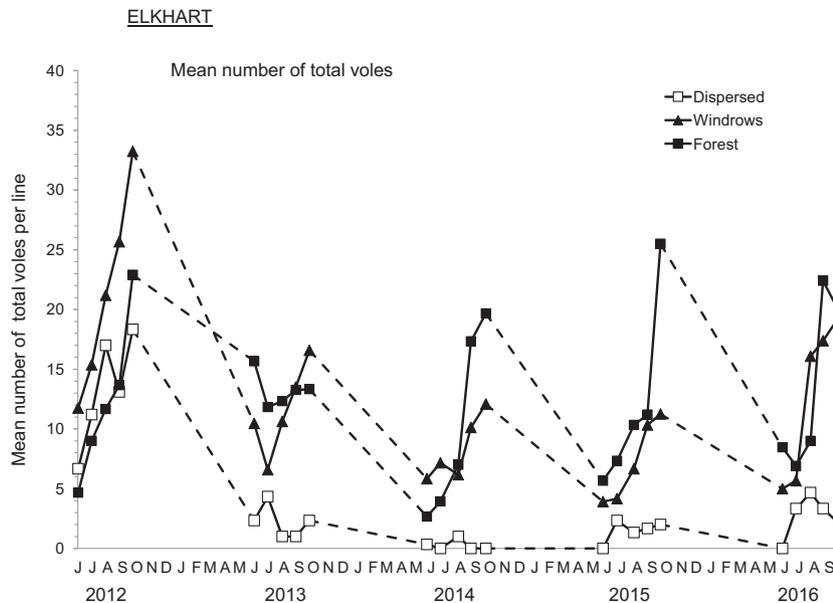


Fig. 3. Mean number of total voles per line in the dispersed, windrow, and forest sites during 2012 to 2016 at the Elkhart study area.

numbers of voles in the dispersed sites in 2013–2016 at Elkhart (Fig. 3) and in both dispersed and windrow sites in 2015–2016 at Golden (Fig. 5). There were no significant treatment \times time interactions for mean abundance of total voles or total small mammals at either study area.

Mean species richness of forest-floor small mammals was significantly different among treatment sites at both Elkhart ($F_{2,6} = 42.74$; $P < 0.01$) and Golden ($F_{2,6} = 11.70$; $P < 0.01$). Mean species diversity followed this same pattern (Table 2). Mean species richness and diversity were highest (DMRT; $P = 0.05$) in the windrow sites at both study areas. Both richness and diversity measures increased significantly ($P < 0.01$) with time at Elkhart, and the significant ($P \leq 0.02$) treatment \times time interaction resulted from a decline in both measurements with time after being relatively high in 2012 in the dispersed sites. There were no significant time or treatment \times time interactions for these diversity measurements at Golden.

Overall mean abundances for individual species recorded at the Elkhart and Golden study areas are listed in Tables 3 and 4, respectively. At Elkhart, mean abundance of red-backed voles was significantly ($F_{2,6} = 37.41$; $P < 0.01$) different among sites with

the windrow and forest sites being higher (DMRT; $P = 0.05$) than the dispersed sites (Table 3). At Golden, mean abundance of red-backed voles was also significantly ($F_{2,6} = 60.54$; $P < 0.01$) different among sites, but with the forest sites being higher (DMRT; $P = 0.05$) than the windrow and both of these sites higher than the dispersed (Table 4). At Elkhart, mean abundance of long-tailed voles was significantly ($F_{2,6} = 44.96$; $P < 0.01$) different among sites, with the windrow sites at higher (DMRT; $P = 0.05$) numbers than the dispersed and forest sites. The pattern was similar at Golden with higher (DMRT; $P = 0.05$) numbers of long-tailed voles in the dispersed and windrow sites than the forest sites (Table 4). Mean abundance of meadow voles was similar among sites at both study areas. Heather voles were most common in the dispersed sites at Elkhart, with similar numbers among sites at Golden. Mean abundance of deer mice was similar among sites at Elkhart; but at Golden deer mouse numbers in the dispersed and windrow sites were higher (DMRT; $P = 0.05$) than in the forest sites. Northwestern chipmunks followed this same pattern at Elkhart, but were at similar abundance levels among sites at Golden. At both study areas, mean abundance of the two shrew species was higher or similar (DMRT; $P = 0.05$) in the windrow than dispersed sites, and in 3 of

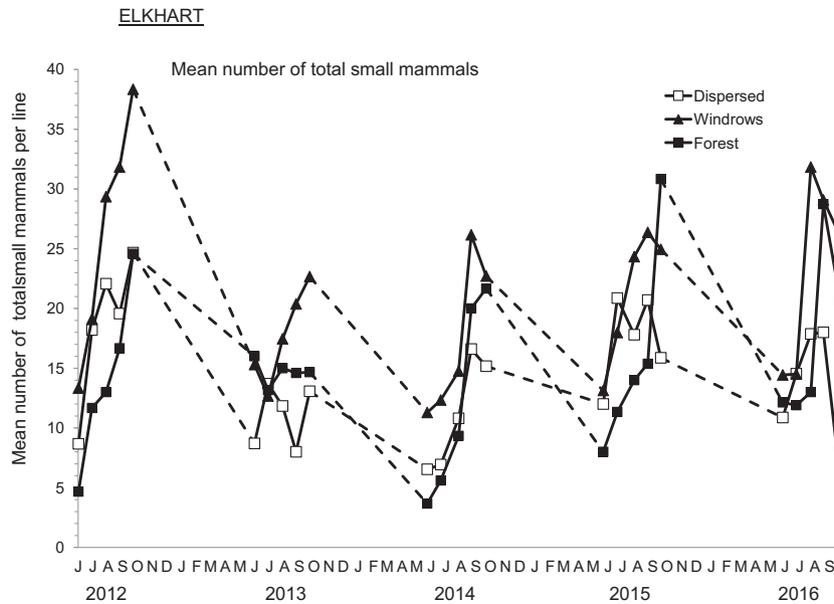


Fig. 4. Mean number of total small mammals per line in the dispersed, windrow, and forest sites during 2012 to 2016 at the Elkhart study area.

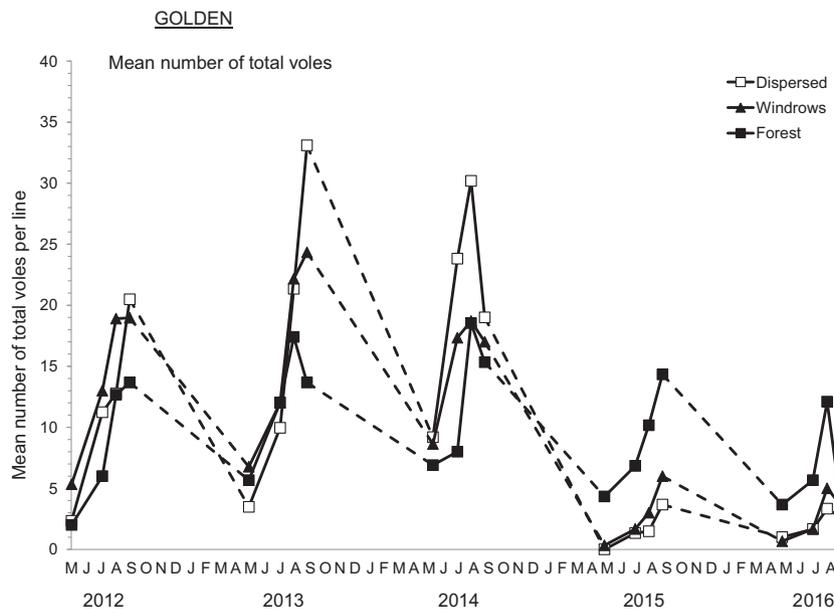


Fig. 5. Mean number of total voles per line in the dispersed, windrow, and forest sites during 2012 to 2016 at the Golden study area.

4 species-study area comparisons tended to be higher in the windrow than forest sites (Tables 3 and 4).

In terms of changes through time, at Elkhart, abundance of red-backed voles and meadow voles declined and those of deer mice, northwestern chipmunks, and the two shrew species increased with time. At Golden, abundance of long-tailed and heather voles declined with time, while those of deer mice and the two shrew species increased.

3.3. Presence of mustelids

Mean presence of mustelids was significantly ($F_{2,15} = 3.86$; $P = 0.05$) different among treatments at the combined study areas (Table 5). The windrow and forest sites were similar and had a higher (DMRT; $P = 0.05$) proportion of presence observations than the dispersed sites. Mean proportion of sampling periods with

mustelid presence ranged from 0.07 to 0.30 in the windrow sites with the 2012, 2013, and 2015 years having the highest levels in the study (Table 5). Mean proportions of mustelid presence ranged from 0.02 to 0.07 and 0.02 to 0.15 for the dispersed and forest sites, respectively. The composite parts of this measurement were: mustelid captures (9 marten and 12 weasels), fecal scats (11 marten and 4 weasels), and disturbed traps (24 marten and 13 weasels). Overall mean levels of presence by marten and small weasels in the windrow sites were 4.2 times higher (non-overlapping 95% CIs) than in the dispersed sites at Elkhart, and 3.3 times higher (overlapping 95% CIs) than dispersed sites at Golden (Fig. 7a + b). When compared to the forest sites, overall mean mustelid presence was 3.6 times higher (non-overlapping 95% CIs) in the windrow sites at Elkhart, but comparable levels in these two sites at Golden (Fig. 7a + b). There were no significant ($P > 0.05$) time or treatment \times time interaction effects.

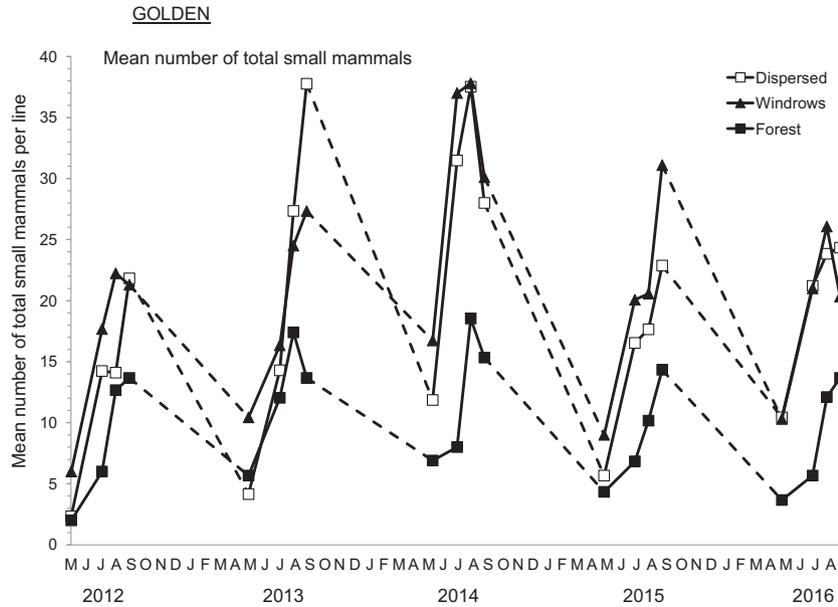


Fig. 6. Mean number of total small mammals per line in the dispersed, windrow, and forest sites during 2012 to 2016 at the Golden study area.

Table 3
Overall mean ($n = 15$; 3 replicate sites \times 5 years) \pm SE abundance per line for each species within the forest-floor small mammal community at the **Elkhart** study area, and results of RM-ANOVA for 2012 to 2016. *F*-values identified by * were calculated using an H-F correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures. Within a row, columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts.

Parameter	Treatment			RM-ANOVA					
	Dispersed	Windrow	Forest	Treatment		Time		Treatment \times time	
				$F_{2,6}$	<i>P</i>	$F_{4,24}$	<i>P</i>	$F_{8,24}$	<i>P</i>
Mean abundance									
<i>Myodes gapperi</i>	2.01c \pm 0.89	8.29b \pm 1.58	11.96a \pm 1.14	37.41	<0.01	6.99	<0.01	1.97	0.10
<i>Microtus longicaudus</i>	0.69b \pm 0.21	3.63a \pm 0.52	0.13b \pm 0.06	44.96	<0.01	7.63	<0.01	4.77	<0.01
<i>Microtus pennsylvanicus</i>	0.97 \pm 0.42	0.25 \pm 0.10	0.05 \pm 0.04	2.91	0.13	5.76*	0.03	3.06*	0.08
<i>Peromyscus maniculatus</i>	0.29a \pm 0.08	0.07b \pm 0.03	0.07b \pm 0.03	11.34	<0.01	1.37*	0.29	0.37*	0.88
<i>Neotamias amoenus</i>	9.45a \pm 1.03	6.47a \pm 0.88	1.86b \pm 0.38	14.24	<0.01	5.15*	<0.01	0.72*	0.65
<i>Sorex monticolus</i>	0.17c \pm 0.05	0.82a \pm 0.21	0.44b \pm 0.10	23.89	<0.01	12.31	<0.01	2.92	0.02
<i>Sorex cinereus</i>	0.00 \pm 0.00	0.07 \pm 0.04	0.05 \pm 0.02	0.72	0.52	2.00*	0.16	1.47*	0.26

Table 4
Overall mean ($n = 15$; 3 replicate sites \times 5 years) \pm SE abundance per line for each species within the forest-floor small mammal community at the **Golden** study area, and results of RM-ANOVA for 2012 to 2016. *F*-values identified by * were calculated using an H-F correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures. Within a row, columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts.

Parameter	Treatment			RM-ANOVA					
	Dispersed	Windrow	Forest	Treatment		Time		Treatment \times time	
				$F_{2,6}$	<i>P</i>	$F_{4,24}$	<i>P</i>	$F_{8,24}$	<i>P</i>
Mean abundance									
<i>Myodes gapperi</i>	0.50c \pm 0.14	2.38b \pm 0.43	5.90a \pm 0.96	60.54	<0.01	10.02*	<0.01	3.34*	0.02
<i>Microtus longicaudus</i>	9.55a \pm 2.51	7.46a \pm 1.51	0.25b \pm 0.17	5.56	0.04	17.46*	<0.01	4.57*	0.01
<i>Microtus pennsylvanicus</i>	0.05 \pm 0.04	0.30 \pm 0.12	0.02 \pm 0.02	1.95	0.22	0.61*	0.60	1.04*	0.43
<i>Peromyscus maniculatus</i>	0.33 \pm 0.12	0.12 \pm 0.07	0.35 \pm 0.15	3.66	0.09	9.66*	<0.01	0.90*	0.53
<i>Peromyscus maniculatus</i>	5.94a \pm 1.37	7.39a \pm 1.60	3.00b \pm 0.65	12.18	<0.01	46.28*	<0.01	5.90*	<0.01
<i>Neotamias amoenus</i>	0.58 \pm 0.23	0.20 \pm 0.11	0.02 \pm 0.02	1.36	0.33	2.05*	0.18	0.72*	0.59
<i>Sorex monticolus</i>	2.03 \pm 0.31	2.83 \pm 0.47	0.57 \pm 0.12	4.89	0.06	14.33*	<0.01	1.92*	0.11
<i>Sorex cinereus</i>	0.20ab \pm 0.08	0.62a \pm 0.14	0.03b \pm 0.02	5.27	0.05	29.89*	<0.01	7.09*	<0.01

Table 5

Annual mean ($n = 6$ replicate sites) \pm SE presence of mustelids (proportion of sampling periods with presence based on live captures, fecal scats, and trap disturbance) per line in the dispersed, windrow, and forest sites at the combined Elkhart and Golden study areas, and results of RM-ANOVA. Within a row, columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts.

Year	Treatment			Treatment		Time		Treatment \times time	
	Dispersed	Windrow	Forest	$F_{2,15}$	P	$F_{4,60}$	P	$F_{8,60}$	P
2012	B 0.02 \pm 0.02	A 0.15 \pm 0.04	A 0.15 \pm 0.09	3.86	0.05	1.60	0.19	1.67	0.12
2013	0.04 \pm 0.02	0.30 \pm 0.09	0.11 \pm 0.05						
2014	0.07 \pm 0.02	0.07 \pm 0.05	0.02 \pm 0.02						
2015	0.04 \pm 0.02	0.11 \pm 0.05	0.09 \pm 0.05						
2016	0.02 \pm 0.02	0.07 \pm 0.04	0.09 \pm 0.03						

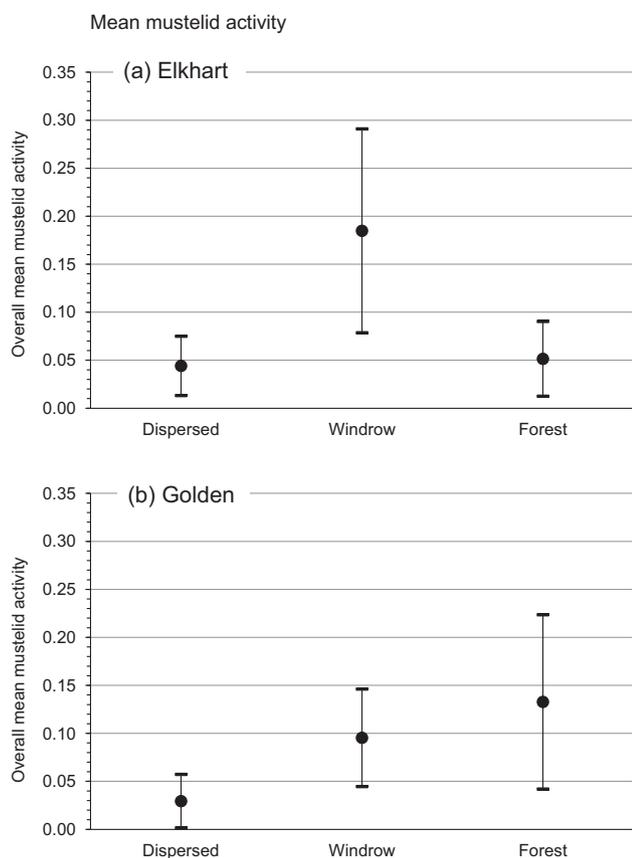


Fig. 7. Overall mean ($n = 3$ replicates sites \times 5 years = 15) \pm 95% CIs mustelid activity (marten and small weasels) per line in the dispersed, windrow, and forest sites during 2012 to 2016 at the (a) Elkhart and (b) Golden study areas.

4. Discussion

4.1. Abundance of small mammals

Virtually all forest-floor and arboreal small mammals are prey for small mustelids and other carnivores. In particular, voles (*Microtus* spp. and *M. gapperi*) are major prey species for marten and the small weasels (Simms, 1979; Martin, 1994; Buskirk and Zielinski, 2003). However, other prey species including shrews (*Sorex* spp.), deer mice, chipmunks (*Neotamias* spp.) and tree squirrels are also important prey items for the short-tailed weasel, particularly in forested habitats (Simms, 1979; Johnson et al., 2000; Edwards and Forbes, 2003). The small mammal prey base available within woody debris structures is likely a critical source of food for mammalian carnivores on forest openings. An analogue for this pattern would be cone middens of red squirrels within forests, which potentially provide a source of small mammal prey for marten and weasels (Pearson and Ruggiero, 2001).

The first part of H_1 , that abundance of vole prey species and total abundance of small mammals would be higher in windrow than dispersed or forest sites, was supported at Elkhart. At Golden, mean total abundance of voles was similar among sites, and hence did not support H_2 , but mean total abundance of small mammals was higher in the dispersed and windrow sites than forest sites. Mean abundance of long-tailed voles were substantially higher at Golden than Elkhart during the first three years of the study before declining to very low numbers in the winter of 2014–15. This pattern fit the population trend of relatively high numbers (49–84/ha) for this microtine in the first three years after clearcut harvesting in the Golden region (Sullivan and Sullivan, 2010). The majority of voles in 2012 at Elkhart were *M. gapperi* who predictably declined on the dispersed sites by the second year after clearcutting (Zwolak, 2009). *M. gapperi*, along with *M. longicaudus*, and sometimes *M. pennsylvanicus*, came to dominate the overall vole population in windrows at Elkhart. The presence of *M. gapperi* populations at mature or old-growth “forest” levels of abundance in our windrows, as recorded at Elkhart, suggested that networks of food sources may also have been present as components of biodiversity. Predators (e.g., marten and small weasels) as components of this biodiversity were, indeed, present on these sites.

The lack of population responses of deer mice and northwestern chipmunks with our windrows of debris was similar to other studies of these generalist species and woody debris on the forest-floor (Craig et al., 2006; Hayes and Cross, 1987; Smith and Maguire, 2004; Waldien et al., 2006; Sullivan et al., 2012). The significant positive response of both shrew species to our windrows is the first time these insectivores have shown a clear pattern with respect to woody debris. Other studies have noted use of woody debris as travel routes by shrews, but with little or no population response (Craig, 1995; McCay and Komoroski, 2004). Accumulations of woody debris may maintain relatively high levels of moisture through time, thereby providing suitable habitat for invertebrates upon which shrews may forage (Wrigley et al., 1979; McCay and Storm, 1997).

4.2. Species richness and diversity of small mammals

The second part of H_1 , that mean species richness and diversity of the overall small mammal community would be higher in windrow than dispersed or forest sites, was supported at Elkhart and Golden, at least for this initial 5-year post-harvest window of investigation. However, other reports of the influence of these structures on richness and diversity are equivocal (Sullivan et al., 2012; Sullivan and Sullivan, 2014). Similarly, Loeb (1999) and Pauli et al. (2006) reported that abundance of small mammals was higher in those sites most affected by natural blowdown of forest trees and consequent high amounts of woody debris. In terms of species richness and diversity, Loeb (1999) reported that species composition of small mammals was similar in blowdown and control sites, while Pauli et al. (2006) found the lowest

species diversity in the sites with extensive blow-down. Conversely, positive relationships between species richness of small mammals and amounts of woody debris were reported by Steel et al. (1999) and Maguire (2002).

The major drawbacks to earlier studies are the timing and scale of construction of woody debris habitats. To avoid contradictory results in a management framework, as noted in the literature and experimentally by Sullivan et al. (2012), large-scale manipulations of woody debris into piles or windrows, as done in our study, are needed to generate unequivocal results in terms of responses in abundance and species richness and diversity of forest-floor small mammals. Piles or windrows need to be at least 2 m in height and 5 m in width or diameter to provide sufficient habitat for forest-floor small mammals and their predators on clearcuts (Sullivan et al., 2012). In addition, *M. gapperi* disappear rapidly from forest sites that are clearcut (Zwolak, 2009), perhaps persisting for one winter after cutting. These structures need to be created at the time of forest harvesting and log processing, or immediately thereafter, to provide sufficient volume of woody material to provide habitat for *M. gapperi* and other small mammal species. Clearly, *M. gapperi* and associated small mammals will persist in these structures for at least five years, at or near abundance levels found in uncut forest.

4.3. Presence of mustelids

This study is the first investigation of the presence of small mustelids in woody debris arranged in windrows on new clearcuts and connected to patches and reserves of uncut forest. H_2 , that these windrows would increase the presence of marten and small weasels in response to abundance of small mammal prey, seemed to be supported, at least when compared to the conventional post-harvest treatment of dispersed woody debris. Overall mean mustelid presence was substantially higher in windrow than dispersed sites over the 5-year study. When viewed separately, mean mustelid presence in windrows was within the range recorded in uncut forest at Golden, but higher in windrows than forest at Elkhart. Thus, these observations fit our results and earlier research findings that small weasels seem to use piles and windrows of woody debris (Lisgo et al., 2002; Sullivan and Sullivan, 2012).

In general, the mammalian carnivore community is negatively affected by clearcutting with loss of preferred prey species, den sites, and other components of forest stand structure (Fisher and Wilkinson, 2005). Thus, woody debris structures on clearcuts corroborate earlier reports by Bull (2002), McComb (2003), and Sullivan et al. (2012) that, in addition to mustelids, several carnivores such as coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and lynx (*Lynx canadensis*) will also use woody debris, particularly logs, as habitat for dens, nest sites, and forage opportunities.

4.4. Study limitations

The two study areas acted as regional replicates with a completely randomized design at each area. We acknowledge the concern that we did not actually intersperse the treatment sites randomly at each study area, per se. However, because operational logistics in building windrows and maximizing distance among treatment sites rather than experimenter bias (Hurlbert, 1984) tended to control assignment of treatments within a study area, this was considered a randomized design. In general, the Interior Cedar Hemlock is a more productive forest ecological zone than the Montane Spruce (Meidinger and Pojar, 1991), and hence the study areas were analyzed separately. These two zones are widely distributed and our reasonably consistent results suggest strongly that inferences are applicable to a wide range of clearcut openings among forest ecosystems in south-central BC. It is important to

note that these inferences reflect mustelid and small mammal prey responses to habitat structures during summer and fall (May to October) only. Population changes resulting from these treatments may not have been the same during other seasons of the year. The 5-year study duration did suggest that there were no dramatic changes in abundance of small mammals from one year to the next during the overwinter periods when data were not available. An exception might be the dramatic decline in abundance of *M. longicaudus* during the overwinter period 2014–15 at Golden. However, this decline was essentially predictable based on the population fluctuations of this microtine on clearcuts in the years immediately post-harvest (Sullivan and Sullivan, 2010).

Identification of captured mustelids and fecal scats were accurate. Fecal scats of mustelids are highly characteristic and we were confident in separating them into marten and small weasels (*Mustela* spp.). However, we were less confident in the identity of the presumed mustelid predator disturbing live-traps as a “predation event”. Other potential predators who might disturb a trap were coyote, lynx, and red fox, all of which were uncommon at the two study areas. It is possible that a fisher (*Martes pennanti*) may have visited our experimental sites, but that would still fit in the mustelid category. The responses of mustelid presence were grouped together to increase sample size, and hence provide a realistic measure of their presence in our treatment sites.

5. Conclusions

Our study is the first to connect windrows to uncut forest patches and reserves and covered a 5-year period since harvest. At both study areas, mean total abundance, species richness, and diversity of small mammals in windrows were maintained at levels higher than in uncut forest sites throughout the 5-year period. This consistent result was likely related to the connectivity between windrows and uncut forests. Strategic management of post-harvest woody debris will help to maintain abundance and diversity of forest mammals, both predator and prey species, on clearcuts. Large-scale conventional harvesting, as well as salvage harvesting of those forests influenced by wildfire and insect outbreaks, typically create large (>100 ha) openings where habitat creation is much needed. It is in these large openings (where windrows are not practical) that a linear configuration of piles of woody debris, at an appropriate scale, should be tested as a means to provide a travel corridor and supply of mammal prey species for mustelids and other mammalian carnivores.

Acknowledgements

We thank the Wood Pellet Association of Canada, Natural Sciences and Engineering Research Council of Canada, Aspen Planers Ltd., Louisiana-Pacific Canada Ltd., the British Columbia Habitat Conservation Trust Foundation, the Westbank First Nation, Jaeden Resources Ltd., Gold Mountain Mining Corp., and the Applied Mammal Research Institute who provided financial and logistical support. T. Ball, D. Gill, D. Gossoo, S. King, A. LaChapelle, G. Murray, and R. Wilson were particularly helpful in assisting with this project.

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