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Original Research

Population Dynamics of Red-backed Voles (*Myodes gapperi*) and Their Relationship to Downed Wood in Managed Forests of Southern British Columbia

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Abstract

Downed wood has long been identified as an important habitat component for many small mammals, particularly for late seral forest species such as the Red-backed Vole (*Myodes gapperi*). We report on the relationship between manipulated volumes of downed wood and Red-backed Vole population dynamics, in both forested and clearcut habitats, and in two distinct ecosystems. We tested the hypotheses (H) for Red-backed Voles that: (H_1) abundance and reproduction would be lower on forested sites with less downed wood; (H_2) a positive relationship between Red-backed Vole population parameters and downed wood will not depend on the presence of alternate forms of cover; and (H_3) retention of downed wood on clearcuts would mitigate the negative effects of harvesting. There were two study areas: a dry Douglas-fir (*Pseudotsuga menziesii*) – Lodgepole Pine (*Pinus contorta*) forest (Opax), and a high-elevation Engelmann Spruce (*Picea engelmannii*) – Subalpine Fir (*Abies lasiocarpa*) forest (Sicamous) in southern British Columbia, Canada. We monitored the responses of Red-backed Voles to three levels of downed wood over a 4-year period in replicated forest and clearcut sites at each area. There were no changes in abundance or reproduction of Red-Backed Voles in response to removal of downed wood on forested sites at either study area, thereby not supporting H_1. Clearcutting negatively affected Red-backed Voles at both study areas; but at Opax, the immediate impact of clearcutting was partially mitigated, at least in the short term, by maintaining >75 m^3/ha of downed wood on site, a result that partially supported H_2 and H_3. Downed wood on Sicamous clearcut sites did not prevent immediate declines of voles after harvest. It is important to retain downed wood in dry ecosystems, where it might act as a moisture reservoir, particularly for Red-backed Voles. For downed wood to be maintained through time,

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larger pieces should be left on site after harvesting as they provide greater amounts of cover and decay more slowly.

Key Words: Abundance, Clearcuts, Douglas-fir Forest, Downed Wood, *Myodes gapperi*, Population Dynamics, Red-backed Voles, Spruce-Fir Forest.

INTRODUCTION

As more old-growth forests are harvested, increasing attention is being focused on the consequences of losing important habitat attributes, such as large amounts of downed wood, understorey cover, or multi-layered forest canopies (Hunter 1990, 1999; Lindenmayer and Franklin 2002). Unmanaged second-growth forests, without silvicultural interventions such as thinning and fertilization, may have different structural characteristics than old-growth forests (Spies *et al.* 1988; Spies and Franklin 1991; Kohm and Franklin 1997), and may provide less suitable habitat for many vertebrate species (Bunnell *et al.* 1999; Thompson *et al.* 2003). In order to maintain structural diversity and biodiversity across the managed landscape, recent research has focused on understanding the function of important habitat components for wildlife, as well as demonstrating the development of late successional structural features (e.g., understorey vegetation, coniferous tree layers, and large trees) in managed forests (Bunnell *et al.* 1999; Sullivan *et al.* 2009, 2013). Downed wood, in particular, provides many important structural and functional features across seral stages for a wide variety of organisms (Harmon *et al.* 1986; McComb and Lindenmayer 1999; Bunnell and Houde 2010).

Downed wood has long been identified as an important habitat component for many small mammals (McComb 2003; Manning and Edge 2008; Fauteux *et al.* 2012). It is particularly important for Red-backed Voles (*Myodes* spp.) (Merritt 1981; Tallmon and Mills 1994; Vanderwel *et al.* 2010), a genus associated with late-seral forests, at least in western North America (Merritt 1981; Raphael 1988). Studies in coniferous and mixed coniferous-deciduous forests reported dramatic declines of *M. gapperi* on clearcuts (Sullivan *et al.* 1999; Klenner and Sullivan 2003; Fisher and Wilkinson 2005), but not necessarily in deciduous forests in the eastern part of the continent (Zwolak 2009). This pattern of Red-backed Vole responses might be related to the more humid microclimates associated with deciduous than coniferous forests, a likely requirement of Red-backed Voles (Zwolak 2009).

Most research on habitat relationships of Red-backed Voles has focussed on the California Red-backed Vole (*M. californicus*), which may have different habitat requirements than the Southern Red-backed Vole (*M. gapperi*) found in forests in the Pacific Northwest. Carey and Johnson (1995) suggested that downed wood was not as important in northern, more mesic forests as in southern forests, and further suggested that forest floor and understorey vegetation were more important factors. Nordyke and Buskirk (1991) and Rosenberg *et al.* (1994) suggested that other forest floor characteristics such as a deep organic soil layer or dense understorey cover may be more strongly related to Red-backed Vole abundance than the amount of downed wood. However, studies have generally been conducted on areas with relatively abundant downed wood, perhaps greater than a required threshold amount to maintain abundance of Red-backed Voles (Bunnell *et al.* 1999). This threshold is germane to the forest manager in terms of how much dispersed downed wood should be left on new cutblocks to provide habitat for various wildlife species.

Moses and Boutin (2001) examined the effect on Red-backed Voles of removing downed wood from clearcuts in a young boreal aspen mixedwood forest, and found that retention of downed wood on the area did not compensate for the loss of the forest canopy. Conversely, Fauteux *et al.* (2012) reported that well-decayed downed wood did seem to compensate for loss of overstory tree cover for Red-back Voles in partially cut boreal forest stands in Quebec. Accumulation of downed wood in piles and windrows on new clearcuts in British Columbia (BC), at a forest-level scale, maintained higher abundances of Red-backed Voles than uniformly dispersed wood (Sullivan *et al.* 2011). Pauli *et al.* (2006) reported higher abundance of Red-backed Voles on sites with extensive blow-down of mature coniferous forest, and hence large amounts of downed wood. However, there has not been an experimental manipulation (i.e., adding and removing wood) of the effects of downed wood on the Southern Red-backed Vole in its optimal forested habitat.

In this paper, we report the results of a multi-year study of the relationship between manipulated volumes of downed wood and Red-backed Vole population dynamics, in both forested and clearcut habitats, and in two distinct ecosystems. We tested the hypotheses (H) that: (H_1) abundance and reproduction of Red-backed Voles would be lower on forested sites with less downed wood; (H_2) a positive relationship between Red-backed Vole population parameters and downed wood will not depend on the presence of alternate forms of cover; and (H_3) retention of downed wood on clearcuts will mitigate harvest effects – specifically, that Red-backed Vole populations will decline faster on clearcut sites without downed wood than on areas with downed wood.

METHODS

Study areas and experimental design

The Opax Mountain Silvicultural Systems Project (hereafter “Opax”) study area (50° 48’ N; 120° 27’ W) was located 20 km northwest of Kamloops, British Columbia, Canada in a multi-storied dry, Douglas-fir (*Pseudotsuga menziesii*) - Lodgepole Pine (*Pinus contorta*) forest which had minor components of Trembling Aspen (*Populus tremuloides*) and Sitka Alder (*Alnus sitchensis*) in moister areas. There were two Interior Douglas Fir (IDF) biogeoclimatic subzones: the dry cool (IDFdk) and very dry hot (IDFxh) (Lloyd *et al.* 1990). Parts of the study area had been harvested with a limited-diameter partial-cut in 1956 to 1957; other areas were unharvested (Klenner and Vyse 1998; Klenner and Sullivan 2009). Understorey vegetation included Birch-leaved Spirea (*Spiraea betulifolia*), Rose (*Rosa* spp.), Soopolallie (*Shepherdia canadensis*), Twinflower (*Linnaea borealis*), Racemose Pussytoes (*Antennaria racemosa*), and Pinegrass (*Calamagrostis rubescens*). The site was covered in up to 0.5 m of snow for five to six months of the year. Clearcut areas were heavily vegetated by two years post-harvest; dominant groups included Rose, Birch-leaved Spirea, Common Snowberry (*Symphoricarpos albus*), Pinegrass, Showy Aster (*Aster conspicuus*), Wild Strawberry (*Fragaria virginiana*), and Racemose Pussytoes. The Opax study area site was divided into fifteen, 20-25-ha harvest treatment areas; 6 at a lower elevation block (1000 m) and 9 at a higher elevation block (1,200 m). Harvest treatments included 20% and 50% volume removal by individual and patch selection. Harvesting was conducted during the winter of 1993-1994. Post-harvest spot screefing (removing the duff layer) with an excavator occurred on clearcuts, followed by planting of conifer seedlings. The study was conducted in the unharvested forest and on the 1.7-ha clearcuts in the harvest treatments with 50% volume removal with the intent of creating low, medium, and high levels of downed wood. We randomly assigned treatments and conducted downed wood manipulations on three 1.4-ha sites in each of the three unharvested blocks and on three 1.7-ha clearcut sites within each of the three harvested blocks. We manipulated the abundance of downed wood on clearcut sites in spring 1994, and on unharvested sites in summer 1995.

The high-elevation Sicamous Creek Silvicultural Systems Project (hereafter "Sicamous") study area was located approximately 120 km east of Opax near Sicamous, British Columbia, Canada (50°50'N, 119°50'W) (Vyse 1999, Klenner and Sullivan 2003). The forest corresponds to the Engelmann Spruce Subalpine Fir (ESSF) biogeoclimatic zone (Meidinger and Pojar 1991) and is representative of the ESSF wet cold subzone (ESSFwc2) described by Lloyd *et al.* (1990). The area was a north-facing slope between 1530 to 1830 m elevation. The forest was dominated by old-growth Subalpine Fir (*Abies lasiocarpa*), with some Engelmann Spruce (*Picea engelmannii*) present. The understorey was dominated by White Rhododendron (*Rhododendron albiflorum*), Black Huckleberry (*Vaccinium membranaceum*) and Oval-leaved Blueberry (*V. ovalifolium*). Snow of a maximum depth 2-3 m was present for up to 9 months (October into June). The study area was divided into 15, 30-ha treatments blocked by elevation (Vyse 1999; Klenner and Sullivan 2003). Harvest treatments ranged from individual tree selection up to 10-ha clearcuts. The study area was harvested during the winter of 1994-1995. Operational site preparation involved soil mounding with an excavator on a 3-m grid, followed by planting in harvested zones. Clearcuts remained sparsely vegetated throughout the study; dominant vegetation included White Rhododendron, Black Huckleberry, Sitka Valerian (*Valeriana sitchensis*) and One-leaved Foamflower (*Tiarella unifoliata*). Within each forested control block and within each 10-ha clearcut block we established three 1.4-ha treatment sites and randomly assigned downed wood treatments (low, medium or high). Downed wood was manipulated on clearcuts during harvesting in winter 1994-95 and site-preparation in August 1995, and on forested sites in summer 1996.

Thus, at each of Opax and Sicamous, the experimental design consisted of three replicates each of forest downed wood at low, medium, and high levels ,i.e., 9 treatment sites; and 3 replicates each of clearcut downed wood at medium and high levels, i.e., 9 treatment sites.

Downed wood

On clearcuts at both Opax and Sicamous downed wood >6 cm in diameter was removed from low treatments during harvesting. The excavator operator removed intact pieces and crushed and scattered logs of decay class 4 or 5 (Maser *et al.* 1979). This prevented small mammals from using tunnels associated with decayed logs, and altered the log microclimate to reduce insects and fungi associated with decayed downed wood (Harmon *et al.* 1986). Additional downed wood was removed from Sicamous clearcuts by hand in August 1995 to reduce volumes further. Medium treatments were not manipulated beyond what occurred during harvesting. On high treatments, downed wood pieces that normally would be removed from the site (e.g., snags) were retained and distributed evenly across the treatment area. Downed wood on all clear-cuts was distributed evenly across each site. After downed wood volumes were measured following treatments, two clearcuts at Opax were further manipulated to more closely approach the intended low, medium and high levels of downed wood.

On forested treatments at Opax and Sicamous, intact pieces of downed wood >6 cm in diameter were removed from low treatments and wood of decay class 4 or 5 was crushed or dug up and scattered over the ground. Methods for achieving medium and high treatments varied between Opax and Sicamous because the high volumes of downed wood at Sicamous made it more difficult and time-consuming to move wood by hand. At Opax, medium treatments had approximately half of the downed wood removed in proportion to the naturally occurring variability in diameter, length and decay class. Downed wood volumes on high treatments at Opax were not manipulated and represented the natural forest condition. At Sicamous, medium treatments were not manipulated and approximately 12 snags were systematically felled on each high treatment.

Downed wood (>1 cm in diameter) volumes were measured using the line intersect method (Van Wagner 1968) in three plots on each vole sampling grid before and after downed wood manipulation. Each plot was an equilateral triangle with 30 m sides. Initial plot point and compass bearing were randomly chosen on the grid.

Vegetation and ground surface cover

Understorey vegetation and ground surface cover were measured in 5.65-m radius vegetation plots centred on every other vole trap station (25 plots per sampling grid) in June and July 1996 at Opax, and July to September 1996 at Sicamous. The sampling circle was divided into four quadrats and visual assessments were made for each variable in each quadrat. Variables measured included: 1) % canopy cover, 2) % cover by shrubs <2-m tall, 3) % cover by shrubs >2-m tall, 4) % cover by herbs and grasses, 5) % cover by moss, 6) % cover by fine debris (including decomposing leaves, needles), 7) % cover by mineral soil (exposed ground), and 8) % protective cover (ground cover from all sources including downed wood and vegetation cover).

Red-backed Vole populations

Red-backed Vole populations were sampled on 1.1-ha grids consisting of 49 stations in a 7 x 7 array spaced 15 m apart. One grid was established in the centre of each downed wood treatment site. At each station, a Longworth-style trap was baited with oats, apple, and coarse brown cotton for nesting material. Number of traps at a station was increased when trap occupancy was greater than 80%. Traps were pre-baited with oats and apple a minimum of one week before trapping commenced each season. During a trapping season, grids were trapped for two consecutive days approximately every three weeks. Traps were set on the evening of days 1 and 2, and checked within four hours after dawn on days 2 and 3. Traps were locked open between trapping sessions to allow animals to move in and out of the traps freely. All animals captured were tagged with a small, individually numbered ear-tag, their gender, weight, and reproductive status recorded, and released at point of capture (Krebs *et al.* 1969). All animals were cared for in accordance with the principles of the Animal Care Committee, University of British Columbia.

We conducted 26 trapping sessions (early summer to September) from 1994-1997 (partial trapping year) at the Opax site. No pre-harvest/downed wood treatment data were collected on clear-cuts. The 1994 trapping season represented pre-treatment data for forested downed wood treatments. We conducted 21 trapping sessions from 1994-1998 (partial trapping year) at the Sicamous site. Data collected in 1994 at Sicamous were pre-harvest/downed wood treatment data for clear-cut treatments; 1994 and 1995 were pre-treatment years for forested treatments. Grids were not sampled during winter at either study area because of logistical difficulties of trapping in snow.

We generated Jolly-Seber (Seber 1982) estimates of population size using Small Mammal Programs for Mark-Recapture Data Analysis (C.J. Krebs, Department of Zoology, University of British Columbia). We calculated the effective trapped area (ETA) for each grid for each year based on mean maximum distance moved (MMDM) by voles between trapping sessions. Half the value of the MMDM was added to the grid size, and used to estimate the total area within which populations were sampled (Wilson and Anderson 1985). Population size estimates were converted to a density estimate by dividing population estimates for each trapping session by the ETA calculated for that year. For analyses of reproduction, juvenile Red-backed Voles were defined as those individuals weighing ≤ 14 g at first capture at Opax, and ≤ 16 g at Sicamous. Unless otherwise stated, all means are presented ± 2 standard errors (SE) of the mean.

Statistical analysis

We compared square-root-transformed downed wood volume data across downed wood treatments with an ANOVA. Significant results were investigated with pairwise contrasts (one-tailed two-sample *t*-tests), after testing for homogeneity of variance with a pairwise *F*-test. We used a Bonferroni adjustment of alpha to compensate for experiment-wise error. To analyse population density, we used a split-plot design in time, where time (split-plot) and block were considered random factors and downed wood treatment was considered a fixed effect. To compensate for the dependence between repeated samples of the same sampling grids, we adjusted degrees of freedom (df) of the split-plot effect and split-plot error term by dividing the df of the numerator (time or interactions between treatment and time) and the denominator (error term B) by the df of the split-plot effect (time). Thus, the df of the split-plot effect (time) becomes one. This adjustment is conservative, and most appropriate when split-plot measures are totally dependent. Therefore, for tests of the split-plot effect and interactions, we used $\alpha = 0.10$ to assess statistical significance. To test main effects, we used the main plot error (Error term A), unless an F-test indicated that Error Terms A and B were not significantly different at $P>0.10$. In this case, we used Error Term B (with adjusted df) as the main plot error term to benefit from the increased df. We used $P=0.05$ when testing main effects.

We assessed reproduction by looking at the proportion of reproductive females and the proportion of juveniles in the population. We compared proportions across downed wood treatments and years with a split-plot in time ANOVA. A female was considered to be in reproductive condition if there was evidence of pregnancy or parturition. Data from 1997 at Opax and 1998 at Sicamous were not included in analyses because those were partial trapping years. We also investigated differences in over-winter condition across downed wood treatments by comparing weights of over-wintered males with a 1-way ANOVA.

Significant effects were investigated with *t*-tests, using a *P* value adjusted for multiple comparisons.

RESULTS

Downed wood

At Opax, downed wood volume varied across treatments on both clearcuts ($F_{2,24}$ = 31.98; P<0.01) and forests ($F_{2,24}$ = 7.80; P<0.01) (Table 1). On clearcuts, low treatment sites had lower downed wood volumes than medium or high sites (t_{16} = 9.92, t_{10} = 6.68, $P_{1\text{-tail}}$ < 0.01 for both), but medium and high sites were similar (t_{12} = 0.78, $P_{1\text{-tail}}$>0.20). On forested sites, low treatments again had lower downed wood volumes than either medium or high sites (t_{16} = 3.50, t_9 = 3.29, $P_{1\text{-tail}}$ < 0.01 for both). Although medium sites tended to have lower downed wood volumes than high sites, the difference was not statistically significant (t_9 = 2.07, $P_{1\text{-tail}}$ = 0.03, where α = 0.017 to compensate for experiment-wise error). At Sicamous, downed wood volumes varied across treatments on both clearcuts ($F_{2,24}$ = 38.09; P<0.01) and forests ($F_{2,24}$ = 78.0, P<0.01). On clearcuts, low treatment sites had lower wood volumes than medium or high sites (t_{16} = 8.2, 7.9, $P_{1\text{-tail}}$<0.01 (Table 1); however, volumes on medium and high sites were similar (t_{16} = 0.4, $P_{1\text{-tail}}$ > 0.10). On forested treatment sites, post-treatment volume of downed wood on low treatments was lower than on medium or high sites (t_{10} = 11.43, t_{12} = 12.63, $P_{1\text{-tail}}$<0.01 for both comparisons); however, volumes on medium and high sites were similar (t_{15} = 1.24, $P_{1\text{-tail}}$ >0.10).

Red-backed Vole populations at Opax

There were 3,148 individual Red-backed Voles captured 9,283 times during the study. Mean ETA was 1.36 ± 0.04 ha (range: 1.10-1.65 ha), which was smaller than the treatment area of 1.7 ha. Eighty-two Red-backed Voles (2.6% of individuals) were captured moving between grids. Most of these movements (54) were one-way emigrations. Mean abundance of Red-backed Voles declined during the study, becoming very low by 1996 (year following treatment) and remained low in 1997 (Table 2a, Figure 1a). Populations were relatively large in spring 1996, but declined during the summer to low levels and remained there for the rest of the study. Mean abundance among downed wood treatments was not significantly different (Table 2).

On clearcuts, mean abundance on low treatment sites declined faster after harvesting than populations on medium or high sites (Table 2b, Figure 1b). Densities on medium and high sites were

Table 1. Mean (± 2 SE) volume of downed wood (m^3/ha) for each treatment site.

Study area	Forest harvest treatment	Replicate	Pre-treatment volume[a] Low	Pre-treatment volume[a] Medium	Pre-treatment volume[a] High	Post-treatment volume (m^3/ha) Low	Post-treatment volume (m^3/ha) Medium	Post-treatment volume (m^3/ha) High
Opax	Clear-cut	1				30.6 (10.6)	113.3[b] (15.3)	79.0 (6.6)
		2				17.9 (3.0)	85.5[b] (39.8)	199.6 (42.7)
		3				27.1 (6.6)	88.3[b] (10.4)	89.7 (42.7)
	Forested	1	109.8 (1.4)	69.9 (15.0)	189.3 (100)	18.3 (12.3)	33.9 (2.5)	189.3[c] (100)
		2	82.6 (31.4)	87.6 (24.6)	148.6 (46.6)	6.9 (2.1)	45.6 (9.7)	148.7[c] (46.6)
		3[d]	32.1 (19.8)	137.3 (96.0)	36.3 (15.3)	6.1 (2.6)	14.7 (4.6)	36.3[c] (15.3)
Sicamous	Clear-cut	1				57.0 (15.1)	453.3[b] (129.4)	330.9 (219.9)
		2				112.9 (41.8)	347.9[b] (80.9)	314.6 (63.5)
		3				60.5 (43.7)	283.3[b] (73.4)	416.9 (32.6)
	Forested	1	388.8 (54.2)	298.7 (100)	201.9 (23.5)	16.5 (11.8)	298.7[c] (100)	186.6 (17.6)
		2	196.0 (48.2)	242.3 (16.6)	251.3 (2.6)	8.7 (2.7)	242.3[c] (16.6)	245.4 (57.8)
		3	344.3 (99.5)	384.2 (86.3)	254.8 (27.0)	6.4 (1.0)	384.2[c] (86.3)	302.1 (55.7)

[a] Pre-treatment data not available for clear-cuts
[b] Site was treated in an operational manner; downed wood was not manipulated beyond what occurred during harvesting (control)
[c] Downed wood was not manipulated and represented the natural forest condition (control)
[d] Data for this block not included in split-plot analyses of population density

approximately four times those on low treatment sites in 1994 (first year post-harvest), and were approximately twice as high in 1995. By 1996 Red-backed Voles were rare on all clearcuts, and across the entire study area.

At Opax, weights of over-wintered male Red-backed Voles at first capture were similar on forests and clearcuts ($F_{1,124}$ = 3.09, $P>0.05$; forest: 17–30 g, n = 99, clearcut: 18–28, n = 27). Mean length of breeding season was similar on forested and clearcut sites (t_{13} = 2.16, $P>0.10$). On forested sites, the proportion of breeding females did not differ significantly among downed wood treatments, but declined across years as the population declined in size (Table 3). The mean proportion of juveniles did not differ significantly among downed wood treatments but did vary across years (29.9% in 1994 to 41.5% in 1995, and 22.7% in 1996) (Table 3). On clearcut sites, the proportion of breeding females was higher on low than on medium or high areas in 1995 and 1996 increasing from 13.9% in 1994 to 22.4% in 1995, and then declining to 9.3% in 1996 (Table 3). The proportion of juveniles was similar among years and downed wood treatments.

Table 2. Results of split-plot analysis of Red-backed Vole abundance data from the Opax study area for a) forest, and b) clearcut sites. Split-plot data are presented for i) split-plot in time (time) with individual samples as split-plots and ii) mean density of voles across years (year) as split-plot. An * indicates effects that are statistically significant.

Effect	Error term	Test
a) *i)*		
Pre-harvest/treatment		
Downed wood	A($F_{4,6}$ = 6.49, $P<0.05$)	$F_{2,4}$ = 0.16, $P>0.50$
Block	A	$F_{2,4}$ = 2.53, $P>0.10$
Time*	B	$F_{1,6}$ = 16.89, $P<0.01$
Downed wood x time interaction	B	$F_{2,6}$ = 0.58, $P>0.50$
Post-treatment		
Downed wood*	B($F_{4,6}$ = 2.42, $P>0.1$)	$F_{2,6}$ = 6.03, $P<0.050$
Block*	B	$F_{2,6}$ = 25.19, $P<0.005$
Time*	B	$F_{1,6}$ = 14.81, $P<0.01$
Downed wood x time interaction	B	$F_{2,6}$ = 0.72, $P>0.50$
ii)		
Downed wood	B($F_{4,6}$ = 1.59, $P>0.1$)	$F_{2,6}$ = 0.46, $P>0.50$
Block*	B	$F_{2,6}$ = 10.87, $P<0.05$
Year*	B	$F_{1,6}$ = 40.44, $P<0.001$
Downed wood x year interaction	B	$F_{2,6}$ = 0.63, $P>0.50$
b) *i)*		
Downed wood	A($F_{4,6}$ = 12.35, $P<0.05$)	$F_{2,4}$ = 3.56, $P>0.10$
Block	A	$F_{2,4}$ = 1.03, $P>0.10$
Time*	B	$F_{1,6}$ = 19.39, $P<0.005$
Downed wood x time interaction	B	$F_{2,6}$ = 2.62, $P>0.10$
ii) Year		
Downed wood*	B($F_{4,6}$ = 2.23, $P>0.1$)	$F_{2,6}$ = 8.35, $P<0.05$
Block	B	$F_{2,6}$ = 1.84, $P>0.10$
Year*	B	$F_{1,6}$ = 4.01, $P<0.10$
Downed wood x year interaction*	B	$F_{2,6}$ = 32.64, $P<0.005$

Red-backed Vole populations at Sicamous

There were 3,733 individual Red-backed Voles captured 10,418 times. Mean ETA of all grids and years was 1.29 ± 0.01 ha. We captured 113 Red-backed Voles (3.0%) on >1 grid. The majority of these captures (77 voles) were emigrants; voles tagged on one grid that subsequently moved, and were captured at least once on another grid. Mean abundance was higher on forested sites than on clearcut sites during the study (Figure 2). While mean population density stayed relatively high and constant on forested sites, populations on clearcuts declined after harvesting (winter 1994-95) and were very small by 1996. Population densities on forested treatment sites were similar among downed wood treatments (Table 4a, Figure 2a). Mean abundance per ha declined from 1994 to 1996 (32.9 to 25.3 to 21.9) and then increased again in 1997 (25.9). On clearcuts, mean abundance declined after harvesting in winter 1994-95, continued to decline in 1996, and remained at very low levels through 1997-1998 (Table 4b, Figure 2b). Mean abundance was similar among downed wood treatment sites post-harvest (Table 4b).

Over-wintered male Red-backed Voles were similar in weight on unmanipulated clearcut and unmanipulated forested sites (weights at first over-wintered capture: n = 12, $\bar{x}$ = 31.0 ± 2.2 g, n = 55, $\bar{x}$ = 29.4 ± 1.1 g; t_{65} = 1.2, P>0.10). On forested sites, proportion of breeding females post-treatment varied over time, but not among downed wood treatments (Table 5a). The proportion of breeding females in 1996 was 40.4%, but declined to 26.2% in 1997. Proportion of juveniles followed the trend in breeding females declining from 21.9% in 1996 to 9.1% in 1997, but was not statistically significant (Table 5b). On clearcuts, proportion of breeding females increased post-harvest from 28.5% in 1995 to 46.1% in 1996, and then declined to 8.6% in 1997 (Table 4a). Proportion of females breeding was similar among downed wood treatments (Table 4a). There were no significant differences in proportion of juvenile voles among treatments or years (Table 4b).

Table 3. Results of split-plot analysis of the reproductive parameters for Red-backed Voles from Opax for a) proportion of population comprised of reproductive females, and b) proportion of population comprised of juveniles. An * indicates effects that are statistically significant.

Effect	Error term	Test
a)		
Forest (post-treatment data)		
Downed wood	B($F_{4,6}$ = 0.39, P>0.1)	$F_{2,6}$ = 0.09, P>0.50
Block	B	$F_{2,6}$ = 0.54, P>0.05
Year*	B	$F_{1,6}$ = 11.77, P<0.05
Downed wood x year interaction	B	$F_{2,6}$ = 0.25, P>0.10
Clearcut		
Downed wood*	B($F_{4,6}$ = 0.55, P>0.1)	$F_{2,6}$ = 5.90, P<0.05
Block	B	$F_{2,6}$ = 1.28, P>0.10
Year*	B	$F_{1,6}$ = 26.44, P<0.01
Downed wood x year interaction	B	$F_{2,6}$ = 1.48, P>0.10
b)		
Forest (post-treatment data)		
Downed wood	A($F_{4,6}$ = 3.49, P<0.1)	$F_{2,4}$ = 0.77, P>0.10
Block	A	$F_{2,4}$ = 0.75, P>0.10
Year*	B	$F_{1,6}$ = 25.85, P<0.01
Downed wood x year interaction	B	$F_{2,6}$ = 0.72, P>0.50
Clearcut		
Downed wood	A($F_{4,6}$ = 0.49, P>0.1)	$F_{2,6}$ = 2.61, P>0.10
Block	B	$F_{2,6}$ = 0.51, P>0.50
Year	B	$F_{1,6}$ = 1.02, P>0.10
Downed wood x year interaction	B	$F_{2,6}$ = 0.94, P>0.10

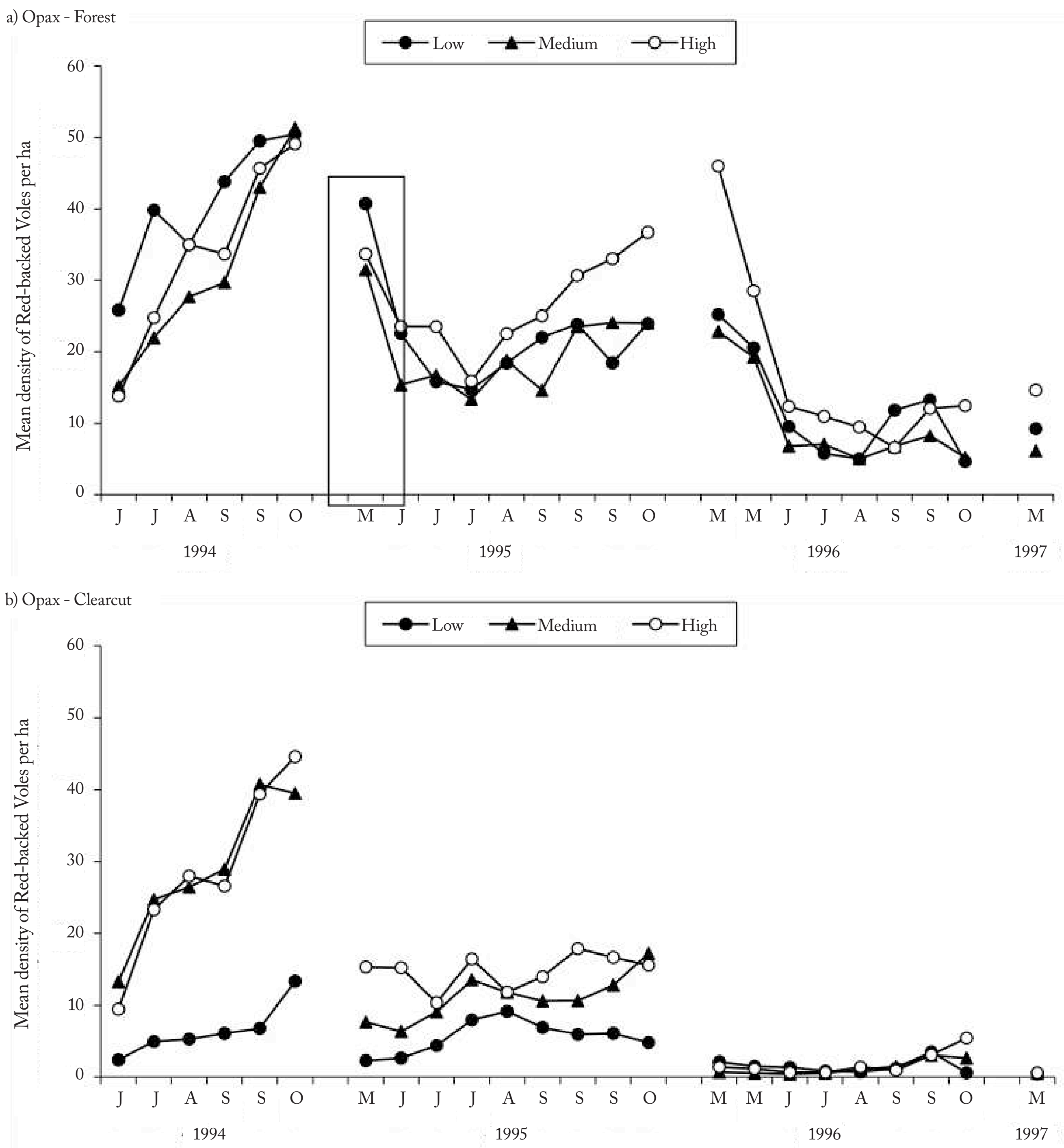

Figure 1. Mean abundance per ha of Red-backed Voles on treatment sites with low, medium and high levels of downed wood at Opax: a) forested sites, and b) clearcut sites. Downed wood manipulations on forested sites occurred in summer 1995. Harvest and downed wood manipulations on clearcut sites occurred in winter 1993-94 to spring 1994 before trapping began. Downed wood manipulations are indicated by an outlined area. M = May, J = June and July, A = August, S = September, O = October.

DISCUSSION

Red-backed Vole populations – Forest treatments

There were no changes in abundance or reproduction of Red-backed Voles in response to removal of downed wood on forested sites at either study area. Thus, H_1, that abundance and reproduction of Red-backed Voles would be lower on sites with less downed wood, was not supported. Red-backed Voles presumably associate with downed wood to satisfy many of their requirements (Merritt 1981; Bunnell *et al.* 1999). Voles consume mycorrhizal fungi, lichens, and occasionally insects (Martell 1981; Gunther *et al.* 1983), all of which are often associated

Table 4. Results of split-plot analysis of Red-backed Vole abundance data from the Sicamous study area for a) forest, and b) clearcut sites. Split-plot data are presented for *i*) split-plot in time (time), and *ii*) split-plots across years (year). An * indicates effects that are statistically significant.

Effect	Error term	Test
a) *i*)		
Pre-harvest/treatment		
Downed wood	A($F_{4,6}$ = 5.09, P<0.05)	$F_{2,4}$ = 0.12, P>0.50
Block	A	$F_{2,6}$ = 0.95, P>0.10
Time*	B	$F_{1,6}$ = 19.76, P<0.01
Downed wood x time interaction	B	$F_{2,6}$ = 1.40, P>0.10
Post-treatment		
Downed wood	A($F_{4,6}$ = 4.11, P<0.1)	$F_{2,4}$ = 0.22, P>0.50
Block	A	$F_{2,4}$ = 0.73, P>0.50
Time*	B	$F_{1,6}$ = 16.41, P<0.01
Downed wood x time interaction	B	$F_{2,6}$ = 0.55, P>0.50
ii)		
Downed wood	B($F_{4,6}$ = 0.61, P>0.1)	$F_{2,6}$ = 0.08, P>0.50
Block	B	$F_{2,6}$ = 0.70, P>0.50
Year*	B	$F_{1,6}$ = 4.65, P<0.10
Downed wood x year interaction	B	$F_{2,6}$ = 0.69, P>0.50
b) *i*)		
Pre-harvest/treatment		
Downed wood	B($F_{4,6}$ = 1.59, P>0.1)	$F_{2,4}$ = 3.32, P>0.10
Block	B	$F_{2,6}$ = 0.50, P>0.50
Time*	B	$F_{1,6}$ = 17.89, P<0.01
Downed wood x time interaction	B	$F_{2,6}$ = 0.56, P>0.50
Post-treatment		
Downed wood	A($F_{4,6}$ = 3.84, P<0.1)	$F_{2,4}$ = 0.31, P>0.50
Block	A	$F_{2,4}$ = 2.12, P>0.10
Time*	B	$F_{1,6}$ = 14.11, P<0.01
Downed wood x time interaction	B	$F_{2,6}$ = 0.68, P>0.10
ii)		
Downed wood	B($F_{4,6}$ = 1.54, P>0.1)	$F_{2,6}$ = 1.35, P>0.10
Block	B	$F_{2,6}$ = 2.57, P>0.10
Year*	B	$F_{1,6}$ = 160.51, P<0.01
Downed wood x year interaction	B	$F_{2,6}$ = 1.24, P>0.10

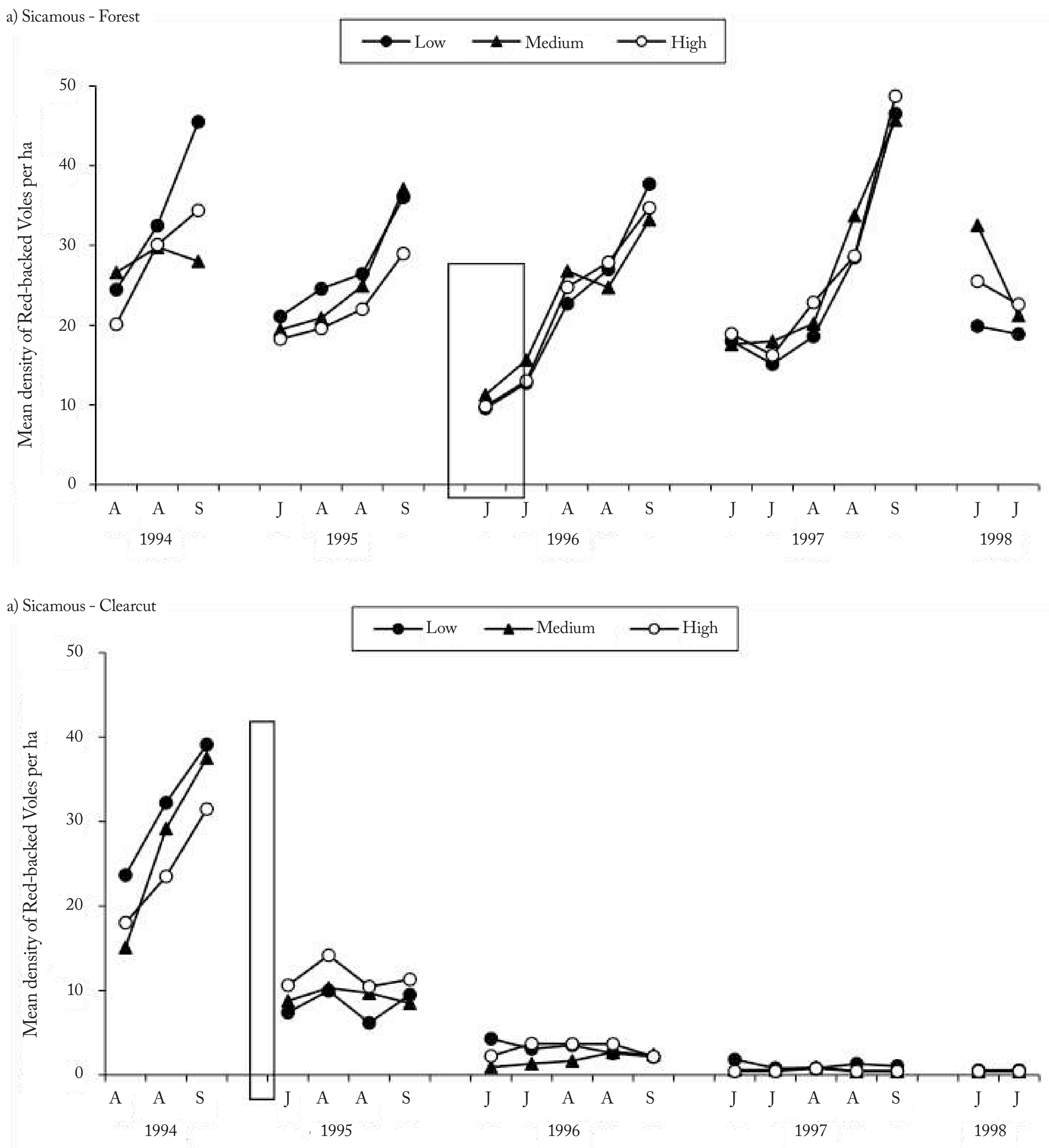

Figure 2. Mean abundance per ha of Red-backed Voles on treatment sites with low, medium and high levels of downed wood at Sicamous: a) forested sites, and b) clearcut sites. Downed wood manipulations on forested sites occurred during summer 1996, and manipulations on clearcut sites occurred during harvesting in winter 1994-95 as indicated by outlined area. J = June and July, A = August, S = September.

with downed wood (Harmon *et al.* 1986; Amaranthus *et al.* 1994). Voles may nest under logs and in stumps (Harmon *et al.* 1986). In addition, voles may be captured next to logs, which suggests that downed wood provides Red-backed Voles with an important structural component of their habitat (Hayes and Cross 1987; Tallmon and Mills 1994).

The lack of response to treatments at Opax might have been hampered by the small population densities across the entire study area beginning in 1996, the year following downed wood treatments. There was some indication that populations on high treatment sites were larger than on low or medium sites by the end of the trapping season in 1995 and beginning of 1996, however, the trend was not statistically significant. The large decline in abundance in 1996 likely overshadowed any potential treatment effects on the study area. Therefore, we could not determine conclusively whether or not downed wood, distributed in a dispersed manner, was an important habitat component for Red-backed Voles in the dry interior forest at Opax. It is not clear why Red-backed Voles declined on the study area in summer 1996. Variability in abundance has been noted in several studies of *Myodes* populations (Rosenberg *et al.* 1994; Boutin *et al.* 1995; Boonstra and Krebs 2012), with summer declines in old-growth forest particularly noted by Sullivan *et al.* (2009).

At Sicamous, population densities were relatively high across all treatment sites during the study. Even with removal of >90% of downed wood on low treatment sites, abundance and reproduction did not differ from unmanipulated sites over the three summers that voles were monitored. There was indirect evidence that Red-backed Voles responded differently to low than to medium or high treatments. The rate of known immigration to low treatment sites was higher than to medium or high sites, and the rate of emigration was higher on medium and high sites than low sites. Without concomitant changes in density or reproductive rates, the meaning of this variation in immigration/emigration rates is unclear.

Table 5. Results of split-plot analysis of the reproductive parameters of the Red-backed Voles from the Sicamous study area: a) proportion of population comprised of reproductive females, and b) proportion of juveniles in the population. An * indicates that the effect is statistically significant.

Effect	Error term	Test
a)		
Forest (post-treatment)		
Downed wood	B($F_{4,6}$ = 1.19, P>0.1)	$F_{2,6}$ = 1.79, P>0.10
Block	B	$F_{2,6}$ = 2.00, P>0.10
Year*	B	$F_{1,6}$ = 12.19, P<0.05
Downed wood x year interaction	B	$F_{2,6}$ = 0.64, P>0.50
Clearcut (post-treatment)		
Downed wood	B($F_{4,6}$ = 0.3, P>0.5)	$F_{2,6}$ = 1.61, P>0.10
Block	B	$F_{2,6}$ = 1.51, P>0.10
Year*	B	$F_{1,6}$ = 9.37, P<0.05
Downed wood x year interaction	B	$F_{2,6}$ = 0.08, P>0.50
b)		
Forest (post-treatment)		
Downed wood	B($F_{4,6}$ = 1.58, P>0.1)	$F_{2,6}$ = 1.06, P>0.10
Block	B	$F_{2,6}$ = 1.34, P>0.10
Year*	B	$F_{1,6}$ = 15.57, P<0.01
Downed wood x year interaction	B	$F_{2,6}$ = 0.55, P>0.50
Clearcut (post-treatment)		
Downed wood	B($F_{4,6}$ = 0.57, P>0.1)	$F_{2,6}$ = 1.71, P>0.10
Block	B	$F_{2,6}$ = 1.39, P>0.10
Year	B	$F_{1,6}$ = 2.27, P>0.10
Downed wood x year interaction	B	$F_{2,6}$ = 0.42, P>0.50

The removal of downed wood would have had an immediate, but probably short-term, effect on the availability of lichens to Red-backed Voles. Long branches, where most arboreal lichens are found, were removed from low treatment sites along with logs. Lichen can form the majority of Red-backed Voles' diets (Gunther *et al.* 1983), and appeared to be an important component of the diet of voles at Opax (Craig 2002). Forests at both study areas contained abundant lichens in the tree canopy, which would fall and eventually replace lichens removed during the treatment.

Downed wood was potentially an important source of thermal cover for Red-backed Voles by mediating temperature extremes in the local environment (Getz 1985), and might be especially important at Opax. High summer temperatures at Opax may have increased stress on vole species with poor kidney efficiencies, like Red-backed Voles (Getz 1985), which are generally considered to be associated with mesic environments (Merritt 1981). Downed wood also might be important in providing structural variability under snow cover. Access to subnivean spaces, where temperatures remain relatively warm and stable is critical to overwinter survival of small mammals (West *et al.* 1980; Pruitt 1984). Access to subnivean spaces would be especially important at Sicamous, where snow 1-2 m deep covered the area for 7-9 months of the year. However, survival rates were similar across downed wood treatments at both study areas during both summer and winter, which suggested that other habitat components on the area provided cover for Red-backed Voles (Craig 2002).

At Sicamous, demographic attributes of Red-backed Vole populations were similar across treatments even though the abundance of downed wood, shrub, herb, and overall cover was much lower on low treatment areas than on medium or high areas. This pattern suggested that characteristics of all sites met some minimum threshold required to maintain relatively abundant Red-backed Vole populations. All of the sampling grids had ≥65% cover from all sources. While canopy cover was low (approximately 11%), understorey cover from shrubs (43-63%), herbs (9-63%) and moss (32-78%) was relatively high. This result did not support H_2, that there is a positive relationship between downed wood and Red-backed Vole populations that does not depend on alternative forms of cover. Thus, in cool, moist forested ecosystems where the vegetative understorey is dense and structurally diverse, downed wood may not be required to maintain Red-backed Voles, at least in the short term.

Red-backed Vole populations – Clearcut treatments

Populations of Red-backed Voles on clearcuts at both study areas declined to very low levels within two years post-harvest. Although Kirkland (1990) reported that Red-backed Voles tend to increase in abundance after clearcutting, Red-backed Vole populations in western North America are negatively affected by removal of the canopy (Fisher and Wilkinson 2005; Zwolak 2009). The response of Red-backed Voles to clearcutting is likely influenced by the amount of downed wood and vegetation left on the area post-harvest (Martell 1983; Sullivan and Boateng 1996), which would affect the forest floor microclimate and, potentially, mycorrhizal fungi (Sullivan *et al.* 1999). Our results suggest that the response is also influenced by the ecosystem in which harvesting occurs.

While clearcutting negatively affected Red-backed Voles at both study areas, the ability of downed wood to mitigate the initial effects of clearcutting varied across study areas. At Opax, the immediate impact of clearcutting was partially mitigated, at least in the short term, by maintaining >75 m^3/ha of downed wood on the site, to partly support H_3, that retention of downed wood on clearcuts will mitigate harvest effects; specifically, that Red-backed Vole populations will decline faster on clearcut sites without downed wood than on areas with downed wood. Population densities were higher for the first two years post-harvest on medium and high sites than low sites. The positive response to the retention of downed wood existed even though the site was sparsely vegetated immediately post-harvest, but became heavily vegetated within two years. This result also partly supported H_2. Other examples supporting this premise have been reported by Fauteux *et al.* (2012) and Sullivan *et al.* (2011).

The importance of downed wood in mitigating the initial effects of clearcutting at Opax was likely related to its importance as a moisture reservoir, especially in a dry, hot ecosystem. Downed wood can hold up to twice its weight in water (Amaranthus *et al.* 1994), and provides an important microenvironment for epigeous fungi (truffles), which tend to be more abundant close to decayed downed wood (Waters *et al.* 1997; Carey *et al.* 1999). While population densities on medium and high treatment areas were still higher than on low treatment areas in 1995 (one year post-harvest), they were lower than in 1994. This trend suggested that the favourable microclimate associated with downed wood in 1994 had declined somewhat by 1995.

Retaining downed wood on clearcut sites at Sicamous had no measurable benefit for Red-backed Vole populations within the first two years after harvesting, contrary to H_3. Downed wood volumes on clearcuts at Sicamous were substantially higher than at Opax; volumes on high treatments were 3-4 times those on Opax clearcuts. Even while populations on forested areas remained high, populations on clearcuts declined to low levels immediately after harvesting, and were rare on clearcuts within two years post-harvest (Klenner and Sullivan 2003). The rate of decline was not influenced by the amount of downed wood, unlike at Opax. This result was similar to that reported by Moses and Boutin (2001) in a boreal mixedwood forest where post-harvest abundance of Red-backed Voles was similar on sites where downed wood had been removed to sites where downed wood was retained. While downed wood volume on clearcuts at Sicamous was relatively high, vegetative cover was low, even in the second growing season post-harvest. Mean overall cover was <50%, with very low shrub (15%), herb (27%) and moss cover (3%). At this high elevation site, downed wood did not appear to influence the immediate response of Red-backed Voles to clearcutting, at least within the downed wood levels studied.

Study limitations

The occasional movement of Red-backed Voles among sampling grids suggested that treatment sites were not completely independent. Ideally, treatment sites would have been more widely spaced on the landscape. The placement of sampling grids was influenced by the operationally sized harvest treatment blocks established as part of two large silvicultural systems projects. In addition, the size of the manipulations, particularly on forested sites, was constrained by the labour-intensive nature of removing downed wood by hand. The main effect of movements would be to reduce variability in Red-backed Vole densities across downed wood treatments within blocks. However, rates of movement were similar across downed wood treatments, ETAs were smaller than the 1.7-ha treatment area size, and 97% of voles sampled were within their respective treatment sites. Thus, the overall experimental design was adequate to test the response of Red-backed Voles to changes in the abundance of dispersed downed wood, within the context described above. However, the low number of replicates (3), inconsistent downed wood manipulations, and intrinsic variability of Red-backed Vole populations over time need to be acknowledged.

MANAGEMENT IMPLICATIONS

In dry ecosystems, such as Opax in the southern interior of BC, downed wood may be particularly important as a moisture reservoir and cover component. On clearcuts at Opax, the removal of downed wood resulted in smaller Red-backed Vole populations. In forested sites, we could not determine whether downed wood was an important habitat component for Red-backed Voles based on population dynamics; however, there was some evidence that removal of downed wood resulted in lower population densities.

In the high-elevation spruce-fir forest at Sicamous, Red-backed Vole abundance did not appear to be determined by the abundance of downed wood. On forested sites with heavy cover from shrubs, herbs, and moss cover (>65%), Red-backed Voles were as abundant on areas with approximately 1% cover by downed wood as areas with 10% cover. The effect of harvesting on Red-backed Voles at the high-elevation system was also not related to the abundance of downed wood. Removal of the forest canopy resulted in the almost complete loss of Red-backed Voles from clearcuts. Retention of downed wood did not modify the site enough to maintain populations, or slow the decline as at Opax.

It is particularly important to retain downed wood in dry ecosystems, where it might act as a moisture reservoir. Red-backed Vole abundance was lower on clearcut areas with only 5% ground cover by downed wood (>7.5 cm in diameter), compared to sites with up to 20% downed wood ground cover. Ground cover of 9-15% by downed wood was normal for clearcuts at Opax. In order for downed wood to be maintained through time, larger pieces should be left on site after harvesting. Larger pieces provide greater amounts of cover, retain more moisture, and also decay more slowly. It takes 80-190 years for a log to fully decompose in this dry ecosystem (Feller 1997). If the presence of wood-boring beetles is a concern, bark could be stripped from large logs, or more medium-sized logs could be left on site. Previous research indicated that burning reduces the amount of downed wood and vegetation, negatively affecting some species of small mammals (Martell 1984; Sullivan *et al.* 1999). Instead of piling and burning downed wood left after harvesting, distribute the material throughout the harvest block to create additional habitat. For example, retention of piles of woody debris near forest edges may be beneficial for American Marten (*Martes americana*) and other small mustelids. However, persistence of Red-backed Voles on clearcuts requires substantial piles or windrows of downed wood (dimensions of at least 2 m in height and 5 m in width or diameter) to provide habitat for this microtine (Sullivan *et al.* 2011, 2012).

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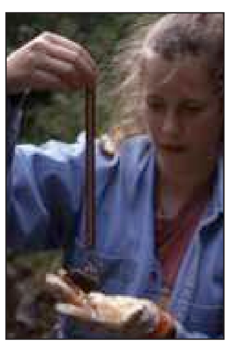

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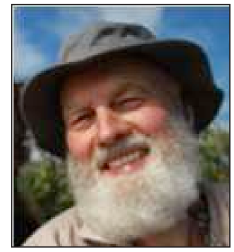

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