

Initial response of small ground-dwelling mammals to forest alternative buffers along headwater streams in the Washington Coast Range, USA

Randall J. Wilk^{a,*}, Martin G. Raphael^a, Christopher S. Nations^b, Jeffrey D. Ricklefs^c

^a USDA Forest Service, Pacific Northwest Research Station, Olympia Forestry Sciences Laboratory, 3625 93rd Avenue, SW, Olympia, WA 98512-9193, United States

^b Western Ecosystems Technology, Inc., 2003 Central Avenue, Cheyenne, WY 82001, United States

^c Washington State Department of Natural Resources, P.O. Box 47016, Olympia, WA 98504-7016, United States

ARTICLE INFO

Article history:

Received 15 April 2010

Received in revised form 3 August 2010

Accepted 5 August 2010

Keywords:

Pacific Northwest

Small mammals

Riparian

Headwater

Buffer

ABSTRACT

We assessed the short-term effects of alternative designs of forested buffer treatments along headwater streams on small ground-dwelling mammals in managed forests in western Washington, USA. Over three summers (one pretreatment and two posttreatment), we trapped 19 mammalian species along 23 streams in the northern Coast Range. We compared faunal communities in unlogged controls with riparian treatments: (1) clearcuts (no buffer) to the stream bank, (2) clearcuts with continuous buffer strips from a few to 20 m each stream side, and (3) clearcuts with small patch (<0.6 ha) buffers left to protect sensitive streamside terrain. We estimated abundance (\hat{N}) of eight common and three less common species with simple models and capture indices, respectively, and analyzed effects of treatments and community measures on relative abundance compared to controls and over time. Habitat and forest stand changes after treatments included reduced live standing trees and canopy, more dead down wood, and increased ground plant species richness, evenness, and diversity, particularly in the patch and no buffers. The forest obligate *Peromyscus keenii* significantly declined in all treatments. No other species declined in strip buffers. Species with statistically greater \hat{N} in treatments included the early-seral microtine *Microtus oregoni*, the semi-arboreal generalist *Tamias townsendii* and the old forest specialist *Myodes gapperi* in all treatments; the generalist *Peromyscus maniculatus* in strip and no buffers; and the early-seral riparian *Zapus trinotatus* in patch buffers. Postlogging trends in \hat{N} were negative for two common shrews, *Sorex monticolus* and *Sorex trowbridgii*. Moist soil denizen *Neurotrichus gibbsii* capture rates were significantly lower in clearcut no buffers. Captures were low for two species of semi-aquatic shrews, *Sorex bendirii* and *Sorex palustris*, but in general, *S. palustris* responded poorly to treatments. Windfall was an important proximate influence on buffer function because persistence was low and created structural diversity in dynamic change. The alternative buffers were ineffective in retaining the habitat and relative abundance of individual small mammal species. Species composition similarity also significantly declined in the clearcuts. Change in species richness, evenness, diversity and total mammals captured in treatments however were not different. Control streams maintained faunal biodiversity but abundance of about half of the species changed following treatment. Steep topography, weather events, and small buffer size advanced habitat changes that influenced small mammal response to treatments. Site-specific data are necessary in logging unit planning along headwater streams, if the management goal is the maintenance of communities observed in undisturbed forest.

Published by Elsevier B.V.

1. Introduction

Forest logging practices along streams in the Pacific Northwest USA include retention of strip buffers intended to maintain streamside riparian habitat, sustain biological diversity, and protect aquatic resources (e.g., FEMAT, 1993; Naiman et al., 1993; Spies et

al., 2002; Richardson et al., 2005). However, some studies show that these buffers may not support wild species at comparable abundances to undisturbed forests before treatment (Richardson and Thompson, 2009). Riparian buffers maintain only certain taxa at levels comparable to unlogged areas so longer-term community dynamics in riparian buffers may be substantially different from undisturbed areas (Marczak et al., 2010).

The narrowest riparian zones are in the stream origins along non-fishbearing first- and second-order or “headwater” streams (order increases at each downstream confluence in the drainage network). In the near-coastal Pacific Northwest, headwater streams

* Corresponding author. Tel.: +1 360 753 7710; fax: +1 360 753 7737.

E-mail addresses: rwilk@fs.fed.us (R.J. Wilk), mraphael@fs.fed.us (M.G. Raphael), cnations@west-inc.com (C.S. Nations), jeffrey.ricklefs@dnr.wa.gov (J.D. Ricklefs).

generally occur at high elevation, are often intermittent or ephemeral, are constrained between ridges under closed canopies, lack flood plains, and are physically unstable owing to winter flooding (Richardson et al., 2005; Richardson and Danehy, 2007). First- and second-order streams may compose up to 80% of the total stream length in many drainage networks, yet are considered to have a small effect upon the lotic continuum compared to the downstream reaches (MacDonald and Coe, 2007; Richardson and Danehy, 2007). Their riparian functionality and biotic response to habitat manipulation is incompletely understood, and there are few studies of the effectiveness of headwater protective buffers on terrestrial fauna.

Forest ground-dwelling small mammals such as shrews, mice, voles, moles, and chipmunks forage upon small vertebrates, insects and plants, alter ground vegetation, mix soil and detritus, spread floral seeds and fungal spores, and are prey to forest carnivores (Hallett et al., 2003). The effect of habitat change by logging on small mammals depends upon the degree to which their ecological requirements are met by the resulting forest condition (Hallett et al., 2003), which can influence critical resources, behaviors and species interactions such as habitat structure, food, foraging behavior, fitness and body size, species communities and interspecies competition (Carey and Johnson, 1995; Lomolino and Perault, 2007). Streamside habitat is ecologically necessary for some species (Anthony et al., 2003), yet the majority of studies on the effects of logging on wildlife are from upland studies (Zwolak, 2009; Marczak et al., 2010).

In British Columbia (BC) Cockle and Richardson (2003) observed that small stream 30-m riparian buffer strips helped lessen the short-term impact of clearcut logging on six small mammal species. In mesic third-order stream riparian forests of the Washington Cascades, Lehmkühl et al. (2008) concluded buffer widths of 60–100 m were effective for refuge and corridor function for small mammals, by measuring spatial relationships of species captures. West (2000) evaluated the effectiveness of two primarily third-order fishbearing stream strip buffer designs in western Washington where capture rates of one species declined but other community differences were small. In a meta-analysis of estimates of the effect of riparian buffers on abundance and density of terrestrial taxa, small mammal densities generally decreased in buffers but the cumulative mean effect size was not significant, reflecting a possible averaging of species responses between abundance at buffer and reference sites (Marczak et al., 2010).

We present research results for small ground-dwelling mammals trapped along western Washington forest first- (and some second-) order headwater streams before and after alternative riparian buffer manipulation. Here both orders (which are physically similar) were part of the research in the headwater rubric if they were fishless—a key regulatory factor in riparian management practices. We initiated this research in part because of the debate over how much protection fishless headwater streams should receive during logging. In Washington State, riparian protection requirements on state and privately managed forests are regulated by the *Forests and Fish Law* (www.forestsandfish.com) or by individually negotiated habitat conservation plans (HCP) between the land owner and the federal agencies charged with protecting at-risk fish and wildlife. On many state and private industrial forests in Washington, headwater streams are not buffered although there are requirements for understory vegetation protection and heavy equipment exclusion on these small, steep channels. Some conservation organizations, however, have argued that the absence of native fishes from headwaters leaves such channels vulnerable to environmental damage during logging, and that other organisms that inhabit the uppermost reaches of the drainage network may suffer habitat loss. They also argue that headwater streams in federally managed forests receive much greater protection under the

Northwest Forest Plan (FEMAT, 1993) than do small watersheds on state and private lands. In order to determine if there was a middle ground between the wide buffers on headwater streams in federal forests and the less protected headwater streams on state forests, the Washington Department of Natural Resources (DNR) implemented a controlled field experiment in which alternative buffering strategies could be evaluated for conservation effectiveness. Our study has relevance to other areas in western North America because the regulation of forest practices often hinges on the presence or absence of fish, with fishless streams typically receiving a lower level of protection during timber harvest.

Our findings are intended to provide a better understanding of alternative buffer designs in the maintenance of streamside small mammal communities by comparing the short-term treatment response of habitat, abundance and composition to measures from prelogging and to measures from uncut reference sites. This research supports the development of a long-term first- and second-order stream conservation strategy as part of the DNR HCP and the proposed adaptive management strategy for western Washington.

2. Study areas

Fieldwork was conducted on DNR-managed State Trust Lands in the Willapa State Province of western Washington State, on the

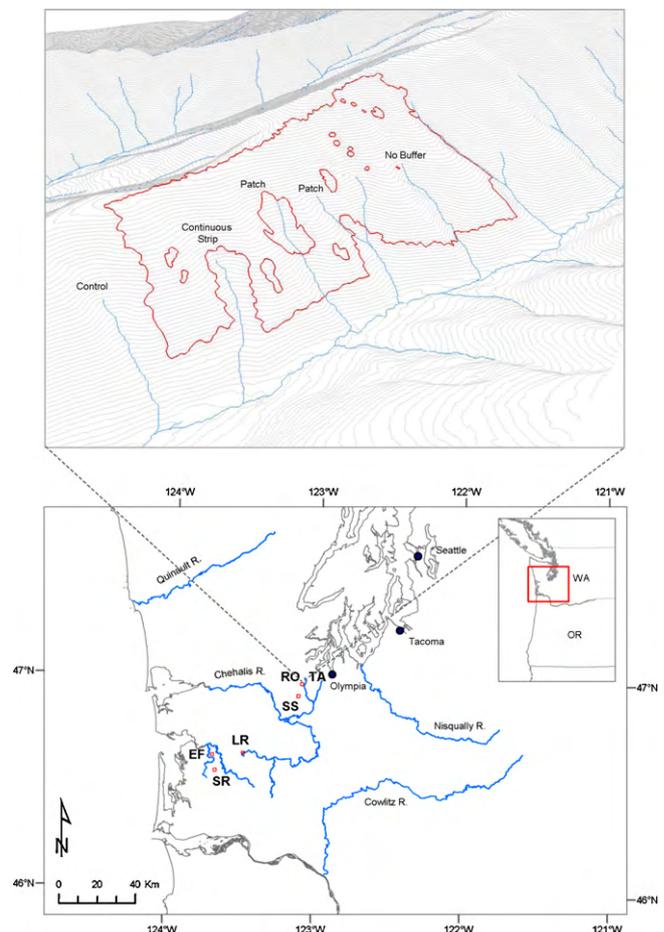


Fig. 1. Western Washington study area, location of the six study blocks, and diagram of the layout of experimental buffer treatments along headwater streams in the Tags block (TA) with one each of control, strip buffer and no buffer treatments, and two patch buffer treatments. Bold lines in diagram show harvest unit outline and cut/retained tree areas. Other block names: RO = Rot, SS = See-saw, LR = Lonely Ridge, EF = Ellsworth Flats, and SR = Split Rue.

northern edge of the Coast Ranges Regional Province (see Franklin and Dyness, 1988). Three cutblocks with 12 streams were in the Black Hills of the Capitol State Forest, west of Olympia, and 3 cutblocks with 11 streams were in the Willapa Hills, east of South Bend (Fig. 1). The highest promontory is 957 m, and the range in elevation of GPS-derived mid-points of trapping arrays was 60–400 m. Stream catchment size ranged 1.2–8.1 ha. Stream reaches, source to confluence, ranged 80–480 m. Stream bankfull width was generally less than 3 m; flow was mostly perennial, but one stream had a dry/trickle bed. Stream aspect varied widely within treatments with one to three streams in each of the four directional quadrants (NE, SE, SW, NW), except for the three patch buffers which were oriented N-NE.

The sites were in managed previously logged and naturally regenerated second-growth coniferous forests of mostly western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*) and western redcedar (*Thuja plicata*), with vine maple (*Acer circinatum*) in the midstory. Some sites had dense patches of salal (*Gaultheria shallon*) in upland ground cover. Devil's club (*Oplopanax horridus*), salmonberry (*Rubus spectabilis*), western sword fern (*Polystichum munitum*) and redwood sorrel (*Oxalis oregana*) characterized streamside vegetation. Stand ages at the time of logging were 61–108 years. Streams assigned to treatments were very similar in measures of environmental and habitat attributes (see Supplement Appendix 1).

In our study area, at least nine species of small mammals occur along aquatic habitat including the benthivorous riparian obligates: marsh shrew (*Sorex bendirii*) and the Pacific water shrew (*Sorex palustris*); riparian associates: the dusky shrew (*Sorex monticolus*), the shrew-mole (*Neurotrichus gibbsii*), the long-tailed vole (*Microtus longicaudus*), the northwestern deer mouse (*Peromyscus keenii*), and the short-tailed weasel (*Mustela erminea*); and species that occur in riparian early-seral habitat that often results from natural habitat disturbance: the creeping vole (*Microtus oregoni*), the Pacific jumping mouse (*Zapus trinotatus*), and the vagrant shrew (*Sorex vagrans*) (Kelsey and West, 1998; West, 2000; Anthony et al., 2003).

3. Methods

3.1. Design and treatments

There were three experimental treatments: (1) clearcuts (no buffer) to the stream bank ($n=7$; one or two per cutblock), (2) clearcuts with continuous buffer strips from a few to 20 m each stream side ($n=7$; one or two per cutblock), and (3) clearcuts with small patch (<0.6 ha in size) buffers left to protect sensitive streamside terrain ($n=3$; in two of the cutblocks). We also had six unmanaged controls, one in each cutblock (henceforth, treatments = buffers = logging; experimentally, alternative buffers include “no buffers” or clearcuts as one of the three alternatives).

Strict adherence to random assignment of treatments was not possible. Control streams were assigned by DNR managers either to one end of the logging unit ($n=4$) or close to treatments ($n=2$). Thus, streams were adjacent or loosely clustered within cutblocks, with buffers assigned *ad hoc*, reflecting the constraints of planning, road building, and access. Treatments occurred late 2003 to early 2005. Pretreatment was in 2003; 2004 was the logging year (60% trapping effort); 2005 was post 1 and 2006 was post 2. The primary focus of this research was 2003, 2005 and 2006. Concurrent plant and stand sampling was done only in pretreatment and post 1.

In post 1, patch buffers were 0.13, 0.56 and 0.59 ha in size. The four control streams located on the ends of logging units were 40, 62, 67 and 91 m from the adjacent treated area clearcut-forest interface; and the two close controls were 137 and 296 m away from

clearcut portions of the nearest treatment (see Fig. 1 for diagram of buffers in one cutblock logging unit).

3.2. Trapping

We trapped during the “dry season”, late May to mid-September, when on average, only ≈ 9 –10% of the annual rainfall occurs (www.ncdc.noaa.gov, Olympia, WA). We centered 18 trapping stations per stream side \approx midpoint between the origin and lower confluence of each stream. Stations were in a zigzag pattern on the bank to 2 m away, and at 5 m intervals apart. We baited one Sherman live trap (76 mm \times 89 mm \times 222 mm) at each station using whole oats, peanut butter, molasses, and raw cotton, and covered it with debris. While bait composition was not optimal for all species, we believe it was effective in capturing a broad number of species, especially the most common ones, known from a pilot study without bait in 2002. We checked traps daily over three nights in five successive trapping bouts that were two to three weeks apart.

We hole-punched small eared species and ear-tagged the larger Townsend's chipmunk (*Tamias townsendii*), assessed and released them. Shrew (*Sorex* spp.) live captures were immediately released unmarked without knowing species, but mortalities were later identified in the laboratory using keys (Carraway, 1995; Van Zyll de Jong, 1983). Identification and age class of the two species of *Peromyscus* (Gitzen, 2006; Kroeger, 2006) and *T. townsendii* (Waldien, 2005) were assigned by weight or tail length criteria, or both.

After logging, the patch buffer trapping arrays were partially inside and partially outside of tree patches. Owing to burying by windthrow, some trapping stations each year were relocated as close to prelogging configuration as possible. Logging altered stream courses in some cases.

3.3. Habitat

We randomly sampled vegetation, forest stand and dead down wood (DDW) in four 3 by 3-m quadrats in each of two 10 by 10-m plots on each stream side, two to 12 m from the bank. There were three arrays in the control, strip buffer, and no buffer, and two each in the patch leave (islands) and patch cut (clearcut portions of the patch buffer treatment).

We recorded ground-story vascular plant species except graminoid *Luzula* spp. because it was difficult to identify. We included trees ≤ 10 cm diameter at breast height (dbh), measured at 1.4 m height and ignored indeterminate seedlings <2 cm tall. We estimated cover in 1% classes to 10% and 5% classes thereafter. DDW was measured using line-intercept sampling (Waddell, 2002).

We estimated forest metrics by using two variable-radius plots per array. We measured basal area (BA) using a 20-BA-factor Spiegel Relaskop. We recorded species, measured quadrat mean diameter (QMD), and uniquely marked all live or dead trees ≥ 10 cm dbh. In post 1, we remeasured live, dead, down, and windthrown trees, but QMD was not remeasured. Overstory canopy was measured using hemispherical photographs from four photo points 1.2 m above ground with a fisheye converter on a digital camera with a 20% mask of the sky (Frazer et al., 1999).

3.4. Analyses

Data processing and preliminary analyses of species abundance from models were done using SAS (SAS Institute, 2003, vers. 9.1.3, Cary, North Carolina) and modeling analysis was conducted using Matlab (Mathworks, 2002, vers. 6.5, Natick, Massachusetts). All other analyses were done with Predictive Analytics Software (SPSS Inc., 2009, vers. 17.0, SPSS, Inc. Chicago, Illinois). Any comparisons we make with other studies are relative because buffer prescriptions, traps, trapping methods, analyses and other factors may differ

among studies, possibly with varied outcomes (see Williams and Braun, 1983; Anthony et al., 2005).

3.5. Community treatment effects

For plant and mammal species richness, evenness and diversity (and mammal captures), forest stand, and DDW, we subtracted prelogging measures from postlogging and compared the mean size change in treatments with controls using one-way analysis of variance (ANOVA), with post hoc tests (Dunnett's *t* or Bonferroni) to determine which treatments were different. We examined prelogging variables for normality using Shapiro-Wilk tests, and transformed data when applicable. Parametric testing of values for live standing trees (stems) ha⁻¹ were transformed log(*x*+1), DDW logs ha⁻¹ and DDW volume (m³ ha⁻¹) were square root transformed; proportion data were arcsine square root transformed (McCune and Grace, 2002). We used the software Palaeontological Statistics (Hammer et al., 2001) to calculate plant and animal diversity indices (Shannon *H'*). The untransformed data are shown, but *P*-values are from the analyses on the values after they were transformed. Because our samples were small and estimates were highly variable in many cases, we set statistical significance $\alpha = 0.10$.

3.6. Abundance of small mammals

All study streams were within the distributional range of all species captured in this study. Trowbridge's shrew (*Sorex trowbridgii*) and *S. monticolus* captures were analyzed using the removal method (Otis et al., 1978; White et al., 1982) because mortality rates were high. Released individuals were treated as if they had not been captured. We pooled captures across all streams to model capture probabilities, *p*. Removals were pooled across trap nights (TN) within each bout treating the bout as a capture occasion.

The removal method goodness-of-fit (GOF) was assessed using a chi-square test (White et al., 1982). Removals are expected to decrease over time, so the "failure criterion" (Otis et al., 1978) of this assumption was calculated for each sequential model to assess whether removals decreased over time. The preferred model was the simplest model that satisfied both the GOF test at $\alpha = 0.10$ and the failure criterion such that $F > 0$, and was primarily used for estimating abundance. The next less parsimonious model was also considered if estimated abundance (\hat{N}) was similar with more precision. Variances were estimated using an asymptotic approximation provided by Otis et al. (1978).

Population sizes for all other species except water shrews and *N. gibbsii* were estimated using the closed population model M_0 , which assumes constant *p* (Otis et al., 1978). The few capture losses (except *M. oregoni*, 32%) were excluded from the analysis as were individuals not known to be either first captures or recaptures (*Z. trinotatus*, 3%). Variances were also estimated using asymptotic approximations (Otis et al., 1978). In rare cases where \hat{N} were not obtained, the population size was the number of new captures with an undefined variance.

We transformed \hat{N} to individuals per stream: $\{(\hat{N}) \times (1/n)\} \pm \{(SE \text{ of } \hat{N}) \times (1/n)\}$, where *n* is the number of streams in a treatment. We then performed six pairwise comparisons for each species, treatment and postlogging year combination using Tukey's test, with the normal approximation. We set statistical significance at $\alpha = 0.10$, due to inherently low statistical power of small samples, with significant *t*-values of 2.052 for within treatment by year comparisons, and *t* = 2.291 for within year, treatment-control comparisons. We did not account for repeated measurements, making the tests very likely conservative in that the standard errors of the differences are overestimated (Baldwin, J., Pacific Southwest Research Station, personal communication).

Captures of the two water shrew species and *N. gibbsii*, were too few to model \hat{N} so we used capture indices (see Hopkins and Kennedy, 2004) and adjusted for sprung traps. Most streams had no captures of these three species, so we transformed capture rates, *n*/100 TN by adding a constant 1 (McCune and Grace, 2002) and converted them to natural logs: $\ln([n/100TN] + 1)$ for repeated measures (Baldwin, J., statistician, PSW Research Station, personal communication). We then performed ANOVA with post hoc tests on the differences in capture rates between postlogging treatments compared to differences in controls. We also used repeated measures ANOVA pairwise comparisons of differences on estimated marginal means between post and pre-capture rates within each treatment with no adjustment for multiple comparisons (least significant difference).

3.7. Small mammal species composition similarity and biological correlates

We calculated Jaccard's index to compare the percentage similarity of species composition (species in common in both locations regardless of abundance; Magurran, 1988) between each treatment stream and the control in each cutblock. We then transformed the percentages with the arcsine square root transformation (multiplied by $2/\pi$) to rescale result to percentages; McCune and Grace, 2002) and conducted ANOVA with post hoc tests. Species representing <0.1% of captures were not included. We also employed simple Pearson bivariate correlations to examine associations between change in habitat and change in the mammal community.

3.8. Percentage of females, productivity, and adult body mass

Because mammal abundance is not always a good indicator of habitat quality (Van Horne, 1983), we considered demographic, body mass, and productivity data measured in the field (live rodents) and laboratory (postmortem). We pooled across patch and no buffers, and across both post 1 and post 2 "impact years" where applicable to increase sample size. We conducted two-sample (*t*-test, Mann-Whitney *U*), multi-sample (one-way ANOVA, Kruskal-Wallis) and chi-square statistical tests on these data. We include additional data from 2002 and 2004 to increase some sample sizes, especially for body mass and percent by sex of water shrews (and *N. gibbsii*) because they are rare or of sensitive status in some regions (e.g., Pacific Water Shrew Recovery Team, 2009), and life history information is incomplete.

4. Results

4.1. Habitat change

Habitat change in post 1 buffers increased as the level of logging increased. Average change in understory plants, forest stand and DDW was greater in the patch and no buffers than in the controls (Tables 1 and 2). Strip buffers were intermediate. Windthrow affected all categories, shown by fewer standing trees and larger amounts of DDW.

4.2. Abundance of small mammals

We captured 3430 individuals of 19 species of small mammals. Two species of *Sorex* and two species of *Peromyscus* accounted for 70% of the captures. *S. trowbridgii* was the only species captured at every stream in every year. We captured nine riparian species with individuals of riparian associates representing 18% of captures, early-seral riparian (10%) and obligates (1%; Table 3).

P. keeni \hat{N} significantly declined in all treatments. No other species declined in strip buffers (Fig. 2). Species with statistically

Table 1

Change in understory/shrub and forest stand measurements in buffer treatments in postlogging compared to controls (first year postlogging–prelogging; $\bar{X} \pm SE$) along headwater streams, western Washington. Patch buffers are split between tree islands (leave) and clearcuts around islands (cut). See Supplement Appendix 1 for prelogging measurements.

Treatment (n)	Understory plants			Forest stand			
	Richness	Evenness	Diversity	Canopy closure (%)	Standing live trees (trees ha ⁻¹)	Basal area (m ² ha ⁻¹)	QMD (cm)
Control (6)	-0.1 ± 0.5	0.01 ± 0.01	-0.01 ± 0.06	0.2 ± 1.2	-109 ± 87	-10 ± 7	-0.0 ± 0.0
Strip buffer (7)	3.4 ± 0.7	0.00 ± 0.01	0.28 ± 0.08	-8.6 ± 3.5	-152 ± 44	-19 ± 4	8 ± 8
P	0.05*	1.00	0.18	0.12	0.98	1.00	0.71
Patch leave (3)	5.5 ± 2.2	-0.00 ± 0.02	0.56 ± 0.14	-23.4 ± 8.7	-120 ± 51	-17 ± 4	-1 ± 2
P	0.01*	1.00	0.01*	0.00*	1.00	1.00	1.00
Patch cut (3)	9.2 ± 0.8	0.13 ± 0.04	0.93 ± 0.07	-67.2 ± 3.9	-273 ± 41	-38 ± 4	-40 ± 4
P	0.00*	0.00*	0.00*	0.00*	0.00*	0.09*	0.00*
No buffer (7)	6.1 ± 1.1	0.15 ± 0.01	0.54 ± 0.10	-69.1 ± 2.6	-518 ± 115	-54 ± 6	-12 ± 6
P	0.00*	0.00*	0.00*	0.00*	0.00*	0.00*	0.37
F _{4,21}	9.87	12.60	13.04	76.84	4.39	10.28	6.68
P	0.00*	0.00*	0.00*	0.00*	0.01*	0.00*	0.00*

* Significantly different from control, ANOVA with post hoc test.

greater \hat{N} in treatments included the early-seral microtine *M. oregoni*, the semi-arboreal generalist *T. townsendii* and the old forest specialist *M. gapperi* in all buffers; the generalist deer mouse *Peromyscus maniculatus* in strip and no buffers; and the early-seral riparian *Z. trinitatus* in patch buffers (Fig. 2). *P. keeni*, along with *M. gapperi*, showed lower \hat{N} along control streams in postlogging (Fig. 2). Trends in \hat{N} were negative for both common shrews, including controls. We captured only 14 individuals of each species of water shrew in 37,260 TN over three years and $n = 49$ of both species including 2002 and 2004. Total captures of *N. gibbsii* ($n = 147$) were not amenable to modeling. Their capture rates in no buffers were significantly lower in both postlogging years than in prelogging (Supplement Appendix 3).

4.3. Small mammal community structure

Average species richness increased 1–2 species in the treatments. *T. townsendii*, *P. maniculatus*, *M. oregoni*, *S. vagrans*, *M. erminea*, and *M. longicaudus* added to species richness in ≥ 1 treatment (Table 3). Losses of numbers of *P. keeni*, *S. trowbridgii* and *S. monticolus* in all treatments were offset by increases of *Z. trinitatus*, *M. oregoni* and *M. gapperi* captures in the patch and no buffers and influenced species evenness. Statistically, there were no significant differences in total captures, species richness, evenness or diversity of small mammals along treated streams (Table 4).

The shifts in species occurrence in treatments were reflected in species composition similarity. Before logging, treatments were 55–60% similar to the species composition of control streams (Table 5). While similarity within controls did not change in time, the clearcut no buffers became more dissimilar to controls (Table 5). Patch buffers showed the strongest similarity to controls among the treatments.

4.4. Biological correlates

We correlated the post 1 mean change in habitat attributes with the mean change in post 1 total small mammal capture attributes (see Supplement Appendix 1 and Table 4 for variables) and found weak but significant associations. In the understory, increases in mammal richness ($r = 0.42$, $P = 0.05$) and diversity ($r = 0.46$, $P = 0.03$) were associated with increases in plant richness. Similarly, mammal richness ($r = 0.35$, $P = 0.10$) and diversity ($r = 0.36$, $P = 0.10$) showed a similar, but weaker association with plant diversity.

At the forest stand level, total mammals captured was positively associated with larger QMD trees ($r = 0.41$, $P = 0.05$). Mammal captures ($r = 0.35$, $P = 0.10$), mammal species richness ($r = 0.44$, $P = 0.04$)

and mammal species diversity ($r = 0.45$, $P = 0.03$) were positively associated with DDW small diameter class (10–30 cm). Mammal richness ($r = 0.37$, $P = 0.08$) also showed a positive association with DDW logs of medium decay class. Mammal richness, evenness, and diversity were negatively associated with DDW soft decay class logs ($r = -0.35$, $P = 0.10$), DDW percent conifer pieces ($r = -0.47$, $P = 0.03$) and DDW logs ≥ 100 cm ($r = -0.36$, $P = 0.09$), respectively.

4.5. Percentage of females, productivity, and adult body mass

After logging, the percentage of captures of C as females increased in patch and no buffers and *S. monticolus* increased in the strip buffers. The percentages of reproductively active females of the two common shrews increased in controls and decreased in patch/no buffers. *S. trowbridgii* also had lower percentage breeding females in strip buffers. *S. monticolus* showed smaller percentages of juvenile captures in the treatments (details are in Supplement Appendixes 4 and 5). Adult female body mass of both common shrews increased in postlogging controls, and female mass of *M. gapperi* in a small sample declined (Table 6). *P. keeni* males and *P. maniculatus* females were heavier in postlogging patch/no buffers, and *P. maniculatus* males were lighter.

We captured 49 water shrews including years 2002 and 2004, but only 32 could be identified to sex and all of these were adults. Forty-five percent of *S. bendirii*, and 20% of *S. palustris* were females. With low captures in prelogging, no *S. bendirii* were breeding. After treatments, female *S. bendirii* had five of eight captures in controls and treatments in reproductive condition. Only 1 of seven male captures was breeding. In prelogging, four of six *S. palustris* were breeding, but this species was nearly absent in postlogging and no reproductively active individuals were captured. There was no differential body mass of either species between pre- and postlogging (see Supplement Appendix 6).

5. Discussion

The effectiveness of alternative buffer treatments for maintaining short-term abundance and population structure of the small mammal community was influenced by the degree of habitat change. Canopy forest conditions we observed in prelogging diminished with increased logging levels which induced lesser riparian protection and increased forest floor habitat complexity. These changes triggered significant responses by small mammals with shifts in \hat{N} in treatments (Fig. 2). Strip buffers appeared to provide more protection of small mammal habitat than the patch buffers and clearcut no buffers when compared to the controls (Tables 1 and 2). Clearcuts did not maintain mammal species com-

Table 2
Change in dead down wood measurements in buffer treatments in postlogging compared to controls (first year postlogging–prelogging; $\bar{X} \pm SE$) along headwater streams, western Washington. Patch buffers are split between tree islands (leave) and clearcuts around islands (cut). See Supplement Appendix 1 for prelogging measurements.

Treatment (n)	Logs (N ha ⁻¹)	Volume (m ³ ha ⁻¹)	Cover (%)	Diameter class (cm)				Decay class			Species class ^a	
				10–30	30–60	60–100	≥100	1 Hard	2–3 Med	4–5 Soft	Decid	Conifer
Control (6)	299 ± 98	-5 ± 31	0.5 ± 0.7	-3 ± 21	20 ± 18	0 ± 0	-18 ± 16	5 ± 7	-1 ± 13	-4 ± 12	10 ± 6	43 ± 11
Strip buffer (7)	493 ± 91	10 ± 33	1.4 ± 0.7	15 ± 12	-6 ± 14	-10 ± 5	1 ± 1	14 ± 7	10 ± 11	-24 ± 8	28 ± 12	25 ± 17
P	0.60	0.95	0.93	0.73	0.48	0.23	0.82	0.97	0.90	0.36	0.34	0.77
Patch leave (3)	611 ± 158	-20 ± 99	0.5 ± 1.7	35 ± 21	-0 ± 12	-1 ± 5	-33 ± 33	12 ± 6	2 ± 7	-14 ± 10	25 ± 7	20 ± 3
P	0.91	1.00	1.00	0.43	0.87	1.00	0.94	1.00	1.00	0.19	0.74	0.58
Patch cut (3)	2149 ± 528	61 ± 55	5.2 ± 2.1	64 ± 25	3 ± 10	-1 ± 1	-67 ± 33	29 ± 18	6 ± 8	-35 ± 26	22 ± 12	40 ± 27
P	0.00*	0.72	0.05*	0.05*	0.92	1.00	0.24	0.65	1.00	0.93	0.85	0.95
No buffer (7)	1522 ± 615	-97 ± 48	-0.7 ± 1.2	21 ± 8	10 ± 17	-1 ± 4	-16 ± 14	43 ± 12	2 ± 6	-31 ± 7	11 ± 5	63 ± 10
P	0.04*	0.72	0.82	0.50	0.99	1.00	1.00	0.06*	1.00	0.32	1.00	0.69
F _{4,21}	4.40	1.14	2.98	1.86	0.56	1.18	1.80	2.16	0.15	1.30	1.00	1.68
P	0.01*	0.37	0.04*	0.16	0.69	0.35	0.17	0.11	0.96	0.30	0.43	0.19

* Significantly different from control, ANOVA with post hoc test.

^a Only pieces identifiable to species; Decid = deciduous.

Table 3
Small mammal species captures and relative occurrence by treatment and year, western Washington stream buffer study 2003, 2005, 2006.

	Control			Strip buffer			Patch buffer			No buffer			Total captures (%)
	Pre-harvest	Post 1	Post 2	Pre-harvest	Post 1	Post 2	Pre-harvest	Post 1	Post 2	Pre-harvest	Post 1	Post 2	
<i>P. keeni</i>	•	•	•	•	•	•	•	•	•	•	•	•	23.79
<i>S. trowbridgii</i>	•	•	•	•	•	•	•	•	•	•	•	•	17.20
<i>S. monticolus</i> (a)	•	•	•	•	•	•	•	•	•	•	•	•	11.31
<i>Sorex</i> unid.	•	•	•	•	•	•	•	•	•	•	•	<	6.91
<i>T. townsendii</i>	<	<	<	•	•	•	•	•	•	•	•	•	6.38
<i>P. maniculatus</i>	<	<	•	<	•	•	•	•	<	•	•	•	5.63
<i>Peromyscus</i> unid.	•	•	•	•	<	•	•	•	•	•	<	•	5.51
<i>M. gapperi</i>	•	<	•	•	•	<	•	•	•	•	•	<	5.45
<i>Z. trinitatus</i> (e)	•	•	•	<	•	•	•	•	•	<	•	•	5.13
<i>N. gibbsii</i> (a)	•	•	<	•	<	<	•	•	<	•	•	<	4.29
<i>M. oregoni</i> (e)	<	<	<	<	<	<	•	•	•	<	•	•	4.17
<i>M. longicaudus</i> (a)	<	<	<	<	<	<	•	•	•	<	•	•	0.99
<i>M. erminea</i> (a)	<	<	<	<	<	<	•	•	•	<	<	<	0.96
<i>S. vagrans</i> (e)	<	<	<	<	<	<	•	•	•	<	<	<	0.79
<i>S. bendirii</i> (o)	<	<	<	<	<	<	<	•	•	•	•	<	0.41
<i>S. palustris</i> (o)	<	<	<	<	<	<	•	•	•	<	<	<	0.41
<i>Glaucomys sabrinus</i>	<	<	<	<	<	<	<	<	<	<	<	<	0.29
<i>S. rohweri</i> ^a	<	<	<	<	<	<	<	<	<	<	<	<	0.23
<i>Scapanus orarius</i>	<	<	<	<	<	<	<	<	<	<	<	<	0.09
<i>Tamias douglasii</i>	<	<	<	<	<	<	<	<	<	<	<	<	0.03
<i>Spilogale gracilis</i>	<	<	<	<	<	<	<	<	<	<	<	<	0.03

Note: • = captured along ≥2/3 of streams; < indicates captured along 1/3–2/3 of streams; a = riparian associate, e = early-seral riparian species, o = riparian obligate species; Post 1 = 1 year postlogging, Post 2 = 2 years postlogging.

^a Previously considered to be *S. cinereus* in western Washington (Rausch et al., 2007; Nagorsen and Panter, 2009).

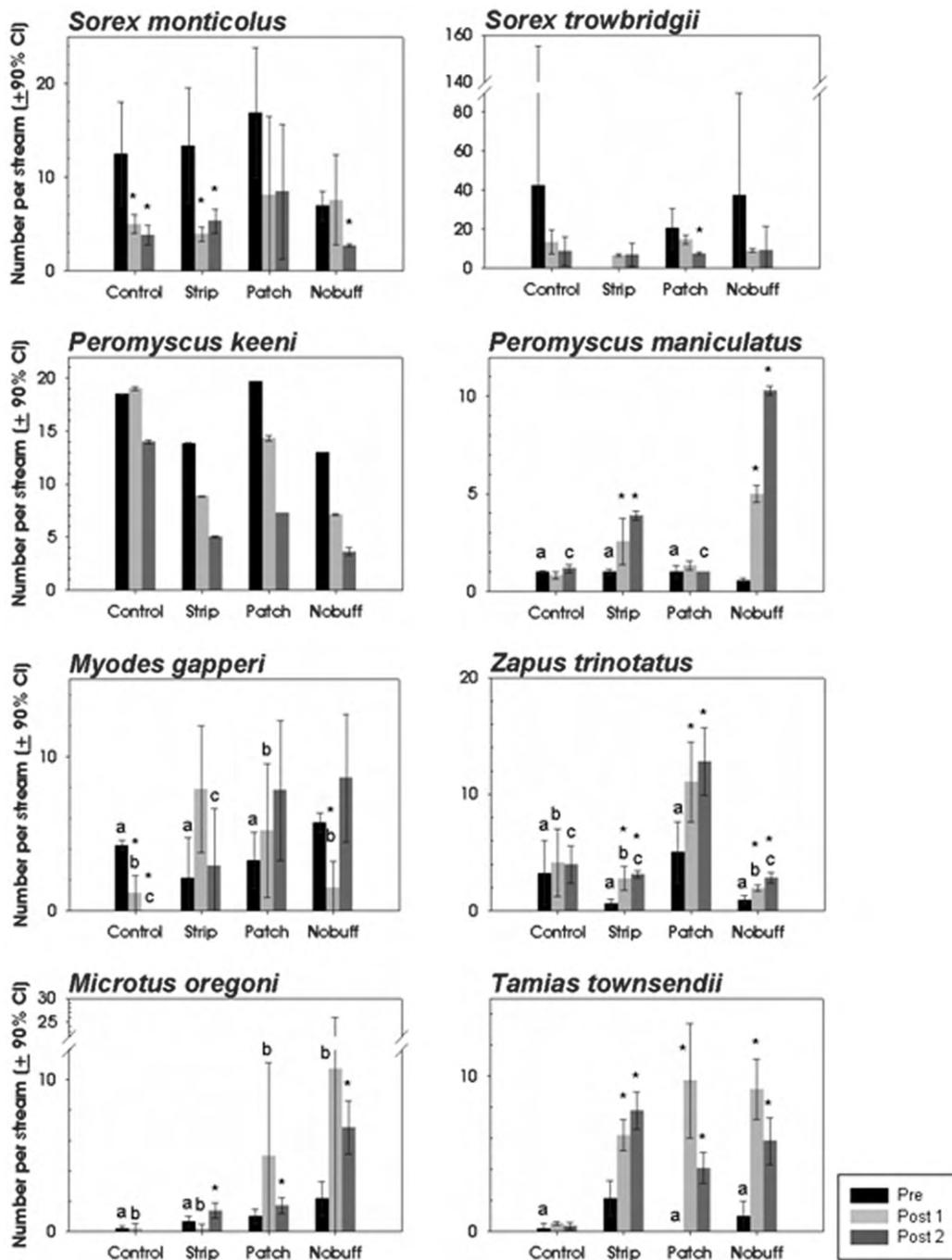


Fig. 2. Estimated abundance (transformed to individuals per stream \pm 90% CI) of eight common small mammal species by treatment type in western Washington stream buffer study, from generalized removal (*S. monticolus* and *S. trowbridgii*) and closed population models M_0 (other six species). For *S. monticolus* and *S. trowbridgii* no within year comparisons of treatments with controls are different. Where bar is missing in *S. trowbridgii* prelogging strip buffer only, there were captures, but no model adequately fit the data. All *P. keeni* pairwise comparisons with controls and prelogging are significantly different. For the other five species the same letters indicate no significant difference from controls in the same year; * indicates within treatment difference from prelogging ($P \leq 0.10$; see methods analyses for t -values). Note scale difference. Control ($n = 6$); strip buffer ($n = 7$); patch buffer ($n = 3$); no buffer ($n = 7$).

position similarity (Table 5). Species richness increased 1–2 more species in the treatments than in controls, but not significantly.

Recent research showed that clearcutting on small streams significantly reduced small mammal species richness in BC (Cockle and Richardson, 2003) or caused a shift in species occurrence in western Washington (West, 2000; like this study). Small mammal species that are negatively affected by clearcutting may also show persistence or increase in abundance after moderate or small-scale disturbance as Gitzen et al. (2007) observed in Washington and Oregon where canopy species *P. keeni*, *S. trowbridgii*, *M.*

gapperi, and *N. gibbsii* showed “greater flexibility” in habitat occupancy than expected in partially logged upland sites of variable retention. Moreover, small mammal species may show different responses to logging owing to effects on factors such as critical resources and species interactions specific to a subarea – even when a treatment has a similar effect on a habitat element across a large geographic region (Gitzen, unpublished). Species that showed increased numbers after buffer manipulation and clearcutting in our study included *P. maniculatus*, *Microtus* spp., and *Tamias* spp., which is consistent with other studies (West, 2000; Cockle and

Table 4
Prelogging values and postlogging change in treatments compared to controls (postlogging year 1 or postlogging year 2 less prelogging value; $\bar{X} \pm SE$) in total captures, species richness, evenness, and diversity of small mammals in buffer treatments along headwater streams, western Washington.

Treatment (n)	Total captures				Species richness				Species evenness				Species diversity					
	Pre		Post 2		Pre		Post 1		Pre		Post 1		Pre		Post 1		Post 2	
	Pre	Post 1	Post 2	Post 1	Pre	Post 1	Post 2	Post 1	Pre	Post 1	Post 2	Post 1	Pre	Post 1	Post 2	Post 1	Post 2	
Control (6)	49 ± 4	-6.5 ± 3.2	-15.7 ± 2.4	-0.5 ± 1.1	7.0 ± 0.4	-0.5 ± 1.1	0.2 ± 0.8	-0.02 ± 0.04	0.01 ± 0.04	1.47 ± 0.07	-0.13 ± 0.18	0.05 ± 0.16	1.47 ± 0.07	-0.13 ± 0.18	0.05 ± 0.16	-0.13 ± 0.18	0.05 ± 0.16	
Strip buffer	42 ± 4	-1.3 ± 5.8	-3.3 ± 5.6	1.1 ± 0.7	6.7 ± 0.5	1.1 ± 0.7	1.4 ± 0.9	0.05 ± 0.03	0.07 ± 0.05	1.47 ± 0.09	0.24 ± 0.11	0.29 ± 0.14	1.47 ± 0.09	0.24 ± 0.11	0.29 ± 0.14	0.24 ± 0.11	0.29 ± 0.14	
<i>P</i> ^a	0.47	0.82	0.26	0.40	0.98	0.40	0.50	0.30	0.95	1.00	0.14	0.44	1.00	0.14	0.44	0.14	0.44	
Patch buffer	52 ± 3	-13 ± 11.1	-4.7 ± 5.2	1.0 ± 1.2	8.0 ± 0.0	1.0 ± 1.2	2.0 ± 0.6	0.06 ± 0.02	0.07 ± 0.01	1.67 ± 0.04	0.22 ± 0.16	0.34 ± 0.06	1.67 ± 0.04	0.22 ± 0.16	0.34 ± 0.06	0.22 ± 0.16	0.34 ± 0.06	
<i>P</i>	0.96	0.90	0.53	0.65	0.75	0.65	0.40	0.38	0.91	0.51	0.34	0.49	0.51	0.34	0.49	0.34	0.49	
No buffer	46 ± 4	-3.0 ± 4.3	-1.0 ± 6.4	0.9 ± 0.8	6.9 ± 0.9	0.9 ± 0.8	1.3 ± 0.6	0.02 ± 0.03	0.00 ± 0.04	1.54 ± 0.12	0.16 ± 0.10	0.17 ± 0.11	1.54 ± 0.12	0.16 ± 0.10	0.17 ± 0.11	0.16 ± 0.10	0.17 ± 0.11	
<i>P</i>	0.88	0.93	0.16	0.55	1.00	0.55	0.59	0.86	0.35	0.91	0.29	0.85	0.91	0.29	0.85	0.29	0.85	
<i>F</i> _{3,19}	0.88	0.20	1.47	0.75	0.43	0.75	0.83	1.13	0.78	0.59	1.58	0.78	0.59	1.58	0.78	1.58	0.78	
<i>P</i>	0.47	0.89	0.25	0.54	0.73	0.54	0.49	0.36	0.52	0.63	0.23	0.52	0.63	0.23	0.52	0.23	0.52	

^a ANOVA post hoc test.

Richardson, 2003; Waldien, 2005; Gitzen et al., 2007; Zwolak, 2009). We also observed concurrent declines in \hat{N} in treatments and controls of three of the four forest endemic species: *P. keeni*, *S. monticolus*, *S. trowbridgii*. The fourth species that declined in controls, *M. gapperi*, increased in treatments (Fig. 2). Concurrent declines we observed of typic forest species suggest that factors other than or in addition to the treatments influenced \hat{N} .

5.1. *Peromyscus keeni*

P. keeni is a coniferous forest obligate species (Hallett et al., 2003; Lawlor, 2003). While populations are expected to decline after logging, neither forest gaps nor fragmentation created less preferable habitat for *P. keeni* in upland forests (Gitzen and West, 2002; Gitzen et al., 2007; Mills et al., 2003). However, riparian treatments in our study exacerbated *P. keeni* average declines of >60% in strip and patch buffers, and >70% in no buffers. To a lesser extent, *P. keeni* also declined in controls (24%). Similarly, *P. keeni* declined \approx 50% on average in third-order stream buffers – but not in controls (West, 2000). While the size of the decline in \hat{N} of *P. keeni* was significant in treatments, the smaller size of change in the controls (Fig. 2) may be biologically inconsequential.

5.2. *Myodes gapperi*

The unexpected increase in \hat{N} of *M. gapperi* in treatments belied their “decline” in the controls. We cannot explain this outcome and we are uncertain whether the difference between four (prelogging) and <1 individual/stream (postlogging; Fig. 2) is biologically important at these relatively low densities. This idiosyncrasy may express the inherently high natural population variation of the species as Carey and Johnson (1995) observed in sites ranging from pristine old-growth to naturally young forests in western Washington. The increase in our treatments of *M. gapperi* indeed fluctuated and was highly variable (Fig. 2). Others reported – in addition to *M. gapperi*, high yearly variation in captures of individual common species in the small mammal community in general in Washington (Gitzen et al., 2007).

In the W-NW United States, *M. gapperi* numbers often decrease after upland logging, and in the E-NE, *M. gapperi* usually increases (Gitzen, unpublished); region may be the primary determinate for *M. gapperi* habitat selection (Pulfer, 2007). In a meta-analysis of postlogging effects on forest small mammals, Zwolak (2009) suggested that declines of *M. gapperi* after upland clearcutting of moist coniferous forest (like our sites) are even greater than in drier sites. Along small stream clearcuts (Cockle and Richardson, 2003) and in partially cut riparian buffers (West, 2000), *M. gapperi* declined in the Pacific Northwest, but not in the controls, as in our study.

In western Washington, *M. gapperi* is more associated with upland habitat than riparian (West, 2000) and is generally considered a mesic old forest species (Merritt, 1981; Sullivan et al., 2009). *M. gapperi* has a purported high need for free water and structurally complex habitat (Verts and Carraway, 1998; Nordyke and Buskirk, 1991; Zwolak, 2009), which may explain their influx along our streamside treatments where both microhabitat features occurred, despite reduced forest canopy. In dryer uplands, habitat structure alone did not explain the inconsistency in responses of *M. gapperi* to variable retention logging among areas Gitzen et al. (2007), which may underscore the importance of headwater streams to *M. gapperi*. *M. gapperi* also is highly adaptive to changing food sources, emphasizing lichens, seeds and fungi (Carey and Johnson, 1995) that may shift in availability following disturbance.

We observed that male *M. gapperi* captures showed lower body mass in patch and no buffers, compared to pretreatment. Thompson et al. (2009) observed males of the closely related western red-backed vole (*Myodes californicus*) moved farther distances,

Table 5Percentage species composition similarity of treatments with controls and across years ($\bar{X} \pm SE$), western Washington stream buffer study.

Treatment	Prelogging	Post 1	P^a	Post 2	P	Within treatments	
						F^b	P
Control	–	52 ± 5	–	56 ± 8	–	0.17	0.69
Strip buffer	61 ± 5	51 ± 7	0.46	45 ± 7	0.16	1.62	0.23
P^a	–	1.00	–	0.59	–	–	–
Patch buffer	58 ± 14	67 ± 13	0.81	56 ± 8	0.99	0.26	0.78
P	–	0.41	–	1.00	–	–	–
No buffer	55 ± 4	48 ± 6	0.63	29 ± 7	0.01*	5.86	0.01*
P	–	0.97	–	0.04*	–	–	–
Within years:							
F^b	0.27	1.03	–	2.89	–	–	–
P	0.76	0.40	–	0.06*	–	–	–

* Significantly different.

^a ANOVA post hoc test compared to controls (columns) or prelogging (rows).^b df : columns: prelogging ($F_{2,14}$); post 1 and post 2 ($F_{3,19}$); rows: control ($F_{1,10}$) strip and no buffers ($F_{2,18}$); patch buffer ($F_{2,6}$).

occupied larger home ranges, and had longer nocturnal activity patterns than females. This tendency for more males than females to disperse through cutover habitat (Mills et al., 2003) may explain the smaller body mass of postlogging captures in treatments owing to energy expenditure and movement into possible streamside sinks, further stressed by changing interspecies competition. Our treatments were probably ecological traps for *M. gapperi* that resulted in population “packing” along streams and reflected the species short-term adaptation by efficient use of limited proximate critical resources unique to headwater streams.

5.3. *Sorex monticolus* and *S. trowbridgii*

The occurrence of six species of shrews in this study, also observed by West (2000) may be the highest reported for the region, owing to forests of high moisture, cool air and a stable food base (Hallett et al., 2003). Treatments however, negatively impacted the two common shrews. Riparian clearcuts also had lower abundance of *S. monticolus* than nearby forested areas (Cockle and Richardson, 2003) in BC, and lower numbers in partially cut strip buffers and controls in Washington (West, 2000). *S. monticolus* also declined in upland variable retention treatments and mature/old-growth in BC

forests until they were absent by the fifth year (see Sullivan et al., 2008; also Sullivan et al., 2009), and Gitzen et al. (2007) observed inconsistent responses to upland variable retention logging in Oregon and Washington.

We observed percentages of breeding females of both species that significantly increased in our postlogging controls which generally extended into the buffers (Supplement). Female captures of both species also had larger body mass in the controls, indicative of better habitat (Craig, 1995). Further, percentages of *S. monticolus* juveniles declined in strip and patch/no buffers, indicative of lower productivity, survival, or both (Supplement). Habitat quality in controls may account for increases in body weight and more breeding females, but declines of \hat{N} by both species in postlogging controls (and treatments) counters the positive effects of habitat and suggests that other factors influenced shrew populations, especially *S. monticolus*. Unlike other shrew species we captured, *S. monticolus* probably does not produce more than one litter of about six young per summer, and annual survival of young is only about four percent (Verts and Carraway, 1998). Most captures of reproductively active individuals in our samples occurred at the onset of trapping (late May) which lasted through the summer. Protracted trapping was detrimental to *S. monticolus* survival and likely, recruitment.

Table 6Mean body mass (g), sample size (n), and P -values for statistical tests^a on seven species of small mammals, western Washington stream buffer study. Postlogging = post 1 (2005) + post 2 (2006) years.

	Control			Strip buffer			Patch/no buffer			P	
	Prelogging	Postlogging	P	Prelogging	Postlogging	P	Prelogging	Postlogging	P	Prelogging	Postlogging
<i>S. trowbridgii</i>											
Female	4.6 (21)	5.0 (43)	0.09*	4.8 (30)	4.8 (40)	0.97	4.6 (41)	4.8 (63)	0.26	0.70	0.35
Male	4.7 (27)	7.8 (34)	0.24	4.5 (24)	4.7 (37)	0.49	4.5 (67)	4.7 (50)	0.11	0.97	0.58
<i>S. monticolus</i>											
Female	4.9 (20)	5.5 (21)	0.05*	5.1 (14)	5.3 (29)	0.67	5.0 (30)	5.2 (30)	0.62	0.75	0.57
Male	5.6 (24)	5.9 (22)	0.40	5.7 (36)	6.1 (27)	0.20	5.6 (43)	5.5 (51)	0.66	0.70	0.04*
<i>N. gibbsii</i> ^a											
Female	7.2 (6)	7.4 (17)	0.67	7.2 (5)	7.7 (13)	0.46	8.1 (10)	7.7 (23)	0.86	0.29	0.56
Male ^b	6.9 (6)	7.1 (12)	0.49	7.2 (5)	7.5 (9)	0.40	7.1 (11)	7.3 (11)	0.38	0.72	0.40
<i>P. keeni</i>											
Female	20.4 (34)	19.6 (52)	0.16	19.5 (19)	20.1 (36)	0.36	19.4 (34)	19.8 (38)	0.64	0.25	0.51
Male	19.4 (59)	19.7 (126)	0.69	19.6 (59)	19.4 (76)	0.68	19.4 (73)	20.2 (56)	0.05*	0.85	0.10*
<i>P. maniculatus</i>											
Female	19.2 (3)	0	–	19.3 (3)	17.1 (14)	0.19	0	19.3 (23)	–	0.90	0.02*
Male	17.0 (1)	19.6 (7)	0.38	19.2 (3)	18.4 (12)	0.61	17.8 (4)	17.4 (34)	0.61	0.48	0.06*
<i>M. gapperi</i>											
Female	19.9 (7)	17.0 (4)	0.06*	18.6 (5)	17.2 (14)	0.55	19.8 (20)	17.5 (12)	0.37	0.85	0.98
Male ^b	21.5 (12)	19.8 (2)	0.53	21.5 (2)	18.7 (18)	0.29	19.7 (20)	17.1 (23)	0.03*	0.47	0.25
<i>M. oregoni</i>											
Female	19.0 (1)	11.0 (1)	–	14.6 (3)	15.2 (9)	0.72	14.6 (6)	15.0 (40)	0.76	0.35	0.36
Male	0	0	–	16.4 (4)	13.4 (9)	0.28	15.3 (11)	14.8 (48)	0.40	0.36	0.14

^a Here data from 2002 pilot study (prelogging columns) and 2004 harvest year (postlogging columns) were added to increase sample sizes.^b ANOVA and/or t -tests; all others: Kruskal–Wallis and/or Mann–Whitney U -tests.* $P \leq 0.010$.

In the nearby lowland Puget Trough, *S. monticolus* breeding occurs before May (Lee, 1995), which would allow for birthing and dispersal of young prior to acute trapping losses (note: the total survival rate for the 3-yr period among captures of *S. monticolus* and *S. trowbridgii* was 20%, but the survival percentages improved in time: 17, 21, and 24%, in pre, post 1 and post 2, respectively; $\chi^2 = 5.661$, $P = 0.06$). Collectively, a number of factors may account for the declines of *S. monticolus*: the “naturally lower” percentage of females we observed in prelogging (whose postlogging percentage increase may have ameliorated further losses); a naturally low birth and survival rate; logging induced landscape alteration on factors such as dispersal, microclimate, food availability, interspecies competition, and predation; a general dependence upon riparian habitat converted to possibly marginal refugia inducing further stress; and the apparent additive capture removals across the study during breeding. *S. trowbridgii* showed similar negative trends to *S. monticolus* and significantly declined in the patch buffers in this study. West (2000) observed nonsignificant declines of *S. trowbridgii* in riparian buffers and uplands along third-order fishbearing streams. This species probably produces >1 litter annually but has a short reproductive period (Verts and Carraway, 1998) that ended about the time our trapping initiated each year. This timing may account for higher percentages of juveniles in postlogging than *S. monticolus*.

5.4. Water shrews

In this region, *S. bendirii* occurs mostly below 650 m (West, 2000; Lehmkuhl et al., 2008; Pacific Water Shrew Recovery Team, 2009) and *S. palustris* occurs mainly >800 m (Conaway, 1952; West, 2000). Our trapping occurred <400 m elevation, yet overall (2002–2006) we captured 62% *S. bendirii* and 38% *S. palustris* with no clear elevation gaps in their distribution. The species are sympatric along Coast Range headwater streams. Our samples were small, but in general, *S. palustris* responded poorly to treatments (Supplement).

5.5. Further considerations

This experiment was driven by factors we could not control, including assignment of sites and treatments, timing of logging (which precluded a scheduled second year of presampling), and oversight of buffer creation. All were influenced by economics and logistics. Narrow buffers like ours inherently have greater variability in effect sizes (Marczak et al., 2010) and the failure to show effects in some cases may reflect sample size or conservative testing of \hat{N} (or the failure of data fitting to models). We believe that factors such as weather that can influence animal activity and capture variation (Corn et al., 1988; MacCracken, 2002) was dampened by summer trapping and the generally even distribution of capture effort. We were unable to create a matching set of capture arrays in adjacent uplands which might have better distinguished which buffers were more productive source habitats or dispersal sinks. Windfall was an important proximate influence on buffer function because it created structural diversity under dynamic change which has been correlated with (but may not be causal) animal abundance (Carey and Harrington, 2001). The postlogging change in total captures in the small mammal community were correlated with several measures of habitat change, which suggests that our \hat{N} of individual species may be reasonable regarding short-term treatment effects; and despite the relative close proximity of some control streams to treatment clearcuts, controls were statistically unchanged in post 1 compared to pretreatment on habitat measures we recorded. Lastly, we caught low numbers of *M. longicaudus*, a riparian associate in western Washington (Anthony et al., 2003) during a year of peak abundance (2006; Sullivan, T.P.,

personal communication), which added to species richness in the patch and no buffers.

6. Conclusion

In the Coast Range, headwater stream alternative buffers were ineffective in retaining the habitat and relative abundance of individual small mammal species in the first two years after creation. Buffer persistence was low. Canopy forest habitat in buffers and small mammal community connectivity to source habitat was absent (clearcuts), isolated (patch buffers), or unidimensional (strip buffers). Minimally, patch buffers need to be connected to remove barriers to dispersal from intervening clearcuts. The postlogging change in total mammals captured, species richness, evenness and diversity in treatments was not significantly different from controls after logging, but the percentage similarity to controls of small mammal species composition declined in the no buffer treatment. Control streams maintained faunal biodiversity but abundance of about half of the species changed following treatment.

Effect sizes associated with buffers <20 m width (the size of this study) are more variable than effect sizes of buffers >50 m and demonstrates a broad insufficiency in maintaining communities in the short-term at levels compared to undisturbed areas (Marczak et al., 2010). The clearcut-forest interface can penetrate up to 40 m into buffers (Brosofske et al., 1997; Harper and MacDonald, 2001) suggesting that our treatments were ecologically breached in the buffer design stage and, one control stream – in the implementation stage (illegally overcut by loggers). Although buffers are intended to be stopgap devices that provide habitat especially in the first two decades before the adjacent forest develops canopy (West, 2000), immediate effects of forest management practices produce imbalanced mammal communities (Carey, 2003, this study). Ultimately, the fundamental measure of a successful riparian buffer design is the persistence of whole communities between the time of logging and canopy closure (West, 2000), without species extirpations. If the management goal is the maintenance of communities observed in undisturbed forest, these considerations, along with the low rate of buffer persistence along headwater streams will require site-specific data (Brosofske et al., 1997; Lee et al., 2004) and an assimilation of the regional research on small stream buffers by forest managers. Factors such as landform, stream orientation, weather, and floral and faunal communities must be included in logging unit planning along headwater streams, because short-term response to buffers by small mammals strongly differs between species and in community composition (Marczak et al., 2010; this study). For example, headwater strip buffers show more wind damage when oriented crosswind than windward (Grizzel and Wolff, 1998), and aggregated retention buffers (patches) of 1 ha, much larger than the patches in our study, appear to be sufficiently large in the short-term for persistence of upland forest-dependent species (Heithecker and Halpern, 2007). Additionally, strip buffers of widths defined by the transition from riparian to upland vegetation or topographic slope breaks may mitigate the impacts of upslope thinning on microclimate above headwater streams (Anderson et al., 2007), and for certain sensitive species, incorporation of upland with riparian forest may be required for adequate conservation function (Semlitsch and Bodie, 2003). A recent vision for “linkage areas” to retain forested ridgelines above headwater streams for species dispersal and habitat connectivity (Olson and Burnett, 2009) would benefit small ground-dwelling mammals.

Acknowledgements

R. Bigley (DNR) coordinated the implementation of the study and partially funded the 2002 pilot study. A.S. Anderson and J.A.

Reed for two field seasons. Others include G. Becker, B. Belanger, S. Crow, M.H. Dennis, M.C. Doyle, K. Gridley, C. Heimborg, J. Heimborg, S. Hull, A. Hyduke, B.T. Kavanagh, S.M. Leach, A. Pauley-Cawley, K.R. Randall, N.C. Rice, W. Scarlett and L.K. Storm. Also H. Shelan-Cole, A.D. Foster, K.I. Wilk, C.L. Sato, Anderson, and S.M. Wilson conducted lab mammal identification. J Baldwin assisted with some statistics. L.G. Sullivan did initial technical editing and P.A. Bison wrote part of the introduction. We thank two anonymous reviewers. Reverence to the beings given to the study; and for the remembrance of Cyggy, Leela, Toby, Swanny, F.H. Jackson and B.A. Howard (RJW).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.08.005.

References

- Anderson, P.D., Larson, D.J., Chan, S.S., 2007. Riparian buffer and density management influences on microclimate of young headwater forests of western Oregon. *For. Sci.* 53, 254–269.
- Anthony, N., Ribic, C.A., Bautz, R., Garland Jr., T., 2005. Comparative effectiveness of Longworth and Sherman live traps. *Wildl. Soc. Bull.* 33, 1018–1026.
- Anthony, R.G., O'Connell, M.A., Pollock, M.M., Hallett, J.G., 2003. Associations of mammals with riparian ecosystems in Pacific Northwest forests. In: Zabel, C.J., Anthony, R.G. (Eds.), *Mammal Community Dynamics Management and Conservation in the Coniferous Forests of Western North America*. Cambridge University Press, Cambridge, United Kingdom, pp. 510–563.
- Brososke, K.D., Chen, J., Naiman, R.J., Franklin, J.F., 1997. Harvesting effects on microclimate gradients from small streams to uplands in western Washington. *Ecol. Appl.* 7, 1188–1200.
- Carey, A.B., 2003. Biocomplexity and restoration of biodiversity in temperate coniferous forest: inducing spatial heterogeneity with variable-density thinning. *Forestry* 76, 127–136.
- Carey, A.B., Harrington, C.A., 2001. Small mammals in young forests: implications for management for sustainability. *For. Ecol. Manage.* 154, 289–309.
- Carey, A.B., Johnson, M.L., 1995. Small mammals in managed, naturally young, and old-growth forests. *Ecol. Appl.* 5, 336–352.
- Carraway, L.N., 1995. A Key to Recent Soricidae of the western United States and Canada based Primarily on Dentaries. Occasional Paper 175, Natural History Museum, Lawrence, KS, USA.
- Cockle, K.L., Richardson, J.S., 2003. Do riparian buffer strips mitigate the impacts of clearcutting on small mammals? *Biol. Conserv.* 113, 133–140.
- Conaway, C.H., 1952. Life history of the water shrew (*Sorex palustris navigator*). *Am. Midl. Nat.* 48, 219–248.
- Corn, P.S., Bury, R.B., Spies, T.A., 1988. Douglas-fir forests in the Cascade Mountains of Oregon and Washington: is the abundance of small mammals related to stand age and moisture? In: Szaro, R.C., Severson, K.E., Patton, D.R. (Eds.), *Management of Amphibians, Reptiles and Small Mammals*. Gen. Tech. Rep. RM-166. USDA Forest Service, Fort Collins, CO, USA, pp. 340–352.
- Craig, V.J., 1995. Relationships between shrews (*Sorex* spp.) and downed wood in the Vancouver watersheds, B.C. M.Sc. Thesis. University of BC, Vancouver, Canada.
- Forest Ecosystem Management Assessment Team (FEMAT), 1993. *Forest Ecosystem Management: An Ecological, Economic and Social Assessment*. U.S. Department of Agriculture, U.S. Department of the Interior, U.S. Department of Commerce, Environmental Protection Agency, Portland, OR, USA.
- Franklin, J.F., Dyrness, C.T., 1988. *Natural Vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, OR, USA.
- Frazer, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap light analyzer (GLA): imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs. Users Manual and Program Documentation, Version 2.0. Simon Fraser University, Burnaby, BC, Canada and the Institute of Ecosystem Studies, Millbrook, New York, USA.
- Gitzen, R.A., 2006. Responses of small mammals to green-tree retention harvests in forests of western Oregon and Washington. Ph.D. Dissertation. University of Washington, Seattle, USA.
- Gitzen, R.A., West, S.D., 2002. Small mammal response to experimental canopy gaps in the southern Washington Cascades. *For. Ecol. Manage.* 168, 187–199.
- Gitzen, R.A., West, S.D., Maquire, C.C., Manning, T., Halpern, C.B., 2007. Response of terrestrial small mammals to varying amounts and patterns of green-tree retention in Pacific Northwest forests. *For. Ecol. Manage.* 251, 142–155.
- Grizzell, J.D., Wolff, N., 1998. Occurrence of windthrow in forest buffer strips and its effect on small streams in northwest Washington. *Northwest Sci.* 72, 214–223.
- Hallett, J.G., O'Connell, M.A., Maguire, C.C., 2003. Ecological relationships of terrestrial small mammals in western coniferous forests. In: Zabel, C.J., Anthony, R.G. (Eds.), *Mammal Community Dynamics Management and Conservation in the Coniferous Forests of Western North America*. Cambridge University Press, Cambridge, United Kingdom, pp. 120–156.
- Hammer, Ø.H., Harper, D.A.T., Ryan, P.D., 2001. PAST: Palaeontological Statistics Software Package for Education and Data Analysis. *Palaeontol. Electron.* 4, 1–9 (vers. 1.81, <http://folk.uio.no/ohammer/past>, 25 April 2008 manual), 88 pp.
- Harper, K.A., MacDonald, S.E., 2001. Structure and composition of riparian boreal forest: new methods for analyzing edge influence. *Ecology* 82, 649–659.
- Heithacker, T.D., Halpern, C.B., 2007. Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. *For. Ecol. Manage.* 248, 163–171.
- Hopkins, H.L., Kennedy, M.L., 2004. An assessment of indices of relative and absolute abundance for monitoring populations of small mammals. *Wildl. Soc. Bull.* 32, 1289–1296.
- Kelsey, K., West, S.D., 1998. Riparian wildlife. In: Naiman, R., Bilbey, R.E. (Eds.), *River Ecology and Management: Lessons for the Pacific Coastal Region*. Springer-Verlag, New York, USA, pp. 235–258.
- Kroeger, M.R., 2006. Identifying Western Washington deer mouse species (*Peromyscus maniculatus* and *Peromyscus keeni*) using molecular techniques and improved morphological analysis. M.Sc. Thesis. University of Washington, Seattle, USA.
- Lawlor, T.E., 2003. Faunal composition and distribution of mammals in western coniferous forests. In: Zabel, C.J., Anthony, R.G. (Eds.), *Mammal Community Dynamics Management and Conservation in the Coniferous Forests of Western North America*. Cambridge University Press, Cambridge, United Kingdom, pp. 41–80.
- Lee, P., Smyth, C., Boutin, S., 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. *J. Environ. Manage.* 70, 165–180.
- Lee, S.D., 1995. Comparison of population characteristics of three species of shrews and the shrew-mole in habitats with different amounts of coarse woody debris. *Acta Theriol.* 40, 415–424.
- Lehmkuhl, J.F., Peffer, R.A., O'Connell, M.A., 2008. Riparian and upland small mammals on the east slope of the Cascade Range, Washington. *Northwest Sci.* 82, 94–107.
- Lomolino, M.V., Perault, D.R., 2007. Body size variation of mammals in a fragmented temperate rainforest. *Conserv. Biol.* 21, 1059–1069.
- MacCracken, J.G., 2002. Response of forest floor vertebrates to riparian hardwood conversion along the Bear River, southwest Washington. *For. Sci.* 48, 299–308.
- MacDonald, L.H., Coe, D., 2007. Influence of headwater streams on downstream reaches of forested areas. *For. Sci.* 53, 148–168.
- Magurran, A.E., 1988. *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, NJ, USA.
- Marczak, L.B., Sakamaki, T., Turvey, S.L., Deguise, I., Wood, S.L.R., Richardson, J.S., 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. *Ecol. Appl.* 20, 126–134.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, OR, USA.
- Merritt, J.K., 1981. *Clethrionomys gapperi*. *Mammal. Species No.* 146.
- Mills, L.S., Schwartz, M.K., Tallmon, D.A., Lair, K.P., 2003. Measuring and interpreting connectivity for mammals in Coniferous Forests. In: Zabel, C.J., Anthony, R.G. (Eds.), *Mammal Community Dynamics Management and Conservation in the Coniferous Forests of Western North America*. Cambridge University Press, Cambridge, United Kingdom, pp. 587–613.
- Nagorsen, D.W., Panter, N., 2009. Identification and status of the Olympic shrew (*Sorex rohweri*) in British Columbia. *Northwest Nat.* 90, 117–129.
- Naiman, R.J., Decamps, H., Pollock, M., 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecol. Appl.* 3, 209–212.
- Nordyke, K.A., Buskirk, S.W., 1991. Southern red-backed vole, *Clethrionomys gapperi*, populations in relation to stand succession and old-growth character in the central Rocky Mountains. *Can. Field-Nat.* 105, 153–175.
- Olson, D.H., Burnett, K.M., 2009. Design and management of linkage areas across headwater drainages to conserve biodiversity in forest ecosystems. *For. Ecol. Manage.* 258, 117–126.
- Otis, D.L., Burnham, K.P., White, G.C., Anderson, D.R., 1978. Statistical inference from capture data on closed animal populations. *Wildl. Monogr.*, 62.
- Pacific Water Shrew Recovery Team, 2009. *Recovery Strategy for the Pacific Water Shrew (*Sorex bendirii*) in British Columbia*. Ministry of Environment, Victoria, BC, Canada.
- Pulfer, T.L., 2007. Habitat selection by the red-backed vole (*Myodes gapperi*) in the Boreal Forest of Northern Ontario. M.Sc. Thesis. University of Guelph, Ontario, Canada.
- Rausch, R.L., Feagin, J.E., Rausch, V.R., 2007. *Sorex rohweri* sp. Nov. (Mammalia, Soricidae) from northwestern North America. *Mammal. Biol.* 72, 93–105.
- Richardson, J.S., Danehy, R.J., 2007. A synthesis of the ecology of headwater streams and their riparian zones in temperate forest. *For. Sci.* 53, 131–147.
- Richardson, J.S., Thompson, R.M., 2009. Setting conservation targets for freshwater ecosystems in forested catchments. In: Villard, M.-A., Jonsson, B.-G. (Eds.), *Setting Conservation Targets for Managed Forest Landscapes*. Cambridge University Press, Cambridge, United Kingdom, pp. 244–263.
- Richardson, J.S., Naiman, R.J., Swanson, F.J., Hibbs, D.E., 2005. Riparian communities associated with Pacific Northwest headwater streams: assemblages, processes, and uniqueness. *J. Am. Water Resour. Assoc.* 41, 935–947.
- Semlitsch, R.D., Bodie, J.R., 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Biol. Conserv.* 17, 1219–1228.
- Spies, T.A., Hibbs, D.E., Ohmann, J.L., Reeves, G.H., Pabst, R.J., Swanson, F.J., Whitlock, C., Jones, J.A., Wemple, B.C., Parendes, L.A., Schrader, B.A., 2002. The ecological basis of forest ecosystem management in the Oregon Coast Range. In: Hobbs, S.D., et al. (Eds.), *Forest and Stream Management in the Oregon Coast Range*. Oregon State University Press, Corvallis, OR, USA, pp. 31–61.

- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., 2008. Influence of variable retention harvests on forest ecosystems: plant and mammal responses up to 8 years postlogging. *For. Ecol. Manage.* 254, 239–254.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., Ransome, D.B., 2009. Stand structure and the abundance and diversity of plants and small mammals in natural and intensively managed forests. *For. Ecol. Manage.* 254, 239–254.
- Thompson, R.L., Chambers, C.L., McComb, B.C., 2009. Home ranges and habitat of western red-backed voles in the Oregon Cascades. *Northwest Sci.* 83, 46–56.
- Van Horne, B., 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* 47, 893–901.
- Van Zyll de Jong, C.G., 1983. Handbook of Canadian Mammals 1 Marsupials and Insectivores. National Museum of Natural Sciences, Ottawa, Canada.
- Verts, B.J., Carraway, L.N., 1998. Land Mammals of Oregon. University of California Press, Berkeley, USA.
- Waddell, K.L., 2002. Sampling coarse woody debris for multiple attributes in extensive resource inventories. *Ecol. Indic.* 1, 139–153.
- Waldien, D.L., 2005. Population and behavioral responses of small mammals to silvicultural and downed wood treatments in the Oregon coast range. Ph.D. Dissertation. Oregon State University, Corvallis, OR, USA.
- West, S.D., 2000. West-side small mammal surveys. In: Effectiveness of Riparian Management Zones in Providing Habitat for Wildlife. Washington Timber Fish & Wildlife Report TFW-LWAG1-00-001. Washington Department of Fish and Wildlife, Olympia, WA, USA, pp. 1–60.
- White, G.C., Anderson, D.R., Burnham, K.P., Otis, D.L., 1982. Capture–Recapture and Removal Methods for Sampling Closed Populations. Los Alamos National Laboratory Report LA-8787-NERP, NM, USA.
- Williams, D.F., Braun, S.E., 1983. Comparison of pitfall and conventional traps for sampling small mammal populations. *J. Wildl. Manage.* 47, 841–845.
- Zwolak, R., 2009. A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. *For. Ecol. Manage.* 258, 539–545.