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Response of terrestrial small mammals to varying amounts and patterns of green-tree retention in Pacific Northwest forests

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Abstract

To sustain native species in managed forests, landowners need silvicultural strategies that retain habitat elements often eliminated during traditional harvests such as clearcut logging. One alternative is green-tree or variable retention. We investigated the response of terrestrial small mammals to experimental harvests that retained large live trees in varying amounts (approximately 100, 75, 40, and 15% of original basal area) and patterns (aggregated versus dispersed) in mature coniferous forests of western Oregon and Washington. Treatments were applied in 36, 13-ha experimental units. We used pitfall traps to sample small mammals for 4 weeks each autumn during 2 years before and 2 years after treatments. We captured 21,351 individuals of 32 species. We analyzed effects of treatments on relative abundance of 12 species. As level of retention declined, we expected species associated with closed-canopy forests to decrease (*Sorex trowbridgii*, *Neurotrichus gibbsii*, *Peromyscus keeni*, *Myodes* [*Clethrionomys*] *californicus*, and *M. gapperi*); species associated with early successional habitats to increase (*S. vagrans*, *P. maniculatus*, *Microtus longicaudus*, and *Microtus oregoni*); and habitat generalists to show little response (*S. monticolus*, *S. pacificus*, and *S. sonomae*). As expected, *M. californicus* declined after harvest, and *P. maniculatus* and *M. longicaudus* increased. *Sorex sonomae* showed an unpredicted decrease. Other species did not show consistent changes. Responses of *S. monticolus*, *S. sonomae*, and *M. gapperi* varied among study areas. For *M. gapperi*, this variation was not explained by differences in habitat structure among areas. For all species, capture rates were similar in dispersed- and aggregated-retention units. Similarity in species composition between harvested sites and controls decreased with decreasing retention. Future sampling of these treatments is needed to assess long-term responses. Based on our initial results, green-tree retention strategies need to be sensitive to regional variation in environmental characteristics and small mammal community composition.

Keywords: Structural retention; Timber harvest; Shrews; Rodents; Forest management

1. Introduction

Forest managers worldwide seek to sustain native species while extracting timber. In many temperate and boreal regions, managers have adopted green-tree retention (Franklin et al., 1997) as an alternative to clearcut logging. Retention of large live trees in small aggregates or dispersed across a harvest unit may help sustain larger populations of forest species than would occur after clearcut harvesting. Green-tree retention may enable breeding populations of closed-canopy species to persist during the period between harvest and subsequent canopy closure. If so, green-tree retention would greatly increase connectivity of local populations for species with low dispersal ability (Matveinen-Huju et al., 2006). Compared to even-aged management, green-tree retention also may increase structural complexity and functional diversity of regenerating forests (Franklin et al., 2002). In time, these forests may support larger populations of mature-forest species and a more diverse fauna, thereby enhancing the ability of "working forests" to sustain native species (Carey et al., 1999; Lindenmayer et al., 2006). Studies from many forest ecosystems are testing these hypotheses (Sullivan et al., 2001; Vanha-Majamaa and Jalonen, 2001; Koivula, 2002; Hyvärinen et al., 2005; Vergara and Schlatter, 2006).

Because of these potential ecological benefits, green-tree retention is now required in harvest units on U.S. federal lands

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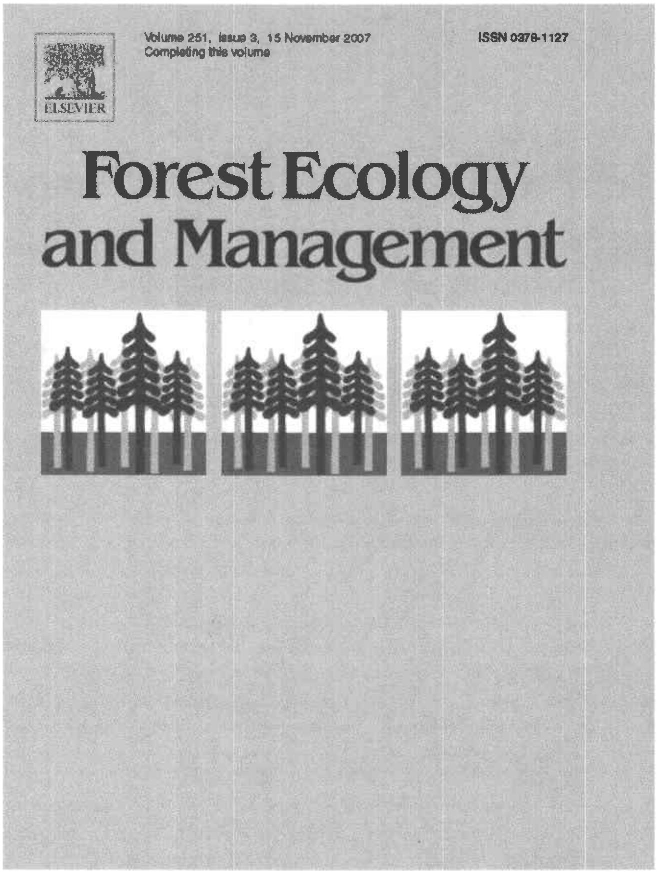
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within the range of the Northern Spotted Owl (western Oregon and Washington, and northern California; USDA and USDI, 1994a). In the Pacific Northwest, researchers and forest managers collaborated to design the Demonstration of Ecosystem Management Options (DEMO) experiment to examine effects of retention amount (proportion of original basal area; 15–100%) and spatial distribution (aggregated or dispersed) on persistence and recovery of forest organisms (Aubry et al., 1999; Franklin et al., 1999). In this paper, we examine effects of DEMO treatments on insectivores and small rodents.

In Pacific Northwest forests, numerous studies have addressed habitat associations of small mammals (e.g., Aubry et al., 1991; Carey and Johnson, 1995) and their comparative abundances in clearcuts versus mature forests (Gashwiler, 1970; Hooven and Black, 1976; Sullivan, 1980; Morrison and Anthony, 1989; Cole et al., 1998). The western Cascades and coastal ranges support a group of species most abundant in closed-canopy forests, a group most abundant in recent clearcuts and riparian areas, and generalists that can be equally abundant across successional stages (Lehmkuhl et al., 1999). As in other forest systems, small mammals of this region respond strongly to changes in the abundance of logs; litter cover and depth; density and composition of herbaceous vegetation and shrubs; and abundance of fruits, seeds, and fungal fruiting bodies (e.g., Carey and Johnson, 1995; Carey et al., 1999).

Previous studies in this region addressed responses of small mammals to partial disturbances such as thinning or shelterwood harvests (Waters and Zabel, 1998; Wilson and Carey, 2000; Suzuki and Hayes, 2003). However, few studies have explicitly examined responses across a range of harvest intensities or to different spatial patterns of overstory removal. Moreover, responses to green-tree retention may differ from responses to other partial-harvest methods, which emphasize silvicultural objectives (tree growth and regeneration). Green-tree retention emphasizes ecological objectives; i.e., managers retain large live trees to maintain forest species and habitat structure. Our study addresses these gaps in knowledge. To our knowledge, this is the first study of green-tree retention to examine effects of both retention amount and pattern on small mammals across multiple forest types and structural conditions.

We predicted that small mammal species associated with closed-canopy forests, early successional species, and habitat generalists would show different responses to retention amount and pattern in the first 2 years after harvest (Lehmkuhl et al., 1999). We anticipated that small mammals would show variable responses among our study areas due to variation in post-harvest habitat conditions. To clarify potential causes of these responses, we quantified treatment effects on key habitat elements. We addressed the following hypotheses:

Hypothesis 1. Closed-canopy species (Trowbridge's shrew, *Sorex trowbridgii*; shrew-mole, *Neurotrichus gibbsii*; Keen's mouse, *Peromyscus keeni*; western red-backed vole, *Myodes* [*Clethrionomys*] *californicus*; southern red-backed vole, *M. gapperi*) would decrease along the retention gradient (from 100 to 15% retention).

Hypothesis 2. Early successional species (vagrant shrew, *S. vagrans*; deer mouse, *P. maniculatus*; long-tailed vole, *Microtus longicaudus*; creeping vole, *Microtus oregoni*) would respond positively to lower levels of retention.

Hypothesis 3. Habitat generalists (montane shrew, *S. monticolus*; Pacific shrew, *S. pacificus*; fog shrew, *S. sonomae*) would show weak or no response to harvest.

Hypothesis 4. The magnitude of response by each species would vary among locations. This variation would be caused by among-location differences in post-harvest habitat conditions.

Hypothesis 5. Pattern of retention (aggregated versus dispersed) would not affect responses.

Hypothesis 6. Small mammal community composition would differ between intact forests (controls) and harvest treatments. Differences would be greatest at the lowest level of retention.

2. Methods

2.1. Experimental design and treatment implementation

The DEMO experiment is a randomized complete-block design with six treatments randomly assigned to six 13-ha experimental units at each of six locations (blocks; Fig. 1). Blocks are located in the southern Oregon Cascades (Watson Falls [WF] and Dog Prairie [DP]); in the southern Washington Cascades (Butte [BU], Little White Salmon [LW], and Paradise Hills [PH]); and in western Washington at the edge of the Coast Range (Capitol Forest [CF]). Before harvest, all blocks supported mature forests (age 65–170 years) dominated by Douglas-fir (*Pseudotsuga menziesii*). Elevations range from 210 to 275 m at CF to 1710 m at DP, with little snow accumulation at CF and snowpack lasting until May or early June at BU and PH. Study sites and vegetation responses to treatment are described by Aubry et al. (1999), Halpern et al. (1999, 2005), Halpern and McKenzie (2001), and Maguire et al. (2006, 2007).

Treatments include four levels of basal-area retention and two retention patterns. These treatments are (1) control (100% retention); (2) 75% aggregated (75%A), with three, 1-ha circular gaps; (3) 40% dispersed (40%D); (4) 40% aggregated (40%A), with five, 1-ha circular aggregates; (5) 15% dispersed (15%D); (6) 15% aggregated (15%A), with two, 1-ha aggregates (Fig. 1). In aggregated-retention treatments, all trees were retained within aggregates; trees >18-cm DBH were removed from harvest areas. In 40%D and 15%D, dominant and co-dominant trees were retained evenly across harvest units. Harvests were completed in autumn 1997 (BU and PH), spring 1998 (CF), or autumn 1998 (WF, DP, and LW). Logs were yarded with helicopters (DP, BU, and LW), suspension cables (CF), or ground-based equipment (WF, PH, and small sections of CF; Halpern and McKenzie, 2001). At four of six blocks, boles were yarded with tree canopies attached to reduce slash accumulation. At WF, some slash was piled on skid paths and burned.

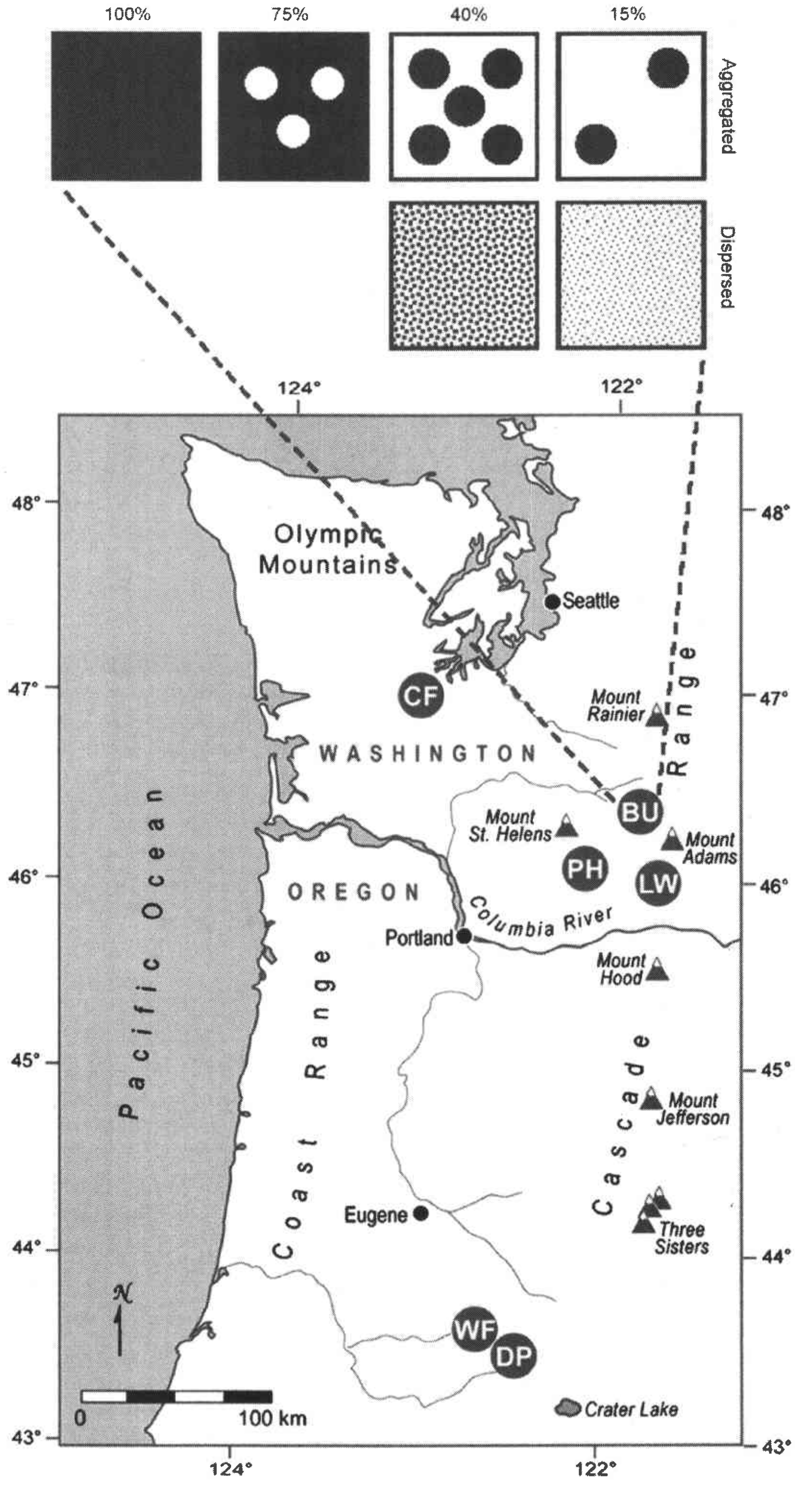

Fig. 1. Location of the six DEMO study blocks and a diagram of the six experimental treatments. In the latter, dark gray areas represent uncut forest (100 and 75% aggregated) or 1-ha forest aggregates (40 and 15% aggregated). Stippled areas represent dispersed retention (40 and 15% dispersed). Block codes from north to south are CF = Capitol Forest, BU = Butte, PH = Paradise Hills, LW = Little White Salmon, WF = Watson Falls, and DP = Dog Prairie. Figure is modified from Halpern et al. (2005), Copyright (2005), with permission from the Ecological Society of America. Schematic is reprinted from Halpern and McKenzie (2001), Copyright (2001), with permission from Elsevier.

2.2. Field and laboratory methods

To sample small mammals, we used an 8×8 or 7×9 permanent, ~8-ha grid in each 13-ha experimental unit. Grid points were 40-m apart. Each grid was surrounded by a similarly treated buffer at least 40-m wide. At each point we installed a single pitfall trap (two No. 10 cans taped together to form a cylinder with diameter ~16 cm and depth ~35 cm) close to logs or other structures when possible (Corn and Bury, 1990). Traps were open continuously for ca. 28 days during autumn of each sampling year (late September to early November). We operated pitfalls as kill traps, filling them partially with water that remained at near-freezing temperatures during autumn sampling. Animals were collected weekly. Treatment units in each block were trapped nearly synchronously: all grids in a block were opened within a 5-day period each year. We sampled small mammals in each experimental unit before treatment ("Pre 2" and "Pre 1": 1995 and 1996) and after treatment ("Post 1" and "Post 2": 1998 and 1999 at BU, PH, and CF; 1999 and 2000 at WF, DP, and LW). University of Washington and Oregon State University Institutional Animal Care and Use committees approved our methods.

During dissections, we recorded species, sex, body measurements (total and tail length, mass) and reproductive data. We used dental or skull characters to identify shrews and voles. We used a tail-length threshold of 96 mm to separate adult *P. keeni* from *P. maniculatus* (Allard et al., 1987). In addition, we identified juveniles (<16 g) with undamaged tails ≤85 mm as *P. maniculatus*. Examination of tail-length histograms for blocks where only *P. keeni* was abundant indicated that most juvenile *P. keeni* were likely to have tails >85 mm by October.

Habitat variables were sampled during concurrent studies of ground conditions, understory vegetation, and forest structure (Halpern and McKenzie, 2001; Halpern et al., 2005; Maguire et al., 2007). These variables were measured at a subset of plots in the sampling grid (32–37 points per experimental unit) before and after harvest.

2.3. Data analysis

2.3.1. Habitat elements

To examine changes in habitat elements important to small mammals, we calculated average values in each experimental unit for five variables: volume ($m^3\,ha^{-1}$) of coarse woody debris (CWD); cover of slash (fine material < 10 cm in diameter originating from harvest; SLASH); cover of exposed mineral soil, including bare skid tracks (SOIL); cover of herbs and low shrubs (species with potential height <1 m; HERB); cover of tall shrubs (species with potential height >1 m; TALL SHRUB). Because residual basal area (BA) deviated somewhat from targeted levels, we used pre- and post-treatment measurements of trees (DBH ≥5 cm) to calculate the percentage of BA retained (%BA). To test for effects of %BA and pattern of retention on habitat variables, we used randomized-block ANCOVA. Pre-treatment values were included as covariates. For SLASH and SOIL, which were largely absent in uncut areas, we analyzed only 40 and 15% treatments. Cover variables were square-root transformed; CWD values were ln-transformed. We used package 'nlme' (Pinheiro and Bates, 2000) in S-PLUS 6.2 (Insightful Corp., 2003) for all linear-model analyses.

2.3.2. Relative abundance of small mammals

To maximize the relevance of this study to forest management, we used grids large enough to encompass within-stand habitat variability, and used pitfall traps because they effectively capture insectivores and small rodents. Because we could not livetrap insectivores in 36 large trap grids simultaneously, we used removal trapping. We used a wide trap spacing so that we did not deplete target populations enough to affect year-to-year population trajectories.

A drawback of this approach is that it did not conform closely to the removal model (which needs rapid depletion of populations to perform effectively; White et al., 1982:118), limiting our ability to account for heterogeneity in detectability (Anderson, 2001). However, we expected that overall detection probabilities for 4 weeks of trapping would converge to similar values among treatments, and that simultaneous trapping of units in each block would account for effects of weather on detectability (Skalski and Robson, 1992:145). For three species (*S. trowbridgii*, *P. keeni*, and *M. gapperi*), the removal model appeared sufficiently valid for us to use it to examine whether our assumptions about detectability were strongly violated. Using program MARK (Huggins and Yip, 1997; White and Burnham, 1999) we fit removal models incorporating effects of treatment, block, time, and weather on detectability. Our analyses indicated that detectability did not vary strongly among treatments for these three species, which were representative of the diverse natural histories of the small mammal assemblage we sampled. This supported our use of relative abundance (captures per 100 trap nights [TN]) to compare treatment effects on populations (Skalski and Robson, 1992). We analyzed relative abundance for five species captured in both states (*S. trowbridgii*, *S. vagrans*, *N. gibbsii*, *P. maniculatus*, and *M. oregoni*), three species captured only in Oregon (*S. pacificus*, *S. sonomae*, and *M. californicus*), and four species captured only in Washington (*S. monticolus*, *P. keeni*, *M. gapperi*, and *M. longicaudus*).

To determine small mammal responses to amount of retention (Hypotheses 1–3), we examined the relationship between capture rates and retention amount (%BA). We used a mixed-effects ANCOVA model appropriate for the randomized-block, repeated-measures design. Response variables were the two post-treatment abundance indices for each site, transformed as ln(captures per 100 TN + 0.1) to improve normality and additivity (Skalski and Robson, 1992). We used pre-treatment relative abundance as a covariate. We report significance of the treatment effect (regression coefficient $\beta_{\%BA}$, the change in transformed capture rates per percentage change in %BA) and the %BA × Time interaction. If %BA × Time was significant, we estimated $\beta_{\%BA}$ separately for each time; if it was not significant, we estimated the coefficient after refitting the model without the interaction term. Appendix A provides more details about these methods.

To examine whether effects of retention varied among blocks (Hypothesis 4), we used likelihood-ratio tests to compare models with and without a random effect modeling among-block variation in $\beta_{\%BA}$. When this among-block variation was present, we estimated block-specific regression coefficients ($\beta'_{\%BA}$). If among-block variation in the effect of %BA was explained by among-block differences in post-harvest habitat conditions, the %BA × block random effect would be unnecessary if we included relevant habitat variables. To examine this scenario, we added CWD and HERB (which was highly correlated with other vegetation variables) to models with and without this random effect, and compared these models again.

To examine effects of retention pattern on capture rates (Hypothesis 5), we conducted a second analysis limited to the two nominal retention amounts (40 and 15%) at which both dispersed and aggregated retention treatments were applied. We used the mixed-effects ANCOVA approach described above to compare dispersed with aggregated retention and to test for a Pattern × Time interaction. We estimated the contrast coefficient for the difference in ln-transformed capture rates, $\bar{x}_{\text{Dispersed}} - \bar{x}_{\text{Aggregated}}$.

Table 1
Total captures of small mammals by study block[a] during four sampling periods between 1995 and 2000

Species	Oregon		Washington				Total
	WF	DP	BU	LW	PH	CF	
Insectivora							
Sorex bendirii	1	2	7	7	7	66	90
Sorex cinereus/rohweri[b]			4	2	17	1	24
Sorex monticolus			443	102	265	283	1093
Sorex pacificus	66	57					123
Sorex palustris	0	1	1	0	1	0	3
Sorex sonomae	122	51					173
Sorex trowbridgii	764	805	1068	1159	651	2338	6785
Sorex vagrans	688	562	95	33	115	133	1626
Sorex species	3	3	22	28	12	45	113
Neurotrichus gibbsii	84	24	189	21	63	180	561
Scapanus orarius	3	3	2	9	7	21	45
Scapanus townsendii						2	2
Rodentia							
Tamias amoenus			5	0	0		5
Tamias siskiyou	10	18					28
Tamias townsendii	0	0	27	11	12	18	68
Tamias species	0	0	4	1	2	0	7
Tamiasciurus douglasii	0	0	4	4	0	3	11
Spermophilus lateralis	1	0					1
Glaucomys sabrinus	4	2	17	2	13	26	64
Thomomys mazama	45	35					80
Thomomys talpoides			1	12	10	0	23
Peromyscus keeni			870	325	214	472	1881
Peromyscus maniculatus	539	832	192	292	49	747	2651
Peromyscus species	0	0	88	91	22	151	352
Myodes californicus	744	469					1213
Myodes gapperi			1227	163	1138	279	2807
Arborimus albipes	1	0					1
Arborimus longicaudus	0	1					1
Phenacomys intermedius	6	0	12	0	42	0	60
Microtus longicaudus	0	0	36	5	7	51	99
Microtus oregoni	180	57	82	112	54	538	1023
Microtus richardsoni	2	5	3	0	2	0	12
Microtus townsendii	0	1	0	0	0	2	3
Microtus species	0	0	1	0	0	0	1
Zapus trinotatus	2	2	16	3	3	231	257
Carnivora							
Mustela erminea	7	6	14	12	8	18	65
Total	3272	2936	4430	2394	2714	5605	21351

Total trap effort was 256,896 trap nights; no value is listed for blocks outside the distributional range of each species.
[a] WF (Watson Falls), DP (Dog Prairie), BU (Butte), LW (Little White Salmon), PH (Paradise Hills), CF (Capitol Forest).
[b] Some shrews identified as *S. cinereus* may be the recently described *S. rohweri* (Rausch et al., 2007).