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Abstract

We evaluated the two-year effects of variable-retention harvest on chipmunk (*Tamias* spp.) abundance (\hat{N}) and habitat in mature coniferous forests in western Oregon and Washington because wildlife responses to density/pattern of retained trees remain largely unknown. In a randomized complete-block design, six treatments were applied to 13-ha units at three sites (blocks): four retention levels of original basal area (BA) in an aggregated tree pattern (100, 75, 40, and 15%) and two retention levels in a dispersed tree pattern (15 and 40%). Log-yarding method differed at each site (suspension cable, shovel-loader, or helicopter). We used an information-theoretic approach to compare six candidate regression models for their ability to predict treatment responses of chipmunk \hat{N} and associated habitat variables. Chipmunk \hat{N} had a positive linear relationship with retention level that predicted a 50% reduction in abundance as % BA retention decreased from 100 to 15% ($R^2 = 0.36$). Disturbed soil cover was strongly related to the interaction of retention level and block (i.e., yarding method and other site-level differences) ($R^2 = 0.82$), and the model predicted disproportionately greater disturbed area for cable yarding (16%) than for shovel (10%) or helicopter (6%) methods as retention decreased from 100 to 15%. Chipmunk \hat{N} had a negative linear relationship with disturbed soil cover that predicted a 70% reduction in the species' abundance as disturbed area increased from 0 to 16% ($R^2 = 0.53$). Retention level and yarding method are important considerations when planning harvesting operations because of their potential impacts to small mammal populations.

Keywords: coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), ecosystem management, log-yarding methods, soil disturbance, Akaike's Information Criterion (AIC)

Introduction

Since variable-retention harvesting of forests was introduced as an alternative to clear-cutting in the Pacific Northwest about 25 years ago, it has been adapted to other conditions and silvicultural systems in various regions of the world (Gustafsson et al. 2012). A primary goal of this

commercial harvesting system is to maintain, create, or restore biological diversity, ecosystem attributes and ecological processes through the manipulation of forest stand basal area (BA, the total cross-sectional area of tree stems at 1.3 m height) and tree distribution pattern (Franklin et al. 1997, Aubry et al. 2009). The Demonstration of Ecosystem Management Options (DEMO) Study was developed to answer questions about the effects of variable-retention harvesting on forest-dwelling organisms in mature coast Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*) forests west of the Cascade Mountain crest in Oregon and Washington (Halpern and Raphael 1999). Ecosystem management has been defined

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as “a strategy or plan to manage ecosystems to provide for all associated organisms, as opposed to a strategy or plan for managing individual species” (FEMAT 1993). Initial findings from DEMO suggest that many components of a functioning forest ecosystem may be better maintained by retaining a combination of large aggregates of trees (≥ 1 ha) and evenly-dispersed trees at levels considerably greater than the current minimum standard of 15% BA retention for the federally-managed forests in the region (USDA and USDI 1994, Aubry et al. 2009).

In Douglas-fir forests, ground-dwelling small mammals (primarily Orders Insectivora and Rodentia), and arboreal squirrels (Family Sciuridae) play numerous ecological roles such as facilitating dispersal of plants and ectomycorrhizal fungi (truffles and mushrooms) and germination of plant seeds, and supporting predator populations (Carey 1995, Luoma et al. 2003, Sidlar 2012). Four studies from DEMO have addressed these species groups. In a pre-treatment study, Cazares et al. (1999) showed the importance of truffle food in the diets of red-backed voles (*Myodes* spp.) and two species of squirrels. In post-treatment research, Jacobs and Luoma (2008) concluded that consumption of truffles by chipmunks (*Tamias* spp.) and red-backed voles showed little change relative to pre-treatment conditions, and speculated that shifts in foraging behaviors compensated for the declining food source. Gitzen et al. (2007) showed how treatments predictably influenced individual species of the ground-dwelling small mammal community; they surmised that regional variation in environmental characteristics and community species composition explained inconsistent responses by some species. Holloway et al. (2012) observed that pattern of retention and landscape context likely influenced the positive threshold response of northern flying squirrels (*Glaucomys sabrinus* Shaw) when BA retention was between 40 and 75%.

Without active management to retain forest legacy structure and complexity, squirrels west of the Cascade Mountain crest generally respond negatively to partial and clear-cut harvesting (Carey 2007). This makes squirrels a potentially suitable group to monitor changes in the overall

forest vertebrate community in relation to management practices (Herbers and Klenner 2007). Semi-arboreal chipmunks (i.e., species that use vertical and horizontal forest structure) may be particularly important in maintaining natural ecosystem processes in these Douglas-fir forests because their abundance and population dynamics differ across different stand age-classes (Rosenberg and Anthony 1993, Hayes et al. 1995, Carey et al. 1999). Their prevalence in older, often unmanaged forests makes their response to variable-retention harvest important to understanding management of biological diversity (Carey 1995, 2001; Carey et al. 1999).

Townsend’s (*T. townsendii* Bachman) and Siskiyou (*T. siskiyou* A. H. Howell) chipmunks occurred abundantly in some DEMO sites during pre-treatment sampling (Lehmkuhl et al. 1999); a third species, the yellow-pine chipmunk (*T. amoenus* J. A. Allen), was known to occur on the edge of the Butte study block near the Cascade Mountain crest. Their habitat associations have been variously described as mesic closed-canopy coniferous forest with structural components that vary with stand age and management history. Forest structural elements often identified as important to chipmunk populations include stratified canopy, shrub understory, snags, and wood debris (Carey 1995, Carey et al. 1999, Waldien et al. 2006). For example, in the central-western Cascades, old forests having large Douglas-fir and western hemlock trees (*Tsuga heterophylla* [Raf.] Sarg.) with well-developed heterogeneous understories of fruit- and seed-bearing shrubs and trees and diverse dietary fungi may provide important habitats for Townsend’s chipmunks (Carey 1995). In contrast, yellow-pine chipmunks seem to prefer younger, more open stands (Sutton 1992). Hence, there is uncertainty about how chipmunks in west-side forests will initially respond to variable-retention harvest. Our primary research objectives were to: (1) describe potential relationships of chipmunk abundance and habitat features to tree retention level, tree distribution pattern, and method of log yarding following variable-retention harvest, and (2) identify primary habitat features that were associated with observed responses of chipmunk abundance to the harvest treatments.

Study Areas

The DEMO Study included six sites (blocks) representing a diversity of physical environments in mature upland forest types within the Douglas-fir zone of western Oregon and Washington (Aubry et al. 2009). Sites occurred across a low to moderate elevation gradient (210 to 1700 m), on gentle to steep slopes (4 to 66%). Perennial streams, wetlands, roads, and existing harvest units were avoided (Aubry et al. 2009). In the chipmunk research, three sites were eliminated owing to the near absence of these species in pre-treatment sampling (Lehmkuhl et al. 1999). This paper focuses on three remaining sites: Capitol Forest in the Black Hills of the Coast Range, Washington Department of Natural Resources; Butte, in the Western Cascades of southern Washington, Gifford Pinchot National Forest; and Watson Falls in the Western Cascades of southern Oregon, Umpqua National Forest (Figure 1). All treatment units within each of the Capitol Forest and Butte blocks were within 2.9 km of each other and some units shared partial borders. Units in the Watson Falls block were within 15 km of each other, occurring in two spatially distinct areas denoted as Mowich Park and Tokatee Airstrip (Cazares et al. 1999). The three sites varied considerably in environmental characteristics, landscape context, and past management history. For example, the Capitol Forest block ranges in elevation from 210 to 275 m, whereas the other blocks range in elevation from 945 to 1310 m. Capitol Forest was in its second forestry rotation, Butte had not been previously harvested, and Watson Falls was salvage-harvested between 1970 and 1978 (Aubry et al. 1999). Before the harvests, study sites in the Capitol Forest block (65-year-old stands) were located within an intensively-managed landscape and the other blocks were generally adjacent to older stands (Butte: 70–80 years old; Watson Falls: 110–130 years old) (Halpern et al. 2005).

Methods

Experimental Design and Modeling Approach

Franklin et al. (1999), Halpern and Raphael (1999), and Aubry et al. (2009) detailed the history and

overview of the DEMO Study. The experimental design was a randomized complete-block with six treatments randomly assigned to 13-ha experimental units at each of the three sites ($n = 18$ experimental units). Treatment targets consisted of five retention levels (100, 75, 40, and 15% of pre-treatment BA) and two tree distribution patterns, resulting in a total of six treatments (Figure 1): (1) non-disturbed control, defined as 100% aggregated (A) BA retention, (2) 75% A retention had merchantable (> 18 cm dbh) trees removed from three 1-ha circular patches (56.4 m radius; 25% of the treatment unit), such that an average of 75% of the overall stand's BA would be retained, (3) 40% A retention had trees retained in 5 circular 1-ha aggregates, such that an average of 40% of the stand's BA would be retained, and merchantable trees in the surrounding "clear-cut" areas were removed, (4) 15% A retention had trees retained in two circular 1-ha aggregates with merchantable trees removed elsewhere, (5) 40% dispersed (D) retention, and (6) 15% D retention. Only dominant and co-dominant trees were retained in dispersed treatments, with leave trees evenly spaced throughout the units. Provisions were made during logging to retain existing snags if permitted by safety considerations, and to leave a target of 6.5 dominant and co-dominant green trees ha^{-1} for snag creation (Aubry 1999). Units were logged between May 1997 and October 1998. Because treatments were defined by target percentage reductions of BA specific to each unit replicate, variation in initial forest structure among sites influenced variation in residual structure among replicates of each treatment (Maguire et al. 2007). Prescriptions were applied uniformly among experimental units within each block to reduce extraneous sources of variation (Halpern and McKenzie 2001).

Owing to variable terrain, methods for log yarding (i.e., transporting of logs to landings) and treating slash differed among the three blocks (Halpern and McKenzie 2001). In the steep terrain of Capitol Forest and Butte (28–53% slope), suspension cables and helicopters were used to yard logs, respectively; and in the gentle terrain of Watson Falls (4–7% slope) tracked shovel-loaders were used. Three to 9% of the area at

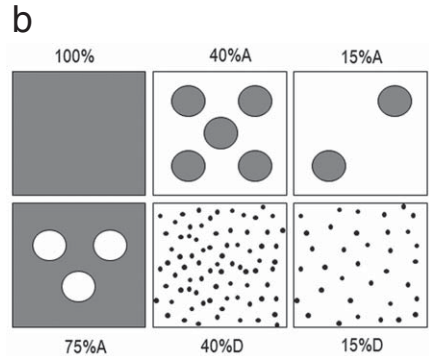


Figure 1. Location (a) and treatment type (b) of the three DEMO study blocks in Washington and Oregon. Study block locations from north to south are indicated by circles; CF = Capitol Forest, BU = Butte, and WF = Watson Falls. Schematic depictions of the six harvest treatments (13-ha units) that occurred in each block are demonstrated using the following patterns: gray-shaded areas represent uncut forest (100 and 75% aggregated [A]) or 1-ha forest aggregates (40% A and 15% A). Stippled areas represent dispersed retention (D) (40% D and 15% D).

Capitol Forest was also yarded by shovel-loader. Additional details are in Halpern and McKenzie (2001).

To address the first research objective, we compared six regression models for their ability to predict responses of chipmunk abundance and associated habitat variables to the experimental treatments (Table 1). Models 1–4 included parameters for estimating the additive effects of each replicate site (block) and potential linear effects of retention level. Model 1 included additional parameters for estimating the effects of tree distribution pattern and its interaction with linear effects of retention level. Model 3 included a parameter for testing potential quadratic effects of retention level. Initial analyses of the data sug-

gested that chipmunk responses to retention level could vary with log-yarding method. Therefore, models 5 and 6 tested for potential interactions between linear effects of retention level and log-yarding method. We addressed the second research objective by comparing regression models of chipmunk abundance to individual habitat element variables to identify those with the best ability to predict treatment responses, and we discuss their biological relevance as they pertain to aspects of the life history of chipmunks.

Chipmunk Sampling

Trapping methods followed Carey et al. (1991). We sampled each experimental unit with 8 x 8 or 9 x 7 grid arrays with one Tomahawk 201

TABLE 1. Description of the six linear regression models that were compared for their ability to describe responses of chipmunk abundance and associated habitat variables to retention level, pattern, and yarding method.

Model	Equation	K	Description
1	$Y = b_{0C} + b_{0H} + b_{0S} + b_1 Ret + b_2 Pat + b_3 Ret * Pat$	7	<u>DEMO experimental design</u> : includes intercepts for each yarding method (i.e., block) and parameters for linear effects of retention level, additive effects of pattern, and linear effects of the interaction of retention level and pattern.
2	$Y = b_{0C} + b_{0H} + b_{0S} + b_1 Ret$	5	<u>Linear model</u> : includes intercepts for each yarding method and a parameter for linear effects of retention level.
3	$Y = b_{0C} + b_{0H} + b_{0S} + b_1 Ret + b_4 Ret^2$	6	<u>Quadratic model</u> : includes intercepts for each yarding method and parameters for linear and quadratic effects of retention level.
4	$Y = b_0 + b_1 Ret$	3	<u>Linear model, reduced</u> : includes a single intercept and a parameter for linear effects of retention level.
5	$Y = b_{0C} + b_{0H} + b_{0S} + b_{1C} Ret + b_{1H} Ret + b_{1S} Ret$	7	<u>Multiplicative model</u> : includes intercepts for each yarding method and parameters for linear effects of the interaction of yarding method and retention level.
6	$Y = b_0 + b_{1C} Ret + b_{1H} Ret + b_{1S} Ret$	5	<u>Multiplicative model, reduced</u> : includes a single intercept and parameters for linear effects of the interaction of yarding method and retention level.

Symbol definitions: K is the number of estimable parameters; Y is the dependent variable (i.e., chipmunk abundance or habitat variable); b_{0C} , b_{0H} , and b_{0S} are intercept coefficients for cable, helicopter, and shovel yarding methods, respectively; b_0 is the intercept coefficient for absence of yarding method effects; b_1 is the slope coefficient for linear effects of retention level (Ret); b_2 is the coefficient for additive effects of pattern (Pat); b_3 is the slope coefficient for the interaction of retention level and pattern; b_4 is the slope coefficient for quadratic effects of retention level (Ret^2); and b_{1C} , b_{1H} and b_{1S} are regression slope coefficients for the interaction of retention level and cable, helicopter, and shovel yarding methods, respectively.

live trap per station at 40 m spacing between stations, covering entire units. In pre-treatment sampling, we alternated trap placement between the ground and a tree bole at a height of ~1.5 m on the nearest large tree. Because of large treeless areas in some units of the aggregated retentions after treatment, we placed all traps on the ground during post-treatment sampling. Although trap placement strategies varied, it is unlikely that their placement differentially biased capture rates within or among blocks because chipmunks have active semi-arboreal life history behaviors, using the ground and trees for foraging, hiding, food caching, nesting, and other purposes. We baited traps with a mixture of peanut butter, rolled oats and molasses, and provided synthetic cotton insulation in nest boxes inside traps. We uniquely marked captured chipmunks with numbered ear tags in addition to recording weight, gender, and reproductive status data.

We sampled Capitol Forest and Butte over two pre-treatment (1995–1996) and two post-treatment years (1998–1999). The 75% A treatment was not sampled in 1995 in both blocks. At Watson Falls, thorough pre-treatment sampling occurred only in 1996 and the two post-treatment years were 1999 and 2000. Sampling occurred after chipmunk breeding had largely ended each year. We trapped for four consecutive 24-h periods each week for two weeks (8 trap-nights [TN]) checking traps daily (trapping bout 1), then suspended trapping for two weeks; we followed this sequence by repeating the 2-week trapping schedule (8 TN, bout 2). This scheme resulted in 16 TN at each trapping station. We initiated trapping between mid- and late September in bout 1, and between mid- and late October in bout 2.

Aspects of the life histories of the Townsend's and Siskiyou chipmunk species are similar. For example, the two species have similar food habits

and diet (Lehmkuhl et al. 1999, Jacobs and Luoma 2008). Therefore, we combined the species into one region-wide analysis. At Butte, there was potential co-occurrence (sympatry) of two chipmunk species—Townsend’s chipmunks and yellow-pine chipmunks. Our methods for handling and caring for captured animals were approved in advance by the Institutional Animal Care and Use Committees of the University of Washington and Oregon State University (see ASM Animal Care and Use Committee 1998).

We estimated chipmunk capture probabilities and maximum likelihood to estimate chipmunk abundance (Williams et al. 2002) for each treatment unit in each year using the whole-unit size (\hat{N} chipmunks 13 ha^{-1}) (Herbers and Klenner 2007). Then we averaged the pre-treatment years and averaged the post-treatment years for each block. We included all ages and sexes, and few individuals were identified as young. We used the Chapman modification of the Lincoln-Petersen estimator for capture-recapture studies to estimate abundance (Williams et al. 2002). Computation of \hat{N} involves the combining of first-marked individual captures from trapping bout 1 with the new captures and recaptures from trapping bout 2, with each counted only once (i.e., without replacement). We added the small number of deaths that occurred in the initial bout (< 10% of all unit-bout-year computations, and mostly involving only one individual) to the abundance estimate ($\hat{N} + \text{deaths}_{n1}$), which adjusted for potential violation of the model population closure assumption (Williams et al. 2002). We assumed that the distribution of population estimates were approximately normal, no significant immigration had occurred and no births had occurred owing to the late-year sampling. Although some post-treatment units had small numbers of chipmunk recaptures, the estimator is less biased and preferred relative to enumeration procedures such as the minimum number known to be alive (Krebs 1999).

Habitat Measurements

Descriptions of experimental units, design layout and sampling of understory vegetation, forest structure, and forest floor conditions (i.e., habitat variables) are detailed in Halpern and Raphael

(1999) and Halpern and McKenzie (2001). We selected 12 habitat variables from a host of variables collected in the DEMO studies because the study plan, scientific literature and expert opinion suggested they had relevance to chipmunks. Some of the selected variables are similar and known to be correlated. In addition to BA, other variables that inherently influenced chipmunk abundance through intentional manipulation of treatments included overstory canopy cover (%), tree density and tree quadratic mean diameter (QMD). Variables that were indirectly influenced by logging operations were disturbed soil cover (%), skid track cover (%), coarse woody debris (CWD) volume ($\geq 10 \text{ cm}$, line-intersect method of Brown [1974]), herb/low shrub cover (%) (potential height < 1 m), tall shrub cover (%) (potential height > 1 m), snag density, and snag average dbh. Disturbed soil cover was defined as the percentage cover of areas (other than skid tracks) where mineral soil had been exposed or deposited (Halpern and McKenzie 2001). A composite variable, wood debris cover (%), was calculated by summing the percentages of slash cover (< 10 cm dia. from logging) and small log cover ($\geq 10 \text{ cm}$ dia. from logs and other CWD resulting from logging and natural events) (from Halpern and McKenzie 2001). Table 2 provides block-level averages for the selected habitat variables.

Analysis

We used an information-theoretic approach (Anderson and Burnham 2002, Burnham and Anderson 2002, Burnham et al. 2011) to identify (1) the best predictors of responses of chipmunk abundance and associated habitat variables to retention level and pattern, and (2) the best individual habitat variable for predicting responses of chipmunk abundance to treatment. The best model had the lowest value for Akaike’s Information Criterion corrected for small sample size ($AIC_c = 0$) and the highest Akaike weight (w_i). We considered models with $w_i \geq 0.7$ to be strong enough for robust inference. For each regression analysis, we plotted the residuals against predicted values to confirm they had a relatively homogenous distribution and did not require any variable transformations. We used SAS 9.4 (SAS Institute, Inc. 2013) for all analyses.

TABLE 2. Estimated Townsend's and Siskiyou chipmunk abundance ($\hat{N} \pm \text{SD}$) and measures of habitat elements ($\bar{x} \pm \text{SD}$) in the post treatment time period for each block in Western Washington and Oregon. Sample size for each block is six. See text for variable definitions.

	Capitol Forest	Butte	Watson Falls
Chipmunk abundance, \hat{N}	16.3 \pm 5.0	25.2 \pm 4.2	22.4 \pm 14.1
Basal area (m ² ha ⁻¹)	29.7 \pm 20.8	29.8 \pm 17.8	24.7 \pm 14.1
Canopy cover (%)	42.2 \pm 25.9	50.1 \pm 26.3	43.2 \pm 22.1
Tree density (<i>n</i> ha ⁻¹)	151.5 \pm 115.0	702.7 \pm 536.1	246.3 \pm 176.2
Live tree QMD (cm)	51.5 \pm 8.8	24.7 \pm 4.1	36.6 \pm 8.5
Disturbed soil cover (%)	9.8 \pm 6.5	3.7 \pm 2.5	7.0 \pm 4.7
Skid track cover (%)	4.7 \pm 3.9	0.3 \pm 0.85	0.8 \pm 0.9
Wood debris cover (%)	42.65 \pm 28.2	49.9 \pm 33.2	45.4 \pm 30.2
CWD volume (m ³ ha ⁻¹)	115.9 \pm 25.5	321.9 \pm 191.4	104.3 \pm 40.1
Low shrub cover (%)	32.6 \pm 21.1	18.0 \pm 6.1	25.6 \pm 14.8
Tall shrub cover (%)	21.1 \pm 8.9	13.0 \pm 3.7	7.9 \pm 6.4
Snags ha ⁻¹	24.2 \pm 12.3	31.9 \pm 12.3	18.3 \pm 10.2
Snag dbh (cm)	50.8 \pm 11.7	56.6 \pm 4.9	54.3 \pm 5.7

Results

The percentage BA retained in each harvested unit was the benchmark for attainment of the experimental treatment objectives in DEMO (Maguire et al. 2007). Implementation of treatments revealed that nominal target BA deviated more widely at Butte and Watson Falls ($\leq 20\%$ absolute) than at Capitol Forest ($\leq 7\%$). Nonetheless, three non-overlapping levels of BA retention were created in the treatments: 15–24% in the 15% retention, 37–60% in the 40% retention, and 71–94% in the 75% retention.

We captured 989 and 737 individual chipmunks before and after treatment, respectively. Capture probabilities across experimental units in trapping bout 1 averaged $0.425 \pm 0.033_{90\%CI}$ and $0.415 \pm 0.022_{90\%CI}$ in pre- and post-treatment sampling, respectively, whereas they averaged $0.365 \pm 0.019_{90\%CI}$ and $0.392 \pm 0.013_{90\%CI}$ in bout 2, respectively. Both the Townsend's and Siskiyou species were approximately equally catchable, which satisfied an assumption of the abundance estimation technique. Ranges of pre-treatment \hat{N} were 6.6–34.0, 30.8–48.9, and 37.0–98.0 chipmunks 13 ha⁻¹ at Capitol Forest, Butte, and Watson Falls, respectively. We identified only one yellow-pine species capture in pre-treatment sampling at Butte.

Influence of Treatments on Chipmunk Abundance

Townsend's and Siskiyou chipmunk abundance had a positive linear relationship with BA retention level ($R^2 = 0.36$) (Figure 2). The selected model (model 4, $w_i = 0.52$) did not include additive effects of blocks (i.e., yarding method); whereas, the second-best model (model 2, $w_i = 0.35$) included these effects (Table 3). Chipmunk abundance was highest in the non-disturbed controls (100% BA), averaging $33.8 \pm 11.2_{90\%CI}$ chipmunks 13 ha⁻¹, and it was lowest in those treatments having the greatest disturbance intensity—15% BA retentions (15% A = $14.8 \pm 7.05_{90\%CI}$ chipmunks 13 ha⁻¹; 15% D = $17.6 \pm 6.15_{90\%CI}$) and the 40% D units ($15.7 \pm 6.2_{90\%CI}$ chipmunks 13 ha⁻¹)—only half or less of that in the non-disturbed controls. The regression model predicted a 50% reduction in chipmunk abundance as retention level decreased from 100 to 15%.

We captured 50 yellow-pine chipmunks in post-treatment sampling at Butte, with the highest \hat{N} in the non-disturbed control, 75% A, and 15% A treatments: $5.0 \pm 2.8_{90\%CI}$ to $8.0 \pm 3.2_{90\%CI}$ chipmunks 13 ha⁻¹. Yellow-pine chipmunk \hat{N} was smaller in the 40% A, 40% D, and 15% D treatments: $1.0 \pm 1.0_{90\%CI}$ to $2.0 \pm 2.0_{90\%CI}$ chipmunks 13 ha⁻¹.

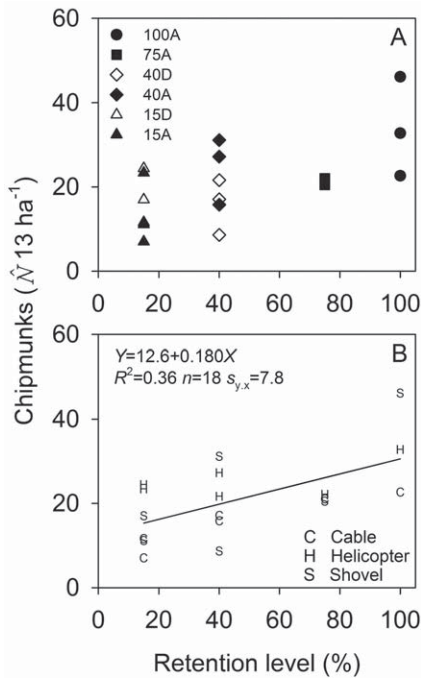


Figure 2. Regression relationship of chipmunk abundance versus retention level. Plotting symbols illustrate variation due to: (A) treatment and (B) yarding method.

Influence of Treatments on Habitat

Harvest operations disturbed the forest floor (i.e., soil and understory vegetation) with an areal extent that was proportional to retention level ($R^2 = 0.82$ and 0.90 ; Figures 3 and 4). In contrast, wood debris cover increased proportionately with decreasing retention level ($R^2 = 0.97$; Figure 5). Disturbed soil cover was best characterized by a regression model that included an interaction between retention level and yarding method (model 5, $w_i = 0.47$, Table 3). Differences in the regression slopes for this model indicated that, as retention level decreased, the percentage area of disturbed soil increased with greater magnitude for cable yarding than for shovel or helicopter yarding methods (Figure 3). At 15% retention, predicted values for disturbed soil cover were 16, 10, and 6% for cable, shovel, and helicopter yarding methods, respectively. Differences in the regression intercepts indicated that, across all retention levels, disturbed soil cover was about 3 percentage points greater for shovel yarding than for helicopter yarding.

TABLE 3. Values of AIC_c and ΔAIC_c (Akaike weights, w_i , below in parentheses) for six linear regression models that predict chipmunk abundance and associated habitat variables that were indirectly influenced by logging operations (not intentionally manipulated by treatments) (see Table 1 for model descriptions). For each variable, bold text indicates the AIC_c value of the model having the lowest AIC_c value and non-bold text indicates differences in AIC_c relative to this model (ΔAIC_c).

Variable	Regression model					
	1	2	3	4	5	6
Chipmunk abundance, \hat{N}	9.52 (0.00)	1.20 (0.28)	4.93 (0.04)	77.46 (0.52)	6.45 (0.02)	2.76 (0.13)
Disturbed soil cover (%)	6.93 (0.01)	0.59 (0.35)	2.31 (0.15)	6.54 (0.02)	43.84 (0.47)	11.33 (0.00)
Skid track cover (%)	9.23 (0.01)	36.63 (0.71)	3.16 (0.15)	5.38 (0.05)	4.24 (0.08)	9.66 (0.01)
Wood debris cover (%)	71.72 (0.99)	14.11 (0.00)	17.60 (0.00)	9.46 (0.01)	22.67 (0.00)	16.26 (0.00)
CWD volume ($m^3 ha^{-1}$)	4.25 (0.08)	179.94 (0.67)	2.92 (0.16)	4.61 (0.07)	8.68 (0.01)	7.14 (0.02)
Low shrub cover (%)	27.93 (0.00)	18.32 (0.00)	22.95 (0.00)	7.06 (0.03)	6.36 (0.04)	66.39 (0.93)
Tall shrub cover (%)	9.54 (0.01)	5.22 (0.06)	6.75 (0.03)	90.36 (0.79)	13.99 (0.00)	3.84 (0.12)
Snags ha^{-1}	7.11 (0.02)	2.28 (0.19)	4.41 (0.06)	92.85 (0.59)	3.27 (0.11)	6.40 (0.02)
Snag dbh (cm)	14.99 (0.00)	4.85 (0.05)	9.42 (0.01)	74.63 (0.61)	10.64 (0.00)	1.26 (0.33)

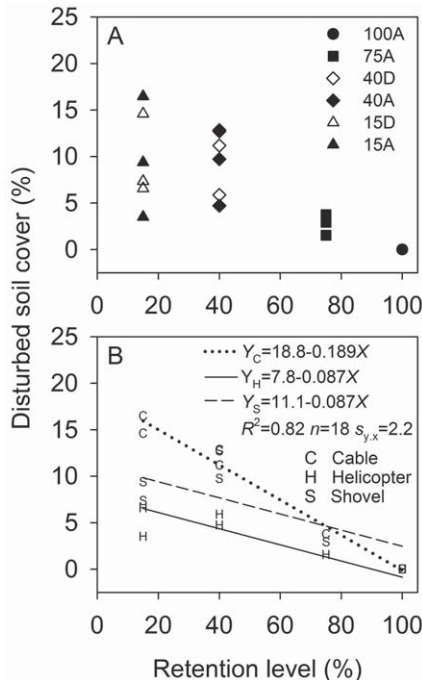


Figure 3. Regression relationship of disturbed soil cover versus the interaction of retention level and yarding method. Plotting symbols illustrate variation due to: (A) treatment and (B) yarding method.

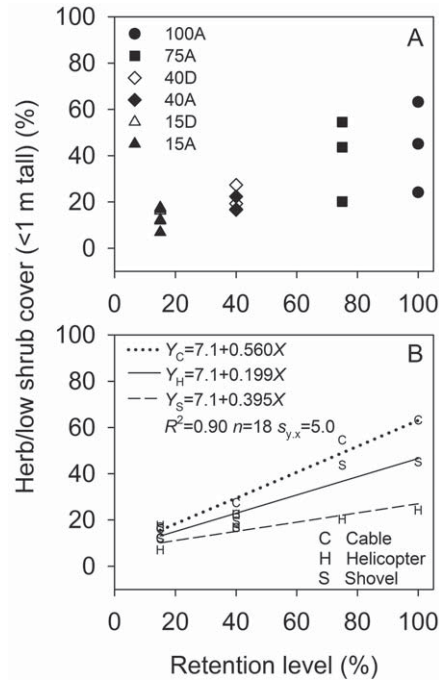


Figure 4. Regression relationship of herb and low shrub cover versus retention level. Plotting symbols illustrate variation due to: (A) treatment and (B) yarding method.

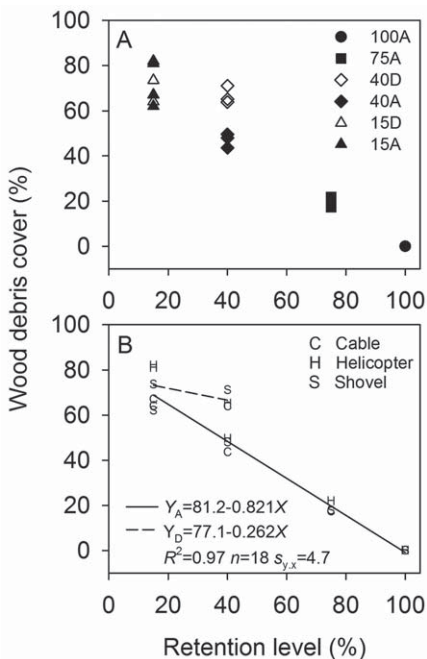


Figure 5. Regression relationship of wood debris cover versus retention level and pattern. Plotting symbols illustrate variation due to: (A) treatment and (B) yarding method. To illustrate differences in the predictive models between aggregated (A) and dispersed (D) patterns, regression intercepts were averaged across blocks.

Cover of herbs and low shrubs was described by model 6 ($w_i = 0.93$), which included a single intercept but separate slopes for each yarding method as found for disturbed soil cover (Table 3, Figure 4). Herb and low shrub cover decreased with decreasing retention level, and the rate of decrease varied among yarding methods as cable > shovel > helicopter. This response was a manifestation of block differences in vegetation cover among the non-disturbed controls and differences in disturbance intensity among yarding methods. As a result, values of herb and low shrub cover converged to a common value with decreasing retention level (i.e., a common regression intercept

= 7.1%). Wood debris cover responded to both level and pattern of tree retention (model 1, $w_i = 0.99$) because deposition of slash increased with decreasing retention, and debris cover was greater in dispersed treatments than in aggregated treatments (Figure 5).

The remaining five habitat variables (i.e., skid track cover, CWD volume, tall shrub cover, snag density, and snag dbh) were best described by linear effects of retention level independent of yarding method (i.e., models 2 or 4, $w_i = 0.6$ to 0.8 , Table 3). Volumes of CWD were reduced by 45% in the 40% D treatment ($92 \text{ m}^3 \text{ ha}^{-1}$, SD 3), and by 17 to 26% ($145 \text{ m}^3 \text{ ha}^{-1}$, SD 104 to $296 \text{ m}^3 \text{ ha}^{-1}$, SD 323) in the other harvested units, compared to < 3% reduction in the non-disturbed controls ($193 \text{ m}^3 \text{ ha}^{-1}$, SD 102). The relatively high wood debris cover (Figure 5) and low CWD volume suggest that CWD piece sizes were small in the 40% D treatments. Snag retention was an objective of the treatments, but some snags were damaged or destroyed during harvest because densities were 21 to 51% lower in harvested units, compared to < 8% lower in the non-disturbed controls.

Relationships of Chipmunk Abundance to Habitat Element Variables

Among the 12 habitat variables, disturbed soil cover was the single best predictor of chipmunk abundance responses to treatment, exhibiting a high value of w_i (0.9) that supports robust inferences (Table 4). Empirical support for disturbed soil cover was more than 23 times (evidence ratio) that of the next model. The other 11 habitat variables did not provide plausible predictive models of chipmunk abundance, obviating the need for model averaging because there were no competing models with the disturbed soil cover model.

Chipmunk abundance declined linearly with increasing cover of disturbed soil (Figure 6, $R^2 = 0.53$). Disturbed soil was the strongest determinant of variation in \hat{N} because it simultaneously accounted for variation in retention level (i.e., overstory density) and variation in disturbance of the forest floor attributable to log-yarding method. No other variable captured this much information regarding treatment effects on chipmunk habitat.

TABLE 4. Values of Akaike's Information Criterion corrected for sample size (AIC_c), difference (ΔAIC_c) from the best model (best model $\Delta AIC_c = 0$), and Akaike weights (w_i) for 12 linear regression models of individual habitat element variables that predict chipmunk abundance (see text for variable descriptions). $K = 3$ for all models. Table includes bottom four variables, which were intentionally manipulated by the treatments.

Variable	AIC_c	ΔAIC_c	w_i
Disturbed soil cover (%)	71.92	0	0.8883
Skid track cover (%)	82.58	10.65	0.0043
Wood debris cover (%)	78.73	6.81	0.0295
CWD volume ($\text{m}^3 \text{ ha}^{-1}$)	83.89	11.97	0.0022
Herb/low shrub cover (%)	83.68	11.76	0.0025
Tall shrub cover (%)	85.03	13.11	0.0013
Snags ha^{-1}	80.61	8.68	0.0116
Snag dbh (cm)	85.62	13.70	0.0009
Basal area ($\text{m}^2 \text{ ha}^{-1}$)	80.03	8.11	0.0154
Overstory canopy cover (%)	78.22	6.29	0.0382
Live trees ha^{-1}	82.87	10.95	0.0037
Live tree QMD	83.99	12.06	0.0021

We observed other variables to be proportional to retention level, and therefore had similar explaining power for this aspect of chipmunk habitat, but only disturbed soil cover integrated habitat responses that were directly disruptive to the movement, feeding, and other life history functions of chipmunks. Also, for low retention levels, only disturbed soil cover differed among log-yarding methods (Figure 3). The same explaining power did not exist for herb/low shrub cover (Figure 4) and wood debris cover (Figure 5). Note also that disturbed soil cover in dispersed treatments always exceeded 5% regardless of retention level (Figure 3).

Discussion

Influence of Treatments on Chipmunk Abundance

Variable-retention harvesting had negative effects on Townsend's and Siskiyou chipmunk populations, and the responses were influenced by the intensity of forest-floor disturbances as determined by log-yarding method. Forest harvest causes an immediate disruption or displacement of the forest

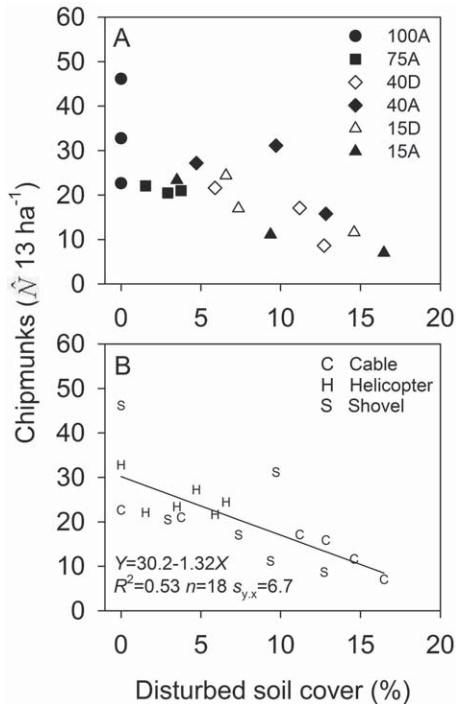


Figure 6. Regression relationship of chipmunk abundance versus disturbed soil cover. Plotting symbols illustrate variation due to: (A) treatment and (B) yarding method.

floor and deposition of logging debris slash that combine to alter abundance and species composition of understory vegetation via plant injury, uprooting or burial (Halpern and McKenzie 2001). The treatment-specific (i.e., retention level) reductions of residual low shrub habitat were indicative of understory fragmentation and discontinuity of cover resulting from this disturbance. Wood debris accumulations (slash and small logs) were indicative of locations where felled trees were topped and their branches removed via breakage or chainsaw. Responses of increased soil disturbance and wood debris cover and reduced herb/low shrub cover with decreased levels of tree retention integrate into a nexus that links forest-floor disturbance to habitat disruption, and ultimately to chipmunk population displacement.

Regression analyses of the habitat variables revealed that responses of chipmunk abundance to the treatments were best explained by a negative linear relationship with disturbed soil cover.

Disturbed soil cover in the dispersed harvest pattern always exceeded 5% regardless of retention level (40 or 15%)—an indication of the unsuitability of the 15% retention levels and each of the dispersed treatments as chipmunk habitat. Reductions in chipmunk abundance were greatest in the 40% D, 15% A, and 15% D treatments, and compared to the non-disturbed controls, these differences were large (i.e., 50% or larger). It is worth noting that the lowest abundances of arboreal flying squirrels also occurred in the 40% D, 15% A, and 15% D treatments in DEMO, and this response was attributed to unsuitable habitat features for the species associated with reductions in tree density and canopy cover (Holloway et al. 2012).

Decrease in Siskiyou Chipmunk Abundance—Differential amounts and distribution of dietary truffles may have contributed to differences in pre-treatment abundance of Siskiyou chipmunks because of their effects on reproductive output (McIntire 1984, Cazares et al. 1999). High chipmunk relative abundances in the Mowich units (3.9 captures 100 TN⁻¹) coincided with high spring truffle biomass (9.8 kg ha⁻¹), compared to significantly lower chipmunk relative abundances (1.5 captures 100 TN⁻¹) and significantly lower truffle biomass (2.3 kg ha⁻¹) in the Airstrip units (Cazares et al. 1999). Harvesting-associated ground disturbance at Watson Falls contributed significantly to the disruption of truffle production (Luoma et al. 2004). Along with large reductions of shrub cover (7 to 78%) and snags (22 to 78%), large declines in chipmunk abundance (54 to 91%) also occurred across harvested units. High predation on truffles by the fungi-eating small mammal community (Amaranthus et al. 1994, Cazares et al. 1999) can also result in chipmunk declines. In an earlier study, high exposure of mineral soil in logging sites treated for slash disposal were surmised to be responsible for reductions in truffle availability to Siskiyou chipmunks in southern Oregon (McIntire 1984). We speculate that the Siskiyou species may be more dependent upon truffles than the Townsend's species owing to the influence of unique biogeographic features and climatic factors on their natural histories in the forests they inhabit.

Relationships of Chipmunk Abundance to Habitat Variables

Our results are consistent with some of the research in managed and natural forests in the Pacific Northwest, which suggests that Townsend's and Siskiyou chipmunks thrive better in habitats maintained for mature or older forests (McIntire 1984, Carey 2007). Following we discuss key features of chipmunk habitat that were modified by the treatments and likely influenced chipmunk abundance.

Shrubs—In managed mature stands and unmanaged old-growth stands of the Pacific Northwest, Townsend's chipmunks were only abundant where shrub cover was > 40% (Carey 1995, Carey et al. 1999). For BA retentions of ≤ 40% we observed values of herb/low shrub cover between 12 and 23% (Figure 4) and considerable variation in abundance of chipmunks (7 to 31 chipmunks 13 ha⁻¹; Figure 2). In the 75% A and non-disturbed controls, chipmunk abundances were more stable and larger, respectively, where herb/low shrub cover varied between 39 and 44% (the 75A treatment reflects only 1 year of data). Chipmunks are highly reliant on continuous horizontal cover of understory vegetation, debris, and other structures for travel, foraging, and hiding when they move about the forest floor (Harestad 1991, Carey 2000), but predation may limit populations in areas with low amounts of escape cover that are provided by dense ericaceous shrubs (Carey 1995, Hayes et al. 1995), such as salal (*Gaultheria shallon* Pursh), which was common at the Capitol Forest site. Furthermore, shrub loss depletes dietary berry/seed sources. Inadequate shrub cover in treatments of ≤ 40% BA retention seems to reflect these detrimental effects.

Wood Debris—Wood debris cover increased with decreasing tree retention. Large-sized wood debris provides hiding, nesting and travel lanes for chipmunks (McComb 2003, Waldien et al. 2006). Piles of wood debris also provide escape cover (Sullivan et al. 2012). In Oregon, CWD cover was a strong predictor of chipmunk carrying capacity, and coupled with complex understory development, accounted for higher Townsend's

chipmunk abundance (Carey et al. 1999). Larger numbers of female Siskiyou chipmunks were associated with logging debris piles compared to non-treated sites (McIntire 1984). Logging debris piles and decayed CWD also help to moderate soil microclimate, which enhances truffle food production (McIntire 1984, Amaranthus et al. 1994, Luoma et al. 2004). In Douglas-fir forests of British Columbia, chipmunk abundance was significantly higher in pile and windrow logging treatments than in untreated forest (Sullivan et al. 2012). However, piled debris that provided refugia for small ground fauna, may also become ecological predation traps for mesocarnivores such as weasels that select these sites for hunting grounds (Lisgo 2002, Manning and Edge 2004, Sullivan et al. 2012). When wood debris is scattered, associations with faunal abundances are inherently weak, owing to high variability in distribution and to measurement scale (Waldien et al. 2006, Bunnell and Houde 2010, Riffell et al. 2011). Such factors contribute to difficulties in assessing chipmunk responses to wood debris. Results of our study showed inverse trends between chipmunk abundance (Figure 2) and amounts of wood debris cover in relation to retention level (Figure 5). This unexpected relationship was likely confounded by other habitat disturbances such as forest-floor disruption, decreases in herb/low shrub cover, predation on chipmunks, and lower retentions of large-piece residual CWD. While wood debris cover was high in the 40% D units, legacy CWD volume reductions were also large—two to three times greater than in the other units. This suggests that smaller-sized pieces populated the landscape, which were less likely to benefit the life history needs of chipmunks and therefore contributed to the unsuitability of that treatment to chipmunks.

Truffles—Truffles are a year-round belowground food source important to chipmunks and other forest small mammals (Maser 1978, McIntire 1984, North et al. 1997). Annual biomass of truffles is highly variable with non-uniform seasonal distributions and sensitivity to changes in soil temperature and moisture (Luoma et al. 2004). This makes truffle production vulnerable

to harvest-associated disturbances to the forest floor because microclimate is best moderated by shady conditions under mature and non-disturbed forest canopies (Heithecker and Halpern 2006). This suggests that there could be potentially large differences in the distribution and abundance of truffles among and within our study sites, owing to the differential effects of log-yarding method on forest-floor disturbance and the rate by which it recovers. For example, low truffle biomass in northwestern Washington was associated with slowly-developing thin organic soil layers after harvesting 60 years earlier (North et al. 1997). When truffle abundance is high, they contribute significantly to chipmunk diets; when low, chipmunks compensate by eating other foods (Jacobs and Luoma 2008). Chipmunks consumed relatively high amounts of other plant materials, in addition to truffles, compared to obligate fungivore flying squirrels and truffle-eating red-backed voles (Jacobs and Luoma 2008) in four DEMO sites, including Watson Falls and Butte. Truffle production was strongly reduced by all levels of retention harvest in another study in three DEMO sites, also including Watson Falls and Butte (Luoma et al. 2004)—particularly in the 15% A, 15% D, and 40% A treatments. Alteration of microclimate and removal of host trees likely accounted for these effects (Luoma et al. 2004). In our study, chipmunk abundances in the 15% retentions and 40% D treatments were lowest. We observed lower numbers of chipmunks in the 40% D treatment, where no effect was detected on autumn truffle biomass, however; and we observed relatively high chipmunk abundances in the 40% A treatment, where strong reductions in truffle production were detected (Luoma et al. 2004). Differences in truffle predation rates may have added to truffle depletions in the 40% A treatment. For example, North et al. (1997) observed that animal consumption of truffles in winter exceeded the available standing crop in younger stands. These studies suggest that forest-floor disturbance likely had strong detrimental effects on truffle production, which probably contributed to the observed declines in chipmunk abundance. In addition, natural recovery of the forest floor to organic conditions that favor

truffle production could take decades depending on disturbance intensity.

Snags—Snags, stumps, and old bird nests in tree branches provide chipmunks sites for food storage, nesting and hiding (Brand 1974, Carey et al. 1997). Townsend's chipmunk densities are related to abundance of large, hard snags in old-growth stands (Rosenberg and Anthony 1993), and Siskiyou chipmunks are associated with large moderately decayed snags (Johnston 2006). With harvest-associated reductions of other habitat features and competition for nesting cavities from wildlife species such as birds and flying squirrels, the availability of suitable snag and down log cavities would seem to assume great importance to chipmunks. For example, higher availability of nesting dens in larger snags may ameliorate other effects of forest harvest for flying squirrels (Holloway et al. 2012). This response also seems tenable for smaller-bodied chipmunks that appear to be more flexible in arboreal and near-ground nest site selection, and may be able to use smaller cavities in smaller trees than flying squirrels. Chipmunk abundances were lowest in our 15% A and 40% D treatments, and snag densities were reduced 41 (40% D) to 51% (15% A); however, retention of larger-sized snags (snag diameter = 57.2 cm [SD 4.6] to 58.9 cm [SD 10.6], compared to 48.3 cm [SD 12.1] in the non-disturbed controls) may have prevented greater declines in chipmunk abundance because they likely provided more nesting cavities. Both treatments also had the lowest snag densities, particularly the 40% D treatment (14.5 snags ha⁻¹ [SD 3.7] compared with 20.1 snags ha⁻¹ [SD 15.2] [15% A] to 27.9 snags ha⁻¹ [SD 23.0] in other treatments and 35.3 snags ha⁻¹ [SD 8.1] in the non-disturbed controls).

Soil Disturbance and Log-Yarding Method

Environmental disturbance in this study was operationally controlled by the log-yarding method used because treatments were implemented consistently across replicated units at each site (Halpern and McKenzie 2001). That is, the method used for each site was based on terrain and topography to minimize environmental damage and to safely and consistently conduct the assigned harvest levels.

Our estimates of disturbed soil cover were conservative because amounts under slash or logs could not be determined (Halpern and McKenzie 2001). Skid track scarification also caused soil disturbance but was treated as a separate variable. Skid track cover is a direct indicator of the area in which logs were dropped and then skidded to landings. Skid track disturbance mostly occurred in cable yarding, whereas disturbed soil cover occurred from all logging activities.

At the lowest retention level, log yarding with suspension cables resulted in the greatest disturbed soil cover (16%)—more than twice as much as for helicopter yarding (6%), and almost twice as much as for shovel-loader yarding (10%) (Figure 3). As expected, helicopter yarding had the lowest disturbance intensity (Halpern and McKenzie 2001), which is also consistent with previous studies. Comparisons of the cable and shovel-loader yarding methods with other studies is challenging however, because often soil compaction, rutting, and other elements are integrated into a single measure of disturbance intensity, compared to our measure of the areal extent of disturbance via percentage cover. For example, tractor logging caused more surface soil disturbance by soil compaction than did “high-lead” clear-cut logging in the Oregon Cascades (Dyrness 1965). On Vancouver Island, British Columbia, and in the northern Rocky Mountains, Montana, overall soil disturbance varied among log-yarding methods as follows: ground-based mobile vehicles > cable > helicopter (Bockheim et al. 1975, Reeves et al. 2011), which was different from our findings of cable > ground-based > helicopter. These differences were likely related to the mobile vehicles used in the ground-based methods. For example, rubber-tired skidders, which are particularly damaging to the soil surface, were also used along with tracked vehicles in Montana, but not in our study. On Vancouver Island, tractor loaders were also used and the leading end of the log was not kept clear of the ground causing high soil disturbance (Bockheim et al. 1975). Moreover, all harvests in these earlier studies were clear-cuts, unlike our study of variable-retention harvests.

Conservation of Forest Structure

In managed forests of the Pacific Northwest, stand structure is an important factor for maintaining Townsend’s chipmunk populations (Rosenberg and Anthony 1993; Carey 1995, 2001). Chipmunk communities may persist, recover quickly or increase from management practices such as in thinned variable-density legacy mosaics if spatial heterogeneity, plant-fungal productivity, biological legacy structure, and complexity are closely reproduced (Carey 2001, Carey and Wilson 2001). Forest legacy retention (trees and snags), multi-species tree management, and retention of shrubs and decadence (wood debris) are examples of management strategies that conserve biological diversity and complexity and promote forest resilience, and general sustainability (Carey 2007). Outside of the tree aggregates, and in dispersed pattern retentions, the treatments in DEMO did not provide this complement of habitat features for chipmunk persistence; only snags were intentionally retained. Our findings suggest that, except for refugia provided by treatments with $\geq 40\%$ retention in an aggregated pattern, short-term forest structure was not adequate for the Townsend’s and Siskiyou chipmunks. In contrast, open canopies likely will foster an expansion of the yellow-pine chipmunk population in the short- to near-term at Butte.

Conclusions

Chipmunks were sensitive to disturbances associated with variable-retention harvest of Pacific Northwestern forests. Within the range of conditions tested, chipmunk populations declined in proportion to the area of disturbed soil, which varied as a result of the interaction of retention level and log-yarding method. The overall declines were continuous along the observed gradient in soil disturbance, with more severe declines occurring in the dispersed pattern. Our results suggest that the current minimum BA retention standard of 15% does not provide suitable short-term habitat for Townsend’s and Siskiyou chipmunks. Dispersed tree patterns with $\leq 40\%$ BA retentions also are not suitable for chipmunks.

Suspension cable and shovel-loader yarding systems were likely to produce disturbances of greater intensity and area than helicopters, and effects attributed to log-yarding method are likely to be stronger than those associated with treatment (i.e., level or pattern of retention) (Halpern and McKenzie 2001, and this study). We also showed how retention level and log-yarding method interacted to produce varying covers of soil disturbance. As retention level decreased below the 75% retention level, the rate of increase in soil disturbance was ranked among yarding methods as cable > shovel-loader = helicopter. For the suspension cable system particularly, relative soil disturbance sharply increased with decreasing retention level. Soil disturbance from cable yarding at the lowest retention level (15%) was more than twice as extensive as from helicopter yarding and almost twice as extensive as from ground-based tracked shovel-loaders.

We suggest that other researchers replicate similar studies and/or collect or review soil disturbance data in forest-fauna studies to confirm relationships like those we observed. It seems likely that other ground-dwelling fauna of similar habitat requirements would respond in a similar negative way to variable-retention harvesting. That we detected relationships with a small sample size suggests that our results may be applicable to a wider range of mature forests in the region. However, replication of each log-yarding method would be a desirable feature to include in future experiments.

Low levels of replication, as in our study, are typical of large-scale forest ecosystem experiments which are expensive and logistically difficult to implement, often resulting in sufficient power to detect only large treatment effects. Observational studies often include greater levels of replication but may be unable to rigorously isolate effects of forest harvesting from other unmeasured factors,

such as pre-existing differences among sites (Block 2013). Our results, integrated with results of other studies, provide a basis for refining hypotheses about potential effects of variable-retention harvesting on chipmunks and related fauna at the forest-floor disturbance level.

The effects of both retention level and log-yarding method are important considerations when planning logging operations, as they seem to differentially influence chipmunk (and likely other small mammal) populations through their effects on the forest floor. Fortunately, the areal extent of such disturbances is known or can be estimated with reasonable certainty for the various log-yarding methods in use today.

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