Fine-Scale Correlates of Small Mammal Abundance in Industrial Forests of Northern California

Author(s): Steven M. Gray, Alexander K. Killion, Gary J. Roloff, Brian P. Dotters and Thomas T. Engstrom

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Steven M. Gray[1,2], Department of Fisheries and Wildlife, 13 Natural Resources Building, Michigan State University, East Lansing, Michigan 48854

Alexander K. Killion, Department of Fisheries and Wildlife, 13 Natural Resources Building, Michigan State University, East Lansing, Michigan 48854

Gary J. Roloff, Department of Fisheries and Wildlife, 13 Natural Resources Building, Michigan State University, East Lansing, Michigan 48854

Brian P. Dotters, Sierra Pacific Industries, 19794 Riverside Avenue, Anderson, California 96007

and

Thomas T. Engstrom, Sierra Pacific Industries, 19794 Riverside Avenue, Anderson, California 96007

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Abstract

Limited information exists on small mammal communities in industrial forests of northern California. Small mammal communities are important components of forest ecosystems and a better understanding of small mammal relationships to fine-scale habitat features in industrial forests can aid management. We developed overall and species-specific models to assess the relationships between small mammals and fine-scale (64 m^2) habitat features (i.e., cover of shrub, forb, grass, rock, mineral soil, forest litter, downed wood, and trees). We also assessed fine-scale land cover category. We trapped small mammals from May to August of 2011–2013 in 65 stands using a web based trapping design that consisted of Sherman and Tomahawk live-traps. We captured 11 small mammal species with the most frequently captured species being *Peromyscus* spp. and California ground squirrels (*Spermophilus beecheyi*) in Sherman and Tomahawk traps, respectively. Pooled small mammal captures in Sherman traps were positively influenced by shrub cover at trapping locations. This relationship was also observed in *Peromyscus* spp. and Allen's chipmunk (*Tamias senex*). We captured more *Peromyscus* spp. and pooled small mammals when a trap was placed in retention rather than clearcuts. In Tomahawk traps, pooled small mammal captures were positively influenced by shrub cover and downed wood. We captured more California ground squirrels in clearcuts opposed to controls and found forest litter to negatively influence ground squirrel captures. Our findings emphasize the importance of fine-scale habitat elements, primarily downed wood, shrub cover, and retention patches on small mammal habitat use in industrial forests of northern California.

Keywords: California ground squirrel, forest management, industrial forests, *Peromyscus* spp., retention patch

Introduction

Interest in the relationships between small mammal populations and intensive forest management partially relates to the growing demand for comprehensive forest management that includes considerations for wildlife, water quality, and aesthetics. Our understanding of the relationships between small mammals and habitats provided by managed forests are based on the evaluation of retention patches (Carey and Wilson 2001, Sullivan and Sullivan 2001, Sullivan et al. 2001, Gitzen et al. 2007), riparian zones (Anthony et al. 1987), downed wood (Carey and Johnson 1995, McComb 2003, Lee 2004, Manning and Edge 2008, Sullivan et al. 2012), and coarse vegetation structure of the managed stand (Carey and Johnson 1995, Sullivan et al. 2000, Sullivan et al. 2009). The influence of fine-scale habitat elements like herbaceous or woody shrub cover, forest litter, small pieces of downed wood, or the amount of exposed mineral soil on small mammal habitat use is less understood. Information on the effects of fine-scale habitat elements can guide forest management, and may be particularly relevant

[1]Author to whom correspondence should be addressed.
Email: stevenmgray4@gmail.com

[2] Current Address: 3120 Cobblestone Ridge, Tecumseh, Michigan 49286

to managers trying to fulfill protected species requirements or forest certification standards.

Occurrence of fine scale habitat features are known to positively influence small mammal survival in moist environments like the Oregon Coast Range (Manning and Edge 2004). These finer scale habitat features may be even more important to small mammals where moisture is limiting during certain times of the year, like in the drier coniferous forests that occur in some parts of the western United States. For example, understory cover was an important covariate on small mammal occupancy in dry ponderosa pine (*Pinus ponderosa*) forests of northern Arizona (Kalies et al. 2012). Similarly, shrub cover and downed wood were the most important habitat characteristics affecting small mammal densities in Arizona (Converse et al. 2006).

Some forest landowners have adopted patch retention strategies in timber harvest areas to supplement wildlife habitat. Retained green trees within timber harvest areas impact small mammal populations, though study results are variable. Sullivan and Sullivan (2001) concluded that small mammal abundance and diversity in harvested conifer forests of British Columbia, Canada, were similar across varying levels of retention due to post-harvest colonization by generalists and early successional species. Gitzen et al. (2007) predicted that small mammal species associated with closed canopy forests would decrease, early successional species would increase, and habitat generalists would show little response to habitat retention in coniferous forests of western Oregon and Washington. Some species did not follow the expected response, leading Gitzen et al. (2007) to suggest that additional factors such as small mammal community composition, latitude, and elevation influenced the response of small mammals to green-tree retention. Green tree retention, particularly in patches, can correspond to unique fine-scale habitat features that are different from surrounding timber harvest areas (Linden and Roloff 2014).

The goal of our research was to explore how small mammal abundance was influenced by fine-scale habitat features in dry industrial forests to better inform retention practices. Our objective was to correlate the number of captured individual small mammals to fine-scale (64 m^2) habitat elements surrounding trap locations. We also evaluated if land cover category (e.g., retention, riparian zone) at a trapping location influenced captures to determine if fine-scale habitat features corresponded to retention practices. We used a combination of live trapping, vegetation sampling, and generalized linear mixed models. Our response variable was the number of uniquely captured individuals at a trap location; this metric represented an indicator to the number of animal home ranges overlapping a location. Our findings provide insight into small mammal habitat use in relation to fine-scale features that can be purposefully managed in industrial forest landscapes of northern California.

Methods

Study Area

This study was conducted in the Klamath Mountain ecoregion of northern California (Trinity County). The landscape of this ecoregion features heterogeneous and intricate vegetation patterns resulting from diverse climate, topography, and parent materials (Sawyer et al. 1977). Soil moisture regimes are xeric with soil temperatures varying from mesic to frigid and some cryic at higher elevations (Miles and Goudey 1997). The climate is considered Mediterranean, with hot and dry summers (Skinner et al. 2006). Average maximum daily temperatures from May through August range from 25 to 34 °C and average precipitation ranges from 3.4 to 0.5 cm. During sampling, the coolest and wettest month is May, with the hottest (August) and driest (July) months toward the end of summer (Weaverville Ranger Station, US Forest Service, Trinity County).

Land uses are predominately forestry, agriculture, tourism, and mining, with 83% of the ecoregion federally owned (Sleeter and Calzia 2008). Historically, fire was the primary disturbance that shaped forest structure in this region (Mohr et al. 2000). Current broad scale disturbances include occasional wildfires and industrial forest management. Vegetation in this region is broadly classified as Douglas-fir (*Pseudotsuga menziesii)*–Ponderosa pine (Miles and Goudey 1997), with industrial forests managed for Douglas-fir, incense-cedar (*Calocedrus decurrens*), and ponderosa pine, and secondarily supporting diverse hardwoods including canyon live oak (*Quercus chrysolepis*), black oak (*Q. kelloggii*), and madrone (*Arbutus menziesii*).

We conducted this project on timberlands owned and managed by Sierra Pacific Industries (SPI). The dominant silviculture regime is small-scale (< 8 ha) clearcutting followed by site preparation that includes various combinations of chemical, mechanical, and fire treatments. Stands in this study were clearcut but contained a diversity of retained structures including riparian buffers (which are called Watercourse and Lake Protection Zones (WLPZ) in California regulatory parlance), retention patches, and occasional single, isolated leave trees. Harvested stands were later replanted (within one year of harvest) and monitored periodically for regeneration success. Stands used for trapping averaged approximately 7–8 ha and were located north and south of Weaverville, CA on elevations ranging from 679 to 1,467 m. We identified all stands in the SPI timber inventory system for northern California that could be categorized into four broadly defined forest development stages: 1) recent clearcuts (3–5 years old), 2) 10–20 year-old plantations, 3) rotation-aged stands (60–80 years old), and 4) WLPZs. We subsequently selected stands that represented a broad spatial distribution (latitude range = 40.5184° – 41.03294°; longitude range = –122.65275° to –123.02216°) and that were reasonably accessible by a logging road.

Small Mammal Trapping

We trapped from May to August of 2011–2013 in 65 stands: 1) recent clearcuts (15 stands), 2) 10–20 year-old plantations (16 stands), 3) rotation-aged stands (16 stands), and 4) WLPZs (18 stands). We used a web-based trapping design with a combination of Sherman (Model LFA, 7.6 x 8.9 x 22.9 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) and Tomahawk (Model 202, 48.3 x 15.2 x 15.2 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin) live traps (Parmenter and McMahon 1989). The web-based design was first described by Anderson et al. (1983) and has been commonly used in small mammal studies (Bagne and Finch 2010).

We placed a single trapping web in a stand. All stands were trapped once. In 2011, we briefly experimented with a smaller web design before settling on the larger web to meet our study objectives. Each trapping web consisted of five spokes containing seven nodes with nodes separated by 7 m. We placed a Sherman live trap at each node, resulting in 35 Sherman traps per web. At the web center and the 3rd and 7th nodes we also placed a Tomahawk live trap, resulting in 11 Tomahawk traps per web. We trapped each web for three (2011) to five (2012–2013) nights, which constituted a trapping period. After each trapping period we moved the trapping webs to the next set of replicate stands. When feasible, one stand of each forest class was trapped during a sampling period to account for broad-scale population fluctuations of small mammals that impacted all stands collectively. We baited traps with a mixture of whole oats, raisins, creamy peanut butter, and molasses. Traps were set under or beside ground cover such as logs or heavy foliage and those at risk of exposure to direct sunlight were shaded. We also applied cotton batting to all traps. For stands containing riparian zones or leave patches, we placed webs so that one or more spokes intersected those retention elements. In the WLPZ forest class, webs were centered on the stream channel yet some spokes extended beyond the WLPZ and into adjacent areas due to the stream course classification and its associated WLPZ protection.

Traps were checked daily between sunrise and noon. Captured animals were marked with a 9-mm passive integrated transponder (PIT) tag injected via a 12-gauge needle subcutaneously in the flank (Model HPT9, Biomark, Boise, ID). We used PIT tags instead of ear tags so that individuals could be identified during subsequent captures with minimal handling, to increase accuracy of individual identification, and to shorten animal handling time (Schooley et al. 1993, Morley 2002). Schooley et al. (1993) found no evidence that PIT tagging increased small mammal mortality.

After marking, animals were released on site for potential recapture. Animals that were seldom captured or those that were not conducive to tagging (e.g., shrews) were released without administering a PIT tag. Capture and handling of animals followed guidelines recommended by the California Department of Fish and Wildlife under scientific collection permit SC-11913, and was reviewed by the Institutional Animal Care and Use Committee at Michigan State University and deemed exempt because field data were collected by SPI employees.

Vegetation Sampling

A 9-m-diameter plot was centered on each individual trap location within a web. The north-south and east-west diameters of the plot were used for point-line transect surveys of ground cover. Points were spaced 1 m apart, starting at 1.5 m and ending at 4.5 m from the individual trap location. We recorded if the point intersected shrub, forb, grass, rock, mineral soil, forest litter, downed wood, or tree. Forest litter included leaves, needles, pine cones, ash, and pulverized slash from timber harvest. Downed wood was defined as downed logs, branches, and discernible woody slash. We did not set a size limit for inclusion in the downed wood category therefore this category could be considered an amalgam of coarse and fine downed wood. We also recorded whether the trap locations were within the clearcut boundary (for 3–5 and 10–20 year old forests), retention patch (60–80 year old trees that were retained during harvesting), riparian zone in a clearcut (clearcut-riparian), control (60–80 year old forests), or riparian zone in a control (control-riparian). Here, control patches correspond to rotation-aged forests and riparian areas were based on buffer requirements around streams associated with the California Forest Practice Rules (CAL FIRE 2014). Retention patch sizes were ≥ 2% of the harvested unit and > 405 m^2.

Data Analysis

We calculated the proportion of each ground cover category within the 9-m-diameter plot. We tested for differences in ground cover among land cover categories using a Kruskal-Wallis rank sum test. A significant finding was followed by a multiple comparisons test to determine homogeneous groupings among land cover categories (Siegel and Castellan 1988). We generated a correlation matrix of ground cover variables using a Kendall tau rank correlation coefficient and identified correlated variables ($P < 0.05$); correlated variables were not included in the same candidate model. Our response variable was the number of unique individuals captured at a trap location over the course of one trapping period for each species. We used generalized linear mixed models (GLMM) with a Poisson distribution in program *R* 3.0.2 for estimating the impact of localized ground cover measures on small mammal species abundance. We also investigated whether the year of sampling or land cover category at each trap (i.e., clearcut, retention, clearcut-riparian, control, or control-riparian zone) influenced small mammal counts for each species. We used a Kruskal-Wallis rank sum test to initially estimate if year or land cover category explained small mammal captures. If we found a significant Kruskal-Wallis effect we included the factors in the GLMMs. We performed the Kruskal-Wallis test as a precursor to GLMM modeling as a means to *a priori* reduce the number of model parameters. We also included a trapping web identifier as a random effect to account for spatial dependencies within webs (Zuur et al. 2009). Using a Kendall tau rank correlation coefficient, we generated a correlation matrix and identified those variable combinations that were correlated ($P < 0.05$). Candidate models were created using the uncorrelated vegetation and land cover variables. We used AICc to rank candidate models and deemed model parameters significant if the 95% confidence intervals did not overlap zero (Burnham and Anderson 2002).

Results

Vegetation and Land Cover at Trap Locations

We sampled 65 stands and recorded vegetation and small mammal data at 2900 trap locations during the summers of 2011–2013. Vegetation measures varied by land cover classification (Table 1). Plots

TABLE 1. Average percent cover (SD; range) of habitat elements within 64 m^2 plots at individual trap locations (*n*) by land cover category in industrial forests of northern California, May–August 2011–2013.

	Land Cover Category				
Habitat Element	Clearcut (*n* = 1308)	Retention (*n* = 146)	Clearcut-riparian (*n* = 70)	Control (*n* = 1007)	Control-riparian (*n* = 369)
Shrub	7 (0.13; 0–100)[a]	7 (0.16; 0–100)[a]	12 (0.19; 0–78)[ab]	7 (0.15; 0–94)[a]	17 (0.19; 0–88)[b]
Forb	10 (0.14; 0–78)[a]	4 (0.07; 0–33)[a]	14 (0.16; 0–89)[ab]	9 (0.13; 0–81)[a]	19 (0.19; 0–88)[b]
Grass	26 (0.22; 0–94)[a]	15 (0.18; 0–69)[b]	15 (0.19; 0–75)[b]	6 (0.11; 0–81)[c]	5 (0.09; 0–63)[c]
Rock	3 (0.08; 0–63)[a]	1 (0.04; 0–25)[ab]	2 (0.04; 0–19)[ab]	1 (0.04; 0–56)[b]	4 (0.09; 0–81)[a]
Mineral Soil	15 (0.17; 0–100)[a]	11 (0.13; 0–50)[a]	8 (0.08; 0–100)[bc]	4 (0.07; 0–56)[b]	2 (0.05; 0–100)[c]
Forest Litter	19 (0.18; 0–89)[a]	38 (0.24; 0–100)[b]	37 (0.28; 0–100)[b]	43 (0.25; 0–100)[c]	30 (0.20; 0–89)[b]
Downed Wood	14 (0.15; 0–75)[ab]	17 (0.16; 0–81)[a]	9 (0.13; 0–56)[c]	12 (0.15; 0–94)[b]	13 (0.13; 0–88)[ab]
Tree	6 (0.09; 0–63)[a]	7 (0.10; 0–50)[ab]	4 (0.09; 0–31)[a]	9 (0.11; 0–94)[c]	9 (0.11; 0–56) [bc]

[a, b, c] Denotes significant differences among land cover categories via multiple comparisons tests.

in riparian zones had greater cover of shrubs (12–17%) and forbs (14–19%) and, according to a multiple comparisons test, were different than clearcut, retention, and controls, which featured similar, lower amounts of these habitat elements (Table 1). Grass cover was highest in clearcuts (26%) and lowest in control and control-riparian plots (5–6%; Table 1). A multiple comparisons test grouped clearcut-riparian and retention, and control plots together, as they featured similar amounts of grass cover, respectively. Clearcut plots had the highest grass coverage and were deemed different from the previous groupings. Rock was relatively uncommon within plots; being most common in control-riparian (4%) and least in control and retention (1%; Table 1). Rock cover was similar in clearcut and control-riparian, and retention and clearcut-riparian plots. Mineral soil cover was highest in clearcut and retention (11–15%) and were different than control (4%) and control-riparian plots (2%; Table 1). Forest litter was lowest in clearcuts (19%) and highest in control plots (43%; Table 1). Forest litter cover differed between clearcuts and control-riparian plots. However, retention, clearcut-riparian, and control plots had similar levels of forest litter. Downed wood was highest in clearcuts, retention patches, and control-riparian zones (13–17%) and lowest in clearcut-riparian (9%; Table 1), with retention, clearcut-riparian, and control plots differing in downed wood cover. Tree stem cover was highest in control (9%) and lowest in clearcut and clearcut-riparian plots (4–6%) with tree cover in controls being distinctly different than in clearcut plots. Collectively, our vegetation results indicate that herbaceous and shrub cover had re-established to levels that were comparable to some of our control land cover categories (Table 1). Based on cover amounts, the vegetative effects of site preparation and planting were negligible 3–5 years after clearcutting in our study.

The most common land cover category at Sherman trap locations was clearcut (*n* = 1308) followed by control (*n* = 1007), control-riparian (*n* = 369), retention (*n* = 146), and clearcut-riparian (*n* = 70). We found that land cover category influenced pooled small mammal counts in Sherman ($\chi^2 = 17.594$, $P = 0.001$) and Tomahawk traps ($\chi^2 = 29.423$, $P = < 0.001$); *Peromyscus* spp. in Sherman traps ($\chi^2 = 17.875$, $P = 0.001$), and California ground squirrels in Tomahawk traps ($\chi^2 = 57.272$, $P = < 0.001$). Land cover category did not influence Allen's chipmunk counts ($\chi^2 = 6.300$, $P = 0.178$). We found that year of sampling influenced pooled small mammals counts in Tomahawk traps ($\chi^2 = 7.431$, $P = 0.024$) and California ground squirrels in Tomahawk traps ($\chi^2 = 7.294$, $P = 0.026$). Year did not influence *Peromyscus* spp. ($\chi^2 = 2.662$, $P = 0.264$), Allen's chipmunk ($\chi^2 = 0.277$, $P = 0.871$), or pooled small mammal counts in Sherman traps ($\chi^2 = 1.865$, $P = 0.394$).

TABLE 2. Average (SE) nightly trap success by land cover category and trap type for all small mammals combined, *Peromyscus* spp. and Allen's chipmunks (Sherman traps), and California ground squirrels (Tomahawk traps) on industrial forests of northern California, May–August 2011–2013.

	Trap Success (Mean, SE)				
	Sherman Traps			Tomahawk Traps	
Land Cover Category[a]	All Small Mammals	*Peromyscus* spp.	Allen's Chipmunk	All Small Mammals	California Ground Squirrel
Clearcut	0.056 (0.004)	0.052 (0.004)	0.001 (< 0.001)	0.060 (0.008)	0.057 (0.008)
Retention Patch	0.107 (0.021)	0.102 (0.021)	0.000 (0.000)	0.048 (0.020)	0.016 (0.011)
Clearcut-riparian	0.056 (0.021)	0.036 (0.016)	0.000 (0.000)	0.085 (0.037)	0.069 (0.035)
Control	0.046 (0.004)	0.042 (0.004)	0.003 (0.001)	0.019 (0.005)	0004 (0.002)
Control-riparian	0.067 (0.007)	0.062 (0.007)	0.004 (0.002)	0.027 (0.010)	0.007 (0.005)

[a] Clearcut = all merchantable trees removed, site prepared and planted 3–5 years ago; Retention Patch = retained merchantable trees within the clearcut boundary; Clearcut-riparian = WLPZ within the clearcut boundary; Control = Rotation-aged (60–80 years old) forests; Control Riparian = WLPZ in rotation-aged forest

Small Mammals

We accumulated 12261 trap nights (87% of the potential trap nights) and caught 11 small mammal species: deer mouse (*P. maniculatus*), brush mouse (*P. boylii*), California ground squirrel, Allen's chipmunk, dusky-footed woodrat (*N. fuscipes*), bushy-tailed woodrat (*N. cinerea*), Trowbridge's shrew (*Sorex trowbridgii*), Douglas squirrel (*Tamiasciurus douglasii*), striped skunk (*Mephitis mephitis*), western harvest mouse (*Reithrodontomys megalotis*), and California vole (*Microtus californicus*). We pooled deer mice and brush mice into *Peromyscus* spp. because field differentiation was not accurate. A total of 380 individuals were marked with a PIT tag; 284 *Peromyscus* spp., 60 California ground squirrels, 13 Allen's chipmunks, 14 dusky-footed woodrats, 5 bushy-tailed woodrats, 3 Douglas squirrels, and 1 California vole. *Peromyscus* spp. was the most frequently captured species in Sherman traps (75% of all captures) whereas California ground squirrel was the most frequently captured species in Tomahawk traps (16% of all captures).

Average nightly capture success in Sherman traps ranged from 0.11 (retention patches) to 0.05 (control) for all small mammals combined (Table 2). *Peromyscus* spp. was most frequently captured in traps located in retention patches (average trap success 0.10) and least frequently captured (< 0.042) in clearcut-riparian and control land cover categories (Table 2). Average nightly captures for Allen's chipmunks in Sherman traps was low overall (< 0.004) with highest trap success in the two control land cover categories (Table 2). Tomahawk traps in clearcut-riparian had the highest trap success (0.085), whereas the lowest success was observed in the controls for all mammals combined (Table 2). We observed highest nightly trap success for California ground squirrels in clearcut-riparian (0.069), and lowest success (< 0.004) in the control cover categories (Table 2).

The random effect (i.e., trap web identifier) adequately accounted for spatial autocorrelation among traps (Appendix 1). We tested 18 candidate GLMMs for commonly captured species in Sherman and Tomahawk traps (Table 3.); we also ran

TABLE 3. Candidate generalized linear mixed models used to estimate the number of individual small mammals at individual trap locations in industrial forests of northern California, May–August 2011–13.

Candidate Models[a]	
1. Forb + Rock + Shrub	10. Grass + Downed Wood
2. Forb + Rock + Tree	11. Forb
3. Grass + Rock	12. Forest Litter
4. Rock + Tree	13. Grass
5. Forb + Shrub	14. Mineral Soil
6. Forb + Rock	15. Rock
7. Forb + Tree	16. Shrub
8. Rock + Shrub	17. Tree
9. Shrub + Downed Wood	18. Downed Wood

[a] Percent cover of forb, rock, tree, grass, shrub, downed wood, mineral soil, and forest litter around individual trap locations.

TABLE 4. Five top-ranking generalized linear mixed models used to estimate the number of individual small mammals (pooled across all species), *Peromyscus* spp., and Allen's chipmunks captured in Sherman traps on industrial forests of northern California, May–August 2011–13. K = the number of estimated model parameters, AICc = Akaike Information Criterion adjusted for small sample sizes, ΔAICc = difference in AIC from top-ranking model, and *w* = weight of evidence.

Species	Model	K	AICc	ΔAICc	*w*
All small mammals[a, b]	Downed Wood + Shrub	8	2635.23	0.00	0.54
	Shrub	7	2636.80	1.57	0.24
	Forb + Shrub	8	2638.78	3.54	0.09
	Rock + Shrub	8	2640.75	3.55	0.03
	Forb + Rock + Shrub	9	2640.75	5.52	0.03
Peromyscus spp.[b]	Shrub	7	2483.13	0.00	0.34
	Downed Wood + Shrub	8	2483.14	0.00	0.34
	Rock + Shrub	8	2484.91	1.78	0.14
	Forb + Shrub	8	2485.08	1.95	0.13
	Forb + Rock + Shrub	9	2486.85	3.71	0.05
Allen's chipmunk	Shrub	3	155.95	0.00	0.27
	Downed Wood + Shrub	4	157.09	1.14	0.15
	Forest Litter	3	157.18	1.23	0.15
	Rock + Shrub	4	157.58	1.63	0.12
	Forb + Shrub	4	157.93	1.98	0.10

[a] *Peromyscus* spp., dusky-footed woodrats, bushy-tailed woodrats, California voles, California ground squirrels, Allen's chipmunks, Douglas squirrels, and Trowbridge's shrews.

[b] Models also included year (2011, 2012, 2013) and category (clearcut, retention, clearcut-riparian, control, or control-riparian zone) factors if deemed significant via *a priori* Kruskal-Wallis rank sum test.

the models for pooled small mammal species by trap type. The top-ranking model for combined small mammal captures in Sherman traps included the proportion of shrub ($ß_1$) and downed wood ($ß_2$) per 64 m^2 and land cover category ($ß_3$ = retention; $ß_4$ = clearcut-riparian; $ß_5$ = control; $ß_6$ = control-riparian; Table 4). This model accounted for 54% of the evidence weight (Table 4.), with shrub and the retention category significant ($ß_1$ = 1.43, 95% CI = 0.86, 1.75; $ß_3$ = 0.44, 95% CI = 0.06, 0.83). This suggests that counts of individual small mammals captured in Sherman traps increased as proportions of shrub increased (Figure 1.) and that we caught more small mammals when a trap was placed in the retention land cover category.

We identified two top-ranking models for the number of individual *Peromyscus* spp. captured in Sherman traps that each accounted for 34% of the evidence weight (Table 4). One top-ranking model included the proportion of shrub ($ß_1$) per 64 m^2 and land cover category ($ß_2$ = retention; $ß_3$ = clearcut-riparian; $ß_4$ = control; $ß_5$ = control-riparian). In this model, both shrub and retention were significant ($ß_1$ = 1.39, 95% CI = 0.79, 1.99; $ß_2$ = 0.44, 95% CI = 0.05, 0.83). The other top-ranking model included the proportion of shrub ($ß_1$) and downed wood ($ß_2$) per 64 m^2, and land cover category ($ß_3$ = retention; $ß_4$ = clearcut-riparian; $ß_5$ = control; $ß_6$ = control-riparian; Table 4.) with the proportion of shrub and the retention land cover category significant ($ß_1$ = 1.44, 95% CI = 0.84, 2.05; $ß_3$ = 0.40, 95% CI = 0.01, 0.80). Both of these models indicated that the number of individual *Peromyscus* spp. at a trap increased as shrub cover increased (Figure 2.) and that more individual *Peromyscus* were captured in retention areas compared to clearcuts.

The top-ranking model for Allen's chipmunks captured in Sherman traps included shrub cover ($ß_1$) per 64 m^2. More individual Allen's chipmunks were captured as shrub cover increased at the trap locations ($ß_1$ = 2.99, 95% CI = 5.63,

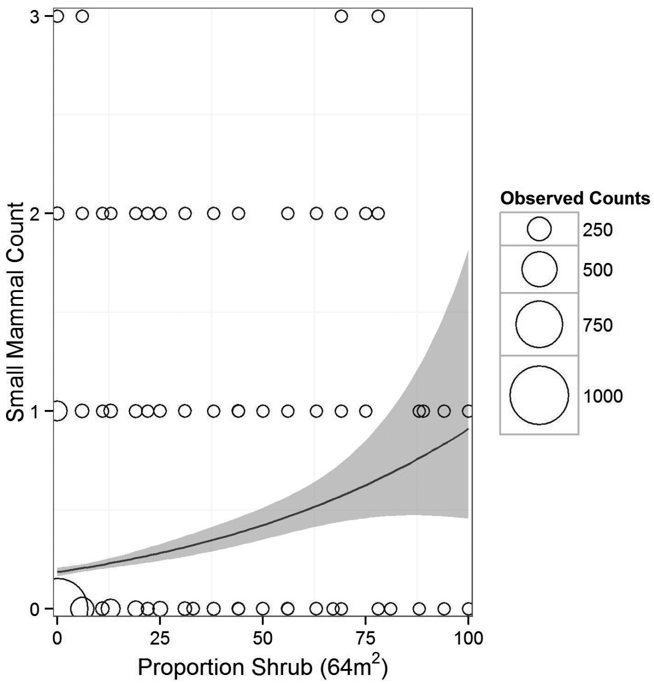

Figure 1. Small mammal counts and shrub cover within the 64 m^2 surrounding Sherman traps in industrial forests of northern California, 2011–2013. Shaded area represents the 95% confidence interval.

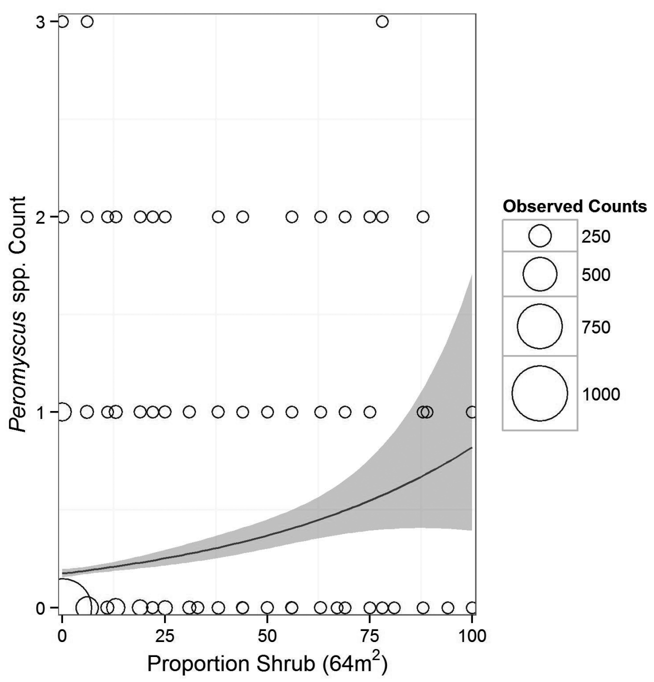

Figure 2. *Peromyscus* spp. counts and shrub cover within 64 m^2 surrounding Sherman traps in industrial forests of northern California, 2011–2013. Shaded area represents the 95% confidence interval.

0.34; Figure 3). We also identified four competing models (Table 4.), but only shrub cover was significant in any of these models.

In Tomahawk traps, a top-ranking model and two competing models were identified (i.e., ΔAICc < 2.0; Table 5). The top-ranking model included the proportion of shrub (ß$_1$; Figure 4a.) and downed wood (ß$_2$; Figure 4b.) within 64 m^2 plots, year (ß$_3$ = 2012, ß$_4$ = 2013), and land cover category (ß$_5$ = retention, ß$_6$ = clearcut-riparian, ß$_7$ = control, ß$_8$ = control-riparian). In this model only downed wood was significant (ß$_2$ = 1.55, 95% CI = 0.25, 2.86); as downed wood cover increased at Tomahawk trap locations the number of individual small mammals increased (Figure 4b). The top competing model consisted solely of the proportion of downed wood (ß$_1$) and this parameter was significant (ß$_1$ = 1.43, 95% CI = 0.12, 2.73). The 3rd ranked model from the Tomahawk traps included the proportion of forest litter (ß$_1$), which was also significant (ß$_1$ = –1.18, 95% CI = –2.34, –0.02); more forest litter resulted in lower small mammal captures in Tomahawk traps.

California ground squirrels were the most frequently captured species in Tomahawk traps. The top-ranking model for California ground squirrels included the proportion of forest litter (ß$_1$) in the 64 m^2 trap area indicating that individual California ground squirrel counts increased as the amount of forest litter decreased (ß$_1$ = –1.71, 95% CI = –3.25, –0.16; Figure 5). In a competing model, the proportion of downed wood (ß$_1$ = 1.98, 95% CI = 0.23, 3.73) and land cover category were significant; we captured more California ground squirrels as downed wood increased and fewer when traps were in controls compared to clearcuts.

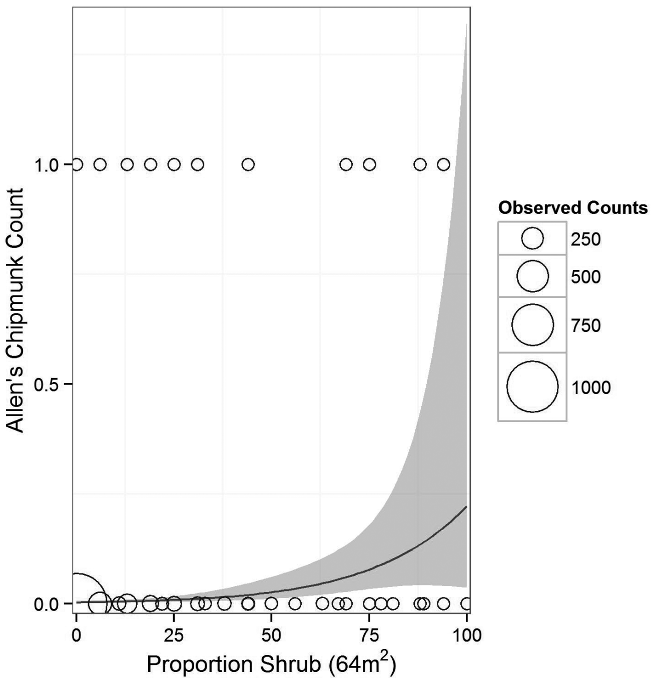

Figure 3. Allen's chipmunk counts and shrub cover within 64 m^2 surrounding Sherman traps in industrial forests of northern California, 2011–2013. Shaded area represents the 95% confidence interval.

Discussion

Our work offers two primary contributions to land managers tasked with considering small mammals in industrial forest landscapes of northern California: 1) small mammal response curves (i.e., Figures 1–5) that can be used to guide management of habitat structures at small scales (64 m^2), and 2) quantitative data on how retention patches and WLPZs contribute to small mammal abundance. For example, our results for Sherman traps indicated that small mammal counts are almost linearly related to shrub cover, so a 25% increase in shrub cover roughly corresponds to a 25% increase in small mammal counts (Figure 1). Our results for Tomahawk traps indicated that downed wood cover should be > 70% to positively affect small mammal counts (Figure 4b). We note that at the plot level in our study (i.e., 64 m^2), the effect of habitat structure on our observed small mammal

TABLE 5. Five top-ranking generalized linear mixed models used to estimate the number of individual small mammals and California ground squirrels caught in Tomahawk traps in industrial forests of northern California, May–August 2011–13. K = the number of estimated model parameters, AICc = Akaike Information Criterion adjusted for small sample sizes, ΔAICc = difference in AIC from top-ranking model, and *w* = weight of evidence.

Species	Model	K	AICc	ΔAICc	*w*
All small mammals[a,b]	Shrub + Downed Wood	10	581.81	0.00	0.25
	Downed Wood	9	582.25	0.44	0.20
	Forest Litter	9	582.39	0.58	0.19
	Grass + Downed Wood	10	583.87	2.06	0.09
	Shrub	9	584.87	3.06	0.05
California ground squirrel[b]	Forest Litter	9	410.04	0.00	0.28
	Downed Wood	9	410.61	0.57	0.21
	Mineral Soil	3	412.08	2.03	0.10
	Shrub + Downed Wood	10	412.09	2.04	0.10
	Grass + Downed Wood	10	412.59	2.55	0.08

[a] Captures of individual *Peromyscus* spp., dusky-footed woodrats, bushy-tailed woodrats, California ground squirrels, Allen's chipmunks, and Douglas squirrels.

[b] Models also included year (2011, 2012, 2013) and category (clearcut, retention, clearcut-riparian, control, or control-riparian zone) factors if deemed significant via *a priori* Kruskal-Wallis rank sum test.

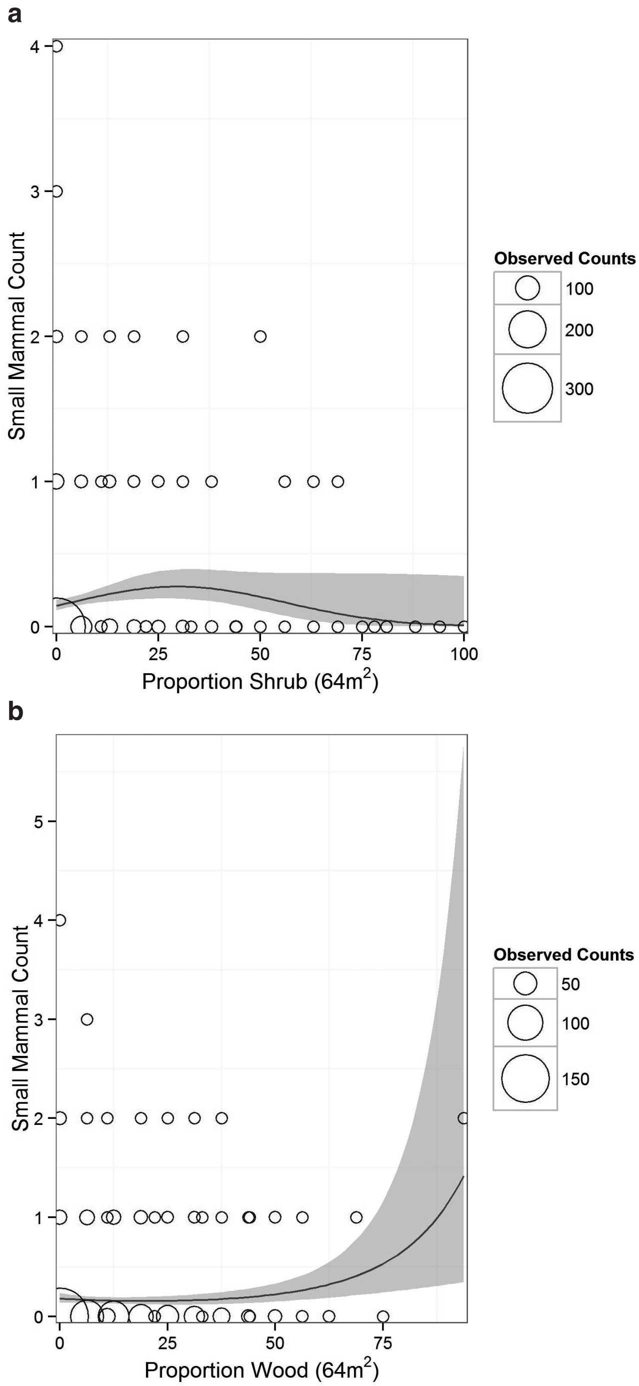

Figure 4. Small mammal counts and a) shrub cover and b) downed wood cover within 64 m^2 surrounding Tomahawk traps in industrial forests of northern California, 2011–2013. Shaded area represents the 95% confidence interval.

responses was small (typically < 1 individual animal), suggesting that multiple small-scale patches of habitat structure will be needed to have an ecologically meaningful effect on small mammal populations. Thus, our response curves can be used to understand the amount of habitat structure (e.g., shrub cover, downed wood cover) needed at small scales to impact small mammal populations and how many of those small scale patches would be required to elicit some larger population-level response.

Our results emphasized the importance of downed wood, shrub cover, and forest litter to small mammals, however some current forest practices reduce these habitat elements during clearcutting so various timber companies rely on WLPZs and the retention of green tree patches to provide important habitat elements. The application of herbicides to control competing vegetation lowers the amount of living woody and herbaceous vegetation during site preparation, although the herbicide effect typically lasts for < 5 years (Morrison and Meslow 1984, Harrington et al. 1995). Fire is also commonly used in some landscapes in northern California after clearcutting to release nutrients, however, burning also reduces vegetative cover and residual downed wood. We found that retention patches positively influenced counts of *Peromyscus* spp. and pooled small mammals. During forest management, retention patches are used to provide wildlife refuge and in some instances aid in seeding and regeneration after a site has been harvested. Our findings are consistent with others that have deemed retention areas an important component in sustaining small mammal populations (Moses and Boutin 2001, Rosenvald and Lohmus 2008, Lindenmayer et al. 2010). Some industrial forest landowners may question the contribution of retention to broader forest stewardship goals and our

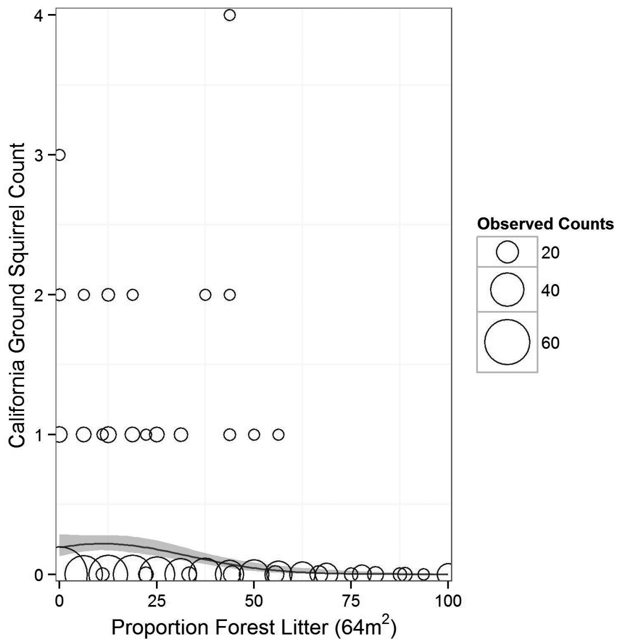

Figure 5. California ground squirrel counts and forest litter cover within 64 m^2 surrounding Tomahawk traps in industrial forests of northern California, 2011–2013. Shaded area represents the 95% confidence interval.

study provides evidence that fine-scale retention can positively affect small mammal communities.

During the 2011–13 field seasons, we captured 11 small mammal species in Sherman and Tomahawk live-traps on dry industrial managed forests in northern California. The most frequently captured species were *Peromyscus* spp. and California ground squirrels in Sherman and Tomahawk traps, respectively. Captures of small mammal species other than *Peromyscus* spp. were low thereby limiting the number of species-specific models that would converge. We found that shrub cover was positively correlated to the number of individual small mammals captured; this relationship held across multiple taxon and trap types. In Tomahawk traps, downed wood cover was also found to positively influence pooled small mammal counts. This result is consistent with other studies from drier environments of the western United States and Canada that collectively found that fine-scale retention of shrubs and downed wood positively affects small mammal habitat use (Manning and Edge 2004, Smith and Maguire 2004, Converse et al. 2006, Coppeto et al. 2006, Kalies et al. 2012). We further found that the land cover class at the trap location impacted small mammal captures, with higher small mammal counts recorded in retention areas. In contrast, counts of California ground squirrels were higher in clearcuts opposed to controls.

Our species-specific analyses found that *Peromyscus* spp. were positively associated with the presence of shrub cover and the retention land cover category. Research results on *Peromyscus* and its relationship with shrub and downed wood are variable. Smith and Maguire (2004) observed little response by deer mice to shrub cover. In contrast, other studies have found a positive response to shrub cover (Carey and Johnson 1995, Kyle and Block 2000). Research on deer mice in relation to retention practices contradict the relationship we observed. Sullivan and Sullivan (2001) found deer mice to be more abundant in clearcuts than in retention areas while other studies did not observe significant differences in deer mouse abundance between clearcuts and retention prescriptions (Klenner and Sullivan 2003, Sullivan et al. 2008).

We found that Allen's chipmunk captures in Sherman traps were positively influenced by the localized amount of shrub cover. Smith and Maguire (2004) found higher abundances of yellow-pine chipmunks (*Tamias amoenus*; a similar species to Allen's chipmunk) in areas of high shrub cover. It is likely that Allen's chipmunks rely on shrubs for forage and thermal cover. Chipmunks use shrubs as cover and have been observed placing burrows near the base of shrubs (Smith and Maguire 2004). In addition, shrubs are used to minimize heat exposure (Chappell 1978) and may produce edible nuts and berries.

We caught more individual California ground squirrels in areas with sparse ground obstruction, like leaves, bark, and downed wood. California ground squirrels tend to occur in open areas, likely related to their apparent affinity for disturbed areas and habitats where predators can be visually detected (Grinnell and Dixon 1918, Owings and Borchert 1975, Ordeñana et al. 2012). In our study area, recently harvested stands apparently provided the fine-scale features conducive to occupancy and use by California ground squirrels.

We acknowledge that the fine-scale habitat associations we documented for the pooled small mammal community were heavily influenced by the most frequently captured species, *Peromyscus* spp., hence our results should be cautiously applied to other species. We also used a web-based random effect as a proxy for unmeasured environmental conditions (e.g., weather, elevation) that are known to influence localized small mammal communities (Converse et al. 2006), but by sampling over 3 years and randomizing when stands were sampled we believe that these factors did not introduce substantial bias into our results.

Our findings underline the importance of fine-scale retained elements, primarily downed wood and shrub cover, on small mammal habitat use. We observed the downed wood effect at multiple scales, including the patch (~ 6.35ha; Gray 2014: Chapter 1) and micro-site (64 m^2; this study). Collectively these results indicate a close, multi-scale relationship between small mammal abundance and downed wood in dry managed forests. Downed wood is important to small mammals because it provides food, cover, and nesting sites (Hallet et al. 2003). Shrub cover also provides food and vertical cover for small mammal species. Retention of these features in an industrial forest could potentially increase small mammal abundance and diversity and contribute to management prescriptions for threatened and endangered predators. However, increasing habitat elements such as downed wood and shrubs in dry forest ecosystems will increase forest floor fuel and could potentially amplify risk of wildfire. Some of our results for downed wood and shrubs suggest that a moderate amount of retention may be optimal for small mammals (i.e., we observed a weak quadratic relationship) and thus we caution against a management philosophy that strives to leave downed wood in uniform abundance. Finding optimal amounts and the configuration of retention elements without increasing wildfire risk or compromising the ability of forest landowners to regenerate harvested sites for desirable tree species is valuable to forest managers. Our study provides insight into fine-scale retention practices that can be used to enhance small mammal habitat.

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