

Preliminary effects of fire and mechanical fuel treatments on the abundance of small mammals in the mixed-conifer forest of the Sierra Nevada

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Abstract

Many western conifer forests were historically affected by frequent, low- to mixed-severity fires. A legacy of fire suppression, logging, grazing and other factors has created current forest habitats that do not reflect historical conditions. The increasing size, severity, and costs of catastrophic forest wildfires are now focusing wildland management and research towards proactive fuel treatments designed to reduce fire hazards across landscapes. As part of the National Fire and Fire Surrogate (FFS) study, we researched the effects of three fuel treatments on small mammal populations within Sierra Nevada mixed-conifer forests. Twelve mixed-conifer stands were selected randomly from a set of available stands. Each stand was assigned to one of four treatment groups: controls, prescribed fire only, mechanical only, and mechanical plus fire combined. Abundance of California ground squirrels (*Spermophilus beecheyi*), long-eared chipmunks (*Tamias quadrimaculatus*), brush mice (*Peromyscus boylii*), and deer mice (*Peromyscus maniculatus*) were monitored both pre- and post-treatment. Only the deer mouse had a significant treatment effect. Deer mice abundance significantly increased from pre- to post-treatment within fire only and mechanical plus fire treatments, and declined within mechanical only treatments. All four species had a significant effect of year, with higher overall abundance in the post-treatment period. In addition to the experimental analysis, models containing stand-level covariates of vegetation and fuel characteristics were examined and compared using model selection procedures. The models only improved upon the experimental analysis for the brush mouse. Brush mice were found to have a positive association with stand-level canopy cover. Our results suggest that burning had a positive effect on deer mice and that mechanical only treatments had a negative effect. For the other three species, the dominant effect of year suggests that other, more regional factors may have affected abundance. Possible explanations included an increase in precipitation from pre- to post-treatment, a major cone crop in 2002, and a major decline in gray fox (*Urocyon cinereoargenteus*) occurrence. For the brush mouse, an evaluation of trap locations within stands indicates that this species was associated with dense clumps of tan oak (*Lithocarpus densiflorus*) or riparian areas. Leaving areas of dense low vegetation cover may benefit this species where fuel reduction treatments are implemented. Our study only documented the immediate impacts of fuel treatments and more research is needed to determine if our results will persist through time.

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1. Introduction

Many western conifer forests were historically affected by frequent, low- to mixed-severity fires (Biswell, 1989; Agee, 1993; Sugihara et al., 2006). Within Sierra Nevada Ponderosa pine (*Pinus ponderosa*) and mixed-conifer forest, fires historically burned at intervals of a few years to decades

(Biswell, 1989; Agee, 1993; Swetnam, 1993; Skinner and Chang, 1996; Taylor and Skinner, 1998; Taylor, 2000; Stephens and Collins, 2004; Moody et al., 2006). These frequent fires were a dominant force that helped shape forest structure and ecosystem processes. A legacy of fire suppression, logging, grazing and other factors has created current forest habitats that do not reflect historical conditions (SNEP, 1996). Few reference forests exist within the U.S. that have not been impacted by management or fire suppression (Stephens and Fulé, 2005). The lack of reference sites makes it difficult to predict what effects restoration treatments will have on forest wildlife species.

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The increasing size, severity, and costs of catastrophic wildfires are now focusing wildland management and research towards proactive fuel treatments designed to reduce fire hazards across landscapes (USDA-USDI, 2000; HFRA, 2003; Stephens and Ruth, 2005). Fuel treatments are designed to reduce surface fuels, reduce ladder fuels, and open the forest canopy (Weatherspoon, 2000; Agee and Skinner, 2005). Restoration via fire is an attempt to reintroduce a natural ecological process into the ecosystem. Mechanical treatments are an attempt to reduce fire hazard without the reintroduction of fire into the landscape. A combination of both mechanical followed by prescribed fire may provide the fastest pathway to restoration of the desired forest structure (Biswell, 1989). All of these treatments have been shown to reduce modeled fire behavior attributes such as intensity, severity, and scorching (Stephens and Moghaddas, 2005a), whereas a majority of traditional silvicultural treatments do not (Stephens and Moghaddas, 2005b). These fuel treatments may result in habitat changes that could affect local small mammal populations. With a lack of reference sites for comparison (Stephens and Fulé, 2005), it is important to research the effects of fuel treatments on wildlife prior to widespread application.

The objective of this study was to determine how three different fuel treatments (with a control) affect small mammal abundance within Sierran mixed-conifer forests (Mayer and Laudenslayer, 1988) of California. Treatments incorporated prescribed fire and mechanical harvesting alone and in combination. In general, treatments simplified surface fuel structure, removed a large portion of the forest midstory and understory vegetation (i.e. “ladder fuels”), and opened the forest canopy (Stephens and Moghaddas, 2005a,c; Kobziar et al., 2006; Collins et al., 2007; Moghaddas and Stephens, 2007). The goal was to determine if these changes to forest structure would result in changes in local small mammal relative abundance. Treatment effects were tested, and a set of models containing stand-level vegetation and fuel covariates in addition to treatment effects were also tested using a model selection framework (Burnham and Anderson, 2002). This study site was part of the larger Fire and Fire Surrogate (FFS) study, in which 13 sites across the U.S. received similar experimental treatments and conducted similar research protocols within forests that were once historically affected by frequent low- to mixed-severity surface fires (Weatherspoon, 2000).

2. Methods

2.1. Study location

The study was conducted in the Sierran mixed-conifer forest region (Mayer and Laudenslayer, 1988) in the north-central Sierra Nevada at the University of California Blodgett Forest Research Station (Blodgett Forest). Blodgett Forest is located at latitude 38°54'45"N, longitude 120°39'27"W, between 1100 and 1410 m above sea level, and encompasses an area of 1780 ha. Tree species in this area include sugar pine (*Pinus lambertiana*), Ponderosa pine, white fir (*Abies concolor*),

incense-cedar (*Calocedrus decurrens*) Douglas-fir (*Pseudotsuga menziesii*), California black oak (*Quercus kelloggii*), tan oak (*Lithocarpus densiflorus*), bush chinquapin (*Chrysolepis sempervirens*) and Pacific madrone (*Arbutus menziesii*). Major shrub species include: deerbrush (*Ceanothus integerrimus*), whitethorn (*Ceanothus cordulatus*), greenleaf manzanita (*Arctostaphylos patula*), and whiteleaf manzanita (*Arctostaphylos viscida*).

Fire was a common ecosystem process in the mixed-conifer forests of Blodgett Forest before the policy of fire suppression began early in the 20th century. Between 1750 and 1900, the median composite fire interval at the 9–15 ha spatial scale was 4.7 years with a fire return interval range of 4–28 years (Stephens and Collins, 2004). Forested areas at Blodgett Forest have been repeatedly harvested and subjected to fire suppression for the last 90 years reflecting a management history common to many forests in California (Laudenslayer and Darr, 1990; Stephens, 2000) and elsewhere in the Western U.S. (Graham et al., 2004).

2.2. Treatments

Twelve mixed-conifer stands (14–29 ha each) with similar stand structure, composition and management histories were selected randomly from a set of possible stands (completely randomized design). The stands considered for experimental selection were under group selection management. Group selection is a form of uneven-age silviculture where small (0.1–1.0 ha) patches are harvested periodically within a stand over a predetermined cutting cycle. Each stand had 20–30% of its area covered by group selection regeneration patches aged 0–30 years. Data from within group selection patches were not analyzed in this paper. Each selected stand was randomly assigned to four treatment groups: control (no manipulation), prescribed surface fire only, mechanical only (thinning and mastication combined), and mechanical plus fire. This resulted in three replicates for each of the four treatments. Work was conducted between July and August for 3 years from 2001 to 2003, with 2001 being the pre-treatment year. In 2002 the first stage of mechanical treatments were completed, and 2003 was the first year post-treatment. The total area for the 12 experimental units was 225 ha.

Control units received no treatment during the study period. Mechanical only treatment units had a two-stage treatment. In the fall of 2001, trees greater than 25 cm in diameter (DBH) were commercially thinned from below to maximize crown spacing while retaining 28–34 m² ha⁻¹ of basal area. In the fall of 2002 approximately 90% of understory conifers and hardwoods between 2 and 25 cm DBH were masticated in place using an excavator-mounted rotary masticator. Masticated material was not removed from the experimental units. Mechanical plus fire experimental units underwent the same treatment as mechanical only units, but in addition, they were prescribed burned using a backing fire (Martin and Dell, 1978) after the mechanical treatment was completed. Fire only units were burned with no pre-treatment using strip head-fires (Martin and Dell, 1978) and all burning was conducted during

a 15-day period (23 October 2002 to 6 November 2002) (Knapp et al., 2004). A full description of treatment implementation techniques and results is provided by Stephens and Moghaddas (2005a,c).

2.3. Vegetation data

Four stand-level fuel and vegetation characteristics were used in models for each small mammal species (see Section 2.5). The goal of the modeling was to determine if stand-level fuel and vegetation characteristics could improve on models containing only treatment effects (the experimental analysis). Many of the fuel and vegetation variables collected were highly correlated, and the four variables were chosen to represent different aspects of the treatments: overstory removal (canopy cover, %), ladder fuel removal (ladder fuel cover, %), the amount of coarse woody debris (CWD volume, $\text{m}^3 \text{ha}^{-1}$) and understory forage and cover characteristics (grass, forb, and shrub cover combined, %). Data were collected on 20 sampling plots centered within a 10 ha area within the each replicate stand (Stephens and Moghaddas, 2005a,c). Plots were systematically located 60 m apart and did not include group selection patches. Canopy cover was estimated using 25 site-tube measurements from a 5×5 grid (5 m spacing) centered on the plot (Gill et al., 2000). Ladder fuel cover was estimated by averaging the amount of live vegetation covering a 2.5 m high and 0.1 m wide cover board located at each cardinal direction 11.3 m from the plot center (Nudds, 1977). Coarse woody debris (CWD) were estimated at 10 of 20 sampling plots. At each plot, a random azimuth was chosen and CWD was measured within a $4 \text{ m} \times 20 \text{ m}$ belt transect (Bate et al., 2004). For each treatment unit, CWD percent cover per hectare, density per hectare, and volume per hectare were computed using equations described by Bate et al. (2004). CWD volume across all decay classes was the covariate used for analysis. Grass, forb and shrub species cover were estimated visually over a 0.04-ha plot in each inventory plot (Collins et al., 2007).

2.4. Small mammal sampling

Small mammal live-trapping was conducted along transects within each replicate stand. A grid-based sampling scheme was not possible due to the presence of group selection harvest units within each stand. Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, WI) were placed at 18 of 20 permanent vegetation sampling plots established within each replicate stand. Sampling plots were located an average of 60 m apart. Sherman live traps (9 in., H.B. Sherman Traps, Tallahassee, FL) were located at the same 18 sampling plots within each replicate, with 18 more traps located between the permanent plots along the transects. Sherman traps were thus located approximately 30 m apart. Trapping was conducted under U.C. Berkeley Animal Care and Use Committee guidelines.

Traps were baited with LabDiet 5001TM (PMI, St. Louis, MO) rodent food pellets and checked in the morning and evening for a total of nine consecutive days. Trapping was conducted between July and August each year, 2001–2003.

Each replicate stand was sampled once per year. Captured animals were batched marked; mice and chipmunks received a small (1 mm) ear notch, whereas squirrels were marked with animal marking paint. The decision to batch mark was based on previous low capture rates at Blodgett Forest (Barrett, unpublished data).

2.5. Data analysis

Data from 2002 were not used in this analysis. In 2002, all stands incorporating mechanical treatments were in various intermediate stages of treatment, and treatments incorporating fire were yet to be burned. In many cases mechanical treatments were being implemented during the actual trapping periods (one stand could not be sampled in 2002). Including 2002 would have included immediate disturbance effects of the treatment manipulation process. The comparison of pre- (2001) and post-treatment (2003) years provided the clearest comparison of actual short-term treatment effects.

For vegetation and fuel data, a one-way ANOVA tested for differences between variables during the pre-treatment period (2001). A one-way ANOVA was also performed on the change from 2001 to 2003 for each variable to test for differences among treatments. For this and all subsequent analyses, $\alpha = 0.10$. A Type I error rate of 0.1 was chosen to reduce the probability of committing a Type II error (concluding no significant difference when there is an actual difference).

Small mammal abundance for each replicate stand was calculated as a “catch per unit effort”. This was calculated as the number of unique animals marked per 100 trap nights, adjusted for inoperable traps. Because the animals were batch-marked and capture rates were low for each replicate, recapture probabilities could not be calculated (Otis et al., 1978). For most replicate stands, the number of unique animals captured per replicate per year was <10 individuals. Such low capture rates probably would have made the estimation of capture probabilities difficult (McKelvey and Pearson, 2001; Hammond and Anthony, 2006). Abundance estimates used in this analysis are thus an index of the actual population abundance. Abundance estimates used in this analysis are only valid if capture probability was similar among replicate stands. Because of this, data used in this analysis should be considered prospective and not confirmatory. New, more flexible methods involving covariates have recently been developed (White, 2005), and future studies should incorporate individual tags and attempt to estimate capture probability.

Abundance data did not conform to the assumptions of normality after various standard transformations. Trapping data were analyzed using generalized estimating equations (GEE's) for each species and implemented in SAS using the “proc GENMOD” procedure (SAS Institute Inc., 2000). Replicate stands were nested within treatment type, and time was a repeated measure. GEE's are particularly suited for the analysis of data based on counts (Liang and Zeger, 1986; Zeger and Liang, 1986; Pedan, 2001; Ballinger, 2004). Two analyses were performed. First, the experimental design was tested using “treatment”, “year” and the “treatment \times year” interaction.

Table 1
Comparison of pre- and post-treatment conditions (2001 vs. 2003) for variables used in generalized estimating equations (GEE) models (\pm S.E.)

Variable	Period	Control	Fire	Mech	Mech + fire
Canopy cover (%)	Pre	69.0 \pm 6.4	68.0 \pm 1.0	66.0 \pm 4.0	63.3 \pm 4.9
	Post	75.0 \pm 5.0 (a)	64.3 \pm 3.4 (a, b)	58.0 \pm 1.0 (b)	50.7 \pm 3.8 (b)
	Change	6.0 \pm 2.0 (a)	-3.7 \pm 2.8 (a, b)	-8.0 \pm 3.5 (b)	-12.7 \pm 2.3 (b)
Grass, forb, and shrub cover (%)	Pre	15.3 \pm 7.8	10.9 \pm 2.3	28.0 \pm 10.5	18.3 \pm 2.7
	Post	17.2 \pm 7.4	13.1 \pm 0.2	19.9 \pm 3.7	13.5 \pm 1.6
	Change	2.0 \pm 1.2	2.1 \pm 2.3	-8.1 \pm 6.9	-4.8 \pm 1.2
Ladder fuel cover (%)	Pre	20.3 \pm 4.7	22.8 \pm 3.3	30.3 \pm 6.2	16.8 \pm 6.2
	Post	20.1 \pm 4.0 (a)	2.5 \pm 0.7 (b)	14.0 \pm 6.0 (a, b)	2.2 \pm 0.1 (b)
	Change	-0.3 \pm 1.6 (a)	-20.3 \pm 3.7 (b)	-16.3 \pm 3.7 (b)	-14.6 \pm 6.2 (a, b)
CWD (m ³ /ha)	Pre	52.3 \pm 15.2	52.7 \pm 3.4	51.5 \pm 10.5	52.0 \pm 11.2
	Post	97.4 \pm 23.1 (a)	9.8 \pm 4.7 (b)	55.1 \pm 15.9 (a, b)	28.6 \pm 17.2 (b)
	Change	45.1 \pm 27.4 (a)	-42.9 \pm 4.5 (b)	3.6 \pm 10.5 (a, b)	-23.4 \pm 21.4 (a, b)

Data were analyzed in a one-way ANOVA for pre-treatment (2001), post-treatment (2003) and the change from pre- to post-treatment. Multiple comparisons were calculated using the Tukey honestly significant difference with $\alpha = 0.10$. For each variable, different letters indicate a significant difference across rows between treatment groups.

This analysis tested for treatment effects, with a significant “treatment \times year” interaction indicating potential differences in the responses of species to the treatments over time. A significant “year” effect indicates that overall abundance was different between pre- and post-treatment. A significant “treatment” effect indicates a difference between treatments across both pre- and post-treatment periods combined. For this analysis, the “treatment \times year” effect tests for a treatment effect and is of the main interest. Coefficients from the model were tested via the Wald chi-square statistic (X^2).

The second analysis included any significant terms from the treatment experimental analysis, with the addition of one of the fuel and vegetation characteristics (canopy cover, ladder fuel cover, CWD, and grass, forb and shrub cover combined). This analysis tested whether the measured covariates could improve upon the models containing only the significant terms from the experimental analysis in explaining abundance for each small mammal species. Significant terms from the experimental analysis were retained and included as terms in all of the covariate models. Models with only the significant experimental terms were treated as the “null” model in this analysis. First, a global model was fitted and tested for overdispersion. The overdispersion parameter from the global model was then used to adjust the reduced models (Burnham and Anderson, 2002). All models for each species conformed to the negative binomial distribution. Model selection was used to compare models using the quasi-likelihood information criterion, corrected for small sample size (QAIC_c) (Burnham and Anderson, 2002). Models were compared using Δ QAIC_c and model weights (w). Models with Δ QAIC_c values between 0 and 2 are considered to have substantial support but essentially no support when Δ QAIC_c > 10 (Burnham and Anderson, 2002). Model weights (w) are dependant on the model set, and are considered as evidence that the model is the best model given the model set (Burnham and Anderson, 2002).

3. Results

A one-way ANOVA determined that there were no significant differences ($\alpha = 0.10$) for the vegetation and fuel

variables during the pre-treatment year (Table 1). A one-way ANOVA was also performed on the change from 2001 to 2003 for each variable to test for amount of habitat change between the treatments. A one-way ANOVA on the change from pre- to post-treatment found significant differences between all treatments except for grass, forb, and shrub cover (Table 1). For canopy cover, the change was significant ($F_{3,11} = 8.70$, $p < 0.01$). Canopy cover in mechanical only and mechanical plus fire was significantly reduced compared to controls (Table 1). Change in canopy cover in the fire only treatment was similar to all treatments (Table 1). For ladder fuel cover, the change was significant ($F_{3,11} = 4.50$, $p = 0.04$), and cover was significantly reduced in the fire only and mechanical only treatments compared to controls (Table 1). Change in ladder fuel cover in the mechanical plus fire treatment was similar to all treatments (Table 1). The change in CWD volume was significant ($F_{3,11} = 4.40$, $p = 0.04$), and CWD was reduced in the fire only treatment compared to controls (Table 1).

The California ground squirrel (*Spermophilus beecheyi*) was the most abundant small mammal captured between in 2001 and 2003 (Table 2). The total number of unique individuals captured was 62 and 133 within the pre- and post-treatment periods, respectively. Deer mice (*Peromyscus maniculatus*) were the next most abundant species with 48 and 61 unique individuals marked in 2001 and 2003, respectively. Fifteen and 61 long-eared chipmunks (*Tamias quadrimaculatus*) were marked in 2001 and 2003, respectively. Brush mice (*Peromyscus boylii*) were the least abundant species captured, with 23 and 44 individuals marked between pre- and post-treatment periods, respectively. Other species captured included: Trowbridge’s shrew (*Sorex trowbridgii*), black-tailed jackrabbit (*Lepus californicus*), western gray squirrel (*Sciurus griseus*), Douglas squirrel (*Tamiasciurus douglasii*), western spotted skunk (*Spilogale gracilis*), and striped skunk (*Mephitis mephitis*).

The abundance of California ground squirrels was similar between treatments across years ($X^2_3 = 0.43$, $p = 0.93$, Table 2). The abundance of California ground squirrels did differ ($X^2_1 = 5.85$, $p = 0.02$) between pre- and post-treatment years, with abundance increasing across all treatments including the

Table 2
Abundance of small mammal species (# per 100 trap nights \pm 1 S.E.) by treatment and year (2001 and 2003)

Species and year	Control	Fire	Mech	Mech + fire	Treatment	Year	Treatment \times year
California ground squirrel (<i>Spermophilus beecheyi</i>)							
2001	3.7 \pm 0.9	4.2 \pm 1.5	2.6 \pm 0.5	3.2 \pm 2.2	$X_3^2 = 0.43, p = 0.93$	$X_1^2 = 5.85, p = \mathbf{0.02}$	$X_3^2 = 2.99, p = 0.39$
2003	5.7 \pm 2.5	7.6 \pm 2.5	11.0 \pm 4.4	8.0 \pm 2.7			
Long-eared Chipmunk (<i>Tamias quadrimaculatus</i>)							
2001	0.2 \pm 0.2	0.7 \pm 0.4	0.7 \pm 0.4	0.0 \pm 0.0	$X_3^2 = 1.86, p = 0.60$	$X_1^2 = 4.71, p = \mathbf{0.03}$	NA
2003	1.7 \pm 1.7	1.7 \pm 1.1	2.4 \pm 1.7	2.1 \pm 1.1			
Brush mouse (<i>Peromyscus boylii</i>)							
2001	1.7 \pm 1.5	0.1 \pm 0.1	0.6 \pm 0.3	0.3 \pm 0.2	$X_3^2 = 2.83, p = 0.42$	$X_1^2 = 4.03, p = \mathbf{0.04}$	$X_3^2 = 3.26, p = 0.35$
2003	1.8 \pm 1.3	1.4 \pm 1.1	1.4 \pm 0.7	0.2 \pm 0.1			
Deer mouse (<i>Peromyscus maniculatus</i>)							
2001	1.9 \pm 1.0	0.5 \pm 0.1	2.0 \pm 0.6	0.2 \pm 0.1	$X_3^2 = 3.42, p = 0.33$	$X_1^2 = 5.22, p = \mathbf{0.02}$	$X_3^2 = 7.54, p = \mathbf{0.06}$
2003	1.3 \pm 0.7	2.0 \pm 0.4	1.2 \pm 0.2	2.3 \pm 0.9			

Statistical results are from generalized estimating equations (GEE's). Significant results are in bold ($p < 0.10$). In 2001, no stands were manipulated. In 2003, all treatments were completed prior to sampling.

control (Table 2). California ground squirrels were at their highest abundance across all years and treatments in the mechanical only treatment in 2003 (Table 2). The interaction effect, treatment \times year, was not significant ($X_3^2 = 2.99, p = 0.39$), confirming a similar response for all treatments across years (Table 2).

The abundance of long-eared chipmunks was similar between treatments across years ($X_3^2 = 1.86, p = 0.60$, Table 2). The abundance of long-eared chipmunks differed significantly ($X_1^2 = 4.71, p = 0.03$) between pre- and post-treatment, with abundance increasing across all treatment groups and the control from pre- to post-treatment (Table 2). Chipmunks reached their highest recorded abundance in the mechanical only treatment in 2003 (Table 2). In the mechanical plus fire treatment, chipmunks increased the most, increasing from 0 in the pre-treatment period to 2.1 chipmunks/100 trap nights in the post-treatment period (Table 2). Testing the treatment \times year interaction was not possible, as the analysis did not converge, but visual examination of the changes indicates that all treatments responded similarly through time (Table 2).

The abundance of brush mice was similar between treatments across years ($X_3^2 = 2.83, p = 0.42$, Table 2). Brush mice abundance was significantly ($X_1^2 = 4.03, p = 0.04$) higher in the post-treatment year (Table 2). Brush mice abundance was highest in the control across both pre- and post-treatment periods (Table 2). Brush mice abundance reached their highest levels in 2003 for the control, fire only, and mechanical only treatments. Abundance remained low across all years in the mechanical plus fire treatment (Table 2). The test for interactions was not significant ($X_3^2 = 3.26, p = 0.35$).

The abundance of deer mice was similar between treatments across years ($X_3^2 = 3.42, p = 0.33$, Table 2). Deer mouse abundance was significantly ($X_1^2 = 5.22, p = 0.02$) higher post-treatment (Table 2). Deer mice exhibited significant ($X_3^2 = 7.54, p = 0.06$) varying patterns in abundance between treatments and years (treatment \times year interaction) (Table 2). Both the control and mechanical only treatments decreased in abundance, whereas treatments incorporating fire (fire only and

mechanical plus fire) increased from pre- to post-treatment (Table 2). The change in abundance from pre- to post-treatment was significantly positive for the fire only ($p < 0.01$) and mechanical plus fire ($p < 0.01$) treatments and negative for the mechanical only treatment ($p < 0.01$). The change from pre- to post-treatment for controls was not significant ($p = 0.37$).

Models containing stand-level variables and any significant term from the experimental analysis (Table 2) were fitted and compared using ΔQAIC_c for each species (Table 3). Significant experimental terms (treatment, year, treatment \times year) formed the "null" model for each species, and were included in each subsequent model containing stand-level covariates. For the California ground squirrel, the null model (year) received the most support ($w = 0.27$, Table 3). Model selection was poor, however, and all models were within $\Delta\text{QAIC}_c < 2.0$. For the long-eared chipmunk, model selection also failed to distinguish between any models (Table 3). All five models had $\Delta\text{QAIC}_c < 2.0$. For the brush mouse, the model containing canopy cover had the highest weight ($w = 0.68$). The coefficient was positive, indicating higher abundance with increasing canopy cover (Table 3). For the deer mouse, the null model (treatment, year, treatment \times year) had the highest weight ($w = 0.36$). Models containing stand-level variables did not improve over the null model for the deer mouse (Table 3).

4. Discussion

4.1. Habitat features

The treatments affected at least one treatment group relative to controls for canopy cover, ladder fuel cover, and CWD volume (Table 1). These results were not unexpected due to the directional nature of the treatments. For canopy cover, both fire and mechanical treatments removed overstory trees via mortality or selective harvest. For ladder fuel cover, fire reduced live vegetation via scorching or mortality, and mechanical methods removed small trees via mastication. For CWD, fire removed dead and down material through combustion. The mechanical only treatment had no effect on

Table 3
Results of habitat models from generalized estimating equations (GEE's)

Model	QAICc	Δ QAICc	w
California ground squirrel (<i>S. beecheyi</i>)			
Null (year)	-455.33	0	0.27
Null + ladder fuel (-)	-455.10	0.23	0.24
Null + grass, forb, and shrub (-)	-454.42	0.92	0.17
Null + coarse woody debris (-)	-454.27	1.06	0.16
Null + canopy cover (-)	-454.17	1.16	0.15
Long-eared chipmunk (<i>T. quadrimaculatus</i>)			
Null (year)	-91.52	0	0.28
Null + grass, forb, and shrub (+)	-91.26	0.26	0.25
Null + coarse woody debris (-)	-90.54	0.98	0.17
Null + ladder fuel (-)	-90.28	1.23	0.15
Null + canopy cover (-)	-90.25	1.26	0.15
Brush mouse (<i>P. boylii</i>)			
Null + canopy cover (+)	-51.72	0	0.68
Null + grass, forb, and shrub (-)	-49.53	2.20	0.23
Null (year)	-45.82	5.90	0.04
Null + ladder fuel (+)	-45.53	6.19	0.03
Null + coarse woody debris (+)	-44.69	7.03	0.02
Deer mouse (<i>P. maniculatus</i>)			
Null (Trt + year + Trt \times year)	-65.61	0	0.36
Null + grass, forb, and shrub (-)	-65.22	0.39	0.29
Null + coarse woody debris (-)	-64.27	1.34	0.18
Null + canopy cover (-)	-63.16	2.45	0.10
Null + ladder fuel (+)	-62.28	3.33	0.07

Species-specific null models consisted of significant terms from the experimental analysis (Table 2). Overdispersion was calculated from the global model and used to adjust QAICc. Signs in parentheses indicate the value of the regression coefficient.

CWD. Although masticated material was left on site, mastication primarily produced material of a smaller size class than what would be classified as CWD (Bate et al., 2004). Understory vegetation (grass, forb, and shrub cover) was not affected by the treatments (Table 1). However, understory vegetation cover was measured less than 1 year post-treatment, and results may diverge through time. A more detailed analysis of changes in vegetation and habitat features at Blodgett Forest is provided elsewhere (Stephens and Moghaddas, 2005a,c; Apigian et al., 2006; Kobziar et al., 2006; Collins et al., 2007; Moghaddas and Stephens, 2007).

4.2. Experimental results

In the experimental analysis, year (pre-treatment vs. post-treatment) was significant for all four small mammal species investigated in this study (Table 2). All four species had higher overall abundance in the post-treatment year when compared to the pre-treatment year. Only deer mice had a significant treatment \times year interaction. Although deer mice were more abundant in 2003 vs. 2001, abundance declined in the mechanical only and control treatments and increased in the fire only and mechanical plus fire treatments (Table 2). Of all the species analyzed in this study, the deer mouse has been the most extensively studied.

The deer mouse is a habitat generalist and is found in many different western forest types and seral stages (Grinnell and

Storer, 1924; Jameson, 1951; Martin and McComb, 2002; Coppeto et al., 2006). In other forest studies, deer mice have generally responded positively (Tester, 1965; Beck and Vogl, 1972; Bock and Bock, 1983; Kyle and Block, 2000; Carey and Wilson, 2001; Klenner and Sullivan, 2003; Suzuki and Hayes, 2003; Muzika et al., 2004; Fantz and Renken, 2005; Perry and Thill, 2005; Greenberg et al., 2006) or minimally (Cole et al., 1998; Waters and Zabel, 1998; Moses and Boutin, 2001; Converse et al., 2006a,b; Craig et al., 2006; Monroe and Converse, 2006) to either forest burning or thinning. A similar pattern was observed across a review of eight other FFS sites, with only one negative response being recorded (Converse et al., 2006b). Based on previous studies within forest ecosystems, the positive response of deer mice to burning at Blodgett Forest is not unexpected, however the negative response to the mechanical only treatment is relatively unexpected.

At Blodgett Forest, both fire and mechanical treatments opened up the forest canopy and midstory (Table 1) (Stephens and Moghaddas, 2005a), but burn treatments also reduced CWD (Table 1) (Stephens and Moghaddas, 2005c) and increased bare mineral soil exposure (Collins et al., 2007; Moghaddas and Stephens, 2007). Food supplementation experiments within burned and unburned grasslands have found greater foraging rates for nocturnal rodents (in which *P. maniculatus* was an abundant species) within burned grasslands (Reed et al., 2004, 2005). At Blodgett Forest, deer mice might have had greater foraging efficiency within burned stands, which may have resulted in higher survival or fecundity, resulting in higher abundance. However, CWD and shrub structure have been found to be important for deer mice while foraging, with mice removing more seeds near structure than from open areas (Roche et al., 1999; Orrock et al., 2004). The use of CWD and other ground structure is believed to reduce exposure to predation. At Blodgett Forest, CWD in the mechanical only stands did not change from pre- to post-treatment (Table 1) (Stephens and Moghaddas, 2005c). However, from pre- to post-treatment 90% of trees between 2 and 25 cm DBH were masticated and the material was left on-site. A significant amount of new ground structure was available despite overstory and midstory tree removal. Coarse woody debris have been cited as important habitat factors for forest-dwelling small mammals, although recent studies on deer mice have been equivocal (Smith and Maguire, 2004; Craig et al., 2006).

It is possible that masticated material left from the mechanical only treatment may have negatively affected deer mice populations at Blodgett Forest. Larger masticated material typically consisted of shards of timber 0.1–1.0 m long and 6–12 cm in DBH. However, smaller material and many small branches with leaves were scattered amongst the larger masticated material. This created a complex structure of relatively small pieces of CWD and smaller fuels. Deer mice have been shown to have a preference for less complex ground surfaces for foraging (Kaufman and Kaufman, 1990; Clark et al., 1991; Reed et al., 2004, 2005), and it is possible that the increase of smaller fuel pieces in mechanical only stands may have negatively affected deer mice foraging efficiency.

For the three other species (California ground squirrel, long-eared chipmunk, and brush mouse), only the year effect was significant (Table 2). Across all treatments combined, these species had a higher abundance in the post-treatment year. At Blodgett Forest, the maximum total linear distance between all replicate stands was 6 km, and many stands were within 1 km of a few other replicate stands. A significant year effect indicates that factors other than treatments likely had a greater affect on the entire population of small mammals at Blodgett Forest. Possible explanations could include weather, seed crops, or changes in predator populations.

Precipitation increased annually from 2001 to 2003 at Blodgett Forest. Total annual precipitation preceding trapping sessions increased from 105 to 130, to 136 cm, 2001 to 2003, respectively (measured from July 1 to June 30th). These amounts were 64%, 81%, and 84% of average rainfall for Blodgett Forest (Blodgett Forest weather station data, 1961–2003). Major sugar pine and moderate Ponderosa pine and Douglas-fir cone crops occurred in 2002 (Frieder Schurr, Blodgett Forest, personal communication). Increased precipitation and cone crop events may have increased the availability of seeds and vegetation across the landscape. Small mammals are known respond positively to food supplementation experiments, and annual increases may have been a result of increased survival, reproduction, reduced territory size, or increased predator vigilance (Koskela et al., 1998; Arenz and Leger, 2000; Dobson and Oli, 2001; Yunger, 2002; Diaz and Alonso, 2003; Huitu et al., 2003; Unangst and Wunder, 2004). Finally, gray fox (*Urocyon cinereoargenteus*) occurrence declined from 53% to 37% to 10% from 2001 to 2003 (Amacher, unpublished camera trap data). Predation is often cited a major limiting factor for small mammal populations, and predator exclusion experiments have shown positive responses from small mammal populations (Klemola et al., 2000; Norrdahl et al., 2002; Yunger, 2004).

An increase in precipitation and cone seed production, coupled with a decrease in a common predator may have helped account for the major effect of year observed for all four species. Simultaneous “top-down” and “bottom-up” effects may have acted to increase small mammal populations across all of Blodgett Forest. However, these explanations are anecdotal. The experiment was designed to test the effects of fuel treatments. The potential causes for year effects are uncontrolled and correlative. The only reasonable conclusion that can be reached from this study is that one or more experimentally uncontrolled factors likely had a greater effect than fire and thinning treatments at Blodgett Forest (Table 2). Longer-term study would be required to determine if treatment stands will diverge in abundance through time.

4.3. Model results

The vegetation and fuel covariate models improved on the experimental models for only the brush mouse (Table 3). For brush mice, the year plus canopy cover model received the most support ($w = 0.68$). However, this result was likely an artifact of the experimental design. Brush mice were primarily captured

in three replicate stands during both pre- and post-treatment periods. All three of these stands had high canopy cover and a high component of tan oak relative to other replicate stands. An inspection of the trap locations within stands found that most brush mouse trappings occurred near riparian areas or tan oak clusters. Brush mice are commonly captured in areas with a high amount of brush or dense, low tree canopy cover (Grinnell and Storer, 1924; Jameson, 1951; Wilson, 1968; Holbrook, 1978; Kalcounis-Rüppell and Millar, 2002; Block et al., 2005). If tan oak relative dominance were added to the analysis post hoc, the null plus tan oak model would have a $w = 0.70$, and canopy cover would be reduced to $w = 0.24$ as the second highest model. At Blodgett Forest, shrub species are sparse within the replicate stands, although dense within some group selection patches within the replicate stands. Within the mature forest, dense patches of low cover are primarily provided by tan oak, California black oak or bush chinquapin clumps. Our results suggest that fuel treatments that significantly reduce low cover of shrubs or trees may have a negative impact on brush mice. Riparian areas that are not harvested or patches of untreated forest with low tree or shrub cover may provide valuable habitat for this species.

5. Conclusions

Only one out of four species, the deer mouse, showed potential effects from forest fuel reduction treatments. Deer mice increased from pre- to post-treatment within the fire only and mechanical plus fire treatments, and decreased in the control and mechanical only treatments. The positive response to fire is generally supported by previous research, however the negative response to the mechanical treatments is of interest. It is possible that an increase of small, masticated material may have had a negative impact on deer mice. More intensive study is needed to confirm this.

Year was the most important factor for the California ground squirrel, long-eared chipmunk, and brush mouse. This indicates that regional factors might have been affecting these small mammal populations at Blodgett Forest. All three of these species were more abundant in the post-treatment period. The period between pre- and post-treatment had higher precipitation, major cone crop events, and a reduction in gray fox occurrence. One or a combination of these factors may have accounted for the global increase of small mammals from 2001 to 2003.

Models involving canopy cover improved on the experimental model for the brush mouse. The brush mouse appeared to be located primarily in areas with high tan oak or riparian canopy cover. Most captures were within the three replicate stands with the highest amount of tan oak density and cover, and individual trapping locations were located within or near tan oak clumps or riparian areas. Leaving patches of dense cover, or untreated riparian areas may be beneficial for brush mice within forests being treated for fuel reduction.

The experiment at Blodgett Forest documented the effects of fuel treatments over a small time frame (1 year pre, 1 year post) and seasonal period (July–August). This might only represent

the immediate effects of fuel treatments. It is unknown whether increases within treatments were from emigration, dispersal, increased reproduction, increased survival, reduced competition, changes in predator populations, or differential capture probabilities. More intensive study would be required to determine which of these factors, if any, were responsible for changes in abundance. The importance of year effects in this study also highlights the need for longer-term study. Observing population changes annually across all treatments may help tease out whether regional effects are more important, or if habitat changes within treatments might cause divergence in abundance through time. Finally, the replication of this experiment was relatively low, and the low replication may not have captured the natural variability within stands across all treatment groups.

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