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The effects of early season and late season prescribed fires on small mammals in a Sierra Nevada mixed conifer forest

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Abstract

Prescribed fire is an important management tool used in the restoration of Sierra Nevada mixed conifer forests where fire has been suppressed over the last century. It is not well known, however, how the timing of prescribed fire affects wildlife populations. We used model selection and multi-model inference methods to compare the effects of early (spring and early summer) and late (late summer and fall) season prescribed fires on small mammal populations, based on 4 years of mark-recapture data collected in Sequoia National Park, California. The effects of prescribed fires on four small mammal metrics were evaluated: deer mouse (*Peromyscus maniculatus*) densities, deer mouse age ratios, lodgepole chipmunk (*Neotamias speciosus*) densities, and total small mammal biomass. For each of these four metrics, the top ranked model in the evaluation of prescribed fire treatment effects contained no prescribed fire effects, but did contain effects of strong year-to-year variation in populations. Models which predicted that fire effects differed depending on the season of fire received only limited support for each of the four metrics. Our results suggest that initial prescribed fires set during the early season will have similar impacts as late season fires on deer mouse populations, lodgepole chipmunk populations, and total small mammal biomass in Sierra Nevada mixed conifer forests.
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Keywords: Fire season; Conifer forest; Small mammal; *Peromyscus*; *Neotamias*; Mark-recapture; Population density

1. Introduction

The importance of reintroducing fire to fire-adapted forests to maintain forest health and to reduce catastrophic wildfires has been widely recognized in recent years (Pruden and Brennan, 1998). How the process of fire should be reintroduced is less certain, particularly since many fire-suppressed forests have developed dramatically different structures than they historically possessed when fire was more frequent (e.g. Parsons and DeBenedeti, 1979; Covington and Moore, 1994). One important issue to be considered is the timing of prescribed fires. Historically, Sierra Nevada mixed conifer forests burned most frequently during the late season (late summer and early fall), when lightning is more common and fuels are drier (Caprio and Swetnam, 1995; Schwilk et al., 2006). Managers often try to mimic this by setting prescribed burns during the late season. However, in forests where fuel loads have accumulated to unnaturally high levels, initial prescribed fires during the late season may be more severe than historic late season fires. Additionally, concerns over the effects of late season prescribed fires on regional air quality, due to the typically stable atmospheric conditions during the fall, have prompted interest in burning more frequently during the early season (spring and early summer; Cahill et al., 1996). Burning earlier in the season may be desirable, particularly for an initial prescribed burn following years of fire suppression, but the ecological consequences of burning during different seasons in mixed conifer forests are not well known.

Small mammals are critical ecosystem components in mixed conifer forests, where they constitute the prey base for many forest predators (Zeilinski et al., 1983; Williams et al., 1992), influence the structure of the vegetative community through seed predation and dispersal (Vander Wall, 1993; Hollander and Vander Wall, 2004; Schnurr et al., 2004), and play an essential role as dispersers of ectomycorrhizal fungi (Pyare and

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Longland, 2001). Small mammal populations can be affected by prescribed fire via direct mortality or indirectly via habitat alteration (Brennan et al., 1998). The amount of direct mortality may depend on the intensity of the fire, as well as the physiological status of the small mammals at the time of the fire (e.g. breeding versus non-breeding). Early season prescribed fires set when many small mammals are reproducing may cause direct mortality significant to the population, particularly for ground nesting species or species that reproduce only once a year during the spring (Erwin and Stasiak, 1979; Smith, 2000). However, habitat alteration by fire often may have a greater impact on small mammal populations than direct mortality from fire (Lyon et al., 1978; Kaufman et al., 1990; Jones, 1992; Smith, 2000). Slocum et al. (2003) found that Florida savanna fires set during the wet season were less intense and patchier than fires during the dry season. Similarly, fires during the early season in a Sierra Nevada mixed conifer forest consumed less fuel, were patchier, and covered less surface area than fires in the late season (Knapp et al., 2005). Areas burned during the early season retained greater cover of coarse woody debris, an important habitat feature for several small mammal species (Lee, 2004; Manning and Edge, 2004), than did areas burned later in the season (Knapp et al., 2005). Similarly, areas burned in the early season had greater understory plant cover 1 year post-fire than did areas burned in the late season (Knapp et al., in press). The season of prescribed burning was also shown to affect the amount of shrub mortality in Sierra Nevada mixed conifer forests (Kauffman and Martin, 1985). Impacts such as these on the structure and composition of vegetative communities depending on the season of fire may have large effects on the amount and quality of food and cover available to small mammals.

Common small mammal species in Sierra Nevada mixed conifer forests are lodgepole chipmunks (*Neotamias speciosus*) and deer mice (*Peromyscus maniculatus*; Jameson and Peeters, 2004). Lodgepole chipmunks are omnivorous, reproduce once a year in the spring, and are commonly found in habitats with partially open canopies and with coarse woody debris, shrubs, and/or rocky areas for cover (Ream, 1981; Best et al., 1994). The fire response of lodgepole chipmunks is not well known, although least chipmunk densities (*N. minimus*) were not affected by a severe wildfire in a ponderosa pine (*Pinus ponderosa*) forest (Converse et al., in press). Eastern chipmunks (*Tamias striatus*) also were not impacted by spring fire in a central Appalachian forest (Rowan et al., 2005), but declined in number following wildfire in a jack-pine (*Pinus banksiana*) forest except where seeds were abundant (Krefting and Ahlgren, 1974). Deer mice are generalists with wide habitat and diet tolerances and strong colonizing abilities (Baker, 1968). With a short gestation time of about 25 days, this species typically has several litters of 3–5 young a year (Layne, 1968). Deer mice appear to take advantage of the increased seed abundance and/or detectibility of seeds from litter removal following fire, and often respond positively to fire (Ream, 1981; Kaufman and Kaufman, 1989; Jones, 1992). However, a few studies have found negative or neutral responses to fire by deer mice (e.g. Gunther et al., 1983; Groves and Steenhof, 1988; Ford et al., 1999). Small mammal species less commonly captured in Sierra Nevada mixed conifer forests include brush mice (*Peromyscus boylii*), long-tailed voles (*Microtus longicaudus*), northern flying squirrels (*Glaucomys sabrinus*), and golden-mantled ground squirrels (*Spermophilus lateralis*). Little is known about the effects of fire on these species.

A factor complicating the study of the effects of fire on small mammals is that most previous studies have used abundance indices, such as minimum number alive or catch per unit effort, to evaluate fire effects. Relative abundance indices often are biased estimates of actual abundance since they do not account for differences in detection probabilities that are likely in small mammal trapping studies; these include differences in detection probabilities between individual animals, over time, or in response to an experimental treatment (Nichols, 1992). The common use of kill-trapping in small mammal-fire effects studies also is problematic, as the impact of fire on population dynamics is difficult to distinguish from the added impact of the kill-trapping mortality (Sullivan et al., 2003). Many studies of fire effects on small mammals also suffer from lack of replication, lack of pre-disturbance data, and/or lack of randomization (Kaufman et al., 1990).

The purpose of our research was to evaluate whether the timing of prescribed fires differentially affected small mammal populations (Monroe, 2005). We examined four metrics for prescribed fire effects: deer mouse densities, deer mouse age ratios, lodgepole chipmunk densities, and total small mammal biomass. Capture–recapture modeling was used to estimate these metrics to ensure they were not confounded by varying detection probabilities. We considered three possible consequences of the prescribed fires on each metric. These included no effect of fire on the metric, a similar effect of fire regardless of the season of the fire, and a different effect depending on the season of the fire. We used model selection and multi-model inference methods to evaluate these possible outcomes for each metric, with the goal of providing information to assist resource managers in making the complicated decisions of how to restore forests with fire.

2. Materials and methods

2.1. Study site and treatments

This study was a component of the National Fire and Fire Surrogates project (Weatherspoon and McIver, unpublished report, 2000). Our study site was located in Giant Forest, an old-growth mixed conifer forest in Sequoia National Park in the southern Sierra Nevada of California. Tree species on the experimental units included, in order of decreasing abundance, white fir (*Abies concolor*), sugar pine (*Pinus lambertina*), incense cedar (*Calocedrus decurrens*), red fir (*A. magnifica*), Jeffrey pine (*Pinus jeffreyi*), ponderosa pine (*Pinus ponderosa*), mountain dogwood (*Cornus nuttallii*), and California black oak (*Quercus kelloggii*). The last major fire at the site before the onset of this study occurred in 1879 (Schwilk et al., 2006). The historic (pre-European settlement) fire regime at the site consisted of fairly frequent (average fire return interval of 27

years), low to moderate intensity, and patchy fires that most commonly burned in the late summer or early fall (Caprio and Swetnam, 1995; Schwilk et al., 2006).

The three treatments applied in this study were late season (fall) prescribed burn, early season (spring) prescribed burn, and no burn (control). We randomly assigned three replicates of each of these treatments to nine experimental units (Fig. 1). Experimental units were 15–20 ha in area, and consisted of a core measurement area of at least 4.5 ha and a surrounding buffer strip that was at least 50 m wide; both the core measurement area and the buffer strip received the assigned treatment. Experimental units were located in proximity to one another (ranged from 100 to 500 m apart) at similar elevations (1900–2150 m), slopes (15–25°), and aspects (west to north-west). Late season prescribed fire treatments were conducted on 28 September, 17 October, and 28 October 2001. Early season prescribed fire treatments were conducted on 20 June and 27 June 2002. All fire treatments were low- to moderate-intensity ground fires. Details of the implementation of the prescribed fire treatments are provided in Knapp et al. (2005).

2.2. Trapping methods

We collected pre-treatment data on small mammals from 9 June–12 August 2001. At each experimental unit, trapping was conducted on a 7 × 7 grid with 25 m spacing between stations. A single extra long Sherman live trap (XLK folding trap; 7.6 cm × 9.5 cm × 30.5 cm; H.B. Sherman Traps, Tallahassee, FL, USA) was placed at each grid point (49 traps per unit), and each unit was sampled once during the pre-treatment period for eight consecutive nights (392 trap-nights per unit). We collected post-treatment small mammal trapping data on control and late season fire units from 20 June–6 September 2002, and on all experimental units from 18 June–4 September 2003, and from 17 June–20 August 2004. Early season burn units in 2002 had been burned too recently to conduct small mammal trapping that summer without damaging the units, i.e. causing high soil erosion. Trapping intensity was increased during the post-treatment trapping period (2002–2004). In addition to trapping the 7 × 7 grid on each unit, we also sampled 20 points located outside of this grid but still within the core measurement area of each unit (69 traps per unit, Fig. 1). These additional points were spaced 50 m from each other, as well as from the 25 m spaced 7 × 7 grid. Trapping these 20 points allowed for small mammal data collection to be standardized with data collection by other researchers from different disciplines within the project. During the post-treatment sampling period, each unit was sampled for nine consecutive nights each summer (621 trap-nights per unit).

Traps were checked once every morning of a trapping session and were left set at all times during the session. Cotton batting and a bait mixture of seed, peanut butter and rolled oats were placed in the traps each morning. Captured small mammals were identified to species and sex, weighed, and individually marked with numbered metal ear tags. For the data analyses, each animal was assigned to an age class (juvenile or adult) based on its mean weight. The weight limit between juvenile and adult for each species was established based on field data and on weight distributions in the literature (Jameson and Peeters, 2004). We considered deer mice adults when ≥13 g, lodgepole chipmunks when ≥40 g, brush mice when ≥14 g, long-tailed voles when ≥35 g, northern flying squirrels when ≥100 g, and golden-mantled ground squirrels when ≥136 g. Black bear (*Ursus americanus*) disturbance of traps was common during the study but varied substantially depending on the unit and year. We noted the disturbance status of every trap for each night, and used these data in the abundance estimation procedure to control for this variation in effective trap effort.

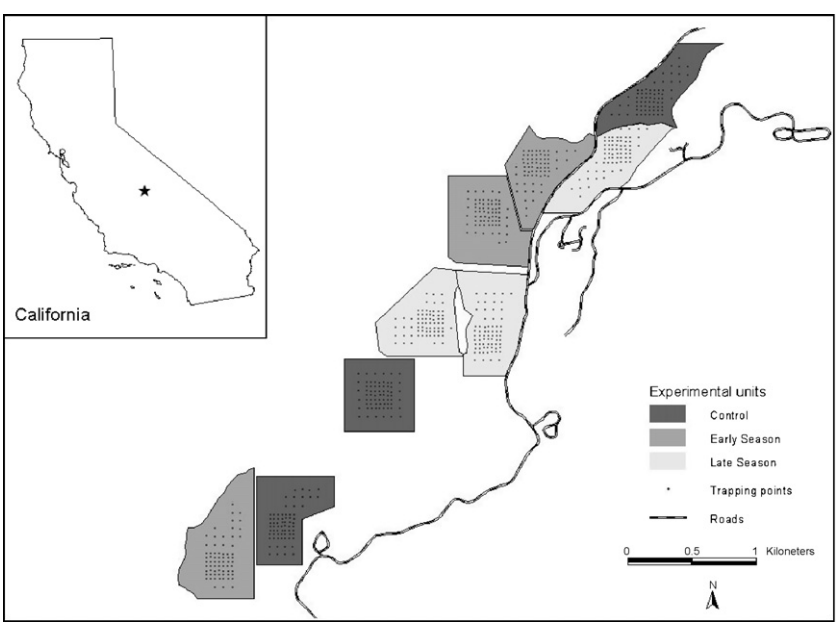

Fig. 1. Map showing location of experimental units and small mammal trapping grids in Sequoia National Park, California.

2.3. Data analyses

We evaluated the effects of prescribed fire treatment on deer mouse densities, deer mouse age ratios (density of juveniles:density of adults), lodgepole chipmunk densities, and total small mammal biomass. The analysis of each of these metrics involved three steps: (1) estimating the abundances of each species per group (groups were either experimental unit per year or age class per experimental unit per year) from the trapping data; (2) converting those abundances to densities, ratios, and biomass; and (3) evaluating the effects of the prescribed fire treatments on those metrics. We conducted each step using an information-theoretic model selection and inference framework (Burnham and Anderson, 2002), in which the relative support given the data for several different a priori hypotheses, in the form of models, was compared using Akaike's Information Criterion (AIC; Akaike, 1973). The small sample size correction was applied to all AIC scores (AIC_c; Hurvich and Tsai, 1989). Interpretations of AIC_c scores were based on AIC_c weights (standardized AIC_c scores; Burnham and Anderson, 2002). Robust estimates of abundances, densities, and treatment effect sizes were made by averaging the models within a model set according to their AIC_c weights.

Estimation of abundance: We estimated abundances for each species using all trapping data, but included grouping factors in each estimation procedure (Bowden et al., 2003). This allowed for enhanced estimation of detection probabilities based on the entire trapping dataset of a species, but still yielded abundance estimates per group. While the grouping factors used for most species were experimental unit and year, large numbers of deer mouse captures allowed for further grouping of deer mouse abundance estimates by age class (juvenile or adult) within experimental units and years.

Detection probabilities in closed mark-recapture analyses are estimates of the probability of capturing or recapturing an animal or group of animals conditional on their presence in the sampled area. These probabilities can be estimated from the capture history data (the record of each animal's capture status at each sampling period) using maximum likelihood methods. In this study, explaining the detection probabilities was not of primary interest; rather accounting for the detection probabilities was a necessary step in order to obtain robust abundance estimates. For estimating detection probabilities and abundances, we used the Huggins' closed-capture model (Huggins, 1989, 1991). This capture–recapture model allows for differing detection probabilities depending on both environmental covariates and individual animal covariates. We determined a set of a priori models of detection probabilities for each analysis (the model sets are described below), and estimated the detection probabilities and the AIC_c weight for each model in the set using Program MARK 3.2 (White and Burnham, 1999). Then, the estimated abundances were calculated from the detection probabilities according to the Huggins' estimator as,

$$\hat{N} = \frac{M_{t+1}}{1-(1-\hat{p}_1)(1-\hat{p}_2)\cdots(1-\hat{p}_t)}, \quad (1)$$

where M_{t+1} is the number of unique individuals marked during t trapping occasions for a particular group and p_t is the estimate of initial capture probability for occasion t, i.e. each night of trapping. The models within the set were then averaged according to their AIC_c weights to produce a vector of model-averaged abundance estimates per group and a model-averaged variance–covariance matrix of those estimated abundances.

The model set used in the deer mouse abundance estimation procedure contained 72 models that incorporated 10 effects in various combinations. We included three of these effects – year, behavior, and effort – in every model as these effects were believed a priori to influence detection probabilities. The behavior effect allowed for recapture probabilities to differ from initial capture probabilities. The effort effect was an environmental covariate that quantified the proportion of traps per unit per night left undisturbed by bears. Additional effects included in only a portion of models included unit, which allowed detection probabilities to vary among experimental units; trap spacing, which allowed detection probabilities to differ depending on the trap spacing on which an animal was first captured (25 m versus 50 m spacing between traps); age, which allowed detection probabilities to vary depending on the age class of the animal (juvenile versus adult); early fire and late fire effects, which distinguished detection probabilities depending on the treatment applied; and, finally, year × early fire and year × late fire interaction effects. Because eight nights of trapping were conducted per experimental unit in 2001, detection probabilities were set to 0 on the ninth night for 2001.

The detection probability model set used for lodgepole chipmunks was the same as that used in the deer mouse abundance estimation, except that models containing both experimental unit and late fire effects were inestimable given the trapping data and therefore were removed from the model set. Inestimability was diagnosed by examining each model for nonsensical abundance estimates, e.g. estimates orders of magnitude larger than estimates in other models.

The detection probability model sets for brush mice, long-tailed voles, northern flying squirrels and golden-mantled ground squirrels were simpler than the deer mouse or lodgepole chipmunk models sets since far fewer capture records were available for these species. In these four model sets, the effort effect was included in every model. The remaining effects were not constrained to every model; they included behavior, year, trap spacing, early fire, and late fire effects. We removed models that were inestimable given the trapping data from these initial model sets, leaving four models in the brush mouse model set, eight models in the long-tailed vole set, eight models in the flying squirrel set, and six models in the golden-mantled ground squirrel set.

Conversion of abundances to densities, age ratios, and total biomass: Converting abundances to densities allowed us to account for the larger area trapped during the post-treatment period, as well as the differing sizes of the experimental units. The conversion to densities from the abundance estimates required estimating effective trapping areas that incorporated edge effects. Edge effects are created by animals whose home ranges do not fall entirely within the trapping grid and by animals

who are lured onto the trapping grid by baited traps, effectively increasing the area trapped beyond that encompassed by the trapping grid (Dice, 1938; Tanaka, 1972). We calculated effective trapping areas by adding the area of a buffer strip with a width 1/2 the mean maximum distance moved (MMDM) to each trapping grid area (Dice, 1938; Wilson and Anderson, 1985). Model selection methods were used to estimate the MMDMs for each species (Converse et al., in press). We determined a set of regression models predicting potential effects on MMDM given the maximum movement data, i.e. the farthest distance between capture gridpoints for each animal, for each species. The deer mouse MMDM model set consisted of models that allowed MMDM to vary by year, by experimental unit, by experimental treatment, or by age class. Models containing year by treatment interactions or year by age interactions were also considered. Finally, a null model in which MMDM did not vary (constant) was included in the set. The lodgepole chipmunk model set was a simplified version of the deer mouse model set since fewer chipmunk movement data were available. This model set contained the constant model and models that allowed MMDM to vary by year or by experimental treatment. Only the constant model was considered for flying squirrels, brush mice, long-tailed voles, and golden-mantled ground squirrels, due to the low number of captures of these species. We calculated effective trapping areas from the MMDMs predicted by each model in a model set, and then averaged over the model set according to the AIC_c weights of each model. We also calculated a model-averaged variance–covariance matrix of the effective trapping areas for each model set (Monroe, 2005).

Densities per group for each species were calculated by dividing the model-averaged abundance estimates by the model-averaged effective trapping areas. The deer mouse age ratios were calculated by dividing the densities of juvenile deer mice per unit per year by the densities of adult deer mice per unit per year. Densities of all species were converted to biomass by multiplying the densities by the cut-off weight between juvenile and adult age classes for each species. We then summed the biomass of each species to calculate the total small mammal biomass per unit per year. Variance–covariance matrices for each metric were calculated through a series of delta method approximations (Seber, 2002; Monroe, 2005). All analyses were computed with SYSTAT v.11 Software (SYSTAT, 2004).

Evaluation of prescribed fire treatment effects on small mammal metrics: We evaluated each of the four metrics for prescribed fire treatment effects using weighted least squares regressions performed within the MATRIX module of SYSTAT v.11 (Draper and Smith, 1998; SYSTAT, 2004). A weighted regression analysis was necessary due to the sampling covariances between the density estimates resulting from the abundance estimation procedure. For each metric, we defined a set of a priori regression models, with each model representing a hypothesis regarding the effects of the prescribed fire treatments on the metric. The same model set was used in the deer mouse density, lodgepole chipmunk density, and total biomass evaluations (Tables 1, 5 and 7). To account for clearly important changes in populations across years, we included a year effect in every model in these model sets. Additionally, three potential prescribed fire effects were compared in these model sets: (1) there was no effect of burning on the metric (year model), (2) early season and late season prescribed fires had the same effect on the metric (year + burn model), and (3) early season and late season prescribed fires had a different effect on the metric (year + early fire + late fire model). Two interaction models were also considered (year × burn and year × early fire + year × late fire), resulting in a set of five models for these metrics. The same effects were employed in the model set used to evaluate the deer mouse age ratio metric, except the year effect was not restricted to every model and a constant model was included, resulting in a set of eight models for this metric (Table 3).

We calculated the weighted regression parameters for each model in a model set according to Draper and Smith (1998). We computed AIC_c scores and AIC_c weights for each model according to Burnham and Anderson (2002) and Converse et al. (in press). Support for the models within a model set was evaluated based on these AIC_c weights. We calculated model-averaged effect sizes by averaging the effect sizes from all models according to the AIC_c model weights. For averaging, effects were considered to have estimates and variances of 0 in models that did not include the effect.

3. Results

3.1. Small mammal captures

A total of 18,498 trapnights were conducted during this study, although 3363 of those were disturbed by bears. We captured 2624 unique individuals a total of 5701 times. These individuals included 1926 deer mice and 563 lodgepole chipmunks. Other species included in the total biomass analysis were brush mice ($n = 36$), long-tailed voles ($n = 34$), northern flying squirrels ($n = 24$), and golden-mantled ground squirrels ($n = 17$). We captured all species known to be resident at the study site, but did not include some species in the analysis because of their low numbers; these were shrews (*Sorex* spp., $n = 14$), Douglas squirrels (*Tamiasciurus douglasii*, $n = 5$), and mountain pocket gophers (*Thomomys monticola*, $n = 5$). The experimental units appeared to be independent as few individuals (0.003%, $n = 9$) were captured in more than one experimental unit.

3.2. Detection probabilities and abundance estimation

There was some evidence that prescribed fire treatments affected small mammal detection probabilities. For each species, except the long-tailed vole and the northern flying squirrel, the detection probability model with the highest AIC_c weight included effects of prescribed fires on detection probabilities. However, the model-averaged 95% confidence intervals of the prescribed fire effects contained 0 for all species. Conversely, there were clear differences in detection probabilities for several other variables. According to the model-averaged effect sizes, deer mice detection probabilities were higher for recaptures than initial captures (effect size = 1.27, S.E. = 0.10), for mice in areas with 25 m trap spacing than those in areas with 50 m trap spacing (effect size = 0.21, S.E. = 0.03), for adult mice than juveniles

Table 1
Model selection results from weighted regression analysis of seasonal prescribed fire treatment effects on deer mouse densities at the Giant Forest study area, Sequoia National Park, California, 2001–2004 ($n = 33$)

Model name	Model structure	K	AIC_c	ΔAIC_c	AIC_c weight
Year	Density = $\beta_0 + \beta_1$(year 2002) + β_2(year 2003) + β_3(year 2004) + ε	5	72.78	0	0.59
Year + burn	Density = $\beta_0 + \beta_1$(year 2002) + β_2(year 2003) + β_3(year 2004) + β_4(burn) + ε	6	74.02	1.24	0.32
Year + early fire + late fire	Density = $\beta_0 + \beta_1$(year 2002) + β_2(year 2003) + β_3(year 2004) + β_4(early fire) + β_5(late fire) + ε	7	77.25	4.48	0.06
Year × burn	Density = $\beta_0 + \beta_1$(year 2002 × control) + β_2(year 2002 × burn) + β_3(year 2003 × control) + β_4(year 2003 × burn) + β_5(year 2004 × control) + β_6(year 2004 × burn) + ε	8	79.21	6.44	0.02
Year × early fire + year × late fire	Density = $\beta_0 + \beta_1$(year 2002 × control) + β_2(year 2002 × late fire) + β_3(year 2003 × control) + β_4(year 2003 × early fire) + β_5(year 2003 × late fire) + β_6(year 2004 × control) + β_7(year 2004 × early fire) + β_8(year 2004 × late fire) + ε	10	87.18	14.41	<0.01

The number of model parameters (K) and the AIC_c scores, delta values, and weights are shown for each model in the model set.

(effect size = 0.30, S.E. = 0.03), and with increased trap effort (effect size = 1.91, S.E. = 0.15). Effect size estimates and standard errors here are on a logit scale to constrain values of capture probabilities to the interval 0–1. The effect sizes are the parameter estimates (β) from the fitted models averaged over the entire model set, and are the difference between the intercept and the effect. Lodgepole chipmunk detection probabilities were higher for recaptures than initial capture rates (effect size = 1.01, S.E. = 0.16), for chipmunks in areas with 25 m trap spacing than those in areas with 50 m trap spacing (effect size = 0.29, S.E. = 0.05), when trap effort increased (effect size = 1.78, S.E. = 0.23), and in 2003 and 2004 compared to 2001 (2003: effect size = 2.51, S.E. = 0.98; 2004: effect size = 2.31, S.E. = 0.98). Lodgepole chipmunk detection probabilities were also higher on experimental units 2 (effect size = 1.21, S.E. = 0.39), 6 (effect size = 1.52, S.E. = 0.38), and 7 (effect size = 1.73, S.E. = 0.37) than on unit 1. Brush mice and golden-mantled ground squirrel detection probabilities were higher when trap effort increased (effect size = 3.46, S.E. = 1.49 and effect size = 3.63, S.E. = 1.38, respectively).

3.3. Evaluation of prescribed fire treatment effects on density metrics

Deer mouse densities: Deer mouse densities ranged widely, from 1.53 individuals/ha (S.E. = 0.61) to 9.11 (S.E. = 1.95) in 2001, from 20.78 (S.E. = 2.17) to 77.12 (S.E. = 7.37) in 2002, from 2.38 (S.E. = 0.68) to 18.11 (S.E. = 0.56) in 2003, and from 12.87 (S.E. = 2.07) to 35.56 (S.E. = 3.78) in 2004. The model selection results from the weighted regression analysis of treatment effects showed strongest support for the model including only the year effect (AIC_c weight = 0.59, Table 1). The year + burn model received the second-most support (AIC_c weight = 0.32). There was little support for unique effects of prescribed fire on deer mouse densities depending on the season of fire (AIC_c weight for the year + early fire + late fire model = 0.06). Models including the year × - prescribed fire interaction term carried less than 3% of the total AIC_c weight.

For each regression analysis, the effect sizes presented are the regression coefficients of the fitted weighted regression models. The model-averaged effect sizes from the deer mouse density analysis indicated that the mean deer mouse density increased an additional 11.88 individuals/ha (S.E. = 5.51, Table 2) in 2002 above the mean density of 1.08 (S.E. = 1.06) in 2001. The 2003 and 2004 effect sizes also indicated an increase in densities compared to 2001, although the 95% confidence intervals for these estimates included 0. The model-averaged burn effect was positive (effect size = 0.64), indicating slightly increased densities on units treated with prescribed fire, although the 95% confidence interval included 0 (S.E. = 1.12).

Table 2
Model-averaged effect sizes (β), standard errors (S.E.), and 95% confidence intervals (CI) from weighted regression analysis of seasonal prescribed fire treatment effects on deer mouse densities at the Giant Forest study area, Sequoia National Park, California, 2001–2004 ($n = 33$)

Parameter	Description	β	S.E.	95% CI
Intercept	–	1.08	1.06	−0.99, 3.15
Year 2002	Difference in mean density between 2001 and 2002	11.88	5.51	1.09, 22.70
Year 2003	Difference in mean density between 2001 and 2003	2.08	1.73	−1.31, 5.47
Year 2004	Difference in mean density between 2001 and 2004	4.28	3.18	−1.95, 10.51
Burn	Difference in mean density between control and burned units (both seasons)	0.64	1.12	−1.56, 2.85
Early fire	Difference in mean density between control and early season fire units	0.12	0.28	−0.43, 0.67
Late fire	Difference in mean density between control and late season fire units	0.13	0.29	−0.44, 0.70

For model averaging, effect sizes and variances were considered to be 0 in models that did not include the effect. Interaction effect sizes are not reported.

Table 3
Model selection results from weighted regression analysis of seasonal prescribed fire treatment effects on deer mouse age ratios (juvenile:adult), at the Giant Forest study area, Sequoia National Park, California, 2001–2004 ($n = 33$)

Model name	Model structure	K	AIC_c	ΔAIC_c	AIC_c weight
Year	Ratio = $\beta_0 + \beta_1$(year 2002) + β_2(year 2003) + β_3(year 2004) + ε	5	53.53	0	0.62
Year + burn	Ratio = $\beta_0 + \beta_1$(year 2002) + β_2(year 2003) + β_3(year 2004) + β_4(burn) + ε	6	55.47	1.94	0.24
Year + early fire + late fire	Ratio = $\beta_0 + \beta_1$(year 2002) + β_2(year 2003) + β_3(year 2004) + β_4(early fire) + β_5(late fire) + ε	7	56.79	3.25	0.12
Year × burn	Ratio = $\beta_0 + \beta_1$(year 2002 × control) + β_2(year 2002 × burn) + β_3(year 2003 × control) + β_4(year 2003 × burn) + β_5(year 2004 × control) + β_6(year 2004 × burn) + ε	8	61.03	7.50	0.01
Constant	Ratio = $\beta_0 + \varepsilon$	2	64.28	10.75	<0.01
Burn	Ratio = $\beta_0 + \beta_1$(burn) + ε	3	66.79	13.25	<0.01
Year × early fire + year × late fire	Ratio = $\beta_0 + \beta_1$(year 2002 × control) + β_2(year 2002 × late fire) + β_3(year 2003 × control) + β_4(year 2003 × early fire) + β_5(year 2003 × late fire) + β_6(year 2004 × control) + β_7(year 2004 × early fire) + β_8(year 2004 × late fire) + ε	10	67.22	13.69	<0.01
Early fire + late fire	Ratio = $\beta_0 + \beta_1$(early fire) + β_2(late fire) + ε	4	68.74	15.21	<0.01

The number of model parameters (K) and the AIC_c scores, delta values, and weights are shown for each model in the model set.

Table 4
Model-averaged effect sizes (β), standard errors (S.E.), and 95% confidence intervals (CI) from weighted regression analysis of seasonal prescribed fire treatment effects on deer mouse age ratios (juvenile:adult) at the Giant Forest study area, Sequoia National Park, California, 2001–2004 ($n = 33$)

Parameter	Description	β	S.E.	95% CI
Intercept	–	0.04	0.07	−0.11, 0.18
Year 2002	Difference in mean ratio between 2001 and 2002	0.51	0.15	0.21, 0.82
Year 2003	Difference in mean ratio between 2001 and 2003	0.04	0.10	−0.16, 0.24
Year 2004	Difference in mean ratio between 2001 and 2004	0.41	0.16	0.09, 0.73
Burn	Difference in mean ratio between control and unburned (both seasons) units	−0.02	0.04	−0.10, 0.06
Early fire	Difference in mean ratio between control and early season fire units	0.00	0.01	−0.03, 0.03
Late fire	Difference in mean ratio between control and late season fire units	−0.01	0.03	−0.07, 0.04

For model averaging, effect sizes and variances were considered to be 0 in models that did not include the effect. Interaction effect sizes are not reported.

Deer mouse age ratios: Age ratios of juvenile to adult deer mice ranged from 0 (S.E. = 0, i.e. no juveniles) to 0.81 (S.E. = 0.77) in 2001, from 0.33 (S.E. = 0.08) to 1.27 (S.E. = 0.16) in 2002, from 0 (S.E. = 0) to 0.89 (S.E. = 0.27) in 2003, and from 0.36 (S.E. = 0.13) to 2.49 (S.E. = 0.65) in 2004. Models lacking a year effect were not supported according to the weighted regression model selection results (Table 3). Among models containing the year effect, there was more support for the year model (AIC_c weight = 0.62) than the year + burn model (AIC_c weight = 0.24) or the year + early fire + late fire model (AIC_c weight = 0.12). The model-averaged effect sizes indicated that age ratios increased (i.e. there were relatively more juveniles) in 2002, 2003, and 2004 than in 2001, although the 95% confidence interval for the 2003 effect included 0 (Table 4). The 95% confidence intervals for the prescribed fire effects (burn, early fire, and late fire) included 0.

Lodgepole chipmunk densities: Lodgepole chipmunk densities ranged from 0 individuals/ha (S.E. = 0) to 2.64 (S.E. = 3.33) in 2001, from 0.33 (S.E. = 0.15) to 10.43 (S.E. = 1.27) in 2002, from 0.42 (S.E. = 0.55) to 5.19 (S.E. = 1.10) in 2003, and from 1.32 (S.E. = 0.27) to 6.85 (S.E. = 0.76) in 2004. The year model (AIC_c weight = 0.64, Table 5) was more strongly

Table 5
Model selection results from weighted regression analysis of seasonal prescribed fire treatment effects on lodgepole chipmunk densities, at the Giant Forest study area, Sequoia National Park, California, 2001–2004 ($n = 33$)

Model name	Model structure	K	AIC_c	ΔAIC_c	AIC_c weight
Year	Density = $\beta_0 + \beta_1$(year 2002) + β_2(year 2003) + β_3(year 2004) + ε	5	70.92	0	0.64
Year + early fire + late fire	Density = $\beta_0 + \beta_1$(year 2002) + β_2(year 2003) + β_3(year 2004) + β_4(early fire) + β_5(late fire) + ε	7	73.21	2.29	0.20
Year + burn	Density = $\beta_0 + \beta_1$(year 2002) + β_2(year 2003) + β_3(year 2004) + β_4(burn) + ε	6	73.90	2.98	0.14
Year × burn	Density = $\beta_0 + \beta_1$(year 2002 × control) + β_2(year 2002 × burn) + β_3(year 2003 × control) + β_4(year 2003 × burn) + β_5(year 2004 × control) + β_6(year 2004 × burn) + ε	8	79.00	8.07	0.01
Year × early fire + year × late fire	Density = $\beta_0 + \beta_1$(year 2002 × control) + β_2(year 2002 × late fire) + β_3(year 2003 × control) + β_4(year 2003 × early fire) + β_5(year 2003 × late fire) + β_6(year 2004 × control) + β_7(year 2004 × early fire) + β_8(year 2004 × late fire) + ε	10	82.35	11.43	<0.01

The number of model parameters (K) and the AIC_c scores, delta values, and weights are shown for each model in the model set.

Table 6
Model-averaged effect sizes (β), standard errors (S.E.), and 95% confidence intervals (CI) from weighted regression analysis of seasonal prescribed fire treatment effects on lodgepole chipmunk densities at the Giant Forest study area, Sequoia National Park, California, 2001–2004 ($n = 33$)

Parameter	Description	β	S.E.	95% CI
Intercept	–	<−0.01	0.48	−0.95, 0.94
Year 2002	Difference in mean density between 2001 and 2002	0.05	0.71	−1.34, 1.43
Year 2003	Difference in mean density between 2001 and 2003	1.08	0.69	−0.25, 2.41
Year 2004	Difference in mean density between 2001 and 2004	1.35	0.86	−0.33, 3.02
Burn	Difference in mean density between control and burned (both seasons) units	−0.02	0.11	−0.22, 0.19
Early fire	Difference in mean density between control and early season fire units	−0.23	0.43	−1.08, 0.62
Late fire	Difference in mean density between control and late season fire units	0.04	0.17	−0.28, 0.36

For model averaging, effect sizes and variances were considered to be 0 in models that did not include the effect. Interaction effect sizes are not reported.

supported than the year + early fire + late fire model (AIC_c weight = 0.20) and the year + burn model (AIC_c weight = 0.14) according to the weighted regression model selection results. There was little support for the year × prescribed fire interaction models based on the AIC_c weights. Chipmunk densities tended to be greater in 2002, 2003, and 2004 than in 2001, although the 95% confidence intervals for these effects included 0 (Table 6). The early season fire effect was slightly negative (effect size = −0.23, S.E. = 0.43), whereas the late season fire effect was slightly positive (effect size = 0.04, S.E. = 0.17), although the 95% confidence intervals for these effects included 0.

Total small mammal biomass: Total small mammal biomass ranged from 50.35 g/ha (S.E. = 30.91) to 193.83 (S.E. = 136.54) in 2001, from 283.45 (S.E. = 32.73) to 1378.45 (S.E. = 116.21) in 2002, from 116.09 (S.E. = 54.56) to 564.56 (S.E. = 151.22) in 2003, and from 252.91 (S.E. = 77.85) to 589.75 (S.E. = 58.47) in 2004. The weighted regression model selection results ranked the year model first (AIC_c weight = 0.60, Table 7) and the year + burn model second (AIC_c weight = 0.24). There was little support for the year + early fire + late fire model or the year × prescribed fire interaction models. Small mammal biomass increased in 2002, 2003, and 2004 compared to 2001, although the 95% confidence interval for 2003 included 0 (Table 8). The model-averaged burn effect (effect size = −14.97) indicated that small mammal biomass decreased on units treated with prescribed fire, although there was considerable uncertainty around this effect (S.E. = 30.59).

Table 7
Model selection results from weighted regression analysis of seasonal prescribed fire treatment effects on small mammal biomass, at the Giant Forest study area, Sequoia National Park, California, 2001–2004 ($n = 33$)

Model name	Model structure	K	AIC_c	ΔAIC_c	AIC_c weight
Year	Biomass = $\beta_0 + \beta_1$(year 2002) + β_2(year 2003) + β_3(year 2004) + ε	5	68.12	0	0.60
Year + burn	Biomass = $\beta_0 + \beta_1$(year 2002) + β_2(year 2003) + β_3(year 2004) + β_4(burn) + ε	6	69.99	1.87	0.24
Year + early fire + late fire	Biomass = $\beta_0 + \beta_1$(year 2002) + β_2(year 2003) + β_3(year 2004) + β_4(early fire) + β_5(late fire) + ε	7	72.15	4.03	0.08
Year × burn	Biomass = $\beta_0 + \beta_1$(year 2002 × control) + β_2(year 2002 × burn) + β_3(year 2003 × control) + β_4(year 2003 × burn) + β_5(year 2004 × control) + β_6(year 2004 × burn) + ε	8	72.18	4.06	0.08
Year × early fire + year × late fire	Biomass = $\beta_0 + \beta_1$(year 2002 × control) + β_2(year 2002 × late fire) + β_3(year 2003 × control) + β_4(year 2003 × early fire) + β_5(year 2003 × late fire) + β_6(year 2004 × control) + β_7(year 2004 × early fire) + β_8(year 2004 × late fire) + ε	10	78.25	10.13	<0.01

The number of parameters (K) and the AIC_c scores, delta values, and weights are shown for each model in the model set.

Table 8
Model-averaged effect sizes (β), standard errors (S.E.), and 95% confidence intervals (CI) from weighted regression analysis of seasonal prescribed fire treatment effects on total small mammal biomass at the Giant Forest study area, Sequoia National Park, California, 2001–2004 ($n = 33$)

Parameter	Description	β	S.E.	95% CI
Intercept	–	46.08	36.17	−24.80, 116.96
Year 2002	Difference in mean biomass between 2001 and 2002	233.11	106.70	23.98, 442.25
Year 2003	Difference in mean biomass between 2001 and 2003	115.68	65.24	−12.19, 243.55
Year 2004	Difference in mean biomass between 2001 and 2004	229.82	96.19	41.29, 418.35
Burn	Difference in mean biomass between control and burned (both seasons) units	−14.97	30.59	−74.917, 44.98
Early fire	Difference in mean biomass between control and early season fire units	−8.09	17.09	−41.58, 25.40
Late fire	Difference in mean biomass between control and late season fire units	−3.98	10.15	−23.87, 15.91

For model averaging, effect sizes and variances were considered to be 0 in models that did not include the effect. Interaction effect sizes are not reported.

4. Discussion

Our results did not show strong differences between the effects of early season and late season fires on any of the four small mammal metrics we examined. Year effects may have obscured prescribed fire treatment effects, but were more important determinants of the small mammal metrics we examined. For deer mice, the model selection results clearly indicated that year effects had a greater influence on total density than prescribed fire effects. Interannual fluctuations of *Peromyscus* densities have frequently been observed and likely are caused by multiple factors including mast seed production, weather, predation, and competition (e.g. Wolff, 1996; Brady and Slade, 2004; Pearce and Venier, 2005). For example, a masting event that occurred at the study site between the 2001 and 2002 summer trapping sessions likely contributed to the substantial increase in deer mouse densities in the latter year. This would be consistent with several studies which have found that *Peromyscus* populations are strongly affected by seed availability. For instance, seed supplementation has led to large increases in deer mouse numbers in some studies (Gilbert and Krebs, 1981; Tait, 1981). In eastern United States deciduous forests, positive correlations between natural yearly fluctuations in seed abundance and white-footed mouse (*Peromyscus leucopus*) abundances are common (Elkinton et al., 1996; Wolff, 1996; McCraken et al., 1999; McShea, 2000; Schnurr et al., 2002). Deer mouse densities in eastern United States deciduous forests also were positively correlated with acorn production (Wolff, 1996). Fewer studies have examined the relationship between seed availability and deer mouse populations in western United States coniferous forests, but Gashwiler (1979) documented greater deer mouse survival and female fecundity in years of high seed production in a western Oregon Douglas fir forest.

A number of other studies have found stronger support for positive prescribed fire impacts on deer mouse densities than reported here (Kaufman et al., 1990; Jones, 1992; Fisher and Wilkinson, 2005). Support for an effect of prescribed burning on deer mouse densities in this study was limited (32% of the total AIC_c weight for the year + burn density model). The model-averaged burn effect size indicated a positive effect of prescribed fire on deer mouse densities, but the 95% confidence interval included 0. The difference between our study and others may be because many past studies did not account for differences in small mammal detection probabilities when estimating abundances or densities. Also, more severe fires than the ground fires implemented in this study may result in stronger positive effects on deer mouse numbers. When examining the effects of a severe wildfire in a ponderosa pine forest on deer mouse densities, Converse et al. (in press) found a strong positive effect of fire even after accounting for treatment effects on deer mouse detection probabilities.

Our results provided little support for differences in deer mouse densities depending on the season of prescribed fire; the year + early fire + late fire model had a low AIC_c weight, and the model-averaged early fire and late fire effect sizes were similar to each another. In contrast, several small mammal habitat components, including coarse woody debris cover, understory cover, and litter cover, were affected differently depending on the season of fire for 1–2 years following the treatments at our study site (Knapp et al., 2005; Knapp et al., in press). The lack of strong evidence that deer mouse densities were affected similarly by fire season suggests that broad-scale factors such as yearly variations in seed availability had a larger influence on deer mouse densities than microhabitat changes. Two other studies have examined the effects of prescribed fires set in different seasons on deer mouse numbers. Martell (1984) also reported no significant difference between catch per unit effort of deer mice on a late season burn versus an early season burn in a black spruce (*Picea mariana*) forest in northcentral Ontario. In contrast, McGee (1982) captured more deer mice per unit effort on a late season burn than on an early season burn in a sagebrush (*Artemisia tridentata*) community in Wyoming. The results of these studies are difficult to extrapolate due to the use of abundance indices to measure deer mouse numbers and to the lack of replication. Although stronger inference can be made from the present study since abundance indices were not used and the treatments were replicated, the level of replication was low (three replicates per treatment) and variation in deer mouse densities was high. A similarly replicated study in a Piedmont oak-shelterwood forest used snap-trapping to measure the effects of fire in winter, spring, or summer on *Peromyscus leucopus* capture rates and also did not find differences depending on the season of fire (Keyser et al., 2001).

The tendency for deer mouse densities to be greater on burned areas does not necessarily indicate that burned habitat is optimal for deer mice, and may reflect dispersal to marginal sink habitat (Van Horne, 1983; Martell, 1984; Fisher and Wilkinson, 2005). Individual deer mice have been observed moving from unburned to burned habitat in a Kansas grassland community, but the age of these animals was not reported (Kaufman et al., 1988). Dispersal sink habitat would be predicted to attract more juvenile deer mice than adult deer mice (Pulliam, 1988). In this regard, burned areas did not appear to act as sink habitat for deer mice during this study since there was limited support for models which predicted differences between the ratio of juveniles to adults on burned and unburned units, and the effect sizes for the burn effects were close to 0. Few studies have examined effects of prescribed fire on small mammal age ratios, but Kirkland et al. (1996) similarly did not find a difference between age ratios of deer mouse populations on burned and unburned units in an Appalachian deciduous forest.

Similar to deer mice, lodgepole chipmunk densities were more strongly affected by year than by prescribed fire. Chipmunk densities may fluctuate naturally between years in response to factors such as mast seed production and weather, so the year effect observed in this study was not surprising (Wolff, 1996; McShea, 2000). The increased heterogeneity of habitat that generally results from complex ground fires is thought to benefit lodgepole chipmunks, although fire effects on lodgepole chipmunks have rarely been examined (Ream, 1981). Meyer (2003) found no effect of prescribed burning on

lodgepole chipmunk densities 1 year after prescribed fires, but in an uncontrolled study, Werner (unpublished data) found that lodgepole chipmunks gradually increased over several years following fire to become almost co-dominant with deer mice. Lodgepole chipmunks may be affected negatively by early season fires since these fires occur during the lodgepole chipmunk breeding season. Although there was more evidence than for deer mice that the season of fire differentially affected lodgepole chipmunk densities, this evidence was still limited; the year + early fire + late fire density model had 20% of the total AIC_c weight and the effect size confidence intervals included 0. Martell (1984) captured a greater number of least chipmunks per unit effort on a late season burned unit than on an early season burn unit, although the difference was not significant. McGee (1982) did not capture any least chipmunks on a late season burned unit, although so few chipmunks were captured on the early season burn unit it was unclear whether the observed difference between the two units was biologically meaningful.

The total small mammal biomass available may influence populations of predator species in Sierra Nevada mixed conifer forests, such as the California spotted owl (*Strix occidentalis occidentalis*). We found limited support (24% of the total AIC_c weight) for an effect of burning on total small mammal biomass. The model-averaged burn effect was negative, although the confidence interval included 0. A differential impact on total small mammal biomass of burning during different seasons was not supported by the model selection results (8% of the total AIC_c weight). Overall, year effects were more important determinants of total small mammal biomass than were prescribed fire treatment effects. Since deer mice and lodgepole chipmunks contributed a considerable portion to total small mammal biomass, it is not surprising that year effects strongly influenced total biomass. Our sampling procedures favored trapping of ground-dwelling small mammal species and may not have sampled the arboreal small mammal community sufficiently, which may explain the lack of a prescribed fire effect on small mammal biomass. Future studies of fire effects on small mammal biomass would benefit from better sampling of these arboreal species, since their contribution to small mammal biomass in the area is not well known and likely is important.

Most studies evaluating the effects of fire on small mammals have relied on relative abundances to evaluate fire effects. Such indices confound detection probabilities with actual abundances and comparisons based on these indices will be biased when detection probabilities differ, for example, among individual animals or in response to experimental treatments. Evidence presented here that small mammal detection probabilities differed by several factors, including factors which could not be controlled for through study design, emphasizes the importance of considering detection probabilities when estimating abundances. Differences in detection probabilities among experimental units are of particular concern when making comparisons of treatment effects across units. For example, the higher chipmunk detection probabilities on units 2, 6, and 7 would have confounded the use of relative abundance indices to compare fire effects on chipmunk numbers. In addition, there was some evidence that detection probabilities for several species were affected by the experimental treatments themselves. Converse et al. (in press) found additional evidence that wildfire influenced small mammal detection probabilities.

Information-theoretic model selection and model-averaging methodology, rather than null hypothesis testing, were employed in the abundance estimation, effective trapping area estimation, and experimental treatment evaluation steps of this study. We preferred these methods to null hypothesis testing because they allow for multiple hypotheses to be considered, they yield quantitative measures with which to compare support for each hypothesis given the data, and they provide robust estimations of effect sizes and variances (Anderson et al., 2000; Johnson and Omland, 2004). This study design improved upon most past studies of effects of fire on small mammals by including controls, pre-treatment data, and randomized replicate treatments. However, the results of this study would have benefited from multiple years of pre-treatment data, especially since few small mammals were captured during the 2001 pre-treatment sampling period, leading to large year effects in the models and complicating the identification of treatment effects. The experimental unit size in this study was larger than in many previous studies, but still smaller than a typical management-oriented prescribed fire. The trade-off for the larger unit size was a low level of replication. This was an important issue as high levels of uncertainty due to the low sample size of experimental units may have obscured real effects of prescribed fire treatments.

Prescribed burning is increasingly implemented on forests throughout the United States to mitigate conditions causing catastrophic wildfires, while restoring the process of fire to fire-adapted ecosystems. Understanding how different methods of prescribed burning will affect these ecosystems therefore is critically important. In fire-suppressed Sierra Nevada mixed conifer forests, early season burns may be an effective method to initially introduce less severe fires (Knapp et al., 2005). The results of this study indicated that effects of early season burns on the small mammal metrics examined were similar to those of late season burns. Systematic differences in deer mouse densities and total small mammal biomass between units burned in different seasons were not supported, and evidence for differential impacts of burning during different seasons on deer mouse age ratios and lodgepole chipmunk densities was limited. Year effects had greater influences on deer mouse densities, deer mouse age ratios, lodgepole chipmunk densities, and total small mammal biomass than did prescribed fire effects. These results only extended over a 3 year post-fire period though, and long-term effects of fire on small mammal populations may differ from those observed here. These results pertain to single fires in mixed conifer habitat where fire had been suppressed for over a century. Fire effects on small mammal populations may differ from those reported here depending on pre-fire habitat quality (Converse et al., in press), and repeated early season burning likely will have stronger impacts on ecosystem structure and small mammal populations

(Robbins and Meyers, 1992). Although potential impacts on rare small mammal species not examined here must also be considered when deciding whether to implement early season burning, this study did not find strong impacts on deer mouse populations, lodgepole chipmunk populations, or total small mammal biomass from early season prescribed fires.

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