

RESEARCH ARTICLE

Response of Small Mammal Populations to Fuel Treatment and Precipitation in a Ponderosa Pine Forest, New Mexico

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Abstract

Mechanical and fire treatments are commonly used to reduce fuels where land use practices have encouraged accumulation of woody debris and high densities of trees. Treatments focus on restoration of vegetation structure, but will also affect wildlife populations. Small mammal populations were monitored before and after dense tree stands were thinned on 2,800 ha in NM, U.S.A. Mammals were live-trapped in upland and riparian habitats from 2002 to 2006 in thinned and unthinned forests. Populations of deer mice (*Peromyscus maniculatus*) and voles (*Microtus* spp.) were estimated using mark–recapture data. An index of abundance was used for chipmunks (*Tamias* spp.) and woodrats (*Neotoma* spp.). Deer mice responded positively to thinning in 2005 in upland and riparian habitats. Voles responded positively to thinning in 2005 and 2006 in riparian habitats. There was no change related to thinning in relative abundance of chipmunks and woodrats or in total

small mammal biomass. Because abiotic processes affect wildlife populations, we also examined response of deer mouse populations to precipitation. After removing treatment effects, populations were modeled with winter and summer precipitation. In both upland and riparian habitats, deer mouse populations had a curvilinear response to precipitation from the preceding winter, while responding negatively to summer rainfall only in riparian habitats. Increases in deer mice populations occurred on thinned sites during a year of high winter precipitation, generally associated with depressed populations, indicating that forest thinning moderated this relationship. Results suggest that precipitation plays a role in determining timing and presence of response to restoration treatments.

Key words: chipmunk, deer mouse, *Microtus*, New Mexico, *Peromyscus maniculatus*, thinning.

Introduction

Small mammals, in addition to being abundant and relatively easy to study, are capable of rapid population growth allowing them to respond quickly to habitat and environmental alterations. In addition, they have important relationships with ecosystem components such as plant community composition (Brown et al. 1986), seed dispersal (Hollander & Vander Wall 2004; Schnurr et al. 2004; Li & Zhang 2003), mycorrhizal fungi dispersal (Pyare & Longland 2001), and predator population dynamics (Zielinski et al. 1983). These characteristics make small mammal populations good subjects for assessing ecosystem health and effects of landscape alterations including natural and anthropogenic disturbances.

Fire is a key component in fire-prone systems that influence ecological and evolutionary processes (Bond & Keeley 2005). Human intervention has altered fire regimes in many

regions, and these alterations are expected to be exacerbated by global climate change as fires are generally expected to burn larger areas with high severity (Kasischke et al. 1995; Goldammer & Price 1998; Stocks et al. 1998; Williams et al. 2001; Westerling et al. 2006). Fire severity, in particular, is of interest where flammable vegetation is close to urban areas or grows in proximity to essential resources such as drinking water. Fires of high severity have a direct and lasting negative impact on water supplies through increased erosion and sedimentation (Cannon et al. 2001). Fuel reduction treatments, such as mechanical thinning and prescribed fire, are commonly used in forested areas to reduce tree density and, consequently, fire severity (Brose & Wade 2002; Storm & Fulé 2007). These treatments, to some extent, also restore historic forest structure (Lynch et al. 2000) and protect forests by enhancing resilience to climate change (Millar et al. 2007).

Fuel reduction strategies strive, in part, to reduce woody debris, a major fuel source for fires. Woody debris created during thinning may provide greater protective cover for small mammals, but eventual removal of these materials may result in reductions of small mammal populations (Converse et al. 2006a). Fuel reduction strategies also seek to reduce tree densities that affect fire size, spread, and severity through

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connectivity in fuels. The resulting reductions in canopy cover may increase herbaceous plant and shrub cover (Moore & Deiter 1992), which may benefit small mammals (Carey & Johnson 1995; Block et al. 2005; Converse et al. 2006c; Lee et al. 2008). On the other hand, more open forests may increase success of predators hunting small mammals (Gese et al. 1995) and predator populations may themselves be affected by treatment and then affect prey populations (Desy & Batzli 1989). Several studies have found positive responses of small mammals to thinning (Wilson & Carey 2000; Suzuki & Hayes 2003; Muzika et al. 2004; Sullivan et al. 2005; Converse et al. 2006a, 2006b), though these were not always linked to the presumed causative sources such as woody debris or herbaceous cover (Converse et al. 2006c; Craig et al. 2006).

Although a number of studies have examined small mammal response to thinning, few include thinning on a large scale or in multiple habitats. In this study, we monitored small mammal populations in upland and riparian areas of a ponderosa pine (*Pinus ponderosa*) forest before and after a large-scale fuel treatment (approximately 2,800 ha). We predicted opening of the forest canopy would increase small mammal populations by increasing plant ground cover and, potentially, food resources. Our study also spanned 6 years during which there was large variation in precipitation patterns. Rainfall directly relates to resource availability and is considered important in population cycles of small mammals, particularly in arid regions (Mutze et al. 1991; Masters 1993; Lima et al. 1999; Ernest et al. 2000; Brown & Ernest 2002; Bradley et al. 2006). Therefore, we used this opportunity to examine rainfall and mammal population patterns and asked how precipitation may have affected small mammal response to thinning.

Methods

Study Area and Treatments

The study took place in the southern Sangre de Cristo Mountains, NM, U.S.A. (35°41'N, 105°50'W). Small mammals were trapped at study sites located within 4 km of the Santa Fe Municipal Watershed outside the city of Santa Fe (Fig. 1). The study sites, ranging from 2,300 to 2,600 m, were primarily ponderosa pine forests with some mixed conifer forest along drainages. The treated site was located along the Santa Fe River in proximity to reservoirs in the Santa Fe Municipal Watershed that supplies drinking water (Fig. 1). Reference sites were on untreated portions of the Santa Fe River, as well as on Little Tesuque and Tesuque Creeks (Fig. 1). Small amounts of piñon-juniper (*Pinus edulis* and *Juniperus* spp.) woodland were present at the lower elevations, particularly along rocky ridges. Riparian areas generally occurred as narrow ribbons of mesic vegetation 25–100 m wide at the bottom of steep mountain sides. Riparian areas along the Santa Fe River were dominated by narrow-leaf cottonwood (*Populus angustifolia*), thin-leaf alder (*Alnus tenuifolia*), and willow (*Salix* sp.), whereas along Tesuque and Little Tesuque Creeks riparian forests were mostly dominated by alder and willow. Away from drainages, the understory was sparsely vegetated

with grasses and forbs. Winter precipitation in the study area falls as rain or snow. Summer monsoons generally bring rain in mid-July and August.

The Santa Fe Municipal Watershed has had a long history of logging, grazing, and homesteading. These activities ceased in 1932 when the watershed was closed to the public, but active fire suppression continued until the treatments described in this study. A total of 2,800 ha of forest within the Santa Fe Municipal Watershed was treated with a combination of mechanical thinning, burning of slash piles, and broadcast burning. Thinning began in February of 2003 and burning of slash piles began in November 2003. Mechanical thinning was primarily complete by the fall of 2004, though application of prescribed fire is ongoing. During 2003, forest thinning was primarily conducted away from trapping locations and after trapping sessions were completed. Thus, we considered 2004 to be the first post-thinning year, although there may have been some disturbance due to increased human activities before this time. Reference sites were a minimum of 150 ha protected from thinning, but were primarily surrounded by similar untreated forest.

Riparian areas along the Santa Fe River were not thinned, but thinning did occur in forests directly adjacent. Thinning reduced tree densities from 500–1200 to 50–100 trees/ha by preferentially removing small trees (mostly <15 cm in diameter). Chainsaws were primarily used to remove trees along with mastication or mechanical shredding. Slash (tree limbs) was piled by hand for future burning. Soil disturbance was minimal during treatment, because no roads were built and no planting or seeding occurred. No wood was removed and, during the study, weather precluded burning of the majority of slash. Ridges were thinned more heavily and no thinning occurred on slopes greater than 40%, thus treatment was not uniform throughout.

Precipitation data were compiled from the Elk Cabin SNOTEL site operated by the U.S. Department of Agriculture Natural Resources Conservation Service located at the upper end of the municipal watershed at an elevation of 2,500 m and near trapping locations (Fig. 1). Data were available in inches and converted to mm after analysis.

Small Mammal Trapping

Small mammals were trapped twice each year, mid-June to mid-July and August, from 2002 to 2006 in riparian and upland habitats following a BACI (before–after control–impact) design (Stewart-Oaten et al. 1986; Underwood 1993). Trapping locations within habitats were chosen randomly, but buffered from other locations by at least 100 m and accessible by roads or trails. In riparian habitats, traps were laid out in linear transects of 100 traps 5 m apart following the water's edge. Three thinned and three reference riparian transects were sampled in 2002–2005. Two thinned and four reference riparian transects were sampled in 2006 in anticipation of expansion of fuel treatments. One thinned transect, where two were in close proximity, was discontinued in 2006. The added reference transect was located at the lower end of

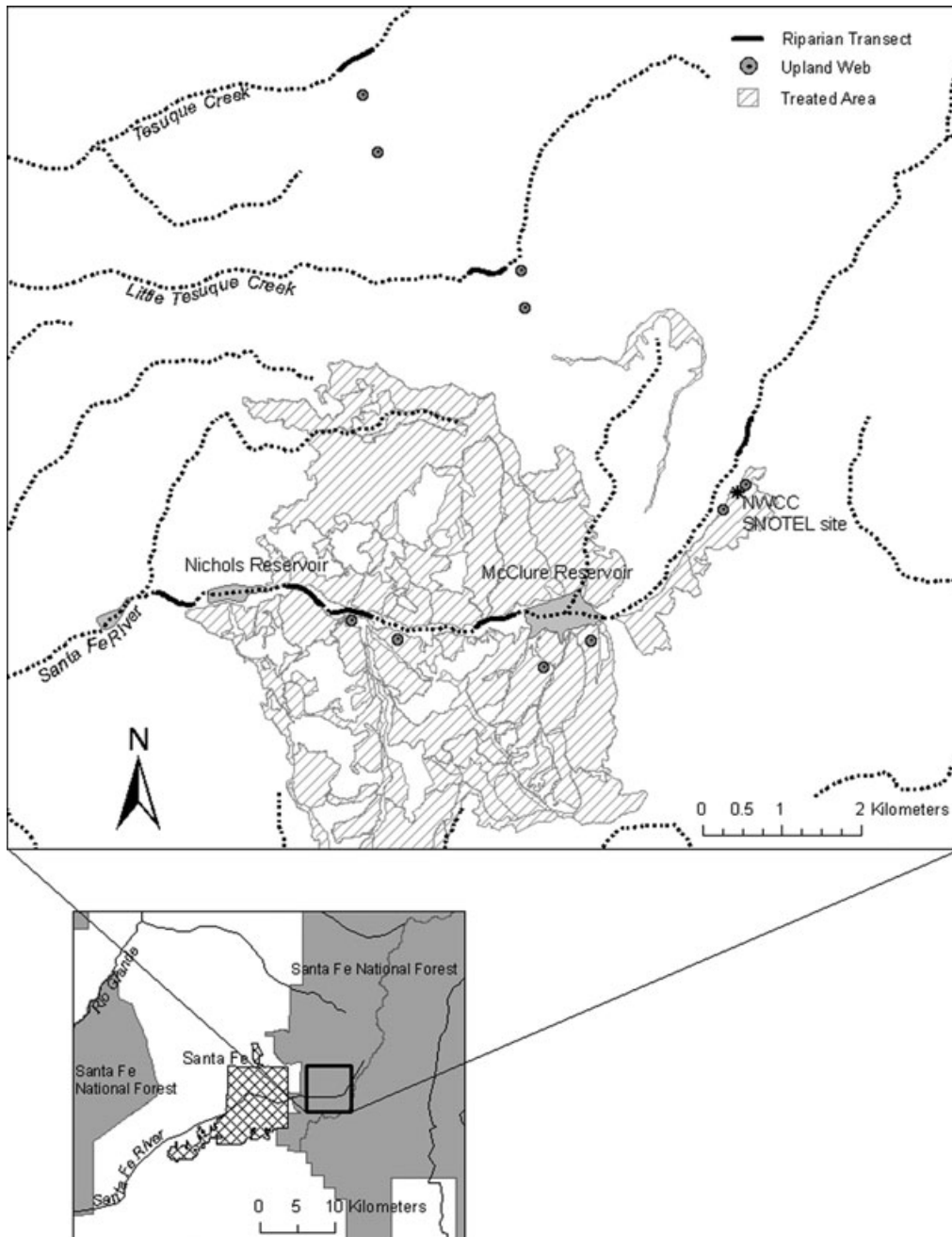


Figure 1. Map of study and trap locations 2002–2006 in riparian and upland habitats near Santa Fe, NM, U.S.A. Transects and webs outside the hatched treated area were used as reference locations. Precipitation data were from the U.S. Department of Agriculture Natural Resources Conservation Service SNOTEL site shown.

the municipal watershed below Nichols Reservoir (Fig. 1). In upland habitats, traps were arranged in a web of 80 traps radiating along eight lines of 10 traps, 5 m apart. Webs were sampled from 2002 to 2005 at six thinned and four reference locations. One reference site with one transect and two webs was not trapped in August of 2002.

Sherman live-traps (7.6 cm × 8.9 cm × 22.9 cm) were baited with rolled or crimped oats and opened at each location

for three consecutive nights. Traps were checked at dawn and captured individuals were identified by species, age, and sex, and uniquely marked with one ear tag. Measurements included ear length, foot length (to the tip of the nail), tail length, and weight. The total biomass was calculated by summing the weights recorded for each unique individual caught per location per trapping period. Mammals were released at the point of capture. All animals and contaminated traps

were processed under the guidelines established for the safe handling of animals potentially infected with hantavirus (Mills et al. 1995)

Small Mammal Populations

We used Program MARK to estimate population sizes for each location in each year, where the number of unique individuals was greater than 30 per year. The trapping schedule followed Pollack's Robust Design (Pollack 1982), but our sample sizes were generally small; so, we estimated populations for each session separately, because the Robust Design would require sufficient data to estimate additional parameters (e.g., survival, availability). Population estimates (N_{est}) were made from mark-recapture data in each session using Huggin's closed capture model, which has been shown to perform well with small sample sizes and was appropriate for our three-night trapping sessions (Huggins 1989, 1991). Too little data precluded evaluating multiple models with multiple parameters in an information-theoretic approach, thus we chose to estimate a single model with minimal parameters to obtain the best possible population estimates. Parameters estimated were probability of capture (p) and probability of recapture (c). Model parameters were estimated collectively for trapping locations within a treatment and habitat type for each session, but thinned and reference areas were estimated separately to account for differences in capture rates that could confound the analysis of thinning effects. Generally, we included a behavioral response ($p \neq c$), except when doing so resulted in nonsensical standard errors and population estimates (e.g., $N_{\text{est}} > 1,000$). Small mammal populations at each trapping location were then calculated using the derived parameters from the resulting models. Trap configuration and number varied by habitat, but was consistent within habitats; thus populations can be compared within, but not between habitats.

Statistical Analysis

Estimated small mammal populations and total biomass were analyzed in a generalized linear mixed model using PROC GLIMMIX (SAS Institute, Inc. 2000). Locations were repeatedly sampled over years and location was designated as the subject of the random effect. The design was unbalanced and denominator degrees of freedom were estimated using the Kenward-Roger method (Kenward & Roger 1997). We evaluated model fit by testing the normality of the residuals and, for nonnormal distributions, using the residual dispersion estimate (X^2/df). The effect of thinning was evaluated using the interaction of time (before vs. after) and treatment (thinned vs. reference). For interactions with a p -value of less than 0.25, we divided time into each post-thinning year to identify when treatment effects occurred. Others (Converse et al. 2006a) have used analyses weighted by the standard errors of the estimates, because the estimation for each location is based on parameter estimates for a group of locations. Because weighted analysis calls for exact estimates of errors (Ryan 1997), which

were not obtainable from our methods in MARK, we present results from unweighted analyses.

For species with captures of unique individuals greater than 10 and less than 30 per year, we used the same analytical methods with number of unique individuals (M_{t+1}) as an index of abundance (McKelvey & Pearson 2001). In 2006, new reference riparian locations were added and these were tested for differences from original reference riparian locations using Welch's t -test.

The southwestern United States has two distinct periods of precipitation, thus we used two measures of precipitation, one for winter and the other for summer. Winter precipitation was the accumulated precipitation from the previous winter period beginning from October and ending 3 months prior to the first day of the trapping session for each location. Small mammal populations have been shown to respond to winter precipitation with a lag of 3 months (Bradley et al. 2006). Summer precipitation was the accumulated precipitation for the 1-month period proceeding the first day of the trapping session for each location. Summer precipitation included monsoonal rainfall, though typically not before mid-July and represented immediate, rather than lagged, effects. Nonlinear effects were suspected based on graphical inspection of the data, and we tested polynomials including the linear, quadratic, and cubic effect for each rainfall parameter. We tested rainfall effects on deer mouse populations using PROC GLIMMIX similar to thinning effects. Populations that were found to be significantly affected by the thinning in the previous analysis were removed from the analysis of precipitation effects to eliminate potentially confounding effects of treatment. Trapping session was included as a categorical variable to account for seasonal population changes attributed to breeding activities between the trapping periods (June/July and August).

We used a stepwise process to model the relationship between rainfall and mammal populations. Trapping session was a covariate and always remained in the models. Additional variables were winter precipitation, summer precipitation, and their higher order polynomials up to the third order. The full model was fit to the data with a generalized linear mixed model as described for the analysis of thinning effect. We removed variables based on their p -values ($p > 0.25$), but required that higher order effects be removed first. Once all variables in the remaining model were significant ($p < 0.05$), variables were added back in to test the validity of the model watching for loss of significance in the selected variables. Fit of the model was reassessed with each step. Graphical representation of the best model of the effect of precipitation on deer mouse populations was created by substituting the observed range of precipitation values for the study into the final equation.

Results

We caught a total of 2,698 individual mammals of 15 species over 5 years. Capture rates averaged 21.3 mammals/100 trap-nights for riparian transects for 2002–2006. For upland webs, mammals were captured at an average rate of 8.6/100 trap-nights for 2002–2005. Four species, or groups of species, had

greater than 10 individuals per year (deer mice, *Peromyscus maniculatus*; voles, *Microtus* spp.; chipmunks, *Tamias* spp.; and woodrats, *Neotoma* spp.). Greater than 30 individuals per year were captured of deer mice and voles.

Deer Mice

Deer mice were the most commonly captured species in both riparian and upland habitats. Captures varied by session, year, and location (Table 1). Population estimates included both probability of initial capture (p) and recapture (c) primarily for riparian locations during August sessions except in 2002. Sessions in 2002, most sessions in June/July, and all upland trapping sessions had lower numbers of captures, so we were unable to include behavioral effects ($p \neq c$) in population estimations. No consistent patterns in the difference between capture probabilities for reference and thinned locations were observed for before (range 25% greater to 10% less on reference) or after thinning (range 17% greater to 29% less on reference). We found no difference between populations in the original reference locations and the added reference locations for 2006 ($F = 0.0$, $p = 0.99$) and thus included data from the new locations. Initial results indicated differences between trapping sessions within a year, but model fit was poor when a variable for session was included; thus we analyzed the sessions separately. The best model fit for treatment effect was obtained with a normal distribution for riparian habitats and a negative binomial distribution for upland habitats ($X^2/df = 2.1$). For both upland and riparian habitats, the interaction of time and treatment was significant. In the June/July session, there was a significant positive effect of thinning in 2005 in riparian habitats, but not upland habitats. In the August session, there was a significant positive effect of thinning in 2005 for both riparian and upland habitats (Table 2). In 2005, deer mouse populations were, on average, 77% higher on thinned than reference in riparian areas and 114% higher in upland areas (Table 1).

Table 1. Means (SE) for number of unique individuals (M_{t+1}) of small mammal species by habitat trapped per treatment across two trapping sessions per year, 2002–2006. For those species where populations were estimated in MARK, the estimated population, N_{est} (SE), is also reported. Treatments were thinned (T) and unthinned or reference (R) with 2002–2003 considered “before” treatment. Upland habitats were not trapped in 2006.

Year	Treatment	Deer mice M_{t+1}		Deer mice N_{est}		Voles M_{t+1}		Chipmunks M_{t+1}		Woodrats M_{t+1}
		Riparian ^a	Upland ^b	Riparian ^a	Upland ^b	Riparian ^a	Riparian ^a	Upland ^b	Riparian ^a	
2002	R	23.0 (7.1)	4.1 (1.3)	30.5 (7.1)	5.1 (1.6)	7.3 (1.8)	13.0 (3.5)	0	1.4 (0.9)	
	T	20.7 (5.3)	4.8 (0.8)	21.7 (5.2)	6.2 (1.1)	0.5 (0.3)	0.5 (0.3)	1.1 (0.4)	2.8 (1.1)	
2003	R	24.7 (4.4)	5.6 (1.1)	27.4 (5.2)	6.5 (1.1)	10.3 (1.7)	13.9 (2.2)	0.6 (0.3)	1.5 (0.8)	
	T	20.7 (4.1)	5.8 (1.1)	23.9 (5.1)	6.7 (1.1)	3.8 (1.0)	6.0 (1.7)	1.3 (0.5)	8.7 (1.3)	
2004	R	31.5 (5.4)	9.8 (1.3)	37.1 (6.5)	12.4 (1.6)	4.2 (1.4)	9.6 (3.2)	1.1 (0.4)	0.5 (0.3)	
	T	23.3 (3.9)	9.7 (2.1)	28.8 (5.2)	11.4 (2.5)	2.0 (1.8)	3.2 (2.9)	2.2 (0.7)	4.0 (0.7)	
2005	R	21.5 (2.5)	3.2 (1.0)	23.3 (2.6)	3.5 (1.1)	3.0 (1.1)	4.5 (1.7)	0.8 (0.3)	0.8 (0.5)	
	T	30.5 (1.6)	7.2 (1.0)	41.2 (1.2)	7.5 (1.0)	5.2 (1.6)	7.8 (2.6)	1.7 (0.6)	3.0 (0.4)	
2006	R	15.1 (2.2)	—	16.7 (2.5)	—	3.5 (1.2)	5.6 (2.0)	—	0.5 (0.3)	
	T	16.8 (0.6)	—	17.9 (0.5)	—	2.3 (0.9)	4.8 (1.7)	—	1.8 (1.1)	

^aNumber of riparian samples 2002–2006; reference = 5, 6, 6, 6, 8; treatment = 6, 6, 6, 6, 4.

^bNumber of upland samples 2002–2005; reference = 6, 8, 8, 8; treatment = 12, 12, 12, 12.

Table 2. Results from generalized linear model for deer mouse populations in two habitats by session including treatment, year (before treatment years combined), and the interactions.

Session 1 (June/July)	Riparian		Upland	
	F	p	F	p
Before vs. 2004	4.84	0.04	3.55	0.07
Before vs. 2005	12.68	0.002	0.47	0.5
Before vs. 2006	0.13	0.72	—	—
Treatment	1.46	0.24	0.59	0.45
Treatment*(2004 vs. before)	1.78	0.2	0.59	0.45
Treatment*(2005 vs. before)	6.61	0.02	0.71	0.4
Treatment*(2006 vs. before)	1.18	0.29	—	—
Session 2 (August)	F	p	F	p
Before vs. 2004	0.52	0.48	20.79	<0.001
Before vs. 2005	0.78	0.39	4	0.05
Before vs. 2006	10.75	0.004	—	—
Treatment	1.63	0.22	1.87	0.18
Treatment*(2004 vs. before)	0.94	0.34	0.22	0.64
Treatment*(2005 vs. before)	7.52	0.01	4.14	0.05
Treatment*(2006 vs. before)	0.34	0.57	—	—

Voies

The most commonly identified vole species was long-tailed vole, *Microtus longicaudus* ($n = 193$), and we combined these with meadow vole, *Microtus pennsylvanicus* ($n = 59$), as we expected their ecological role and, thus, response to thinning would be similar. All captures were from riparian transects. Populations were estimated using MARK with no behavioral response to trapping ($p = c$). Best model fit was obtained with a lognormal distribution ($X^2/df = 0.7$). Trapping session was not significant and was removed from the model ($F = 0.05$, $p = 0.82$). The time by treatment interaction was significant ($F = 7.93$, $p = 0.007$). Populations were positively affected by thinning when compared with reference areas in 2005 and

2006, but not 2004 ($F = 6.05$, $p = 0.02$; $F = 6.05$, $p = 0.02$; $F = 1.22$, $p = 0.28$, respectively).

Chipmunks

Two species of chipmunks were captured in upland habitats, least chipmunk, *Tamias minimus* ($n = 156$) and Colorado chipmunk, *Tamias quadrivittatus* ($n = 32$). These were combined because their ecological roles were expected to be similar. A lognormal distribution fit best ($X^2/df = 0.4$). Trapping session was not significant and was removed ($F = 0.20$, $p = 0.66$). There was no effect of thinning on chipmunk populations (treatment \times time, $F = 0.32$, $p = 0.57$).

Woodrats

Woodrats were caught primarily in riparian habitats ($n = 146$ vs. 37) and were primarily identified as Mexican woodrat, *Neotoma mexicana* ($n = 141$), with fewer individuals of white-throated woodrat, *Neotoma albigula* ($n = 42$). These species were combined because, like voles, we felt the response to thinning would be similar. Upland populations that were small were not evaluated. Riparian captures were variable by year and tended to be lower on reference than thinned areas (Table 1). The best fit for the riparian data was a lognormal distribution ($X^2/df = 0.7$). Woodrat abundance differed between trapping sessions ($F = 8.4$, $p = 0.01$) with the usual increase during the summer, and fit of the model was not improved by analyzing these separately; thus, session was retained in the model. There was also no effect of thinning (treatment \times time, $F = 0.02$, $p = 0.88$).

Total Biomass

Average total biomass was higher on thinned than reference sites before thinning (1,309 vs. 995 g). In the post-thinning period, biomass was lower with an average of 808 g in thinned areas and 664 g on reference locations. The best fitting model for biomass was a lognormal model with an unstructured covariance matrix. Fit was improved by analyzing trapping sessions separately. For upland habitats in June/July and August, there was no effect of thinning (treatment \times time, $F = 0.94$, $p = 0.34$ and $F = 0.45$, $p = 0.51$, respectively).

Table 3. Parameter estimates from selected generalized linear model of the relationship between deer mouse populations and precipitation. Populations were sampled in June/July and again in August, thus this estimate reflects breeding activities. Winter precipitation is accumulated from October to 3 months before the trapping session. Summer precipitation is accumulated for 1 month before the trapping session. For upland habitats, summer rainfall was non-significant when included in the model and removed. Precipitation data was modeled in inches.

Variable	Riparian			Upland		
	Estimate	SE	p	Estimate	SE	p
Intercept	3.07	0.38	<0.001	1.07	0.4	0.01
June/July to August	0.60	0.14	<0.001	0.62	0.14	<0.001
Winter precipitation	0.13	0.06	0.05	0.27	0.08	0.001
(Winter precipitation) ²	-0.006	0.003	0.04	-0.01	0.004	<0.001
Summer precipitation	-0.07	0.03	0.01	—	—	—

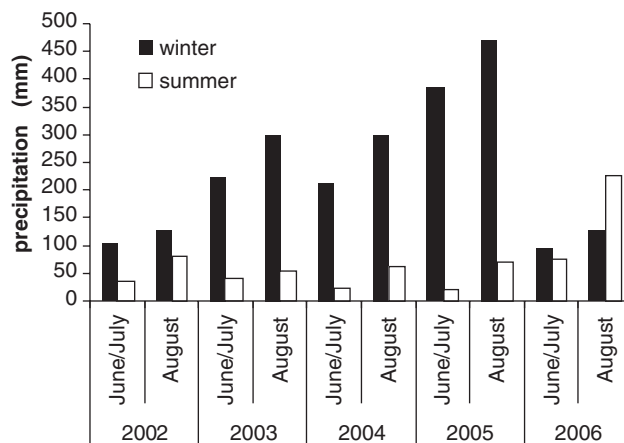


Figure 2. Accumulated precipitation for each trapping session 2002–2006. Winter is precipitation accumulated from October to 3 months before trapping. Summer is precipitation accumulated in 1 month before trapping.

Precipitation

Precipitation varied considerably during the study period ranging from 80 to 480 mm for winter and 10 to 270 mm for 1 month accumulation in summer (Fig. 2). The effect of trapping session on deer mouse population size, which was included in all models, was significant, positive, and approximately equal for both habitats (Table 3). The best fit for precipitation models was a lognormal distribution with an unstructured covariance matrix. The effect of winter precipitation was nonlinear with a positive influence on deer mouse populations at low levels and a negative influence at higher levels. Slope was zero (inflection point) at 270 mm of precipitation. The amount of summer precipitation had a negative linear effect on deer mouse populations for riparian habitats (Fig. 3) and no effect in upland habitats. Upland populations had a similar pattern to those shown in Figure 3 with a slope of zero at 260 mm and no effect of summer rainfall.

Discussion

We found positive or neutral effects of thinning on the small mammal species examined. Positive effects lasted 2 years or

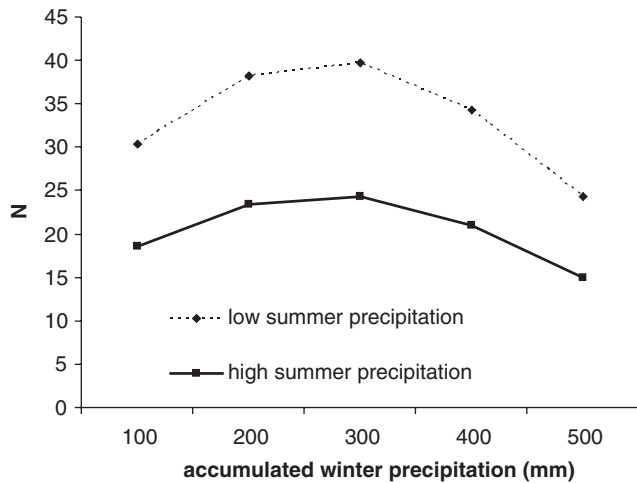


Figure 3. Model results from generalized linear model of the response of August deer mouse populations to observed range of winter (accumulated in the preceding winter with 3 month lag) and summer (accumulated in the 1 month prior with no lag) precipitation in riparian habitats 2002–2006. Low summer precipitation was 25 mm and high summer precipitation was 200 mm. N is the population size (e^x) calculated from the equation estimated by the model, which was fitted with a lognormal distribution. Upland populations had a similar relationship with winter precipitation without the negative effect of summer precipitation.

less out of four post-thinning years. Positive effects of thinning on small mammals have been attributed to increases in downed woody debris (Manning & Edge 2004; Converse et al. 2006a, 2006b), herbaceous understory plants (Suzuki & Hayes 2003; Manning & Edge 2004; Converse et al. 2006a), and habitat heterogeneity (Carey & Wilson 2001; Muzika et al. 2004), all of which were potential factors in our study area. In riparian areas, where thinning did not occur, small mammals may be using resources in thinned areas adjacent to the narrow riparian areas, or predator populations in the area may have been negatively impacted by thinning. Changes in predator populations may better explain the positive response of voles as they are unlikely to use areas outside the riparian zone. More work is needed to evaluate thinning effects on predation.

In addition to deer mice, chipmunks and woodrats were expected to respond positively to thinning because of increases in woody debris (Converse et al. 2006a; Lehmkühl et al. 2006), but we found no response. However, we were unable to correct for differences in capture probability due to small sample sizes and there was considerable variation in captures of these species among trapping locations before thinning that could have masked effects. Additionally, these were the largest of the species studied and may not be affected by the same predators.

Our finding of a curvilinear effect of rainfall is consistent with others (Brown & Ernest 2002). It also provides an explanation for why there has been inconsistency in correlating rainfall and small mammal populations. For summer rainfall, we found a negative effect in riparian areas, a response that has been attributed to flooding (Kemper & Bell 1985; Elliot &

Root 2006). Though water was regulated on parts of the Santa Fe River, the summer thunderstorms are intense and flooding occurs even where water is regulated by dams. Flooding does not occur on the steep slopes of the upland areas and we did not find the same effect of summer precipitation there indicating that soils, slope, and other physical attributes of the landscape that relate to flooding potential may be important covariates in the precipitation relationship. Winter precipitation, on the other hand, was measured 3 months before trapping, and its effects were not adequately explained by flooding. Much of the winter precipitation is snowfall and at moderate to high levels may limit access to food (Korslund & Steen 2006) and delay seed germination and plant growth.

Thinning effects were removed when modeling precipitation and deer mouse populations, but 2005, a wet year, was the year where we saw a positive response to thinning. The model predicts that at 2005 winter precipitation levels, populations should decrease, but we saw the opposite effect on thinned areas. Thinning of the forest canopy may increase snow accumulation, but also accelerate melting (Troendle & Leaf 1981; Kirchhoff & Schoen 1987). In thinned forests, earlier melting of snow along with increased plant cover and seed production may have alleviated the negative effects of high winter precipitation predicted by the model. Similarly, canopy removal can also reduce snow sublimation thereby increasing water availability to plants (Pomeroy & Gray 1995; Stottlemeyer & Troendle 2001). Thus, abiotic factors such as precipitation may interact with forest thinning and natural disturbances to affect wildlife populations.

We could identify the same treatment effects using M_{t+1} as with N_{est} , but observed variation in capture probabilities supports adjusting for probability of capture, especially when data are collected in only a few years. There was, however, no consistent pattern in capture probability by treatment or time indicating that site differences were at least as important as thinning in affecting capture rates.

Conclusions

The lack of negative effects on small mammals indicates that ecosystem function remained intact following large-scale thinning with minimal soil disturbance in this watershed. Some species were positively affected for a short period as well. Precipitation likely influenced the timing of small mammal response to thinning, thus abiotic influences need to be considered when evaluating treatment effects and may be closely tied to detection of effects. In addition to precipitation, results suggest that habitat type, flooding potential, and capture probabilities are important when examining changes in small mammal populations.

Implications for Practice

- This and other studies indicate that forest thinning with minimal ground disturbance is compatible with sustainable small mammal populations.

- Abiotic factors such as precipitation or habitat type may influence timing and presence of response of small mammals to restoration treatments and should be taken into account during study design and analysis.
- Because a detectable response was related to factors that varied annually, researchers need to anticipate this variability by planning for multi-year studies.

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LITERATURE CITED

- Block, W. M., J. L. Ganey, P. E. Scott, and R. King. 2005. Prey ecology of Mexican spotted owls in pine-oak forests of northern Arizona. *The Journal of Wildlife Management* **69**:619–629.
- Bond, W. J., and J. E. Keeley. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable systems. *Trends in Ecology and Evolution* **20**:387–394.
- Bradley, R. D., J. D. Hanson, B. R. Amman, B. D. Baxter, F. S. Carroll, N. D. Durish, et al. 2006. Rapid recovery of rodent populations following severe drought. *The Southwestern Naturalist* **51**:87–93.
- Brose, P., and D. Wade. 2002. Potential fire behavior in pine flatwood forests following three different fuel reduction techniques. *Forest Ecology and Management* **163**:71–84.
- Brown J. H., D. W. Davidson, J. C. Munger, and R. S. Inouye. 1986. Experimental community ecology: the desert granivore system. Pages 41–61 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper & Row, New York.
- Brown, J. H., and S. K. M. Ernest. 2002. Rain and rodents: complex dynamics of desert consumers. *BioScience* **52**:979–987.
- Cannon, S. H., E. R. Bigio, and E. Mine. 2001. A process for fire-related debris flow initiation, Cerro Grande Fire, New Mexico. *Hydrological Processes* **15**:3011–3023.
- Carey, A. B., and M. L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. *Ecological Applications* **5**:336–352.
- Carey, A. B., and S. M. Wilson. 2001. Induced spatial heterogeneity in forest canopies: response of small mammals. *The Journal of Wildlife Management* **65**:1014–1027.
- Converse, S. J., W. M. Block, and G. C. White. 2006a. Small mammal population and habitat responses to forest thinning and prescribed fire. *Forest Ecology and Management* **228**:263–273.
- Converse, S. J., G. C. White, and W. M. Block. 2006b. Small mammal responses to thinning and wildfire in ponderosa pine-dominated forest of the southwestern United States. *The Journal of Wildlife Management* **70**:1711–1722.
- Converse, S. J., G. C. White, K. L. Farris, and S. Zack. 2006c. Small mammals and forest fuel reduction: national-scale responses to fire and fire surrogates. *Ecological Applications* **16**:1717–1729.
- Craig, V. J., W. Klenner, M. C. Feller, and T. P. Sullivan. 2006. Relationships between deer mice and downed wood in managed forest of southern British Columbia. *Canadian Journal of Forest Research* **36**:2189–2203.
- Desy, E. A., and G. O. Batzli. 1989. Effects of food availability and predation on prairie vole demography: a field experiment. *Ecology* **70**:411–421.
- Elliot, A. G., and B. G. Root. 2006. Small mammal responses to silvicultural and precipitation-related disturbance in northeastern Missouri riparian forests. *Wildlife Society Bulletin* **34**:485–501.
- Ernest, S. K. M., J. H. Brown, and R. R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos* **88**:470–482.
- Gese, E. M., R. L. Ruff, and R. L. Crabtree. 1995. Intrinsic and extrinsic factors influencing coyote predation of small mammals in Yellowstone National Park. *Canadian Journal of Zoology* **74**:784–797.
- Goldammer, J. G., and C. Price. 1998. Potential impacts of climate change on fire regimes in the tropics based on MAGICC and a GISS GCM-derived lightning model. *Climatic Change* **39**:273–296.
- Hollander, J. L., and S. B. Vander Wall. 2004. Effectiveness of six species of rodents as dispersers of singleleaf piñon pine (*Pinus monophylla*). *Oecologia* **138**:57–65.
- Huggins, R. M. 1989. On the statistical analysis of capture-recapture experiments. *Biometrika* **76**:133–140.
- Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* **47**:725–732.
- Kasischke, E. S., N. L. Christensen Jr., B. J. Stocks. 1995. Fire, global warming, and the carbon balance of boreal forests. *Ecological Applications* **5**:437–451.
- Kemper, C., and D. T. Bell. 1985. Small mammals and habitat structure in lowland rainforest forest of Peninsular Malaysia. *Journal of Tropical Ecology* **1**:5–22.
- Kenward, M. G., and J. H. Roger. 1997. Small sample inference for mixed effects from restricted maximum likelihood. *Biometrics* **53**:983–997.
- Kirchhoff, M. D., and J. W. Schoen. 1987. Forest cover and snow: implications for deer habitat in southeast Alaska. *The Journal of Wildlife Management* **51**:28–33.
- Korslund, L., and H. Steen. 2006. Small rodent winter survival: snow conditions limit access to food resources. *Journal of Animal Ecology* **75**:156–166.
- Lee, E.-J., W.-S. Lee, and S.-J. Rhim. 2008. Characteristics of small rodent populations in post-fire silvicultural management stands within pine forest. *Forest Ecology and Management* **255**:1418–1422.
- Lehmkuhl, J. F., K. D. Kistler, and J. S. Begley. 2006. Bushy-tailed woodrat abundance in dry forests of eastern Washington. *Journal of Mammalogy* **87**:371–379.
- Li, H., and Z. Zhang. 2003. Effect of rodents on acorn dispersal and survival of the Liaodong oak (*Quercus liaotungensis* Koidz.). *Forest Ecology and Management* **176**:387–396.
- Lima, M., J. E. Keymer, and F. M. Jaksic. 1999. El Niño-southern oscillation-driven rainfall variability and delayed density dependence cause rodent outbreaks in western South America: linking demography and population dynamics. *American Naturalist* **153**:476–491.
- Lynch, D. L., W. H. Romme, and M. L. Floyd. 2000. Forest restoration in southwestern ponderosa pine. *Journal of Forestry* **98**:17–24.
- Manning, J. A., and W. D. Edge. 2004. Small mammal survival and downed wood at multiple scales in managed forests. *Journal of Mammalogy* **85**:87–96.
- Masters, P. 1993. The effects of fire-driven succession and rainfall on small mammals in spinifex grassland at Uluru National Park, Northern Territory. *Wildlife Research* **20**:803–813.
- McKelvey, K. S. and D. E. Pearson. 2001. Population estimation with sparse data: the role of estimators versus indices revisited. *Canadian Journal of Zoology* **79**:1754–1765.

- Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications* **17**:2145–2151.
- Mills, J. N., T. L. Yates, J. E. Childs, R. R. Parmenter, T. G. Ksiazek, P. E. Rollin, and C. J. Peters. 1995. Guidelines for working with rodents potentially infected with Hantavirus. *Journal of Mammalogy* **76**:716–722.
- Moore, M. M., and D. A. Deiter. 1992. Stand density index as a predictor of forage production in northern Arizona pine forest. *Journal of Range Management* **45**:267–171.
- Mutze, G. J., B. Green, and K. Newgrain. 1991. Water flux and energy use in wild house mice (*Mus domesticus*) and the impact of seasonal aridity on breeding and population levels. *Oecologia* **88**:529–538.
- Muzika, R. M., S. T. Grushecky, A. M. Liebhold, and R. L. Smith. 2004. Using thinning as a management tool for gypsy moth: the influence on small mammal abundance. *Forest Ecology and Management* **192**:349–359.
- Pollack, K. H. 1982. A capture-recapture design robust to unequal probabilities of capture. *The Journal of Wildlife Management* **46**:757–760.
- Pomeroy, J., and D. Gray. 1995. Snow cover: accumulation, relocation, and management. National Hydrology Research Institute, Saskatoon, Canada.
- Pyare, S. and W. S. Longland. 2001. Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. *Journal of Mammalogy* **82**:681–689.
- Ryan, T. P. 1997. Modern regression methods. John Wiley and Sons, New York.
- SAS Institute, Inc. 2000. SAS/STAT user's guide. SAS Institute, Cary, North Carolina.
- Schnurr, J. L., C. D. Canham, R. S. Ostfeld, and R. S. Inouye. 2004. Neighborhood analyses of small-mammal dynamics: impacts on seed predation and seedling establishment. *Ecology* **85**:741–755.
- Stewart-Oaten, A., W. W. Murdoch, and K. R. Parker. 1986. Environmental impact assessment: "pseudoreplication" in time? *Ecology* **67**:929–940.
- Stocks, B. J., M. A. Fosberg, T. J. Lynham, L. Mearns, B. M. Wotton, Q. Yang, et al. 1998. Climate change and forest fire potential in Russian and Canadian boreal forests. *Climatic Change* **38**:1–13.
- Storm, B. A., and P. Z. Fulé. 2007. Pre-wildfire fuel treatments affect long-term ponderosa pine forest dynamics. *International Journal of Wildland Fire* **16**:128–138.
- Stottleyer, R., and C. A. Troendle. 2001. Effect of canopy removal on snowpack quantity and quality, Fraser Experimental Forest, Colorado. *Journal of Hydrology* **245**:165–176.
- Sullivan, T. P., D. S. Sullivan, P. M.F. Lindgren, and D. B. Ransome. 2005. Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest II: diversity and population dynamics of forest floor small mammals. *Forest Ecology and Management* **205**:1–14.
- Suzuki, N., and J. P. Hayes. 2003. Effects of thinning on small mammals in Oregon coastal forests. *The Journal of Wildlife Management* **67**:352–371.
- Troendle, C. A., and C. F. Leaf. 1981. Effects of timber harvest in the snow zone on volume and timing of water yield. Pages 231–243 in D. Baumgartner, editor. Proceedings of the interior west watershed management symposium. Washington State University Cooperative Extension, Spokane.
- Underwood, A. J. 1993. The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. *Australian Journal of Ecology* **18**:99–116.
- Westerling, A., H. Hidalgo, D. Cayan, and T. Swetnam. 2006. Warming and earlier spring increases western U.S. forest wildfire activity. *Science* **313**:940–943.
- Williams, A., D. Karoly, and N. Tapper. 2001. The sensitivity of Australian fire danger to climate change. *Climatic Change* **49**:171–191.
- Wilson, S. M., and A. B. Carey. 2000. Legacy retention versus thinning: influences on small mammals. *Northwest Science* **74**:131–145.
- Zielinski, W. J., W. D. Spencer, and R. H. Barrett. 1983. Relationship between food habits and activity patterns of pine martens. *Journal of Mammalogy* **64**:387–396.