EFFECTS OF BURNING AND THINNING ON LODGEPOLE CHIPMUNKS (*NEOTAMIAS SPECIOSUS*) IN THE SIERRA NEVADA, CALIFORNIA

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ABSTRACT—Prescribed burning and mechanical thinning are widely used to manage fuels in North American forests, but few studies have examined the relative impacts of these treatments on wildlife. Using a fully factorial and completely randomized design, we examined the shortterm effects of prescribed burning (no burn vs. burn), mechanical thinning (no thin, light thin, and heavy thin), and combinations of these treatments on the capture rate and demographic parameters of Lodgepole Chipmunks (Neotamias speciosus) in mixed-conifer forests in the southern Sierra Nevada of California. Chipmunks were sampled in eighteen 4-ha treatment plots during the summer of 1999 and 2000 (pre-treatment) and 2002 and 2003 (post-treatment). Although burning and thinning caused significant changes in forest structure, neither treatment had a significant effect on the capture rate or most demographic parameters of N. speciosus. Body mass of males (2002 and 2003) and the ratio of males to females (2003) decreased following burning. Body mass and percentage reproductive females were positively correlated with the total number of White Fir (Abies concolor) cones produced across treatments and years, possibly reflecting a positive association between chipmunk reproduction and food availability. These results suggest that prescribed burning and mechanical thinning may have minor or no short-term effects on the capture rate and demography of N. speciosus in mixed-conifer forests of the Sierra Nevada, but effects over longer periods have not been investigated.

Key words: *Neotamias speciosus*, Lodgepole Chipmunk, capture rate, fire, thinning, cones, Sierra Nevada, California

Fire is an integral component of many ecosystems throughout the world (Dickman and Rollinger 1998), facilitating tree regeneration, nutrient cycling, and understory vegetation dynamics (Attiwill 1994; Chang 1996; Stephen and Han 2006). Decades of fire exclusion in western North American forests have changed stand structure and composition, increased the incidence of insect and disease outbreaks, and greatly amplified the frequency and extent of high-intensity catastrophic fires (Agee 1993; Skinner and Chang 1996; Husari and McKelvey 1996; Dickman and Rollinger 1998). Prescribed fire has been used to manage fuels and restore forest ecosystems to a desired condition (McKelvey and others 1996). Although there are many challenges to reintroducing fire to Sierra Nevada forests, under suitable conditions prescribed fire management has the potential to reduce fire intensity and tree mortality, restore stand structure to a desired range of conditions, and improve habitat for wildlife (Biswell 1989; Chang 1996; Allen and others 2002; Stephens and Moghaddas 2005a). However, implementation of prescribed burning programs in California often is limited by air quality restrictions, containment concerns, and fire management budgets (Husari and McKelvey 1996).

Mechanical thinning is an alternative to prescribed burning for reducing fuels in forests. Selective removal of understory fuels has been proposed to reduce the intensity of stand-replacing crown fires (Helms and Tappeiner 1996), but thinning may have different effects on forest ecosystems compared to prescribed fire. For instance, thinning treatments may increase soil compaction and decrease total above-ground carbon by removing trees (Helms and Tappeiner 1996), whereas burning may increase nutrient availability in the short term and, unintentionally or intentionally, cause significant tree death (Chang 1996). Thinning does not enhance reproduction and seed germination in plants that require heat or smoke treatment, but it can enhance vegetation growth, seed and fruit production, and regeneration of plants that require physical disturbance or increased light, moisture, and nutrient availability (Chang 1996; Keeley and Fotheringham 1997; Wayman and North 2007). Mechanically thinned forest stands have a different composition of hypogeous fungal sporocarps (truffles) than burned stands (Meyer, North, and Kelt 2005). Burning may favor larger-diameter and more fire-resistant tree species such as Ponderosa Pine (Pinus ponderosa) and Douglas-Fir (Pseudotsuga menziesii) (Agee 1993) that often are preferred timber species. Some types of prescribed burning or selective mechanical thinning may increase the density of larger-diameter snags that provide important nest cavities for wildlife (Carey and others 1997; Stephens and Moghaddas 2005b). Consequently, wildlife species attracted to these post-fire habitat conditions may not be favored following thinning treatments (Chang 1996).

Chipmunks (*Neotamias* spp.) are abundant and important components of western North American forests and are very responsive to changes in management (Carey 1995, 2000; Carey and others 1999; Sullivan and Klenner 2000) and natural environmental variability (Chappell 1978; Sharples 1983). In the Sierra Nevada, chipmunks disperse tree and shrub seeds (Vander Wall 1993, 1994) as well as ectomycorrhizal fungal spores (Pyare and Longland 2001; Meyer, Kelt, and North 2005; Meyer, North, and Kelt 2005) that may be critical for forest regeneration. Many chipmunk species in the Sierra Nevada, such as the Lodgepole Chipmunk (Neotamias speciosus), are prey for Pine Martens (Zielinski and others 1983) and Northern Goshawks (Schnell 1958; Maurer 2000), and are occasionally in the diet of California Spotted Owls (Poopatanapong 2000). The Lodgepole Chipmunk also is of particular interest in California forests because it occurs in many forest types (Broadbooks 1999), is more dependent than other sympatric chipmunk species on overstory trees for nest and refuge sites (Best and others 1994), and one subspecies (N. s. cal*lipeplus*) is currently recognized as a sensitive species in California (USDA Forest Service 2001).

Availability of food resources is an important factor influencing the capture rate and demography of sciurids in many western North American forests (Sullivan and Sullivan 1982; Klenner and Krebs 1991; Dodd and others 2003; Ransome and Sullivan 2004). In the Sierra Nevada, conifer seeds and understory vegetation (seeds, flowers, fruits, and leaves of shrubs and herbs) are primary foods in the diet of N. speciosus and other chipmunk species (Tevis 1952, 1953; Chappel 1978; Best and others 1994). Food availability is positively associated with reproduction, body mass, and capture rate in tree squirrels of North America (Sullivan and Sullivan 1982; Buchanan and others 1990; Koprowski 1991; Vlasman and Fryxell 2002). However, very little information has been published on the relationship between food abundance (particularly conifer seeds) and the capture rate and reproduction of chipmunks despite their importance in food webs of coniferous forests in western North America.

The purpose of our study was to examine the short-term effects of prescribed burning, mechanical thinning, and combinations of these treatments on capture rate and demographic parameters of *N. speciosus*. A 2nd objective was to assess annual differences in capture rate and demographic parameters and their relationship to food availability (conifer cones, understory vegetation) during post-treatment years. We predicted that, in the short-term (≤ 2 y), burn-



FIGURE 1. Location and layout of research plots at the Teakettle Experimental Forest, Fresno Co., California. Black dots on bottom right panel indicate location of trap stations in a plot. Treatment plot codes in the left panel include unburned (U), burned (B), no thin (N), light 'CASPO' thin (C), and heavy 'Shelterwood' thin (S).

ing, thinning, and their combination would decrease capture rate, mean body mass, and reproduction of chipmunks by decreasing understory food availability (shrubs, herbs) in treated stands. We also predicted positive relationships between food availability (conifer cones, shrubs, and herbaceous plants) and chipmunk capture rate, female body mass, and reproduction across post-treatment plots.

METHODS

Study Area and Experimental Design

Our study was conducted at Teakettle Experimental Forest, a 1300-ha mixed-conifer forest in the southern Sierra Nevada, Fresno County, California (Fig. 1). Teakettle is at 1800 to 2400 m elevation and is characterized by a strongly Mediterranean-influenced montane climate, with hot, dry summers and 125 cm mean annual precipitation that falls almost exclusively in the form of snow from November to April (North and others 2002). Our site is an oldgrowth forest characterized by a multi-layered canopy and numerous large (>100 cm diameter at breast height; dbh) and old (>200 y) trees, snags, and decayed logs. Dominant trees include White Fir (Abies concolor), Red Fir (A. magnifica), Sugar Pine (Pinus lambertiana), Jeffrey Pine (P. jeffreyi), and Incense Cedar (Calocedrus decurrens). Dominant understory plants include Mountain Whitethorn (Ceanothus cordulatus), Bush Chinquapin (Chrysolepis sempervirens), Greenleaf Manzanita (Arctostaphylos patula), Pinemat Manzanita (Arctostaphylos neva-

densis), and Snowberry (Symphoricarpos mollis) (North and others 2002). Old-growth rather than 2nd-growth forest was selected for thinning and burning treatments because it is (1) a baseline for historic forest conditions indicating how ecosystem processes respond to disturbance; (2) less variable than stands with different management histories, thereby allowing plots to have similar pre-treatment conditions; and (3) representative of unharvested Sierra Nevada mixed-conifer forest stands that, compared to historic conditions, have significantly altered stand structure and composition (North and others in press), regeneration (Gray and others 2005), and tree mortality conditions (Smith and others 2005) following a long history of fire exclusion. The last widespread fire of low to high severity at the study site was in 1865 (North and others 2004).

For this experiment, we used a full factorial set of treatments in a completely randomized design. Six treatments were produced by crossing 2 levels of burning (no burn vs. prescribed burn) with 3 levels of thinning (none, light thin, and heavy thin): (1) no burn or thin (control); (2) light thin only; (3) heavy thin only; (4) burn only; (5) light thin followed by burn; and (6) heavy thin followed by burn. We established 18 replicate 4-ha plots, and all plots but 1 were randomly assigned to each treatment (Fig. 1). The single exception was a plot that was randomly assigned to 1 of the 3 unthinned treatments because it contained a perennial stream around which US Forest Service regulations did not permit tree harvest. All plots were separated by untreated buffer zones composed of homogenous upland stands ranging from ≥ 50 to 150 m. The spatial placement of plots was determined following cluster analysis of mapped sample quadrats, indicating that all pre-treatment plots were considered statistically similar with respect to all overstory and understory habitat variables measured in this study (North and others 2002). We believe that plots were of adequate size (4 ha) to maintain independence among treatments because (1) there was a minimum distance of 150 to 250 m between grid points of any 2 plots, which is approximately 60 to 160 m greater than the average maximum distance moved by N. speciosus (90 m; Monroe 2005), and (2) only 3.4% of the individuals captured post-treatment in our study were from >1 plot, and these individuals were excluded

from post-treatment analyses. In July to September 2000 and July to August 2001, 12 plots were thinned following 2 prescriptions: 6 lightintensity CASPO (California Spotted Owl guidelines) plots and 6 high-intensity shelterwood plots. Under CASPO thinning, no trees >76 cm diameter were harvested and at least 40% of the canopy cover (~75% using hemispherical digital photos) was left in place after harvest. With shelterwood regeneration harvest ('shelterwood thinning'), all trees >25 cm dbh were removed except for approximately 22 dominant, evenly spaced trees per hectare. Shelterwood guidelines followed practices used on several National Forests in the Sierra Nevada before CASPO regulations and were modeled on common silvicultural prescriptions (Smith 1986). Compared to controls, the CASPO and shelterwood thinned plots had significantly lower canopy cover and fewer large diameter (\geq 50 cm) trees and snags than controls, but only shelterwood thinned plots had fewer understory shrubs (Table 1). In early November 2001, after the 1st substantial fall rain, 9 plots were treated with prescribed burns. At this time, mean daytime temperature was 13°C and relative humidity ranged between 25 to 70%. The percentage of ground cover burned was significantly different among no thin (11%), CASPO (52%), and shelterwood (71%) plots that were prescribed-burned (no thin and CASPO: P = 0.04; no thin and shelterwood: P= 0.01; CASPO and shelterwood: P = 0.02). All thinned plots with the exception of CASPOthinned-without-burning had significantly lower canopy cover and number of large trees and snags than controls, while only plots that were heavily thinned (shelterwood) had lower shrub cover than controls (Table 1).

Sampling of Chipmunks and Food Resources

We used a 3 \times 3 grid with 50 m spacing between traps to sample chipmunks in each plot (Fig. 1). At each grid point, we placed a single Tomahawk live trap (model 201) 1.5 m above ground on the trunk of the closest large (>70 cm dbh) tree. We limited our sampling effort to only 9 traps per plot because more intensive small mammal sampling created impacts on concurrent collaborative research in our study plots (North and Chen 2005), and ground trap sampling was discontinued at the beginning of our study due to heavy losses of ground traps

TABLE 1. Mean values of stand structure and conifer cone variables measured in treatment plots at Teakettle Experimental Forest (2002 to 2003). Within a row, values with different superscript letters are significantly different (P < 0.05) from other values within the same row using Tukey's HSD test. Numbers in parentheses indicate pre-treatment (1999 to 2000) values (no pre-treatment stand structure values were significantly different using Tukey's HSD test).

	No burn			Burn			
Stand variable	No thin (control)	Light thin ²	Heavy thin ³	No thin	Light thin ²	Heavy thin ³	
Density of large trees ¹ (no./ha) Density of large snags ¹	68.3 ^{a,b} (68.3)	41.7 ^{b,c} (77.0)	22.5 ^c (67.8)	77.9 ^a (77.9)	41.2 ^c (77.3)	24.6 ^c (72.9)	
(no./ha)	(, , , , , , , , , , , , , , , , , , ,	9.8 ^{a,b} (13.7)	8.3 ^b (11.3)	8.4 ^b (10.7)	9.2 ^b (11.4)	8.5 ^b (14.8)	
Canopy cover (%) Shrub cover (%)		72.3 ^{a,c} (81.2) 5.7 ^{a,b} (14.8)	62.7 ^d (80.1) 1.5 ^b (14.4)	79.9 ^a (79.4) 15.8 ^a (27.6)			
Herbaceous plant cover (%) <i>Pinus jeffreyi</i> cones (no./ha)	7.4 ^a (4.9) 219 (270)	5.1 ^a (3.7) 63 (231)	4.9 ^a (2.4) 271 (360)	8.1 ^a (3.8) 760 (141)	17.1 ^b (3.2) 417 (131)	16.9 ^b (1.1) 253 (144)	
Abies concolor cones (no./ha) Pinus lambertiana cones	1541 (3605)	594 (1065)	688 (696)	3583 (2967)	1943 (2667)	341 (3208)	
$\frac{\text{(no./ha)}}{^{1} \geq 50 \text{ cm dbh.}}$	967 (977)	793 (522)	702 (1018)	914 (1359)	211 (723)	970 (1560)	

² Light (CASPO) thinning, no trees >76 cm diameter were harvested and at least 75% of the canopy cover (using hemispherical digital photos) was left in place after harvest.

³ Heavy (shelterwood) thinning, all trees >25 cm dbh were removed except for approximately 22 dominant, evenly spaced trees per hectare.

by repeated Black Bear (Ursus americanus) activity. In 1999 to 2000 (pre-treatment) and 2002 to 2003 (post-treatment), we set traps in each plot for 3 consecutive days in early summer (June) and 4 consecutive days in mid-summer (July to August), for a total of 45 trap-nights per plot per year. Traps were baited with a mixture of peanut butter and rolled oats and were provided with a small cardboard shelter and polyethylene stuffing material for thermal insulation. We checked traps at dawn and dusk and closed them in the event of heavy rain. We marked all captured chipmunks with individually numbered metal ear tags, and recorded their body mass, sex, reproductive condition, and age class (juvenile or adult). We used pelage characteristics to determine age class (color markings are brighter and stronger on juveniles than adults). We assessed reproductive condition based on scrotum color and position of the testes in males and degree of enlargement, redness, and turgidity of mammae in females (Best and others 1994). All captured animals were handled in accordance with the American Society of Mammalogists Animal Care and Use Committee (1998) guidelines and an approved Institutional Animal Care and Use Committee (IACUC) protocol.

We sampled conifer cone abundance and herbaceous plant cover in all 4-ha plots to evaluate potential relationships between food availability and chipmunk variables (capture rate, reproductive condition) across treatments and years. We estimated conifer cone abundance by selecting and marking a single randomly selected overstory tree (>80 cm dbh) of the 3 most common overstory tree species (Abies concolor, P. jeffreyi, and P. lambertiana) within each of 18 treatment plots. In July of 2000, 2002, and 2003, we used 10×40 binoculars to count the number of cones that were visible in each tree from a single station that was 25 m from the tree in a fixed randomly selected direction. The low number of sample trees surveyed in each plot (n = 1 per species) does not account for variation in cone estimates among trees within a stand. To estimate the mean percent cover of shrubs and herbaceous plants, we visually estimated plant cover in a sample of nine 10-m² circular quadrats in each plot (1 at each trap station) in July to August of 2000, 2002, and 2003.

Analysis

The number of captures and recaptures varied greatly among treatments, with few or no recaptures in some plots, so we calculated capture rate of *N. speciosus* among treatments. Capture rate (CR) was expressed as a modification of the formula of Nelson and Clark (1973):

$$CR = [I/(T - S/2)] \times 100$$

where I = number of individuals captured, T = number of traps multiplied by the number of nights traps were opened (trapnights), and S = number of traps sprung across all nights of effort. Capture rate is expressed as a percentage of traps with ≥ 1 capture and was positively correlated with Nelson and Clark's (1973) capture rate values (Pearson's R = 1.000 and 0.972 for 2002 and 2003, respectively) and is a useful and simple estimator of true abundance of small mammals, including chipmunks (Waters and Zabel 1998; Carey and others 1999). We also calculated the total number of individuals captured, as these counts were proportional to population size in small-mammal populations (Slade and Blair 2000).

We analyzed all pre-treatment stand structure variables (density of large trees and snags; canopy, shrub, and herbaceous plant cover) and N. speciosus variables (capture rate, sex ratio, percent breeding females, male and female body mass) with 3-way mixed-model analysis of variance (ANOVA) to test for differences among treatments (burning, thinning; fixed factors) and pre-treatment year (random factor). There were no significant pre-treatment differences (all P > 0.05) in any of these variables. Data were evaluated for normality with the Kolmogorov-Smirnov test and for homoscedasticity with Levene's test. Sex ratios were square-root transformed and female body mass and number of A. concolor and P. jeffreyi cones were log-transformed to improve the fit to parametric assumptions of normality and homoscedasticity. All analyses were conducted with Statistica 6.0 (StatSoft Inc., Tulsa, Oklahoma) and an α level of 0.05.

We used 3-way mixed-model ANOVAs and a single multivariate analysis of variance (MAN-OVA) to test for the effect of fire (2 levels; fixed factor), thinning (3 levels; fixed factor), and post-treatment year (2 years; random factor) on chipmunk capture rate and demographic variables [sex ratio of all individuals, percent of females in breeding condition (females lactating or pregnant), and male and female body mass]. Trapping periods for early- and mid-summer (n = 3 and 4 d, respectively) were not analyzed separately. A small percent (3.4%) of captured individuals was found in more than a single treatment plot and we excluded these individuals from analysis to maximize the independence of treatment plots in our sample.

TABLE 2. Summary of *Neotamias speciosus* and conifer cone variables measured in pre-treatment (1999 and 2000) and post-treatment (2002 and 2003) stands at Teakettle Experimental Forest. Capture rate, percent breeding females, female body mass, and conifer cone variables are presented as mean $\pm s_{\hat{x}}$.

Capture variable	1999	2000	2002	2003
Number of in-				
dividuals ¹	109	106	296	256
Number of				
captures	190	241	461	491
Capture rate				
(%)	8 ± 2	12 ± 2	41 ± 4	28 ± 3
Percent breed-				
ing females	36 ± 5	65 ± 5	39 ± 6	80 ± 3
Female body				
mass (g)	56 ± 1	59 ± 1	60 ± 1	66 ± 1
Pinus jeffrei				
cones (no./				
ha)	_	14 ± 6	21 ± 4	97 ± 24
Abies concolor				
cones (no./				
ha)	_	96 ± 42	19 ± 11	87 ± 20
Pinus lamberti-				
ana cones				
(no./ha)	_	154 ± 31	142 ± 18	102 ± 26

¹ Total number of individual chipmunks captured during sampling (excludes recaptures).

The total number of conifer (A. concolor, P. jeffreyi, and P. lambertiana) cones per year was calculated as the total number of visible cones per large (\geq 50 cm dbh) tree \times the number of large trees per hectare in each plot. We used 2-way ANOVAs to examine the effect of burn and thin treatments on the total number of cones for each of the 3 conifer species. We used singlefactor ANOVAs to examine differences in the number of conifer cones per tree (3 conifer species) and understory plant cover (shrubs, herbaceous plants) between 2002 and 2003. We used Pearson's product-moment correlation to examine relationships between the availability of food resources (A. concolor, P. lambertiana, and P. jeffreyi cone abundance, cover of shrubs and herbaceous plants), chipmunk capture rate, and body mass of females.

RESULTS

We captured 1383 chipmunks from 1999 to 2003, with the majority (69%) of captures from post-treatment (2002 to 2003) censuses (Table 2). Burning and thinning had no effect on *N. speciosus* capture rate (Tables 3, 4, 5), but capture rate was greater in 2002 than 2003 (Table

 (0.61 ± 0.32)

 59.9 ± 10.1

 (64.2 ± 13.1)

 55.7 ± 1.1

 (58.9 ± 2.7)

 60.7 ± 1.7

 (69.1 ± 2.9)

nation. Numbers in	parentheses in	dicate pre-trea	atment (1999 to	2000) values.			
	No burn			Burn			
- Chipmunk variable	No thin (control)	Light thin	Heavy thin	No thin	Light thin	Heavy thin	
Capture rate ¹	25.0 ± 5.4 (9.0 ± 3.5)	40.0 ± 5.0 (5.3 ± 5.5)	35.7 ± 8.8 (9.5 ± 2.8)	33.7 ± 4.3 (12.2 ± 4.7)	32.7 ± 8.7 (12.9 ± 6.1)	38.4 ± 5.4 (11.1 ± 1.9)	
Total number of individuals captured/year	12.7 ± 2.1 (5.7 ± 2.2)	$\begin{array}{c} 18.0 \pm 1.6 \\ (3.3 \pm 1.4) \end{array}$	16.7 ± 3.6 (6.0 ± 1.8)	$\begin{array}{c} 16.3 \pm 1.9 \\ (7.7 \pm 2.9) \end{array}$	16.3 ± 4.6 (8.2 ± 1.6)	$\begin{array}{c} 18.7 \pm 2.3 \\ (7.0 \pm 1.2) \end{array}$	
Sex ratio	2.44 ± 0.48	1.41 ± 0.35	1.18 ± 0.16	1.29 ± 0.22	1.44 ± 0.34	0.85 ± 0.11	

 (0.74 ± 0.12)

 51.5 ± 13.4

 (64.0 ± 12.8)

 58.0 ± 1.2^2

 (58.7 ± 1.7)

 60.9 ± 1.7

 (69.9 ± 2.9)

 (0.45 ± 0.22)

 (53.1 ± 10.8)

 78.8 ± 6.7

 54.7 ± 1.1

 (59.0 ± 1.0)

 67.3 ± 3.2

 (67.7 ± 2.3)

TABLE 3. Mean $\pm s_r$ of *Neotamias speciosus* variables measured in post-treatment stands at Teakettle Experimental Forest. Post-treatment years (2002 to 2003) are pooled, such that n = 6 for each treatment combina

¹ The percent of traps with ≥ 1 capture.

(male:female) Percent breeding

Male body mass (g)

females

Female body

mass (g)

> (67.5 ± 3.5) ² For this value, n = 5 (no male captures in 1 treatment plot in 2003).

 (2.67 ± 1.15)

 51.3 ± 14.7

 (54.2 ± 19.8)

 57.6 ± 1.0

 (56.9 ± 1.9)

 63.2 ± 1.9

2). Overall, demographic variables of N. speciosus (percent of breeding females, male and female body mass, sex ratio) were similar across treatments both pre- and post-treatment (Tables 3, 5), although body mass of males and sex ratio were lower in burned than unburned plots (Tables 4, 5). The percent of breeding females and female body mass were greater in 2003 than 2002 (Table 2), with a significant interaction between year, thin, and burn treatments for percentage of reproductive females (Table 5). Across all plots, females averaged 9% and 17% heavier than males in 2002 and 2003,

respectively, although non-breeding females were only 6.5% heavier than males in 2003.

 (1.03 ± 0.18)

57.2 ± 15.2

 (51.3 ± 9.1)

54.3 ± 1.7

 (56.7 ± 1.8)

 64.9 ± 2.8

 (67.3 ± 2.1)

Estimates of P. jeffreyi cone abundance was 3.2 times greater in burned compared to unburned plots but was not different among thin treatments (Tables 1, 6). Cone abundance for A. concolor or P. lambertiana did not differ among burn or thin treatments. Cone abundance for both A. concolor and P. jeffreyi were 4.6 times greater in July 2003 than July 2002, but the abundance of P. lambertiana cones was similar between years (Tables 2, 6). Understory herbaceous plant and shrub cover was 1.7 times

TABLE 4. Mean $\pm s_{\bar{x}}$ of *Neotamias speciosus* variables measured in post-treatment stands at Teakettle Experimental Forest. Treatments are grouped by burning (no burn, burn) or thinning (no thin, light thin, heavy thin) to allow direct comparison within a treatment group. Post-treatment years (2002 to 2003) and treatments are pooled such that n = 12 (no thin, light thin, heavy thin) or n = 18 (no burn, burn). Numbers in parentheses indicate pre-treatment (1999 to 2000) values.

Chipmunk variable	No burn	Burn	No thin	Light thin	Heavy thin
Capture rate ¹	33.6 ± 3.9	34.9 ± 3.5	29.4 ± 3.6	36.4 ± 4.9	37.0 ± 5.0
*	(7.9 ± 1.6)	(12.1 ± 1.8)	(10.6 ± 2.8)	(9.1 ± 2.0)	(10.3 ± 1.7)
Total number of individ-	15.7 ± 1.5	17.1 ± 1.7	14.5 ± 1.5	17.2 ± 2.3	17.7 ± 2.1
uals captured/year	(5.0 ± 1.0)	(7.6 ± 1.1)	(6.7 ± 1.8)	(5.8 ± 1.2)	(6.5 ± 1.0)
Sex ratio (male:female)	1.71 ± 0.25	1.19 ± 0.14	1.87 ± 0.31	1.42 ± 0.23	1.00 ± 0.10
	(1.39 ± 0.47)	(0.79 ± 0.14)	(1.46 ± 0.61)	(0.86 ± 0.17)	(0.82 ± 0.17)
Percent breeding females	54.2 ± 7.1	64.9 ± 6.9	65.1 ± 8.8	58.5 ± 8.7	55.1 ± 8.8
0	(60.5 ± 8.6)	(50.9 ± 4.7)	(53.6 ± 10.2)	(56.5 ± 7.4)	(55.5 ± 6.4)
Male body mass (g) ²	57.1 ± 0.6	54.5 ± 0.7	56.2 ± 0.8	55.0 ± 1.0	56.1 ± 0.9
	(58.1 ± 1.1)	(57.3 ± 0.8)	(57.8 ± 1.2)	(57.4 ± 1.5)	(57.8 ± 0.9)
Female body mass (g)	61.6 ± 1.0	64.4 ± 1.6	65.2 ± 1.9	62.8 ± 1.7	61.0 ± 1.4
	(68.8 ± 1.7)	(68.2 ± 1.4)	(67.6 ± 1.9)	(68.0 ± 1.6)	(69.8 ± 2.1)

¹ The percent of traps with \geq 1 capture

² For unburned plots, n = 17; heavy thinned plots, n = 11 (no male captures in 1 plot in 2003).

 (0.89 ± 0.31)

 $58.7\,\pm\,12.4$

 (48.3 ± 4.6)

 $54.4\,\pm\,0.7$

 (56.8 ± 0.7)

 61.1 ± 2.1

 (69.7 ± 3.3)

TABLE 5. MANOVA and ANOVAs for effects of burning, thinning, and year on *Neotamias speciosus* variables at Teakettle Experimental Forest (2002 to 2003).

Dependent variable	Factor	Wilk's λ	F	df	Р
ANOVA	burn		0.069	1,24	0.795
Capture rate	thin		0.875	2,24	0.430
*	burn $ imes$ thin		0.804	2,24	0.459
	year		5.961	1,24	0.022
	burn $ imes$ year		0.590	1,24	0.450
	thin $ imes$ year		0.196	2,24	0.823
	burn $ imes$ thin $ imes$ year		0.103	2,24	0.902
MANOVA	burn	0.583	3.573	4,20	0.024
Sex ratio, percent breeding females,	thin	0.621	1.344	8,40	0.250
male and female body mass	burn $ imes$ thin	0.661	1.152	8,40	0.351
	year	0.361	8.843	4,20	< 0.001
	burn $ imes$ year	0.901	0.550	4,20	0.701
	thin $ imes$ year	0.834	0.474	8,40	0.867
	burn $ imes$ thin $ imes$ year	0.513	1.979	8,40	0.075
ANVOAs					
Sex ratio	burn		4.350	1,24	0.048
	year		2.270	1,24	0.146
	burn $ imes$ thin $ imes$ year		3.399	1,24	0.051
Percent breeding females	burn		2.676	1,24	0.115
-	year		39.478	1,24	< 0.001
	burn $ imes$ thin $ imes$ year		4.232	1,24	0.027
Male body mass	burn		7.663	1,23	0.011
	year		1.867	1,23	0.185
	burn $ imes$ thin $ imes$ year		1.272	1,23	0.299
Female body mass	burn		2.549	1,24	0.123
-	year		11.966	1,24	0.002
	burn $ imes$ thin $ imes$ year		0.571	1,24	0.573

greater in 2003 (21.3 \pm 5.2) than 2002 (12.2 \pm 4.6; $F_{1,34} = 7.675$, P = 0.009). There were essentially no correlations between female body mass and the abundance of shrubs (R = 0.267, P = 0.115) or herbaceous plants (R = -0.074, P= 0.666). There were weak positive correlations between female body mass or reproduction and the number of A. concolor cones (body mass: R = 0.447, P = 0.007; reproduction: R =0.461, P = 0.005), but no correlation with the number of cones of *P. lambertiana* (body mass: R = -0.198, P = 0.262; reproduction: R =-0.069, P = 0.697) or *P. jeffreyi* (body mass: *R* = 0.287, P = 0.089; reproduction: R = 0.255, P= 0.133); and no correlation between chipmunk capture rate and the number of cones of A. concolor (R = -0.191, P = 0.272), *P. lambertiana* (*R* = 0.103, P = 0.560), or P. jeffreyi (R = -0.059, P)= 0.739).

DISCUSSION

Our study was conducted with limited sampling effort over 2 seasons in 1 location and therefore may not provide robust estimates of capture rate, demographic variables, or food abundance for N. speciosus. Additionally, our treatment plots were relatively small in size (4 ha) and may not be completely independent with respect to chipmunk capture rate and demographic variables. Despite or because of these limitations, we did not detect an immediate effect of mechanical thinning on the capture rate or demographic parameters of N. speciosus at Teakettle. In the Cascade Mountains of northeastern California, N. speciosus was more frequently captured in shelterwood-thinned units than in unthinned old- or 2nd-growth forest stands (Waters and Zabel 1998). Similarly in the northern Sierra Nevada, N. speciosus was more frequently captured in open, heavily thinned stands with scattered trees than in closed-canopy stands or clear-cuts with an extremely high or low density of trees (Sharples 1983). One key difference between these studies and ours is that both Waters and Zabel (1998) and Sharples (1983) sampled their thinned stands 7 to 16 y after thinning, allowing time for the forest understory to develop a

TABLE 6. ANOVAs for effects of burning, thinning, and year on cone abundance of 3 tree species at Teakettle Experimental Forest (2002 to 2003).

Conifer species	Factor	F	df	Р
Pinus	burn	8.583	1,24	0.007
jeffreyi	thin	0.972	2,24	0.393
,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	burn $ imes$ thin	3.138	2,24	0.062
	year	10.109	1,24	0.004
	$burn \times year$	0.409	1,24	0.529
	thin \times year	0.412	2,24	0.667
	$burn \times thin$	1.487	2,24	0.246
	imes year			
Abies	burn	0.002	1,23	0.965
concolor	thin	0.846	2,23	0.442
	burn $ imes$ thin	0.211	2,23	0.811
	year	16.653	1,23	< 0.001
	$burn \times year$	0.002	1,23	0.962
	thin \times year	1.046	2,23	0.576
	$burn \times thin$	0.703	2,23	0.506
	imes year			
Pinus	burn	0.433	1,22	0.518
lambertiana	thin	1.744	2,22	0.198
	burn $ imes$ thin	1.627	2,22	0.219
	year	3.969	1,22	0.059
	burn × year	0.080	1,22	0.780
	thin \times year	0.610	2,22	0.552
	$burn \times thin$	3.925	2,22	0.035
	\times year			

dense shrub and herb understory. In 2ndgrowth forest stands of the northern Sierra Nevada, for example, N. speciosus was associated with a greater coverage and diversity of understory shrubs (Coppeto and others 2006). Such understory vegetation is a diverse source of seeds, fruits, flowers, and leaves that provide food for N. speciosus (Tevis 1952, 1953; Best and others 1994). In contrast, we sampled immediately (1 to 2 y) after thinning treatments when the forest understory was largely undeveloped, although several herbaceous species increased in abundance immediately following treatments particularly in thin combined with burn treatments (Wayman and North 2007). The lack of understory food resources for N. speciosus in the thinned plots in our study may partially explain the lack of significant increase in N. speciosus capture rate immediately following thinning.

Our study also failed to detect an effect of prescribed burning on *N. speciosus* capture rate or female-related demographic parameters, possibly as a result of our limited sample effort or small size of treatment plots. However, prescribed fire was not expected to increase the

capture rate of N. speciosus at Teakettle given the low-severity impact of burning on forest stand structure. Burning had no notable effect on any stand structure variables, with the exception that fewer large-diameter snags were in burned-only compared to control plots, and herbaceous plant cover was greater in thinwith-burn plots compared to control, thin-only, or burn-only plots (Table 1). In mixed-conifer forest of the southern Sierra Nevada, latespring and fall prescribed burning had no immediate effect on densities of N. speciosus, although annual changes in density were substantial (Monroe 2005). In contrast, N. speciosus was more frequently captured in intensively burned stands where tree cover was 30 times lower and understory shrub and herb cover was 8 and 7 times greater, respectively, than in unburned stands (Sharples 1983). In a mature Giant Sequoia (Sequoiadendron giganteum) forest stand, N. speciosus capture rate gradually increased 4 to 5 y following prescribed burning, when the cover of understory vegetation returned to pre-burn levels (Werner 2000).

Body mass and the percentage of reproductive female chipmunks were positively associated with cone crop of A. concolor and P. jeffreyi across years and treatment plots at Teakettle. Conifer seeds are a high-energy and primary food resource in the diet of N. speciosus and other squirrels of the Sierra Nevada (Tevis 1952, 1953) and positively associated with reproduction (Wauters and others 2004) and detection rates (Buchanan and others 1990) in tree squirrels (Sciurus, Tamiasciurus spp.). Given that there was nearly a 5-fold difference in the number of A. concolor and P. jeffreyi cones between 2002 and 2003, it is possible that this greater food availability in 2003 may have increased nutritional intake in females and enhanced the onset of reproduction during this year. Other primary food resources such as hypogeous fungal sporocarps (truffles) were similar in abundance between the summers of 2002 and 2003 (Meyer, North, and Kelt 2005).

Although our study was exploratory and based on limited sampling, our results represent a 1st experimental study directly comparing the effects of burning and mechanical thinning on chipmunk capture rate in the Sierra Nevada. Despite having different impacts on forest stand structure, both burning and thinning had similar, non-significant short-term ef-

fects on N. speciosus capture rate and demographic variables. Previous studies (for example, Tevis 1956; Sharples 1983; Waters and Zabel 1998) indicate that these similarities in chipmunk capture rate may change as the forest understory develops to provide individuals with more food resources and cover from predators. However, while more intensive thinning and burning treatments may potentially benefit Lodgepole Chipmunk populations in the longterm, they are predicted to have the opposite impact on populations of more sensitive, forestdependent species, such as the Northern Flying Squirrel (Glaucomys sabrinus; Meyer and others 2007). We recommend future research focus on these more sensitive species of the Sierra Nevada to critically evaluate the effects of prescribed burning and mechanical thinning on forest wildlife.

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LITERATURE CITED

- AGEE JK. 1993. Fire ecology in Pacific Northwest forests. Washington DC: Island Press. 493 p.
- ALLEN CD, SAVAGE M, FALK DA, SUCKLING KF, SWETNAM TW, SCHULKE T, STACEY PB, MORGAN P, HOFFMAN M, KLINGEL JT. 2002. Ecological restoration of southwestern Ponderosa Pine ecosystems: a broad perspective. Ecological Applications 12:1418–1433.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416– 1431.
- ATTIWILL PM. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63:247–300.
- BEST TL, CLAWSON RG, CLAWSON JA. 1994. Tamias speciosus. Mammalian Species 478:1–9.

BISWELL HH. 1989. Prescribed burning in California

wildlands vegetation management. Berkeley, CA: University of California Press. 274 p.

- BROADBOOKS HE. 1999. Lodgepole Chipmunk *Tamias* speciosus. In: Wilson DE, Ruff S, editors. Smithsonian book of North American mammals. Washington DC: Smithsonian Institution Press. p 386– 388.
- BUCHANAN JB, LUNDQUIST RW, AUBRY KB. 1990. Winter populations of Douglas' Squirrels in different-aged Douglas-fir forests. Journal of Wildlife Management 54:577–581.
- CAREY AB. 1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecological Applications 5:648–661.
- CAREY AB. 2000. Effects of new forest management strategies on squirrel populations. Ecological Applications 10:248–257.
- CAREY AB, KERSHNER J, BISWELL B, DOMINGUEZ DE TOLEDO L. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildlife Monographs 142:1–71.
- CAREY AB, WILSON TM, MAGUIRE CC, BISWELL BL. 1997. Dens of Northern Flying Squirrels in the Pacific Northwest. Journal of Wildlife Management 61:684–699.
- CHANG C. 1996. Ecosystem responses to fire and variations in fire regimes. In: Erman DC, editor. Sierra Nevada Ecosystem Project, final report to Congress, vol. 2, assessment and scientific basis for management options. Davis, CA: Wildlands Center Research Report. p 1071–1100.
- CHAPPELL MA. 1978. Behavioral factors in the altitudinal zonation of chipmunks (*Eutamias*). Ecology 59:565–579.
- COPPETO SA, KELT DA, VAN VUREN DH, WILSON JA, BIGELOW S. 2006. Habitat associations of small mammals at two spatial scales in the northern Sierra Nevada. Journal of Mammalogy 87:402–413.
- DICKMAN DI, ROLLINGER JL. 1998. Fire for restoration of communities and ecosystems. Bulletin of the Ecological Society of America 79:157–160.
- DODD NL, STATES JS, ROSENSTOCK SS. 2003. Tasseleared Squirrel population, habitat condition, and dietary relationships in north-central Arizona. Journal of Wildlife Management 67:622–633.
- GRAY AN, ZALD HSJ, KERN RA, NORTH M. 2004. Stand conditions associated with tree regeneration in Sierran mixed-conifer forests. Forest Science 51:198–210.
- HELMS JA, TAPPEINER JC. 1996. Silviculture in the Sierra. In: Erman DC, editor. Sierra Nevada Ecosystem Project, final report to Congress, vol. 2, assessment and scientific basis for management options. Davis, CA: Wildlands Center Research Report. p 439–476.
- HUSARI SJ, MCKELVEY KS. 1996. Fire management policies and programs. In: Erman DC, editor. Si-

erra Nevada Ecosystem Project, final report to Congress, vol. 2, assessment and scientific basis for management options. Davis, CA: Wildlands Center Research Report. p 1101–1118.

- KEELEY JE, FOTHERINGHAM CJ. 1997. Trace gas emissions and smoke-induced seed germination. Science 276:1248–1250.
- KLENNER W, KREBS CJ. 1991. Red Squirrel population dynamics I. The effect of supplemental food on demography. Journal of Animal Ecology 60:961– 978.
- KOPROWSKI JL 1991. Response of Fox Squirrels and Gray Squirrels to a late spring-early summer food shortage. Journal of Mammalogy 72:367–372.
- MAURER J. 2000. Nesting habitat and prey relations of the Northern Goshawk in Yosemite National Park [thesis]. Davis, CA: University of California, Davis. 97 p.
- MCKELVEY KS, SKINNER CN, CHANG C, ERMAN DC, HUSARI SJ, PARSONS DJ, VAN WAGTENDONK JW, WEATHERSPOON CP. 1996. An overview of fire in the Sierra Nevada. In: Erman DC, editor. Sierra Nevada Ecosystem Project, final report to Congress, vol. 2, assessment and scientific basis for management options. Davis, CA: Wildlands Center Research Report. p 1033–1040.
- MEYER MD, KELT DA, NORTH M. 2005. Fungi in the diets of Northern Flying Squirrels and Lodgepole Chipmunks in the Sierra Nevada. Canadian Journal of Zoology 83:1581–1589.
- MEYER MD, KELT DA, NORTH M. 2007. Microhabitat associations of Northern Flying Squirrels in burned and thinned forest stands of the Sierra Nevada. American Midland Naturalist 157:202– 211.
- MEYER MD, NORTH MP, KELT DA. 2005. Short-term effects of fire and forest thinning on truffle abundance and consumption by *Neotamias speciosus* in the Sierra Nevada of California. Canadian Journal of Forest Research 35:1061–1070.
- MONROE ME. 2005. The effects of prescribed fires in different seasons on small mammals in a Sierra Nevada mixed conifer forest [dissertation]. Davis, CA: University of California, Davis. 124 p.
- NELSON L, CLARK FW. 1973. Correction for sprung traps in catch/effort calculations of trapping results. Journal of Mammalogy 54:295–298.
- NORTH M, CHEN J. 2005. Introduction to the special issue on Sierran mixed-conifer research. Forest Science 51:185–186.
- NORTH M, INNES J, ZALD H. In press. Comparison of thinning and prescribed fire restoration treatments to Sierran mixed-conifer historic conditions. Canadian Journal of Forest Research.
- NORTH M, OAKLEY B, CHEN J, ERICKSON H, GRAY A, IZZO A, JOHNSON D, MA S, MARRA J, MEYER M, PURCELL K, RAMBO T, RIZZO D, ROATH B, SCHOW-ALTER T. 2002. Vegetation and ecological charac-

teristics of mixed conifer and Red Fir forests at Teakettle Experimental Forest Experimental Forest. Berkeley, CA: USDA Forest Service. General Technical Report PSW-GTR-186. 52 p.

- PYARE S, LONGLAND WS. 2001. Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. Journal of Mammalogy 82:681–689.
- POOPATANAPONG A. 2000. Effects of California Spotted Owl (*Strix occidentalis occidentalis*) predation on Northern Flying Squirrel (*Glaucomys sabrinus*) population, behavior, and demography [thesis]. Reno, NV: University of Nevada, Reno. 96 p.
- RANSOME DB, SULLIVAN TP. 2004. Effects of food and den-site supplementation on populations of *Glaucomys sabrinus* and *Tamiasciurus douglasii*. Journal of Mammalogy 85:206–215.
- SCHNELL JH. 1958. Nesting behavior and food habits of Goshawks in the Sierra Nevada of California. Condor 60:377–403.
- SHARPLES FE. 1983. Habitat use by sympatric species of *Eutamias*. Journal of Mammalogy 64:572–579.
- SKINNER CN, CHANG C. 1996. Fire regimes, past and present. In: Erman DC, editor. Sierra Nevada Ecosystem Project final report to Congress, Vol. II, Assessments and scientific basis for management options. Davis, CA: Wildlands Center Research Report. p 1041–1069.
- SLADE NA, BLAIR SM. 2000. An empirical test of using counts of individuals captured as indicies of population size. Journal of Mammalogy 81:1035– 1045.
- SMITH DM. 1986. The practice of silviculture. 8th ed. New York, NY: John Wiley and Sons. 527 p.
- SMITH TF, RIZZO DM, NORTH M. 2005. Patterns of mortality in an old-growth mixed-conifer forest of the southern Sierra Nevada, California. Forest Science 51:266–275.
- STEPHEN H, HAN C. 2006. Understory vegetation dynamics in North American boreal forests. Critical Reviews in Plant Sciences 25:381–397.
- STEPHENS SL, MOGHADDAS J. 2005a. Experimental fuel treatment impacts on forest structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest. Forest Ecology and Management 214:21–36.
- STEPHENS SL, MOGHADDAS J. 2005b. Fuel treatment effects on snags and coarse woody debris in a Sierra Nevada mixed conifer forest. Forest Ecology and Management 214:53–64.
- SULLIVAN TP, KLENNER W. 2000. Response of Northwestern Chipmunks (*Tamias amoenus*) to variable habitat structure in young Lodgepole Pine forest. Canadian Journal of Zoology 78:283–293.
- SULLIVAN TP, SULLIVAN DS. 1982. Population dynamics and regulation of Douglas Squirrel (*Tamiasciurus douglasii*) with supplemental food. Oecologia 53:264–270.

- TEVIS L. 1952. Autumn foods of chipmunks and Golden-mantled Ground Squirrels in the northern Sierra Nevada. Journal of Mammalogy 33: 198–205.
- TEVIS L. 1953. Stomach contents of chipmunks and mantled squirrels in northeastern California. Journal of Mammalogy 34:316–224.
- TEVIS L. 1956. Responses of small mammal populations to logging of Douglas-fir. Journal of Mammalogy 37:189–196.
- USDA FOREST SERVICE. 2001. Pacific Southwest Region sensitive animal species by forest. Retrieved January 15, 2007, from http://www.fs.fed.us/r5/ projects/sensitive-species/sensitive-animals.html.
- VANDER WALL SB. 1993. Cache site selection by chipmunks (*Tamias* spp.) and its influence on the effectiveness of seed dispersal in Jeffrey Pine (*Pinus jeffreyi*). Oecologia 96:246–252.
- VANDER WALL SB. 1994. The role of animals in dispersing a "wind-dispersed" pine. Ecology 73: 614–621.
- VLASMAN KL, FRYXELL JM. 2002. Seasonal changes in territory use by Red Squirrels, *Tamiasciurus hud*-

sonicus, and responses to food augmentation. Canadian Journal of Zoology 80:1957–1965.

- WATERS JR, ZABEL CJ. 1998. Abundances of small mammals in fir forests in northeastern California. Journal of Mammalogy 79:1244–1253.
- WAUTERS LA, MATTHYSEN E, ADRIAENSEN F, TOSI G. 2004. Within-sex density dependence and population dynamics of Red Squirrel *Sciurus vulgaris*. Journal of Animal Ecology 73:11–25.
- WAYMAN RB, NORTH M. 2007. Initial response of a mixed-conifer understory community to burning and thinning restoration treatments. Forest Ecology and Management 239:32–44.
- WERNER HW. 2000. Fire effects monitoring on wildlife. In: Caprio AC, editor. Annual fire report on research, inventory, and monitoring. Three Rivers, CA: USDI National Park Service, Sequoia and Kings Canyon National Parks. 9 p.
- ZEILINSKI WJ, SPENCER WD, BARRETT RH. 1983. Relationship between food habits and activity patterns of Pine Martens. Journal of Mammalogy 64: 387–396.

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