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SMALL MAMMALS AND FOREST FUEL REDUCTION: NATIONAL-SCALE RESPONSES TO FIRE AND FIRE SURROGATES

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Abstract. Forest fuel reduction treatments are increasingly used by managers to reduce the risk of high-severity wildfire and to manage changes in the ecological function of forests. However, comparative ecological effects of the various types of treatments are poorly understood. We examined short-term patterns in small-mammal responses to mechanical thinning, prescribed-fire, and mechanical thinning/prescribed-fire combination treatments at eight different study areas across the United States as a part of the National Fire and Fire Surrogate (FFS) Project. Research questions included: (1) do treatments differ in their effect on small mammal densities and biomass? and (2) are effects of treatments consistent across study areas? We modeled taxa-specific densities and total small-mammal biomass as functions of treatment types and study area effects and ranked models based on an information-theoretic model selection criterion. Small-mammal taxa examined, including deer mice (*Peromyscus maniculatus*), yellow-pine chipmunks (*Tamias amoenus*), and golden-mantled ground squirrels (*Spermophilus lateralis*), as well as all *Peromyscus* and *Tamias* species, had top-ranked models with responses varying both by treatment type and study area. In each of these cases, the top-ranked model carried between 69% and 99% of the total weight in the model set, indicating strong support for the top-ranked models. However, the top-ranked model of total small-mammal biomass was a model with biomass varying only with treatment (i.e., treated vs. untreated), not by treatment type or study area; again, this model had strong support, with 75% of the total model weight. Individual species and taxa appear to have variable responses to fuel reduction treatment types in different areas; however, total small-mammal biomass appears generally to increase after any type of fuel reduction. These results suggest that there is substantial variability in taxa-specific responses to treatments and indicate that adaptive management policies may be necessary when applying fuel reduction treatments in areas where management of small-mammal populations is of interest. Adaptive management can be used by managers who are conducting fuel reduction treatments to reduce uncertainty as to which treatments are locally optimal for meeting objectives for the management of small-mammal populations.

Key words: fire; forest; fuel reduction; mark–recapture; Peromyscus; *population density; small mammal;* Spermophilus; Tamias; *thinning.*

Introduction

Many forests in the United States that historically experienced frequent, low- to moderate-severity fires have undergone reductions in fire frequency and changes in forest structure since Euro-American settlement. Causes include fire suppression, grazing, logging, farm abandonment in the southeast United States, and climatic variation (Dodge 1972, Kilgore and Taylor 1979, Bonnicksen and Stone 1982, Arno et al. 1995, Cowell 1998, Allen et al. 2002). In some cases, a result of decreased fire frequency has been increased fuel loads, resulting in increased risk of high-severity wildfire and changes in the ecological function of forests (Covington and Moore 1994, Stephens 1998). There is interest among land managers and scientists in developing and applying treatments to reduce forest fuels, but it is necessary to understand the potential effects of forest fuel reduction on forest ecology prior to implementing treatments (Covington et al. 1997, Wagner et al. 2000, Block et al. 2001).

Two primary types of fuel reduction treatments have been widely applied: prescribed fire and mechanical treatments (e.g., thinning). Prescribed fire is thought to simulate the historical disturbance and fuel reduction process. A common mechanical substitute for fire is "thinning from below," i.e., removing smaller trees whose lower branches carry fire into forest canopies, while retaining larger trees (Covington and Moore 1994, Arno et al. 1995). Thinning is also frequently used in

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combination with prescribed fire to reduce fuel loads so that prescribed-fire treatments are less severe (e.g., Covington et al. 1997, Fulé et al. 2001*a*, *b*). Prescribed fire, mechanical thinning, and combination treatments are effective in reducing forest fuels and fire risk in some cases (Martinson and Omi 2002, Pollet and Omi 2002). However, the comparative ecological effects of these treatments are unclear. It is important to evaluate the ecological effects of these treatments to inform management decision-making and to determine whether mechanical treatments or mechanical treatments in combination with prescribed fire are ecologically appropriate surrogates for fire.

The National Fire and Fire Surrogate (FFS) Project was conceived as a cooperative effort among federal land management agencies, universities, and private organizations to investigate the relative effects of fire and fire surrogate treatments on forest ecology and fire risk (P. Weatherspoon and J. McIver, *unpublished manuscript* [*available online*]).[4] The FFS Project experimental approach applied a similar study design and sampling scheme to 13 study areas across the United States, thereby allowing for both local- and broad-scale inferences. Through the FFS Project, researchers monitored treatment effects on several ecological response variables in the general areas of wildlife, vegetation, fuels and fire behavior, soils, entomology, and pathology.

Because the FFS Project approach has been applied at a large number of spatially disjunct study areas, it is possible to draw conclusions about the generality of the effects of treatments through cross-study area analyses. A primary emphasis of the original FFS Project study proposal was on providing such information. If effects of treatments were found to be largely consistent across study areas, land managers' abilities to predict the outcome of management actions would be strengthened. Conversely, if effects were found to be highly divergent, increased site-specific analyses would be warranted before widespread adoption of particular management actions. One approach would be to conduct such analyses in the context of adaptive management (Walters 1986), wherein monitoring and analysis of the outcomes of management actions are used to reduce uncertainties about optimal management practices at the local scale.

Within the wildlife component of the FFS Project, small-mammal populations were identified as a response variable of interest. Small-mammal communities comprise an important component of the vertebrate biomass and biodiversity of forests, and they influence forest vegetation structure through consumption and dispersal of seeds and hypogeous fungi (Tevis 1956, Gashwiler 1970, Maser et al. 1978, Price and Jenkins 1986). Furthermore, small mammals are an important food source for forest predators (e.g., Koehler and Hornocker 1977, Long and Smith 2000, Ward 2001).

[4] ⟨www.fs.fed.us/ffs⟩

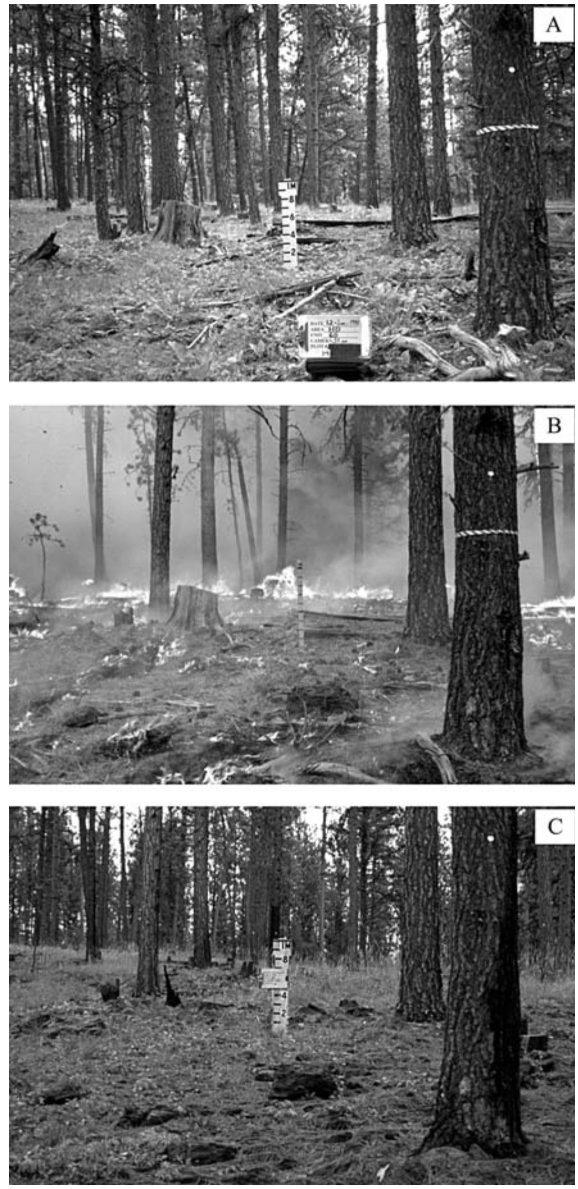

FIG. 1. Images of a portion of an experimental unit at the Hungry Bob study area (HBOB), northeastern Oregon, USA, that underwent a thinning/prescribed-fire fuel reduction treatment: (A) in the summer of 1998 before thinning, (B) in the fall of 2000 after thinning and during prescribed fire, and (C) in the summer of 2001. Photos are courtesy of A. Youngblood, USDA Forest Service, Pacific Northwest Research Station.

Here we examine initial (i.e., within two years posttreatment) small-mammal responses to mechanical thinning, prescribed-fire, and thinning/prescribed-fire combination treatments (Fig. 1) across eight FFS Project study areas distributed throughout the United States. In a large, spatially disjunct study such as this, variation in methods, treatments, and timing at different study areas is to be expected, despite a concerted effort to standardize methods and to apply treatments in similar ways. Capturing and explaining the full range of this variation was not our focus. Our emphasis, instead, was on the examination of general responses of small-mammal populations and communities to treatments. We believe this information to be of primary interest to managers who are interested in predicting the effects of forest management actions on wildlife populations and other components of forest ecology. Therefore, we focused on two primary research questions. (1) Do thinning, prescribed-fire, and thinning/prescribed-fire combination treatments differ in their effects on small-mammal densities and total small-mammal biomass? (2) Are results generally similar across study areas?

Methods

Study areas, treatments, and data collection

The FFS Project network was composed of 13 study areas in the United States, including eight in the western United States (Arizona, California [three], Montana, New Mexico, Oregon, and Washington) and five in the eastern United States (Alabama, Florida, North Carolina, Ohio, and South Carolina). Eight of these study areas provided data to the analyses herein. The remaining five study areas either had very low numbers of small mammals or their data collection and site-specific analysis timeline did not permit participation. Study areas included here were located in five western states (Arizona, California [two], Montana, New Mexico, and Oregon) and two eastern states (Alabama and Florida).

The basic study design was established by the FFS Project national study proposal. The study areas were divided into experimental units; each unit was assigned to a treatment type (typically a thinning treatment, a prescribed-fire treatment, and a thinning/prescribed-fire combination treatment) or to a control. There were typically at least three experimental units assigned to each of these categories at each study area. At certain study areas, the experimental units were spatially grouped into multiple blocks, so that a block represented one replicate of each treatment type. Treatments were designed and implemented by individual study area leaders, resulting in individual variation in methods used, including thinning methods and intensity, season of burning, etc. In addition, certain study areas (primarily the eastern study areas) carried out additional treatments such as herbicide treatments or mowing. These treatments were not included here; only mechanical removal of trees and prescribed-fire treatments were considered. All sampling within the experimental units was keyed to a permanent grid system of sampling points, typically spaced 50 m apart, although in some cases, small-mammal sampling occurred at a finer scale than the permanent sampling grid. Small-mammal sampling consisted of live-trapping and marking animals (mark–recapture) to allow for the estimation of population abundance (see Plate 1). Small-mammal sampling was conducted during summer months (May–September), with the majority of trapping occurring during July and August. Abbreviated study area descriptions are presented below; study areas are presented in order from western-most to eastern-most. More-detailed study area descriptions are provided in the FFS Project national study proposal (P. Weatherspoon and J. McIver, *unpublished manuscript* [see footnote 4]). A summary of relevant study area activities is supplied in Table 1.

Plate 1. A lodgepole chipmunk (*Tamias speciosus*) captured during trapping by M. E. Monroe in August 2002 at the Sequoia National Park study area of the Fire and Fire Surrogate Project, and photographed just prior to marking with ear tags. The plastic bag visible in the photograph was used for handling and weighing the animal. Photo credit: K. Farris.

The Southern Cascades study area (CASC) was located on the Klamath National Forest in northern California, in mixed-conifer forest dominated by ponderosa pine and white fir (*Abies concolor*). The area consisted of 12 experimental units that were not grouped into blocks. Units were assigned to thinning (three units), prescribed-fire (three units), and thinning/prescribed-fire (three units) treatments, and to controls (three units). Thinning was conducted between the fall of 1998 and the fall of 1999, before pretreatment small-mammal data were collected. Therefore, estimation of the effect of thinning at this study area rests on the assumption that thinning and control units were fairly similar before treatments. Slash was scattered after thinning. Prescribed burning was conducted in the fall of 2001 and fall of 2002. Experimental units were 6.25 ha, with a 50-m buffer, for a total treated area of ~12.25 ha. Small-mammal trapping was conducted in May–August 2001 (mid-treatment) and 2003 (posttreatment). One Model XLK Sherman live trap (7.6 × 9.5 × 30.5 cm;

TABLE 1. Timing and characteristics of the National Fire and Fire Surrogate Project study design and data used in the small-mammal analyses.

		Thin		Prescribed fire		Thinning/prescribed fire		
Area†	Sampling	Period	*n*	Period	*n*	Period	*n*	Controls‡
CASC	2001, 2003	fall 1998	1	fall 2002	3	fall 1998/fall 2001	1	3
		summer 1999§	2			fall 1999/fall 2001	1	
						summer 1999/fall 2001§	1	
SEQU	2001–2003	NA		fall 2001	3	NA		3
				spring 2002	3			
HBOB	2000–2001	fall 1998§	4	fall 2000	4	fall 1998/fall 2000§	4	3
PLAT	2000–2003	winter 2002–2003	6	NA		NA		6
LUBR	2000, 2002	winter 2001–2002	3	spring 2002	3	winter 2001–2002/spring 2002	3	3
JEMZ	2001–2003	winter 2002–2003	1	NA		NA		3
GULF	2001–2003	spring 2002	3	spring 2002	3	spring 2002/spring 2002	3	3
MYAK	2000–2002	NA		summer 2000	2	NA		1
				summer 2001	1			

† Study areas are Southern Cascades, California (CASC); Sequoia National Park, California (SEQU); Hungry Bob, Oregon (HBOB); Southwest Plateau, Arizona (PLAT); Lubrecht Forest, Montana (LUBR); Jemez Mountains, New Mexico (JEMZ); Gulf Coast, Alabama (GULF); and Myakka River, Florida (MYAK).

‡ Controls received no treatment throughout the study.

§ At these study areas, thinning occurred before initial small-mammal sampling, so estimation of the effect of thinning rests on the assumption that thinning and control units were similar before treatments.

H. B. Sherman Traps, Tallahassee, Florida, USA) and one Model 201 Tomahawk live trap (12.7 × 12.7 × 40.6 cm; Tomahawk Live Trap, Tomahawk, Wisconsin, USA) were placed at each permanent sampling point, which were arranged in 6 × 6 dimensional grids with 50-m spacing between points. Animals were marked by clipping fur in unique patterns.

The Sequoia National Park study area (SEQU) was located on the Sequoia National Park in east-central California, in mixed-conifer forest dominated by white fir, sugar pine (*Pinus lambertiana*), and incense cedar (*Calocedrus decurrens*). The study area consisted of nine experimental units that were not grouped into blocks. Units were assigned to two different thinning treatments (three units each) and to controls (three units). The treatments consisted of spring burning and fall burning; thinning was not implemented on this study area. Fall burns were conducted in the fall of 2001; spring burns were conducted in the spring of 2002. The two burning treatments were not distinguished in the analyses herein. Small-mammal sampling was conducted from June to September in 2001 (pretreatment), 2002 (posttreatment, no spring burn experimental units trapped), and 2003 (posttreatment). Experimental units were irregularly shaped, between 15 and 20 ha in size, including a 50-m buffer between the permanent sampling grid and the edge of the treated area. Small-mammal trapping was conducted at all 36 permanent sampling points in experimental units with 50-m trap spacing on the outer portion of sampling grids, but trap spacing was decreased to 25 m on the interior of the sampling grids. In 2001, only the interior of the sampling grids was trapped. Model XLK Sherman live traps were placed at all trapping points, and animals were marked with ear tags.

The Hungry Bob study area (HBOB) was located in the Blue Mountains of northeast Oregon on the Wallowa-Whitman National Forest, in mixed-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*). The study area consisted of 16 experimental units, 15 of which were included in this analysis. Experimental units were not grouped into blocks and were highly variable in size and shape, and some units were composed of smaller subunits separated in space. Units were assigned to thinning (four units), prescribed-fire (four units), and thinning/prescribed-fire (four units) treatments, and to controls (three units). Thinning was conducted in the fall of 1998, before pretreatment small-mammal data were collected, so estimation of the effect of thinning (as for CASC) rests on the assumption that thinning and control units were fairly similar before treatments. Slash was scattered after thinning. Prescribed burning was conducted in the fall of 2000. Treated areas ranged in size from 8 to 66 ha, although the permanent sampling grids were much smaller than this, consisting of between 19 and 30 sampling points spaced ≥50 m apart. Small-mammal data were collected in June–August 2000 (mid-treatment) and 2001 (posttreatment). Traps were placed at all permanent sampling points, i.e., ≥50 m apart, with one Model LFA Sherman live trap (7.6 × 8.9 × 22.9 cm) and one Model 201 Tomahawk live trap at each sampling point. Animals were marked by clipping fur in unique patterns.

The Southwest Plateau study area (PLAT) was located in north-central Arizona on ponderosa pine forest. Three blocks comprised the study area, with two on the Coconino National Forest and one on the Kaibab National Forest. While one unit in each block was assigned to thinning, prescribed-fire, and thinning/prescribed-fire treatments and to a control, prescribed burning was not completed before data collection for these analyses was completed. Therefore, two units in each block were analyzed as thinned units and two as controls. Thinning was completed during the winter of 2002–2003; slash was piled after thinning. Experimental units were ~6.25 ha in size, with an additional 50-m buffer, resulting in a total treated area of ~12.25 ha. Pretreatment data were collected in July–August 2000, 2001, and 2002; posttreatment data were collected in July 2003. In 2000–2001, small mammal sampling was conducted at all permanent sampling points, which were arranged generally in 6 × 6 dimensional grids, but sometimes varied slightly from that pattern, with 50-m spacing between points. In 2002–2003 (and on two experimental units in 2001 as part of a pilot study), trapping intensity was increased by adding additional trapping points to decrease trap spacing to 25 m. One Model LFA Sherman live trap was placed at every trapping point, and one Model XLF15 Sherman live trap (10.2 × 11.4 × 38.1 cm) was placed at every other trapping point. All captured animals were individually marked with ear tags.

The Lubrecht Forest study area (LUBR) was located on the University of Montana's Lubrecht Forest in western Montana on mixed-conifer forest dominated by ponderosa pine and Douglas-fir. Experimental units were arranged in three blocks with four experimental units per block. Units were assigned to thinning (three units), prescribed-fire (three units), and thinning/prescribed-fire (three units) treatments, and to controls (three units). Thinning was completed in January–March 2001; slash was scattered after thinning. Prescribed burning was completed in May–June 2002. Experimental units were 6.25 ha, with an ~50-m buffer, resulting in a total treated area of ~12.25 ha. Small-mammal sampling was conducted in July–August 2000 (pretreatment) and 2002 (posttreatment) on smaller trapping grids centered within the experimental units (7 × 7 dimensional grids with 25-m spacing). One Model LFA Sherman live trap was placed at every trapping point, and animals were individually marked with ear tags and/or toe-clipping.

The Jemez Mountains study area (JEMZ) was located west of Los Alamos, New Mexico, on the Santa Fe National Forest, in mixed-conifer forest dominated by ponderosa pine with lesser amounts of Douglas-fir, southwestern white pine (*Pinus strobiformis*), and quaking aspen (*Populus tremuloides*). Data presented here come from one block. Thinning was completed on one of four experimental units on this block during the winter of 2002–2003; slash was piled and/or scattered after thinning. Therefore, one unit was included in the analyses as a thinned unit, and the remaining three experimental units on this block were included as controls. Prescribed burning was not completed at this study area by 2005. Experimental units were 6.25 ha, with a 50-m buffer, resulting in a total area of 12.25 ha. Pretreatment small-mammal data were collected in August 2001 and 2002; posttreatment data were collected in August 2003. In 2001, small-mammal sampling was conducted at all permanent sampling points, which were arranged in 6 × 6 dimensional grids with 50 m between points (i.e., 6.25 ha). In 2002–2003, trapping intensity was increased by adding additional trapping points to decrease trap spacing to 25 m. One Model LFA Sherman live trap was placed at every trapping point, and one Model XLF15 Sherman live trap was placed at every other trapping point. All captured animals were individually marked with ear tags.

The Gulf Coast study area (GULF) was located in longleaf pine (*Pinus palustris*) forest on the Auburn University Solon Dixon Forestry Education Center in southern Alabama. The study area consisted of 15 experimental units, 12 of which were included here. Experimental units were grouped into three blocks, with the exception of two experimental units that were not included in a block. Units included in the analyses were assigned to thinning (three units), prescribed-fire (three units), and thinning/prescribed-fire (three units) treatments, and to controls (three units). Thinning was conducted during February–April 2002, and burning was conducted after thinning during April–May 2002. Slash was piled away from retained trees and left in the experimental units after thinning. Experimental units consisted of 12.25-ha sampling grids surrounded by a 20-m buffer, resulting in a total treated area of ~15 ha. Small mammals were trapped during July–August 2001 (pretreatment) and July 2002 and 2003 (posttreatment). Small-mammal sampling occurred on a smaller scale than the permanent sampling grid, in 10 × 10 dimensional trapping grids with 10-m spacing between trapping points. One Model LFA Sherman live trap was placed at each trapping point. Animals were marked with ear tags and/or toe-clipping.

The Myakka River study area (MYAK) was located on the Myakka River State Park in southwest Florida on forest dominated by longleaf pine and slash pine (*Pinus elliottii*). Sixteen experimental units were arranged in three blocks, but data from only four experimental units (two at each of two blocks) were used here. Burning of one unit at block 1 occurred in August of 2001; the other unit was included as a control. Burning of both units at block 2 occurred in July of 2000. Experimental units were ~6.25 ha with a 50-m buffer, resulting in a total treated area of ~12.25 ha. Experimental units at block 1 were sampled for small mammals in June–July 2000 and 2002. Experimental units at block 2 were sampled for small mammals in June–July 2000 and 2001. One Model LFA or Model XLK Sherman live trap was placed at each permanent sampling point, in 6 × 6 dimensional grids with 50-m spacing between points. Animals were marked by clipping fur in unique patterns.

Data analysis

The data analysis took place in three steps. First, we estimated abundance for each small-mammal species each year in each experimental unit, based on the mark–recapture data. Second, we converted abundance

TABLE 2. Variables and numbers of models used in the National Fire and Fire Surrogate Project for small-mammal abundance estimation.

Study area†	Abundance estimation variables	Total models
CASC	mixture,‡ behavior,§ year, unit, thin, fire, thin × fire	40
SEQU	behavior, disturbance, trap density, age,‡ year, unit, fall fire, spring fire, fall fire × year	80
HBOB	mixture, behavior, year, unit, thin, fire, thin × fire	40
PLAT	behavior, time of day, trap effort, age, year or trapping session(year), block or unit, thin	72
LUBR	behavior, age, year, block or unit, thin, fire, thin × fire	60
JEMZ	behavior, time of day, age, year or trapping session(year), unit, thin	24
GULF	behavior, age, year, unit, thin, fire, thin × year, fire × year, thin × fire	68
MYAK	behavior, age, year, block or unit, fire	24

† Study areas are Southern Cascades, California (CASC); Sequoia National Park, California (SEQU); Hungry Bob, Oregon (HBOB); Southwest Plateau, Arizona (PLAT); Lubrecht Forest, Montana (LUBR); Jemez Mountains, New Mexico (JEMZ); Gulf Coast, Alabama (GULF); and Myakka River, Florida (MYAK).
‡ Age and mixture denote effects used to model individual heterogeneity in capture probabilities.
§ Behavior effect denotes an effect to estimate trap-happy or trap-shy responses to capture.

estimates to density estimates by dividing abundance by trapping area. Finally, we conducted weighted least-squares regression analyses to examine the effects of treatments on small-mammal densities and total small-mammal biomass.

Throughout the analysis, we employed an information-theoretic philosophy of model selection and inference (Burnham and Anderson 2002). Tools employed included model selection based on Akaike's Information Criterion (AIC; Akaike 1973) corrected for small sample size (AIC_c; Hurvich and Tsai 1989) and model-averaging based on Akaike weights (Burnham and Anderson 2002). At each step in the analysis, statistical model sets were specified a priori, to strengthen inference (Anderson et al. 2001).

Abundance estimation.—The focus of abundance estimation, using mark–recapture techniques, is on the estimation of detection probabilities to correct counts for animals not sampled by the capture process. Detection probabilities may be highly dynamic over space and time (Nichols 1992, Anderson 2001) and may also be influenced by habitat modifications (Converse et al., *in press*); therefore, estimation of detection probabilities is necessary for robust inference about population abundances. We used the conditional likelihood closed model (Huggins 1989, 1991) to estimate detection probabilities and abundance. The conditional likelihood model generates estimates of capture rates based on animal encounter histories and uses these rates to generate estimates of abundance. This model is preferred because it allows for variation in detection probabilities over time and due to behavioral responses of captured animals, and it also allows for the inclusion of covariates (e.g., age) to model individual heterogeneity in capture probabilities (White 2002). This model also has favorable numerical properties when most of the animals are captured in a sampled area (Converse 2005).

Abundance estimation was carried out for each species at a study area in which at least 10 individuals were captured. All data for a given species at a given study area were combined into one analysis to facilitate efficient estimation of detection probabilities and hence abundance; abundance estimates were obtained on each experimental unit each year by grouping captured animals accordingly. Variables that might influence detection probabilities were identified. These variables were then used in various combinations to build candidate models for estimation of detection probabilities. For example, animals on burned experimental units may have a different capture probability than animals on control experimental units; thus burning would be included as a variable in a subset of models of detection probability. Different model sets were devised for each study area to take into account the unique sampling conditions at each. Effort was also made to keep the model sets relatively small (maximum 80 models; Table 2), as recommended by Burnham and Anderson (2002). Model sets were devised a priori, based on consultations with researchers who collected data, to integrate study-area-specific details of trapping and treatment conditions.

Estimation of abundance was conducted in Program MARK 3.2 (White and Burnham 1999). We ran the entire specified model set for each species at each study area and then deleted any models in which abundances were inestimable and models that were logically nonsensical (e.g., an age effect if all captured individuals of a species were adults). We then model-averaged the abundance estimates and variance–covariance matrices to account for model selection uncertainty. We based model-averaging on Akaike weights; model-averaged estimates were computed based on Burnham and Anderson (2002) and model-averaged variance–covariance matrices were computed based on Burnham and Anderson (2004).

Densities, biomass, and variance–covariance matrices.—Density was calculated as the abundance of a given species divided by the area of the trapping grid in each experimental unit (as individuals per hectare). Density estimation in mark–recapture studies generally proceeds by estimating effective trapping area, computed as the area of the trapping grid expanded by the area of an additional buffer strip, to account for animals whose home ranges only partially overlap the trapping area.

Table 3. Numbers of unique individuals of small-mammal species captured at the National Fire and Fire Surrogate Project study areas, including all species of which at least 10 individuals were captured at a study area.

Common and scientific names	Mass† (g)	Study areas‡								Total
		CASC	SEQU	HBOB	PLAT	LUBR	JEMZ	GULF	MYAK	
Southern red-backed vole, *Cleithrionomys gapperi*	20	0	0	0	0	74	0	0	0	74
Northern flying squirrel, *Glaucomys sabrinus*	45	0	14	0	0	0	0	0	0	14
Southern flying squirrel, *Glaucomys volans*	60	0	0	0	0	0	0	11	0	11
Long-tailed vole, *Microtus longicaudus*	30	0	21	0	0	0	23	0	0	44
Mexican woodrat, *Neotoma mexicana*	100	0	0	0	19	0	21	0	0	40
Golden mouse, *Ochrotomys nuttalli*	20	0	0	0	0	0	0	40	0	40
Brush mouse,§ *Peromyscus boylii*	14	0	36	0	2	0	0	0	0	38
Cotton mouse, *Peromyscus gossypinus*	25	0	0	0	0	0	0	401	16	417
Deer mouse, *Peromyscus maniculatus*	14	19	1389	83	486	541	265	0	0	2783
Columbian ground squirrel, *Spermophilus columbianus*	340	0	0	10	0	0	0	0	0	10
Golden-mantled ground squirrel, *Spermophilus lateralis*	150	73	10	39	21	0	0	0	0	143
Cotton rat, *Sigmodon hispidus*	80	0	0	0	0	0	0	0	232	232
Yellow-pine chipmunk, *Tamias amoenus*	36	49	0	766	0	234	0	0	0	1049
Gray-collared chipmunk, *Tamias cinereicollis*	50	0	0	0	304	0	0	0	0	304
Cliff chipmunk, *Tamias dorsalis*	50	0	0	0	11	0	0	0	0	11
Least chipmunk, *Tamias minimus*	35	0	0	0	0	0	99	0	0	99
Allen's chipmunk, *Tamias senex*	70	387	0	0	0	0	0	0	0	387
Lodgepole chipmunk, *Tamias speciosus*	30	0	335	0	0	0	0	0	0	335
Red squirrel, *Tamiasciurus hudsonicus*	140	0	0	37	0	0	0	0	0	37
Total		528	1805	935	843	849	408	452	248	6068

† The minimum adult mass (g) used to compute total small-mammal biomass.

‡ Study areas are Southern Cascades, California (CASC); Sequoia National Park, California (SEQU); Hungry Bob, Oregon (HBOB); Southwest Plateau, Arizona (PLAT); Lubrecht Forest, Montana (LUBR); Jemez Mountains, New Mexico (JEMZ); Gulf Coast, Alabama (GULF); and Myakka River, Florida (MYAK).

§ Brush mice were combined with deer mice prior to abundance analysis, because of small numbers and difficulty in distinguishing among juveniles of these species.

Methods to estimate buffer strip width (Wilson and Anderson 1985) or newer methods in which density is calculated based on the spatial arrangement of traps used by animals (Efford 2004) were not feasible in this case because of the irregular shape of some trapping grids. Therefore we calculated a naïve density estimate (Wilson and Anderson 1985) by drawing a convex polygon (i.e., all outer angles $\geq$180°) around all points in the trapping grid. The convex polygon area was necessary because some trapping grids were not rectangular.

We also computed total small-mammal biomass (in grams per hectare) for each study area. We used minimum adult mass (in grams) as a multiplier to convert density estimates to biomass estimates for each species, then summed the total estimated biomass over all species at each study area. We determined minimum adult masses from a combination of literature sources (Hamilton and Whitaker 1979, Jameson and Peeters 1988, Hilton and Best 1993, Fitzgerald et al. 1994, Whitaker 1996) and judgments based on discussions with study area researchers and examination of data sets. We used minimum adult mass to provide a single, objective multiplier so that results would not be confounded by different estimates of mass at each study area. We also thought that minimum adult mass, rather than mean adult mass, was more appropriate, as some individuals in the population were subadults. Masses used to compute biomass are provided in Table 3.

Variance–covariance matrices of the density estimates and total biomass estimates were necessary for the weighted regression analysis (see *Analysis of treatment effects*). These matrices were computed by delta method transformations of the variance–covariance matrices of the abundance estimates for each species provided by Program MARK (Seber 2002). Weighted analysis cannot be conducted with variances of zero because the variance–covariance matrix is singular. Variances of zero occurred in the abundance variance–covariance matrix for a species when no animals of that species were caught on a given experimental unit in a given year. In order to provide positive variances in these cases, we fit a linear regression (PROC REG; SAS Institute 2003) of the natural log of positive variances against their corresponding density estimates and determined the regression intercept (Franklin 1997). The exponential of the regression intercept then served as the variance for the zero-density estimates.

Analysis of treatment effects.—The analysis of treatment effects was conducted under a weighted least-squares regression analysis (Draper and Smith 1998) in PROC IML (SAS Institute 2003). A traditional (i.e., unweighted) regression analysis was inappropriate because of the sampling covariances between the density estimates that were induced by the abundance estimation procedure. The computational details, including effect size and variance estimation and computation of

AIC_c in a weighted regression context, are provided in Converse et al. (*in press*).

We specified multiple a priori models describing predicted responses to treatments. We considered four structures on treatment effects: by category (thinned, prescribed fire, thinned/prescribed fire) or treatment only (i.e., treated vs. untreated), and nested within study area or not. We also considered two alternative blocking structures: by study area or by year nested within study area. We did not consider year without nesting it within study area because the study areas were far enough apart that high temporal autocorrelation was not expected. We considered a total of 12 structural models in each analysis.

We used these structural models in six separate analyses, each of which had a different response variable. We limited analyses to response variables that spanned multiple study areas because the focus was on cross-study area effects. We adopted the a priori rule that a species had to appear on at least three study areas and have a minimum of 100 total individuals captured to warrant an individual analysis. This resulted in three species-level response variables: golden-mantled ground squirrel (*Spermophilus lateralis*) density, yellow-pine chipmunk (*Tamias amoenus*) density, and deer mouse (*Peromyscus maniculatus*) density. We further considered genus-level response variables, including all chipmunk (*Tamias*) species and all *Peromyscus* spp. Finally, as an overall community metric, we included total small-mammal biomass as a response variable.

Results

Six-thousand sixty-eight (6068) individuals of 19 small mammal species captured on the eight study areas were included in the analyses (Table 3). This represented all species of which $\geq$10 individuals were captured at a study area. The most wide-ranging genus, *Peromyscus*, was captured on all eight study areas, including deer mice and brush mice (*P. boylii*) in the West and cotton mice (*P. gossypinus*) in the East. The second most wide-ranging genus was *Tamias* (chipmunks), of which at least one species occurred at all six western study areas; also, the eastern chipmunk (*T. striatus*) was observed at GULF, but its capture numbers (three individuals) were too small to meet our criteria for inclusion in the analysis. The most wide-ranging species was the deer mouse, which was caught on all six of the western study areas and was the most commonly captured species on four of these study areas. The golden-mantled ground squirrel was the second most widely distributed species, caught at four western study areas. The yellow-pine chipmunk (*T. amoenus*) was caught at three western study areas. All other species were caught at two or fewer study areas.

The results of the analysis of small-mammal responses to treatments indicated that for the species-level response variables (golden-mantled ground squirrels, yellow-pine chipmunks, and deer mice), as well as the genus-level response variables (*Tamias* and *Peromyscus*), the top-ranked model (as determined by AIC_c) included, in all cases, a treatment effect that was specific to treatment type nested within study area, i.e., treatment effects varied by treatment type and study area. The top-ranked model for total biomass, however, included a treatment effect that was not specific to either treatment category or study area, i.e., all treatment types had the same effect, and the effect was the same across study areas. Because support for the top-ranked model was substantial (>68%) in all cases, we based our inference on the top-ranked model for each analysis.

Analysis of golden-mantled ground squirrel densities resulted in a top-ranked model, [Density {treatment category (study area)}], with 78% of the model weight. Estimated thin effects ranged from −0.03 to 0.27 and were negative at HBOB and PLAT and positive at CASC (Fig. 2A). Estimated fire effects ranged from −0.03 to 0.10 and were negative at CASC and positive at SEQU and HBOB. Estimated thinning/prescribed-fire effects were 0.04 and 1.18 at HBOB and CASC, respectively. Estimated 95% confidence intervals on the effects included zero in all cases except for the positive prescribed-fire effect at SEQU and the positive thinning/prescribed-fire effect at CASC.

Modeling results for yellow-pine chipmunk densities indicated that the top-ranked model was [Density {study area + treatment category (study area)}], with 69% of the model weight. Estimated thin effects ranged from −2.01 to 6.78 and were negative at HBOB and positive at CASC and LUBR (Fig. 2B). Estimated prescribed-fire effects ranged from −0.32 to 1.42 and were negative at LUBR and positive at CASC and HBOB. Estimated thinning/prescribed-fire effects ranged from −3.17 to 0.77 and were negative at HBOB and LUBR and positive at CASC. In all but one case (positive LUBR thinning effect), 95% confidence intervals included zero.

Analysis of deer mouse densities indicated that the top model was [Density {year (study area) + treatment category (study area)}], with >99% of the weight. Estimated thinning effects ranged from −0.26 to 5.29 and were negative at CASC and PLAT and were positive at HBOB, LUBR, and JEMZ (Fig. 2C). Estimated prescribed-fire effects ranged from −0.84 to 14.39 and were negative at SEQU and positive at CASC, HBOB, and LUBR. Estimated thining/prescribed-fire effects ranged from −6.86 to 0.31 and were negative at LUBR and positive at CASC and HBOB. All 95% confidence intervals included zero with the exception of the positive thinning effect at JEMZ, the positive prescribed-fire effect at LUBR, and the negative thinning/prescribed-fire effect at LUBR.

The top-ranked model for all *Tamias* spp. was [Density {study area + treatment category (study area)}], with 99% of the model weight. Estimated thinning effects ranged from −2.01 to 6.84 and were negative at HBOB and were positive at CASC, PLAT, LUBR, and JEMZ (Fig. 2D). Estimated precribed-fire effects ranged from −1.01 to 1.42 and were negative at

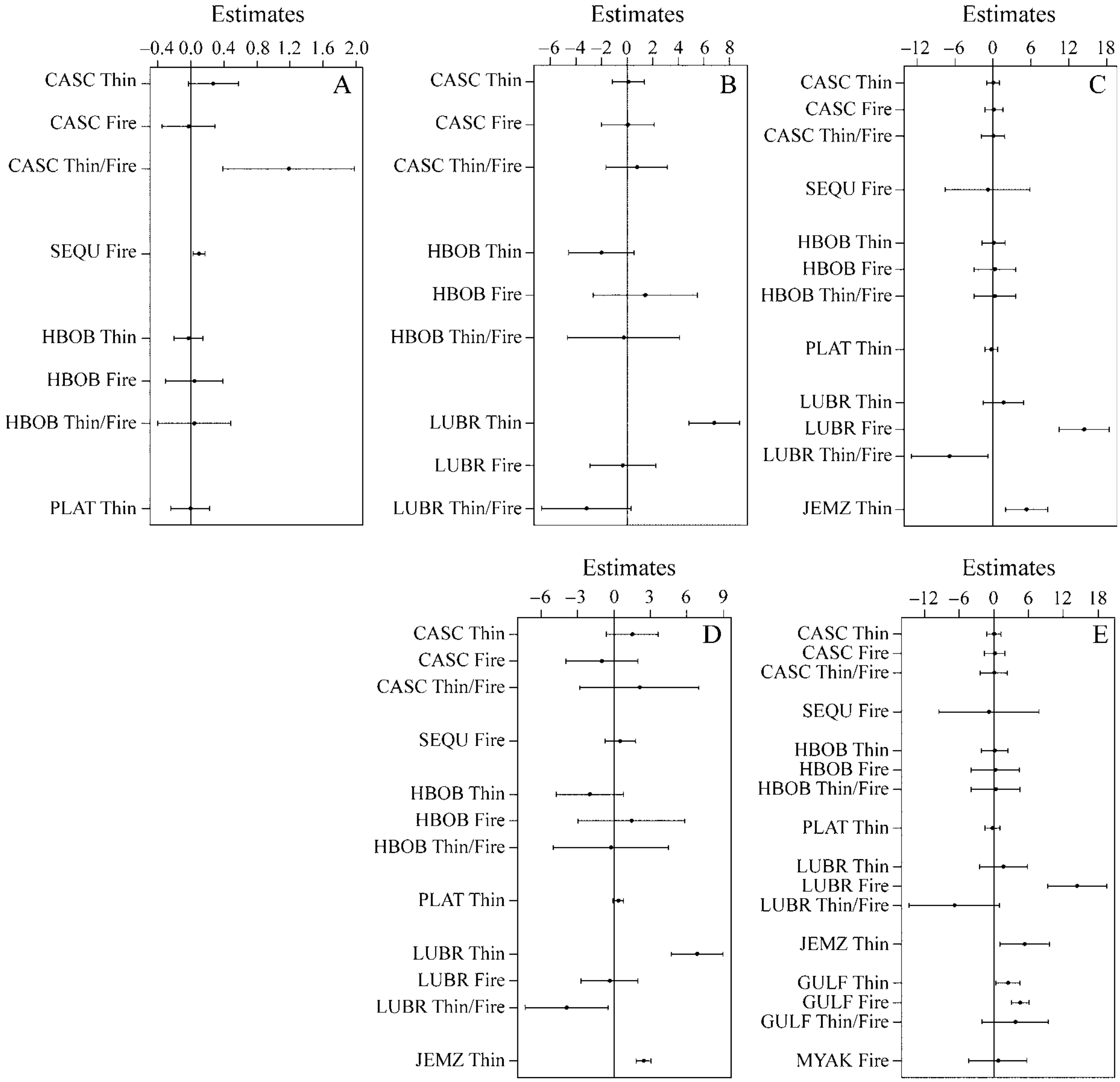

FIG. 2. Effect size estimates and 95% confidence intervals for taxa-specific responses to thinning, prescribed-fire, and thinning/prescribed-fire combination treatments at the National Fire and Fire Surrogate study areas. Estimates and confidence intervals are based on the top-ranked (according to the corrected Akaike Information Criterion, AIC_c) model of population responses to treatments (see *Methods*). Study areas are presented in order from west to east (top to bottom within each panel; see Table 1 for explanations of abbreviations). Taxa presented are (A) golden-mantled ground squirrels; (B) yellow-pine chipmunks; (C) deer mice; (D) *Tamias* spp.; and (E) *Peromyscus* spp.

CASC and LUBR and positive at SEQU and HBOB. Estimated thinning/prescribed-fire effects ranged from −3.91 to 2.08 and were negative at HBOB and LUBR and positive at CASC. All 95% confidence intervals included zero with the exception of two positive thinning effects (LUBR and JEMZ) and the negative thinning/prescribed-fire effect at LUBR.

The top-ranked model of *Peromyscus* spp. densities was [Density {year (study area) + treatment category (study area)}], with 98% of the weight. Estimated thinning effects ranged from −0.26 to 5.29 and were negative at CASC and PLAT and were positive at HBOB, LUBR, JEMZ, and GULF (Fig. 2E). Estimated prescribed-fire effects ranged from −0.84 to 14.39; estimated effects were negative at SEQU and were positive at CASC, HBOB, LUBR, GULF, and MYAK. Estimated thinning/prescribed-fire effects ranged from −6.86 to 3.68; estimated effects were negative at LUBR and positive at CASC, HBOB, and GULF. All 95% confidence intervals included zero with the exception of positive thinning effects at JEMZ and GULF and positive prescribed-fire effects at LUBR and GULF.

The top-ranked model of total small-mammal biomass was [Biomass {year (study area) + treatment}] with

75% of the model weight. The treatment effect estimate was 40.4 (95% CI = 9.1, 71.7).

Discussion

The results of this cross-study-area, multi-taxa analysis indicate that densities of individual taxa of small mammals have variable short-term responses to different treatment types and that treatment effects are different at different study areas. We found no evidence that mechanical thinning is ecologically equivalent to fire, that is, thinning does not appear to operate ecologically as a fire surrogate with respect to populations of individual small-mammal taxa. Further, we found that even within a treatment type, the direction (positive or negative) of treatment effects varied across study areas. Conversely, the best approximating model for total small-mammal biomass was a simpler model, with a treatment effect that did not vary by study area or treatment type. Therefore, while prediction of responses of a particular small-mammal species to a treatment is difficult given present information, it is reasonable to predict that total small-mammal biomass should increase with thinning, prescribed-fire, or thinning and prescribed-fire combination treatments.

Responses of small mammals to fuel reduction treatments are likely determined by responses of critical habitat components, including shrub and herbaceous vegetation and coarse woody debris. Understory vegetation, which provides a source of cover, as well as vegetation and seed food sources (Ahlgren 1966, Goodwin and Hungerford 1979, Kyle and Block 2000, Wilson and Carey 2000), and coarse woody debris, which provides nesting and travel cover and insect and fungal food sources (Hayes and Cross 1987, Graves et al. 1988, Loeb 1999, Bowman et al. 2000, Carey and Harrington 2001), strongly influence small-mammal populations, and these components of small-mammal habitat may have quite different responses to thinning and prescribed fire. Thinning has been shown to increase herbaceous cover by 1–2 growing seasons after treatment (Clary 1975, Covington et al. 1997), as has prescribed fire within the first few growing seasons after fire (Bock and Bock 1983, Harris and Covington 1983, Oswald and Covington 1983, 1984), but positive herbaceous vegetation response after fire may be delayed compared to thinning because of fire-related damage to vegetation. Thinning is expected to increase coarse woody debris through slash deposits, while prescribed fire leads to short-term declines in coarse woody debris (Covington and Sackett 1984, Arno et al. 1995). Combined thinning/prescribed-fire treatments have been shown to result in increased herbaceous vegetation and decreased coarse woody debris (Converse et al. 2006).

Given potential differences in responses of habitat components, it is reasonable to expect that small-mammal populations would respond differently by treatment type. In addition, the individual taxa responses documented here indicate that treatment effects are quite variable within a treatment type at different study areas. While differences in timing and execution of treatments at different study areas are possible confounding factors, this study has documented greater variability in short-term treatment responses than previous research. Experimental and quasi-experimental studies have provided evidence for short-term increases in deer mouse populations after forest thinning (Ahlgren 1966, Carey and Wilson 2001, Suzuki and Hayes 2003, Hadley and Wilson 2004, Converse et al., *in press*; but see also Sullivan et al. [2001]). Similarly for fire: evidence from experimental and quasi-experimental examinations of prescribed fire in forests and woodlands have documented increased densities of deer mice immediately after prescribed fire (Tester 1965, Ahlgren 1966, Bock and Bock 1983) and wildfire (Krefting and Ahlgren 1974, Martell 1984, Kyle and Block 2000, Converse et al., *in press*). Short-term positive responses to thinning have also been documented for a number of chipmunk species (Carey 2001, Carey and Wilson 2001, Sullivan et al. 2001, Hadley and Wilson 2004, Converse et al., *in press*). While less is known about chipmunk responses to fire, information available suggests negligible to slightly negative responses (Kyle and Block 2000, Converse et al., *in press*; but see also Martell [1984]). The highly variable responses to treatments by golden-mantled ground squirrels documented in this study are one of the few examinations of effects of forest management on this species (but see Converse et al. 2006).

Total small-mammal biomass had consistent responses across treatment types and study areas. Overall positive responses of small-mammal communities have been linked to increases in habitat complexity (Goodwin and Hungerford 1979, Monthey and Soutiere 1985, Clough 1987, Carey and Johnson 1995, Wilson and Carey 2000, Carey and Harrington 2001). It is not known whether small-mammal habitat complexity generally increases with thinning and prescribed-fire treatments. Increased habitat complexity may be realized through changes in understory vegetation, which has been shown to increase after both thinning and fire (Clary 1975, Bock and Bock 1983, Harris and Covington 1983, Oswald and Covington 1983, 1984, Covington et al. 1997). However, coarse woody debris sometimes declines immediately after fire (Covington and Sackett 1984, Arno et al. 1995), which may reduce that component of habitat complexity in the short term.

If treatment responses of individual species are highly variable, information allowing better prediction of the direction and magnitude of responses would be helpful in guiding the placement and extent of fuel reduction treatments. There is some indication that pretreatment conditions may influence the direction of small-mammal responses to fuel reduction treatments. In finer-scale analyses of treatment effects at PLAT, effects of thinning on deer mice, gray-collared chipmunks, and total small-mammal biomass were positive on experimental units which, prior to treatment, were comprised of forests with densely packed small trees (Converse et al., *in press*). However, effects were negligible to negative on experimental units with pretreatment forests composed of larger, more widely spaced trees, even though total tree basal area was similar across the experimental units. Differences in pretreatment conditions across study areas may have had an influence on the differences in treatment responses documented here.

In addition to pretreatment conditions, additional factors that may have caused differences in the treatment responses we observed include both characteristics of the sites and of the treatments. Characteristics of the site causing variability may include predator or pathogen populations, weather conditions, landscape context of study sites, etc. Characteristics of treatments that may have caused observed differences in treatment responses include the time of year that treatments were carried out, the time elapsed between treatment application and posttreatment monitoring, operating characteristics of thinning contractors, weather and fuel conditions during prescribed-fire treatments, etc. These and similar factors deserve closer consideration by researchers and managers examining small-mammal responses to fuel reduction treatments.

Differences in responses by taxa across different study areas indicate that the ability of managers to predict short-term responses of individual small-mammal taxa to fuel reduction treatments is currently limited. Predicting longer term responses may be even more difficult. Therefore, it is not possible to make prescriptive recommendations about population management based on our results. Our results indicate that, when managers are interested in maintaining a particular small-mammal species while conducting fuel reduction treatments, it is necessary for them to determine which of a suite of possible treatments is most effective in their area. In order to do this, an adaptive management philosophy may be useful.

Adaptive management (Walters 1986) is an iterated decision-making process with a focus on modifying decisions over time based on knowledge gained from monitoring the outcomes of previous management decisions. Adaptive management involves four basic components: (1) identification of management objectives, (2) representation of current knowledge and system uncertainty, (3) identification of alternative management actions, and (4) a monitoring system that allows for further learning after actions are implemented. Adaptive management can be used to reduce uncertainty about a given management question by learning from the application of alternate management strategies; this can be done while managers move forward in achieving fuels management goals. An important benefit of adaptive management is that it can be used by individual managers who do not have adequate spatial replicates to conduct a traditional experiment. In our results, we found that traditional experimental replication, i.e., replication over space, was inadequate to identify optimal approaches for management of small mammals because responses were different in different areas. However, on a local scale, managers could use replication over time to reduce their uncertainty about which fuel reduction treatment is most effective in their area. Managers can then optimize their management for a given set of objectives by modifying their decisions over time as they reduce their uncertainty about which fuel reduction treatment is best suited to meet those objectives.

In areas managed for overall small-mammal biomass, e.g., in raptor foraging areas, a reasonable hypothesis for managers at the outset of fuel reduction planning is that total biomass will increase with fuel reduction treatments. For instance, thinning and prescribed fire have been recommended for the maintenance of foraging areas for northern goshawks (*Accipiter gentilis*) and Mexican spotted owls (*Strix occidentalis lucida*) in the American Southwest (Reynolds et al. 1996). However, monitoring of prey responses to treatments is still warranted, as local conditions may result in significant variations in responses, and knowledge of long-term responses of small mammals to forest fuel reduction treatments is still limited.

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