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DISSERTATION

SMALL MAMMAL RESPONSES TO FOREST RESTORATION AND FUEL REDUCTION

Submitted by

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In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 2005

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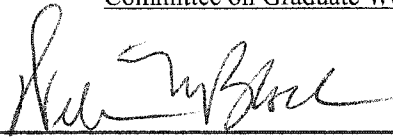
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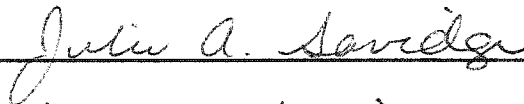
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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY SARAH J. CONVERSE ENTITLED SMALL MAMMAL RESPONSES TO FOREST RESTORATION AND FUEL REDUCTION BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

SMALL MAMMAL RESPONSES TO FOREST RESTORATION AND FUEL REDUCTION

Forest restoration and fuel reduction treatments have been recommended for many North American forests that have undergone changes in their fire regimes. I examined how such treatments impact small mammal populations. I further considered potential biases in interpreting historical fire-scar data, which have been used to recommend fire return intervals for treatments in modern forest management, and I developed improved estimators for parameters of historical fire regimes.

In Chapter 1, as part of a national experiment, the Fire and Fire Surrogate Program, I evaluated the effects of forest thinning on small mammal population densities and total small mammal biomass in ponderosa pine-dominated forests at 2 study areas in northern Arizona and northern New Mexico, USA. I also evaluated the effects of wildfire on small mammal population densities after a wildfire burned a portion of one study area. I refined statistical methods to efficiently estimate small mammal population densities and to model the impacts of disturbance on densities; these methods involve estimation of abundance and effective trapping area in combined analyses across space and time followed by a weighted regression analysis of treatment effects. I hypothesized that habitat changes post-disturbance would be the largest determinant of population responses to thinning and wildfire within 1 year of disturbances. This hypothesis was largely supported, as predicted positive responses to thinning were documented for deer mice (*Peromyscus maniculatus*), gray-collared chipmunks (*Tamias cinereicollis*), and least chipmunks (*T. minimus*). Predicted positive responses to wildfire were also observed for deer mice, while predicted negative responses to wildfire were not supported for chipmunks. Total biomass of small mammal populations generally increased following both thinning and wildfire. I argue that my statistical methods, combined with rigorous attention to experimental design, provide a template for similar experimental investigations.

In Chapter 2, I examined changes in small mammal habitat and densities of 4 small mammal species, including deer mice, gray-collared chipmunks, golden-mantled ground squirrels (*Spermophilus*

lateralis), and Mexican woodrats (*Neotoma mexicana*), 2-3 years after variable-intensity thinning and prescribed fire treatments in ponderosa pine forests of northern Arizona, USA. These treatments were designed to simultaneously reduce high-severity fire risk while returning forests to conditions more representative of pre-European settlement structure and function. Treatments resulted in increased herbaceous vegetation and decreased woody debris, 2 important components of small mammal habitat in these forests. Small mammal populations varied strongly across years during the course of the study. Small mammal densities were influenced by both treatments and identified habitat variables. Deer mouse densities were negatively related to tree densities. Gray-collared chipmunks were negatively related to tree densities, positively related to woody debris, and negatively related to treatment. Golden-mantled ground squirrels did not appear to vary strongly with treatment or treatment-related habitat changes. Mexican woodrats were positively, but weakly, related to woody debris. Overall, forest thinning can be expected to increase densities of small mammals in these forests, and retention of slash in fuel reduction/restoration treatments may further positively influence small mammal densities in the post-treatment community. However, reduction of woody debris with frequent prescribed fire entries may reduce small mammal densities. Further work is necessary to better understand links between herbaceous vegetation and small mammal populations in southwestern ponderosa pine forests, as well as population dynamics and habitat needs of less common species such golden-mantled ground squirrels and Mexican woodrats.

In Chapter 3, I examined general patterns of small mammal responses to mechanical thinning, prescribed fire, and mechanical thinning/prescribed fire combination treatments at 8 different study areas across the United States as a part of the Fire and Fire Surrogate Program. Research questions included 1) do treatments differ in their impact on small mammal densities and biomass, and 2) are effects of treatments consistent across study areas? I 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, yellow-pine chipmunks (*T. amoenus*), and golden mantled ground squirrels, as well as all *Peromyscus* and *Tamias* species, had top-ranked models with responses varying both by treatment type and study area. However, the top-ranked model of total small mammal biomass was a model with biomass varying only with treatment, not by treatment type or study area. Individual species and taxa appear to have variable

responses to fuel reduction treatment types in different areas; however, total small mammal biomass appears to generally increase after any type of fuel reduction. These results highlight the variability in taxa-specific responses to treatments and suggest the importance of adaptive management policies and careful site-specific analyses when applying fuel reduction treatments.

In Chapter 4, I describe an analogy between models designed to estimate occupancy of sites by animal species and the estimation of fire size and mean fire return interval. Information on characteristics of historical fire regimes in ponderosa pine forests is increasingly being used to understand ecological function and to set management guidelines for these forests. Better methods for estimating parameters of historical fire regimes from fire-scarred samples are needed. I provide estimators for both size and return interval of fire when detection probabilities of fires are < 1 . The sampling method involved requires identification of sites that are geographically closed to fire and the sampling of fire-scar recorder trees within those sites. Simulations suggest that at least 3 recorder trees per site would be necessary to obtain relatively unbiased and precise estimates of parameters. I introduce model assumptions, sampling considerations and ideas for advanced applications of this approach. The model described exists in a likelihood framework, thus facilitating information-theoretic model selection and inference.

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CHAPTER 1:
SMALL MAMMAL RESPONSES TO THINNING AND WILDFIRE IN
PONDEROSA PINE-DOMINATED FORESTS OF THE SOUTHWESTERN USA

INTRODUCTION

Recently, researchers have focused substantial effort on investigating changes in fire regimes and stand structure of ponderosa pine-dominated forests of the southwestern USA (Cooper 1960, Covington and Moore 1994, Moore et al. 1999, Fulé et al. 2001, Allen et al. 2002). These forests apparently experienced frequent fires (2-20 year return interval; Moore et al. 1999) of low to moderate severity in the recent past resulting in a park-like appearance with mature trees interspersed in forest openings. However, since European settlement of the region, fire suppression, grazing, and logging are thought to have resulted in levels of tree densities and forest fuels outside the historic range of variability, thereby increasing the potential for high-severity wildfires (Cooper 1960, Savage and Swetnam 1990, Covington and Moore 1994, Arno et al. 1995). To reduce this potential, managers are interested in the development and application of treatments, including mechanical thinning and prescribed fire, designed to remove excess fuels while moving these forests toward historical structural conditions and disturbance intervals (e.g., Covington et al. 1997, Moore et al. 1999, Lynch et al. 2000). Such fuel reduction treatments have recently been officially sanctioned on USA federal lands through the 2003 Healthy Forests Restoration Act.

Information allowing better prediction of the potential effects of fuel reduction treatments is needed to guide management decisions such as type, timing, extent, area, and location of treatments. To provide such information, the national Fire and Fire Surrogate (FFS) Program was conceived as a cooperative effort among federal land-management agencies, universities, and private organizations to investigate the relative impacts of fire and fire surrogate treatments (i.e., mechanical thinning) on forest ecology and fire risk in forests throughout the USA that evolved with short-interval, low- to moderate-severity fire regimes (P. Weatherspoon and J. McIver, US Forest Service, unpublished report). The FFS

experimental approach applies a similar study design and sampling scheme to 13 study areas across the country, including 2 study areas in ponderosa pine-dominated forests of Arizona and New Mexico. Through the FFS Program, researchers are monitoring treatment effects on several ecological response variables in the general areas of wildlife, vegetation, fuels and fire behavior, soils, entomology, and pathology.

Compared to forests treated with fuel reduction techniques, untreated forests appear to be at higher risk for severe wildfire (Fulé et al. 2001, Martinson and Omi 2002, Pollet and Omi 2002). Therefore, understanding how effects of fuel reduction treatments differ from the effects of severe wildfires, which may occur more commonly in the absence of fuel reduction treatments, should also help to guide management decisions. Responses to prescribed fire and thinning can generally be examined experimentally; however, studying wildfire is limited to quasi-experimental approaches, and data on pre-wildfire conditions are rarely available.

Within the wildlife component of the FFS Program, small mammal populations have been identified as a response variable of interest. Small mammal communities comprise an important component of the vertebrate biomass and biodiversity of forests, and likely have a substantial role in shaping forest successional patterns through seed consumption and dispersal and hypogeous fungi dispersal (Tevis 1956, Gashwiler 1970, Maser et al. 1978, Price and Jenkins 1986). Small mammals also are important as food sources for predatory species of management concern in southwestern forests, including northern goshawks (*Accipiter gentilis*; Reynolds et al. 1996, Long and Smith 2000) and Mexican spotted owls (*Strix occidentalis lucida*; Ward and Block 1995, Sureda and Morrison 1998).

Little reliable information is available regarding small mammal responses to forest thinning, prescribed fire, or wildfire; such information is sorely needed to understand the effects of treatments on populations (Whelan 1995). Three major flaws in the existing literature include reliance on abundance indices, non-optimal sampling methods such as kill-trapping, and lack of pre-disturbance data. The majority of the extant work employs indices of abundance as response variables (e.g., Tester 1965, Bock and Bock 1983, Masters et al. 1998, Steventon et al. 1998, Wilson and Carey 2000, Carey 2001). Inference from abundance indices rests on the problematic assumption that the probability of detecting animals is constant across space and time (Nichols 1992, Anderson 2001). When comparing across areas that have

been differentially influenced by a habitat disturbance, this assumption seems unrealistic because changes in habitat likely influence animals' behavior and thus capture probabilities (Block et al. 2001).

Additionally, some investigators have relied on indices from small mammal kill-trapping (e.g., Ahlgren 1966, Krefting and Ahlgren 1974, Martell 1984, Kirkland et al. 1996, Ford et al. 1999, Suzuki and Hayes 2003), which may reduce the power of investigations to detect effects because the investigation itself is a mortality factor that may influence local population dynamics. Finally, lack of pre-disturbance information degrades the utility of much existing research. In studies of wildfire, information on pre-fire populations is generally unavailable, and investigators rely on comparisons to nearby unburned areas (e.g., Krefting and Ahlgren 1974, Martell 1984, Kirkland et al. 1996, Kyle and Block 2000). However, even in the case of planned forest disturbances, investigators have frequently failed to gather pre-prescribed fire (e.g., Ahlgren 1966, Bock and Bock 1983), or pre-thinning (e.g., Monthey and Soutiere 1985, Steventon et al. 1998) data.

This work began as an investigation of small mammal responses to thinning treatments in southwestern ponderosa pine-dominated forests, conducted within the FFS Program at the Southwest Plateau study area in northern Arizona, and at the Jemez Mountains study area in northern New Mexico. In addition to these treatments, a high-severity wildfire, the Lakes Fire, burned through a portion of the Jemez Mountains study area in 2002 after 2 years of small mammal data had been gathered, allowing me the rare opportunity to assess small mammal responses to wildfire in ponderosa-pine dominated forests through examination of pre- and post-fire populations. I evaluated short-term responses (6 months to 1 year post-disturbance) to forest thinning and wildfire. These responses were evaluated through changes in population densities of dominant species and changes in total small mammal community biomass. In addition to an examination of treatment responses, I also evaluated the challenges and opportunities associated with large-scale habitat experiments in the context of this work.

Responses of small mammal populations to wildfire and thinning can be considered to occur in 2 stages. The first stage is proximal mortality caused by the disturbance itself. Wildfire will most likely be a greater proximal source of small mammal mortality from burns or suffocation (Tevis 1956, Chew et al. 1959) compared to thinning, although thinning operations, if large and intense enough, probably result in some immediate mortality or emigration by small mammals.

The second stage of post-disturbance response is a demographic response to altered habitat conditions after treatment, either through changes in survival, fecundity, or migration, or combinations thereof. The second stage of response spans a gradient across short-term to long-term changes in habitat conditions. The impact of disturbance on vegetation communities is expected to be highly dynamic over time (e.g., Oswald and Covington 1983, Oswald and Covington 1984), and thus the time period included in post-disturbance sampling will determine the measurable responses. I examined responses from 6 months to 1 year post-disturbance, which I characterize as short-term. Because I sampled small mammals in late summer, these responses were measured after 1 growing season post-disturbance.

Thinning and wildfire are expected to differ in their short-term, i.e., 1-2 growing seasons post-disturbance, impact on the structural characteristics of small mammal habitat. Critical components of small mammal habitat in forests include the herbaceous layer, which provides a source of food through both vegetation and seeds (Ahlgren 1966, Goodwin and Hungerford 1979, Kyle and Block 2000, Wilson and Carey 2000), coarse woody debris, which provides nesting cover, 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), and the overstory canopy, which influences the density of the herbaceous layer (Clary 1975, Moore and Deiter 1992), and provides food through seed production (Gashwiler 1970, Gashwiler 1979, Carey and Johnson 1995).

In general, a negative relationship exists between herbaceous density and tree density (Clary 1975, Moore and Deiter 1992, Sullivan et al. 2001), and thinning increases herbaceous cover by 1-2 growing seasons after treatment (Clary 1975, Covington et al. 1997), presumably due to increased light and/or nutrient availability. Thinning method and treatment of slash will influence the coarse woody debris available immediately after thinning, depending on whether slash is removed, lopped and scattered, or piled. If slash contains pine cones, it may increase the short-term availability of seeds to forest floor small mammals.

Immediately after fire, the biomass of the herbaceous layer (e.g., grasses, forbs, seedlings) will generally be reduced due to proximal mortality from the fire. However, in the first few growing seasons after fire, a recovery of this component to greater than pre-fire levels can be expected, based on data on prescribed fire (Bock and Bock 1983, Harris and Covington 1983, Oswald and Covington 1983, Oswald

and Covington 1984). Fire intensity will impact the level and type of herbaceous recovery. Armour et al. (1984) found similar forb cover among unburned, low-intensity burned, and high-intensity burned sites, but lower grass cover on high intensity burned sites, apparently due to smoldering of the litter layer and resultant mortality of grass rhizomes. Soil seed sources may also be impacted differentially by variable-severity fire – if soil seed sources are destroyed by the wildfire, forbs with wind-dispersed seeds, rather than grasses, may be prominent in the short-term post-fire community (Harris and Covington 1983). Fire also leads to short-term declines in coarse woody debris (Covington and Sackett 1984, Arno et al. 1995, Chapter 2), although, again, the extent of the reduction is probably variable and dependent on fire intensity. Reduction in the overstory also is highly dependent on fire conditions and partially dependent on pre-fire stand conditions. Griffis et al. (2001) documented substantially higher tree mortality after wildfire in unthinned stands versus after prescribed fire in thinned stands.

Different effects on habitat are likely to result in different responses of the small mammal communities in affected areas. I hypothesized that habitat needs, rather than proximal mortality due to disturbance, would be the driving force behind changes in densities 6 months to 1 year post-disturbance. I then predicted demographic responses based on information on habitat needs for the dominant species found on the study areas.

I predicted that deer mice (*Peromyscus maniculatus*) in ponderosa pine-dominated forests would exhibit positive short-term responses to thinning. Deer mice are early seral-stage generalists known to benefit from disturbances of many kinds (Fitzgerald et al. 1994). They are highly omnivorous, with a diet composed primarily of seeds, but also including insects and herbaceous material. I expected thinning to increase the availability of food sources in 3 possible ways: first through increased availability of herbaceous vegetation and associated seeds, second through increased availability of herbivorous insects, and third, through increased availability of pine seeds readily harvested from slash piles. In addition, I also expected that the presence of slash would provide generous amounts of cover. Deer mice have been positively linked with both coarse woody debris cover and herbaceous and/or shrub cover (Goodwin and Hungerford 1979, Carey and Johnson 1995, Kyle and Block 2000, Carey and Harrington 2001, Carey and Wilson 2001, Manning and Edge 2004).

For similar reasons, I also predicted that chipmunk species, including gray-collared (*Tamias cinereicollis*) and least (*T. minimus*) chipmunks would exhibit positive short-term responses to thinning. Chipmunks are omnivorous, primarily feeding on herbaceous material and seeds (Hilton and Best 1993, Fitzgerald et al 1994). They are associated with forest openings and use logs and stumps for feeding, observation, and nesting cover. I expected that thinning would immediately increase the availability of both openings and logs and stumps and would also increase food availability, as discussed for deer mice.

I predicted positive responses of deer mice to wildfire. In the short-term, I expected that wildfire would increase important food sources for deer mice through increased seed availability from early-colonizing forbs or forbs released from competition, and/or increased availability of seeds in the soil seed bank once forest floor litter was reduced by fire (Ahlgren 1966). Though coarse woody debris should decline after fire, I expected that increases in food sources would compensate for this loss. Ream's (1981) review of small mammal-fire associations suggested positive responses to fire by deer mice.

Conversely, I predicted that chipmunks in ponderosa pine-dominated forests would respond negatively to wildfire. While wildfire may increase seed availability, herbaceous vegetation plays a relatively large role in chipmunk diets (Hilton and Best 1993, Fitzgerald et al. 1994), and I expected herbaceous vegetation to be less available after wildfire than before. Also, in the short-term wildfire will tend to reduce the availability of coarse woody debris, and I predicted that this reduction would influence responses by chipmunks to wildfire. Ream's (1981) review suggested that chipmunks would more likely respond positively to fire if rock, shrub, or woody cover remained.

STUDY AREA

The study area design was established by the FFS Program national study proposal (P. Weatherspoon and J. McIver, US Forest Service, unpublished report). The 2 southwestern study areas in the FFS Program were each comprised of 3 study sites. Study sites were further divided into 4 experimental units, each assigned to a treatment type (thin, prescribed burn, thin/prescribed burn combination, control). Treatments were not assigned to the study sites randomly, but were assigned primarily by convenience, i.e., both thin and thin/prescribed burn treatments next to each other, similarly for burn and thin/prescribed burn. Because prescribed burning was not completed on the southwestern study areas within the time frame of this research, only the thinning portion of the FFS Program study

design is examined here. Sampling within the experimental units was keyed to a permanent grid system of 36 points placed 50 m apart, generally in a 6 x 6 array, but sometimes in an oblong or non-rectangular array. The total area of each sampling grid was approximately 6.25 ha. A 50-m buffer surrounded the sampling grid, e.g., total size of the treated areas was approximately 12.25 ha. Table 1.1 provides a summary of the assignment of experimental units to treatments under the original FFS design and under this study.

The Southwest Plateau study area (SPSA) was located on the Coconino and Kaibab National Forests west of Flagstaff, Arizona, between 2,100 and 2,300 m elevation. It was composed of 1 study site, SP-A, located on the Kaibab National Forest (35°N, 112°W), and 2 study sites, SP-B and SP-C, located approximately 25 km east of SP-A and < 5 km from each other on the Coconino National Forest (35°N, 111°W), and. At all 3 SPSA study sites, experimental units were arranged in a 2 x 2 square block, with experimental units adjacent within the blocks. Ponderosa pine was the sole tree species throughout the 3 study sites, with the exception of a few (less than 20% of basal area; J. Bailey, Northern Arizona University, unpublished data) Gambel oak (*Quercus gambelii*) and alligator juniper (*Juniperus deppeana*) at SP-A. Common understory plants included (J. Bailey, Northern Arizona University, unpublished data) yarrow (*Achillea millefolium*), pine dropseed (*Blepharoneuron tricholepis*), sedges (*Carex* spp.), Wheeler's thistle (*Cirsium wheeleri*), trailing fleabane (*Erigeron flagellaris*), Arizona fescue (*Festuca arizonica*), Wright's deervetch (*Lotus wrightii*), and squirreltail (*Sytanion hystrix*), though drought conditions in the southwest USA at the time of the study likely resulted in relatively low herbaceous cover. The SP-A site had a few low rocky ridges, but otherwise the sites lacked substantial topographic relief. All of the SPSA study sites had been pre-commercial thinned during the previous 30 years, with at least 2 prior entries of thinning.

The Jemez Mountains study area (JMSA) was located entirely on the Santa Fe National Forest west of Los Alamos, New Mexico (35°N, 106°W), at elevations ranging from 2,400 to 2,600 m. Data presented here were gathered at 2 study sites, JM-B and JM-C. Data from the third study site (JM-A) were not included in this analysis because no treatments were completed there. Both the JM-B and JM-C study sites were dominated by ponderosa pine, with lesser amounts of southwestern white pine (*Pinus strobiformis*), Douglas-fir (*Pseudotsuga menziesii*), Gambel oak, and aspen (*Populus tremuloides*).

Common understory shrubs (J. Bailey, Northern Arizona University, unpublished data) included Wood's rose (*Rosa woodsii*), kinnikinnick (*Arctostaphylos uva-ursi*), and Oregon grape (*Berberis repens*). Common herbaceous plants included yarrow (*Achillea millefolium*), Kaibab pussytoes (*Antennaria rosulata*), sedges (*Carex* spp.), Arizona fescue (*Festuca arizonica*), muttongrass (*Poa fendleriana*), and squirreltail (*Sitanion hystrix*). Both the JM-B and JM-C sites included hills and rocky ridges. Information on management history was not available for the study sites, but the stands had undergone logging in the past. At the JM-B site, 2 experimental units were located adjacently and were < 1 km from the 2 other experimental units, which were located adjacently. At the JM-C site, the experimental units were arranged in a string along the northern edge of a mesa top. The JM-B and JM-C sites were separated by approximately 12 km.

METHODS

Small Mammal Trapping

Two different levels of small mammal capture effort were used in this study. The sampling grid in each experimental unit provided the basic structure for small mammal trapping grids. The FFS national protocol called for trapping at 50-m intervals, keyed to the permanent sampling grid points (S. Zack, Wildlife Conservation Society, and B. Laudenslayer, US Forest Service, unpublished report). In 2000 at the SPSA, each trapping grid consisted of 1 large (7.6 x 8.9 x 22.9 cm) Sherman folding live-trap at every grid point, and 1 extra-large (10.2 x 11.4 x 38.1 cm) Sherman folding live-trap at every other grid point. The same design was then carried out in 2001 at both the SPSA and JMSA, except that a pilot study to evaluate the utility of an expanded trapping effort was made on 2 of the experimental units at the SPSA. The expanded effort consisted of placing trap lines between the grid points, thus decreasing trap spacing to 25 m. Large Sherman live-traps were placed at these points for a total of 121 large traps (compared to 36 in the original design) and extra-large Sherman live-traps were placed at the original grid points for a total of 36 traps (compared to 18 in the original design). Converse et al. (2004) evaluated the expanded trapping effort and concluded that it resulted in increased capture probabilities and sample sizes. Thus, the expanded trapping effort was applied to both study areas in subsequent years.

Small mammal trapping was conducted annually from 2000-2003 at the SPSA and from 2001-2003 at the JMSA. Trapping occurred in July and August during 2 consecutive 5-day sessions at each

study area. Half the experimental units at each study site, randomly assigned, were trapped in the first session and the other half in the second session. Traps were positioned along small mammal trails, at the openings of burrow holes, and/or in proximity to downed woody debris. A wood shingle was used to shade and insulate traps. Polyester filling was placed at the back of each trap for insulation along with approximately 20 mL of a bait mixture of rolled oats and chicken feed. A small amount of bait was also trailed into the entrance of each trap. Traps were checked during both morning and afternoon to yield 10 trapping occasions on each unit each year. During trapping, the following data were recorded for each animal: trap location and size, species, new or recapture, individual identity, age class, sex, mass, reproductive condition, and release condition. Animals were individually identified with 2 unique ear tags.

Treatments

On both study areas, thinning treatments were designed to simultaneously retain the largest trees and create clumps of trees separated by larger, semi-open spaces. This is thought to more closely simulate historical conditions in these forests (Covington et al. 1997). On the SPSA, 2 experimental units at both the SP-B and SP-C sites were thinned during the fall of 2002 with piling of slash completed in the spring of 2003. Thinning began on 2 experimental units at the SP-A site in the fall of 2002 but was not completed until the spring of 2003. At the SP-A site, trees were felled primarily with a feller-buncher and slash was piled. At the SP-B and SP-C sites, trees were hand-felled and slash was piled after short-distance skidding; slash piles were slightly smaller and more numerous at the SP-B and SP-C sites than at the SP-A site. Slash was left after the treatments and was still in the units during small mammal trapping in 2003. At the JMSA, 1 experimental unit at the SP-B site was thinned in the spring of 2003. Though some piles existed, slash was generally not piled but was left scattered on the ground and was still in the unit during the trapping season of 2003. Thinning was not completed at the remaining unit slated for thinning at the SP-B site because of logistical difficulties. Disturbance of the soil after thinning was more severe at the JMSA than at the SPSA, presumably due to the thinning methods used and the greater topographic relief at the JMSA.

The Lakes Fire (approximately 1,700 ha total) burned through the entire JM-C site at the JMSA in late August 2002. Tree mortality was nearly complete throughout the majority of the 4 experimental units. Needles and small branches were consumed on a majority of the trees, and ground cover was almost

completely consumed except in some small clearings, leaving bare soil throughout the site. The burned slope to the north of the JM-C site was treated by the US Forest Service with aerial seeding on 11-12 October 2002, with the goal of reducing post-fire erosion. Seeded grasses, including mountain brome (*Bromus marginatus*; 30% of mix), slender wheatgrass (*Elymus trachycaulus*; 30%), annual rye grass (*Lolium multiflorum*; 30%), and barley (*Hordeum vulgare*; 10%), were applied at a nominal density of approximately 25 kg/ha. While aerial seeding was not intended for the JM-C experimental units, due to the presence of seeded grasses in June 2004 it was apparent that some seeds had blown into the north portion of the experimental units.

Data Analysis

The analysis of responses to thinning and wildfire occurred in 4 steps. First, I estimated abundances for each species each year in each experimental unit, based on the mark-recapture data. Second, I estimated effective trapping area for each species each year in each unit through models of mean maximum distance moved. Third, I calculated species-specific densities, total small mammal biomass, and variance-covariance matrices for densities and biomass in each unit each year. Finally, I conducted weighted least-squares regression analyses to examine the effects of habitat disturbances on densities of the most common small mammal species at each study area and on total biomass at each study area.

Throughout the analysis, I employed an information-theoretic philosophy of model selection and multi-model inference (Burnham and Anderson 2002). Model selection was based on Akaike's Information Criterion (AIC; Akaike 1973) with a small sample correction (AIC_c; Hurvich and Tsai 1989) and model-averaging was based on Akaike weights (Burnham and Anderson 2002). At each step in the analysis, I specified statistical model sets *a priori*, to strengthen inference and lessen the risk of identifying spurious effects (Anderson et al. 2001).

Abundance Estimation.—Abundance estimates for each unit in each year were obtained through the Huggins conditional likelihood approach (Huggins 1989, 1991). The Huggins approach allows for the modeling of individual heterogeneity, behavioral responses to capture, and time effects on capture probabilities (Model M_{tbi} ; Otis et al. 1978). The Huggins conditional likelihood generates estimates of initial capture ($p_i, i = 1, \dots, t$) and recapture rates ($c_i, i = 2, \dots, t$) for t occasions based on animal encounter

histories and uses these rates to generate estimates of abundance with a Horvitz-Thompson type estimator, as

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

where M_{t+1} is the number of unique individuals marked on a grid during t trapping occasions, i.e., the minimum known population size, and p_t is the estimate of initial capture rate for occasion t . One benefit of the Huggins approach is the ability to use individual-specific covariates to model heterogeneity in capture probabilities (Huggins 1991, Pollock 2002, White 2002). An additional benefit over the full closed-capture likelihood of Otis et al. (1978) is the improved numerical properties of the Huggins estimator in some cases; for these data, the full likelihood models sometimes would generate abundance estimates equal to M_{t+1} with an estimated variance of 0.

I used age class as an individual covariate to account for heterogeneity in capture rates. I classified animals as either adults or subadults based primarily on mass, and secondarily on external evidence of reproductive status if there was uncertainty in mass measurements (McCravy and Rose 1992). I used a combination of field observations and information available in the literature (Hilton and Best 1993, Fitzgerald et al. 1994) to define typical minimum masses of adult animals. Deer mice and brush mice (*Peromyscus boylii*) were defined as adult when ≥ 14 g, long-tailed voles (*Microtus longicaudus*) when ≥ 30 g, least chipmunks when ≥ 35 g, gray-collared chipmunks and cliff chipmunks (*Tamias dorsalis*) when ≥ 50 g, Mexican woodrats (*Neotoma mexicana*) when ≥ 100 g, and golden-mantled ground squirrels (*Spermophilus lateralis*) when ≥ 150 g.

Estimation of abundance was conducted in Program MARK 3.2 (White and Burnham 1999). Experimental units in each year of the study were treated as groups in the analysis, and thus abundance estimates were obtained for each unit in each year, i.e., I combined data across experimental units and years to obtain abundance estimates for each experimental unit in each year and I used auxiliary variables to model differences in detection probabilities across experimental units and years (Bowden et al. 2003). This approach is useful because of its increased efficiency, especially when small sample sizes occur at the scale where abundance estimates are desired.

I proposed *a priori* models to describe capture probabilities and estimate abundance. I included a time of day effect (a.m. versus p.m. trap check) and a behavioral response to capture in all models, because observations during data collection indicated that these were clearly important factors. The only exception to this was long-tailed voles at the JMSA, where a behavior effect was not estimable and thus was deleted from all models. At both study areas, I included age of individual, either year or session within year, and either unit or site as effects in the models. For the SPSA analyses, I also included trapping effort (low effort = 50 m trap spacing, high effort = 25 m trap spacing) and treatment (thinning). For the JMSA analysis, I also included treatment (thinning or wildfire), but trap effort was not considered in the JMSA analysis because trap effort was nested within year. I included all possible combinations of the effects for a total of 72 abundance estimation models in both the SPSA and JMSA analyses.

Abundance estimation was conducted for all marked species, but in the cases of species with small sample sizes, many models were not included because effects were not estimable or were poorly estimable (e.g., Mexican woodrats were never caught at the JM-C site on the JMSA, therefore a wildfire effect was not estimable). To determine estimability, abundance estimates were examined for each model and models were deleted if estimates were nonsensical, e.g., estimates on the order of thousands or more individuals. Such abundance estimates can be expected with the Huggins conditional likelihood approach when very small detection probabilities occur in the denominator of equation (1), as may occur with inestimable effects in the models (Pollock 2002).

I model-averaged the abundance estimates and variance-covariance matrices to account for model selection uncertainty. I used AIC_c for model selection, computed model-averaged estimates based on Burnham and Anderson (2002), and model-averaged variance-covariance matrices based on Burnham and Anderson (2004).

Effective Trapping Area.—Estimation of abundance via mark-recapture methods from a trapping grid results in an estimate that pertains to an unknown total area. Because density is of more interest as a response variable than abundance, I used mean maximum distance moved (MMDM) to estimate the areas to which abundance estimates applied (Wilson and Anderson 1985). I calculated the maximum distance moved between any 2 traps for each marked animal with ≥ 2 captures in a unit in one year. I specified multiple ANOVA (PROC GLM; SAS Institute 2003) models to estimate MMDM. For the analyses at both

study areas, I proposed candidate models with MMDM varying by year, unit, site, or a constant model. For the SPSA analysis, I additionally considered treatment (thinning) and trapping effort. For the JMSA analysis, I also considered treatment (thinning or wildfire). Thus, I examined 6 models in the analyses at each study area. Only single-variable models and a smaller model set, as compared to the abundance estimation procedure, was considered because less information is available in the capture-recapture data on movement than on capture probability. This is because each animal contributes at most one piece of information to the estimation of MMDM, whereas each animal contributes information to estimation of capture probabilities equal to the number of capture occasions in which an animal is at risk of capture.

For each model, I added a buffer strip, with a width of one-half the model-averaged MMDM, to the area of each trapping grid to estimate the effective trapping area (Otis et al. 1978, Wilson and Anderson 1985). The variance of effective trapping area for each model was calculated by a delta-method transformation of the variance of MMDM (Wilson and Anderson 1985). Covariances across the effective trapping area estimates were calculated based on the correlation matrix of the estimates, e.g., for model MMDM{year} the covariance across experimental units within a year was computed as

$$\text{cov}(E_{it}, E_{jt}) = \sqrt{\text{var}(E_{it}) * \text{var}(E_{jt})}, \quad (2)$$

where $\text{var}(E_{it})$ is the variance of the effective trapping area estimate in unit i in year t and $\text{var}(E_{jt})$ is the variance of the effective trapping area estimate in unit j in year t , because $\text{corr}(E_{it}, E_{jt}) = 1$. Then, for model MMDM{year}, correlations, and therefore covariances, in estimates between years would be 0. I then model-averaged the estimates and variance-covariance matrices of effective trapping area from each model to obtain model-averaged estimates and variances-covariance matrices, based on the computed AIC_c for each ANOVA model (Burnham and Anderson 2002).

Densities, Biomass, and Variance-Covariance Matrices.— Species-specific densities were calculated in each unit each year as the abundance divided by the effective trapping area. For the analysis of total biomass, I used the minimum adult mass, in grams, as a multiplier to convert density estimates to biomass estimates, and then summed the total estimated mass over all marked species at each study area. Variance-covariance matrices of the density estimates and total biomass estimates were necessary for the weighted regression analysis. These matrices were computed by delta method transformations of the

model-averaged variance-covariance matrices of the abundance estimates provided by Program MARK and the model-averaged variance-covariance matrices of effective trapping area (Seber 2002).

Weighted analysis cannot be conducted with variances of 0 because the variance-covariance matrix is singular. Variances of 0 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, I 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 0 density estimates. This method was used for the most common species at each study area, analyzed singly, as well as for the less common species, which were not analyzed singly, before they were included in the analysis of total biomass. The only exception was the long-tailed vole, which was only caught on 1 experimental unit in 1 year, thus making a regression impossible.

Analysis of Treatment Effects.—The analysis of treatment effects was conducted under a weighted least-squares regression framework (Draper and Smith 1998). A traditional (i.e., unweighted) regression analysis was inappropriate because of the non-0 sampling covariances between the abundance estimates, which were induced by the abundance and effective trapping area estimation procedures.

I specified multiple *a priori* models describing predicted responses of densities to treatments. I used site, year, and treatments as factors in the models. While abundance and effective trapping area were estimated at a unit scale each year (because trapping was conducted at a unit scale), I did not model treatment effects at a unit scale. Treating units as replicates would represent pseudo-replication (Hurlbert 1984) because thinning treatments were carried out essentially as one operation at each study site, and because the wildfire also represented a single “treatment”. In the SPSA data analysis, thinning was treated as 3 factors by nesting thinning within the 3 study sites. Thinning was treated in this way because important interaction effects were evident after an initial set of model runs with thinning treated as a common effect across all sites and interactions included between site and thinning. To keep the model set balanced, thus allowing the calculation of valid relative importance values (described below), this initial set of models was revised to provide for estimation of thinning effects differently at each study site. In the JMSA analysis, there were 2 treatments, thinning and wildfire, and interactions were not considered

because treatments were naturally nested within sites. I ran all combinations of the variables, for a total of 8 models in the SPSA analysis and 16 models in the JMSA analysis.

A vector of effect sizes ($\hat{\beta}_i$) was estimated, and a variance-covariance matrix of the effects ($\hat{\Sigma}_i$) was computed for each model (i) in the weighted analyses. Computation of $\hat{\beta}_i$ and $\hat{\Sigma}_i$ follow from Draper and Smith (1998) as

$$\hat{\beta}_i = (X_i'V^{-1}X_i)^{-1}X_i'V^{-1}Y \quad (3)$$

and

$$\hat{\Sigma}_i = (X_i'V^{-1}X_i)^{-1}\hat{\sigma}_i^2 \quad (4)$$

where X_i is the design matrix of model i , V is the variance-covariance matrix of the model-averaged density estimates, Y is the vector of model-averaged density estimates, and $\hat{\sigma}_i^2$ is estimated from the residual sum of squares of the model, divided by the appropriate degrees of freedom, resulting in an unbiased estimator,

$$\hat{\sigma}_i^2 = \frac{(Y - X_i\hat{\beta}_i)'V^{-1}(Y - X_i\hat{\beta}_i)}{(n - K_i)} \quad (5)$$

where n is the sample size of Y estimates and K_i is the number of parameters in model i plus 1 for the estimation of $\hat{\sigma}_i^2$.

Integral to estimating AIC for model i is the recognition that the joint likelihood function for β_i and σ_i^2 is given by

$$\mathcal{L}(\beta_i, \sigma_i^2 | Y, X_i, V) = \frac{1}{\sqrt{|\sigma_i^2 V|} (2\pi)^n} \exp\left(-\frac{1}{2}(Y - X_i\beta_i)'(\sigma_i^2 V)^{-1}(Y - X_i\beta_i)\right) \quad (6)$$

Substituting the maximum likelihood estimators of $\hat{\beta}_i$, given above, and $\hat{\sigma}_i^2$, given as

$$\hat{\sigma}_i^2 = \frac{(Y - X_i\hat{\beta}_i)'V^{-1}(Y - X_i\hat{\beta}_i)}{(n)} \quad (7)$$

into the right side of equation (6) results in a $\log \mathcal{L}$ function proportional to

$$\log \mathcal{L}(\beta_i, \sigma_i^2 | Y, X_i, V) \propto -\frac{1}{2}n\log(\sigma_i^2) \quad (8)$$

and AIC is computed, as in Burnham and Anderson (2002), as

$$AIC_i = n \log \hat{\sigma}_i^2 + 2K_i. \quad (9)$$

The small sample correction of AIC (AIC_c ; Hurvich and Tsai 1989) was then computed for each model. All calculations were carried out in PROC IML (SAS Institute 2003). Based on the computed AIC_c for each model, information-theoretic model selection and multi-model inferential methods were employed (Burnham and Anderson 2002). These included model-averaged effect sizes and standard errors, as well as relative importance values, calculated by summing the Akaike weights across all models in which a given variable appears (Burnham and Anderson 2002). Recent work has indicated that a relative importance value, based on Akaike weights, of ≥ 0.40 suggests that a variable is having an effect on the process of interest (G. C. White, Colorado State University, unpublished data).

RESULTS

Two species were caught most commonly at each study area, with all other species contributing less than 25 total individuals per study area (Table 1.2, 1.3). At the SPSA, deer mice (Figure 1.1) and gray-collared chipmunks (Figure 1.2) were the dominant species. Estimated deer mouse densities ranged from 0 (SE = 0) to 8.5 (SE = 1.6) individuals/ha, and gray-collared chipmunk densities ranged from 0 (SE = 0) to 3.3 (SE = 0.4) individuals/ha. Total small mammal biomass at the SPSA also included Mexican woodrats, golden-mantled ground squirrels, and cliff chipmunks (Figure 1.3). At the JMSA, deer mice (Figure 1.4) and least chipmunks (Figure 1.5) were the dominant species. Estimated deer mouse densities ranged from 0.4 (SE = 0.2) to 9.6 (SE = 0.9) individuals/ha, and least chipmunk densities ranged from 0 (SE = 0) to 1.9 (SE = 0.7) individuals/ha. Total small mammal biomass also included long-tailed voles, Mexican woodrats, and golden-mantled ground squirrels (Figure 1.6). Small mammal community composition appeared to be generally stable before and after treatments, with the exception of the appearance of long-tailed voles after thinning on unit G on the JMSA (Table 1.3). At both study areas, some *Peromyscus* captures were brush mice (*P. boylii*) rather than deer mice, but these individuals were combined with deer mice before analysis was conducted because numbers were low and because of the difficulty in distinguishing the species, at least in the younger age classes; all *Peromyscus* are referred to as deer mice throughout this report. Two adult brush mice were captured on the SPSA, 1 at the SP-A site in 2001 and 1 at the SP-A site in 2002; 5 were captured at the JMSA, all of them at the JM-C site in 2001. Field crews

captured, but did not mark, an additional 3 small mammal species at the SPSA, including rock squirrels (*Spermophilus variegatus*), Mexican voles (*M. mexicanus*), and Abert's squirrels (*Sciurus abertii*). At the JMSA, additional species captured, but not marked, included rock squirrels, dwarf shrews (*Sorex nanus*), and mountain cottontails (*Sylvilagus nuttallii*). Species that were not marked were treated as such because they were captured only incidentally and, in the case of Mexican voles, were protected species.

There existed evidence that disturbance (thinning or wildfire) impacted both capture probabilities and movements of animals (Appendix 1A). Top ranked models of capture probabilities included a thinning effect for gray-collared chipmunks at the SPSA and for least chipmunks at the JMSA, and a wildfire effect appeared in the top ranked capture probabilities model for deer mice at the JMSA. Based on results from these top models, thinning had a positive impact on capture probabilities of both gray-collared chipmunks (effect size = 1.23, SE = 0.47) and least chipmunks (effect size = 1.56, SE = 0.33), while wildfire had a negative impact on capture probabilities of deer mice (effect size = -0.86, SE = 0.20). The top model of mean maximum distance moved by gray-collared chipmunks at the SPSA included a thinning effect in which MMDM was larger in thinned than in unthinned experimental units (unthinned MMDM = 96.30, SE = 4.41; thinned MMDM = 122.62, SE = 12.74).

Predicted positive responses of deer mice to thinning were supported everywhere but the SP-B study site on the SPSA. The top-ranked weighted regression model included only the thinning effect; this model carried 65% of the total model weight (Table 1.4). Thinning had a high relative importance value (0.76), i.e., thinning was associated with models that carried 76% of the total weight. The thinning effect was positive at both the SP-A and SP-C sites, but the effect was negative at the SP-B site, although in all cases the 95% confidence intervals on the model-averaged estimates included 0 (Table 1.5). At the JMSA, the top-ranked model, with 59% of the total weight, included year, thinning, and wildfire effects (Table 1.6). The relative importance value of the positive thinning effect was 0.89, and the 95% confidence interval did not include 0 (Table 1.7).

Deer mice also exhibited predicted positive responses to wildfire. At the JMSA, as noted above, the top-ranked regression model for deer mice included year, thinning, and wildfire effects (Table 1.6). The relative importance value of the positive wildfire effect was 0.77, with a 95% confidence interval that only marginally included 0 (Table 1.7).

Predicted positive responses of gray-collared and least chipmunks to thinning were also largely supported. At the SPSA, the top-ranked model for gray-collared chipmunks had a weight of 95% and included site and thinning effects (Table 1.8). The relative importance value of thinning was high (1.00; Table 1.9). Very few gray-collared chipmunks were ever captured at the SP-A study site, and the estimate of the thinning effect there was nearly 0. Elsewhere, exhibiting a similar pattern as for the deer mouse analysis, the estimate of the thinning effect at the SP-C site was positive while the estimate at the SP-B site was negative, though only at the SP-C site did the 95% confidence interval exclude 0 (Table 1.9). For least chipmunks at the JMSA, the top-ranked model had a weight of 47% and included site and thinning effects (Table 1.10). The relative importance value of the positive thinning effect was 0.96 and the 95% confidence interval did not include 0 (Table 1.11).

The predicted negative response by least chipmunks to wildfire was not supported. The top-ranked model for least chipmunks at the JMSA did not include a wildfire effect (Table 1.10), the relative importance value of the wildfire effect was 0.19, and the effect estimate was nearly 0 (Table 1.11).

Total biomass generally increased as a result of thinning at the SPSA, where the top model included site and thinning effects (Table 1.12) and had a model weight of 73%. The relative importance value of thinning (0.92) was high, and the effect was positive at the SP-A and SP-C study sites and negative at the SP-B site, but only the SP-C estimate had a 95% confidence interval that did not include 0 (Table 1.13). At the JMSA, the top-ranked biomass model included a wildfire effect, with a weight of 28% (Table 1.14). The top-ranked model including a thinning effect had a weight of 11%. The estimated effect of the wildfire was positive and the relative importance value was 0.56; the relative importance value for the positive thinning effect was a low 0.23 (Table 1.15). In both cases the 95% confidence intervals included 0.

DISCUSSION

Experimental Design and Inference

Difficulties in conducting and monitoring large-scale habitat manipulations include problems with relevance of the spatial and temporal scale of treatment and monitoring, classical experimental design issues such as randomization and replication, and the appropriateness of the response variables monitored (Smith 1999, Block et al. 2001). I confronted many of these issues with regard to the design and

implementation of this study, including experimental units that were smaller than desired, a temporal scale that was shorter than desired, non-randomization of treatments, lack of replication, and the use of density, rather than an underlying demographic rate, as the response variable. Difficulties with the wildlife investigations in the FFS Program were predictable because the wildlife portion of the study was overlaid on a design targeted to monitor vegetative and fuel responses to treatments (Block et al. 2001), and selection of the size and location of study blocks and assignment and administration of the treatments was not controlled by wildlife investigators. Additional constraints were a function, as commonly occurs, of budgetary limitations. Clearly more information on ecological effects of fire management and fuel reduction is needed. However, I believe my results are relatively robust predictions of short-term small mammal density responses to thinning and wildfire in southwestern ponderosa pine forests.

The size of the thinned areas at the SPSA was 2 experimental units combined for a total treated area of approximately 24 ha, while at the JMSA the single thinned experimental unit represented approximately half this area. Although the sizes of the treatments studied here represent an improvement over experimental treatments that have been criticized for being overly small (e.g., see Smith's (1999) analysis of Von Trebra et al. (1998)), concern may justifiably exist about the applicability of this research to larger-scale management actions. If treated areas are small relative to areas used by small mammals, small mammal responses may qualitatively differ from responses to larger-scale treatments. This may occur if animals respond not to the treatments themselves, but to the habitat edges induced by the treatments. However, the capture-recapture data from this study indicate that animals were responding to the treatments, because animals appeared to be using areas that were generally smaller than the treated areas. If large numbers of animals appeared in more than one experimental unit in a given year at study sites where experimental units were directly adjacent, i.e., the study sites at the SPSA, this would indicate that animals used and responded to larger areas than the experimental units. Individuals were occasionally captured in more than one experimental unit at a given site, but the incidence of this was relatively uncommon. Few individual deer mice (12 of 486 = 2.5%) or gray-collared chipmunks (19 of 304 = 6.3%) at the SPSA had encounter histories in >1 experimental unit in a single year. To more rigorously address this issue *post hoc*, I calculated \bar{p}^* , the mean probability of capture at least once on a given experimental unit, given presence, by dividing the total number of capture histories, M_{t+1} , for a given species by the

sum of the abundance estimates for that species. These rates were $486/1226 = 0.40$ for deer mice and $304/426 = 0.71$ for gray-collared chipmunks at the SPSA. From this, the expected number of animals occurring on 2 experimental units in a single year can be calculated as

$$\hat{N}(2 \text{ units}) = \frac{M_{t+1,2 \text{ units}}}{(\hat{p}^*)^2}, \quad (10)$$

where $M_{t+1,2 \text{ units}}$ represents the number of individuals captured on 2 experimental units in a single year, resulting in expected numbers of 75 deer mice and 38 gray-collared chipmunks. This indicates that only approximately 6.1% of deer mice and 8.9% of chipmunks would be expected to occur on 2 experimental units in a given year. Therefore, it is reasonable to conclude that animals in this study were primarily responding to the treatments themselves, at least over the late summer period in which I sampled populations. However, future investigations can further increase the size of experimental units and thereby reduce the influence of induced edge by monitoring small mammals before and after thinning or prescribed fire treatments planned as part of large-scale forest management actions (Block et al. 2001).

The temporal scale of investigation, and therefore the scale of inference, are also limited here, and continued monitoring of these and other experiments will be necessary to understand long-term responses to treatments. While Sullivan et al. (1999:1382) state that “the major changes to habitat and small mammals are likely to occur in the immediate post-treatment period after harvesting,” this is still an open question because small mammal results from long-term, continuously monitored experiments of forest management systems are not currently available. Populations may change with time since treatment as successional sequences move forests toward conditions similar to pre-treatment conditions, similar to historic conditions, or into entirely novel conditions. Extant examinations of responses at longer time scales since disturbance examine only snap-shots of the post-treatment time series (e.g., Wilson and Carey 2000).

Because treatments were not randomly assigned to experimental units, but instead were assigned based on convenience, the inferences of this research are weakened, and the design is more correctly termed quasi-experimental (Block et al. 2001). While the scope of collected pre-treatment data mitigates this problem to some degree, it does not overcome it completely. Recognizing the importance of

randomization in experimental design cannot be overemphasized when planning and executing large-scale experiments.

Another shortcoming of this experiment was that the replication of the disturbances was limited. The thinning treatment was replicated 3 times at the SPSA and once again at the JMSA, but the wildfire event was not replicated. The response of deer mice and chipmunks to thinning was consistent, and consistent with expectations, across the majority of replicates, but additional replication of thinning operations is necessary to understand the consistency in small mammal responses to thinning over larger spatial scales and more diverse conditions. A large-scale analysis of treatment effects across the majority of the 13 national FFS study areas is presented in Chapter 3. Because of the unpredictable nature of wildfire, an opportunity to examine changes in pre- and post-wildfire data is rare. Therefore, though the wildfire results presented here do not capture the variability of wildfire responses because of the lack of replication, they do represent the only examination, to my knowledge, of pre- and post-wildfire small mammal populations in forested habitat.

While I estimated density responses to treatments, investigations of the mechanisms resulting in changes in density would increase understanding of small mammal population dynamics in relation to fuel reduction treatments; underlying demographic rates are sometimes a more reliable indicator of habitat quality than population density (Van Horne 1983). Further studies of immigration, survival, and reproduction after thinning and fire would elucidate these processes. For example, it has been suggested that immigrants make up a substantial component of post-fire small mammal populations (Tevis 1956, Tester 1965), but it is not known to what extent animals may survive fire. Mark-recapture data collected in a design such as the one used here should allow for the estimation of survival and emigration responses to treatments under the robust design (Kendall et al. 1995). However, I was limited in my ability to estimate these demographic responses because dominant small mammal species on the study areas had either low annual survival rates and so were rarely captured in multiple years (deer mice) or tag loss occurred between yearly trapping sessions (chipmunks). Furthermore, improved marking methods, e.g., passive integrative transponders (PIT tags), could reduce mark loss.

The strength of the approach described here is that it provides a statistically rigorous and efficient method for the modeling of changes in population densities across space and time. Variances on densities

are reduced by combining data across trapping grids and years, as compared to estimating densities in separate analyses for each grid in each year. Combining data to estimate abundance in multiple areas has been previously described by Bowden et al. (2003); here I add the additional component of time. This approach is both efficient and allows for the removal of the impacts of treatments or other variables of interest, e.g., year or site, on detection probabilities and movement of animals. I provide a method for modeling densities that accounts for the sampling covariances induced by the combined analysis, thus leading to rigorous estimates of effect sizes and uncertainty. Further, the emphasis I place on multi-model inference increases the robustness of the estimates. While the methods I used to estimate population density may be biased high in some cases (see Parmenter et al. 2003), true densities were of less interest in this analysis than density estimates that were unbiased with respect to the variables (thinning, wildfire, year, site) included in the weighted regression analysis; such unbiased estimates will lead to unbiased estimates of effect sizes.

In the large majority of publications examining responses of small mammal populations to forest management, investigators have relied on indices of abundance (minimum known alive or catch per unit effort) to examine responses to treatments. However, the use of methods for estimating detection probabilities are preferable to reliance on the assumption, required in the use of indices, that detection is equal across years, sites, treatments, etc. My results indicate that detection probabilities vary not only temporally and spatially, but also with treatments, which is to be expected as habitat conditions change post-treatment resulting in changes in behavior and movements of animals. Thus, treatment effects on abundance and detection probabilities are confounded in studies where detection probabilities are not estimated. Relying on indices of abundance may lead to misinterpretations of responses to thinning and wildfire.

Small Mammal Responses to Treatments

While I generally found support for the positive predicted responses of deer mice and chipmunks to thinning, there were inconsistencies in the thinning responses at the SPSA. These inconsistencies occurred at one study site, the SP-B site, where estimated responses to thinning by both deer mice and chipmunks were slightly negative. This site had the largest pre-treatment small mammal populations

(Figures 1.1, 1.2, 1.3), indicating that, perhaps, small mammal populations were not as limited by habitat conditions before the thinning treatments.

This result prompts interest in the characteristics of the pre-treatment habitat at SP-B that were supporting larger small mammal populations. The small mammal populations at the SP-A site were generally quite small and composed of different species (i.e., small numbers of cliff chipmunks occurred in addition to small numbers of gray-collared chipmunks), the SP-A site was relatively far geographically from the other 2 sites, and the SP-A site consisted of substantially different habitat, given the presence of Gambel's oak and alligator juniper, so here I focus on comparisons between the SP-B and SP-C sites. Pre-treatment total tree basal area was similar at the 2 study sites (BA = 35.6 m²/ha, range = 34.3 – 38.3 at SP-B, BA = 34.2 m²/ha, range = 24.9 – 43.1 at SP-C), but average tree density was 540 trees/ha (range = 387-701) at the SP-B site, and 798 trees/ha (range = 611-906) at the SP-C site (J. Bailey, Northern Arizona University, unpublished data). Therefore, the trees at the SP-C site were on average smaller as well as more numerous, and indeed, the average percentage of all trees \leq 40 cm was 88% (range 87% to 92%) at SP-B, compared to 98% (range 98% to 99%) at SP-C. Stands of this type, with small, closely-spaced trees, appear to limit populations of deer mice and chipmunks (Hamilton and Cook 1940). Based on our results, thinning of such stands may result in the greatest short-term response in populations of these species. This result highlights the importance of pre-disturbance conditions in determining responses to thinning and wildfire. If habitat is poor for small mammals before disturbance, it appears to be more likely to improve after disturbance. The thinned experimental unit at the JM-B site, where strong positive responses by both deer mice and least chipmunks were observed, also had stands that were thick with small trees and had few openings prior to treatment.

Positive responses to thinning have previously been suggested in deer mice (Wilson and Carey 2000, Carey and Wilson 2001, Suzuki and Hayes 2003). Immediate increases in deer mouse populations after thinning may be due to increases in invertebrate food sources (Ahlgren 1966), herbaceous food and cover (Wilson and Carey 2000), conifer seed in slash piles, and coarse woody debris cover (Carey and Johnson 1995, Suzuki and Hayes 2003, but see Hadley and Wilson 2004). The treatment of slash after thinning seems to have critical importance for small mammal responses (Goodwin and Hungerford 1979). The presence of slash, whether piled (SPSA study area) or scattered (JMSA study area), appeared to

provide focal points for small mammal activity in this study. Slash both harbors insect food sources (Ahlgren 1966) and facilitates animal movement and foraging (Hayes and Cross 1987, Graves et al. 1988, Loeb 1999). Further information on demographic processes leading to increased densities after thinning is needed. Increased food sources and/or cover may increase survival rates after thinning; evidence exists that survival of deer mice is influenced nonlinearly by herbaceous cover and coarse woody debris (Manning and Edge 2004). Conifer seed abundance also appears to influence both survival and fecundity of deer mice (Gashwiler 1979).

Positive responses of deer mice to prescribed fire and wildfire, including severe wildfire, have been documented (Tester 1965, Ahlgren 1966, Krefting and Ahlgren 1974, Bock and Bock 1983, Martell 1984, Kyle and Block 2000), and these responses appear to be linked to increased food sources, such as increases in forb cover even with severe wildfire (Kyle and Block 2000), and an increase in conifer seed availability in jack pine (*Pinus banksiana*) forests, where jack pine cones release seeds in response to heating (Krefting and Ahlgren 1974). The availability of seed food sources may have increased after the wildfire in this study if forb or pine seeds in the soil were exposed by a reduction in the litter layer, or if some pine seeds survived the fire in the canopy, were released during the fall after the fire, and were more easily located by mice during the fall or following spring. Also, some small unburned or lightly burned patches remained in the area of the fire, generally where old logging roads had created small clearings, and these areas may have allowed for easy foraging by deer mice. However, the possibility exists that the positive response of deer mice was due partly to the grass seeding operation carried out in October of 2002, in which an unknown amount of grass seed intended for the side of the mesa apparently drifted into the experimental units. It is unfortunate that this uncertainty exists, as it is unlikely that many opportunities to examine pre- and post- wildfire small mammal populations will occur. Experimental introductions of grass seed after prescribed fire could be used to separate out this confounding.

Coarse woody debris was almost certainly reduced after the wildfire (Covington and Sackett 1984, Arno et al. 1995, Chapter 2) but this did not appear to hamper deer mice in their search for cover, despite the strong relationships documented between deer mice abundance and coarse woody debris (Goodwin and Hungerford 1979, Graves et al. 1988, Carey and Johnson 1995). After the wildfire, mice were observed using burned-out stumps for hiding and escape cover. Manning and Edge (2004) found that deer mouse

survival in an Oregon mixed-conifer forest was linked non-linearly with coarse woody debris and fern cover. They suggested that the moderate amount of coarse woody debris and fern cover that was linked with highest survival rates, as compared to higher levels of woody debris and fern cover, was explainable by either reduced predatory efficiency with reduced habitat complexity or reduced competition.

Least and gray-collared chipmunks generally exhibited positive responses to thinning, as predicted. Strong relationships with understory vegetation (Carey 2000, Carey 2001) and an association with coarse woody debris and stumps (Fitzgerald et al. 1994, but see Hadley and Wilson 2004) may have spurred this increase. Positive responses to thinning have been documented for other chipmunk species (Carey 2000, Wilson and Carey 2000, Carey 2001, Carey and Wilson 2001, Sullivan et al. 2001, Hadley and Wilson 2004).

For least chipmunks, the increased availability of food sources, either from forb or pine seeds in the soil bank or aerially-applied grass seeds, may have offset the effect of the loss of coarse woody debris after the wildfire, thus explaining the lack of a negative response by chipmunks to wildfire in this study. Such a pattern has been suggested in a study of jack pine (*Pinus banksiana*) burns for eastern chipmunks (*Tamias striatus*; Krefting and Ahlgren 1974). This hypothesis has also been suggested by research indicating that Townsend's chipmunks (*T. townsendii*) are more common in thinned stands with greater understory vegetation when compared to legacy retention stands with greater amounts of coarse woody debris (Carey 2000).

The critical determinants of forest floor small mammal biomass appear to be coarse woody debris and understory vegetation (Carey and Johnson 1995, Simon et al. 2002). Vertically and horizontally heterogeneous vegetation communities also result in greater richness and abundance of small mammal communities (Carey and Harrington 2001). My results, and others (Monthey and Soutiere 1985, Carey and Johnson 1995, Masters et al. 1998, Wilson and Carey 2000, Carey and Wilson 2001, Suzuki and Hayes 2003) indicate that small mammal biomass appears to respond positively to increased herbaceous vegetation and habitat complexity with thinning disturbances in ponderosa pine and other coniferous forests, assuming the pre-disturbance habitat is relatively poor, (but see Hadley and Wilson 2004, where red-backed voles' (*Clethrionomys gapperi*) dominance of the small mammal community resulted in highest biomass in less disturbed areas). In many low-elevation pine forests of western North America, where deer

mice and chipmunks are the dominant species in the small mammal community, positive biomass responses to thinning may be due to an increase in food availability and coarse woody debris. A positive, though not strong, response to wildfire was documented at the JMSA, though a positive response to thinning was not supported there. However, the variances of the biomass estimates were large and thus model selection favored simpler models. Presumably, increases in biomass in the growing season after wildfire would be driven by an increase in food sources, though again, I am not able to separate the effects of natural food increases after fire from the potential effects of the aerial seeding operation.

MANAGEMENT IMPLICATIONS

Thinning treatments are currently proposed for wide-scale fuel reduction in many forests throughout the United States, especially the western USA. The 2003 Healthy Forests Restoration Act encourages the use of selective thinning for managing wildfire risk and ecological goals. Therefore, forest managers will increasingly find themselves in the position of evaluating the appropriateness of thinning treatments on larger areas.

Generally, total biomass of forest small mammals may be expected to initially increase with thinning treatments in ponderosa pine forests, where deer mice and chipmunks are often dominant species, at least in forests with relatively poor small mammal habitat prior to treatments. Typically, these are areas that would receive increased management attention because of high fuel loadings – areas with high numbers of small trees, few openings, and few larger trees. However, where deer mouse and chipmunk habitat is already fairly good, i.e., in areas with a relatively high number of forest openings and adequate coarse woody debris and herbaceous ground cover, thinning treatments may not increase small mammal populations. If there is concern for small mammal populations (for example, in areas managed for raptor foraging), management attention should be focused on reducing fuel loadings and opening canopies in forest stands with the densest structure, rather than in forests with larger, more widely-spaced trees. Site-specific analysis will be critical to making appropriate decisions about treatment application (Brown et al. 2004).

The responses of small mammal biomass to the high-severity wildfires that may result from passive management, or periodically occur in higher-elevation forests with historically-infrequent fires, are

less clear. Where deer mice are dominant, total small mammal biomass may increase after high-severity wildfire. This may not hold where chipmunks compose a larger portion of the small mammal community.

Treatment of slash after thinning is an important consideration when designing treatments. I evaluated treatments where slash was left in the treated area and either piled or scattered. In both cases, slash appeared to serve as focal areas of small mammal activity, and slash piles appeared to provide abundant small mammal cover. Therefore, it seems likely that thinning would not increase biomass as strongly if slash were immediately removed.

Management attention may focus on small mammal biomass if concern exists about the food base for small mammal predators, such as forest raptors (e.g., goshawks, spotted owls). In these cases, thinning treatments designed to increase small mammal biomass must be balanced against additional habitat needs of the predator species of interest, e.g., denser closed-canopy stands to facilitate goshawk fledgling survival (Reynolds et al. 1996, Long and Smith 2000).

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Table 1.1. Original assignment of experimental units at study sites at the Southwest Plateau study area (SPSA), northern Arizona, and the Jemez Mountains study area (JMSA), northern New Mexico, to treatments under the Fire and Fire Surrogate Program (FFS) design, and the treatments examined under this study.

Study Area	Site	Design	Experimental Unit			
			1	2	3	4
SPSA	SP-A	FFS	Thin	Thin/Burn	Control	Burn
		This study	Thin	Thin	Control	Control
	SP-B	FFS	Control	Burn	Thin	Thin/Burn
		This study	Control	Control	Thin	Thin
	SP-C	FFS	Control	Thin/Burn	Thin	Burn
		This study	Control	Thin	Thin	Control
JMSA	JM-A	FFS	Burn	Thin/Burn	Thin	Control
		This study	Excluded	Excluded	Excluded	Excluded
	JM-B	FFS	Burn	Thin/Burn	Thin	Control
		This study	Control	Control	Thin	Control
	JM-C	FFS	Control	Thin	Thin/Burn	Burn
		This study	Wildfire	Wildfire	Wildfire	Wildfire

Table 1.2. Sample sizes (M_{t+1}) of individual animals for species captured at the Southwest Plateau study area, northern Arizona, from 2000-2003.

Year	Site	M_{t+1}					
		Mexican woodrat	Brush mouse	Deer mouse	Golden-mantled ground squirrel	Gray-collared chipmunk	Cliff chipmunk
2000	SP-A	1	0	24	0	7	2
	SP-B	4	0	30	1	82	0
	SP-C	5	0	45	1	27	0
2001	SP-A	0	1	14	0	1	3
	SP-B	2	0	26	2	81	1
	SP-C	2	0	30	1	16	0
2002	SP-A	0	1	9	0	0	1
	SP-B	0	0	69	10	37	0
	SP-C	0	0	57	0	17	0
2003	SP-A	0	0	29	1	2	4
	SP-B	2	0	58	5	9	0
	SP-C	3	0	95	0	25	0
Total		19	2 ^a	486	21	304	11

^aBrush mice were combined with deer mice for analyses.

Table 1.3. Sample sizes (M_{t+1}) of individual animals for species captured at the Jemez Mountains study area, northern New Mexico, from 2001-2003.

Year	Site	M_{t+1}					
		Long-tailed vole	Mexican woodrat	Brush mouse	Deer mouse	Golden-mantled ground squirrel	Least chipmunk
2001	JM-B	0	5	0	44	0	25
	JM-C	0	0	5	30	7	8
2002	JM-B	0	7	0	57	0	43
	JM-C	0	0	0	61	1	30
2003	JM-B	23	9	0	163	0	31
	JM-C	0	0	0	204	4	16
Total		23	21	5 ^a	559	12	153

^aBrush mice were combined with deer mice for analyses.

Table 1.4. Model selection results from weighted regression analysis of treatment effects on deer mouse densities at the Southwest Plateau study area, northern Arizona, 2000-2003. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K).

Model	AIC_c	ΔAIC_c	Weight	K
Density{thin}	8.294	0.000	0.65264	5
Density{constant}	11.038	2.745	0.16547	2
Density{site + thin}	12.315	4.021	0.08741	7
Density{site}	12.989	4.696	0.06238	4
Density{year + thin}	15.095	6.801	0.02177	8
Density{year}	17.602	9.308	0.00621	5
Density{site + year}	19.518	11.225	0.00238	7
Density{site + year + thin}	20.151	11.857	0.00174	10

Table 1.5. Estimated relative importance values, model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on deer mouse densities at the Southwest Plateau study area, northern Arizona, 2000-2003.

Variable	Relative Importance	Level	Effect	SE	95% CI
Intercept	1.00000	-	0.270	0.108	(0.059, 0.481)
Site	0.15391	Difference SP-A, SP-B	-0.006	0.033	(-0.071, 0.059)
		Difference SP-A, SP-C	0.047	0.104	(-0.156, 0.251)
Year	0.03210	Difference 2000, 2001	0.002	0.010	(-0.018, 0.023)
		Difference 2000, 2002	-0.004	0.014	(-0.031, 0.024)
		Difference 2000, 2003	0.004	0.012	(-0.019, 0.028)
Thin	0.76356	SP-A Thinned	0.241	0.236	(-0.222, 0.704)
		SP-B Thinned	-0.170	0.145	(-0.453, 0.113)
		SP-C Thinned	1.111	0.859	(-0.572, 2.795)

Table 1.6. Model selection results from weighted regression analysis of treatment effects on deer mouse densities at the Jemez Mountains study area, northern New Mexico, 2001-2003. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K).

Model	AIC_c	ΔAIC_c	Weight	K
Density{year + thin + fire}	46.499	0.000	0.58891	6
Density{site + year + thin + fire}	49.555	3.056	0.12779	7
Density{site + year + thin}	50.310	3.811	0.08762	6
Density{year + thin}	50.359	3.860	0.08550	5
Density{year + fire}	51.922	5.423	0.03912	5
Density{year}	52.047	5.547	0.03676	4
Density{site + year}	52.876	6.377	0.02428	5
Density{site + year + fire}	54.716	8.217	0.00968	6
Density{thin + fire}	62.666	16.167	0.00018	4
Density{site + thin + fire}	64.180	17.681	0.00009	5
Density{fire}	66.575	20.075	0.00003	3
Density{thin}	67.756	21.256	0.00001	3
Density{site + fire}	67.845	21.346	0.00001	4
Density{constant}	68.669	22.170	0.00001	2
Density{site + thin}	70.570	24.071	0.00000	4
Density{site}	71.074	24.575	0.00000	3

Table 1.7. Estimated relative importance values, model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on deer mouse densities at the Jemez Mountains study area, northern New Mexico, 2001-2003.

Variable	Relative Importance	Level	Effect	SE	95% CI
Intercept	1.00000	-	0.775	0.398	(-0.006, 1.555)
Site	0.24948	Difference JM-B, JM-C	0.128	0.242	(-0.347, 0.602)
Year	0.99966	Difference 2001, 2002	0.407	0.429	(-0.434, 1.247)
		Difference 2001, 2003	3.152	0.653	(1.872, 4.431)
Thin	0.89010	Thinned	3.360	1.681	(0.065, 6.656)
Fire	0.76581	Wildfire	1.781	1.289	(-0.746, 4.308)

Table 1.8. Model selection results from weighted regression analysis of treatment effects on gray-collared chipmunk densities at the Southwest Plateau study area, northern Arizona, 2000-2003. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K).

Model	AIC_c	ΔAIC_c	Weight	K
Density{site + thin}	83.688	0.000	0.95348	7
Density{site + year + thin}	90.721	7.033	0.02833	10
Density{thin}	91.841	8.153	0.01618	5
Density{constant}	97.292	13.604	0.00106	2
Density{site}	98.952	15.263	0.00046	4
Density{year + thin}	99.108	15.419	0.00043	8
Density{year}	104.012	20.324	0.00004	5
Density{site + year}	105.224	21.536	0.00002	7

Table 1.9. Estimated relative importance values, model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on gray-collared chipmunk densities at the Southwest Plateau study area, northern Arizona, 2000-2003.

Variable	Relative Importance	Level	Effect	SE	95% CI
Intercept	1.00000	-	0.019	0.059	(-0.095, 0.134)
Site	0.98229	Difference SP-A, SP-B	0.333	0.102	(0.133, 0.533)
		Difference SP-A, SP-C	0.060	0.067	(-0.071, 0.192)
Year	0.02881	Difference 2000, 2001	-0.002	0.007	(-0.016, 0.011)
		Difference 2000, 2002	-0.003	0.007	(-0.017, 0.012)
		Difference 2000, 2003	-0.005	0.012	(-0.029, 0.018)
Thin	0.99842	SP-A Thinned	-0.014	0.140	(-0.289, 0.261)
		SP-B Thinned	-0.177	0.111	(-0.394, 0.040)
		SP-C Thinned	0.968	0.237	(0.505, 1.432)

Table 1.10. Model selection results from weighted regression analysis of treatment effects on least chipmunk densities at the Jemez Mountains study area, northern New Mexico, 2001-2003. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K).

Model	AIC_c	ΔAIC_c	Weight	K
Density{site + thin}	65.895	0.000	0.47212	4
Density{thin}	67.988	2.093	0.16581	3
Density{site + thin + fire}	69.110	3.214	0.09464	5
Density{year + thin}	69.225	3.329	0.08935	5
Density{thin + fire}	69.878	3.983	0.06445	4
Density{site + year + thin}	70.286	4.391	0.05255	6
Density{site}	72.557	6.661	0.01689	3
Density{year + thin + fire}	72.630	6.734	0.01628	6
Density{constant}	73.863	7.968	0.00879	2
Density{site + year + thin + fire}	74.056	8.161	0.00798	7
Density{site + fire}	75.441	9.545	0.00399	4
Density{fire}	75.608	9.713	0.00367	3
Density{year}	77.062	11.167	0.00178	4
Density{site + year}	78.194	12.298	0.00101	5
Density{year + fire}	79.460	13.564	0.00054	5
Density{site + year + fire}	81.783	15.887	0.00017	6

Table 1.11. Estimated relative importance values, model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on least chipmunk densities at the Jemez Mountains study area, northern New Mexico, 2001-2003.

Variable	Relative Importance	Level	Effect	SE	95% CI
Intercept	1.00000	-	0.275	0.285	(-0.284, 0.833)
Site	0.64934	Difference JM-B, JM-C	-0.194	0.187	(-0.560, 0.172)
Year	0.16965	Difference 2001, 2002	0.044	0.088	(-0.129, 0.217)
		Difference 2001, 2003	-0.001	0.042	(-0.083, 0.081)
Thin	0.96317	Thinned	1.317	0.477	(0.382, 2.253)
Fire	0.19172	Wildfire	-0.021	0.077	(-0.171, 0.130)

Table 1.12. Model selection results from weighted regression analysis of treatment effects on total small mammal biomass at the Southwest Plateau study area, northern Arizona, 2000-2003. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K).

Model	AIC_c	ΔAIC_c	Weight	K
Biomass{site + thin}	8.978	0.000	0.72829	7
Biomass{site + year + thin}	11.650	2.672	0.19149	10
Biomass{site}	13.621	4.644	0.07144	4
Biomass{site + year}	17.816	8.838	0.00877	7
Biomass{constant}	34.457	25.479	0.00000	2
Biomass{thin}	37.625	28.647	0.00000	5
Biomass{year}	38.961	29.984	0.00000	5
Biomass{year + thin}	40.997	32.019	0.00000	8

Table 1.13. Estimated relative importance values, model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on small mammal biomass at the Southwest Plateau study area, northern Arizona, 2000-2003.

Variable	Relative Importance	Level	Effect	SE	95% CI
Intercept	1.00000	-	16.344	11.867	(-6.925, 39.593)
Site	1.00000	Difference SP-A, SP-B	96.417	15.238	(66.551, 126.283)
		Difference SP-A, SP-C	39.285	13.906	(12.030, 66.540)
Year	0.20027	Difference 2000, 2001	-4.737	8.438	(-21.275, 11.801)
		Difference 2000, 2002	-4.982	8.839	(-22.306, 12.342)
		Difference 2000, 2003	-6.751	11.787	(-29.854, 16.351)
Thin	0.91978	SP-A Thinned	6.520	23.913	(-40.349, 53.389)
		SP-B Thinned	-42.308	32.098	(-105.219, 20.604)
		SP-C Thinned	70.056	30.887	(9.517, 130.595)

Table 1.14. Model selection results from weighted regression analysis of treatment effects on total small mammal biomass at the Jemez Mountains study area, northern New Mexico, 2001-2003. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K).

Model	AIC_c	ΔAIC_c	Weight	K
Biomass{fire}	-100.831	0.000	0.28327	3
Biomass{year}	-100.125	0.706	0.19899	4
Biomass{thin + fire}	-98.869	1.962	0.10621	4
Biomass{site + fire}	-98.427	2.404	0.08515	4
Biomass{constant}	-98.388	2.443	0.08350	2
Biomass{year + thin}	-97.243	3.588	0.04710	5
Biomass{site + year}	-96.947	3.884	0.04062	5
Biomass{year + fire}	-96.942	3.889	0.04052	5
Biomass{site}	-96.358	4.474	0.03025	3
Biomass{thin}	-95.998	4.833	0.02528	3
Biomass{site + thin + fire}	-95.896	4.935	0.02402	5
Biomass{site + thin}	-94.017	6.814	0.00939	4
Biomass{year + thin + fire}	-93.981	6.851	0.00922	6
Biomass{site + year + thin}	-93.833	6.998	0.00856	6
Biomass{site + year + fire}	-93.347	7.485	0.00671	6
Biomass{site + year + thin + fire}	-89.935	10.897	0.00122	7

Table 1.15. Estimated relative importance values, model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on total small mammal biomass at the Jemez Mountains study area, northern New Mexico, 2001-2003.

Variable	Relative Importance	Level	Effect	SE	95% CI
Intercept	1.00000	-	130.776	98.079	(-61.459, 323.012)
Site	0.20592	Difference JM-B, JM-C	-3.467	31.474	(-65.157, 58.222)
Year	0.35294	Difference 2001, 2002	-43.312	50.083	(-141.475, 54.852)
		Difference 2001, 2003	4.519	44.701	(-83.094, 92.132)
Thin	0.23099	Thinned	59.137	139.482	(-214.248, 332.521)
Fire	0.55632	Wildfire	66.008	81.983	(-94.679, 226.694)

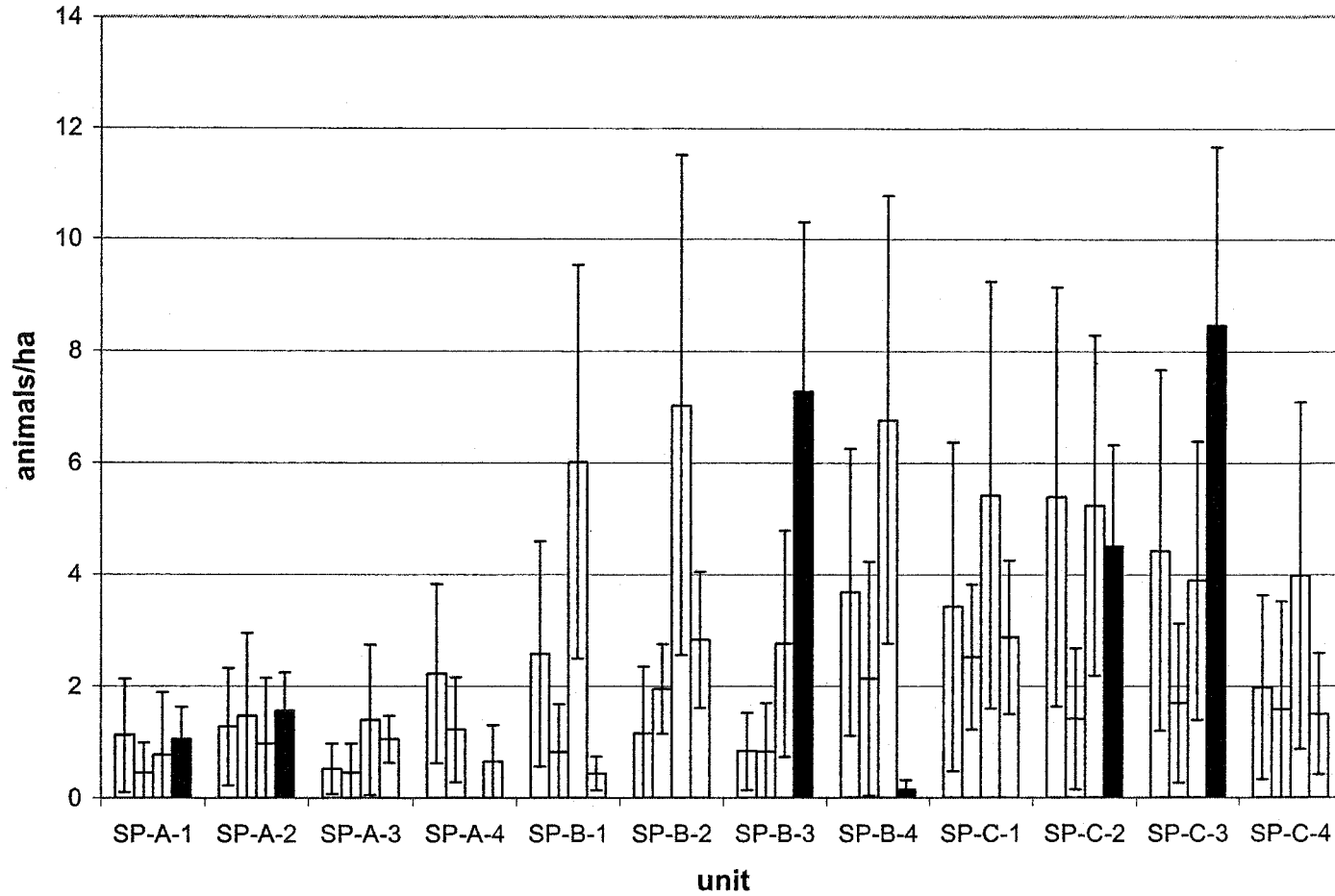


Figure 1.1. Density estimates and 95% confidence intervals for deer mice at the SP-A study site (units 1-4), the SP-B study site (units 1-4), and the SP-C study site (units 1-4) at the Southwest Plateau study area, northern Arizona. Bars within experimental unit groupings represent years 2000, 2001, 2002, and 2003 from left to right. Black bars represent thinned experimental units.

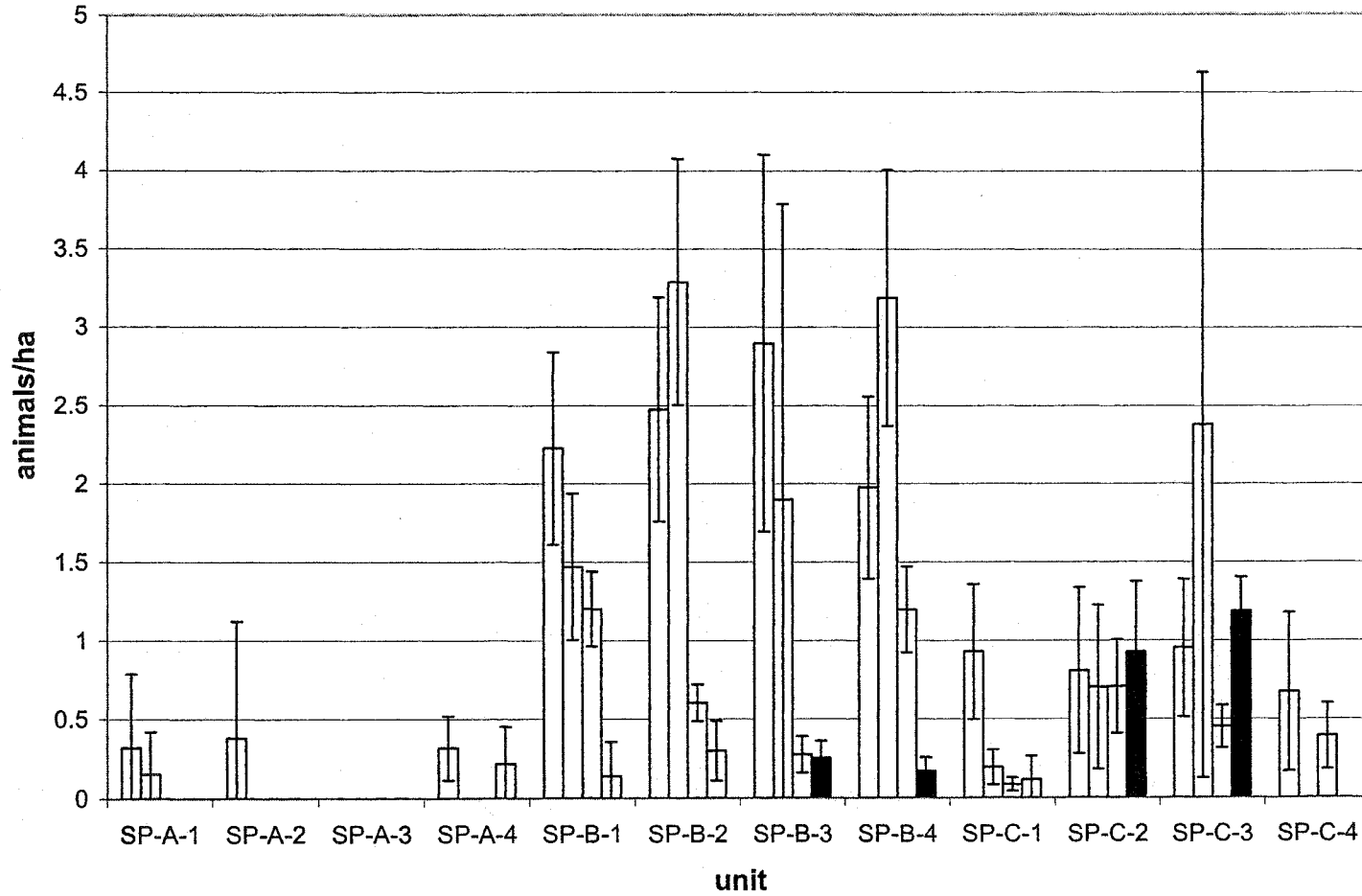


Figure 1.2. Density estimates and 95% confidence intervals for gray-collared chipmunks at the SP-A study site (units 1-4), the SP-B study site (units 1-4), and the SP-C study site (units 1-4) at the Southwest Plateau study area, northern Arizona. Bars within experimental unit groupings represent years 2000, 2001, 2002, and 2003 from left to right. Black bars represent thinned experimental units.

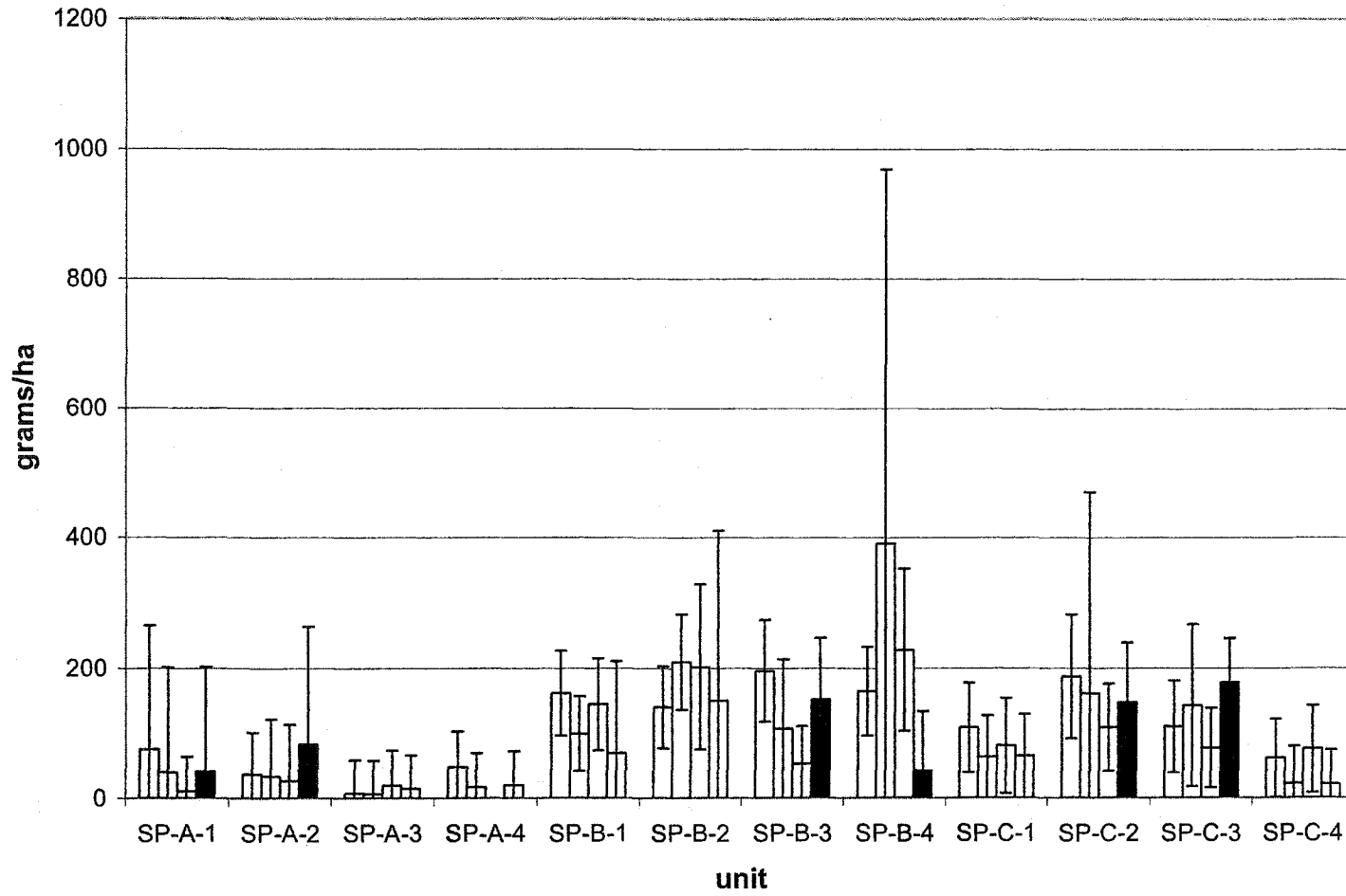


Figure 1.3. Estimates and 95% confidence intervals for total small mammal biomass at the SP-A study site (units 1-4), the SP-B study site (units 1-4), and the SP-C study site (units 1-4) at the Southwest Plateau study area, northern Arizona. Bars within experimental unit groupings represent years 2000, 2001, 2002, and 2003 from left to right. Black bars represent thinned experimental units.

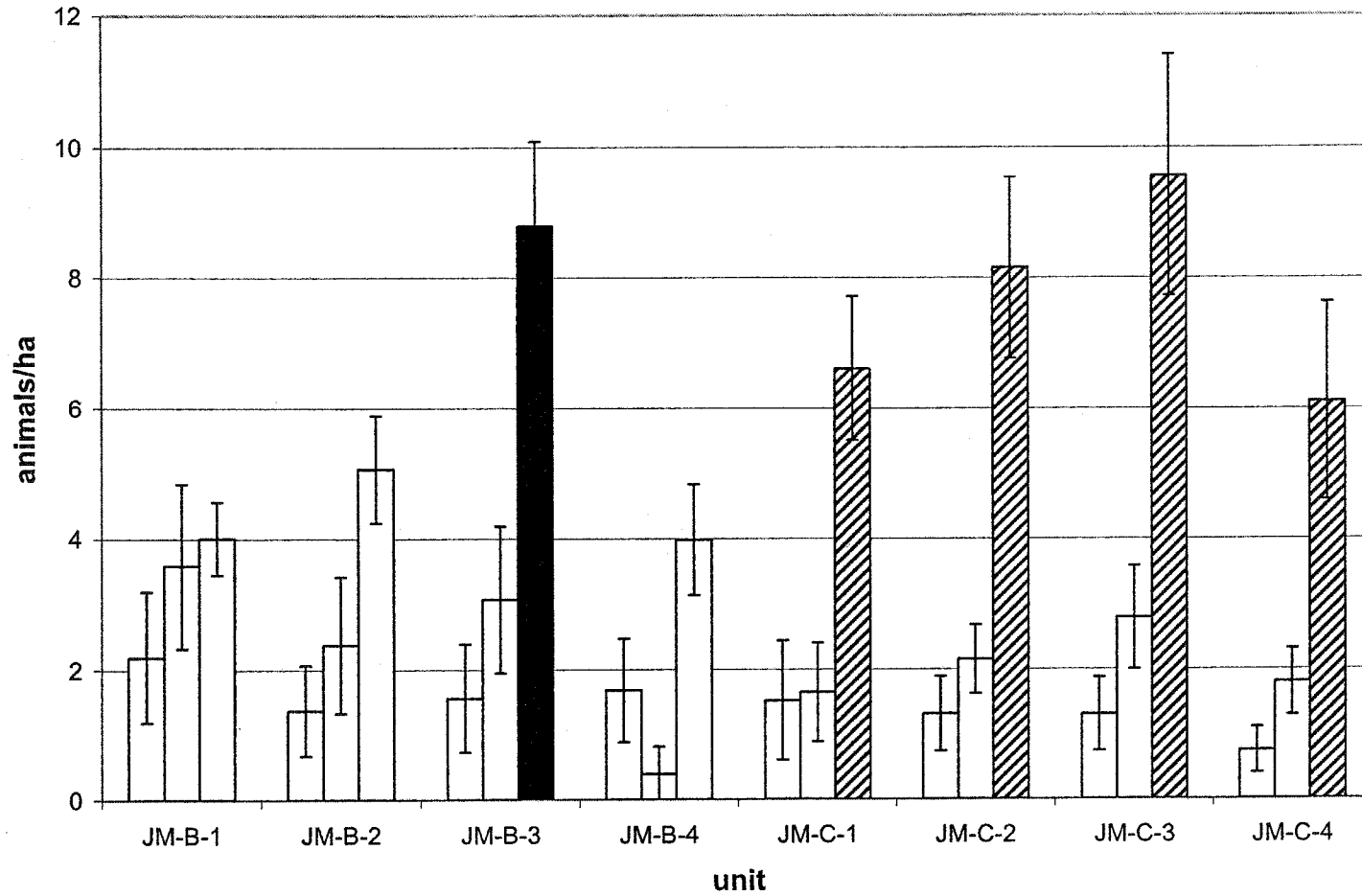


Figure 1.4. Density estimates and 95% confidence intervals for deer mice at the JM-B study site (units 1-4) and the JM-C study site (units 1-4) at the Jemez Mountains study area, northern New Mexico. Bars within experimental unit groupings represent years 2001, 2002, and 2003 from left to right. The black bar represents the thinned experimental unit and the striped bars represent burned experimental units.

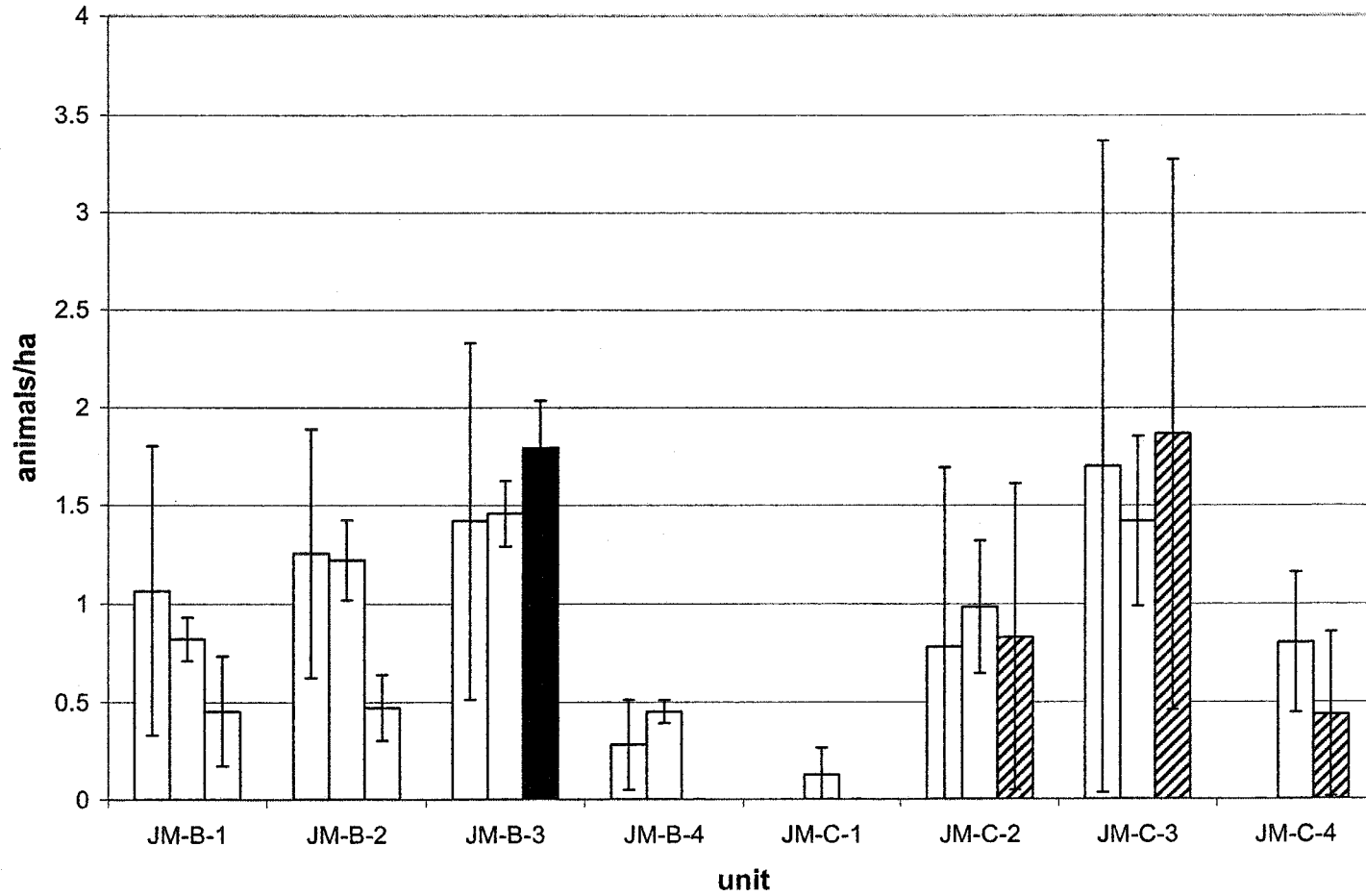


Figure 1.5. Density estimates and 95% confidence intervals for least chipmunks at the JM-B study site (units 1-4) and the JM-C study site (units 1-4) at the Jemez Mountains study area, northern New Mexico. Bars within experimental unit groupings represent years 2001, 2002, and 2003 from left to right. The black bar represents the thinned experimental unit and the striped bars represent burned experimental units.

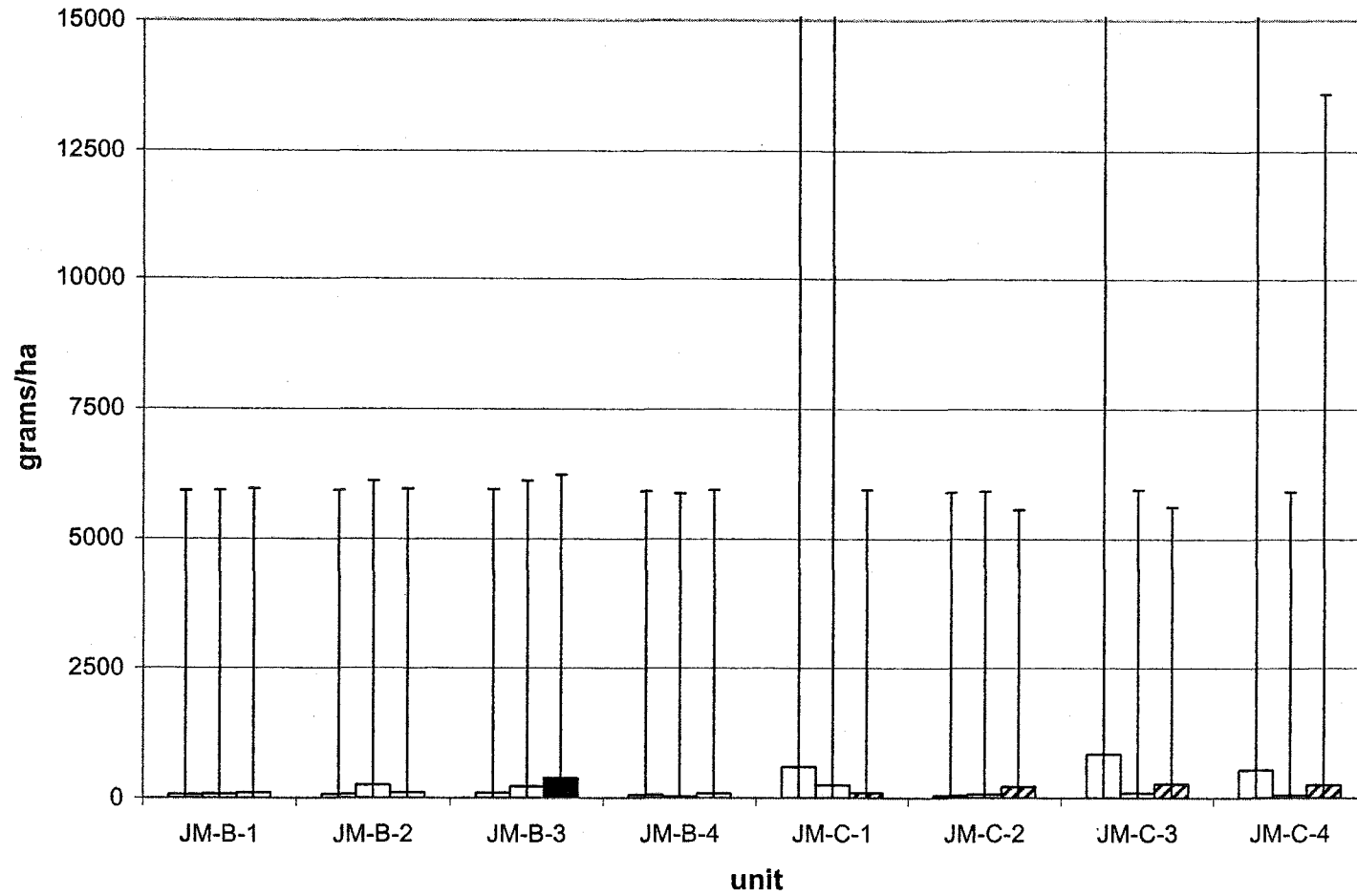


Figure 1.6. Estimates and 95% confidence intervals for total small mammal biomass at the JM-B study site (units 1-4) and the JM-C study site (units 1-4) at the Jemez Mountains study area, northern New Mexico. Bars within experimental unit groupings represent years 2001, 2002, and 2003 from left to right. The black bar represents the thinned experimental unit and the striped bars represent burned experimental units.

APPENDIX 1A:

**MODEL SELECTION RESULTS FROM MODELING OF CAPTURE PROBABILITIES AND MEAN MAXIMUM DISTANCE MOVED FOR
SMALL MAMMAL SPECIES CAPTURED ON FIRE AND FIRE SURROGATE PROGRAM STUDY AREAS IN NORTHERN ARIZONA AND
NORTHERN NEW MEXICO, USA**

Table 1A.1. Initial capture (p) and recapture probability (c) models and model selection results for Mexican woodrats at the Southwest Plateau study area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m.) = c (behavior)}	113.144	0.000	0.35294	3
{ p (a.m. + effort) = c (behavior)}	113.543	0.399	0.28913	4
{ p (a.m. + thin) = c (behavior)}	115.033	1.890	0.13722	4
{ p (a.m. + site) = c (behavior)}	116.390	3.246	0.06965	5
{ p (a.m. + year) = c (behavior)}	116.397	3.253	0.06938	5
{ p (a.m. + effort + site) = c (behavior)}	117.248	4.104	0.04534	6
{ p (a.m. + thin + site) = c (behavior)}	118.404	5.261	0.02543	6
{ p (a.m. + year + site) = c (behavior)}	120.098	6.954	0.01091	7

Table 1A.2. Initial capture (p) and recapture probability (c) models and model selection results for deer mice at the Southwest Plateau study area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m. + age + effort + year + site) = c (behavior)}	3200.887	0.000	0.50661	10
{ p (a.m. + age + effort + thin + year + site) = c (behavior)}	3202.873	1.986	0.18768	11
{ p (a.m. + age + effort + year) = c (behavior)}	3203.073	2.186	0.16979	8
{ p (a.m. + age + effort + thin + year) = c (behavior)}	3205.077	4.190	0.06235	9
{ p (a.m. + age + effort + session(year) + site) = c (behavior)}	3206.976	6.089	0.02413	14
{ p (a.m. + age + effort + year + unit) = c (behavior)}	3207.942	7.055	0.01488	19

Table 1A.3. Initial capture (p) and recapture probability (c) models and model selection results for golden-mantled ground squirrels at the Southwest Plateau study area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
$\{p \text{ (a.m. + year)} = c \text{ (behavior)}\}$	194.310	0.000	0.40748	6
$\{p \text{ (a.m. + thin + year)} = c \text{ (behavior)}\}$	195.342	1.032	0.24325	7
$\{p \text{ (a.m. + age + year)} = c \text{ (behavior)}\}$	195.841	1.531	0.18953	7
$\{p \text{ (a.m. + age + thin + year)} = c \text{ (behavior)}\}$	196.695	2.385	0.12368	8

Table 1A.4. Initial capture (p) and recapture probability (c) models and model selection results for gray-collared chipmunks at the Southwest Plateau study area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
$\{p \text{ (a.m. + age + effort + thin + session(year) + unit) = } c \text{ (behavior)}\}$	3199.840	0.000	0.49517	23
$\{p \text{ (a.m. + age + effort + thin + session(year)) = } c \text{ (behavior)}\}$	3201.832	1.991	0.18296	15
$\{p \text{ (a.m. + age + effort + thin + session(year) + site) = } c \text{ (behavior)}\}$	3201.872	2.032	0.17926	15
$\{p \text{ (a.m. + age + thin + session(year) + unit) = } c \text{ (behavior)}\}$	3204.719	4.879	0.04319	22
$\{p \text{ (a.m. + age + effort + session(year) + unit) = } c \text{ (behavior)}\}$	3205.526	5.686	0.02885	22
$\{p \text{ (a.m. + age + effort + thin + unit) = } c \text{ (behavior)}\}$	3206.190	6.350	0.02070	16
$\{p \text{ (a.m. + age + effort + session(year)) = } c \text{ (behavior)}\}$	3206.402	6.562	0.01861	12

Table 1A.5. Initial capture (p) and recapture probability (c) models and model selection results for cliff chipmunks at the Southwest Plateau study area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m.) = c (behavior)}	92.601	0.000	1.00000	3

Table 1A.6. Initial capture (p) and recapture probability (c) models and model selection results for long-tailed voles at the Jemez Mountains study area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight. Behavioral effects of capture were not estimable so were omitted.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m.) = c }	131.269	0.000	0.72338	2
{ p (a.m. + age) = c }	133.192	1.923	0.27662	3

Table 1A.7. Initial capture (p) and recapture probability (c) models and model selection results for Mexican woodrats at the Jemez Mountains study area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m. + age + year) = c (behavior)}	151.774	0.000	0.27512	6
{ p (a.m. + age + thin + year) = c (behavior)}	152.464	0.690	0.19484	7
{ p (a.m. + thin + year) = c (behavior)}	152.533	0.760	0.18817	6
{ p (a.m. + year) = c (behavior)}	153.338	1.564	0.12585	5
{ p (a.m. + thin + year + unit) = c (behavior)}	154.026	2.252	0.08921	10
{ p (a.m. + year + unit) = c (behavior)}	155.992	4.219	0.03338	9
{ p (a.m. + age + thin + year + unit) = c (behavior)}	156.158	4.384	0.03072	11
{ p (a.m. + age + year + unit) = c (behavior)}	156.853	5.080	0.02170	10
{ p (a.m. + thin) = c (behavior)}	157.646	5.873	0.01460	4
{ p (a.m.) = c (behavior)}	158.012	6.238	0.01216	3

Table 1A.8. Initial capture (p) and recapture probability (c) models and model selection results for deer mice at the Jemez Mountains study area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m. + age + fire + year + site) = c (behavior)}	4162.729	0.000	0.36643	8
{ p (a.m. + age + fire + thin + year + site) = c (behavior)}	4163.170	0.441	0.29392	9
{ p (a.m. + age + fire + session(year) + site) = c (behavior)}	4164.444	1.716	0.15540	11
{ p (a.m. + age + fire + thin + session(year) + site) = c (behavior)}	4165.763	3.034	0.08037	12
{ p (a.m. + age + fire + year) = c (behavior)}	4168.000	5.271	0.02626	7
{ p (a.m. + age + fire + thin + year) = c (behavior)}	4168.462	5.733	0.02084	8
{ p (a.m. + age + fire + year + unit) = c (behavior)}	4169.135	6.406	0.01489	14
{ p (a.m. + age + fire + thin + year + unit) = c (behavior)}	4169.340	6.611	0.01344	15
{ p (a.m. + age + fire + session(year)) = c (behavior)}	4169.611	6.882	0.01174	10

Table 1A.9. Initial capture (p) and recapture probability (c) models and model selection results for golden-mantled ground squirrels at the Jemez Mountains study area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m.) = c (behavior)}	81.509	0.000	0.35369	3
{ p (a.m. + fire) = c (behavior)}	82.299	0.790	0.23829	4
{ p (a.m. + age) = c (behavior)}	83.459	1.950	0.13344	4
{ p (a.m. + year) = c (behavior)}	83.920	2.410	0.10599	5
{ p (a.m. + age + fire) = c (behavior)}	84.311	2.801	0.08716	5
{ p (a.m. + age + year) = c (behavior)}	86.130	4.621	0.03509	6
{ p (a.m. + fire + year) = c (behavior)}	86.137	4.627	0.03498	6
{ p (a.m. + age + fire + year) = c (behavior)}	88.387	6.878	0.01135	7

Table 1A.10. Initial capture (p) and recapture probability (c) models and model selection results for least chipmunks at the Jemez Mountains study area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
$\{p(\text{a.m.} + \text{thin} + \text{session}(\text{year}) + \text{site}) = c(\text{behavior})\}$	1695.219	0.000	0.40672	10
$\{p(\text{a.m.} + \text{fire} + \text{thin} + \text{session}(\text{year}) + \text{site}) = c(\text{behavior})\}$	1696.950	1.731	0.17121	11
$\{p(\text{a.m.} + \text{age} + \text{thin} + \text{session}(\text{year}) + \text{site}) = c(\text{behavior})\}$	1697.241	2.022	0.14799	11
$\{p(\text{a.m.} + \text{thin} + \text{year} + \text{site}) = c(\text{behavior})\}$	1698.614	3.395	0.07450	7
$\{p(\text{a.m.} + \text{fire} + \text{thin} + \text{year} + \text{site}) = c(\text{behavior})\}$	1698.933	3.714	0.06351	8
$\{p(\text{a.m.} + \text{age} + \text{fire} + \text{thin} + \text{session}(\text{year}) + \text{site}) = c(\text{behavior})\}$	1698.969	3.750	0.06239	12
$\{p(\text{a.m.} + \text{age} + \text{thin} + \text{year} + \text{site}) = c(\text{behavior})\}$	1699.763	4.544	0.04194	8
$\{p(\text{a.m.} + \text{age} + \text{fire} + \text{thin} + \text{year} + \text{site}) = c(\text{behavior})\}$	1700.439	5.220	0.02991	9

Table 1A.11. Mean maximum distance moved (MMDM) models and model selection results for Mexican woodrats ($n = 5$) at the Southwest Plateau study area. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{MMDM (constant)}	50.201	0.000	1.00000	2

Table 1A.12. Mean maximum distance moved (MMDM) models and model selection results for deer mice ($n = 249$) at the Southwest Plateau study area. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{MMDM (effort)}	2076.831	0.000	0.30501	3
{MMDM (year)}	2076.904	0.073	0.29410	5
{MMDM (constant)}	2077.241	0.410	0.24846	2
{MMDM (thin)}	2078.726	1.895	0.11828	3
{MMDM (site)}	2081.241	4.410	0.03362	4

Table 1A.13. Mean maximum distance moved (MMDM) models and model selection results for golden-mantled ground squirrels ($n = 13$) at the Southwest Plateau study area. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{MMDM (constant)}	114.157	0.000	0.76076	2
{MMDM (effort)}	116.471	2.314	0.23924	3

Table 1A.14. Mean maximum distance moved (MMDM) models and model selection results for gray-collared chipmunks ($n = 206$) at the Southwest Plateau study area. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{MMDM (thin)}	1689.955	0.000	0.31410	3
{MMDM (year)}	1690.100	0.145	0.29215	5
{MMDM (effort)}	1690.859	0.904	0.19986	3
{MMDM (constant)}	1691.237	1.282	0.16546	2
{MMDM (site)}	1694.759	4.804	0.02843	4

Table 1A.15. Mean maximum distance moved (MMDM) models and model selection results for cliff chipmunks ($n = 4$) at the Southwest Plateau study area. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{MMDM (constant)}	51.348	0.000	1.00000	2

Table 1A.16. Mean maximum distance moved (MMDM) models and model selection results for long-tailed voles ($n = 5$) at the Jemez Mountains study area. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{MMDM (constant)}	34.631	0.000	1.00000	2

Table 1A.17. Mean maximum distance moved (MMDM) models and model selection results for Mexican woodrats ($n = 13$) at the Jemez Mountains study area. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{MMDM (constant)}	102.440	0.000	0.58499	2
{MMDM (year)}	103.127	0.687	0.41501	4

Table 1A.18. Mean maximum distance moved (MMDM) models and model selection results for deer mice ($n = 408$) at the Jemez Mountains study area. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{MMDM (year)}	3141.492	0.000	0.98256	4

Table 1A.19. Mean maximum distance moved (MMDM) models and model selection results for golden-mantled ground squirrels ($n = 5$) at the Jemez Mountains study area. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{MMDM (constant)}	44.814	0.000	0.99995	2

Table 1A.20. Mean maximum distance moved (MMDM) models and model selection results for least chipmunks ($n = 104$) at the Jemez Mountains study area. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{MMDM (year)}	830.441	0.000	0.000	4
{MMDM (thin)}	832.378	1.937	1.937	3
{MMDM (constant)}	835.652	5.211	5.211	2
{MMDM (site)}	836.752	6.311	6.311	3
{MMDM (fire)}	837.157	6.716	6.716	3

CHAPTER 2:
**SMALL MAMMAL POPULATION AND HABITAT RESPONSES TO VARIABLE-INTENSITY
FOREST THINNING AND PRESCRIBED FIRE IN NORTHERN ARIZONA, USA**

INTRODUCTION

Changes in the structure and function of ponderosa pine (*Pinus ponderosa*) forests of the southwestern United States (USA) have been documented and discussed extensively, with concerns over these changes increasing during the last decade (Cooper 1960, Dodge 1972, Covington and Moore 1994, Fulé et al. 1997, Mast et al. 1999, Allen et al. 2002). Historical data indicate that in the period before Euro-American settlement of the southwestern USA, ponderosa pine forests in the region experienced relatively frequent ground fires of predominantly low to moderate severity (Moore et al. 1999). This disturbance pattern resulted in open stands of ponderosa pine with rich herbaceous understories. Changes in land use and management in the southwestern USA since Euro-American settlement in the mid-nineteenth century, including extensive fire suppression, grazing, and logging, are believed to have resulted in increased tree densities, loss of the open structure of forests, declines in the biomass of herbaceous understories, and increased risk of high-severity wildfire (Cooper 1960, Savage and Swetnam 1990, Covington and Moore 1994, Arno et al. 1995).

Researchers and managers have developed fuel reduction treatments, frequently consisting of mechanical removal (i.e., thinning) of smaller trees followed by prescribed burning, to reduce the risk of high-severity wildfire in southwestern ponderosa pine forests (Covington et al. 1997; Lynch et al. 2000; Fulé et al. 2001a,b). These treatments appear to be effective in reducing high-severity wildfire risk (Fulé et al. 2001a,b; Martinson and Omi 2002; Pollet and Omi 2002). The ecological impacts of such treatments, however, are more difficult to assess. In some cases, fuel reduction treatments are billed as forest restoration techniques in that they are designed to replicate what is known about pre-EuroAmerican settlement (hereafter, pre-Euro-settlement) forest conditions (Covington et al. 1997, Moore et al. 1999,

Lynch et al. 2000). Implicit in the use of forest restoration as an ecological management approach is the assumption that restoration of historic forest conditions will provide for current forest ecological values, such as native wildlife diversity. Assessing this assumption is critical to a careful evaluation of restoration as a method for maintaining forest ecological values, especially in light of changing climatic conditions and introduction of exotic species since EuroAmerican settlement (Wagner et al. 2000).

Information about fuel reduction/restoration treatment effects on small mammal communities in southwestern ponderosa pine forests is necessary for an understanding of broader ecological responses to treatments. Small mammals impact 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 mammal populations are food sources for predator populations in southwestern forests (e.g., Mexican spotted owls, *Strix occidentalis lucida*, and northern goshawks, *Accipiter gentilis*; Ward and Block 1995, Reynolds et al. 1996, Sureda and Morrison 1998, Long and Smith 2000, Ward 2001, Block et al. 2005). Before managers adopt particular restoration or fuel reduction treatments, it is necessary to understand the potential impacts on small mammal habitats and populations.

Unfortunately, much of the existing information on small mammal responses to forest thinning and prescribed fire is limited in its inferential strength. Most examinations of forest management impacts on small mammals are based on indices of abundance (e.g., Tester 1965, Bock and Bock 1983, Masters et al. 1998, Steventon et al. 1998, Wilson and Carey 2000, Carey 2001). Inference from abundance indices requires the assumption that the probability of detecting animals is constant across space, time, and treatment (Nichols 1992, Anderson 2001). However, both thinning and fire influence detection probabilities and movements of small mammals (Chapter 1) as would be expected with major changes in habitat structure. Therefore, the use of indices will result in biased estimates of treatment effects, and methods, such as mark-recapture, for estimating true abundance or density are necessary for valid inference.

Small mammal communities in southwestern ponderosa pine are dominated by 2 taxa, including deer mice (*Peromyscus maniculatus*) and one of several species of chipmunks (*Tamias* spp.). Deer mice are small (12-20 g) nocturnal murid rodents with omnivorous habits. Deer mice are common throughout much of North America and are found frequently in early successional habitats (Fitzgerald et al. 1994).

The chipmunk species considered in this study, the gray-collared chipmunk (*Tamias cinereicollis*), is native to Arizona and New Mexico. It is a medium-sized (20-70 g) omnivorous diurnal sciurid rodent that inhabits open woodlands (Hilton and Best 1993). Important habitat components for both deer mouse and chipmunk populations include herbaceous vegetation, which provides seed and vegetation food sources (Ahlgren 1966, Goodwin and Hungerford 1979, Kyle and Block 2000, Wilson and Carey 2000), and forest floor woody debris, which is used for nesting and travel cover and as a source of invertebrate foods (Hayes and Cross 1987, Graves et al. 1988, Hilton and Best 1993, Bowman et al. 2000, Carey and Harrington 2001).

High herbaceous density is related to lower tree density in southwestern ponderosa pine forests (Clary 1975, Moore and Deiter 1992), presumably due to increased light, water, and nutrient availability under sparser tree canopies, and while burning may reduce herbaceous cover in the immediate aftermath of fire, there is evidence that herbaceous vegetation quickly recovers to greater than pre-fire levels after prescribed burns (Bock and Bock 1983, Harris and Covington 1983, Oswald and Covington 1983, Oswald and Covington 1984). Thus, increases in herbaceous cover with thinning and prescribed burning treatments are expected. Woody debris will be influenced by treatments – post-thinning slash should increase the amount of available woody debris immediately after thinning to a variable degree, depending on whether slash is removed, piled, or scattered. Prescribed fire is expected to result in immediate reductions in woody debris (Covington and Sackett 1984, Arno et al. 1995), but high spatial variability in woody debris availability may result, depending on fire behavior and severity and initial woody debris loadings. There is a need for better information on how forest thinning and prescribed fire treatments influence these components of small mammal habitat, and whether changes in these components alone allow prediction of changes in small mammal populations.

Positive responses to forest thinning treatments have been demonstrated for both chipmunks (Carey 2000, Carey 2001, Carey and Wilson 2001, Sullivan et al. 2001, Hadley and Wilson 2004, Chapter 1) and deer mice (Carey and Wilson 2001, Suzuki and Hayes 2003, Chapter 1), as have positive responses of deer mice to prescribed fire (Tester 1965, Ahlgren 1966, Bock and Bock 1983). Much less is known about potential responses to treatments of 2 other small mammal species in southwestern ponderosa pine forests: golden-mantled ground squirrels (*Spermophilus lateralis*) and Mexican woodrats (*Neotoma*

mexicana). Golden-mantled ground squirrels are large (120-300 g), diurnal sciurids native to the western USA and southwestern Canada; they are omnivorous and inhabit meadows, shrublands, open woodlands, and disturbed forest (Goodwin and Hungerford 1979, Bartels and Thompson 1993, Fitzgerald et al. 1994). Given golden-mantled ground squirrels' use of relatively open woodlands, positive responses to fuel reduction/restoration treatments appear likely. Mexican woodrats are medium-sized (70-200 g) nocturnal murid rodents with omnivorous habits, inhabiting the southwestern USA, Mexico, and Central America. This woodrat species appears to be most closely linked with the presence of certain physical characteristics of habitats such as rocky slopes and outcrops (Cornely and Baker 1986, Fitzgerald et al. 1994, Sureda and Morrison 1999, Ward 2001, Block et al. 2005) but has also been linked positively with woody debris volume (Ward 2001) and shrubs (Sureda and Morrison 1999, Ward 2001, Block et al. 2005). Relationships of any of these 4 small mammal species to variable disturbance intensity, e.g., variable intensity thinning, are not known.

I considered small mammal habitat and population responses to fuel reduction/restoration treatments in southwestern ponderosa pine forests. The objectives of the study were to examine the effects of restoration treatments on critical components of small mammal habitat 2 to 3 years after treatments were completed, where treatments consisted of variable-intensity thinning followed by prescribed burning, and to investigate how treatments and habitat components influenced small mammal population densities over the same time period.

STUDY AREA

The Fort Valley Study Area (FVSA) was located on and proximal to the Fort Valley Experimental Forest, Coconino National Forest, northwest of Flagstaff, Arizona, USA, at 35° N, 111° W. The FVSA was located at 2,300 m elevation with flat to gently rolling topography. A small drainage was located in experimental units 5 and 6, with steep stream banks and associated rocky outcrops. Ponderosa pine dominated the canopy in the FVSA, with only an occasional southwestern white pine (*Pinus strobiformis*) or tree-sized Gambel's oak (*Quercus gambelii*). Understory shrubs were sparse, but the most common species were Wood's rose (*Rosa woodsii*) and buckbrush (*Ceanothus fendleri*).

Three replicate blocks, or sites, comprised the FVSA, and each site in turn consisted of 4 experimental units. The experimental units were 14.2 ha (35 acres) in size. An experimental unit at each

site was assigned randomly to a control and to each of 3 treatments (described below). At site 1, experimental units 1-4 were contiguous; at site 2, units 5-7 were contiguous, but not contiguous with unit 8; and at site 3, experimental units 9-12 were not contiguous. Experimental units within all of the sites were < 1.5 km from each other. Fulé et al. (2001a) provide further description of the study area.

METHODS

Treatments

Fuel reduction/restoration treatments were designed and described by Fulé et al. (2001a). Thinning activities were based around remnant (i.e., living or evidence of dead) pre-Euro-settlement trees. All living trees of pre-Euro-settlement origin in the experimental units were recorded; trees were presumed to be of pre-Euro-settlement origin if they were of large size and had yellowed bark (ponderosa pine bark changes from black to yellow as trees age). Also, snags, logs, and stumps of pre-Euro-settlement origin were recorded. Then, a 9.1 m- (30 ft) or, if that area was inadequate, an 18.3 m- (60 ft) radius area was searched around each remnant. Post-Euro-settlement trees were retained in that area as follows: for the 1.5-2 treatment, 1.5 trees (i.e., 3 trees for every 2 pre-Euro-settlement remnants) ≥ 40.6 cm (16 in) diameter at breast height (dbh) or 3 trees < 40.6 cm dbh were retained; in the 2-4 treatment, 2 trees ≥ 40.6 cm dbh or 4 trees < 40.6 cm dbh were retained; and in the 3-6 treatment, 3 trees ≥ 40.6 cm dbh or 6 trees < 40.6 cm dbh were retained. All living remnants were also retained. Therefore, the 1.5-2 treatment represented nominally the largest reduction in post-Euro-settlement trees, followed by the 2-4 treatment, and then the 3-6 treatment.

Thinning was conducted during 1999, but all treated experimental units were not completed simultaneously. By the time of small mammal trapping in 1999 (late summer), all thinning was complete (defined as all activity completed except for road blading and closure) except for on experimental unit 5 and half of experimental unit 6. These units were completed in the fall of 1999. Treatment units were then prescribed burned during the spring of 2000 (units 1, 2, and 4) and the spring of 2001 (units 5, 6, 7, 10, 11, and 12). Control units (3, 8, and 9) received neither thinning nor burning.

Treatment of slash from thinning operations differed by site because of the use of different thinning contractors and resulting differences in thinning methods used. At sites 1 and 2, slash was chopped and scattered, while at site 3, slash was piled.

Habitat Sampling and Variable Construction

All sampling (i.e., habitat sampling and small mammal trapping) was conducted at 2 sampling grids located in each of the experimental units. Grids were placed at least 50 m from the experimental unit boundaries and at least 100 m from the other sampling grid within the experimental unit. The location of sampling grids was constant throughout the study. Grids consisted of 22 sampling stations, arranged in 2 parallel lines spaced 20 m apart, each with 11 sampling stations also placed 20 m apart – thus yielding a sampling grid of nominally 20 m x 200 m, or 0.4 ha.

Five-m radius habitat plots were centered on each of the sampling stations. Pre-treatment vegetation sampling was conducted from mid October to early December in 1998 and post-treatment sampling was conducted from late September to early November in 2003. All trees in the habitat plots were tallied; trees were defined as woody plants taller than 2 m with dbh \geq 10 cm. Additionally, each log \geq 2 m in length and with a midpoint diameter \geq 10 cm was measured, including its length and diameter. A random transect 10 m long was placed across the diameter of the habitat plot, and point intercept data were recorded at 1-m intervals on characteristics of ground and tree cover, including grasses, forbs, rocks, lichens, moss, woody debris, dung, litter and woody vegetation cover.

Metrics calculated based on the habitat sampling data included percent change in the number of trees from 1998 to 2003, which served as a measure of thinning intensity, as well as 2 metrics relating to small mammal habitat, including percent change in herbaceous vegetation from 1998 to 2003, and percent change in woody debris volume from 1998 to 2003. The number of trees was assessed by averaging the number of trees in each of the 22 habitat plots within a sampling grid. An index of herbaceous vegetation was constructed by summing the number of points on each of the 10-m point intercept transects that intersected either a grass or a forb, then averaging these counts over each sampling grid. Woody debris calculations for a sampling grid were based on the average volume of logs in the habitat plots; volume was calculated by assuming that logs were cylindrical. I assessed the percent change in each metric by averaging the grid values over the 2 grids within an experimental unit, and computing the percent change in the metric for that unit as

$$\frac{2003 \text{ Metric} - 1998 \text{ Metric}}{1998 \text{ Metric}} \quad (1)$$

Inference was based on the experimental unit scale, rather than the sampling grid scale, to avoid problems of pseudoreplication (Hurlbert 1984). For each metric, the standard error of the percent change was calculated based on a delta-method transformation of the standard error of the original data (Seber 2002), and 95% confidence intervals were constructed in order to examine differences in the metrics between treated and control units and across treatment intensities.

Small Mammal Trapping

Small mammal trapping was conducted at each of the sampling grids. One large (7.6 x 8.9 x 22.9 cm) and 1 extra-large (10.2 x 11.4 x 38.1 cm) folding Sherman live-trap were placed in the vicinity of each sampling station, for a total of 44 traps per sampling grid. Traps were positioned along small mammal trails, at the openings of burrow holes, and/or in proximity to rocks or woody debris. A wood shingle was used to shade and insulate traps. Cotton batting was placed at the back of each trap for insulation, and approximately 20 mL of a bait mixture of rolled oats and chicken feed was placed in each trap, with an additional small amount of bait placed outside trap entrances.

Small mammal trapping was conducted from 2 September to 5 October in 1998, from 16 September to 19 October in 1999, from 28 August to 29 September in 2001, from 10 September to 8 October in 2002, and from 9 September to 10 October in 2003 during 3 trapping sessions in each year. Sampling grids were randomly selected for trapping during 1 of the 3 trapping sessions, with the 2 trapping grids within each experimental unit precluded from being trapped in the same session. Trapping sessions were terminated once approximately 90% of the captured animals on a trapping occasion were recaptures, yielding trapping sessions of between 8 and 11 trapping occasions (i.e., 4 to 5.5 days of 2 trapping occasions per day). Because thinning was not completed as of the beginning of trapping in 1999, experimental unit 5 was not trapped and only the completed half (i.e., 1 sampling grid) of experimental unit 6 was trapped in 1999. No trapping was conducted during 2000, complete post-treatment sampling was conducted in 2001-2003.

Traps were checked in the morning and afternoon, and the following data were recorded: trap location and size, species, new or recapture, individual identity, age class, sex, mass, and release condition. Animals were individually identified with 2 unique ear tags.

Small Mammal Data Analysis

The estimation and modeling of small mammal densities is similar to that described in Chapter 1. Inference was based on estimates of true density, rather than on indices of abundance in which changes in detection probabilities across time, space, and treatments are ignored (Nichols 1992, Anderson 2001, Chapter 1). First, I estimated abundance for each species each year (1998-1999, 2001-2003) in each sampling grid, based on the mark-recapture data. Second, I estimated effective trapping area at the same scale as for abundance. Third, I calculated species' densities and variance-covariance matrices at a unit scale in each year (1998-1999, 2001-2003), by combining abundance and area to calculate density (individuals per ha) and then averaging density estimates over the 2 trapping grids in each experimental unit. Finally, I modeled unit-scale densities from the first and last years of the study (1998 and 2003) with weighted least-squares regression analyses as a function of year, site, treatment, and habitat variables. I calculated species densities based on the trapping data from all years to increase the precision of estimates, but I conducted density modeling based on only the 1998 and 2003 density estimates because my primary interest was in linking densities to the habitat variables which were measured in those years.

Throughout the analyses, I employed an information-theoretic philosophy of model selection with a focus on multi-model 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). Before the analysis was begun, statistical model sets were specified (i.e., *a priori*), to strengthen inference (Anderson et al. 2001).

Abundance Estimation.—Abundance estimates for each sampling grid in each year of trapping were obtained through analysis of the mark-recapture data using the Huggins conditional likelihood model (Huggins 1989, 1991). The Huggins conditional likelihood model provides for estimation of detection probabilities under the assumption of population closure, and allows for behavioral responses to capture, time effects on detection probabilities, and individual heterogeneity in detection probabilities through inclusion of individual covariates (Model M_{ibh} ; Otis et al. 1978). The Huggins conditional likelihood estimates initial capture ($p_i, i = 1, \dots, t$) and recapture rates ($c_i, i = 2, \dots, t$) for t occasions based on animal encounter histories and uses these rates to generate estimates of abundance, as

$$\hat{N} = \frac{M_{t+1}}{1 - (1 - \hat{p}_1)(1 - \hat{p}_2) \dots (1 - \hat{p}_t)}, \quad (2)$$

where M_{t+1} is the number of unique individuals marked on a grid during t trapping occasions, i.e., the minimum known population size, and p_t is the estimate of initial capture rate for occasion t .

I used age class as an individual covariate to account for individual heterogeneity in detection probabilities. I classified animals as either adults or subadults based on mass and external evidence of reproductive status (McCravy and Rose 1992). Deer mice were defined as adults when ≥ 14 g, gray-collared chipmunks when ≥ 50 g, Mexican woodrats when ≥ 100 g, and golden-mantled ground squirrels when ≥ 150 g, based on field observations and information in the literature (Hilton and Best 1993, Fitzgerald et al. 1994).

Estimation of abundance was conducted in Program MARK 3.2 (White and Burnham 1999). I proposed several *a priori* models of detection probabilities. Effects in models of detection probability included 2 that were in all models based on *a priori* considerations: behavioral responses to capture and time of day (i.e., a.m. versus p.m. trap check). Additional effects considered were age of animal, year, experimental unit, and 2 variables to estimate the effects of treatments on detection probabilities. The first of these variables was a bivariate prescribed fire effect (applied on all treatment units beginning in 2001). The second of these variables was the average number of trees per habitat plot, where the average was calculated for each experimental unit. The number of trees variable was used to model changes in habitat conditions due to thinning. Because reduction in the number of trees was primarily due to thinning activities (prescribed fire did not result in tree mortalities), this variable represented an estimate of thinning intensity. Thus, 1998 measures of the number of trees were applied to estimation of detection probability in 1998, and 2003 measures of the number of trees were applied in all subsequent years, i.e., all years post-thinning. I further modeled an interaction effect between treatment (fire * number of trees) and post-treatment year (i.e., the interaction effect applied in 2001-2003). A total of 36 abundance models were considered.

Abundance estimation was conducted for each of the 4 marked species. Estimates from each model were checked and models that produced nonsensical estimates (i.e., estimates on the order of hundreds or thousands of individuals on a single trapping grid) were deleted. Such nonsensical estimates

occur under the Huggins conditional likelihood when effects in the models are not estimable or are poorly estimable. I model-averaged abundance estimates and variance-covariance matrices across the remaining models. Model-averaged abundance estimates were computed based on Akaike weights as described in Burnham and Anderson (2002) and model-averaged variance-covariance matrices were computed based on Burnham and Anderson (2004).

Effective Trapping Area.—I used the mean maximum distance moved (MMDM) method to estimate effective trapping area (Wilson and Anderson 1985), the area to which an abundance estimate applies. I calculated the maximum distance moved between any 2 traps for each marked animal with ≥ 2 captures in a given sampling grid in a given year. I specified regression models (PROC REG; SAS Institute 2003) to determine model weights and estimate values of MMDM. Only single parameter models were considered, including MMDM as a constant value across sampling grids and years, and as a function of year, experimental unit, fire, number of trees, and the interaction between treatment (fire * number of trees) and post-treatment year, for a total of 6 regression models of MMDM. Fewer, less complex models were considered than in the abundance analysis because less information is available in the mark-recapture data to estimate movements as compared to detection probabilities (Chapter 1). I computed AIC_c for each of the regression models (Burnham and Anderson 2002). I then calculated a vector of MMDM estimates under each model across the sampling grids and years based on the regression coefficients, along with a variance-covariance matrix across the grids and years based on a delta-method transformation of the variance-covariance matrix of the regression coefficients (Seber 2002). I then calculated effective trapping area under each model by adding a buffer strip with a width of one-half the model-averaged MMDM to the area of each trapping grid (Otis et al. 1978, Wilson and Anderson 1985), and calculated the variance-covariance matrix of effective trap area under each model using a delta-method transformation of the MMDM variance-covariance matrix, which was then converted from m^2 to ha. Finally, I model-averaged the vectors of effective trapping area and their variance-covariance matrices across all models, as described in Burnham and Anderson (2002).

Densities and Variance-Covariance Matrices.—Species-specific densities were calculated on each sampling grid in each year as the abundance divided by the effective trapping area for that grid. These estimates were then averaged across the 2 sampling grids in each experimental unit to calculate the average

density within an experimental unit in each year. A series of delta-method transformations was used to convert the variance-covariance matrices of abundance and effective trapping area at the grid scale to a variance-covariance matrix of density at the experimental unit scale (Seber 2002). Inference was based on the unit scale, rather than the grid scale, as noted for the habitat analysis, to avoid problems of pseudoreplication (Hurlbert 1984).

Weighted regression analysis cannot be conducted with variances of 0 because the variance-covariance matrix is singular. Variances of 0 occurred in the density 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, I 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 0 density estimates.

Treatment Effects Analysis.—The analysis of treatment effects was conducted under a weighted least-squares regression analysis (Draper and Smith 1998) in PROC IML (SAS Institute 2003). The computational details of the analysis, including calculation of AIC_c , regression coefficients, and variance estimates are provided in Chapter 1.

My interest was in modeling species densities in 1998 and 2003 in order to examine impacts of the vegetation variables, which were measured in those years, on densities. Therefore, I extracted the 1998 and 2003 portions of the vectors of density estimates and variance-covariance matrices from those for the vectors and matrices for all years (1998-1999, 2001-2003). I specified multiple *a priori* models describing responses of small mammal densities to treatments and to habitat components. Effects in the models included 2 blocking effects, year and site (year was included in all models based on *a priori* considerations). Additionally, 2 habitat effects were considered, including herbaceous vegetation and woody debris, as well as 2 treatment effects, including treatment intensity (number of trees) and a bivariate treatment effect (treated, control). The herbaceous vegetation effect was constructed from the indices of herbaceous vegetation for each experimental unit in each year of the study. The woody debris effect was constructed from the average volume of woody debris in each habitat plot for each experimental unit in each year. The treatment intensity effect was constructed from the average number of trees in habitat plots

for each of the experimental units in each year. The bivariate treatment effect was modeled on treated units in 2003. I considered all combinations of the effects for a total of 32 density models.

For each of the effects, I constructed relative importance values (Burnham and Anderson 2002), and used these metrics to rank the treatment and habitat variables in order of their importance in influencing densities. Relative importance values are calculated by summing the weights over all models in a balanced set which include a given effect. Simulation studies have suggested that relative importance values of 0.40 or higher indicate that a given variable is having an effect on the process of interest (G. C. White, Colorado State University, unpublished data).

RESULTS

Habitat Components

Confidence intervals (95%) indicated that percent change in trees, percent change in herbaceous cover, and percent change in woody debris were different between treated experimental units and controls (Table 2.1). All variables also differed to some degree by treatment type.

On average, the number of trees declined 71% on experimental units that received the 1.5-2 treatment, 75% on 2-4 experimental units, and 55% on 3-6 experimental units. As expected, the 1.5-2 treatment resulted in a larger decline in the number of trees than the 3-6 treatment, but, unexpectedly, the 1.5-2 treatment resulted in a slightly smaller decline in the number of trees than the 2-4 treatment, an apparent result of variations in the number of pre-Euro-settlement remnants on the experimental units. The percent change in the number of trees on control units between 1998 and 2003 was not statistically different than 0 (Table 2.1). The number of trees ranged from 4,500 – 7,900 per ha prior to treatment (all experimental units). After treatment, the number of trees on 1.5-2 units ranged from 1,000 – 2,313 per ha, the 2-4 units ranged from 1,400 – 1,900 per ha, and the 3-6 units ranged from 2,000 – 3,200 per ha.

Overall, herbaceous cover increased substantially with fuel reduction/restoration treatments. Herbaceous cover increased 199% on the 1.5-2 treatment units, 208% on the 2-4 treatment units, and 62% on the 3-6 treatment. The percent changes on the 1.5-2 and 3-6 treatment units were statistically different from each other (Table 2.1), but neither was statistically different from the change on 2-4 treatment units. The percent change in herbaceous cover on control units did not differ statistically from 0.

Finally, woody debris declined after treatment on all the treated units. The decline was 44% on 1.5-2 units, 78% on 2-4 units, and 78% on 3-6 units. There was no statistical difference between the 2-4 and 3-6 treatments, but the 1.5-2 treatment was different from the 2-4 and 3-6 treatments (Table 2.1). Change in woody debris on control units did not differ statistically from 0. Pre-treatment woody debris volume ranged from approximately 1.3 – 6.0 m³/m² (all experimental units); post treatment volumes on treated units ranged from approximately 0.3 – 2.4 m³/m².

Small Mammal Populations

During small mammal trapping at the FVSA, 5 species were captured (Table 2.2). These were deer mice, brush mice (*Peromyscus boylii*), gray-collared chipmunks, golden-mantled ground-squirrels, and Mexican woodrats. Deer mice and brush mice were combined in all analyses, and are herein referred to as deer mice, because so few brush mice were captured (4 total individuals; Table 2.2), and because these species may be difficult to distinguish in some cases, e.g., as juveniles.

For all 4 small mammal species monitored, estimated densities were generally higher in the first 2 years of the study (1998-1999) than in the last 3 years (2001-2003). These differences were most apparent for deer mice, golden-mantled ground squirrels, and woodrats (Figures 2.1 – 2.4). Deer mouse densities averaged 18.18 (SE = 0.15, range = 5.46 – 31.20) individuals per hectare in 1998-1999, and 5.95 (SE = 0.06, range = 0 – 17.35) in 2001-2003. Gray-collared chipmunk densities averaged 3.45 (SE = 0.02, range = 0.46 – 7.99) individuals per hectare in 1998-1999, and 2.33 (SE = 0.02, range = 0 – 7.01) in 2001-2003. Golden-mantled ground squirrel densities averaged 1.48 (SE = 0.01, range = 0 – 5.78) individuals per hectare in 1998-1999, and 0.43 (SE = 0.00, range = 0 – 3.36) in 2001-2003. Mexican woodrat densities averaged 2.09 (SE = 0.01, range = 0 – 6.06) individuals per hectare in 1998-1999, and 0.14 (SE = 0.00, range = 0 – 1.79) in 2001-2003.

Modeling of detection probabilities for the estimation of abundance indicated support for detection probabilities varying over individuals, time, space, and treatments (Appendix 2A). Age effects appeared in the top AIC_c-ranked models of detection probabilities for deer mice, gray-collared chipmunks, and golden-mantled ground squirrels; year effects appeared in the top models for deer mice, gray-collared chipmunks, and Mexican woodrats; unit effects appeared in the top models for deer mice and gray-collared chipmunks;

and the fire effect, number of trees effect, and treatment * year interaction terms all appeared in the top model for gray-collared chipmunks.

Modeling results from the MMDM analysis indicated some support for movements varying by treatment (Appendix 2A). The top model for gray-collared chipmunks contained the treatment * year effect. The top-ranked models for all other species were constant models.

The top-ranked model of deer mouse densities was model (year + site + trees), with a weight of 0.13 (Table 2.3). The second-ranked model, with nearly equal weight, was model (year + site). Site had the highest relative importance value, 0.87, while the number of trees variable had a relative importance of 0.42 and a negative effect size (Table 2.4). All other relative importance values were < 0.40.

For gray-collared chipmunks, the top-ranked model, with a weight of 0.29, was model (year + site + trees + woody debris + treatment; Table 2.5). The second-ranked model, which also had high weight (0.26), was model (year + site + trees + herbaceous + woody debris + treatment). Of the variables in the top model, the variable with the largest relative importance was woody debris (1.00), followed by number of trees (0.97), treatment (0.82), and site (0.71). Herbaceous vegetation, which appeared in the second-ranked model, had a relative importance of 0.50. Woody debris had a positive regression coefficient, while number of trees, treatment, and herbaceous vegetation had negative regression coefficients.

For golden-mantled ground squirrels, the top-ranked model included only the year effect, and had a weight of 0.14 (Table 2.7). The relative importance values for each of the site, habitat, and treatment variables were < 0.40 (Table 2.8).

In the analysis of Mexican woodrat densities, the top model was model (year) with a weight of 0.11; however, model (year + woody debris) was ranked nearly as high, with a ΔAIC_c value of 0.16 and a weight of 0.10 (Table 2.9). The relative importance value for the woody debris effect was 0.60, and the effect size was positive, though small (Table 2.10). All other effects had relative importance values < 0.40.

DISCUSSION

The fuel reduction/restoration treatments examined in this study resulted in changes in small mammal habitat components, with herbaceous vegetation increasing after treatments and woody debris declining. The greatest recorded increase in herbaceous vegetation was slightly more than a doubling of the index of herbaceous vegetation on the 2-4 treatment units, indicating that treatments affected large

increases in herbaceous vegetation within 2-3 growing seasons after treatment. These findings are supported by studies indicating increases in herbaceous vegetation in ponderosa pine and other forests by 1-2 growing seasons after thinning and/or prescribed fire (Clary 1975, Bock and Bock 1983, Harris and Covington 1983, Covington et al. 1997, Carey and Wilson 2001, Griffis et al. 2001), and based on the demonstrated negative relationship between overstory density and herbaceous vegetation in these forests (Moore and Deiter 1992). Woody debris volume declined between 44% and 78% after treatments. This decline was least pronounced with the 1.5-2 treatment, a result that was likely due to local variations in the volume of deposited slash and fire intensity; the smaller decline in the 1.5-2 treatment was apparently not due to an overall greater amount of woody debris inputs from slash, based on the percent change in number of trees. Covington and Sackett (1984) documented declines of approximately 60% in woody debris after prescribed fire in southwestern ponderosa pine; similar to the values recorded here. Therefore, for both herbaceous vegetation and woody debris, treatment-related habitat changes were approximately as expected.

Estimated densities of small mammals were generally lower during the last 3 years of this study than during the first 2 years. Deer mouse densities estimated from nearby study sites (within 50 km) during the period 2000 to 2003 (0 – 8.5 individuals per ha; Chapter 1) were similar or even smaller than those estimated in 2001-2003 for this study (0 – 17.35 individuals per ha). Similarly, for gray-collared chipmunks, estimates were comparable or slightly smaller in nearby study sites than in this study (0 – 3.3 individuals per ha in nearby study sites compared to 0 – 7.01 individuals per ha in this study). Reduced population densities in 2001-2003 may have been due at least partially to weather patterns. The southwestern USA was experiencing a drought during the early 2000s, and lack of rainfall may inhibit development of food sources for small mammals. Total precipitation in the Flagstaff area from September to April was 41 cm in 1997-1998, 35 cm in 1998-1999, 32 cm in 2000-2001, 12 cm in 2001-2002, and 32 cm in 2002-2003 (Flagstaff-Pulliam Airport data, National Climatic Data Center, available at www.ncdc.noaa.gov/oa/ncdc.html). The changes in small mammal populations across years in this study may have made it difficult to detect additional effects of treatments or treatment-related habitat changes.

Woody debris was the best predictor of both gray-collared chipmunk and Mexican woodrat densities. A positive relationship between gray-collared chipmunk densities and woody debris was

expected, based on chipmunks' use of logs and stumps for traveling, nesting, and feeding platforms (Hilton and Best 1993). A weak positive relationship between Mexican woodrats and woody debris has previously been documented (Ward 2001), and woody debris may also provide cover and foraging opportunities for Mexican woodrats, but physical characteristics of the habitat, such as availability of rocky slopes, may be a more important determinant of Mexican woodrat population densities. Deer mouse populations have also been tied to the availability of woody debris (Carey and Johnson 1995, Menzel et al. 1999, Carey and Harrington 2001, Suzuki and Hayes 2003), and while a positive regression coefficient for the effect of woody debris on deer mice was estimated in this study (Table 2.4), an important relationship was not indicated, based on the low relative importance value of woody debris in the deer mouse analysis. Previous research suggesting that availability of slash may have a positive impact on post-thinning chipmunk and deer mouse densities in southwestern ponderosa pine forests (Goodwin and Hungerford 1979, Chapter 1) implies that leaving post-thinning slash piles where possible may help to support local small mammal populations.

Surprisingly, strong positive links between herbaceous vegetation and small mammal densities were not supported in this study. However, gray-collared chipmunk densities were negatively, though weakly, linked with herbaceous vegetation. Deer mouse populations have been shown to respond to increases in herbaceous food and cover after thinning (Wilson and Carey 2000, Carey and Wilson 2001), though Hadley and Wilson (2004) demonstrated a negative relationship between deer mice and herbaceous cover in forests where deer mice competed with southern red-backed voles (*Clethrionomys gapperi*). Also, chipmunk densities were highest in thinned stands with understory development in the Pacific Northwest (Carey 2000, Wilson and Carey 2000, Carey 2001, Sullivan et al. 2001). It is necessary to investigate more closely the relationship between herbaceous vegetation and densities of small mammals in these forests. An alternate metric, such as total herbaceous biomass, may be more appropriate than the point intercept-based metric used here.

Treatment effects, including thinning intensity (modeled as number of trees) and the bivariate treatment variable, were important predictors of both deer mouse and gray-collared chipmunk densities. The average number of trees had a negative impact on both deer mouse and gray-collared chipmunk densities. This finding supports previous research that both deer mice and chipmunks benefit from thinning

in southwestern ponderosa pine forests (Goodwin and Hungerford 1979, Chapter 1), and Pacific Northwest forests (Wilson and Carey 2000, Carey and Wilson 2001). Deer mice also increased after thinning in Oregon Douglas-fir forests (*Pseudotsuga menziesii*), though the populations did not appear to vary by thinning intensity (Suzuki and Hayes 2003). Gray-collared chipmunk densities in this study were also related to the bivariate treatment effect, though with a negative regression coefficient. The bivariate treatment effect simultaneously modeled the effect of thinning and prescribed fire. Thinning had a positive impact on gray-collared chipmunks, but thinning and prescribed fire combined had a negative impact on gray-collared chipmunks, presumably because prescribed fire reduced woody debris availability. This lends further support to the result that woody debris is the strongest determinant of chipmunk densities.

Overall, increases in habitat complexity, particularly development of understories, appear to positively influence small mammal populations (Goodwin and Hungerford 1979, Montney and Soutiere 1985, Carey and Johnson 1995, Clough 1997, Wilson and Carey 2000, Carey and Harrington 2001) in southwestern ponderosa pine and other forests. One important component of small mammal habitat in many forests is shrubs, which provide for habitat complexity and frequently provide a source of food (e.g., Carey and Johnson 1995, Block et al. 2005). However, shrubs were relatively infrequent on the Fort Valley study area, and therefore I did not expect, and thus did not estimate, relationships between small mammals and shrub cover.

Questions exist over whether knowledge of historical conditions in southwestern ponderosa pine forests is adequate to restore these conditions. For instance, historical mean fire return intervals, as frequently reconstructed for southwestern ponderosa pine forests using fire scar techniques, may underestimate the length of fire-free intervals (Baker and Ehle 2001). If such information is used to determine rates of prescribed fire entry in current forest management, the result may be a reduction in woody debris below levels historically experienced by small mammals in these forests, and potential declines in small mammal populations. The results of this study underscore how overly-frequent burning could negatively impact at least one dominant small mammal species (gray-collared chipmunks) in these forests. Furthermore, even if historical knowledge was adequate and restoration of historical conditions was possible, it is unclear that restoring historical conditions would result in conservation of all forest ecological values (Wagner et al. 2000). In light of changing climatic conditions, the presence of exotic

plant species, and significant land area in human uses, such as cities and suburban areas, restoring conditions present in southwestern forests prior to Euro-settlement may not be the best way to conserve forest ecological values. Certainly, monitoring of treated areas will be necessary, and an adaptive management philosophy (Walters 1986) may be beneficial to the management of forests to reduce fire risk and provide for ecological values. Brown et al. (2004) further cautioned that appropriate use of thinning and prescribed fire to manage forest ecological values would include careful attention to site-specific conditions.

There is a need to carefully assess ecological effects of fuel reduction and restoration treatments over longer time periods. In this study, major changes in population densities over the course of the study may have masked additional effects of treatments or habitat variables; studying populations over longer time periods will reduce the impact of high temporal variation on the estimation of treatment effects. Furthermore, the lack of consistency in the timing of treatments may have reduced the quality of information available in the data. Better controlled, longer-term experiments with multiple re-entries of thinning and/or prescribed fire are needed to elucidate effects of potential southwestern ponderosa pine management strategies on forest ecology. Researchers should seek opportunities to partner with forest management agencies to make such experiments feasible.

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Table 2.1. Vegetation changes with 3 levels of thinning treatment (described in text) followed by burning. Vegetation was measured in 1998 and 2003.

Block	Unit	Treatment	% Change in Trees (95% CI)	% Change in herbaceous (95% CI)	% Change in woody debris (95% CI)
1	1	1.5-2	-86.8 (-87.0, -86.7)	175.4 (93.3, 257.5)	-65.0 (-70.8, -59.2)
2	6	1.5-2	-59.3 (-60.4, -58.2)	241.7 (47.2, 436.1)	-34.2 (-59.4, -8.9)
3	10	1.5-2	-66.1 (-66.9, -65.3)	180.0 (89.7, 270.3)	-32.7 (-96.5, 31.1)
		Mean	-70.8 (-71.2, -70.3)	199.0 (122.5, 275.5)	-43.9 (-52.6, -35.3)
1	2	2-4	-82.3 (-82.6, -82.0)	237.8 (-49.7, 525.2)	-77.6 (-81.2, 74.0)
2	7	2-4	-67.3 (-67.6, -67.0)	293.8 (51.5, 536.0)	-74.0 (-76.4, -71.7)
3	12	2-4	-75.9 (-76.2, -75.6)	91.5 (49.4, 133.6)	-83.7 (-84.4, -83.0)
		Mean	-75.2 (-75.3, -75.0)	207.7 (81.6, 333.8)	-78.4 (-80.4, -76.5)
1	4	3-6	-57.5 (-58.8, -56.3)	36.4 (-2.9, 75.6)	-76.9 (-83.1, -70.7)
2	5	3-6	-51.7 (-52.9, -50.5)	100.0 (4.7, 195.3)	-84.3 (-84.9, -83.7)
3	11	3-6	-55.6 (-57.0, -54.3)	48.1 (36.1, 60.1)	-72.2 (-74.6, -69.8)
		Mean	-55.0 (-55.7, -54.2)	61.5 (26.9, 96.1)	-77.8 (-79.9, -75.7)
1	3	Control	1.3 (-0.8, 3.4)	-10.3 (-31.8, 11.3)	9.3 (-36.8, 55.4)
2	8	Control	0.5 (-3.6, 4.5)	-6.3 (-44.0, 31.5)	-7.4 (-41.6, 26.8)
3	9	Control	4.7 (-2.1, 11.5)	15.7 (7.7, 23.7)	25.9 (-56.3, 108.1)
		Mean	2.1 (-0.6, 4.9)	-0.3 (-15.0, 14.5)	9.3 (-9.9, 28.4)

Table 2.2. Numbers of unique individuals captured in each trapping grid each year for 5 species of small mammals caught on the Fort Valley study area, northern Arizona, 1998-1999 and 2001-2003.

Species	M_{t+1}					Total
	1998	1999	2001	2002	2003	
Mexican woodrat	21	39	1	3	3	67
Golden-mantled ground squirrel	50	43	23	13	8	137
Gray-collared chipmunk	97	135	78	85	79	474
Deer mouse	442	247	45	146	111	995
Brush mouse	0	1	0	1	2	4 ^a

^aDeer mice and brush mice were combined for analyses.

Table 2.3. Model selection results from weighted regression analysis of deer mouse densities at the Fort Valley study area, northern Arizona, 1998 and 2003. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
Density{year + site + trees}	85.579	0.000	0.13230	5
Density{year + site}	85.579	0.001	0.13226	4
Density{year + site + treatment}	85.888	0.309	0.11334	5
Density{year + site + woody debris + treatment}	86.575	0.997	0.08038	6
Density{year + site + trees + woody debris}	86.694	1.115	0.07576	6
Density{year + site + trees + herbaceous}	87.556	1.977	0.04922	6
Density{year + site + herbaceous}	87.723	2.144	0.04529	5
Density{year + site + woody debris}	87.877	2.298	0.04193	5
Density{year + site + trees + treatment}	88.121	2.543	0.03711	6
Density{year + site + trees + herbaceous + woody debris}	88.202	2.623	0.03564	7
Density{year + site + herbaceous + treatment}	88.263	2.684	0.03457	6
Density{year + site + herbaceous + woody debris + treatment}	88.578	2.999	0.02953	7
Density{year}	88.815	3.236	0.02624	2
Density{year + site + trees + woody debris + treatment}	88.999	3.420	0.02393	7
Density{year + herbaceous}	89.502	3.924	0.01860	3
Density{year + herbaceous + treatment}	89.854	4.275	0.01560	4

continued

Table 2.3. continued

Model	AIC_c	ΔAIC_c	Weight	K
Density{year + site + herbaceous + woody debris}	90.024	4.445	0.01433	6
Density{year + trees + herbaceous}	90.163	4.585	0.01337	4
Density{year + site + trees + herbaceous + treatment}	90.195	4.616	0.01316	7
Density{year + site + trees + herbaceous + woody debris + treatment}	90.459	4.880	0.01153	8

Table 2.4. Estimated relative importance values, model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on deer mouse densities at the Fort Valley study area, northern Arizona, 1998 and 2003.

Variable	Relative Importance	Level	Effect	SE	95% CI
Intercept	1.00000	-	14.828	2.631	(9.671, 19.985)
Year	1.00000	Difference 1998, 2003	-10.381	1.401	(-13.128, -7.635)
Site	0.87028	Difference Site 1, Site 2	0.222	1.014	(-1.765, 2.209)
		Difference Site 1, Site 3	-1.859	1.194	(-4.200, 0.482)
Trees	0.41685	Continuous	-0.234	0.385	(-0.988, 0.519)
Herbaceous	0.30229	Continuous	-0.140	0.357	(-0.840, 0.561)
Woody debris	0.34465	Continuous	0.016	0.030	(-0.044, 0.076)
Treatment	0.38554	Treated	0.716	1.280	(-1.794, 3.226)

Table 2.5. Model selection results from weighted regression analysis of gray-collared chipmunk densities at the Fort Valley study area, northern Arizona, 1998 and 2003. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
Density{year + site + trees + woody debris + treatment}	45.404	0.000	0.29165	7
Density{year + site + trees + herbaceous + woody debris + treatment}	45.654	0.250	0.25740	8
Density{year + trees + herbaceous + woody debris + treatment}	46.837	1.433	0.14248	6
Density{year + trees + woody debris + treatment}	47.129	1.726	0.12307	5
Density{year + site + trees + herbaceous + woody debris}	48.250	2.846	0.07027	7
Density{year + site + trees + woody debris}	48.602	3.199	0.05892	6
Density{year + trees + herbaceous + woody debris}	50.908	5.504	0.01860	5
Density{year + site + woody debris}	51.204	5.800	0.01605	5

Table 2.6. Estimated relative importance values, model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on gray-collared chipmunk densities at the Fort Valley study area, northern Arizona, 1998 and 2003.

Variable	Relative Importance	Level	Effect	SE	95% CI
Intercept	1.00000	-	2.895	1.269	(0.407, 5.383)
Year	1.00000	Difference 1998, 2003	-0.344	0.377	(-1.083, 0.396)
Site	0.70663	Difference Site 1, Site 2	0.197	0.306	(-0.403, 0.796)
		Difference Site 1, Site 3	0.417	0.331	(-0.232, 1.066)
Trees	0.96911	Continuous	-0.516	0.204	(-0.915, -0.117)
Herbaceous	0.49612	Continuous	-0.144	0.193	(-0.522, 0.234)
Woody debris	0.99802	Continuous	0.054	0.014	(0.026, 0.081)
Treatment	0.82304	Treated	-1.352	0.879	(-3.074, 0.370)

Table 2.7. Model selection results from weighted regression analysis of golden-mantled ground squirrel densities at the Fort Valley study area, northern Arizona, 1998 and 2003. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
Density{year}	11.140	0.000	0.14248	2
Density{year + site}	11.615	0.474	0.11239	4
Density{year + woody debris}	12.626	1.486	0.06778	3
Density{year + trees + woody debris}	12.713	1.573	0.06490	4
Density{year + trees}	12.811	1.671	0.06178	3
Density{year + herbaceous}	13.302	2.162	0.04834	3
Density{year + treatment}	13.437	2.297	0.04518	3
Density{year + site + woody debris}	13.589	2.449	0.04188	5
Density{year + site + trees}	13.690	2.550	0.03982	5
Density{year + site + treatment}	14.008	2.868	0.03396	5
Density{year + trees + treatment}	14.025	2.885	0.03368	4
Density{year + site + herbaceous}	14.084	2.943	0.03271	5
Density{year + trees + woody debris + treatment}	14.333	3.193	0.02887	5
Density{year + site + trees + woody debris}	14.588	3.448	0.02541	6
Density{year + woody debris + treatment}	14.633	3.493	0.02485	4

continued

Table 2.7. continued

Model	AICc	ΔAIC_c	Weight	<i>K</i>
Density{year + herbaceous + woody debris}	14.698	3.558	0.02405	4
Density{year + trees + herbaceous + woody debris}	14.923	3.783	0.02149	5
Density{year + trees + herbaceous}	15.176	4.036	0.01894	4
Density{year + site + woody debris + treatment}	15.611	4.470	0.01524	6
Density{year + herbaceous + treatment}	15.682	4.541	0.01471	4
Density{year + site + trees + herbaceous}	15.856	4.716	0.01348	6
Density{year + site + herbaceous + woody debris}	15.944	4.803	0.01290	6
Density{year + site + trees + treatment}	16.030	4.890	0.01236	6
Density{year + trees + herbaceous + treatment}	16.418	5.278	0.01018	5

Table 2.8. Estimated relative importance values, model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on golden-mantled ground squirrel densities at the Fort Valley study area, northern Arizona, 1998 and 2003.

Variable	Relative Importance	Level	Effect	SE	95% CI
Intercept	1.00000	-	0.198	0.235	(-0.262, 0.659)
Year	1.00000	Difference 1998, 2003	-0.170	0.137	(-0.438, 0.098)
Site	0.37557	Difference Site 1, Site 2	0.024	0.060	(-0.094, 0.142)
		Difference Site 1, Site 3	0.104	0.150	(-0.190, 0.398)
Trees	0.36257	Continuous	-0.025	0.044	(-0.110, 0.061)
Herbaceous	0.24203	Continuous	-0.001	0.019	(-0.039, 0.037)
Woody debris	0.36664	Continuous	0.002	0.004	(-0.005, 0.009)
Treatment	0.26325	Treated	-0.019	0.084	(-0.182, 0.145)

Table 2.9. Model selection results from weighted regression analysis of Mexican woodrat densities at the Fort Valley study area, northern Arizona, 1998 and 2003. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
Density{year}	40.500	0.000	0.10623	2
Density{year + woody debris}	40.655	0.155	0.09831	3
Density{year + trees + woody debris}	40.832	0.332	0.09000	3
Density{year + site + herbaceous + woody debris}	41.365	0.865	0.06893	6
Density{year + site}	41.403	0.903	0.06764	4
Density{year + site + woody debris}	41.771	1.271	0.05626	5
Density{year + woody debris + treatment}	41.970	1.470	0.05095	4
Density{year + trees}	42.139	1.639	0.04681	3
Density{year + herbaceous + woody debris}	42.762	2.262	0.03429	4
Density{year + herbaceous}	42.799	2.299	0.03366	3
Density{year + treatment}	42.800	2.300	0.03364	3
Density{year + trees + herbaceous + woody debris}	43.296	2.796	0.02625	5
Density{year + trees + woody debris + treatment}	43.302	2.802	0.02618	5
Density{year + site + herbaceous}	43.417	2.917	0.02471	5
Density{year + site + woody debris + treatment}	43.428	2.928	0.02457	6
Density{year + site + trees + woody debris}	43.591	3.091	0.02265	6

continued

Table 2.9. continued

Model	AICc	ΔAIC_c	Weight	<i>K</i>
Density{year + trees + treatment}	43.661	3.161	0.02188	4
Density{year + site + trees}	43.869	3.369	0.01971	5
Density{year + site + treatment}	43.882	3.382	0.01959	5
Density{year + site + trees + herbaceous + woody debris}	43.918	3.418	0.01923	7
Density{year + site + herbaceous + woody debris + treatment}	44.048	3.547	0.01803	7
Density{year + trees + herbaceous}	44.379	3.879	0.01528	4
Density{year + herbaceous + woody debris + treatment}	44.453	3.952	0.01472	5
Density{year + herbaceous + treatment}	45.189	4.689	0.01019	4

Table 2.10. Estimated relative importance values, model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on Mexican woodrat densities at the Fort Valley study area, northern Arizona, 1998 and 2003.

Variable	Relative Importance	Level	Effect	SE	95% CI
Intercept	1.00000	-	0.152	0.220	(-0.278, 0.583)
Year	1.00000	Difference 1998, 2003	-0.239	0.148	(-0.529, 0.052)
Site	0.37806	Difference Site 1, Site 2	0.071	0.108	(-0.140, 0.282)
		Difference Site 1, Site 3	0.071	0.105	(-0.136, 0.278)
Trees	0.32907	Continuous	-0.013	0.028	(-0.068, 0.042)
Herbaceous	0.30335	Continuous	0.019	0.044	(-0.067, 0.104)
Woody debris	0.56907	Continuous	0.005	0.006	(-0.006, 0.016)
Treatment	0.26211	Treated	0.009	0.078	(-0.144, 0.161)

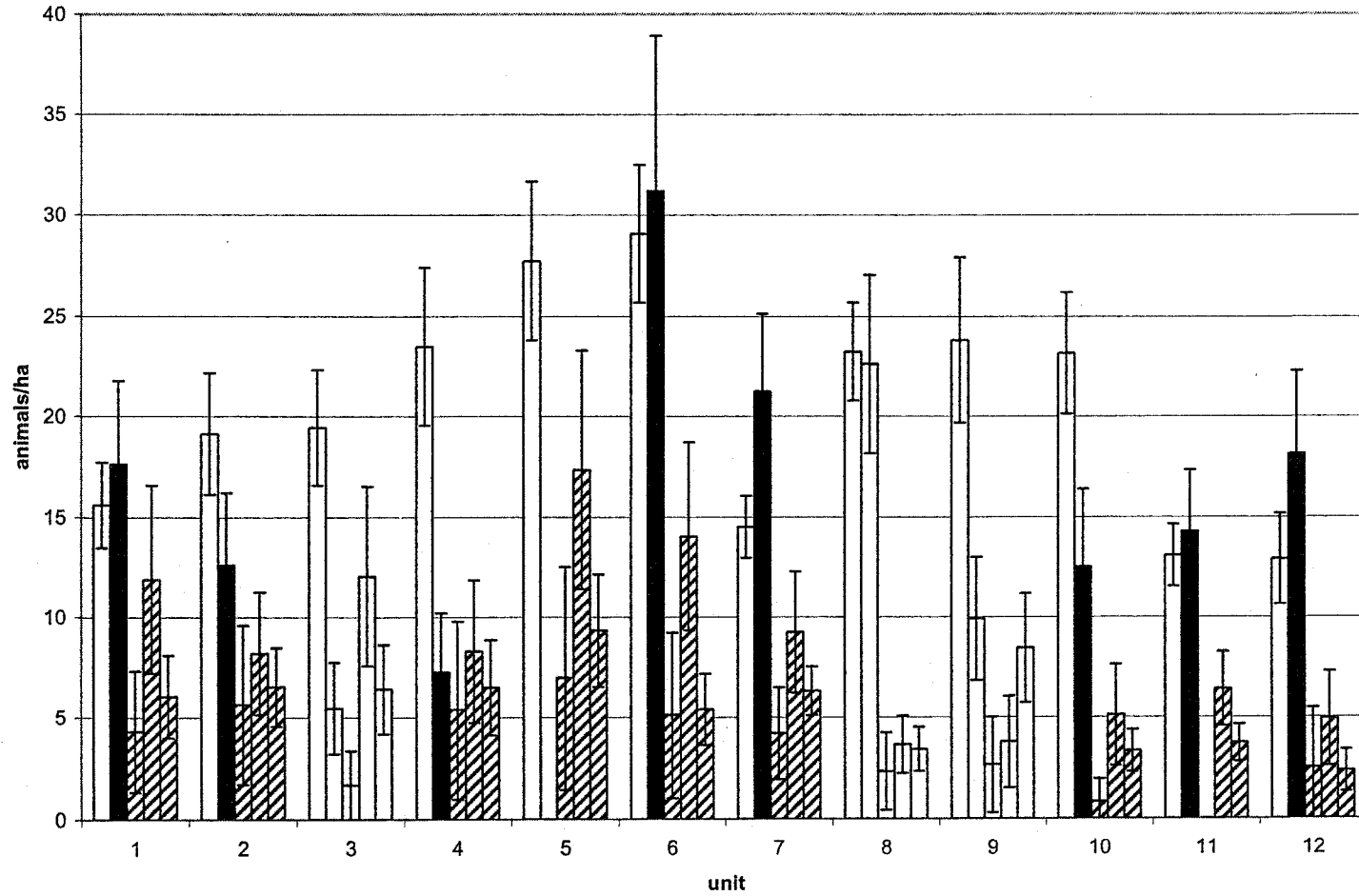


Figure 2.1. Density estimates and 95% confidence intervals for deer mice at the Fort Valley study area, northern Arizona. Bars within experimental unit groupings represent years 1998, 1999, 2001, 2002, and 2003 from left to right. Black bars represent thinned experimental units and striped bars represent thinned and burned experimental units.

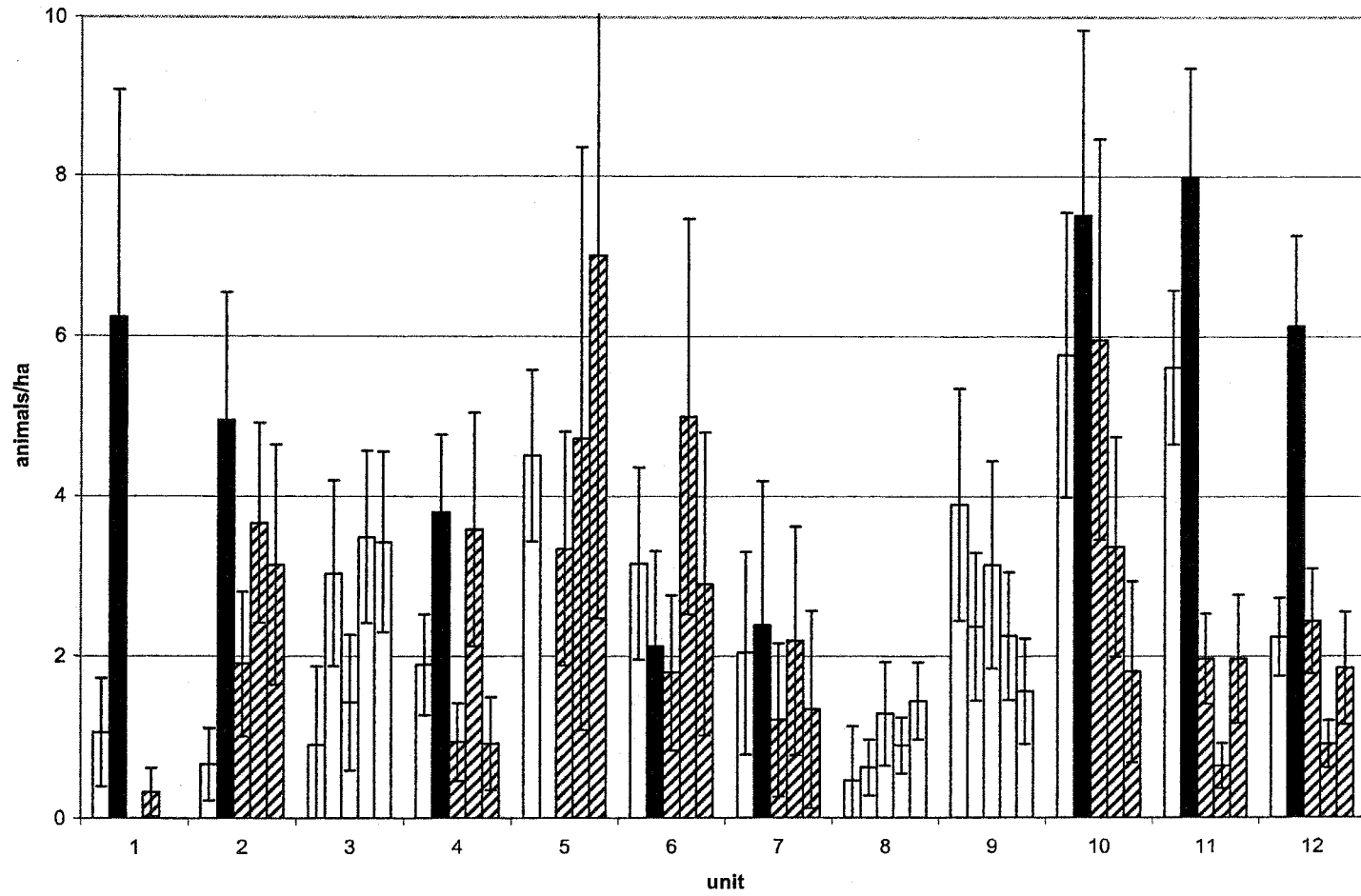


Figure 2.2. Density estimates and 95% confidence intervals for gray-collared chipmunks at the Fort Valley study area, northern Arizona. Bars within experimental unit groupings represent years 1998, 1999, 2001, 2002 and 2003 from left to right. Black bars represent thinned experimental units and striped bars represent thinned and burned experimental units.

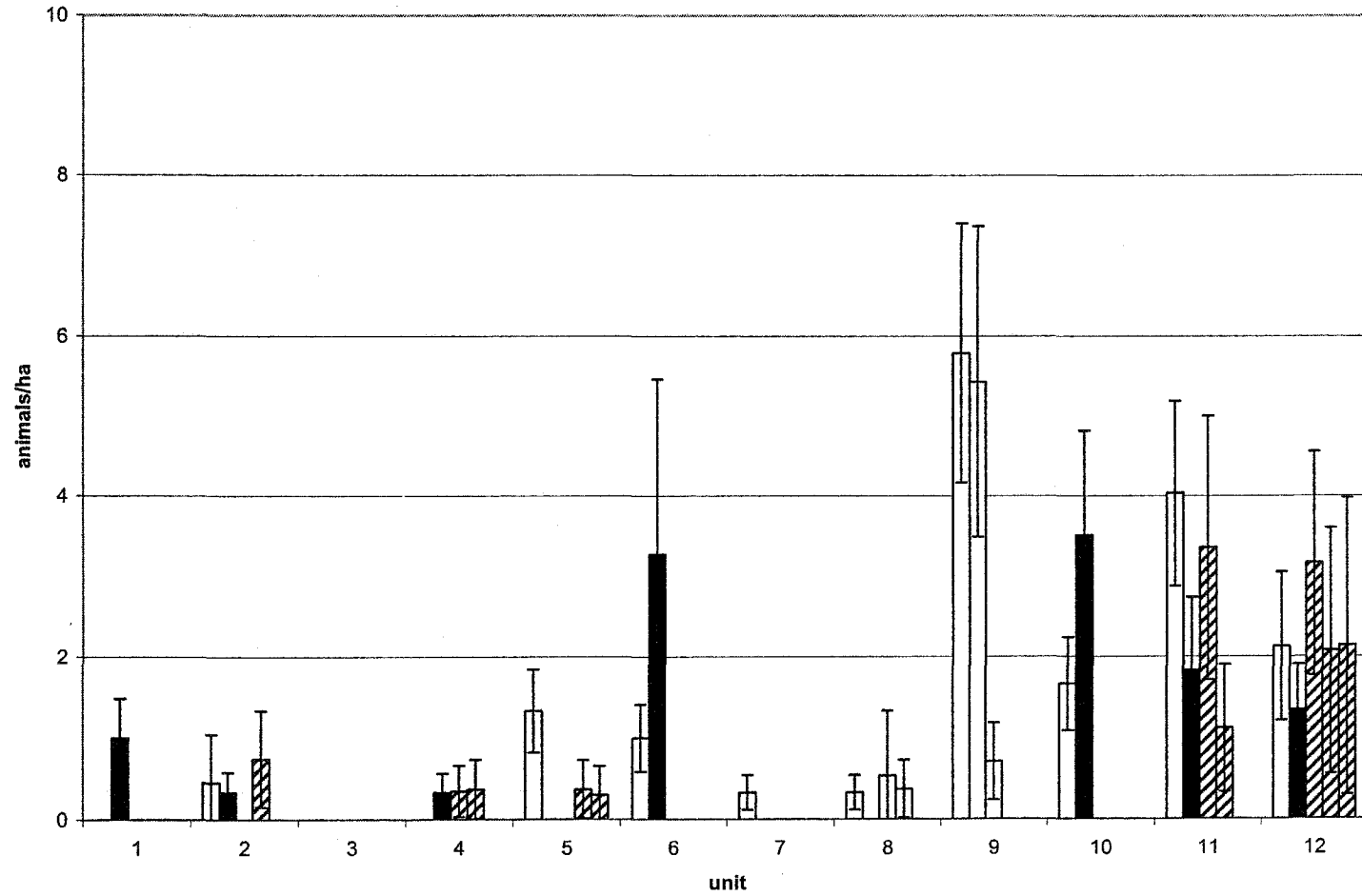


Figure 2.3. Density estimates and 95% confidence intervals for golden-mantled ground squirrels at the Fort Valley study area, northern Arizona. Bars within experimental unit groupings represent years 1998, 1999, 2001, 2002 and 2003 from left to right. Black bars represent thinned experimental units and striped bars represent thinned and burned experimental units.

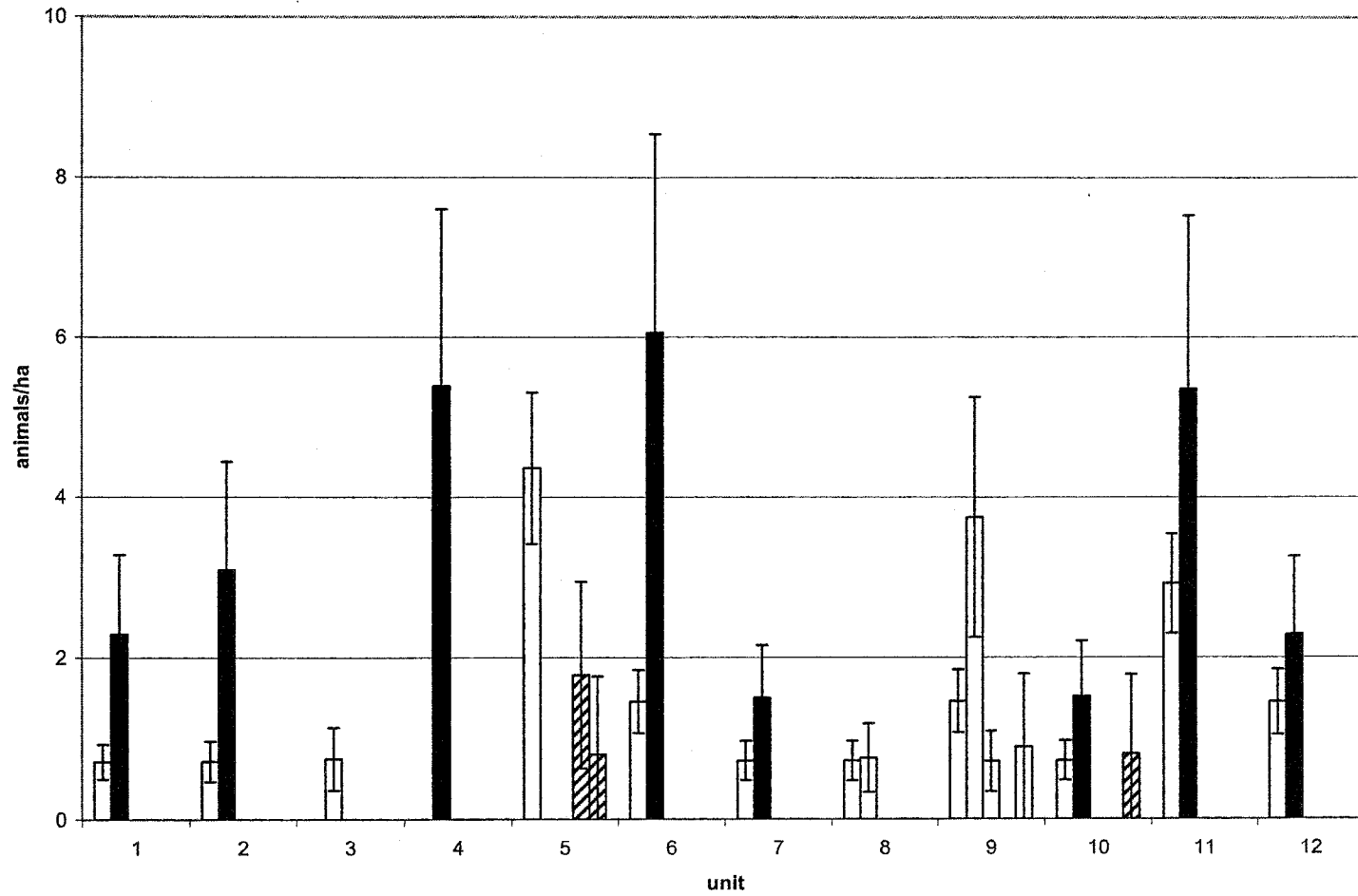


Figure 2.4. Density estimates and 95% confidence intervals for Mexican woodrats at the Fort Valley study area, northern Arizona. Bars within experimental unit groupings represent years 1998, 1999, 2001, 2002 and 2003 from left to right. Black bars represent thinned experimental units and striped bars represent thinned and burned experimental units.

APPENDIX 2A:

**MODEL SELECTION RESULTS FROM MODELING OF CAPTURE PROBABILITIES AND MEAN MAXIMUM DISTANCE MOVED FOR
SMALL MAMMAL SPECIES CAPTURED ON THE FORT VALLEY STUDY AREA, NORTHERN ARIZONA, USA**

Table 2A.1. Initial capture (p) and recapture probability (c) models and model selection results for deer mice at the Fort Valley Experimental Forest, Arizona. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m. + age + year + unit) = c (additive)}	7000.559	0.000	0.37745	19
{ p (a.m. + age + year + unit + fire) = c (additive)}	7001.796	1.237	0.20337	20
{ p (a.m. + age + year + unit + trees) = c (additive)}	7002.127	1.568	0.17233	20
{ p (a.m. + age + year + unit + trees + fire + treatment * year) = c (additive)}	7002.292	1.733	0.15871	24
{ p (a.m. + age + year + unit + trees + fire) = c (additive)}	7003.724	3.165	0.07756	21

Table 2A.2. Initial capture (p) and recapture probability (c) models and model selection results for gray-collared chipmunks at the Fort Valley Experimental Forest, Arizona. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m. + age + year + unit + stems + fire + treatment * year) = c (additive)}	4241.424	0.000	0.64371	24
{ p (a.m. + year + unit + trees + fire + treatment * year) = c (additive)}	4245.173	3.749	0.09876	23
{ p (a.m. + age + unit) = c (additive)}	4246.240	4.816	0.05794	15
{ p (a.m. + age + year + unit + fire) = c (additive)}	4246.682	5.258	0.04644	20
{ p (a.m. + age + year + unit) = c (additive)}	4247.220	5.796	0.03550	19
{ p (a.m. + age + unit + fire) = c (additive)}	4247.466	6.042	0.03139	16
{ p (a.m. + age + unit + trees) = c (additive)}	4248.172	6.748	0.02205	16
{ p (a.m. + age + year + unit + trees + fire) = c (additive)}	4248.688	7.264	0.01704	21
{ p (a.m. + age + year + unit + trees) = c (additive)}	4248.801	7.377	0.01610	20
{ p (a.m. + age + unit + trees + fire) = c (additive)}	4249.457	8.033	0.01160	17

Table 2A.3. Initial capture (p) and recapture probability (c) models and model selection results for golden-mantled ground squirrels at the Fort Valley Experimental Forest, Arizona. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m. + age) = c (additive)}	1172.222	0.000	0.36126	4
{ p (a.m. + age + trees) = c (additive)}	1172.767	0.545	0.27516	5
{ p (a.m. + age + fire) = c (additive)}	1173.966	1.744	0.15104	5
{ p (a.m. + age + trees + fire) = c (additive)}	1174.755	2.533	0.10182	6
{ p (a.m. + age + year) = c (additive)}	1177.273	5.051	0.02890	8
{ p (a.m.) = c (additive)}	1177.905	5.683	0.02107	3
{ p (a.m. + age + year + fire) = c (additive)}	1178.752	6.530	0.01380	9
{ p (a.m. + trees) = c (additive)}	1178.904	6.682	0.01279	4
{ p (a.m. + age + year + trees) = c (additive)}	1179.269	7.046	0.01066	9

Table 2A.4. Initial capture (p) and recapture probability (c) models and model selection results for Mexican woodrats at the Fort Valley Experimental Forest, Arizona. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m. + year) = c (additive)}	521.299	0.000	0.15285	7
{ p (a.m. + fire) = c (additive)}	521.527	0.227	0.13642	4
{ p (a.m. + age + fire) = c (additive)}	521.608	0.309	0.13100	5
{ p (a.m. + age + year) = c (additive)}	522.143	0.844	0.10023	8
{ p (a.m.) = c (additive)}	522.171	0.872	0.09886	3
{ p (a.m. + age) = c (additive)}	522.414	1.114	0.08756	4
{ p (a.m. + trees + fire) = c (additive)}	523.060	1.761	0.06338	5
{ p (a.m. + age + trees + fire) = c (additive)}	523.189	1.889	0.05943	6
{ p (a.m. + year + trees) = c (additive)}	523.273	1.973	0.05698	8
{ p (a.m. + trees) = c (additive)}	523.919	2.619	0.04126	4
{ p (a.m. + age + year + trees) = c (additive)}	524.180	2.880	0.03621	9
{ p (a.m. + age + trees) = c (additive)}	524.202	2.902	0.03581	5

Table 2A.5. Mean maximum distance moved models and model selection results for deer mice ($n=536$) at the Fort Valley Experimental Forest, Arizona. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{MMDM (constant)}	3450.976	0.000	0.51043	2
{MMDM (fire)}	3452.312	1.336	0.26173	3
{MMDM (trees)}	3452.989	2.013	0.18657	3
{MMDM (year)}	3456.553	5.577	0.03140	6

Table 2A.6. Mean maximum distance moved models and model selection results for gray-collared chipmunks ($n=290$) at the Fort Valley Experimental Forest, Arizona. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{MMDM (treatment * year)}	2186.252	0.000	0.38972	7
{MMDM (constant)}	2186.886	0.634	0.28385	2
{MMDM (stems)}	2188.813	2.561	0.10828	3
{MMDM (fire)}	2188.916	2.664	0.10285	3
{MMDM (year)}	2188.954	2.702	0.10092	6
{MMDM (unit)}	2192.852	6.600	0.01437	13

Table 2A.7. Mean maximum distance moved models and model selection results for golden-mantled ground squirrels ($n=79$) at the Fort Valley Experimental Forest, Arizona. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{MMDM (constant)}	598.542	0.000	0.48712	2
{MMDM (trees)}	600.391	1.850	0.19317	3
{MMDM (fire)}	600.493	1.952	0.18358	3
{MMDM (year)}	601.091	2.550	0.13613	6

Table 2A.8. Mean maximum distance moved models and model selection results for Mexican woodrats ($n=37$) at the Fort Valley Experimental Forest, Arizona. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{MMDM (constant)}	194.211	0.000	0.38523	2
{MMDM (fire)}	194.652	0.441	0.30897	3
{MMDM (year)}	195.898	1.687	0.16571	6
{MMDM (trees)}	196.234	2.023	0.14008	3

CHAPTER 3:
SMALL MAMMAL RESPONSES TO FOREST FUEL REDUCTION:
NATIONAL-SCALE RESULTS FROM THE FIRE AND FIRE SURROGATE PROGRAM

INTRODUCTION

Many United States (USA) forests 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 USA, and climatic variation (Dodge 1972, Kilgore and Taylor 1979, Bonnicksen and Stone 1982, Arno et al. 1995, Cowell 1998, Allen et al. 2002). A result of decreased fire frequency is 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). Among land managers and scientists, there is interest in developing and applying treatments to reduce forest fuels, but before widespread adoption of fuel reduction treatments, it is necessary to understand the potential effects of forest fuel reduction on forest ecology (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 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. 2001a,b). Prescribed fire, mechanical thinning, and combination treatments are effective in reducing forest fuels and fire risk (Martinson and Omi 2002, Pollet and Omi 2002). However, the comparative ecological effects of these treatments are not known (P. Weatherspoon and J. McIver, US Forest Service, unpublished report). It is important to evaluate the ecological impacts of these treatments, and to determine whether

mechanical treatments, or mechanical treatments in combination with prescribed fire, are ecologically appropriate surrogates for fire.

To provide such information, the national Fire and Fire Surrogate (FFS) Program was conceived as a cooperative effort among federal land-management agencies, universities, and private organizations to investigate the relative impacts of fire and fire surrogate treatments on forest ecology and fire risk (P. Weatherspoon and J. McIver, US Forest Service, unpublished report). The FFS experimental approach applies a similar study design and sampling scheme to 13 study areas across the USA, thereby allowing for both local and large-scale inferences. Through the FFS study, researchers are monitoring 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 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 study proposal was on providing such information (P. Weatherspoon and J. McIver, US Forest Service, unpublished report). If impacts of treatments were found to be largely consistent across study areas, land managers' abilities to predict the impacts of management actions would be strengthened. Conversely, if impacts were found to be highly divergent, increased site-specific analyses would be warranted before widespread adoption of particular management actions.

Within the wildlife component of the FFS study, small mammal populations were identified as a response variable of interest (P. Weatherspoon and J. McIver, US Forest Service, unpublished report). Small mammal communities comprise an important component of the vertebrate biomass and biodiversity of forests, and they impact 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 comprise an important food source for forest predators (e.g., Koehler and Hornocker 1977, Long and Smith 2000, Ward 2001).

Here I examine initial (i.e., within 2 years post-treatment) small mammal responses to mechanical thinning, prescribed fire, and thinning/prescribed fire combination treatments across 8 FFS study areas distributed throughout the USA. In a large-scale study such as this, significant variation in methods, treatments, and timing at different study areas is expected. Capturing and explaining the full range of this

variation was not my focus. My emphasis, instead, was on the examination of general responses of small mammal populations and communities to treatments. Therefore, I focused on 2 primary research questions. First, do thinning, prescribed fire, and thinning/prescribed fire combination treatments differ in their effects on small mammal densities and total small mammal biomass? Second, are results generally similar across study areas?

METHODS

Study Areas, Treatments, and Data Collection

The FFS network was composed of 13 study areas in the USA, including 8 in the western USA (Arizona, California (3), Montana, New Mexico, Oregon, and Washington) and 5 in the eastern USA (Alabama, Florida, North Carolina, Ohio, and South Carolina). Eight of these study areas provided data to the analyses herein. The remaining 5 study areas either had very low numbers of small mammals or their data collection and analysis timeline did not permit participation. It was necessary to assess the data set from each study area to determine whether and how much of the data set was appropriate for inclusion in these analyses. Study areas included in the analyses spanned 5 western states (Arizona, California (2), Montana, New Mexico, and Oregon) and 2 eastern states (Alabama and Florida).

The study area design was established by the FFS national study proposal (P. Weatherspoon and J. McIver, US Forest Service, unpublished report). The study areas were divided into experimental units; each unit was assigned to a treatment type (typically thin, prescribed burn, thin/prescribed burn combination, and control). At certain study areas, the experimental units were grouped into blocks, or study sites, but this was not universally true. There were at least 3 experimental units assigned to each treatment. 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 sites (primarily the eastern study sites) 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 included. 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. Detailed study area descriptions are provided in the FFS national study proposal (P. Weatherspoon and J. McIver, US Forest Service, unpublished report) and are available on the FFS website at <http://www.fs.fed.us/ffs/>. A summary of study area activities is supplied in Table 3.1.

The Gulf Coast study area (GCSA) was located in long-leaf pine (*Pinus palustris*) forest on the Auburn University Solon Dixon Forestry Center in southern Alabama. The study area consisted of 15 experimental units, 12 of which were included; an additional 3 experimental units were assigned to an herbicide and burn treatment and therefore were excluded. Experimental units were not closely grouped into study sites. Thinning was conducted during February-April 2002 and burning was conducted immediately 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 approximately 15 ha. Small mammals were trapped during July-August 2001 (pre-treatment) and July 2002 and 2003 (post-treatment). Small mammal sampling occurred on a smaller scale than the permanent sampling grid, in 10 x 10-dimensional trapping grids with 10-m spacing between trapping points. One large (7.6 x 8.9 x 22.9 cm) Sherman live-trap was placed at each trapping point. Animals were marked with ear tags and/or toe-clipping.

The Hungry Bob study area (HBSA) 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. An additional control unit was omitted because the sampling points were arranged in a straight line, thus precluding the calculation of population density with the methods described below. Experimental units were not grouped into study sites, and were highly variable in size and shape, and some units were composed of smaller subunits separated in space. Thinning was conducted, before the FFS study commenced, in the fall of 1998 before pre-treatment small mammal data were collected; 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 the late summer of 2000 (mid-treatment) and 2001 (post-treatment). Traps were placed at all permanent

sampling points, i.e., ≥ 50 m apart, with 1 large Sherman live-trap and 1 #201 (12.7 x 12.7 x 40.6 cm) Tomahawk live-trap at each sampling point. Animals were marked by clipping fur in unique patterns.

The Jemez Mountains study area (JMSA) 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 aspen (*Populus tremuloides*). While 3 study sites were initially identified, 1 study site was destroyed by a wildfire and no treatments were completed on a second during the initial phase of the study; therefore data presented here come from 1 study site. Thinning was completed on 1 of 4 experimental units on this study site during the winter of 2002-2003; slash was piled and/or scattered after thinning. 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. Pre-treatment small mammal data were collected in 2001 and 2002; post-treatment data were collected in 2003. In 2001, small mammal sampling was conducted at all permanent sampling points, which were arranged in 6 x 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. Two sizes of Sherman live-traps were used, with large traps at every trapping point and extra-large traps (10.2 x 11.4 x 38.1 cm) at every other trapping point. All captured animals were individually marked with ear tags.

The Lubrecht Forest study area (LFSA) 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 3 study sites with 4 experimental units per site. 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 approximately 50-m buffer, resulting in a total treated area of approximately 12.25 ha. Small mammal sampling was conducted in July-August 2000 (pre-treatment) and 2002 (post-treatment) on smaller trapping grids centered within the experimental units (7 x 7-dimensional grids with 25-m spacing). One large Sherman live-trap was placed at every trapping point and animals were individually marked with ear tags and/or toe-clipping.

The Myakka River study area (MRSA) 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 3 study sites, but data from only 4 experimental units (2 at each of 2 study sites) were

used here. Treatments included burning, mowing, and chopping vegetation; only experimental units treated with prescribed burns were included. Furthermore, an escaped fire and flooding precluded use of some experimental units. Experimental units were approximately 6.25 ha with a 50-m buffer, resulting in a total treated area of approximately 12.25 ha. Burning of 1 unit at site 1 occurred in August of 2001, burning of both units at site 2 occurred in July of 2000. Experimental units at site 1 were sampled for small mammals in June-July 2000 and 2002. Experimental units at site 2 were sampled for small mammals in June-July 2000 and 2001. One large or extra-large kangaroo rat (7.6 x 9.5 x 30.5) Sherman live-trap was placed at each permanent sampling point, in 6 x 6-dimensional grids with 50-m spacing between points. Animals were marked by clipping fur in unique patterns.

The Southern Cascades study area (SCSA) was located on the Klamath National Forest in northern California on mixed-conifer forest dominated by ponderosa pine and Douglas-fir. The area consisted of 12 experimental units that were not grouped into study sites. Thinning was conducted in the fall of 1998 (1 thin/burn unit, 1 thin only unit), the summer of 1999 (2 thin only units, 1 thin/burn unit), and the fall of 1999 (1 thin/burn unit), before pre-treatment small mammal data were collected; slash was scattered after thinning. Prescribed burning was conducted in the fall of 2001 (3 thin/burn units) and fall of 2002 (3 burn only units). Experimental units were 6.25 ha, with a 50-m buffer, for a total treated area of approximately 12.25 ha. Small mammal trapping was conducted in May-August 2001 (mid-treatment) and 2003 (post-treatment). One extra-large kangaroo rat Sherman live-trap and 1 #201 Tomahawk live-trap were placed at each permanent sampling point, which were arranged in 6 x 6-dimensional grids with 50-m spacing between points. Animals were marked by clipping fur in unique patterns.

The Sequoia National Park study area (SNSA) was located on the Sequoia National Park in east-central California, in mixed-conifer forest dominated by ponderosa pine, sugar pine (*Pinus lambertiana*) and white fir (*Abies concolor*). The study area consisted of 9 experimental units that were not grouped into study sites. The treatments consisted of spring burning and fall burning; thinning was not implemented on this National Park Service study area. The 2 burning treatments were combined in this analysis. Fall burns were conducted in the fall of 2001, spring burns were conducted in the spring of 2002. Small mammal sampling was conducted from June-September in 2001 (pre-treatment), 2002 (post-treatment, no spring burn experimental units trapped), and 2003 (post-treatment). 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 on the interior of the sampling grids, trap spacing was decreased to 25 m. Extra-large kangaroo rat Sherman live-traps were placed at all trapping points, and animals were marked with ear tags.

The Southwest Plateau study area (SPSA) was located in north-central Arizona on ponderosa pine forest. Three study sites comprised the study area, with 2 on the Coconino National Forest and 1 on the Kaibab National Forest. Thinning was completed on 2 of the 4 experimental units on all 3 replicate study sites during the winter of 2002-2003; slash was piled after thinning. Prescribed burning was not completed at the SPSA before data collection for these analyses was completed. Experimental units were approximately 6.25 ha in size, with an additional 50-m buffer, resulting in a total treated area of approximately 12.25 ha. Pre-treatment data were collected in July 2000, 2001, and 2002; post-treatment data were collected in July 2003. In 2000, small mammal sampling was conducted at all permanent sampling points, which were arranged generally in 6 x 6-dimensional grids, but sometimes varied slightly from that pattern, with 50-m spacing between points. In 2002-2003, trapping intensity was increased by adding additional trapping points to decrease trap spacing to 25 m. Two sizes of Sherman live-traps were used, with large traps at every trapping point and extra-large traps at every other trapping point. All captured animals were individually marked with ear tags.

Data Analysis

The data analysis took place in 3 steps. First, I estimated abundance for each species each year in each experimental unit, based on the mark-recapture data. Second, I converted abundance estimates to density estimates by dividing abundance by trapping area. Finally, I conducted weighted least-squares regression analyses to examine the effects of treatments on small mammal densities and total small mammal biomass.

Throughout the analysis, I employed an information-theoretic philosophy of model selection and multi-model inference (Burnham and Anderson 2002). Tools employed included model selection based on Akaike's Information Criterion (AIC; Akaike 1973) corrected for 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 impacted by habitat modifications (Chapter 1, Chapter 2). Therefore, reliance on index values of relative abundance to evaluate population responses to treatments will result in unreliable inference. I used the conditional likelihood closed model (Huggins 1989, 1991) to model detection probabilities and estimate abundance. The conditional likelihood approach allows for individual heterogeneity, behavioral response to capture, and time effects on capture probabilities (Model M_{tbi} ; Otis et al. 1978), and has previously been used to estimate abundance of small mammals (Converse et al. 2004, Chapter 1, Chapter 2). The conditional likelihood model generates estimates of initial capture rates (p_i , $i = 1, \dots, t$) and recapture rates (c_i , $i = 2, \dots, t$) for t occasions based on animal encounter histories and uses these rates to generate estimates of abundance. This model is preferred because it allows for the inclusion of individual covariates, e.g., age, to model individual heterogeneity in capture probabilities (White 2002) and has favorable numerical properties when most of the animals are captured in a sampled area (personal observation). The conditional likelihood model estimates abundance, based on capture rates, as

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

where M_{t+1} is the number of unique individuals marked on a grid during t trapping occasions, i.e., the minimum known population size, and p_t is the estimate of initial capture rate for occasion t .

Abundance estimation was carried out for each species at a study area of which at least 10 individuals were captured. All data for a given species at a given study area were combined into one large 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 impact detection probabilities were identified, and model sets were devised wherein models of detection probabilities were based on various combinations of the variables of interest. 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), 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. Variables included in abundance models are summarized by study area in Table 3.2.

Based on previous analyses (Chapter 1, Chapter 2) indicating the importance of behavioral responses to capture in modeling small mammal detection probabilities, I generally considered behavioral responses to capture in all abundance models, unless models did not perform well (i.e., unstable abundance estimates, inestimable detection probabilities). In these cases, behavior was treated as a variable that could be included or not (HBSA, SNSA). A behavior effect was not estimable for cotton mice and cotton rats at the MRSA, nor for long-tailed voles or northern flying squirrels at the SNSA, so behavior was deleted from the model sets for these species.

A challenge in valid estimation of animal abundance is the proper modeling of individual heterogeneity in capture probabilities (Otis et al. 1978, Williams et al. 2002). I used 2 approaches to account for individual heterogeneity. The first was age of individual animals. Animals were classified by researchers at each study area as either adults or subadults based on mass and/or external evidence of reproductive status (McCrary and Rose 1992). When age of individual animals did not perform well in the models, I used mixture models to account for heterogeneity in capture probabilities (Pledger 2000). Larger amounts of heterogeneity were evident when trap spacing was larger, so, for example, at the HBSA and the SCSA, initial model runs demonstrated that heterogeneity was so great that abundance estimates were not reliable (e.g., estimates were orders of magnitude larger than estimates in other models).

Estimation of abundance was conducted in Program MARK 3.2 (White and Burnham 1999). I ran the entire specified model set for each species at each study area, and then deleted any models where estimates were not identifiable or where the models themselves were logically nonsensical (e.g., an age effect if all captured individuals of a species were adults). I then model-averaged the abundance estimates and variance-covariance matrices to account for model selection uncertainty. I 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. Generally, density estimation in mark-recapture studies proceeds by estimating effective trapping area, computed as the area of the trapping grid expanded by the area of an additional buffer strip of width W . Methods to estimate buffer strip width (Wilson and Anderson 1985a) 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 (see Discussion and Figure 1). Therefore, I calculated a naïve density estimate (Wilson and Anderson 1985a) by drawing a convex polygon (i.e., all outer angles $\geq 180^\circ$) around all points in the trapping grid. The convex polygon area was necessary because some trapping grids were irregularly shaped, i.e., were not rectangular (at the HBSA, MRSA, SNSA, and SPSA).

Variance-covariance matrices of the density estimates and total biomass estimates were necessary for the weighted regression analysis. 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 0 because the variance-covariance matrix is singular. Variances of 0 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, I 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 0 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 , are provided

in Chapter 1. Based on the computed AIC_c for each model, I computed model-averaged effect sizes and standard errors for each variable (Burnham and Anderson 2002).

I specified multiple *a priori* models describing predicted responses to treatments. I considered 4 structures on treatment effects – by category (thin, burn, thin/burn) or not (treatment), and nested within study area or not. I additionally considered 2 alternative blocking structures – by study area or by year nested within study area. I 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. I considered a total of 12 structural models in each analysis.

Because the focus was on cross-study area effects, I limited analyses to taxa that spanned multiple study areas. I adopted the *a priori* rule that a species had to appear on at least 3 study areas and have a minimum of 100 total individuals captured to warrant an individual analysis. This resulted in 3 species-level response variables: golden-mantled ground squirrel (*Spermophilus lateralis*) density, yellow-pine chipmunk (*Tamias amoenus*) density, and deer mouse (*Peromyscus maniculatus*) density. I further considered genus-level response variables, including all chipmunk (*Tamias*) species and all *Peromyscus* spp. Therefore, I was able to examine responses of the dominant taxa in many western forests with historically short-interval fire regimes (i.e., lower elevation forests), including deer mice and chipmunks, as well as one of the dominant taxa in forests throughout the US, *Peromyscus*. While the golden-mantled ground squirrel was not dominant in the capture data from any of the study areas, it was common enough across the western study areas to support an individual analysis.

As an overall community metric, I considered total small mammal biomass. For the analysis of total biomass, I used minimum adult mass, in grams, as a multiplier to convert density estimates to biomass estimates, then summed the total estimated biomass over all species at each study area. I determined minimum adult masses from a combination of literature sources (Hamilton and Whitaker 1979, Jameson and Peeters 1988, Fitzgerald et al. 1994, Hilton and Best 1993, Whitaker 1996) and judgments based on discussions with study area researchers and examination of data sets. Masses used to compute biomass are provided in Table 3.3.

RESULTS

There were 6,068 individuals of 19 species captured on the 8 study areas (Table 3.3). The most wide-ranging species was the deer mouse, which was caught on all 6 of the western study areas and was, in all but 1 case (SCSA) the most commonly captured species on the western study areas. The most widely ranging genus, *Peromyscus*, was captured on all 8 study areas, including deer mice in the west and cotton mice (*P. gossypinus*) in the east. The second most widely ranging genus was *Tamias* (chipmunks), of which at least 1 species occurred at all 6 western study areas. The eastern chipmunk (*T. striatus*) was also observed at the GCSA, but its capture numbers (3 individuals) were too small for abundance analysis. Only one chipmunk species, the yellow-pine chipmunk (*T. amoenus*) was caught at more than 1 study area. The golden-mantled ground squirrel was the only other widely distributed species, caught at 4 western study areas. Three species, including long-tailed voles (*Microtus longicaudus*), Mexican woodrats (*Neotoma mexicana*), and brush mice (*P. boylii*) were caught at 2 study areas, but all were caught in small numbers. Because of the small capture numbers, and because of difficulties in distinguishing amongst *Peromyscus* spp., brush mice were combined with deer mice at the study areas where both were caught.

Modeling of detection probabilities for abundance estimation indicated that detection probabilities varied in different times, areas, and conditions, including over treatments (Appendix 3A). Populations for which a thinning and/or prescribed burning effect appeared in the top-ranked model of detection probabilities included golden mice (*Ochrotomys nuttalli*) and cotton mice (*Peromyscus gossypinus*) at the GCSA; least chipmunks (*Tamias minimus*) at the JMSA; southern red-backed voles (*Clethrionomys gapperi*), deer mice, and yellow-pine chipmunks at the LFSA; golden-mantled ground squirrels and yellow-pine chipmunks at the SCSA; deer mice, golden-mantled ground squirrels, and lodgepole chipmunks (*T. speciosus*) at the SNSA; and gray-collared chipmunks (*T. cinereicollis*) at the SPSA.

For analysis of 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 both treatment category and study area, i.e., treatment effects were different by treatment type and study area and in all cases the top model received strong support. The top 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.

Analysis of golden-mantled ground squirrel densities resulted in a top-ranked model, [Density {treatment category (study area)}], with 82% of the model weight (Table 3.4). No clear pattern was evident in the 3 study area burn effects (2 positive regression coefficients, 1 negative), or 3 study area thin effects (2 negative regression coefficients, 1 positive), though both of the 2 study area thin/burn effects were positive (Table 3.5). Estimated 95% confidence intervals on the treatment effects included 0 in all cases.

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 (Table 3.6). Two of 3 regression coefficients for study area burn effects were negative, while 1 was positive; similarly for the 3 study area thin effects and 3 study area thin/burn effects (Table 3.7). In all but one case (positive LFSA thin effect), 95% confidence intervals included 0.

Analysis of deer mouse densities indicated that the top model was [Density {year (study area) + treatment category (study area)}] with 100% of the weight (Table 3.8). Three of 4 study area burn effects were positive, as were 3 of 5 study area thin effects and 2 of 3 study area thin/burn effects (Table 3.9). All 95% confidence intervals included 0 with the exception of a positive burn effect at the LFSA and a positive thin effect at the JMSA.

The top-ranked model for all *Tamias* spp. was [Density {study area + treatment category (study area)}], with 99% of the model weight (Table 3.10). Two of 4 regression coefficients for study area burn effects were positive; 4 of 5 regression coefficients for study area thin effects were positive; and 1 of 3 study area thin/burn effects was positive (Table 3.11). All 95% confidence intervals included 0 with the exception of 2 positive thin effects (JMSA and LFSA).

The top-ranked model of *Peromyscus* spp. densities was [Density {year (study area) + treatment category (study area)}], with 98% of the weight (Table 3.12). Five of 6 study area burn effects were positive, 4 of 6 study area thin effects were positive, and 3 of 4 study area thin/burn effects were positive (Table 3.13). All 95% confidence intervals included 0 with the exception of positive burn effects at the GCSA and LFSA and positive thin effects at the GCSA and JMSA.

The top ranked model of total small mammal biomass was [Biomass {year (study area) + treatment}] with 76% of the model weight (Table 3.14). The positive treatment effect had a 95% confidence interval that only marginally included 0 (Table 3.15).

DISCUSSION

Small Mammal Responses to Treatments

The results of this cross-study area, multi-taxa analysis indicate that densities of individual taxa of small mammals have variable responses to different treatment types at different study areas. The direction (positive or negative) of treatment effects was variable across study areas, even within a treatment type. 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. It is important to note, however, that high variances on estimates of total small mammal biomass probably caused the selection of a simpler approximating model for biomass, rather than estimated treatment effects that were highly precise and similar over treatment types and areas.

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), have been shown to be important determinants of forest small mammal populations, and these components of small mammal habitat may have quite different responses to thinning and prescribed fire. Thinning increases herbaceous cover by 1-2 growing seasons after treatment (Clary 1975, Covington et al. 1997), as does prescribed fire within the first few growing seasons after the disturbance (Bock and Bock 1983, Harris and Covington 1983, Oswald and Covington 1983, Oswald and Covington 1984), but vegetation response after fire is likely delayed by post-prescribed fire vegetation recovery. 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 burning treatments

have been shown to result in increased herbaceous vegetation and decreased coarse woody debris (Chapter 2).

Given potential differences in responses of habitat components, it is reasonable to expect that small mammals 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. However, differences in timing and execution of treatments at different study areas are possible confounding factors. For instance, climate variability at different sites in different years, or differences in treatment execution, such as whether slash was piled or scattered after thinning, may have caused some of the differences in study area effects. Despite these complications, this study has documented greater variability in treatment responses than previous research. For example, deer mouse populations have been thought to almost universally demonstrate positive responses to forest disturbance, including thinning operations (Wilson and Carey 2000, Carey and Wilson 2001, Suzuki and Hayes 2003, Chapter 1, Chapter 2, but see Hadley and Wilson 2004). Positive responses of deer mice have also been documented for both prescribed fire and wildfire (Tester 1965, Ahlgren 1966, Krefting and Ahlgren 1974, Bock and Bock 1983, Martell 1984, Kyle and Block 2000). Similarly for chipmunks, positive responses to thinning have been documented for a number of species (Carey 2000, Wilson and Carey 2000, Carey 2001, Carey and Wilson 2001, Sullivan et al. 2001, Hadley and Wilson 2004, Chapter 1, Chapter 2). Less information is available on chipmunk responses to fire, but what information is available suggests negligible to negative responses (Chapter 1, Chapter 2). The highly variable responses to treatments by golden-mantled ground squirrels documented in this study are one of the few examinations of impacts of forest management on this species (but see Chapter 2).

One response variable examined here, total small mammal biomass, had consistent responses across treatment types and study areas. This result is supported further by additional research (Goodwin and Hungerford 1979, Monthey and Soutiere 1985, Carey and Johnson 1995, Clough 1997, Wilson and Carey 2000, Carey and Harrington 2001) indicating that increases in habitat complexity result in overall positive responses by small mammal communities. Any type of treatment that increases habitat complexity, i.e., by increasing herbaceous vegetation, may result in higher small mammal populations. However, while it is reasonable as a coarse prediction to expect that small mammals should respond

positively to any type of forest disturbance, there is almost certainly high variability in responses of total biomass to fuel reduction treatments.

If treatment responses 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 pre-treatment conditions may impact the direction of small mammal responses to fuel reduction treatments. In finer-scale analyses of treatment effects at the SPSA, responses of deer mice, gray-collared chipmunks and total small mammal biomass to thinning were shown to be positive on experimental units which, prior to treatment, were comprised of forests with densely-packed small trees, whereas responses were negligible to negative on experimental units with pre-treatment forests composed of larger, more widely spaced trees, even though total tree basal area was similar across the experimental units (Chapter 1). Differences in pre-treatment conditions across study areas may have had an important influence on the differences in treatment responses documented here.

Differences in responses by taxa across different study areas indicate that the ability of managers to predict responses of small mammal communities to fuel reduction treatments is currently limited. Given this constraint, an adaptive management philosophy is probably warranted (Walters 1986), wherein management actions are conceived as experiments designed to reduce uncertainty about the effects of management on response variables of interest, at least in areas managed for small mammals, such as raptor foraging areas. Focus should be placed on determining the pre-treatment conditions or other variables that impact responses of small mammals to treatments. Once such information is available, careful site-specific analyses can be used to predict responses at specific sites (Brown et al. 2004).

Experimental Design and Inference

A difficulty I faced in estimating small mammal densities in this study was in the estimation of effective trapping area, the area to which a mark-recapture-based estimate of abundance applies. The approach used in similar analyses (Chapter 1, Chapter 2) was to estimate effective trapping area using model selection and the mean maximum distance moved method (Wilson and Anderson 1985a) in which a buffer strip, estimated from the mean of the maximum distance moved by animals on a trapping grid, is added to the area of the trapping grid. These analyses have indicated that treatments can impact movements of animals and thus effective trapping area; therefore, the most robust estimates of treatment

effects will be based on empirical estimates of effective trapping area. However, the shape and size of trapping grids on some of the experimental units included in this analysis were such that estimation of mean maximum distance moved was not feasible. In particular, portions of some trapping grids at the HBSA were composed of a single line of traps (Figure 1). Movements, and thus mean maximum distance moved, could not be reliably estimated in such a grid, and use of the area of the trapping grid itself to calculate density was not possible because a line has no area. Therefore, the convex polygon method that I used to estimate the area of the trapping grid and thus calculate density was the most plausible, objective method available to complete this analysis. In many cases (i.e., on rectangular grids), the convex polygon area was the same as the naïve area described by Wilson and Anderson (1985a). Investigators interested in estimating small mammal densities or density-based treatment responses should use either trapping webs (Anderson et al. 1983, Wilson and Anderson 1985b) or large-dimension, regularly shaped (i.e. square or rectangular) trapping grids to facilitate the estimation of movement and thus effective trapping area by methods such as mean maximum distance moved (Wilson and Anderson 1985a) or to estimate density directly with the recently-developed method of Efford (2004). The FFS study was not designed primarily for wildlife investigations; instead wildlife sampling was added to a design intended for vegetation and other types of investigations. As Block et al. (2001) note, such a situation often results in compromised quality of wildlife investigations. If movements were strongly impacted by treatments, then estimates of treatment effect size reported here may be biased. Because I focus on patterns of treatment responses by treatment type and over space, rather than on estimation of treatment effect size, my inference should be less dependent on the importance of treatment effects on animal movements.

A common concern of many wildlife researchers involved in the FFS program was the small size of the experimental units – total treated area was generally less than 13 ha, although some study areas (i.e., HBSA) had larger or smaller treated areas. Future studies investigating small mammal responses to forest management treatments should attempt to increase the size of treated areas. Overly small treatment areas result in a larger potential edge effect, where animals respond to the creation of a habitat edge induced by treatments rather than to the treatments themselves. Possibly, edge effects were present in data sets included in this analysis, although a more detailed analysis of the data from the SPSA (Chapter 1) indicated that animals likely were responding to the treatments themselves rather than the induced edge on the

approximately 12.25 ha experimental units there. Partnering with forest management agencies that are implementing large-scale fuel reduction treatments should provide researchers with opportunities to study responses on larger spatial scales.

Furthermore, there is a need to assess ecological effects of fuel reduction and restoration treatments over longer time periods; this research only considered responses over the first 1-2 years post-treatment. The FFS study was originally conceived as a 5-year study, but continued work on existing FFS study areas could provide much needed information on long-term impacts of treatments, as well as on impacts of multiple re-entries of fuel reduction treatments.

A primary strength of my analytic approach was the use of response variables (density and biomass) that had been corrected for variable detection probabilities, particularly detection probabilities varying by treatments. Rather than estimate detection probabilities and hence true abundance, most investigators examining small mammal responses to forest management have relied on indices of abundance (minimum known alive or catch per unit effort) to estimate treatment effects (e.g., Tester 1965, Bock and Bock 1983, Masters et al. 1998, Steventon et al. 1998, Wilson and Carey 2000, Carey 2001). When comparing across areas that have been differentially influenced by a habitat disturbance, the assumption of equal detection probabilities required for valid use of index values seems particularly unrealistic because habitat changes may influence behavior and thus detection rates (Block et al. 2001). In addition to this analysis, other work (Chapter 1, Chapter 2) has indicated that detection probabilities vary over space, time, and treatments.

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Table 3.1. Timing and characteristics of FFS Program study design and data contributed to analyses, for Gulf Coast Study Area – Alabama (GCSA), Hungry Bob Study Area – Oregon (HBSA), Jemez Mountains Study Area – New Mexico (JMSA), Lubrecht Forest Study Area – Montana (LFSA), Myakka River Study Area – Florida (MRSA), Southern Cascades Study Area – California (SCSA), Sequoia National Park Study Area – California (SNSA), and Southwest Plateau Study Area – Arizona (SPSA).

Area	Sampling	Thinning (Replicates)	Burning (Replicates)	Thinning/Burning (Replicates)	Controls
GCSA	2001-2003	Spring 2002 (3)	Spring 2002 (3)	Spring 2002/Spring 2002 (3)	3
HBSA	2000-2001	Fall 1998 (4)	Fall 2000 (4)	Fall 1998/Fall 2000 (4)	3
JMSA	2001-2003	Winter 2002-2003 (1)	NA	NA	3
LFSA	2000, 2002	Winter 2001 (3)	Spring 2002 (3)	Winter 2001/Spring 2002 (3)	3
MRSA	2000-2002	NA	Summer 2000 (2), Summer 2001 (1)	NA	1
SCSA	2001, 2003	Fall 1998 (1), Summer 1999 (2)	Fall 2002 (3)	Fall 1998/Fall 2001 (1), Fall 1999/Fall 2001 (1), Summer 1999/Fall 2001(1)	3
SNSA	2001-2003	NA	Fall 2001 (3), Spring 2002 (3)	NA	3
SPSA	2000-2003	Winter 2002-2003 (6)	NA	NA	6

Table 3.2. Variables and number of models used in FFS Program small mammal abundance estimation, for Gulf Coast Study Area – Alabama (GCSA), Hungry Bob Study Area – Oregon (HBSA), Jemez Mountains Study Area – New Mexico (JMSA), Lubrecht Forest Study Area – Montana (LFSA), Myakka River Study Area – Florida (MRSA), Southern Cascades Study Area – California (SCSA), Sequoia National Park Study Area – California (SNSA), and Southwest Plateau Study Area – Arizona (SPSA).

Study Area	Abundance Estimation Variables	Total Models
GCSA	^a Behavior, Age, Year, Unit, Thin, Burn, Thin*Year, Burn*Year, Thin*Burn,	68
HBSA	^a Mixture, Behavior, Year, Unit, Thin, Burn, Thin*Burn	40
JMSA	^a Behavior, ^a Time of day, Age, Year <i>OR</i> Session(Year), Unit, Thin	24
LFSA	^a Behavior, Age, Year, Site <i>OR</i> Unit, Thin, Burn, Thin*Burn	60
MRSA	^{a,b} Behavior, Age, Year, Site <i>OR</i> Unit, Burn	24
SCSA	^a Mixture, Behavior, Year, Unit, Thin, Burn, Thin*Burn	40
SNSA	^{a,b} Behavior, ^a Disturbance, Trap Density, Age, Year, Unit, Fall Burn, Spring Burn, Fall Burn*Year	80
SPSA	^a Behavior, ^a Time of day, Trap effort, Age, Year <i>OR</i> Session(Year), Site <i>OR</i> Unit, Thin	72

^aThe denoted variable appeared in all models in the set based on *a priori* considerations.

^bA behavior effect was not estimable for cotton mice or cotton rats at the MRSA, or for long-tailed voles or northern flying squirrels at the SNSA.

Table 3.3. Unique number of individuals captured for small mammal species at 8 FFS study areas, including Gulf Coast Study Area – Alabama (GCSA), Hungry Bob Study Area – Oregon (HBSA), Jemez Mountains Study Area – New Mexico (JMSA), Lubrecht Forest Study Area – Montana (LFSA), Myakka River Study Area – Florida (MRSA), Southern Cascades Study Area – California (SCSA), Sequoia National Park Study Area – California (SNSA), and Southwest Plateau Study Area – Arizona (SPSA).

Species	Mass (g) ^a	GCSA	HBSA	JMSA	LFSA	MRSA	SCSA	SNSA	SPSA	Total
Southern red-backed vole (<i>Clethrionomys gapperi</i>)	20	0	0	0	74	0	0	0	0	74
Northern flying squirrel (<i>Glaucomys sabrinus</i>)	45	0	0	0	0	0	0	14	0	14
Southern flying squirrel (<i>Glaucomys volans</i>)	60	11	0	0	0	0	0	0	0	11
Long-tailed vole (<i>Microtus longicaudus</i>)	30	0	0	23	0	0	0	21	0	44
Mexican woodrat (<i>Neotoma mexicana</i>)	100	0	0	21	0	0	0	0	19	40
Golden mouse (<i>Ochrotomys nuttalli</i>)	20	40	0	0	0	0	0	0	0	40
Brush mouse (<i>Peromyscus boylii</i>)	14	0	0	0	0	0	0	36 ^b	2 ^b	38 ^b
Cotton mouse (<i>Peromyscus gossypinus</i>)	25	401	0	0	0	16	0	0	0	417
Deer mouse (<i>Peromyscus maniculatus</i>)	14	0	83	265	541	0	19	1389	486	2783
Columbian ground squirrel (<i>Spermophilus columbianus</i>)	340	0	10	0	0	0	0	0	0	10
Golden-mantled ground squirrel (<i>Spermophilus lateralis</i>)	150	0	39	0	0	0	73	10	21	143
Cotton rat (<i>Sigmodon hispidus</i>)	80	0	0	0	0	232	0	0	0	232

continued

Table 3.3. continued

Species	Mass (g) ^a	GCSA	HBSA	JMSA	LFSA	MRSA	SCSA	SNSA	SPSA	Total
Yellow-pine chipmunk (<i>Tamias amoenus</i>)	36	0	766	0	234	0	49	0	0	1049
Gray-collared chipmunk (<i>Tamias cinereicollis</i>)	50	0	0	0	0	0	0	0	304	304
Cliff chipmunk (<i>Tamias dorsalis</i>)	50	0	0	0	0	0	0	0	11	11
Least chipmunk (<i>Tamias minimus</i>)	35	0	0	99	0	0	0	0	0	99
Allen's chipmunk (<i>Tamias senex</i>)	70	0	0	0	0	0	387	0	0	387
Lodgepole chipmunk (<i>Tamias speciosus</i>)	30	0	0	0	0	0	0	335	0	335
Red squirrel (<i>Tamiasciurus hudsonicus</i>)	140	0	37	0	0	0	0	0	0	37
Total		452	935	408	849	248	528	1805	843	6068

^aMass used to compute total small mammal biomass.

^bBrush mice were combined with deer mice prior to abundance analysis.

Table 3.4. Model selection results from weighted regression analysis of golden-mantled ground squirrel densities from 4 FFS study areas. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
Density{treatment category (study area)}	-166.935	0.000	0.81563	10
Density{treatment}	-161.526	5.409	0.05457	3
Density{study area + treatment category (study area)}	-160.548	6.387	0.03347	13
Density{treatment (study area)}	-160.207	6.727	0.02822	6
Density{study area}	-159.543	7.392	0.02025	5
Density{treatment category}	-159.495	7.440	0.01977	5
Density{study area + treatment}	-158.478	8.457	0.01189	6
Density{constant}	-158.133	8.802	0.01001	2

Table 3.5. Estimated model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on golden-mantled ground squirrel densities from 4 FFS study areas.

Variable	Level	Effect	SE	95% CI
Treatment	Treatment	0.006	0.011	(-0.017, 0.028)
Treatment (Study Area)	Treatment HBSA	0.000	0.002	(-0.004, 0.004)
	Treatment SCSA	0.008	0.016	(-0.023, 0.038)
	Treatment SNSA	0.003	0.006	(-0.009, 0.014)
	Treatment SPSA	0.000	0.004	(-0.008, 0.008)
Treatment Category	Burn	0.002	0.004	(-0.007, 0.011)
	Thin	0.001	0.003	(-0.005, 0.006)
	Thin/Burn	0.003	0.007	(-0.011, 0.017)
Treatment Category (Study Area)	Burn HBSA	0.034	0.155	(-0.270, 0.337)
	Burn SCSA	-0.025	0.144	(-0.307, 0.257)
	Burn SNSA	0.083	0.049	(-0.014, 0.179)
	Thin HBSA	-0.026	0.079	(-0.181, 0.129)
	Thin SCSA	0.231	0.171	(-0.105, 0.567)
	Thin SPSA	-0.009	0.103	(-0.211, 0.194)
	Thin/Burn HBSA	0.037	0.199	(-0.352, 0.427)
	Thin/Burn SCSA	1.005	0.528	(-0.030, 2.041)

Table 3.6. Model selection results from weighted regression analysis of yellow-pine chipmunk densities from 3 FFS study areas. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
Density{study area + treatment category (study area)}	184.150	0.000	0.68572	13
Density{treatment category (study area)}	186.435	2.286	0.21870	11
Density{year (study area) + treatment category (study area)}	188.352	4.202	0.08390	16

Table 3.7. Estimated model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on yellow-pine chipmunk densities from 3 FFS study areas.

Variable	Level	Effect	SE	95% CI
Treatment	Treatment	0.000	0.001	(-0.002, 0.002)
Treatment (Study Area)	Treatment HBSA	-0.001	0.009	(-0.018, 0.017)
	Treatment LFSA	0.019	0.038	(-0.057, 0.094)
	Treatment SCSA	-0.001	0.004	(-0.009, 0.008)
Treatment Category	Burn	0.000	0.001	(-0.002, 0.001)
	Thin	0.000	0.000	(0.000, 0.000)
	Thin/Burn	0.000	0.001	(-0.002, 0.003)
Treatment Category (Study Area)	Burn HBSA	1.879	2.188	(-2.408, 6.167)
	Burn LFSA	-0.628	1.649	(-3.860, 2.604)
	Burn SCSA	-0.101	1.062	(-2.182, 1.981)
	Thin HBSA	-1.392	1.593	(-4.514, 1.730)
	Thin LFSA	6.400	1.460	(3.539, 9.262)
	Thin SCSA	-0.064	0.670	(-1.378, 1.250)
	Thin/Burn HBSA	-0.695	2.330	(-5.261, 3.871)
	Thin/Burn LFSA	-2.831	2.111	(-6.968, 1.306)
	Thin/Burn SCSA	0.916	1.247	(-1.527, 3.360)

Table 3.8. Model selection results from weighted regression analysis of deer mouse densities from 6 FFS study areas. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
Density {year (study area) + treatment category (study area)}	326.319	0.000	0.99967	29

Table 3.9. Estimated model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on deer mouse densities from 6 FFS study areas.

Variable	Level	Effect	SE	95% CI
Treatment	Treatment	0.000	0.000	(0.000, 0.000)
Treatment (Study Area)	Treatment HBSA	0.000	0.000	(-0.001, 0.001)
	Treatment JMSA	0.002	0.004	(-0.005, 0.009)
	Treatment LFSA	0.002	0.005	(-0.007, 0.011)
	Treatment SCSA	0.000	0.000	(0.000, 0.000)
	Treatment SNSA	0.000	0.002	(-0.003, 0.003)
	Treatment SPSA	0.000	0.000	(-0.001, 0.000)
Treatment Category	Burn	0.000	0.000	(0.000, 0.000)
	Thin	0.000	0.000	(0.000, 0.000)
	Thin/Burn	0.000	0.000	(0.000, 0.000)

continued

Table 3.9. continued.

Variable	Level	Effect	SE	95% CI
Treatment Category (Study Area)	Burn HBSA	0.254	1.662	(-3.004, 3.511)
	Burn LFSA	14.387	2.018	(10.432, 18.341)
	Burn SCSA	0.128	0.715	(-1.273, 1.529)
	Burn SNSA	-0.835	3.402	(-7.502, 5.833)
	Thin HBSA	0.113	0.923	(-1.697, 1.923)
	Thin JMSA	5.291	1.688	(1.982, 8.600)
	Thin LFSA	1.666	1.614	(-1.498, 4.831)
	Thin SCSA	-0.003	0.507	(-0.997, 0.991)
	Thin SPSA	-0.264	0.504	(-1.252, 0.724)
	Thin/Burn HBSA	0.315	1.670	(-2.959, 3.588)
	Thin/Burn LFSA	-6.855	3.067	(-12.866, -0.845)
	Thin/Burn SCSA	0.009	0.930	(-1.813, 1.831)

Table 3.10. Model selection results from weighted regression analysis of chipmunk densities from 6 FFS study areas. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
Density{study area + treatment category (study area)}	397.864	0.000	0.99390	19

Table 3.11. Estimated model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on chipmunk densities from 6 FFS study areas.

Variable	Level	Effect	SE	95% CI
Treatment	Treatment	0.000	0.000	(0.000, 0.000)
Treatment (Study Area)	Treatment HBSA	0.000	0.001	(-0.002, 0.001)
	Treatment JMSA	0.001	0.001	(-0.002, 0.003)
	Treatment LFSA	0.001	0.002	(-0.003, 0.005)
	Treatment SCSA	0.000	0.001	(-0.001, 0.001)
	Treatment SNSA	0.000	0.000	(-0.001, 0.001)
	Treatment SPSA	0.000	0.000	(0.000, 0.001)
	Treatment Category	Burn	0.000	0.000
Thin		0.000	0.000	(0.000, 0.000)
Thin/Burn		0.000	0.000	(0.000, 0.000)

continued

Table 3.11. continued.

Variable	Level	Effect	SE	95% CI
Treatment Category (Study Area)	Burn HBSA	1.433	2.247	(-2.971, 5.838)
	Burn LFSA	-0.371	1.200	(-2.724, 1.981)
	Burn SCSA	-1.003	1.513	(-3.968, 1.963)
	Burn SNSA	0.496	0.640	(-0.760, 1.751)
	Thin HBSA	-1.996	1.421	(-4.781, 0.789)
	Thin JMSA	2.436	0.320	(1.809, 3.062)
	Thin LFSA	6.838	1.083	(4.715, 8.961)
	Thin SCSA	1.494	1.096	(-0.655, 3.643)
	Thin SPSA	0.351	0.212	(-0.064, 0.766)
	Thin/Burn HBSA	-0.273	2.427	(-5.029, 4.484)
	Thin/Burn LFSA	-3.909	1.740	(-7.319, -0.498)
	Thin/Burn SCSA	2.075	2.511	(-2.848, 6.997)

Table 3.12. Model selection results from weighted regression analysis of *Peromyscus* spp. densities from 8 FFS study areas. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
Density{year(study area) + treatment category (study area)}	526.074	0.000	0.98094	39
Density{year (study area) + treatment (study area)}	533.958	7.884	0.01904	31

Table 3.13. Estimated model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on *Peromyscus* spp. densities from 8 FFS study areas.

Variable	Level	Effect	SE	95% CI
Treatment	Treatment	0.000	0.000	(0.000, 0.000)
Treatment (Study Area)	Treatment GCSA	0.078	0.155	(-0.225, 0.382)
	Treatment HBSA	0.003	0.026	(-0.048, 0.055)
	Treatment JMSA	0.101	0.207	(-0.305, 0.507)
	Treatment LFSA	0.130	0.259	(-0.378, 0.637)
	Treatment MRSA	0.013	0.066	(-0.116, 0.142)
	Treatment SCSA	0.001	0.013	(-0.024, 0.026)
	Treatment SNSA	-0.016	0.106	(-0.223, 0.191)
	Treatment SPSA	-0.005	0.019	(-0.042, 0.032)
Treatment Category	Burn	0.000	0.000	(0.000, 0.000)
	Thin	0.000	0.000	(0.000, 0.000)
	Thin/Burn	0.000	0.000	(0.000, 0.000)

continued

Table 3.13. continued.

Variable	Level	Effect	SE	95% CI
Treatment Category (Study Area)	Burn GCSA	4.467	0.854	(2.793, 6.140)
	Burn HBSA	0.251	2.102	(-3.868, 4.370)
	Burn LFSA	14.117	2.847	(8.537, 19.697)
	Burn MRSA	0.675	2.531	(-4.286, 5.636)
	Burn SCSA	0.125	0.910	(-1.659, 1.909)
	Burn SNSA	-0.819	4.348	(-9.342, 7.704)
	Thin GCSA	2.388	1.106	(0.220, 4.555)
	Thin HBSA	0.109	1.144	(-2.133, 2.350)
	Thin JMSA	5.192	2.249	(0.783, 9.601)
	Thin LFSA	1.635	2.087	(-2.456, 5.726)
	Thin SCSA	-0.003	0.640	(-1.256, 1.251)
	Thin SPSA	-0.259	0.647	(-1.527, 1.008)
	Thin/Burn GCSA	3.614	2.929	(-2.126, 9.355)
	Thin/Burn HBSA	0.311	2.118	(-3.841, 4.462)
	Thin/Burn LFSA	-6.727	4.034	(-14.633, 1.179)
Thin/Burn SCSA	0.007	1.178	(-2.303, 2.316)	

Table 3.14. Model selection results from weighted regression analysis of total small mammal biomass from 8 FFS study areas. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
Biomass{year (study area) + treatment}	432.503	0.000	0.76300	24
Biomass{year (study area) + treatment category}	435.667	3.164	0.15688	26
Biomass{year (study area)}	437.055	4.552	0.07836	23

Table 3.15. Estimated model-averaged effect sizes, standard errors (SE), and 95% confidence intervals (CI) from weighted regression analysis of treatment effects on total small biomass from 8 FFS study areas.

Variable	Level	Effect	SE	95% CI
Treatment	Treatment	30.812	21.506	(-11.341, 72.964)
Treatment (Study Area)	Treatment GCSA	0.085	0.175	(-0.259, 0.429)
	Treatment HBSA	-0.165	0.983	(-2.093, 1.762)
	Treatment JMSA	3.908	33.809	(-62.358, 70.174)
	Treatment LFSA	-0.078	0.440	(-0.941, 0.785)
	Treatment MRSA	0.306	1.635	(-2.899, 3.511)
	Treatment SCSA	-0.066	0.206	(-0.470, 0.337)
	Treatment SNSA	-0.189	0.424	(-1.020, 0.643)
	Treatment SPSA	0.139	0.307	(-0.464, 0.741)
Treatment Category	Burn	5.329	9.837	(-13.952, 24.610)
	Thin	9.377	16.777	(-23.506, 42.259)
	Thin/Burn	-16.802	31.310	(-78.170, 44.565)

continued

Table 3.15. continued.

Variable	Level	Effect	SE	95% CI
Treatment Category (Study Area)	Burn GCSA	0.001	0.003	(-0.004, 0.007)
	Burn HBSA	0.004	0.017	(-0.030, 0.037)
	Burn LFSA	-0.003	0.009	(-0.021, 0.015)
	Burn MRSA	0.005	0.026	(-0.045, 0.055)
	Burn SCSA	-0.003	0.006	(-0.015, 0.010)
	Burn SNSA	-0.003	0.007	(-0.016, 0.010)
	Thin GCSA	0.002	0.004	(-0.005, 0.009)
	Thin HBSA	-0.003	0.016	(-0.036, 0.029)
	Thin JMSA	0.062	0.530	(-0.976, 1.100)
	Thin LFSA	0.002	0.010	(-0.017, 0.022)
	Thin SCSA	0.003	0.009	(-0.014, 0.021)
	Thin SPSA	0.002	0.005	(-0.007, 0.012)
	Thin/Burn GCSA	-0.006	0.012	(-0.029, 0.018)
	Thin/Burn HBSA	-0.005	0.019	(-0.041, 0.032)
	Thin/Burn LFSA	0.002	0.010	(-0.018, 0.022)
Thin/Burn SCSA	0.012	0.028	(-0.043, 0.067)	

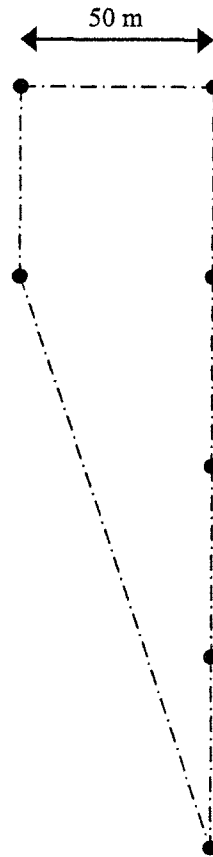


Figure 1. Layout of an example small mammal trapping grid at the HBSA, where black dots represent trap locations. Such trapping grid layouts precluded empirical estimation of effective trap area. A convex polygon (dashed line) was therefore used to calculate effective trap area, and thus small mammal density. Most trapping grids at the HBSA were larger than this example, but many had similarly problematic layouts.

APPENDIX 3A:
MODEL SELECTION RESULTS FROM MODELING OF CAPTURE PROBABILITIES FOR SMALL MAMMAL SPECIES CAPTURED ON
EIGHT FIRE AND FIRE SURROGATE PROGRAM STUDY AREAS, USA

Table 3A.1. Initial capture (p) and recapture probability (c) models and model selection results for southern flying squirrels at the Gulf Coast Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (age) = c (behavior)}	77.681	0.000	0.50970	3
{ p (.) = c (behavior)}	79.208	1.527	0.23754	2
{ p (age + thin) = c (behavior)}	79.872	2.191	0.17042	4
{ p (thin) = c (behavior)}	81.326	3.646	0.08235	3

Table 3A.2. Initial capture (p) and recapture probability (c) models and model selection results for golden mice at the Gulf Coast Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (year + thin + burn + (thin * year)) = c (behavior)}	347.420	0.000	0.19303	7
{ p (year + burn) = c (behavior)}	348.204	0.784	0.13041	5
{ p (year + thin + burn) = c (behavior)}	348.229	0.809	0.12880	6
{ p (age + year + thin + burn + (thin * year)) = c (behavior)}	349.224	1.804	0.07831	8
{ p (thin + burn) = c (behavior)}	349.544	2.124	0.06674	4
{ p (age + year + burn) = c (behavior)}	349.980	2.560	0.05366	6
{ p (age + year + thin + burn) = c (behavior)}	350.012	2.592	0.05281	7
{ p (year + burn + (burn * year)) = c (behavior)}	350.268	2.849	0.04646	6
{ p (year + thin + burn + (burn * year)) = c (behavior)}	350.327	2.907	0.04512	7
{ p (burn) = c (behavior)}	351.128	3.709	0.03022	3
{ p (age + thin + burn) = c (behavior)}	351.514	4.094	0.02492	5
{ p (age + year + burn + (burn * year)) = c (behavior)}	352.059	4.640	0.01897	7
{ p (age + year + thin + burn + (burn * year)) = c (behavior)}	352.126	4.706	0.01836	8
{ p (.) = c (behavior)}	352.173	4.753	0.01793	2
{ p (year) = c (behavior)}	352.241	4.821	0.01733	4

continued

Table 3A.2. continued.

Model	AIC _c	ΔAIC _c	Weight	K
{p (thin) = c (behavior)}	352.244	4.825	0.01730	3
{p (age + burn) = c (behavior)}	352.795	5.375	0.01314	4

Table 3A.3. Initial capture (p) and recapture probability (c) models and model selection results for cotton mice at the Gulf Coast Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
$\{p(\text{age} + \text{year} + \text{unit} + \text{thin} + \text{burn} + \text{thin} * \text{year}) = c(\text{behavior})\}$	3620.012	0.000	0.19851	19
$\{p(\text{year} + \text{unit} + \text{thin} + \text{burn} + \text{thin} * \text{year}) = c(\text{behavior})\}$	3620.822	0.810	0.13238	18
$\{p(\text{age} + \text{year} + \text{unit} + \text{thin} + \text{burn}) = c(\text{behavior})\}$	3620.960	0.949	0.12354	18
$\{p(\text{year} + \text{unit} + \text{thin} + \text{burn}) = c(\text{behavior})\}$	3621.569	1.557	0.09114	17
$\{p(\text{age} + \text{year} + \text{unit} + \text{thin} + \text{burn} + \text{thin} * \text{burn} + \text{thin} * \text{year}) = c(\text{behavior})\}$	3621.946	1.935	0.07545	20
$\{p(\text{age} + \text{year} + \text{unit} + \text{thin} + \text{burn} + \text{burn} * \text{year}) = c(\text{behavior})\}$	3622.456	2.444	0.05850	19
$\{p(\text{year} + \text{unit} + \text{thin} + \text{burn} + \text{thin} * \text{burn} + \text{thin} * \text{year}) = c(\text{behavior})\}$	3622.736	2.724	0.05084	19
$\{p(\text{age} + \text{year} + \text{unit} + \text{thin} + \text{burn} + \text{thin} * \text{burn}) = c(\text{behavior})\}$	3622.893	2.882	0.04699	19
$\{p(\text{year} + \text{unit} + \text{thin} + \text{burn} + \text{burn} * \text{year}) = c(\text{behavior})\}$	3622.979	2.967	0.04503	18
$\{p(\text{age} + \text{year} + \text{unit} + \text{thin} + \text{burn} + \text{thin} * \text{burn} + \text{thin} * \text{year} + \text{burn} * \text{year}) = c(\text{behavior})\}$	3623.388	3.377	0.03669	21
$\{p(\text{year} + \text{unit} + \text{thin} + \text{burn} + \text{thin} * \text{burn}) = c(\text{behavior})\}$	3623.482	3.470	0.03502	18
$\{p(\text{year} + \text{unit} + \text{thin} + \text{burn} + \text{thin} * \text{burn} + \text{thin} * \text{year} + \text{burn} * \text{year}) = c(\text{behavior})\}$	3624.101	4.089	0.02569	20
$\{p(\text{age} + \text{year} + \text{unit} + \text{thin} + \text{burn} + \text{thin} * \text{burn} + \text{burn} * \text{year}) = c(\text{behavior})\}$	3624.426	4.415	0.02184	20
$\{p(\text{year} + \text{unit} + \text{thin} + \text{burn} + \text{thin} * \text{burn} + \text{burn} * \text{year}) = c(\text{behavior})\}$	3624.937	4.925	0.01692	19

Table 3A.4. Initial capture (p) and recapture probability (c) models and model selection results for deer mice at the Hungry Bob Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (mix + year) = c (.)}	471.250	0.000	0.27560	4
{ p (mix) = c (.)}	472.135	0.885	0.17705	3
{ p (mix + year + burn) = c (.)}	472.479	1.230	0.14902	5
{ p (mix + year + thin) = c (.)}	472.672	1.422	0.13536	5
{ p (mix + burn) = c (.)}	474.028	2.778	0.06871	4
{ p (mix + thin) = c (.)}	474.395	3.145	0.05719	4
{ p (mix + thin + burn) = c (.)}	474.707	3.458	0.04892	5
{ p (mix + year + thin + burn) = c (.)}	474.715	3.465	0.04873	6
{ p (mix + thin + burn + thin * burn) = c (.)}	476.344	5.094	0.02158	6
{ p (mix + year + thin + burn + thin * burn) = c (.)}	476.725	5.475	0.01784	7

Table 3A.5. Initial capture (p) and recapture probability (c) models and model selection results for Columbian ground squirrels at the Hungry Bob Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (mix) = c (.)}	50.707	0.000	1.00000	3

Table 3A.6. Initial capture (p) and recapture probability (c) models and model selection results for golden-mantled ground squirrels at the Hungry Bob Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (mix) = c (.)}	223.421	0.000	0.46065	3
{ p (mix + thin) = c (.)}	224.633	1.212	0.25135	4
{ p (mix) = c (behavior)}	225.289	1.868	0.18102	4
{ p (mix + thin) = c (behavior)}	226.341	2.920	0.10699	5

Table 3A.7. Initial capture (p) and recapture probability (c) models and model selection results for yellow-pine chipmunks at the Hungry Bob Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (mix + unit + year) = c (.)}	5057.478	0.000	0.60654	18
{ p (mix + unit + year + burn) = c (.)}	5059.404	1.926	0.23160	19
{ p (mix + unit + burn) = c (.)}	5061.518	4.040	0.08047	18
{ p (mix + unit + year + thin + burn + thin * burn) = c (.)}	5062.860	5.382	0.04114	21
{ p (mix + unit) = c (.)}	5063.776	6.297	0.02603	17
{ p (mix + unit + thin + burn + thin * burn) = c (.)}	5064.994	7.516	0.01415	20

Table 3A.8. Initial capture (p) and recapture probability (c) models and model selection results for red squirrels at the Hungry Bob Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
$\{p(\text{mix}) = c(\cdot)\}$	158.043	0.000	0.60573	3
$\{p(\text{mix} + \text{year}) = c(\cdot)\}$	158.902	0.859	0.39427	4

Table 3A.9. Initial capture (p) and recapture probability (c) models and model selection results for long-tailed voles at the Jemez Mountains Study Area. Capture probabilities were modeled to produce derived abundance estimates Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m.) = c (behavior)}	128.940	0.000	0.73889	3
{ p (a.m. + age) = c (behavior)}	131.020	2.080	0.26111	4

Table 3A.10. Initial capture (p) and recapture probability (c) models and model selection results for Mexican woodrats at the Jemez Mountains Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m. + year + age) = c (behavior)}	151.774	0.000	0.20343	6
{ p (a.m. + year + unit + thin) = c (behavior)}	151.819	0.046	0.19882	9
{ p (a.m. + year + thin + age) = c (behavior)}	152.464	0.690	0.14406	7
{ p (a.m. + year + thin) = c (behavior)}	152.533	0.760	0.13914	6
{ p (a.m. + year) = c (behavior)}	153.338	1.564	0.09306	5
{ p (a.m. + year + unit) = c (behavior)}	153.808	2.034	0.07357	8
{ p (a.m. + year + unit + thin + age) = c (behavior)}	153.929	2.155	0.06924	10
{ p (a.m. + year + unit + age) = c (behavior)}	154.646	2.873	0.04837	9
{ p (a.m. + thin) = c (behavior)}	157.646	5.873	0.01079	4

Table 3A.11. Initial capture (p) and recapture probability (c) models and model selection results for deer mice at the Jemez Mountains Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m. + year + age) = c (behavior)}	2043.405	0.000	0.42832	6
{ p (a.m. + year + thin + age) = c (behavior)}	2044.182	0.777	0.29037	7
{ p (a.m. + session(year) + age) = c (behavior)}	2045.401	1.997	0.15784	9
{ p (a.m. + session(year) + thin + age) = c (behavior)}	2047.342	3.937	0.05981	10
{ p (a.m. + year + unit + thin + age) = c (behavior)}	2048.932	5.527	0.02701	10
{ p (a.m. + year + unit + age) = c (behavior)}	2049.168	5.763	0.02400	9

Table 3A.12. Initial capture (p) and recapture probability (c) models and model selection results for least chipmunks at the Jemez Mountains Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c , Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
$\{p \text{ (a.m. + year + thin)} = c \text{ (behavior)}\}$	1132.426	0.000	0.33634	6
$\{p \text{ (a.m. + session(year) + thin)} = c \text{ (behavior)}\}$	1132.922	0.496	0.26249	9
$\{p \text{ (a.m. + year + thin + age)} = c \text{ (behavior)}\}$	1133.752	1.326	0.17333	7
$\{p \text{ (a.m. + session(year) + thin + age)} = c \text{ (behavior)}\}$	1134.958	2.532	0.09485	10
$\{p \text{ (a.m. + year + unit + thin)} = c \text{ (behavior)}\}$	1135.829	3.403	0.06137	9
$\{p \text{ (a.m. + session(year) + unit + thin)} = c \text{ (behavior)}\}$	1137.310	4.884	0.02926	12
$\{p \text{ (a.m. + year + unit + thin + age)} = c \text{ (behavior)}\}$	1137.564	5.138	0.02577	10
$\{p \text{ (a.m. + session(year) + unit + thin + age)} = c \text{ (behavior)}\}$	1139.314	6.888	0.01074	13

Table 3A.13. Initial capture (p) and recapture probability (c) models and model selection results for southern red-backed voles at the Lubrecht Forest Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (age + year + thin) = c (behavior)}	384.205	0.000	0.29804	5
{ p (age + year) = c (behavior)}	384.748	0.544	0.22710	4
{ p (age + year + thin + burn) = c (behavior)}	385.969	1.764	0.12338	6
{ p (age + year + burn) = c (behavior)}	386.757	2.552	0.08321	5
{ p (age + site + year + thin) = c (behavior)}	387.074	2.870	0.07098	7
{ p (age + site + year) = c (behavior)}	387.537	3.332	0.05633	6
{ p (age + year + thin + burn + thin * burn) = c (behavior)}	387.906	3.702	0.04682	7
{ p (age + site + year + thin + burn) = c (behavior)}	389.074	4.869	0.02612	8
{ p (age + site + year + burn) = c (behavior)}	389.609	5.404	0.01999	7
{ p (age) = c (behavior)}	390.203	5.998	0.01485	3

Table 3A.14. Initial capture (p) and recapture probability (c) models and model selection results for deer mice at the Lubrecht Forest Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (age + unit + year + thin + burn) = c (behavior)}	3561.396	0.000	0.63300	17
{ p (age + unit + year + thin + burn + thin * burn) = c (behavior)}	3563.411	2.015	0.23112	18
{ p (age + unit + year + burn) = c (behavior)}	3565.219	3.823	0.09358	16
{ p (age + unit + year + thin) = c (behavior)}	3567.665	6.270	0.02754	16

Table 3A.15. Initial capture (p) and recapture probability (c) models and model selection results for yellow-pine chipmunks at the Lubrecht Forest Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (age + site + thin) = c (behavior)}	1498.503	0.000	0.23377	6
{ p (age + site + thin + burn) = c (behavior)}	1499.245	0.742	0.16133	7
{ p (age + unit + year + thin + burn) = c (behavior)}	1499.688	1.185	0.12926	16
{ p (age + site + year + thin) = c (behavior)}	1500.526	2.023	0.08502	7
{ p (age + site + thin + burn + thin * burn) = c (behavior)}	1500.811	2.308	0.07372	8
{ p (age + unit + thin + burn) = c (behavior)}	1501.066	2.563	0.06489	15
{ p (age + site + year + thin + burn) = c (behavior)}	1501.183	2.680	0.06120	8
{ p (age + unit + year + thin + burn + thin * burn) = c (behavior)}	1501.521	3.018	0.05168	17
{ p (age + site + year + thin + burn + thin * burn) = c (behavior)}	1502.555	4.052	0.03082	9
{ p (age + unit + burn) = c (behavior)}	1502.756	4.253	0.02788	14
{ p (age + unit + thin + burn + thin * burn) = c (behavior)}	1503.113	4.610	0.02332	16
{ p (age + thin) = c (behavior)}	1504.282	5.779	0.01300	4
{ p (age + unit + thin) = c (behavior)}	1504.664	6.162	0.01074	14
{ p (age + unit + year + burn) = c (behavior)}	1504.806	6.303	0.01000	15

Table 3A.16. Initial capture (p) and recapture probability (c) models and model selection results for cotton mice at the Myakka River Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
$\{p(.) = c(.)\}$	85.577	0.000	0.39863	1
$\{p(\text{site}) = c(.)\}$	86.366	0.789	0.26871	2
$\{p(\text{burn}) = c(.)\}$	87.635	2.058	0.14245	2
$\{p(\text{site} + \text{burn}) = c(.)\}$	88.417	2.840	0.09636	3
$\{p(\text{year}) = c(.)\}$	89.795	4.218	0.04838	3
$\{p(\text{year} + \text{site}) = c(.)\}$	89.919	4.342	0.04548	4

Table 3A.17. Initial capture (p) and recapture probability (c) models and model selection results for cotton rats at the Myakka River Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (age + unit) = c (.)}	1091.789	0.000	0.46904	5
{ p (age + unit + burn) = c (.)}	1093.744	1.955	0.17645	6
{ p (unit) = c (.)}	1095.237	3.448	0.08366	4
{ p (age + year + unit) = c (.)}	1095.823	4.035	0.06238	7
{ p (age + site) = c (.)}	1096.570	4.782	0.04294	3
{ p (unit + burn) = c (.)}	1097.003	5.215	0.03458	5
{ p (age) = c (.)}	1097.181	5.392	0.03165	2
{ p (age + site + burn) = c (.)}	1098.418	6.629	0.01705	4
{ p (age + year) = c (.)}	1098.893	7.104	0.01344	4
{ p (age + burn) = c (.)}	1099.059	7.271	0.01237	3
{ p (year + unit) = c (.)}	1099.164	7.375	0.01174	6

Table 3A.18. Initial capture (p) and recapture probability (c) models and model selection results for deer mice at the Southern Cascades Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (mix) = c (.)}	101.469	0.000	1.00000	3

Table 3A.19. Initial capture (p) and recapture probability (c) models and model selection results for golden-mantled ground squirrels at the Southern Cascades Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (mix + burn) = c (.)}	346.687	0.000	0.39049	4
{ p (mix + year) = c (.)}	347.609	0.921	0.24634	4
{ p (mix) = c (.)}	348.086	1.399	0.19406	3
{ p (mix + year + burn) = c (.)}	348.361	1.674	0.16911	5

Table 3A.20. Initial capture (p) and recapture probability (c) models and model selection results for yellow-pine chipmunks at the Southern Cascades Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (mix + thin) = c (.)}	284.246	0.000	0.27942	4
{ p (mix + thin + burn) = c (.)}	285.426	1.180	0.15489	5
{ p (mix + year + thin) = c (.)}	286.034	1.788	0.11427	5
{ p (mix + thin) = c (behavior)}	286.221	1.975	0.10407	5
{ p (mix + thin + burn) = c (behavior)}	287.379	3.133	0.05833	6
{ p (mix + year + thin + burn) = c (.)}	287.525	3.280	0.05420	6
{ p (mix + year + thin) = c (behavior)}	288.061	3.815	0.04147	6
{ p (mix + year) = c (.)}	288.141	3.896	0.03984	4
{ p (mix + burn) = c (.)}	288.376	4.130	0.03543	4
{ p (mix) = c (.)}	289.313	5.067	0.02218	3
{ p (mix + year + thin + burn) = c (behavior)}	289.485	5.240	0.02034	7
{ p (mix + burn) = c (behavior)}	289.580	5.334	0.01941	5
{ p (mix + year + burn) = c (.)}	289.740	5.495	0.01791	5
{ p (mix + year) = c (behavior)}	289.859	5.614	0.01687	5
{ p (mix) = c (behavior)}	290.364	6.118	0.01311	4

Table 3A.21. Initial capture (p) and recapture probability (c) models and model selection results for Allen's chipmunks at the Southern Cascades Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (mix + unit) = c (behavior)}	2377.072	0.000	0.36376	15
{ p (mix + unit + burn) = c (behavior)}	2378.929	1.857	0.14374	16
{ p (mix + year + unit) = c (behavior)}	2378.984	1.913	0.13980	16
{ p (mix + unit + thin) = c (behavior)}	2379.105	2.034	0.13159	16
{ p (mix + year + unit + burn) = c (behavior)}	2380.953	3.881	0.05224	17
{ p (mix + unit + thin + burn) = c (behavior)}	2380.964	3.893	0.05194	17
{ p (mix + year + unit + thin) = c (behavior)}	2381.020	3.948	0.05052	17
{ p (mix + unit + thin + burn + thin * burn) = c (behavior)}	2381.994	4.922	0.03104	18
{ p (mix + year + unit + thin + burn) = c (behavior)}	2382.991	5.919	0.01886	18
{ p (mix + year + unit + thin + burn + thin * burn) = c (behavior)}	2384.022	6.951	0.01126	19

Table 3A.22. Initial capture (p) and recapture probability (c) models and model selection results for northern flying squirrels at the Sequoia National Park Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
$\{p(\text{effort}) = c(\cdot)\}$	109.104	0.000	0.29568	2
$\{p(\text{effort} + \text{spring burn}) = c(\cdot)\}$	109.126	0.021	0.29255	3
$\{p(\text{effort} + \text{trap density}) = c(\cdot)\}$	110.472	1.368	0.14922	3
$\{p(\text{effort} + \text{trap density} + \text{spring burn}) = c(\cdot)\}$	111.025	1.921	0.11318	4
$\{p(\text{effort} + \text{year}) = c(\cdot)\}$	112.550	3.445	0.05280	4
$\{p(\text{effort} + \text{year} + \text{trap density}) = c(\cdot)\}$	112.877	3.773	0.04483	5
$\{p(\text{effort} + \text{year} + \text{spring burn}) = c(\cdot)\}$	113.405	4.301	0.03443	5
$\{p(\text{effort} + \text{year} + \text{trap density} + \text{spring burn}) = c(\cdot)\}$	114.781	5.677	0.01731	6

Table 3A.23. Initial capture (p) and recapture probability (c) models and model selection results for long-tailed voles at the Sequoia National Park Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (effort) = c (.)}	151.920	0.000	0.32907	2
{ p (effort + fall burn) = c (.)}	153.686	1.766	0.13612	3
{ p (effort + spring burn) = c (.)}	153.771	1.851	0.13045	3
{ p (effort + trap density) = c (.)}	153.838	1.918	0.12613	3
{ p (effort + fall burn + spring burn) = c (.)}	154.111	2.191	0.11003	4
{ p (effort + trap density + fall burn) = c (.)}	154.892	2.972	0.07445	4
{ p (effort + trap density + spring burn) = c (.)}	155.793	3.873	0.04746	4
{ p (effort + trap density + fall burn + spring burn) = c (.)}	155.843	3.923	0.04629	5

Table 3A.24. Initial capture (p) and recapture probability (c) models and model selection results for deer mice at the Sequoia National Park Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
$\{p(\text{effort} + \text{year} + \text{unit} + \text{age} + \text{trap density} + \text{fall burn} + \text{fall burn} * \text{year}) = c(\text{behavior})\}$	13382.473	0.000	0.51021	17
$\{p(\text{effort} + \text{year} + \text{unit} + \text{age} + \text{trap density} + \text{fall burn} + \text{spring burn} + \text{fall burn} * \text{year}) = c(\text{behavior})\}$	13382.582	0.109	0.48322	18

Table 3A.25. Initial capture (p) and recapture probability (c) models and model selection results for golden-mantled ground squirrels at the Sequoia National Park Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (effort + spring burn) = c (behavior)}	101.828	0.000	0.50449	4
{ p (effort + fall burn + spring burn) = c (behavior)}	103.600	1.772	0.20801	5
{ p (effort + trap density + spring burn) = c (behavior)}	104.019	2.191	0.16869	5
{ p (effort + trap density + fall burn + spring burn) = c (behavior)}	105.795	3.967	0.06942	6
{ p (effort) = c (behavior)}	108.619	6.790	0.01692	3
{ p (effort + fall burn) = c (behavior)}	108.769	6.941	0.01569	4
{ p (effort + trap density) = c (behavior)}	109.652	7.823	0.01009	4

Table 3A.26. Initial capture (p) and recapture probability (c) models and model selection results for lodgepole chipmunks at the Sequoia National Park Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (effort + year + trap density + fall burn + spring burn + fall burn * year) = c (behavior)}	3053.664	0.000	0.22003	9
{ p (effort + year + age + trap density + fall burn + spring burn + fall burn * year) = c (behavior)}	3053.685	0.021	0.21777	10
{ p (effort + year + age + trap density + fall burn + fall burn * year) = c (behavior)}	3054.763	1.099	0.12703	9
{ p (effort + year + trap density + spring burn) = c (behavior)}	3054.893	1.229	0.11900	7
{ p (effort + year + trap density + fall burn + fall burn * year) = c (behavior)}	3054.899	1.235	0.11869	8
{ p (effort + year + age + trap density + spring burn) = c (behavior)}	3055.705	2.041	0.07930	8
{ p (effort + year + trap density + fall burn + spring burn) = c (behavior)}	3056.665	3.001	0.04907	8
{ p (effort + year + age + trap density + fall burn + spring burn) = c (behavior)}	3057.438	3.774	0.03334	9
{ p (effort + year + trap density) = c (behavior)}	3059.004	5.340	0.01524	6
{ p (effort + year + age + trap density) = c (behavior)}	3059.750	6.086	0.01049	7

Table 3A.27. Initial capture (p) and recapture probability (c) models and model selection results for Mexican woodrats at the Southwest Plateau Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m.) = c (behavior)}	113.144	0.000	0.35294	3
{ p (a.m. + effort) = c (behavior)}	113.543	0.399	0.28913	4
{ p (a.m. + thin) = c (behavior)}	115.033	1.890	0.13722	4
{ p (a.m. + site) = c (behavior)}	116.390	3.246	0.06965	5
{ p (a.m. + year) = c (behavior)}	116.397	3.253	0.06938	5
{ p (a.m. + effort + site) = c (behavior)}	117.248	4.104	0.04534	6
{ p (a.m. + thin + site) = c (behavior)}	118.404	5.261	0.02543	6
{ p (a.m. + year + site) = c (behavior)}	120.098	6.954	0.01091	7

Table 3A.28. Initial capture (p) and recapture probability (c) models and model selection results for deer mice at the Southwest Plateau Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m. + age + effort + year + site) = c (behavior)}	3200.887	0.000	0.50661	10
{ p (a.m. + age + effort + thin + year + site) = c (behavior)}	3202.873	1.986	0.18768	11
{ p (a.m. + age + effort + year) = c (behavior)}	3203.073	2.186	0.16979	8
{ p (a.m. + age + effort + thin + year) = c (behavior)}	3205.077	4.190	0.06235	9
{ p (a.m. + age + effort + session(year) + site) = c (behavior)}	3206.976	6.089	0.02413	14
{ p (a.m. + age + effort + year + unit) = c (behavior)}	3207.942	7.055	0.01488	19

Table 3A.29. Initial capture (p) and recapture probability (c) models and model selection results for golden-mantled ground squirrels at the Southwest Plateau Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m. + year) = c (behavior)}	194.310	0.000	0.40748	6
{ p (a.m. + thin + year) = c (behavior)}	195.342	1.032	0.24325	7
{ p (a.m. + age + year) = c (behavior)}	195.841	1.531	0.18953	7
{ p (a.m. + age + thin + year) = c (behavior)}	196.695	2.385	0.12368	8

Table 3A.30. Initial capture (p) and recapture probability (c) models and model selection results for gray-collared chipmunks at the Southwest Plateau Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
$\{p \text{ (a.m. + age + effort + thin + session(year) + unit)} = c \text{ (behavior)}\}$	3199.840	0.000	0.49517	23
$\{p \text{ (a.m. + age + effort + thin + session(year))} = c \text{ (behavior)}\}$	3201.832	1.991	0.18296	15
$\{p \text{ (a.m. + age + effort + thin + session(year) + site)} = c \text{ (behavior)}\}$	3201.872	2.032	0.17926	15
$\{p \text{ (a.m. + age + thin + session(year) + unit)} = c \text{ (behavior)}\}$	3204.719	4.879	0.04319	22
$\{p \text{ (a.m. + age + effort + session(year) + unit)} = c \text{ (behavior)}\}$	3205.526	5.686	0.02885	22
$\{p \text{ (a.m. + age + effort + thin + unit)} = c \text{ (behavior)}\}$	3206.190	6.350	0.02070	16
$\{p \text{ (a.m. + age + effort + session(year))} = c \text{ (behavior)}\}$	3206.402	6.562	0.01861	12

Table 3A.31. Initial capture (p) and recapture probability (c) models and model selection results for cliff chipmunks at the Southwest Plateau Study Area. Capture probabilities were modeled to produce derived abundance estimates. Model selection results include AIC_c , relative AIC_c (ΔAIC_c), Akaike weight, and number of parameters (K), for those models with at least 1% of the Akaike weight.

Model	AIC_c	ΔAIC_c	Weight	K
{ p (a.m.) = c (behavior)}	92.601	0.000	1.00000	3

CHAPTER 4:
AN OCCUPANCY MODEL TO RECONSTRUCT HISTORICAL FOREST FIRE REGIMES
FROM FIRE SCARS

INTRODUCTION

Historical ecological data have been used to understand ecosystem structure and function as well as to set guidelines for ecosystem management (Swetnam et al. 1999, Romme et al. 2000). Ponderosa pine (*Pinus ponderosa*) forests, particularly forests in the southwestern United States, constitute an ecosystem in which historical data have played a relatively large role in informing ecological knowledge and management planning. A major focus of current research and management efforts in ponderosa pine forests is on restoring ecosystem structure and function that were apparently modified after EuroAmerican settlement in the mid-nineteenth century (Covington and Moore 1994, Moore et al. 1999, Allen et al. 2002). Changes in ecosystem structure and function appear to be linked to changes in the fire regime in these forests, notably transition from a pre-EuroAmerican settlement fire regime of frequent, low-severity fires to long fire-free periods in the early 20th century, followed by current trends toward fires of increasing size and severity. There is tremendous research and management interest in the use of fuel reduction or restoration treatments, consisting primarily of thinning and prescribed fire, to restore forests to pre-EuroAmerican settlement conditions, with more open forests, richer herbaceous understories, and lower risk of severe wildfire (Covington et al. 1997; Lynch et al. 2000; Fulé et al. 2001*a,b*). Historical data have been used to investigate drivers of historical fire regimes (Swetnam 1990), document changes in fire regimes since EuroAmerican settlement (Fulé et al. 1997) and investigate the causes of these changes (Savage and Swetnam 1990).

A major source of historical data on fire regimes in ponderosa pine forests is from fire scars in tree growth annuli, including live trees, dead logs, snags, and stumps (Dieterich 1980, Stokes 1980, Dieterich and Swetnam 1984, Swetnam and Dieterich 1985, Baisan and Swetnam 1990). Fires that occur at the base

of a tree may, in some cases, lead to physiological damage to the tree, thus resulting in an identifiable scar in the annulus for that year. Growth annuli can be cross-dated using dendrochronological techniques, leading to high temporal resolution in scar dating (Baisan and Swetnam 1990, Swetnam et al. 1999), i.e., scars and therefore fires can be dated to annual resolution. The formation of the first scar on a tree leads to a much higher probability of subsequent scarring due to the flammability of exposed wood and resin (Johnson and Gutsell 1994, Swetnam et al. 1999), resulting in what is referred to as a recorder tree. Recorder trees can be identified by prominent triangular injuries near their bases; these injuries are sampled by removing a wedge or cross-section from the tree at the site of the injury. The samples are then prepared, cross-dated with known regional dendrochronologies, and fire scars are dated to year and sometimes to season. Such studies are particularly suited for southwestern ponderosa pine forests because dead recorders, such as snags, logs, and stumps, tend to be well preserved due to the low decay rates in these dry forests, thereby increasing the amount of historical information available (Covington et al. 1997).

Fire scar data have been used to assess various parameters of the historical fire regime, primarily fire return interval and spatial extent of fires. However, there have been objections to the methods used to assess these parameters, and there is uncertainty about the strength of inference from fire scar datasets (Johnson and Gutsell 1994, Minnich et al. 2000, Veblen 2000, Baker and Ehle 2001). There is a need for more robust inferential methods as fire-scar studies are used not just to lend scientific support to the reintroduction of fire, but to make recommendations for the management of prescribed fire regimes, for example, intervals between burns and the size of burns (Swetnam et al. 1999, Baker and Ehle 2001). The underlying uncertainty in fire scar studies lies in the fact that all fires are not recorded as scars on recorder trees, and, furthermore, scars can be destroyed by more recent fires, so the probability of detecting a fire on a recorder tree given that a fire occurred at the base of the tree is < 1 . Formally, the probability of detecting a fire is equal to the probability that a fire occurred, multiplied by the probability that a scar was formed given that a fire occurred, multiplied by the probability that the scar was retained given that it formed:

$$\text{Pr}(\text{detecting fire}) = \text{Pr}(\text{fire occurred}) * \text{Pr}(\text{scar formed} | \text{fire occurred}) * \text{Pr}(\text{scar retained} | \text{scar formed}).$$

Fire return interval is the interval between successive fires in a specified area (Romme 1980), e.g., at a recorder tree. The mean fire return interval is the average of fire return intervals across time in a defined area. Fire return intervals as currently constructed are frequently termed composite mean fire

return intervals (Dieterich 1980). All fires recorded anywhere in a forested stand of variable area are added together and the composite mean fire return interval (CMFI) is the average of the intervals between all fires in the stand. It can be seen, however, that the CMFI depends on the area sampled, because some recorded fires may not have burned the entire sampled stand, and as stand size increases, more fires will have occurred in the stand (Baker and Ehle 2001, Morgan et al. 2001). Therefore, CMFI is a description of the average number of years during which no fire burned anywhere in the stand. Any given point in a stand, however, possibly burned less often than this. As an attempt to correct for this problem, some workers have calculated CMFI based on scars that appeared on a certain percentage of the trees (e.g., 10% or more and 25% or more of trees; Savage and Swetnam 1990, Fulé et al. 1997, Fulé et al. 2003), thereby attempting to reduce the impact of small fires on the calculation of CMFI. However, this method may change the value of CMFI substantially (e.g., Swetnam 1990), and rules for including only a certain proportion of fire-scarred samples are *ad hoc* and inherently arbitrary. Additionally, no estimator of precision is available for CMFI (Morgan et al. 2001). Rather than basing inference solely on the mean of intervals between fires as in the CMFI, some investigators have also computed the Weibull median probability interval, which may better reflect central tendencies than the mean, though the ecological interpretation of the parameters of the Weibull distribution is difficult (Grissino-Mayer 1999). The use of the Weibull distribution does not solve the difficulties associated with study area size.

No quantitatively rigorous method is available to estimate the proportion of an area burned in a given year from historical data (Minnich et al. 2000, Morgan et al. 2001, Fulé et al. 2003). The relative proportion of recorder trees in a stand that have a scar in a given year has been used as an index of fire size and/or severity (Swetnam and Dieterich 1985, Fulé et al. 1997). However, size and severity cannot be separated using this method because the detection probabilities of fires are not estimated. Presumably, more severe fires have a higher probability of scarring trees, though this assumption has not been directly tested. Dieterich (1980) noted that it is not possible to use widely spaced scars in the same year to surmise that the area between the scars burned in that year, as multiple disjunct fires may have burned one stand in a given year. Again, there is no method for estimating the uncertainty around an estimate of fire extent (Morgan et al. 2001).

Here I propose a method to estimate both the mean fire return interval in such a way as to eliminate the confounding factor of sampling scale, as well as the proportion of an area burned in a year. These statistics may be estimated through application of theory developed to estimate site occupancy probabilities in animal populations with imperfect detection probabilities (MacKenzie et al. 2002, Tyre et al. 2003). The similarities between estimating detection probabilities for animals and detection probabilities for fires from fire scars in tree rings suggest that useful insights could be gleaned from the theory behind models designed to correct for imperfect detection of animals. The method I present includes the specification of statistical models in a likelihood framework, which allows for the use of information-theoretic model selection and model-based inferential methods (Burnham and Anderson 2002), for example, in the consideration of models allowing for the inclusion of various types of covariates. Such modeling efforts should yield useful insights into mechanisms of both fire occurrence and detection.

Occupancy Model and Analogy to Fire Occupancy

The proposed model for analysis of fire scar datasets is the model of MacKenzie et al. (2002), hereafter referred to as the occupancy model. This model is equivalent to the zero-inflated binomial model of Tyre et al. (2003). The occupancy model was designed to estimate the proportion of sites on a landscape occupied by a species (primarily applied to animal species) when the probability of detecting the species is < 1 . Use of the method requires that multiple visits to a site (occasions) be undertaken, during which the species is either detected or not, over a period of time during which the population can be assumed to be closed to extinction and colonization. Through this sampling scheme, the probability of detection at each occasion (p_i) and the proportion of occupied sites (ψ) can be estimated. The occupancy model also allows for missing values on some sites at some occasions, for example, if some sites were not sampled on a particular occasion due to logistical constraints.

The analogous application of the occupancy model to fire scar studies involves the selection of sites on a landscape of interest that are small enough that they can be assumed “closed” to fire, so that the entire site either burned or did not burn in a given year. Each site must contain ≥ 1 recorder trees that were active, that is, alive and capable of recording a fire, in each year to which inference is desired. Some portion of the sites would need to have ≥ 2 recorder trees in order to estimate detection probability of fire within a site. The data then consist of binomial “encounter histories” for each site and year combination in

the data set (Table 4.1), in which “occasions” are represented by recorder trees located within a site, so that multiple recorder trees at a site are substituted for repeat visits to a site over time. From this data, inference may be made to a landscape of sites or a time series of years, including the annual percent of area burned or the return interval of fire.

Two parameters are estimable, including

$$p_t = \text{Pr}(\text{tree } t \text{ has fire scar} \mid \text{fire burned in vicinity of tree } t)$$

and (if encounter histories for each site and year combination are grouped by site for analysis)

$$\psi_s = \text{Proportion of sampled years in which a fire burned at site } s$$

or (if encounter histories for each site and year combination are grouped by year for analysis)

$$\psi_y = \text{Proportion of sampled sites in which a fire burned in year } y$$

Estimation of the parameters occurs through specification of the probability structure associated with each of the encounter histories. For illustration purposes, consider the first detection probability in Table 4.1: 0110. The probability of observing this encounter history is equal to $\psi(1 - p_A)p_B p_C(1 - p_D)$, that is, the site was occupied (ψ), no fire was observed at recorder tree A ($1 - p_A$), fires were observed at both recorder tree B (p_B) and C (p_C), and no fire was observed at recorder tree D ($1 - p_D$). The second encounter history in Table 4.1 is 0000, with probability structure $\psi(1 - p_A)(1 - p_B)(1 - p_C)(1 - p_D) + (1 - \psi)$. This encounter history could have arisen from one of 2 possibilities: either site s was unoccupied in year y ($1 - \psi$) or it was occupied (ψ) but a fire was not detected at recorder trees A, B, C, or D [$(1 - p_A)(1 - p_B)(1 - p_C)(1 - p_D)$]. Summarizing the probability structure for all possible encounter histories results in the joint likelihood function of MacKenzie et al. (2002) for estimation of ψ and each of the p_t detection probabilities:

$$\mathfrak{L}(\psi, p_t) = \left\{ \psi^n \prod_{t=1}^T p_t^{n_t} (1 - p_t)^{n - n_t} \right\} \left\{ \psi \prod_{t=1}^T (1 - p_t) + (1 - \psi) \right\}^{N - n} \quad (1)$$

where T is the number of recorder trees per site, N is the total number of sites or years, n_t is the number of sites or years where a fire was detected at recorder tree t , and n is the number of sites or years where a fire was detected at ≥ 1 recorder tree. In practice, multiple groups of sites or years could be analyzed simultaneously, with some cross-group estimation of parameters. This would increase modeling efficiency while inducing a covariance across the multiple estimated ψ_s or ψ_y .

Then, estimators of interest allowing inference to the entire study area include mean fire return interval (MFI):

$$\text{MFI} = \frac{N_S}{\sum_s \psi_s} \quad (2)$$

where N_S is the total number of sites analyzed. This estimator is the inverse of the mean (across sites, where sites are represented by groups in the analysis) of the proportion of sampled years in which a fire occurred, for example, $\bar{\psi}_s = 0.3$ implies an MFI of $1/0.3 = 3.4$ years. The variance estimator for MFI can be derived using a delta method approximation (Seber 2002) as:

$$\text{var}(\text{MFI}) = \left\{ \frac{N_S}{\left(\sum_s \psi_s \right)^2} \right\}^2 \left(\text{var} \sum_s \psi_s \right) = \left\{ \frac{N_S}{\left(\sum_s \psi_s \right)^2} \right\}^2 \left[\sum_s \left\{ \text{var}(\psi_s) + \sum_{t, s \neq t} \text{cov}(\psi_s, \psi_t) \right\} \right] \quad (3)$$

The second parameter of interest is

$$\text{Average Fire Size} = \frac{\sum_y \psi_y}{N_Y} * A \quad (4)$$

where N_Y is the total number of years analyzed (where years are represented by groups in the analysis) and A is the size of the study area. Here, the estimator of variance is

$$\text{var}(\text{Average Fire Size}) = \left(\frac{A}{N_Y} \right)^2 \left(\text{var} \sum_y \psi_y \right) = \left(\frac{A}{N_Y} \right)^2 \left[\sum_y \left\{ \text{var}(\psi_y) + \sum_{z, y \neq z} \text{cov}(\psi_y, \psi_z) \right\} \right] \quad (5)$$

One important difference from the occupancy model, when analyzing fire scar data, is that a model with fully time-specific detection probabilities is not sensible. This is because there is no relation between tree t at site A and tree t at site B; trees are not arranged in a meaningful order in each site as occasions are arranged in time in the occupancy model.

Sampling

Additional criticisms of fire scar studies have focused on the sampling methods employed. These criticisms have primarily concerned the non-random sampling of fire-scarred trees. Selective, or targeted,

sampling of trees has been the standard method of fire-scar sampling, whereby a landscape of interest is searched for the trees with the longest and largest record of fire-scars and these trees are sampled to calculate statistics such as CMFI (Swetnam and Dieterich 1985, Baisan and Swetnam 1990, Swetnam and Baisan 1996, Fulé et al. 1997, Fulé et al. 2003). This method has received criticism (Johnson and Gutsell 1994, Baker and Ehle 2001) because of its nonrandom nature, though Swetnam and Baisan (1996) contend that because of the high heterogeneity in the fire scar records in recorder trees, caused by factors such as the position of the tree in the landscape, bark thickness, etc., it is inefficient to sample trees as if they all belong to the same population. Critics counter that the non-random nature of selection will result in unknown bias in calculation of statistics such as CMFI. Bias could be induced if, for example, trees with a tendency to incur greater numbers of scars occurred in areas that also tended to receive more fires.

In the model presented here, sampling to produce a fire scar dataset would consist of selecting random points in a landscape to which inference is desired, then censusing (or less likely, selecting a random sample of) recorder trees in a circle of radius r around the random point. Random sampling of sites and a census or random sample of recorder trees within sites insures that the sampling process is not correlated with aspects of the fire regime, and that statistical inference is supported (Johnson and Gutsell 1994, Minnich et al. 2000). Each circle of radius r would comprise a site. The radius r should be constant across sites and r should be adequate to provide 1 or more recorder trees at each site/year combination, but not so large as to risk serious violation of the assumption of spatial closure. Furthermore, placing a site across geologic features that would lead to a lack of spatial closure, such as cliffs, rivers, etc., should be avoided. One important consideration is that it is not possible to know in the field what years a given recorder tree will cover, i.e., whether a recorder tree will be “active” in a given year. Therefore, maximizing the number of possible samples per site will maximize the information available in the dataset, thereby leading to the most precise, unbiased estimates of fire regime parameters.

Within sites, recorder trees will generally be recognized by an external injury at the tree’s (or log’s, snag’s, etc.) base. To be considered a recorder tree, a tree must have some non-negligible probability of recording an interval between fire events, because the interval between fire events is of primary interest for inference. Once a tree is first scarred, it then becomes a “recorder” tree that is available for further scarring, until its death. Johnson and Gutsell (1994) correctly contend that the tree pith-to-first scar period

and the last scar-to-tree death period do not represent real fire-free intervals. Inclusion of the pith-to-first scar portion of the sample has been argued for (Baker and Ehle 2001) but would not be valid because before the tree is first scarred, it is not available for scarring, and thus cannot record the interval between fires.

Sampling would ideally include taking an entire cross section of the tree in order to most accurately cross-date the sample and establish the year of fire (Stokes 1980, Madany et al. 1982, Dieterich and Swetnam 1984, Swetnam and Dieterich 1985, Baisan and Swetnam 1990). Some fires may be recorded on only one side of a fire scar (Stokes 1980), therefore an entire cross section would increase detection probability.

Model Assumptions

The following are assumptions required in order to make valid inference from the analysis:

- Sites are geographically closed to fire, i.e., every point in a site experiences the same fires as every other point in the same site.
- Trees are homogenous with respect to detection probability of fires. This assumption can be relaxed if appropriate tree-specific covariates can be identified to model detection probability.
- Wildfire is not stand-replacing.
- At least 1 active fire scarred tree can be located in each site.

When estimating spatial extent of fire:

- Sites are independent samples.
- Sites are homogenous with respect to probability of fire occupancy. This assumption can be relaxed if appropriate site-specific covariates can be identified to model ψ_y .
- Sites are homogenous with respect to detection probability of fires. This assumption can be relaxed if appropriate site-specific covariates can be identified to model detection probability.

When estimating fire return interval:

- Years are independent samples.
- Years are homogenous with respect to probability of fire occupancy. This assumption can be relaxed if appropriate year-specific covariates can be identified to model ψ_s .

- Years are homogenous with respect to detection probability of fires. This assumption can be relaxed if appropriate year-specific covariates can be identified to model detection probability.

SIMULATION METHODS

Historical datasets do not allow the investigator control over the probability of fire detection, and only allow limited control over the number of recorder trees included in a site (by expanding the size of the site). Furthermore, it is likely that homogeneity assumptions may be frequently violated. I therefore simulated data under a simple site- or year-specific model (i.e., with only 1 analysis group) to determine the effect of the number of recorder trees (T), the probability of fire detection (p), and heterogeneity in detection across trees in a site on estimator performance. Data were simulated and analyses of the data were conducted in Program MARK 3.2 (White and Burnham 1999), which allows for user-specified simulation and analysis of data under the occupancy model. In all simulations, sample size of number of sites (N_S) or years (N_Y) was 100, and the proportion of sites or years occupied was 0.3 (i.e., $\psi = 0.3$). Results of each simulation scenario are based on 6000 simulations. I calculated relative bias

$\left(\text{RB} = \frac{E(\psi) - \psi}{\psi} \right)$, expected variance (EV), mean square error = $\text{RB}^2 + \text{EV}$, and confidence interval coverage (CI coverage) of ψ for each simulation scenario.

For the first set of simulations, I examined the impact of the number of recorder trees (T) and the probability of fire detection (p) on estimator performance for ψ . I generated data under model $p(\cdot)$, so that detection probability was constant across recorder trees within a site and across sites. I then considered various numbers of recorder trees (T) per site, over 4 levels: 2, 3, 4, or 5 recorder trees per site. I simultaneously varied detection probability (p) over 3 levels: 0.25, 0.50, and 0.75. Therefore, 9 scenarios were considered, with each of the combinations of number of recorder trees and detection probability levels. For each simulation, I used the generating model to analyze the data, model $p(\cdot)$.

I designed a second set of simulations to examine the impact of heterogeneity in detection across trees within a site on estimator performance for ψ . In this case, the detection probability was not constant, but varied across recorder trees. I generated data under model $p(t)$, where detection varied by recorder tree. I specified $T = 3$, and a mean detection probability (\bar{p}) of 0.5. I then considered 4 different scenarios: (1) $\bar{p} = 0.5$, standard deviation = 0 (no heterogeneity: $p_1 = p_2 = p_3 = 0.50$); (2) $\bar{p} = 0.5$, standard deviation =

0.05 (low heterogeneity: $p_1 = 0.45, p_2 = 0.50, p_3 = 0.55$); (3) $\bar{p} = 0.5$, standard deviation = 0.1 (moderate heterogeneity: $p_1 = 0.40, p_2 = 0.50, p_3 = 0.60$); and (4) $\bar{p} = 0.5$, standard deviation = 0.2 (high heterogeneity: $p_1 = 0.30, p_2 = 0.50, p_3 = 0.70$). I then used model $p(\cdot)$ to analyze the data estimated under $p(t)$.

RESULTS

The number of samples in a site (T) had an important impact on relative bias (RB) of ψ . At low numbers of recorder trees and low detection probabilities, there was a positive RB on ψ , i.e., it was overestimated (Figure 4.1). RB on ψ was seriously high (over 0.4) with only 2 recorder trees and $p = 0.25$. This was partly due to a relatively large number of simulations (15%) in which ψ was estimated to be 1. This extreme overestimate of ψ occurred in a maximum of less than 0.2% of simulations in all other simulation scenarios. With $p = 0.5$ and $p = 0.75$, RB of ψ was under 0.1 for all levels of T . With $p = 0.25$, at least $T = 4$ was required to achieve a RB under 0.1. Results were similar for expected variance (EV) (Figure 4.2). EV of ψ was highest at $p = 0.25$ with $T = 2$ and $T = 3$. The results for mean square error (MSE; Figure 4.3) further illustrate the point that $T = 2$ and $p = 0.25$ results in poor performance of the estimator of ψ . Confidence interval (CI) coverage similarly was poor at $T = 2$ and $p = 0.25$, although most other levels resulted in CI coverage near nominal (Figure 4.4).

Results from the heterogeneity simulations indicate increasing RB, EV, and MSE with increasing levels of heterogeneity (Table 4.2). The direction of the RB was the same as above, i.e., increasing positive bias on ψ with increasing levels of heterogeneity. CI coverage was near nominal for all heterogeneity simulation scenarios.

DISCUSSION

Sampling and Analysis Considerations

Simulations suggest that obtaining at least 3 recorder trees in a site should be a goal of investigators implementing this analysis, unless detection probabilities are known to be high. Low decomposition rates in southwestern ponderosa pine forests should support greater numbers of recorder trees in these forests, and some minimum estimates of expected detection probabilities suggest that detection probabilities above 0.25 may be possible to achieve. Fulé et al. (1997) found a maximum proportion of recorder trees scarred per year of 63%. Swetnam (1990) noted that in regional fire years

(years where fires were widespread), up to 80% of recorder trees recorded fires. Swetnam and Dieterich (1985) had a maximum of 62-65% of recorder trees scarred in some years. However, it is important to note that each of these studies relied on targeted sampling, seeking out the trees in a landscape which recorded the most fires for the longest period, thus these rates may not be as high on a site-by-site basis. The simulations presented here assume that each site would have the same number of recorder trees. Estimators may not perform as well if this represents a mean number of recorder trees with some large variance, i.e., some sites have as few as 1 recorder tree, while other sites have more recorder trees.

One problematic assumption of the model may be the assumption of independence across sites and/or years. Highly synchronous fire regimes may result in an area where there are few barriers to fire spread (Dieterich 1980, Swetnam and Dieterich 1985, Swetnam 1990, Baisan and Swetnam 1990, Fulé et al. 1997, Fulé et al. 2003), creating fire regimes that are spatially autocorrelated. Furthermore, fire regimes may be temporally autocorrelated (Morgan et al. 2001), whereby fire burning in year y may influence the probability of fire burning in year $y + 1$ because of fuel consumption in year y . Such lack of independence results in underestimation of uncertainty about the estimated parameters. One method for dealing with spatial autocorrelation is to pick a larger study area and choose sites randomly within it, such that sites are not frequently directly adjacent. Additionally, goodness-of-fit and variance inflation should be an integral part of any analysis. MacKenzie and Bailey (2004) present a general χ^2 goodness-of-fit test for the occupancy model to determine lack of model fit and to estimate a variance inflation factor (\hat{c}). The calculation of \hat{c} is based on the ratio of the calculated χ^2 goodness-of-fit statistic to a parametric bootstrap-based χ^2 statistic. However, the test is most sensitive to assumption violations in p rather than in ψ . Especially with sparser data sets, it would be sensibly conservative to inflate variances by \hat{c} even if a significant lack of fit is not demonstrated by the test statistic.

An additional potentially problematic assumption is the assumption of homogeneity in probability of fire occurrence or detection across sites within a year or years within a site, as well as the assumption of homogeneity in detection probabilities across trees within a site. Application of individual covariates to model differences will be useful (discussed below) but all sources of heterogeneity may not be identifiable. Eventually, mixture distributions may be applied to the occupancy model to better deal with heterogeneity;

though fitting mixture distributions will require higher numbers of recorder trees per site. Goodness-of-fit testing and variance inflation will serve to correct for some degree of extra-binomial variation.

Applications

Because the occupancy model is likelihood-based, it lends itself to information-theoretic model selection and inferential methods (Burnham and Anderson 2002). Model selection tools include AIC (Akaike's Information Criterion; Akaike 1973), AIC_c (small sample correction of AIC; Hurvich and Tsai 1989), or $QAIC_c$ (when extra-binomial variation is present; Lebreton et al. 1992, Burnham and Anderson 2002). Interesting applications of the modeling approach described herein rely on model selection to evaluate evidence for hypotheses about mechanisms resulting in fire occurrence and/or scar formation and retention. Here I consider 3 types of predictor variables, those which are tree-specific, site-specific, or year-specific.

Tree-specific covariates could be used to model the fire detection process. For example, a tree-specific covariate of interest would be the age of each recorder tree during a given year. Note that this covariate would always be specific to trees within each site (analogous to a time-dependent individual covariate in the occupancy model). Using such a covariate, an investigator could entertain 2 possible hypotheses, represented by models $p(\text{age})$ or $p(\cdot)$, that is, formation and retention (detection) of a scar is a function of the age of the tree, or it is not. Model selection methods would allow evaluation of the weight of evidence for each of these hypotheses. Such approaches could allow for better information on the mechanisms of fire scar formation (Johnson and Gutsell 1994).

Site-specific predictors are variables associated with a site that may be related either to fire occurrence or detection probability. These variables will generally apply to all years at a site simultaneously. For example, average slope of a site may have an impact on scarring probability. Note that when these covariates are used in estimation of ψ_y , the proportion of sites burned in a given year, they are individual covariates, that is, they apply to individual encounter histories within a dataset that is grouped by year. Alternately, when these covariates are used in estimation of ψ_s , the proportion of years burned at a given site, they apply to all members of the group of years at a given site.

Year-specific predictors are associated with a specific year in a dataset, and will generally apply to all sites simultaneously. These variables would be individual covariates when estimating ψ_s , but group

covariates when estimating ψ_y . Examples include climate variables (Swetnam 1990) that may be used to predict fire events in a given year. Also, climate variables may influence fire severity and in turn impact detection probability. Additional examples of year-specific covariates include the degree of human settlement, or effort spent on fire suppression. Modeling the impacts of such covariates would allow a rigorous analysis of mechanisms resulting in post-European settlement declines in fire occurrence.

Finally, estimation of variability in fire regimes over time and space is needed (Morgan et al. 2001). Random effects and variance components analyses are suited to applications of these kinds, and large datasets, with multiple sites and years, would allow for estimation of temporal and spatial process variance in fire regime parameters (Burnham et al. 1987). For instance, variance components analysis of multiple computed ψ_s over a landscape would give an estimate of the variance in fire return intervals over space, or similarly, variance components analysis of multiple computed ψ_y would provide an estimate of the variance in area burned over years.

An empirical analysis based on the modeling framework described here will highlight further challenges and opportunities associated with this approach. Some appropriate data sets may be extant, if based on a random sample or census of recorder trees in a study area of interest, where all samples are geographically referenced. I recommend that a random sample or census of recorder trees and geographic referencing of samples should be standard practice for all future fire history investigations. Year-, site-, and tree-specific covariates of potential interest should also be identified prior to sampling.

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Table 4.1. Example encounter “histories” for estimating mean fire return interval (a) and proportion of area burned (b). A “0” denotes a fire was not recorded by a given recorder tree, a “1” denotes a fire was recorded.

Scenario	Site	Year	Recorder A	Recorder B	Recorder C	Recorder D
a	A	1	0	1	1	0
	A	2	0	0	0	0
	A	3	0	0	NA ^a	NA
	A	4	0	1	0	1
	A	5	0	0	0	0
	A	6	1	1	0	NA
	A	7	0	0	0	NA
	A	8	1	1	NA	NA
b	A	1	0	1	1	0
	B	1	0	0	0	0
	C	1	0	0	NA	NA
	D	1	0	1	0	1
	E	1	0	0	0	0
	F	1	1	1	0	NA
	G	1	0	0	0	NA
	H	1	1	1	NA	NA

^aFor illustration, NA denotes a recorder tree that was Not Active during a particular site/year combination.

Table 4.2. Simulation results ($n = 6000$ for each level) for proportion occupied at 4 levels of heterogeneity in within-site detection rates. Results are based on 3 recorder trees per site. At no heterogeneity, $p_1 = p_2 = p_3 = 0.5$. At low heterogeneity, $p_1 = 0.45, p_2 = 0.5, p_3 = 0.55$. At moderate heterogeneity, $p_1 = 0.4, p_2 = 0.5, p_3 = 0.6$. At high heterogeneity, $p_1 = 0.3, p_2 = 0.5, p_3 = 0.7$.

Heterogeneity Level	Relative Bias	Expected Variance	Mean Square Error	CI Coverage
None ($\bar{p} = 0.5, SD = 0$)	0.0162	0.0030	0.0033	0.9517
Low ($\bar{p} = 0.5, SD = 0.05$)	0.0223	0.0031	0.0036	0.9553
Moderate ($\bar{p} = 0.5, SD = 0.1$)	0.0287	0.0031	0.0039	0.9463
High ($\bar{p} = 0.5, SD = 0.2$)	0.0606	0.0033	0.0070	0.9537

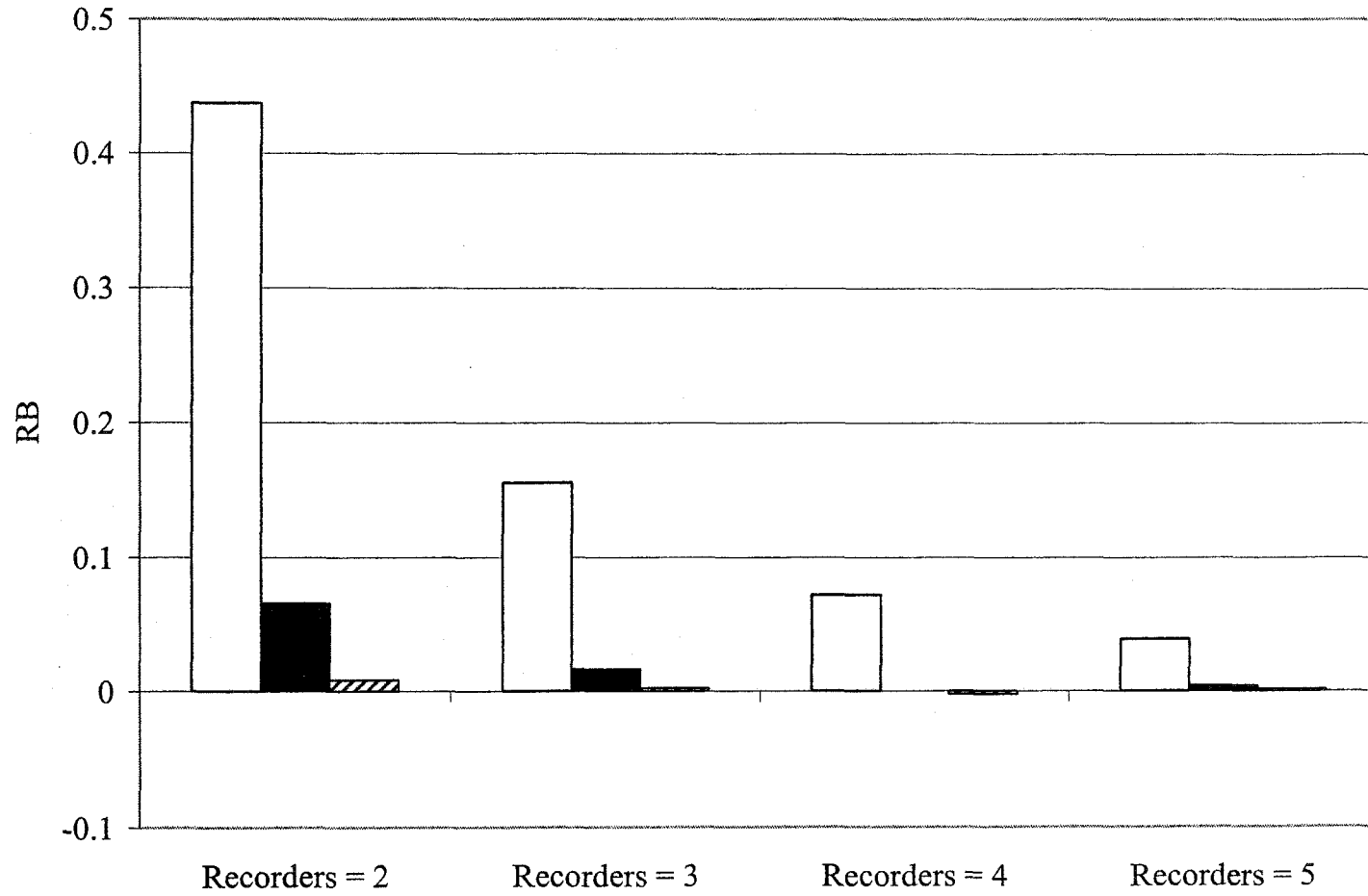


Figure 4.1. Relative bias (RB) in proportion of sites occupied ($n = 6000$ simulations), under 3 levels of detection probability (p) and 4 levels of number of recorder trees per site (t). Simulations are based on a true $\psi = 0.3 = 30\%$ of 100 sites occupied. White bars represent $p = 0.25$, black bars represent $p = 0.50$, and striped bars represent $p = 0.75$.

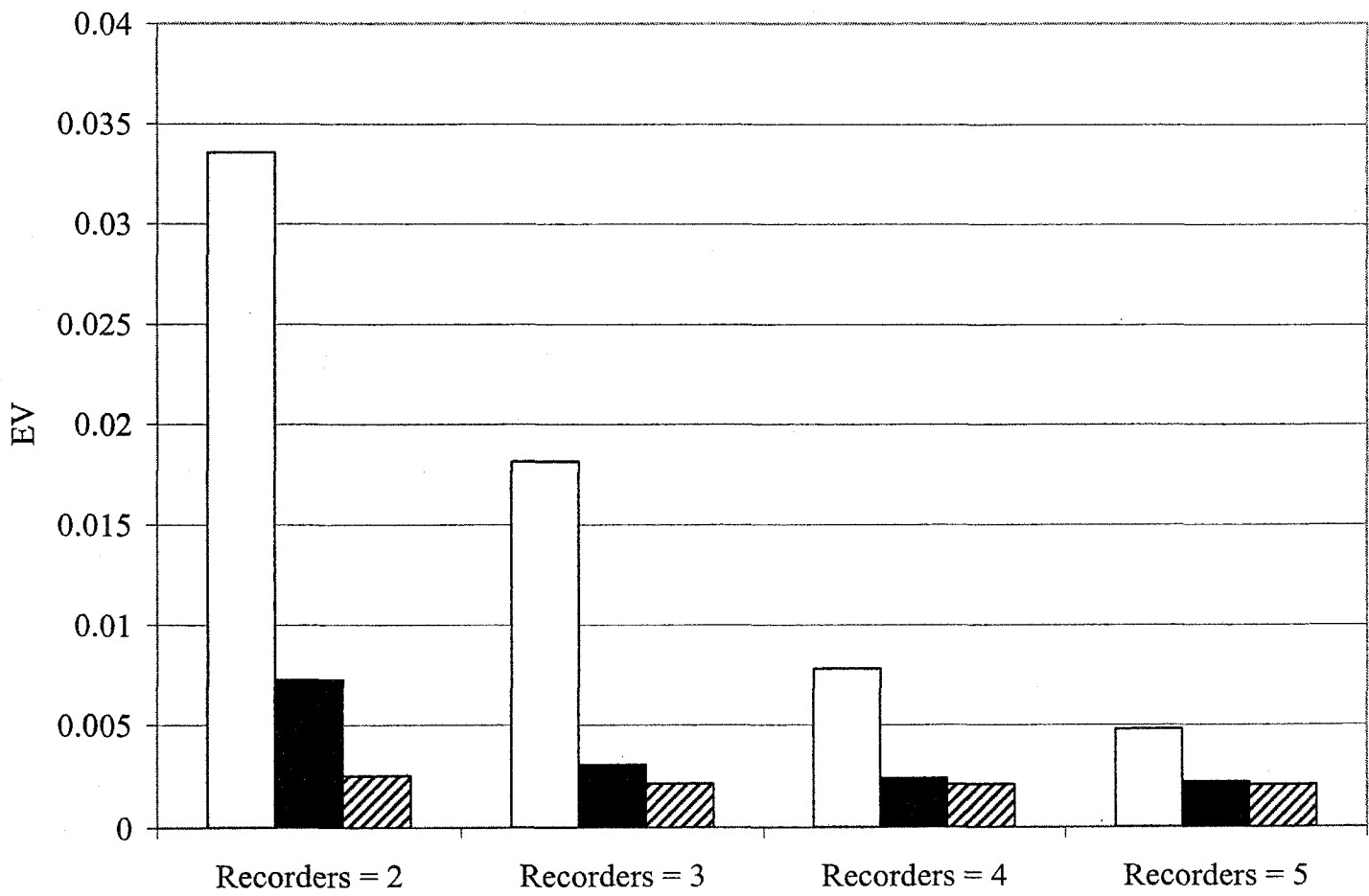


Figure 4.2. Expected variance (EV) of proportion of sites occupied ($n = 6000$ simulations), under 3 levels of detection probability (p) and 4 levels of number of recorder trees per site (t). Simulations are based on a true $\psi = 0.3 = 30\%$ of 100 sites occupied. White bars represent $p = 0.25$, black bars represent $p = 0.50$, and striped bars represent $p = 0.75$.

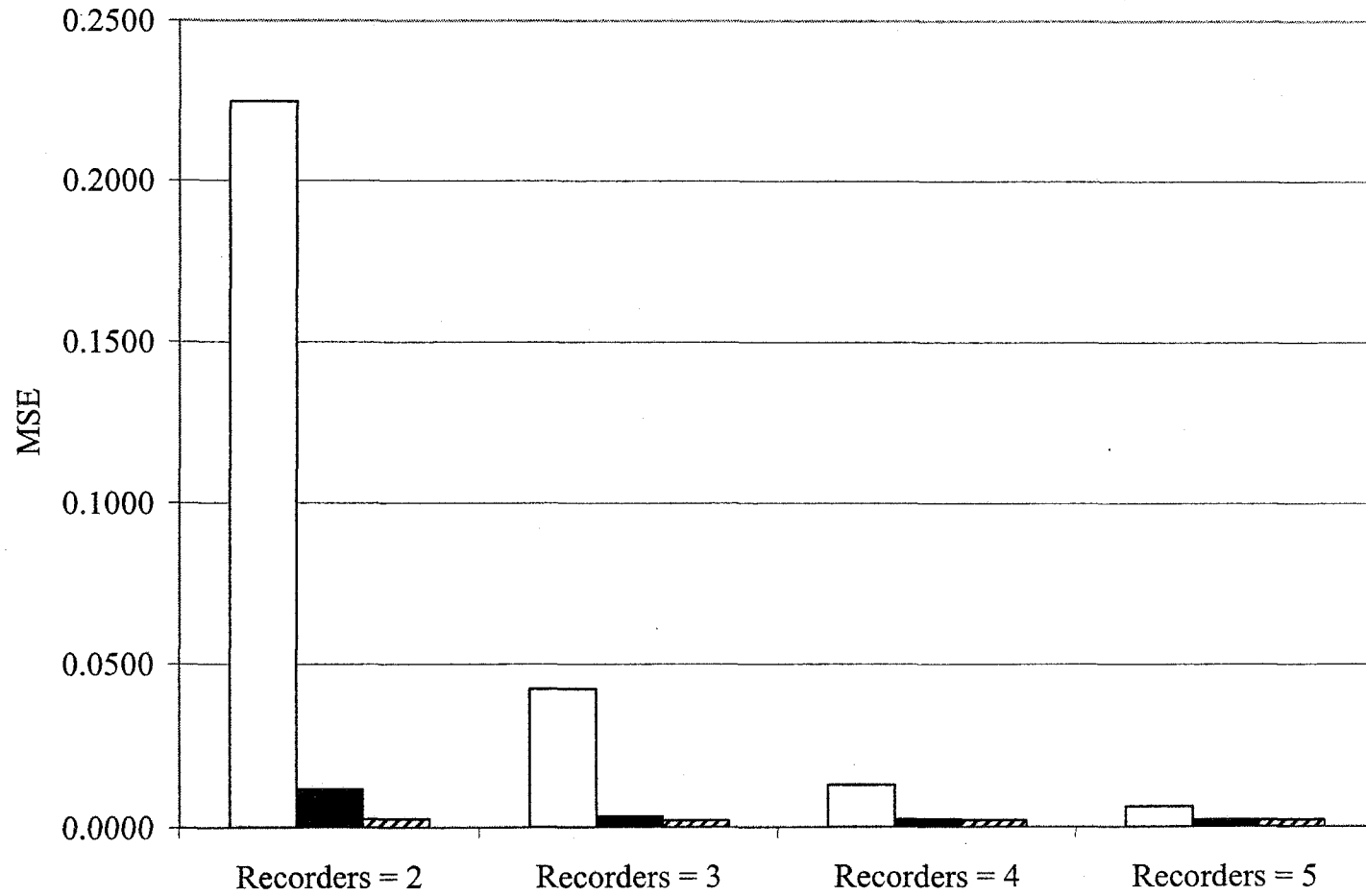


Figure 4.3. Mean square error (MSE) of proportion of sites occupied ($n = 6000$ simulations), under 3 levels of detection probability (p) and 4 levels of number of recorder trees per site (t). Simulations are based on a true $\psi = 0.3 = 30\%$ of 100 sites occupied. White bars represent $p = 0.25$, black bars represent $p = 0.50$, and striped bars represent $p = 0.75$.

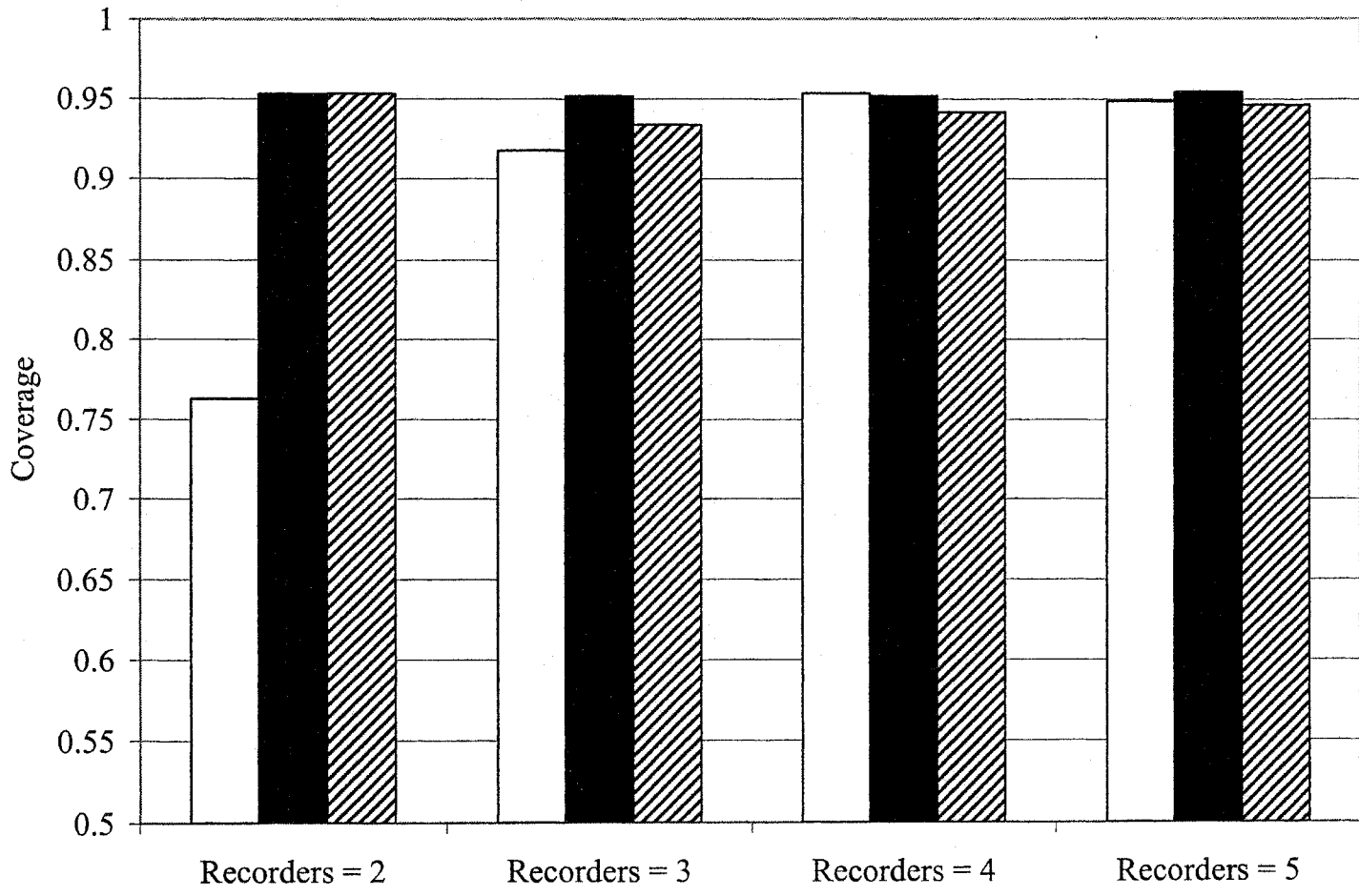


Figure 4.4. Achieved confidence interval coverage (Coverage; 95% nominal) for proportion of sites occupied ($n = 6000$ simulations), under 3 levels of detection probability (p) and 4 levels of number of recorder trees per site (l). Simulations are based on a true $\psi = 0.3 = 30\%$ of 100 sites occupied. White bars represent $p = 0.25$, black bars represent $p = 0.50$, and striped bars represent $p = 0.75$.