



AN ABSTRACT OF THE DISSERTATION OF

Joseph B. Fontaine for the degree of Doctor of Philosophy in Wildlife Science presented on November 29, 2007.

Title: Influences of High Severity Fire and Postfire Logging on Avian and Small Mammal Communities of the Siskiyou Mountains, Oregon, USA.

Abstract approved:

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W. Douglas Robinson

High severity fire is a historical and integral disturbance process in coniferous forest types. Compounded disturbances such as multiple fires or post-disturbance management activities are increasingly common, but ecological responses are not well understood and may represent novel types of disturbances. I studied bird and small mammal communities in the mixed severity fire regime of the Siskiyou Mountains of southwestern Oregon, USA, at various points in time after one or two high severity fires in and around the historic 200,000-ha Biscuit Fire. Post-disturbance time intervals included 2-4 years after a single fire, 17-18 years after a single fire, 2-3 years after a repeat fire (15 year interval between fires), and >100 years since stand-replacement fire (mature/old-growth forest). Additionally, I examined the response of these communities to postfire salvage logging of the Biscuit Fire.

Avian species richness did not differ significantly among habitats. Among the recently burned habitats, bird density was highest 17-18-years after fire and lowest 2

years after a single fire. Sites 17-18 years postfire were dominated by broad-leaved shrubs. Ordination of community data revealed two distinct gradients in avian species composition, one relating to tree structure (live, dead-sound, dead-decayed) and another relating to shrub volume and height. Bird density was positively related to shrub height and volume; increases in broad-leaved plants following fire were associated with significant increases in bird density.

Immediately after a single high severity fire event, small mammal communities transitioned from low abundance and high species richness to high abundance and low species richness dominated by deer mice. Partial recovery to a pre-burn state was evident 17 years after fire with wood rats being present but vole species still absent relative to unburned mature forest. Repeat fire was associated with heightened abundance of deer mice and herbaceous cover. Postfire salvage logging created a significant pulse of woody debris but no significant changes in densities or biomass of small mammals were observed. Fire effects on small mammal communities were much larger than those of postfire salvage logging in the short term. Longer term studies of changes in small mammal communities following salvage logging are needed over decades and greater time scales to fully evaluate the impacts of the management activity.

To examine bird response to postfire salvage logging, we used point counts to measure changes in densities and occurrence for 17 common bird species. Response was measured at two spatial scales (20 ha and 2 ha) relative to two measures of salvage logging: proportion of surrounding area logged and logging intensity (basal area removed). The 20-ha scale comprised the logging unit as well as unit edges and surrounding unlogged areas, while the 2-ha scale comprised only the logging unit and not

surrounding edges. At the 20-ha scale, we found a positive response in the density of shrub-associated species (house wren, lazuli bunting, black-headed grosbeak [scientific names given in Appendix A]) and edge-associated species (olive-sided flycatcher, yellow-rumped warbler) and little evidence of negative responses, save for a reduction in density of Hammond's flycatcher. At the 2-ha scale, shrub-associates again responded positively but not edge-associates. Brown creeper responded negatively at the 2-ha scale and five species had suggestive negative trends but they were not significant suggesting that, except for shrub nesting species, bird use of salvage units is associated with edges and not interior portions of salvage units. The lack of a strong negative response to salvage logging of the Biscuit Fire suggests that the small logging unit sizes relative to the burn area, as well as extensive snag retention in riparian buffers, tended to retain many bird species in the burn landscape.

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Influences of High Severity Fire and Postfire Logging on Avian and Small Mammal  
Communities of the Siskiyou Mountains, Oregon, USA

by  
Joseph B. Fontaine

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Joseph B. Fontaine, Author

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My dissertation work has been an extremely multidisciplinary experience bridging fire science, forest ecology, landscape ecology, and wildlife ecology to name a few. I consider myself fortunate to work in such a multidisciplinary environment with the constant challenge of synthesizing ideas and research results across disciplinary boundaries. I have had the good luck of working with Dan Donato from the beginning to the end and at every step along the way. Our collaborative effort has been fantastic and deeply rewarding.

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## CONTRIBUTION OF AUTHORS

Daniel C. Donato assisted with study design, data collection, and writing of chapters 2-4.

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Influences of High Severity Fire and Postfire Logging on Avian and Small Mammal  
Communities of the Siskiyou Mountains, Oregon, USA

by  
Joseph B. Fontaine

## CHAPTER 1: INTRODUCTION

The study of ecological response to disturbance and succession has a rich history in ecology reaching back to some of the earliest ecological theories and principles (Cowles 1899, Clements 1936, Chapman 1938). Recognition of the ubiquitous nature of disturbance led to the development of concepts such as community succession and climax. Subsequent bodies of work have developed around the study of different forms of disturbance striving to increase understanding of how disturbance acts to maintain diversity and ecosystem function across temporal and spatial scales (Connell and Slatyer 1977, Sousa 1984, Petraitis 1989, Agee 1993, Dale et al. 2005). Understanding of ecological response to disturbance is increasingly relevant as scientists strive to understand the consequences of and potential responses to climate change, land use change, and alteration of natural disturbance regimes.

Fire is a principal agent of disturbance throughout many ecosystems including dry forest types of North America (Agee 1993). Many ecosystems and species are considered fire-dependent (e.g. longleaf pine (*Pinus palustris*) ecosystems, black-backed woodpecker (*Picoides arcticus*)) and, in the absence of fire, gradually disappear as succession proceeds. Thus, recurrent disturbance via fire is necessary for the maintenance of particular community types and species. Recurrent disturbance over short intervals (e.g. <20 years) by low severity fire and long intervals (e.g. >200 years) by high severity fire is well known from fire history studies (Pyne et al. 1996, Swetnam et al. 1999). However, high severity fires recurring over short time scales have received little attention despite their known occurrence in several vegetation types, notably

chaparral and mixed conifer forests (Zedler et al. 1983, Agee 1993, Delitti et al. 2005).

Increasing wildfire activity across much of western North America with higher frequency of large wildfires (Westerling et al. 2006) raises the probability of recurrent short-interval high severity fires. A second fire may simply reset a successional clock, creating communities indistinguishable from those occurring after just one fire, or repeat fires may provide a novel set of ecological conditions, structuring a community unique from that following a single fire event. Limited evidence from recent fire ecology studies suggests that repeated short-interval fires may be unique (Zedler et al. 1983, Delitti et al. 2005, Johnstone 2006), although the influence of inter-fire interval, vegetation type, and environmental conditions remain poorly understood. Additionally, it is unknown whether repeat burn communities and single-fire communities will transition into similar communities over time. Rate of change in post-fire communities and the timescale over which they retain early successional characteristics are not well understood.

A second form of short-interval compound disturbance is postfire (salvage) logging, a frequently practiced management activity on many forested lands after high severity fire. Post-fire logging is often implemented with the goals of recovering economic value of fire-killed trees, funding post-fire replanting of conifers, and reducing the risk of future fire (McIver and Starr 2001). The role of natural disturbance in producing the spatial heterogeneity necessary for maintaining biodiversity may be altered by salvage logging. Salvage can reduce forest regeneration (Donato et al. 2006), alter vegetation composition (Stuart et al. 1993, Rumbaitis del Rio 2006), reduce densities of cavity nesting birds (Hutto and Gallo 2006, Koivula and Schmiegelow 2007, Saab et al. 2007), and increase the severity of future fire (Thompson et al. 2007). Additionally, the

impact of two disturbances--e.g. fire and timber harvest--over a short time scale (<2-3 years) have been hypothesized to alter successional trajectories of ecological systems (Stuart et al. 1993, Paine et al. 1998, Romme et al. 1998).

Despite the widespread practice of salvage logging, land managers have little information available to them describing ecological response to salvage logging. Moreover, while implementing salvage logging, public land managers frequently are confronted with multiple management objectives calling for both maintenance of biodiversity as well as harvest of fire-killed trees. For example, National Forests are “to provide a framework to contribute to sustaining native ecological systems by providing ecological conditions to support diversity of native plant and animal species in the plan area” (USDA 2005).

Utilizing a unique configuration of recent and older fires in the Klamath-Siskiyou Mountains of southwestern Oregon USA, we examined the response of bird and terrestrial small mammal communities to fire over short and decadal time scales as well as their short term response to postfire salvage logging and repeated high severity fire. We posed three principal research questions. 1) How do bird and small mammal communities change following one high severity fire at short (2-4 years postfire) and intermediate (17-18 years postfire) time scales, 2) How do these same communities respond to repeated high severity fire with a 15 year interval between fires, and 3) What is the short-term response to postfire salvage logging of bird and small mammal communities? An understanding of how communities change following a single disturbance provides a context against which to compare response to repeated fire and postfire salvage logging.

Chapter 2 explores the response of bird communities to high severity fire at two time scales and response to repeated high severity fire. We examined bird community structure, density, and species richness in sites representing various times since high-severity fire (range 2 – 100+ yr), and immediately following a second high severity fire that occurred 15 years after an initial high severity fire. Using ordination, we identified the dominant environmental gradients associated with bird community structure as well as species associated with particular habitats. These comparisons serve to explore and identify the effects of fire, early plant succession, and recurrent disturbance on bird communities.

In chapter 3, we examined the response of terrestrial small mammal communities to fire over short and decadal time scales as well as their short term response to postfire salvage logging and repeated high severity fire. The abundance of small mammals, community composition, and reproductive condition were measured and evaluated relative to the environmental conditions present. Our objectives were to (1) characterize small mammal communities with distinct disturbance histories (unburned, single fire, repeat fire, single fire + logging) and (2) examine relationships among habitat metrics and small mammal species abundance, richness, and total biomass. With expectations of increased fire frequencies as climate changes and with interest in postfire management, the response of small mammals to the compound disturbances of salvage logging and repeated high severity fire provide important data on post-disturbance wildlife community dynamics.

The objective of chapter 4 was to address bird response to salvage logging in two ways. First, we examined differences in response to extent (area logged) and intensity

(basal area removed) of salvage logging. Area logged was used to test whether areal extent of logging, regardless of intensity, influenced bird species occurrence; harvest intensity was used as a continuous measure of stand-level structural change (stem removal) associated with different salvage treatments. Second, we examined response to salvage at two spatial scales (2-ha and 20-ha) to examine bird use of actual salvage units (2-ha) versus the edge habitats generated by salvage logging (20-ha). Comparisons of effect estimates from mixed linear and logistic models were evaluated using 95% confidence intervals and an information theoretic approach to evaluate the strength of evidence for differing responses to logging metrics at two spatial scales.

**CHAPTER 2: BIRD COMMUNITIES FOLLOWING HIGH SEVERITY FIRE:  
RESPONSE TO SINGLE AND REPEAT FIRES IN THE SISKIYOU  
MOUNTAINS, OREGON, USA**

**ABSTRACT**

Fire is a widespread natural disturbance agent in most conifer-dominated forests. In light of climate change and the effects of fire exclusion, high severity (stand-replacement) fire has become a prominent land management issue. Post-fire management is often focused on reducing the risk or impact of repeat fires over short time scales (sometimes referred to as ‘reburns’), but little information exists on the effects of such short-interval fires, particularly with regard to vertebrate taxa. We studied bird communities in the mixed severity fire regime of the Klamath-Siskiyou ecoregion of Oregon, USA, at various points in time after one or two high severity fires in and around the historic 200,000-ha Biscuit Fire. Response times included 2-4 years after a single fire, 17-18 years after a single fire, 2-3 years after a repeat fire (15 year interval between fires), and >100 years since stand-replacement fire (mature/old-growth forest). Using point counts, bird communities were sampled 2004-2006 with 2-8 point counts per site and 6-19 sites per habitat type. Avian species richness did not differ significantly among habitats. Among the recently burned habitats, bird density was highest 17-18-years after fire and lowest 2 years after a single fire. 17-18 year post-fire sites were dominated by broad-leaved shrubs. Ordination of community data revealed two distinct gradients in species composition, one relating to tree structure (live, dead-sound, dead-decayed) and another relating to shrub volume and height. Bird density was positively related to shrub height

and volume; increases in broad-leaved plants following fire were associated with significant increases in bird density. Contrary to expectations, repeated high severity fire did not reduce species richness, and bird densities were greater in those habitats than in once-burned habitats. Broad-leaved hardwoods and shrubs, and the disturbances that mediate their abundance and structural diversity on the landscape, appear to play a major role in structuring avian communities in the Klamath-Siskiyou region. In light of these results, extended periods of early seral broadleaf dominance and short-interval high severity fires may be important to the conservation of avian biodiversity in this region.

## INTRODUCTION

In most coniferous forests, fire is a widespread and dominant ecological process promoting and maintaining ecosystem structure, function, and biodiversity at multiple spatial scales (Pickett and White 1985, Agee 1993, Attiwill 1994, Pyne et al. 1996, Lindenmayer et al. 2004, Vandvik et al. 2005). Throughout large portions of North America, fire exclusion over the last century has greatly reduced the frequency and extent of fires (Agee 1993, Pyne et al. 1996, Fule and Laughlin 2007) leading to, among other things, reductions in naturally generated early seral conditions (Noss et al. 2006). In places where high severity fire occurs, post-fire intervention such as salvage logging frequently is implemented to reduce the likelihood of recurrent fire and recoup economic value (McIver and Starr 2001). Although recurrent high severity fires are anticipated to be detrimental to ecosystem function (e.g. Brown et al. 2003), little information is available on this topic despite intense management interest (Donato et al. 2006, Stokstad 2006) and the potentially profound impact of multiple disturbances over short intervals on ecosystems (Sousa 1984, Foster et al. 1998, Paine et al. 1998, Noss et al. 2006).

Disturbance regimes are characterized by frequency and intensity of perturbations. Recurrent disturbance by low severity fire is well known from fire history studies, particularly in dry forest types (Pyne et al. 1996, Swetnam et al. 1999). However, high severity fires recurring over short time scales have received little attention despite their known occurrence in several vegetation types, notably chaparral and mixed conifer forests (Zedler et al. 1983, Agee 1993, Delitti et al. 2005). Increasing wildfire activity across much of western North America with higher frequency of large wildfires (Westerling et al. 2006) raises the probability of recurrent short-interval high severity fires. Thus, managers and policy makers have an increased need to better understand the ecological consequences of short-interval, high severity fire on ecosystems, particularly in light of the stated goal of most post-fire rehabilitation to reduce risk of reburn (McIver and Starr 2001, Brown et al. 2003). A second fire may simply reset a successional clock, creating communities indistinguishable from those occurring after just one fire, or repeat fires may provide a novel set of ecological conditions, structuring a community unique from that following a single fire event. Limited evidence from recent fire ecology studies suggests that repeated short-interval fires may be unique (Zedler et al. 1983, Delitti et al. 2005, Johnstone 2006), although the influence of inter-fire interval, vegetation type, and environmental conditions remain poorly understood. Additionally, it is unknown whether repeat burn communities and single-fire communities will transition into similar communities over time. Rate of change in post-fire communities and the timescale over which they retain early successional characteristics are not well understood. Studies of bird communities from frequent fire forest types such as longleaf pine (*Pinus palustris*, 1-

3 year surface fire return interval) suggest that early seral vertebrate species decline rapidly in the absence of recurrent fire (Engstrom et al. 1984).

Many species of birds are adapted to, or dependent upon, disturbances such as fire or insect outbreaks in all or portions of their distribution (MacArthur 1958, Brennan 1998). Fire heavily influences vertical and horizontal heterogeneity of vegetation; characteristics well known to structure avian communities in terms of abundance and species richness (MacArthur and MacArthur 1961, Holmes et al. 1979). Recognition of the importance of post-fire early seral habitats for birds and the uniqueness of post-fire bird communities has been documented across many ecosystem types ranging from boreal regions to Mediterranean systems to pine forests of the southwestern and southeastern U.S. (Brennan 1998, Herrando et al. 2003, Bock and Block 2005, Hannon and Drapeau 2005). However, most work has focused on cavity-nesting birds within continental interior forest types immediately after high severity fire. Little is known about community-wide bird response to fire, particularly over longer time scales (but see Schieck and Song 2006) and multiple disturbances. Following high severity fire(s), rates of vegetation recovery, successional pathways, and subsequent disturbances will impact the length of time that sites retain early seral bird communities. This is key information for forest managers tasked with conserving disturbance dependent bird species as well as landscape scale avian biodiversity.

Our objectives were to compare bird communities at different times since stand-replacement fire and use the unique opportunity presented by the 200,000 ha Biscuit Fire which burned over a pre-existing 15-year old fire to assess the effect of short-interval high severity fire on bird communities. We examined bird community structure, density,

and species richness in sites representing various times since high-severity fire (range 2 - >100 yr), and immediately following a second high severity fire that occurred 15 years following an initial high severity fire. Using ordination, we identified the dominant environmental gradients associated with bird community structure as well as species associated with particular habitats. These comparisons serve to explore and identify the effects of fire, early plant succession, and recurrent disturbance on bird communities.

## METHODS

### *Study Area and Fire History*

The Klamath-Siskiyou region in northwestern North America is characterized by a Mediterranean climate and a mixed severity fire regime in which fires burn every 5-75 years (Agee 1993, Taylor and Skinner 1998). The mixed severity fire regime is among the most complex and least understood ecological disturbance regimes; the combination of surface and stand-replacement fire over varying spatial and temporal scales results in a complex mosaic of plant communities and successional stages on the landscape (Agee 1993). In stand-replacement patches, rapid vegetation recovery and resulting fuel continuity create the potential for recurrent high severity fires over short (~decadal) time scales (Thompson et al. 2007). The fire prone nature of forests in the region, concerns over impacts of climate change, and land-use objectives specifying conifer-dominated forests have led to an increased need for information describing ecological responses to mixed severity fire.

In July 2002, at least two separate lightning strikes ignited fires in Southwestern Oregon which became the 200,000 ha Biscuit Fire. The Biscuit Fire completely reburned the 38,000 ha 1987 Silver Fire while the nearby 8,000 ha 1987 Galice Fire remained

outside the Biscuit Fire perimeter. Forest types in the study area include the upper portion of the mixed evergreen zone, trending into the white fir zone (Franklin and Dyrness 1973), and are dominated by conifer species such as Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), and white fir (*Abies concolor*). Typical evergreen hardwoods include Pacific madrone (*Arbutus menziesii*), tanoak (*Lithocarpus densiflorus*), and canyon live-oak (*Quercus chrysolepis*) and shrubs such as manzanita (*Arctostaphylos sp.*) and ceanothus (*Ceanothus sp.*). Elevations spanned 400-1400m on a full range of aspects, primarily on slopes  $>20^\circ$ . We studied disturbance(s) consisting of high severity fire ( $>95\%$  tree mortality) and post-fire (salvage) logging after fire.

### *Study Design*

Substituting space for time, we took advantage of the landscape configuration of the two 1987 fires and one 2002 fire to establish geographically proximate study sites with distinct disturbance histories (Table 2.1). Each site was comprised of similar potential vegetation types generally dominated by Douglas-fir (Franklin and Dyrness 1973); all sites were mature to old-growth conifer-dominated forests prior to fire. Areas sampled experienced a combination of zero, one, or two recent fire events (in cases of the latter, burns were separated by 15 years); all burns experienced some degree of salvage logging (Table 2.1). In this study, fire and salvage logging (harvest of fire-killed trees) were confounded for all fires. All high severity fire patches within forested portions of the Galice Fire were salvage logged as well as many of those in the Silver and Biscuit fires. Due to a paucity of stands that burned with high severity in 1987 and were not salvage logged, our results describe responses to the combination of fire and salvage logging.

Sites with differing disturbance histories were located as close to one another as possible to ensure maximum similarity prior to fire. A site, the experimental unit of this study, was defined as a relatively homogeneous area of similar stand condition and high fire severity ranging in size from ~10-50 ha. The quasi-treatments (referred to as treatments for brevity in the remainder of the paper) allow examination of community response to stand replacement fire at short and intermediate (~decadal) time scales. Because burned sites were preexisting and not selected randomly, inference from our results may be limited to our study sites.

#### *Vegetation and Environmental Data.*

Vegetation and environmental data were collected at each point count station using a circular plot with a 10m radius centered on the point with the goal of characterizing vegetation in three general strata (ground, shrub, canopy). At the vegetation plot scale, points were randomly placed. These data allowed us to assess plant species composition of plots as well as vertical vegetation structure and their correlation with bird community composition and abundance (MacArthur and MacArthur 1961). Environmental data included physiographic characteristics (elevation, slope, aspect, distance from ocean), ground cover (percent cover of forbs and grass, litter, bare soil, rock, wood, moss/lichen), and live and dead woody vegetation characteristics (species, height, percent cover). Within plots, each tree was identified to species and classified as live or dead and assigned a decay class (Cline et al. 1980), dbh, and height. Shrub species were divided into two categories based on life history and growth form. The first category included species capable of re-sprouting and obtaining large stature and biomass (shrubs: 26 species), and the second smaller low-stature shrubs generally less than 0.5m

in height and having little secondary growth (low shrubs: 39 species). Large re-sprouting shrubs were tallied by individual, percent cover estimated by species, and the diameter and height of live and dead stems were estimated. Low growing shrubs were identified to species and percent cover estimated.

#### *Bird Data.*

Avian point counts were conducted during days with no precipitation and light to no wind from mid-May to early-July. Point counts were conducted from just after dawn until 10:00 am, using standard point counting techniques for five minutes (Ralph et al. 1993); observers recorded all birds seen and heard and their distance using an unlimited radius. To maximize accuracy of distance estimation and proper bird identification, observers were trained extensively prior to beginning point counts, used range finders in the field, and performed double observer counts for a subset of points. Point counts were visited 1-3 times each year from 2004-2006. Number of point counts per site and per treatment varied based on the size of each site and number of sites in each treatment, respectively (Table 2.1). To reduce spatial dependence and edge effects, individual point counts were spaced at 225-250m intervals and were >75m from edges creating a regular grid of point counts within each site.

#### *Data Analysis*

*Vegetation and Environmental Data.* Vegetation data from plots were averaged to generate site-level estimates of cover classes, total shrub volume, live and dead shrub heights, and basal area of trees >2m tall and >10cm diameter at breast height (live conifers, live hardwoods, sound snags, and soft snags). For comparison of treatments, sites were averaged and 95% confidence intervals constructed.

*Bird Data.* Our goal was to examine community level patterns along a gradient of disturbance and succession. Thus, our approach focused on community level metrics (richness and bird density), ordination, and indicator species analysis.

*Species Richness.* We used EstimateS (Colwell 2006) to estimate species richness by treatment and year. Comparisons of communities with varying abundance structures must be corrected by the number of individuals in order to compare unbiased estimates of species richness (Gotelli and Colwell 2001). Using data truncated at 100m, rarefaction curves were generated by treatment and site and estimated species richness (alpha diversity) was recorded for the same number of individuals as determined by the treatment with the lowest sampling intensity (180 individuals, burned 1987 in 2005). Ninety-five percent confidence intervals were estimated by EstimateS via resampling using 2000 Monte Carlo randomizations. Additionally, at the same numbers of individuals, the estimated asymptote of species richness (gamma diversity) was calculated for each treatment by year combination using a Michaelis Menton equation.

*Avian Density.* Density of birds per hectare was estimated for each site using program DISTANCE 5.0 (Thomas 2006). Application of distance sampling and program DISTANCE allows for estimation of bird densities unbiased by differences in detectability between habitats (Buckland et al. 2001). Following methods outlined in Buckland et al (2001), aural detections were truncated at probability of detection  $\sim 0.10$  and detection functions were modeled using a hazard rate or half normal key function with a simple polynomial expansion. Data for each of the 10 treatment-by-year combinations were modeled separately. Top models were selected on the basis of  $\Delta AICc$  and overall fit (Buckland et al. 2001, Burnham and Anderson 2002). Site level bird

density estimates were averaged within treatment and their 95% confidence intervals estimated. Further details of this analysis are given in Appendix A.

*Community Analysis.* We used ordination as the primary means of analyzing our community data to examine community response to fire and associated vegetation gradients. Community data are rarely linear and often possess high levels of heterogeneity; thus the application of non-parametric statistical techniques not dependent on traditional assumptions of linearity and normality are often the best approach to analysis of community data (McCune and Grace 2002). Nonmetric Multidimensional Scaling (NMS, Kruskal 1964) using a Sørensen distance measure was used for ordinations. NMS is an iterative multivariate ordination technique based on ranked distances among sample units (McCune and Grace 2002). Ordinations were implemented using PC-ORD 5.04 (McCune and Mefford 2006) and standard procedures outlined in McCune and Grace (2002).

Ordinations were evaluated as sample units (sites) in species or trait space. Using overlays of categorical variables describing disturbance history, we assessed whether communities or traits occurring in different habitat types were differentiated by the NMS ordination. Overlays of environmental variables with  $R^2$  values  $>0.25$  with at least one axis were used to evaluate correlates of community gradients. Ordination axes were rotated to load the number of times burned onto axis 1. Finally, Multi-Response Permutation Procedures (MRPP) using Sørensen distance were used to assess the strength of *a priori* groups (i.e. treatments) as measured by species composition. MRPP is a non-parametric procedure for testing the hypothesis of no difference between pre-defined

groups (McCune and Grace 2002). The A-statistic from MRPP provides a useful estimate of effect size and within-group homogeneity of *a priori* defined groups.

*Indicator Species Analysis.* Indicator species analysis (ISA, Dufrene and Legendre 1997) was conducted on species site-level data (McCune and Mefford 2006) to assess the strength of species associations with particular treatments and to aid interpretation of ordinations. ISA identifies species associated with groups (i.e. treatments) by calculating an indicator value that is a composite of both frequency and abundance of species in defined groups. High indicator values reflect both high abundance and prevalence within a group. Significance of indicator values was assessed using Monte Carlo simulations with 1000 randomizations; *P*-values represent the probability of a similar observation relative to randomized data. Because of the high number of significance tests used in this method, we only report *P*-values <0.005.

## RESULTS

### *Vegetation Response*

Effects of fire were evident in vegetation data reflecting the transition of biomass from live to dead pools and the combustion of ground cover (Fig. 2.1). Dead tree (snag) basal area in recently once-burned sites was similar to live conifer basal area in unburned stands (Fig. 2.1a), reflecting overstory mortality. Height of live shrubs in the burned in 1987 stands broadly overlapped with height of dead shrubs in repeat burned stands (Fig. 2.1b), suggesting pre-fire similarity in structure and response to the 1987 fires. Basal area of sound snags and dead shrub height in the recently burned treatment overlapped that of live conifers and shrubs in unburned forest, suggesting similar pre-fire structure. Shrub response was substantially greater in repeat burn stands than burn 2002 stands with

shrubs in repeat burn stands achieving greater volume and height than shrubs in burn 2002 stands (Fig. 2.1c). By four years after fire B02 shrub height, but not volume, began to approach that of repeat burn stands two years after fire (Fig. 2.1b-c), underscoring the rapid post-fire shrub response in repeat burn stands. Additional effects of the Biscuit Fire included a reduction in litter cover and an increase in bare ground (Fig 2.1d); repeat burn stands had higher forb cover than any other treatment type (Fig 2.1d).

Dominant shrubs such as tanoak, madrone, snowbrush, and chinquapin were present in all treatments while repeat burn stands had reduced amounts of Sadler oak (*Quercus sadleriana*) and burn 1987 stands had the highest cover of madrone (Table 2-2).

#### *Avian Species Richness and Density*

From 2004-2006, four observers conducted 884 point counts, recording 8788 detections of 70 bird species across the 4 treatments (Table 2.1, see Appendix B for a complete species list). Estimates of species richness per point count overlapped for all treatments and years; the highest estimated richness was in burn 1987 stands and the lowest estimate was in burn 2002 stands during 2004, two years after fire. Total species richness per treatment displayed the same pattern (Fig. 2.2a). Avian densities exhibited significant differences between treatments (Fig. 2.2b); Burn 2002 stands had the lowest densities of birds in all three years while the other three treatments showed similar densities with overlapping 95% confidence intervals. Repeat burn stands showed a significant increase in density from 2004 to 2005 (2 and 3 years after fire), mirroring the increase in shrub volume over the same period (Fig. 2.1c, 2.2b). Lower bird density but comparable richness of burn 2002 stands suggests that burn 2002 bird communities occurred at lower densities but were composed of more species per individuals sampled.

### *Community Analysis.*

Ordination of the site-level dataset using average abundance resulted in a 2-dimensional solution (Fig. 2.3a, final stress = 17.3, instability = 0.001) and total  $R^2=0.82$ . The  $R^2$  represents the proportion of variance in the original distance matrix represented by the Euclidean ordination space (straight line distance between two points in a Cartesian coordinate system). The strongest gradient (axis 1,  $R^2=0.47$ ) in the site ordination was associated with number of times burned and tree composition, grading from live conifers to sound snags to soft snags (Fig. 2.3a). The second axis ( $R^2=0.50$ ) corresponded to a shrub gradient with low elevation, shrub-dominated burned sites on one end and higher elevation burned sites with a smaller shrub component at the opposite end. Fire effects such as duff and litter consumption as well as tree and shrub mortality were reflected by the correlation vectors (Fig. 2.3a) and large correlation coefficients (Table 2.3). Elevation and shrub volume vectors (Fig. 2.3a) were pointed in nearly opposite directions, reflecting the decreased prevalence of large stature shrubs at the highest elevation sites. Plots of species revealed groups associated with each treatment type (Fig. 2.3b). Particularly evident were species groupings with mature forest and burn 2002 treatments, while species in repeat burn and burn 1987 treatments were somewhat intermixed. The MRPP test using treatments as *a priori* groups yielded a large A-statistic ( $A=0.227$ ,  $P<0.0001$ ), reflecting the distinct qualities of species assemblages in each treatment and high within group homogeneity.

There was a significant association between shrub stature and overall avian density (Fig. 2.4). The intercept and slope estimates (95% CIs) from a linear regression

of shrub height against bird density did not overlap zero (Fig. 2.4; intercept =1.07(0.27-1.86); slope= 1.92(1.30-2.54)).

### *Indicator Species Analysis*

Species with significant indicator values were identified for all treatments (Fig. 2.3b, Table 2.4). Unburned and repeat burned treatments had the largest numbers of indicator species, reflecting their unique composition. Single burn treatments (burn 2002 and burn 1987) had smaller numbers of indicator species and traits. Significant indicator values ranged from 35 (green-tailed towhee) to 75 (lazuli bunting). Several rare species with significant associations but low indicator values were identified (green-tailed towhee, golden-crowned kinglet, winter wren) while species with high indicator values reflected both abundance and restricted occurrence (lazuli bunting, hermit warbler, hairy woodpecker, Fig. 2.3b).

## DISCUSSION

### *Repeat burn response*

We found that a repeat burn did not merely “reset” the successional clock, but also resulted in vegetation characteristics and bird communities distinct from both recent and older single burn treatments. The repeat burn had the largest number of indicator species, most of which were associated with shrubs (see Fig. 2.3b, Table 2.4). Shrub volume was higher in repeat burn sites relative to recent single burn sites despite both treatments having the same time since last fire. We hypothesize that the rapid shrub response, together with larger, more abundant dead shrubs and snags in more advanced stages of decay offer a unique set of structural attributes favored by certain bird species.

Ordination results are consistent with the expectation that, over time, twice burned and once burned avian communities may converge. Convergence of bird community composition could occur after once-burned stands possess a more developed shrub component, small snags fall resulting in more open stands, and large snags advance to decay class 3 or greater, losing their bark and fine branches. By four years postfire, Lazuli Buntings –a strong indicator species for the repeat fire treatment- were much more prevalent in recent single burn sites with the greatest degree of shrub development (Fontaine, unpublished data) thus supporting the hypothesis of community convergence. Schieck and Song (2006) reviewed bird community succession in boreal forests, noting that logged and burned communities within the same forest type converged once snags fell and communities became dominated by shrub-associated birds after ~25 years. However, convergence of communities may be more strongly influenced by site-scale differences in disturbance regime (i.e. likelihood of subsequent reburns) and physiographic conditions (i.e. aspect, soil type, elevation).

The prevalence of shrub-associated species with the repeat burn reflects its unique nature and is a novel result for a dry forest type. Previous studies have shown (Jehle et al. 2006) and reviews (e.g. Saab and Powell 2005) have hypothesized a negative response of shrub nesting birds to fire. However, these observations and hypotheses come from less productive systems where post-fire shrub response is slower and with higher rates of ungulate herbivory (Verts and Carraway 1998). Previous studies from longer time periods following fire and similar climate (Raphael et al. 1987) have reported a positive relationship between shrub-associated species and shrub-dominated post-fire plant communities. Research from boreal forests with similar shrub response rates (mostly

resprouting aspen) have found results similar to ours over comparable time scales (e.g. Morissette et al. 2002). The Mediterranean climate and prevalent resprouting shrubs are distinct from forest types in the interior west dominated by a continental climatic regime where shrubs may have slower or less vigorous responses.

### *Single fire response*

Given the relatively simplified stand structure immediately following a high severity fire, it is not surprising that we documented low bird densities occurring in recently severely burned stands (B02 treatment). Low bird densities have been shown in a variety of forest types following high severity fire spanning from ponderosa pine to spruce dominated forests (Saab and Powell 2005, Schieck and Song 2006) as well as similar Mediterranean vegetation types in Spain (Herrando et al. 2003) and Australia (Wooller and Calver 1988). In contrast, the lack of a decline in species richness in recently once-burned sites may be a consequence of the mixed severity fire regime with a high degree of fine scale spatial heterogeneity. Remnant green trees, complex topography, smaller patch size, and regenerating shrubs may support more species than other forests immediately following high severity fire. However, this hypothesis is difficult to evaluate because the relationship between sampling effort, bird densities, and species richness have not been evaluated in previous studies of postfire bird communities (Bock and Lynch 1970, Smucker et al. 2005, Kotliar et al. 2007). Alternatively, our results of no change in richness may stem from a large pool of disturbance-adapted species that simply replace those associated with closed canopy conifer forest.

Within the ordination (see Fig. 2.3a-b), recently single burned sites ranged across a greater portion of the ordination space than any other treatment likely reflecting a

diverse set of post-fire vegetation responses varying with site conditions (elevation, soil type, plant association, etc). At one end of the gradient were higher elevation stands with a reduced shrub component dominated by Douglas-fir and white fir snags while at the other end, and closer to twice burned sites, were lower elevation stands with co-dominant Douglas-fir and tanoak with a much more pronounced post-fire shrub response. Species associated more with snags and bare ground (indicator species: hairy woodpecker, Townsend's solitaire, dark-eyed junco) clustered towards the higher elevation single burn sites. These species associations are likely the most consistent with past work from interior western forests with a reduced shrub component (Hutto 1995, Kotliar et al. 2002, Saab et al. 2005). Species associated more with shrubs occurred in sites from all burned treatments with a larger shrub component (lower elevation, greater tanoak, madrone, and snowbrush component).

Studies across a range of forest types have reported unique assemblages of birds following single high severity fires (Kotliar et al. 2002, Saab and Powell 2005, Schieck and Song 2006) and several recent studies have underscored the importance of fire severity in understanding bird species response to fire (Smucker et al. 2005, Kotliar et al. 2007). Additionally, the need for increased understanding of longer term response of birds as habitats develop following fire has been cited multiple times (e.g. Hutto 1995, Kotliar et al. 2002, Saab and Powell 2005) but few studies have addressed this question, particularly in drier forest types with more frequent fire (see Schieck and Song 2006 for a review of boreal forests). In our study, we measured communities 2-4 years after fire (B02 treatment) and 17-18 years after fire (B87 treatment). These temporal comparisons suggest vegetation recovery is rapid in this system and, after 17-18 years, sites are

dominated by early seral shrubs and components of an early seral bird community. Patterns of bird density and species richness are consistent with the extensive literature linking vegetation complexity with avian densities (MacArthur and MacArthur 1961, Wiens 1989).

Fire size also may play a role in the patterns we observed. The Silver (38,000 ha) and Biscuit (200,000 ha) fires were both considered large, with the latter being the largest forest wildfire in Oregon's recorded history. Past studies of postfire avian ecology have generally been conducted on smaller fires; no studies that we are aware of have examined the influence of overall fire size on avian communities. Of 23 studies examining fire effects on bird communities reviewed by Kotliar et al (2002), most were 400-1400 ha with just four larger than 1400 ha. Most studies of larger fires have been conducted in boreal forest types (Schieck and Song 2006). Our study provides data on avian communities in a landscape-scale wildfire across a portion of the large environmental gradients characteristic of the Klamath-Siskiyou region.

#### *Study Limitations*

The results presented in this paper are from sites that experienced stand replacement fire and post-fire salvage logging 1-3 years after the initial fire event. Post-fire salvage logging directly influences stand structure via tree removal and also may have indirect effects, one of which may be alteration of shrub communities (Stuart et al. 1993). Few published studies have examined the effects of post-fire salvage logging on vegetation communities, particularly over longer time scales (McIver and Starr 2001). This study is retrospective without any pre-fire data. Thus, effects of fire are confounded with pre-existing spatial variation in environmental conditions and bird densities: a

potential problem that may lead to spurious conclusions (Parker and Wiens 2005). We strove to closely match physiographic conditions (elevation, slope, soil, etc) and vegetation composition (plant association group) between treatments as well as maximize proximity. While these issues cannot be fully addressed, the strong pattern in the bird data and obvious effects due to fire (i.e. tree mortality, changes in shrub stature, litter consumption) suggest that this confounding source of variation is not exerting a large influence on our dataset.

### *Management Implications*

Knowledge of the strong relationship between bird community composition and vegetation structure is a powerful tool for land managers. Given information on habitat associations, land managers may anticipate effects of fire and associated vegetation management on bird communities. Our data suggest that relative to a single burn, the effect of a repeat burn on bird communities is to increase overall density without a decrease in species richness. Thus, if species richness and abundance are management goals, repeated high severity fire has no negative and potentially positive consequences for birds via the creation of a unique, shrub-dominated habitat type. Identification of important pyrogenic vegetation structure for birds (e.g. snags, seeding and resprouting shrubs) may aid in designing post-fire management plans.

Early and mid-successional stands are characterized by diverse bird communities that compose a significant fraction of landscape scale biodiversity (Raphael et al. 1987, Hutto 1995, Hobson and Schieck 1999, Morissette et al. 2002, Smucker et al. 2005). In the Klamath-Siskiyou region, these stands often are dominated by broad-leaved evergreen hardwoods which provide critical nesting and foraging habitat (Seavy 2006).

In addition, the importance to wildlife of snags in varying states of decay has been widely recognized across a variety of forest types (Lehmkuhl et al. 2003b, Saab et al. 2004).

Patterns of shrub regeneration following fire and their relation to wildlife have generally been overlooked in forested systems of the United States; lack of shrub regeneration in shrub steppe habitats has been noted widely as problematic for recovery of bird communities (Jehle et al. 2006). Work from Mediterranean-type landscapes in Australia (Wooller and Calver 1988) and Spain (Herrando et al. 2003) have noted a large portion of the post-fire bird community is associated with broad-leaved evergreen shrubs.

In the Klamath-Siskiyou region, intensive research and management strategies have been directed at finding effective ways to diminish shrub dominance in order to quickly establish and accelerate conifer development (Hobbs et al. 1992). However, recent work suggests that conifer establishment and eventual dominance in shrubfields is the typical sequence following wildfire in the Klamath-Siskiyou region (Shatford et al. 2007), with the length of time between establishment and dominance quite variable. This protracted establishment period allows for diverse early successional communities to persist on the landscape for a period of time. Thus, in areas where management objectives call for late successional conifer-dominated conditions as well as maintaining native biological diversity, increased tolerance for a longer early successional phase of shrub dominance likely will benefit wildlife species, many of which are of conservation concern (Brennan 1998).

## LITERATURE CITED

- Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.
- Attiwill, P. M. 1994. The burning continent: Forest ecosystems and fire management in Australia. Institute of Public Affairs, West Perth, WA, Australia.
- Bock, C. E., and W. M. Block. 2005. Fire and birds in the southwestern United States. *Studies in Avian Biology* **30**:14-32.
- Bock, C. E., and J. F. Lynch. 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. *Condor* **72**:182-189.
- Brennan, L. A., R.T. Engstrom, W.E. Palmer, S.M. Hermann, G.A. Hurst, L.W. Burger, C.L. Hardy. 1998. Whither wildlife without fire? Pages 402-414 *in* transactions of the 63rd North American Wildlife and Natural Resource Conference.
- Brown, J. K., E. D. Reinhardt, and K. A. Kramer. 2003. Coarse woody debris: managing benefits and fire hazard in the recovering forest. Pages 1-16 *in* R. M. R. Station, editor. USDA Forest Service.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: Estimating abundance of biological populations. Oxford University Press, Oxford; New York.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd edition. Springer, New York.
- Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *Journal of Wildlife Management* **44**:773-786.
- Colwell, R. K. 2006. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.0.0. *in*.
- Delitti, W., A. Ferran, L. Trabaud, and V. R. Vallejo. 2005. Effects of fire recurrence in *Quercus coccifera* L. shrublands of the Valencia Region (Spain): I. plant composition and productivity. *Plant Ecology* **177**:57-70.
- Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2006. Post-wildfire logging hinders regeneration and increases fire risk. *Science* **311**:352.
- Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* **67**:345-366.

- Engstrom, R. T., L. C. Robert, and W. W. Baker. 1984. Breeding bird populations in relation to changing forest structure following fire exclusion: A 15-year study. *Wilson Bulletin* **96**:437-450.
- Foster, D. R., D. H. Knight, and J. F. Franklin. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* **1**:497-510.
- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. Pacific Northwest Forest and Range Experiment Station, USDA Forest Service, Portland, OR.
- Fule, P. Z., and D. C. Laughlin. 2007. Wildland fire effects on forest structure over an altitudinal gradient, Grand Canyon National Park, USA. *Journal of Applied Ecology* **44**:136-146.
- Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**:379-391.
- Hannon, S. J., and P. Drapeau. 2005. Bird responses to burning and logging in the boreal forest of Canada. *Studies in Avian Biology* **30**:97-115.
- Herrando, S., L. s. Brotons, and S. Llacuna. 2003. Does fire increase the spatial heterogeneity of bird communities in Mediterranean landscapes? *Ibis* **145**:307-317.
- Hobbs, S. D., S. D. Tesch, P. W. Owston, R. E. Stewart, J. C. Tappeiner, and G. E. Wells, editors. 1992. Reforestation practices in Southwestern Oregon and Northern California. Forest Research Laboratory, Oregon State University, Corvallis, OR.
- Hobson, K. A., and J. Schieck. 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. *Ecological Applications* **9**:849-863.
- Holmes, R. T., J. R. E. Bonney, and S. W. Pacala. 1979. Guild structure of the Hubbard Brook bird community: A multivariate approach. *Ecology* **60**:512-520.
- Hutto, R. L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology* **9**:1041-1058.
- Jehle, G., J. A. Savidge, and N. B. Kotliar. 2006. Green-tailed Towhee response to prescribed fire in montane shrubland. *Condor* **108**:634-646.
- Johnstone, J. F. 2006. Response of boreal plant communities to variations in previous fire-free interval. *International Journal of Wildland Fire* **15**:497-508.

- Kotliar, N. B., S. J. Hejl, R. L. Hutto, V. A. Saab, C. P. Melcher, and M. E. McFadzen. 2002. Effects of fire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. *Studies in Avian Biology* **25**:49-64.
- Kotliar, N. B., P. L. Kennedy, and K. Ferree. 2007. Avifaunal responses to fire in southwestern montane forests along a burn severity gradient. *Ecological Applications* **17**:491-507.
- Kruskal, J. B. 1964. Nonmetric multidimensional scaling: A numerical method. *Psychometrika* **29**:115-129.
- Lehmkuhl, J. F., R. L. Everett, R. Schellhaas, P. Ohlson, D. Keenum, H. Riesterer, and D. Spurbeck. 2003. Cavities in snags along a wildlife chronosequence in eastern Washington. *Journal of Wildlife Management* **67**:219-228.
- Lindenmayer, D. B., D. R. Foster, J. F. Franklin, M. L. Hunter, R. F. Noss, F. A. Schmiegelow, and D. Perry. 2004. Salvage harvesting policies after natural disturbance. *Science* **303**:1303.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* **39**:599-619.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* **42**:594-598.
- McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.
- McCune, B., and M. J. Mefford. 2006. PC-ORD. Multivariate Analysis of Ecological Data. Version 5.04. *in*. MjM Software, Gleneden Beach, Oregon, U.S.A.
- McIver, J. D., and L. Starr. 2001. A literature review on the environmental effects of postfire logging. *Western Journal of Applied Forestry* **16**:159-168.
- Morissette, J. L., T. P. Cobb, R. M. Brigham, and P. C. James. 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. *Canadian Journal of Forest Research* **32**:2169-2183.
- Noss, R. F., J. F. Franklin, W. L. Baker, T. Schoennagel, and P. B. Moyle. 2006. Managing fire-prone forests in the western United States. *Frontiers in Ecology and the Environment* **4**:481-487.
- Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* **1**:535-545.

- Parker, K., and J. A. Wiens. 2005. Assessing recovery following environmental accidents: Environmental variation, ecological assumptions, and strategies. *Ecological Applications* **15**:2037-2051.
- Pickett, S. T. A., and P. S. White. 1985. *The Ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, FL.
- Pyne, S. J., P. L. Andrews, and R. D. Laven. 1996. *Introduction to wildland fire*, 2nd edition. Wiley, New York.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. *in* USDA Forest Service, General Technical Report PSW-GTR-144. www. Pacific Southwest Research Station, Berkeley, CA.
- Raphael, M. G., M. L. Morrison, and M. P. Yoder-Williams. 1987. Breeding bird populations during twenty-five years of postfire succession in the Sierra Nevada. *Condor* **89**:614-626.
- Saab, V. A., J. Dudley, and W. L. Thompson. 2004. Factors influencing occupancy of nest cavities in recently burned forests. *Condor* **106**:20-36.
- Saab, V. A., and H. D. W. Powell. 2005. Fire and avian ecology in North America: Processes influencing pattern. *Studies in Avian Biology* **30**:1-13.
- Saab, V. A., H. D. W. Powell, N. B. Kotliar, and K. R. Newlon. 2005. Variation in fire regimes of the Rocky Mountains: Implications for avian communities and fire management. *Studies in Avian Biology* **30**:76-96.
- Schieck, J., and S. J. Song. 2006. Changes in bird communities throughout succession following fire and harvest in boreal forests of western North America: Literature review and meta-analyses. *Canadian Journal of Forest Research* **36**:1299-1318.
- Seavy, N. E. 2006. Effects of disturbance on animal communities: Fire effects on birds in mixed-conifer forest. Dissertation. University of Florida, Gainesville, FL.
- Shatford, J. P. A., D. E. Hibbs, and K. J. Puettmann. 2007. Conifer regeneration after forest fire in the Klamath-Siskiyou: How much, how soon? *Journal of Forestry* **105**:139-146.
- Smucker, K. M., R. L. Hutto, and B. M. Steele. 2005. Changes in bird abundance after wildfire: Importance of fire severity and time since fire. *Ecological Applications* **15**:1535-1549.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**:353-391.

- Stokstad, E. 2006. Salvage logging research continues to generate sparks. *Science* **311**:761.
- Stuart, J. D., M. C. Grifantini, and L. Fox, III. 1993. Early successional pathways following wildfire and subsequent silvicultural treatment in Douglas-fir/hardwood forests, NW California. *Forest Science* **39**:561-572.
- Swetnam, T. W., C. D. Allen, and J. L. Betancourt. 1999. Applied historical ecology: Using the past to manage for the future. *Ecological Applications* **9**:1189-1206.
- Taylor, A. H., and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. *Forest Ecology and Management* **111**:285-301.
- Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B. and Marques, T.A. 2006. Distance 5.0 Beta 5. *in*. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. <http://www.ruwpa.st-and.ac.uk/distance/>.
- Thompson, J. R., T. A. Spies, and L. M. Ganio. 2007. Re-burn severity in managed and unmanaged vegetation in a large wildfire. *Proceedings of the National Academy of Science* **104**:10743-10748.
- Vandvik, V., E. Heegaard, I. E. Maren, and P. A. Aarrestad. 2005. Managing heterogeneity: the importance of grazing and environmental variation on post-fire succession in heathlands. *Journal of Applied Ecology* **42**:139-149.
- Verts, B. J., and L. N. Carraway. 1998. Land mammals of Oregon. University of California Press, Berkeley, CA.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* **313**:940-943.
- Wiens, J. A. 1989. The ecology of bird communities. Cambridge University Press, Cambridge; New York.
- Wooller, R. D., and M. C. Calver. 1988. Changes in an assemblage of small birds in the understorey of dry sclerophyll forest in south-western Australis after fire. *Australian Wildlife Research* **15**:331-338.
- Zedler, P. H., C. R. Gautier, and G. S. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* **64**:809-818.

Table 2.1. Disturbance history and sampling intensity of four treatments 2004-2006 in the Klamath-Siskiyou mountains, Oregon, USA.

Description†	Fire 1987	Fire 2002	Years since fire	N-2004‡	N-2005‡	N-2006‡
Mature Forest	No	No	>100	12	9	7
				5.3 (0.54)	5.6 (0.58)	5.7 (0.57)
				870	572	391
-----				13	19	17
Recent Burn (2002)	No	Yes	2-4	6.9 (0.89)	7.2 (0.75)	7.2 (0.78)
				944	1233	777
-----				7	6	
Old Burn (1987)	Yes	No	17-18	2.5 (0.53)	2.8 (0.70)	NA
				386	180	
-----				7	7	
Repeat burn	Yes	Yes	2-3	7.3 (0.68)	7.9 (0.80)	NA
				834	582	

†All three burned treatments were partially salvage logged 1-3 years following high severity fire.

‡In each year, the number of sites, mean point count stations per site (standard error) and total avian detections after truncation are presented. Point counts per site ranged from 2-14.

Table 2.2. Percent cover of surface classes and dominant shrubs across treatments 2004-2006.

Category /Species	NB	B02			B87	RB	
	2004	2004	2005	2006	2004	2004	2005
rock	4.9 (2.3)	45.0 (3.7)	24.3 (4.6)	23.4 (3.4)	10.3 (3.7)	29.7 (4.4)	22.8 (4.8)
soil	2.7 (0.9)	18.9 (2.2)	17.5 (2.3)	24.9 (3.2)	13.7 (5.2)	11.6 (1.2)	9.4 (2.1)
litter	63.4 (4.0)	18.2 (2.9)	16.1 (3.0)	17.6 (2.0)	48.1 (7.8)	9.4 (3.9)	11.6 (2.3)
wood	10.8 (1.7)	4.9 (0.9)	17.7 (2.9)	12.9 (2.2)	17.2 (3.2)	5.7 (1.1)	17.1 (4.0)
moss-lichen	9.1 (3.0)	2.6 (1.6)	2.4 (1.0)	3.7 (1.2)	2.0 (1.0)	1.3 (1.1)	4.5 (1.1)
herb	9.5 (4.3)	10.6 (3.6)	21.2 (4.5)	17.6 (2.0)	9.2 (3.5)	42.6 (6.7)	34.1 (7.6)
subshrub‡	6.6 (2.8)	9.1 (3.3)	10.9 (1.9)	14.7 (2.8)	9.3 (1.0)	6.6 (1.5)	12.2 (3.1)
<i>Arbutus menziesii</i>	0.3 (0.2)	0.9 (0.3)	1.2 (0.4)	1.8 (0.6)	4.6 (1.5)	2.5 (0.9)	4.9 (1.5)
<i>Arctostaphylos sp.</i>	1.8 (1.2)	0.1 (0.03)	2.1 (0.9)	1.8 (0.8)	3.1 (1.9)	0.9 (0.7)	2.3 (1.6)
<i>Castanopsis chrysophylla</i>	0.6 (0.4)	1.5 (0.6)	2.2 (0.8)	2.5 (0.7)	6.9 (2.2)	0.8 (0.4)	1.1 (0.7)
<i>Ceanothus integerrimus</i>	0 (0)	0 (0)	0.7 (0.3)	1.6 (0.9)	1.8 (1.7)	3.4 (2.4)	5.7 (2.8)
<i>Ceanothus velutinus</i>	0 (0)	0.3 (0.1)	1.4 (0.6)	3 (1.4)	9.6 (5.4)	9.4 (3.1)	16.8 (6.2)
<i>Eriodictyon californicum</i>	0 (0)	0 (0)	0.6 (0.6)	0.8 (0.5)	1.3 (1.3)	0 (0)	1 (1.0)
<i>Lithocarpus densiflorus</i>	14 (3.2)	9.4 (2.0)	11.4 (2.4)	11.5 (2.3)	13.7 (4.6)	10.6 (1.8)	20.1 (2.4)
<i>Quercus sadleriana</i>	2 (0.9)	2.2 (1.0)	4.9 (2.0)	1.8 (1.0)	6.4 (5.6)	0.2 (0.2)	0 (0)
<i>Quercus sp.</i>	12.9 (3.7)	4.6 (1.4)	7.2 (1.8)	4.1 (0.9)	4.8 (1.5)	3.2 (0.9)	4.4 (1.0)
<i>Umbellularia californica</i>	1.4 (1.4)	0.6 (0.6)	0.6 (0.4)	0.7 (0.5)	0 (0)	0 (0.02)	0.1 (0.1)
<i>Vaccinium sp.</i>	7.2 (5.1)	1.8 (1.3)	2 (0.8)	1.9 (0.8)	0.6 (0.4)	0.1 (0.03)	0.5 (0.2)

Notes: Numbers represent means (standard error) of percent cover values across sites within each treatment by year (see Table 1 for number of sites per treatment).

‡Common genera of subshrubs include *Gaultheria*, *Berberis*, *Ribes*, and *Rubus*.

Table 2.3. Correlation coefficients ( $R^2 > 0.25$ ) of environmental variables with axes of site-level ordination using nonmetric multidimensional scaling (NMS).

Predictor	Description	Units	Axis 1	Axis 2
#Burns	Number of times burned	0,1, or 2	0.82	-0.03
LiveCon	Basal area of live conifers	$\text{m}^2 \cdot \text{ha}^{-1}$	-0.79	-0.21
LiveHW	Basal area of live hardwoods	$\text{m}^2 \cdot \text{ha}^{-1}$	-0.57	-0.25
BiscSnag	Basal area of fresh snags	$\text{m}^2 \cdot \text{ha}^{-1}$	0.42	0.50
ShrbHtLv	Height of live shrubs	m	-0.30	-0.65
ShrbHtDd	Height of dead shrub	m	0.56	-0.12
ShrbVol	Shrub volume	$\text{m}^3 \cdot \text{ha}^{-1}$	-0.26	-0.62
%Rock	Percent cover of rock	%	0.42	0.43
%Litter	Percent cover of litter	%	-0.82	-0.30
Elev	Elevation	m	-0.14	0.56

*Notes:* Total variance explained by the ordination was 0.82 (Axis 1 = 0.47, Axis 2 = 0.35).

Table 2.4. Indicator species associated with treatments.

Treatment association	Species	Indicator value	<i>P</i> -value
B02	hairy woodpecker (HAWO)	71.2	0.0002
B02	dark-eyed junco (DEJU)	48.4	0.0002
B02	Townsend's solitaire (TOSO)	47.3	0.0002
B87	wren (WREN)	69.6	0.0002
B87	orange-crowned warbler (OCWA)	52.2	0.0002
B87	black-headed grosbeak (BHGR)	42.4	0.0008
B87	acorn woodpecker (ACWO)	32.1	0.0028
NB	Pacific-slope flycatcher (PSFL)	71.8	0.0002
NB	hermit warbler (HEWA)	70.5	0.0002
NB	hermit thrush (HETH)	67.3	0.0002
NB	red-breasted nuthatch (RBNU)	49.1	0.0002
NB	brown creeper (BRCR)	48.2	0.0002
NB	chestnut-backed chickadee (CBCH)	46.3	0.0008
NB	black-throated gray warbler (BTYW)	40.4	0.0024
NB	winter wren (WIWR)	37.9	0.0004
NB	golden-crowned kinglet (GCKI)	37.5	0.0004
RB	lazuli bunting (LAZB)	74.7	0.0002
RB	rufous hummingbird (RUHU)	56.8	0.0002
RB	spotted towhee (SPTO)	53.9	0.0002
RB	fox sparrow (FOSP)	52.3	0.0002
RB	Nashville warbler (NAWA)	41.5	0.0022
RB	white-crowned sparrow (WCSP)	40.8	0.001
RB	green-tailed towhee (GTTO)	34.9	0.0004

Figure 2.1. Above-ground structural characteristics of treatments sampled: (a) Basal area ( $\text{m}^2/\text{ha}$ ) of live conifers, live hardwood (HW: hardwood), sound snags, soft snags, and hardwood snags; (b) Shrub height (m) of dead and live shrubs; (c) volume ( $\text{m}^3/\text{ha}$ ) from 2004-2006; and (d) ground cover classes in 2004 showing fire effects. High severity fire killed and consumed much of the aboveground vegetation which was followed by a rapid recovery of the shrub layer.

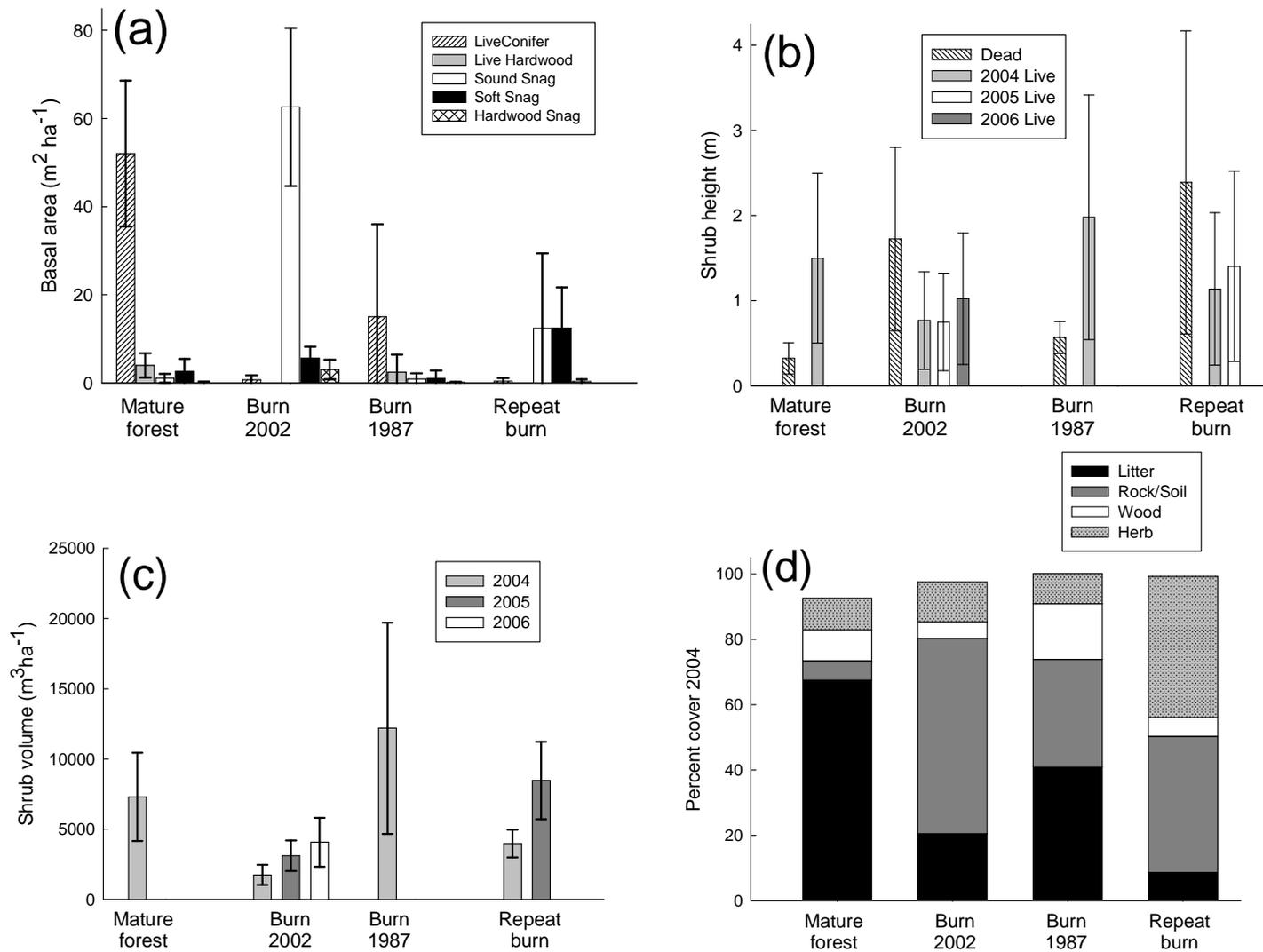


Figure 2.1

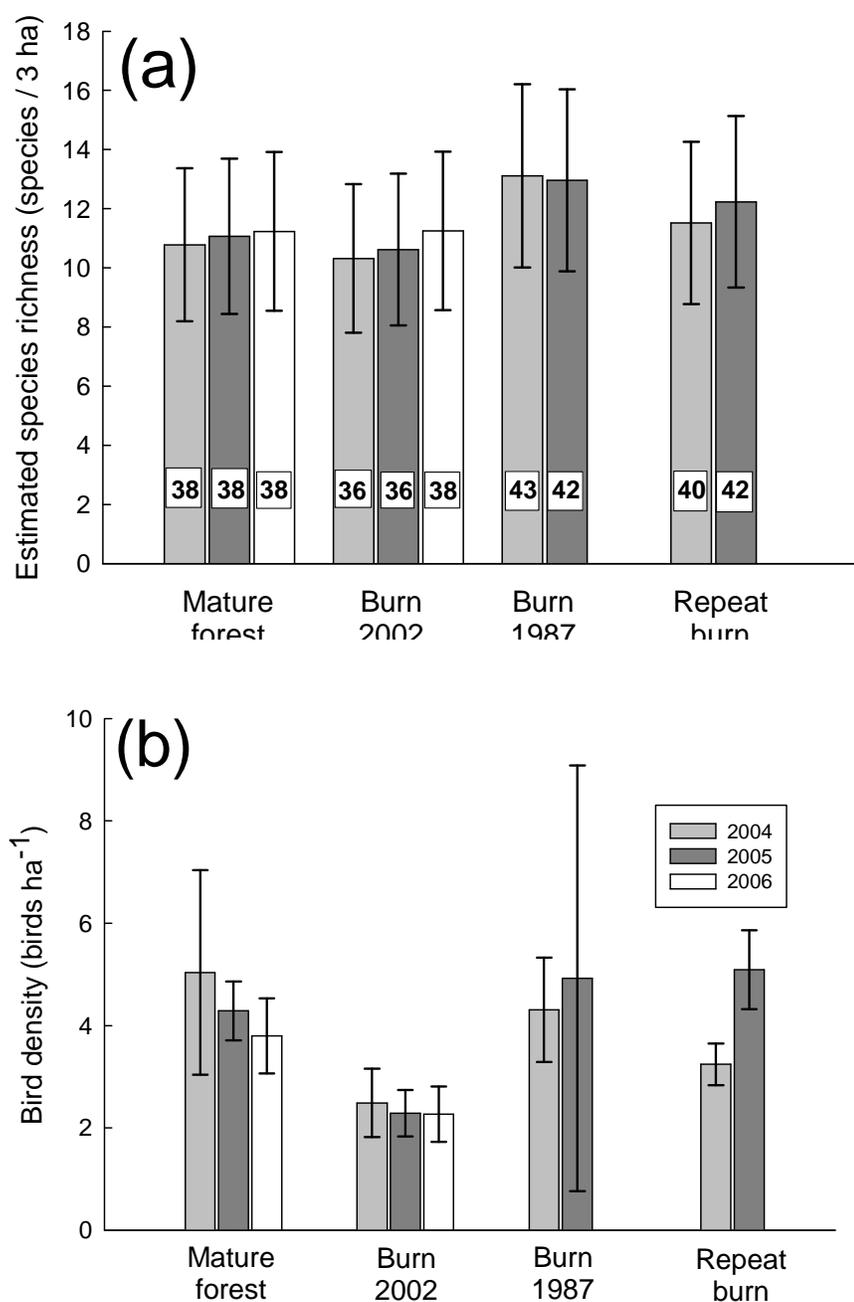


Figure 2.2. Bird species richness and density by treatment. (a) Species richness (estimated species per point, 95% CIs with total estimated richness in boxes) and (b) mean (birds per ha, 95% CIs) bird densities by treatment 2004-2006. Species richness was not significantly impacted by high severity fire while overall density showed an initial decrease followed by a rapid recovery.

Figure 2.3. Ordination of sites (2004-2006) in species space. (a) Ordination of sites (2004-2006) in species space using nonmetric multidimensional scaling (NMS) and (b) the same ordination with species maximum values plotted. The disturbance histories are associated with distinct bird communities (MRPP,  $A=0.23$ ,  $P<0.0001$ ). Environmental correlates with the ordination axes ( $R^2>0.25$ , Table 2.3) are shown (#Burns: Number of times burned; ShrbHtDd: Height of dead shrubs (m); ShrbVol: Volume of live shrubs ( $m^3/ha$ ); ShrbHtLv: Height of live shrubs; LiveHW: Basal area of live hardwood trees; LiveCon: Basal area of live conifer trees; %Litter: percent cover of litter; Elev: Elevation(m); BiscSnag: Basal area of sound snags; %Rock: percent cover of rock. Significant indicator species are emphasized with the symbol of the associated treatment; see Table 2.4 for common names of significant indicator species and Appendix B for a complete list of species and scientific names.

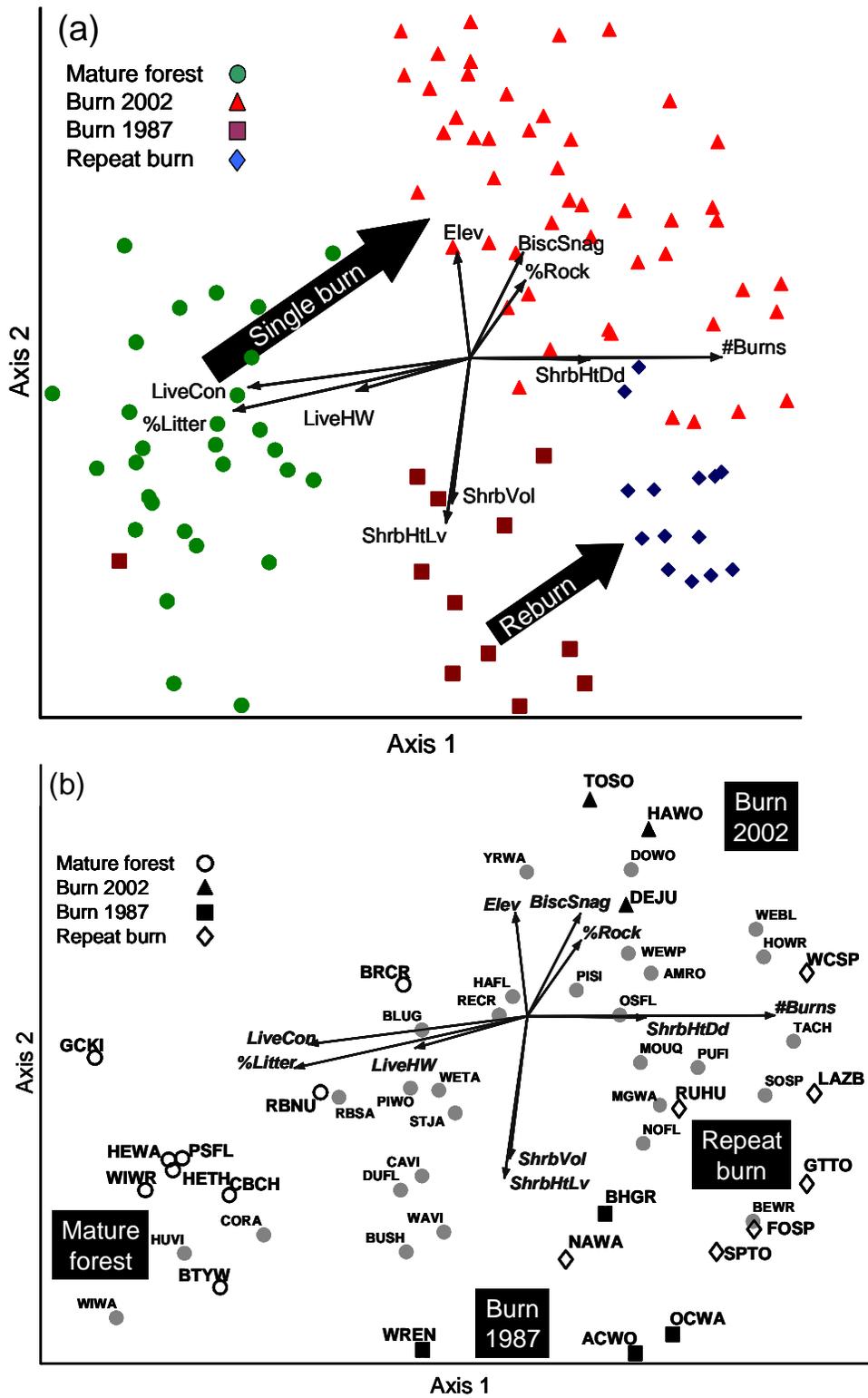


Figure 2.3

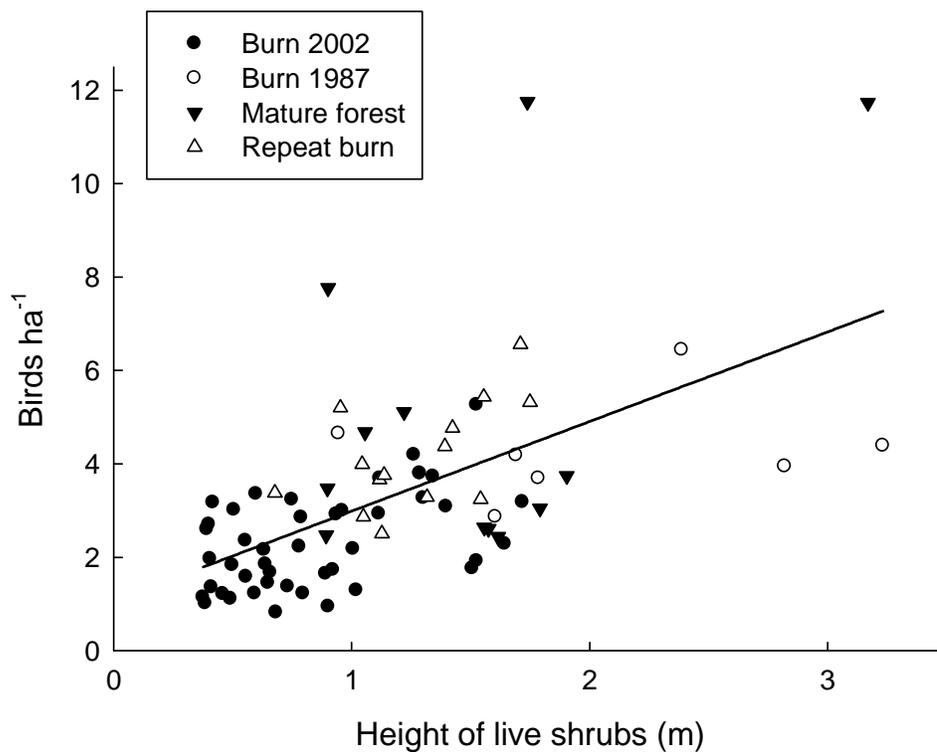


Figure 2.4. Live shrub height (m) and bird density (birds ha<sup>-1</sup>) 2004-2006 with least squares linear regression line. Each point represents one site per year. Shrub stature had a strong relationship with post-fire bird density; 95% confidence intervals for the slope and intercept coefficients did not overlap zero: intercept = 1.07 (0.27-1.86); slope = 1.92 (1.30-2.54).

**CHAPTER 3: RESPONSE OF SMALL MAMMALS TO HIGH SEVERITY  
FIRE, REPEAT BURNING, AND POSTFIRE SALVAGE LOGGING IN THE  
SISKIYOU MOUNTAINS, OREGON, USA**

**ABSTRACT**

Ecological responses to compound disturbances, such as recurrent fire or fire plus postfire management activities, may differ from disturbance events that are widely spaced in time (e.g. one fire or single-entry tree harvest in a century). In the Siskiyou Mountains of southwestern Oregon, we examined the composition and abundance of small mammal communities at different times following differing combinations of high severity fire and postfire salvage logging. Small mammals were sampled at two and seventeen years following a single high severity fire, two years following a second high severity fire (with a fifteen year interval between fires), one year after postfire salvage logging of a severely burned stand, and in mature stands with >100 years since fire. Immediately after a single high severity fire event, small mammal communities transitioned from low abundance and high species richness to high abundance and low species richness dominated by deer mice. Partial recovery to a pre-burn state was evident 17 years after fire with wood rats being present but vole species still absent. Repeat fire was associated with heightened abundance of deer mice and herbaceous cover. Postfire salvage logging created a significant pulse of woody debris but no significant changes in densities or biomass of small mammals were observed. Fire effects on small mammal communities were much larger than those of postfire salvage logging in the short term. Longer term studies of

changes in small mammal communities following salvage logging are needed over decades and greater time scales to fully evaluate the impacts of this management activity.

## INTRODUCTION

Ecological response to disturbance is of fundamental importance to ecosystem function and community structure and composition (Connell and Slatyer 1977, Sousa 1984, Agee 1993). Compounded disturbances such as multiple fires or management activities are increasingly common, but responses are not well understood and may represent novel types of disturbance responses (Paine et al. 1998). Post-disturbance land management, itself a compound disturbance, is frequently implemented to avoid or reduce the severity and intensity of future disturbances (e.g. postfire salvage logging to reduce risk/severity of future fire) (Donato et al. 2006, Thompson et al. 2007). Type, intensity, extent, and time between disturbances interact to determine whether successional pathways are altered from those observed after infrequent disturbance events (Paine et al. 1998).

In forested ecosystems, two principal forms of disturbance are fire and tree harvest. Fire frequency and severity generate a complex mosaic of forest ages and types across landscapes. The recurrent nature of fire acts to maintain landscape complexity and early successional habitats and associated disturbance-dependent species (Agee 1993, Franklin et al. 2002). High severity fire and tree harvest may both simplify forest structure at fine spatial scales but, depending on spatial extent, may increase landscape-scale heterogeneity (Franklin et al. 2002). High intensity fire-related combustion of litter and woody debris and the killing of understory and overstory vegetation reduces stand-scale complexity. Similarly, clearcut harvest tends to reduce stand-scale complexity via

the cutting of overstory trees and subsequent yarding disturbance. In combination -- the harvest of fire-killed trees after fire, or postfire salvage logging-- has received heightened attention given the nature of the combined disturbance and increased prevalence of fire in western North America (McIver and Starr 2001, Donato et al. 2006). Large fires on public lands in the western United States over the last 20 years have underscored the need for additional research on the influence of fire and postfire logging on a variety of ecosystem attributes including both vegetation and wildlife (Kotliar et al. 2002, Westerling et al. 2006, Thompson et al. 2007).

Small mammal communities constitute an important portion of forest biodiversity by contributing to a wide variety of ecosystem processes. Small mammals disperse ectomycorrhizal fungi through truffle consumption (Carey and Johnson 1995, Meyer et al. 2005) and influence vegetation structure through consumption and dispersal of seeds and hypogeous fungi (Gashwiler 1967, Carey and Johnson 1995, Meyer et al. 2005). Forest predators of management concern such as northern spotted owl (*Strix occidentalis caurina*), Mexican spotted owl (*S. o. lucida*) and northern goshawk (*Accipiter gentilis*) are predators of small mammals (Rosenberg et al. 2003, Morrison 2006). Small mammal response to fire and logging has been addressed in previous studies examining high intensity disturbance (e.g. high severity fire and clearcutting) (Cook 1959, Sullivan et al. 1999, Fisher and Wilkinson 2005). Habitat factors associated with small mammal species presence/absence include volume of woody debris, herbaceous cover, shrub prevalence, and seral stage (Carey and Johnson 1995, Fisher and Wilkinson 2005, Converse et al. 2006a). Following logging or fire, deer mice, chipmunk species, and total small mammal biomass tend to increase (Fox 1990, Fisher and Wilkinson 2005, Converse

et al. 2006c). Responses of other small mammals to fire and logging vary widely depending on forest type and fire severity (e.g. voles such as *Clethrionomys gapperi* may increase/decrease following logging or fire in differing forest types (Fox 1983, Craig et al. 2006)).

Few studies have examined the influence of repeated fire or postfire logging on small mammal communities. In a review of postfire logging effects, McIver and Starr (2001) found only one field study, from Israel (Haim and Izhaki 1994), examining the influence of postfire logging on small mammals. Effects of repeated fire have been addressed in prairie (Beck and Vogl 1972) and shrub-dominated systems (Fox 1990) but not in forested ecosystems. Utilizing a unique configuration of recent and older fires in the Klamath-Siskiyou Mountains of southwestern Oregon USA, we examined the response of terrestrial small mammal communities to fire over short and decadal time scales as well as their short term response to postfire salvage logging and repeated high severity fire. The abundance of small mammals, community composition, and reproductive condition were measured and evaluated relative to the environmental conditions present. Our objectives were to (1) characterize small mammal communities with distinct disturbance histories (unburned, single fire, repeat fire, single fire + logging) and (2) examine relationships among habitat metrics and small mammal species abundance, richness, and total biomass. With expectations of increased fire frequencies as climate changes and with interest in postfire management, the response of small mammals to the compound disturbances of salvage logging and repeated high severity fire provide important data on post-disturbance wildlife community dynamics.

## METHODS

### *Study area and fire history*

The Klamath-Siskiyou region in northwestern North America is characterized by a Mediterranean climate and a mixed-severity fire regime in which fires burn every 5-75 years (Agee 1993, Taylor and Skinner 1998). The mixed-severity fire regime is among the most complex and least understood ecological disturbance regimes; the combination of surface and stand-replacement fire over varying spatial and temporal scales results in a complex mosaic of plant communities, age structures, and successional stages on the landscape (Agee 1993). In stand-replacement patches, rapid vegetation recovery and resulting fuel continuity create the potential for recurrent high severity fires over short (~decadal) time scales (Thompson et al. 2007).

In July 2002, at least two separate lightning strikes ignited fires in southwestern Oregon which became the 200,000 ha Biscuit Fire. The Biscuit Fire completely reburned the 38,000 ha 1987 Silver Fire while the nearby 8,000 ha 1987 Galice Fire remained outside the Biscuit Fire perimeter (Fig 3.1). Forest types in the study area are the upper portion of the mixed evergreen zone, trending into the white fir zone (Franklin and Dyrness 1973), dominated by conifer species including Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), and knobcone pine (*Pinus attenuata*). Typical evergreen hardwoods include Pacific madrone (*Arbutus menziesii*), tanoak (*Lithocarpus densiflorus*), chinquapin (*Chrysolepis chrysophylla*), and canyon live-oak (*Quercus chrysolepis*) and shrubs such as manzanita (*Arctostaphylos sp.*) and ceanothus (*Ceanothus sp.*).

We took advantage of the landscape configuration of the two 1987 fires and one 2002 fire to establish study sites with differing disturbance histories (Fig 3.1). Sites

sampled were selected on the basis of their disturbance histories and spatial proximity to one another: all were mature to old-growth conifer-dominated forests prior to high severity fire (>95% canopy mortality). Each site was a relatively homogeneous area of similar stand condition and high fire severity ranging in size from ~10-50 ha. Plots were located at least 300 m from one another within sites (range 1-3 plots per site). Soils were largely metavolcanic and metasedimentary in origin with a few sites having coarse-grained igneous type soils; ultramafic soil types were avoided. Elevations spanned 400-1400m on a full range of aspects, on slopes primarily >20°. Plots experienced a combination of zero, one, or two recent fire events (in cases of the latter, burns were separated by 15 years); all burns experienced some degree of salvage logging (Table 3.1).

Salvage logging occurred during the fall, winter, and spring of 2004-2005. We devoted our sampling effort in 2005 to quantifying the effects of salvage; thus our 2004 data were used to investigate the effects of fire and our 2005 data were applied to examining the influence of salvage logging. We employed a paired plot design where salvage logged and unlogged plots were located near one another (range 250-700m) within a site. Salvage logging consisted of handfelling and cable yarding <1 year after fire with snag retention levels of 4-6 ha<sup>-1</sup> in the case of the Galice Fire, hand felling and helicopter yarding 1-2 years after fire with snag retention levels of 12-17 ha<sup>-1</sup> in the case of the Silver Fire, and for the Biscuit Fire hand felling and cable/helicopter yarding 2-3 years after fire with minimum snag retention of 9-16 snags per hectare greater than 48 cm dbh (USDA Forest Service 2004 pg G-22). All plots were located in salvage units > 3 ha in size. In this study, fire and salvage logging were confounded for the 1987 fires. The different disturbance histories (referred to as treatments hereafter) allow examination of

small mammal response to stand replacement fire at short and intermediate (~decadal) time scales. Because burned sites were preexisting and not selected randomly, inference from our results are limited to our study sites.

### *Vegetation sampling*

Plots (1-ha) were sampled for vegetation and small mammals during the summers of 2004-2005. Vegetation data were collected using a design similar to the Forest Inventory and Analysis program (USDA 2003) as part of a parallel study (Donato et al. 2006). Briefly, woody debris were measured in four 75m planar intercept transects originating from the center of the plot (Brown 1974). Ground cover (litter, bare soil, herbaceous plants) was estimated ocularly on 4 nonoverlapping circular subplots positioned over the hectare plot 35m from one another. Shrub biomass and tree basal area was computed from measurements of individual shrubs and trees occurring on each subplot. Herbaceous plant cover was the combination of forbs, grasses, and low stature shrubs with little secondary growth such as *Berberis sp.*, *Gaultheria shallon*, *Ribes sp.*, and other species of similar stature. Mass ( $\text{kg ha}^{-1}$ ) of live shrubs was estimated using field measurements of shrub crown volume and basal diameter of stems in combination with allometric equations (Donato 2008). Volume of coarse woody debris was estimated using standard measurements and equations outlined in Brown (1974) and Harmon and Sexton (1996). Vegetation data used in this paper include cover of litter, bare soil, and herbaceous plants; basal area of live and dead trees, mass of downed woody debris, and shrub biomass (live and dead).

### *Small mammal trapping*

Mammal trapping was conducted from July-August in 2004 and 2005.

Trapping grids of 10 x 10 traps with 10m spacing were established using large (7.6 cm x 8.9 cm x 22.9 cm) Sherman live-traps baited with peanut butter and rolled oats, placed near logs or runways to maximize capture rates. Grids were trapped for 3 (range 2-4) consecutive nights for one trapping occasion; daytime trapping was not conducted to avoid heat-based mortality. We recorded the following data for each captured animal: trap number, species, weight, sex, and evidence of reproduction (lactating females, scrotal males). Each captured animal received a temporary mark (red permanent ink on an ear) indicating the night of its capture, allowing us to assess the number of times each animal had been captured.

#### *Data analysis*

We first calculated treatment means and 95% confidence intervals of small mammal densities, observed species richness, and total biomass as well as vegetation/habitat characteristics such as tree densities, coarse woody debris, and ground cover. We examined the influence of high severity fire, postfire salvage logging, and habitat characteristics on small mammals using additive linear models with multimodel inference within an information theoretic framework (Burnham and Anderson 2002).

*Small mammals.* Abundance of small mammal species was estimated using mark-recapture data. Following the suggestions of McKelvey and Pearson (2001), we report the unique number of individuals ( $M_{t+1}$ ) captured per plot. This estimate of population size is known to be negatively biased (Otis et al. 1978); however, given the modest number of captures (<50) per plot in most small mammal studies (see McKelvey and Pearson 2001 for a review), other estimators may exhibit greater bias and

inconsistency when underlying sources of heterogeneity in trapping probabilities cannot be adequately assessed. Under these conditions, McKelvey and Pearson (2001) show that  $M_{t+1}$  was the most robust to changes in underlying population attributes (e.g. heterogeneity in trapping probabilities over time, behavior, etc.), had the smallest coefficients of variation over a broad range of capture probabilities, and outperformed population estimators in detecting changes in population size. In addition, an observed high correlation ( $r^2 > 0.7$ ) between  $M_{t+1}$  and population estimators suggests relatively constant bias (McKelvey and Pearson 2001). In our study, estimated capture probabilities using program CAPTURE (White et al. 1978) showed broad overlap across treatments suggesting no consistent differences in capture probability by treatment (Fig 3.2b; one-way ANOVA  $F_{5,24} = 0.64$ ,  $P=0.67$ ). Thus, bias in  $M_{t+1}$  was not due to disturbance history and, rather, likely came from individual-level heterogeneity in capture probabilities (e.g. age, gender, reproductive condition). Furthermore, estimates of population size ( $N\text{-hat}$ ), obtained from program CAPTURE had low precision but a high correlation with  $M_{t+1}$  suggesting that  $M_{t+1}$  is reliable index of population size (spearman  $r=0.88$ , Fig 3.2b).

Abundance of small mammal species was converted to density (individuals  $\text{ha}^{-1}$ ) using a naïve estimate of effective trapping area (1 hectare trapping grids). Species with  $>10$  captures were compared across treatments (deer mice (*Peromyscus maniculatus*), pinyon mice (*P. truei*), and chipmunks (*Tamias sp.*)). The two chipmunk species (*Tamias townsendii* and *T. siskiyouensis*) in the study area were pooled due to overlapping characteristics and difficulty in field identification to species (Verts and Carraway 1998). For the community level metrics of species richness and total biomass,

all species were included. Biomass was the sum of weights of all individuals.

Shannon diversity and evenness of the small mammal community as well as the proportion of reproductive deer mice were calculated for each plot. Lack of overlap of confidence intervals with means of other treatments was interpreted as evidence for statistical difference between groups while asymmetrical overlap of means (intervals overlap one mean but not the other) was interpreted as suggestive evidence of a statistical difference between groups (Ramsey and Schafer 2002).

*Evaluation of disturbance effects and habitat relationships.* We evaluated the effect of high severity fire in 1987 and 2002, salvage logging, and vegetation variables on small mammal metrics using ordinary least squares regression performed with the linear model function within R v2.5.1 (R Development Core Team 2007). Due to multiple study objectives, our vegetation and small mammal plots did not have complete spatial overlap. Thus, we performed the analysis using a subset of data for which we had both small mammal data and intensive vegetation measurements (n=14 plots in fire analysis, 11 plots in salvage analysis). For our analysis of fire effects, we included indicator variables for high severity fire in 1987 or 2002 and four vegetation variables based on published literature: rotten coarse woody debris volume, sound coarse woody debris volume, cover of herbaceous plants, and biomass of live shrubs. The salvage analysis included the four habitat variables plus an indicator variable for salvage logging. We used an all subsets approach to give each predictor equal consideration but given the modest size of the data sets, we constrained our models to no more than the intercept plus three predictors for the fire analysis and the intercept plus two predictors for the salvage analysis. No interactions were considered and we avoided models with highly correlated

predictors. For the salvage analysis, we did not include salvage logging and sound coarse woody debris in the same model due to their high correlation (spearman  $r=0.87$ ). This resulted in a model set of 42 models for the fire analysis and 15 models for the salvage analysis.

Models were evaluated using an information theoretic model selection and inference framework (Burnham and Anderson 2002), in which the relative support given the data for hypotheses in the form of models was compared using Akaike's information criterion (AIC, Akaike 1973). We applied the small sample size correction (AIC<sub>c</sub>) to all AIC calculations (Hurvich and Tsai 1989). Interpretation was based on model weights ( $w_i$ ) and relative importance values of each predictor (sum of model weights containing each predictor, (Burnham and Anderson 2002)) and parameter estimates with 95% confidence intervals. For each predictor, we report its parameter estimate and 95% confidence interval from the top model containing that predictor. To evaluate the relative importance of predictors we summed the weights ( $w_i$ ) of the models containing each predictor (see Burnham and Anderson 2002). We used relative importance values of 0.40 and greater as a cutoff to identify predictors that were likely influencing the process of interest (see Converse et al. 2006a).

## RESULTS

### *Vegetation Response*

*Fire Effects.* Direct effects of fire on vegetation were evident; comparison of unburned and burned sites in 2002 as well as the 1987 burn with the repeat burn reflected the effects of high severity fire in 2002 via the consumption of litter, increased bare soil, killed trees, and top-killed shrubs (Fig 3.3). Herbaceous cover in repeat burned stands

exceeded that of all other disturbance histories (Fig 3.3), likely reflecting the early seral condition of repeat burn stands at the time of the second fire. Sound coarse woody debris levels were larger in stands two years after fire relative to mature forests. Smaller volume of rotten coarse woody debris two years after a single burn compared with that of mature forests likely reflected combustion due to fire of wood in advanced stages of decay.

*Salvage Logging.* Postfire salvage logging altered stand structure via the removal of standing fire-killed trees (Fig 3.4a) and increased volume of sound coarse woody debris on the forest floor (Fig 3.4b). Other ground cover metrics such as live shrub mass and cover of bare ground, herbs, and litter showed no difference between logged and unlogged plots one year after logging (Fig 3.4c).

#### *Small Mammal Response*

*Fire Effects.* Four treatments were sampled in the summer of 2004 with 4-5 stands per treatment. We captured 473 individuals of 9 species (Table 3.1). Overall patterns of community composition and abundance yielded a pattern of higher species richness and lower total abundance in mature forest and 1987 burn treatments and lower richness and higher abundance in the more recent 2002 burn and repeat burn treatments (Fig 3.5). However, high variability within treatments led to large confidence intervals that overlapped means in most cases. Similarly, mean diversity and evenness varied markedly across treatments; however, broad overlap in confidence intervals reflected no difference between treatments.

Deer mice showed the strongest response, exhibiting low densities in mature forest and the highest densities in areas burned in 2002 (both single and repeat burns, Fig

3.5) as well as the highest proportion of reproductive individuals (Table 3.2).

Estimates of the proportion of reproductive deer mice were highest in sites burned in 2002 (burn 2002 and repeat burn) and significantly lower in mature forest and burn 1987 treatments (Table 3.2). Deer mouse densities in the repeat burn were greater than the single burn (Fig 3.4). Pinyon mice were found in low densities in mature forest and sites 17 years after fire in 2004 and, by 2005, had re-colonized areas burned in 2002 (3 years postfire, Fig 3.5-6). Chipmunks (*Tamias* sp) were captured most frequently in sites burned in 1987 (Fig 3.5).

The top-ranked model for deer mouse density was (intercept + burn 2002 + herb) with a weight of 0.30 (Table 3.3). Burn 2002 and herb cover had importance values of 0.98 and 0.67, respectively with confidence intervals of the parameter estimates not overlapping zero (Table 3.4). The estimate for burn 1987 did not overlap zero but had a very low relative importance value suggesting low biological significance (Table 3.4). Model results for pinyon mouse and chipmunk densities reflected the low number of captures with no predictors having importance values >0.40 (Table 3.4), multiple models with  $\Delta AIC_c$  values of <2 (Table 3.3), and all parameter estimates overlapping zero (Table 3.4). The top biomass model included sound coarse woody debris and the intercept (Table 3.3) with sound coarse woody debris having a relative importance value of 0.44 and a parameter estimate broadly overlapping zero (Table 3.4). Top ranking models of species richness included a positive effect of rotten coarse woody debris (confidence interval not overlapping zero) and a weak negative effect of burning in 2002 (Table 3.3, Table 3.4). These are consistent with the tendency for highest species richness to be in mature forests (Fig 3.5).

*Salvage Effects.* We assessed the influence of salvage logging on small mammals in the first growing season following logging and prior to fuels reduction activities. We sampled 13 plots (6 unlogged, 7 logged), capturing 453 individuals of 3 species (Table 3.1). Little variation in community composition was apparent between logged and unlogged stands aside from a slight increase in chipmunks in salvage logged stands (Fig 3.6). For small mammals, the effects of the 2002 Biscuit Fire appeared much stronger than that of postfire salvage logging. None of our five response variables (densities of 3 species, total biomass, species richness) was strongly related to salvage logging. Salvage logging was not in any of the top models (Table 3.3), parameter confidence intervals overlapped zero, and importance values were never  $>0.40$  (Table 3.5). Herb cover was the only predictor associated with any of our response variables, with a negative estimate for pinyon mouse density and species richness (Table 3.5).

## DISCUSSION

Our study of fire and salvage effects on terrestrial small mammals was retrospective in nature with non-randomly selected plots. Site selection for the salvage logging portion of our study was non-random (because land managers determine potential salvage units) but employed a paired plot design in which logged and unlogged plots were within 500m of one another (e.g. a natural experiment). Thus, inference regarding the short-term effects of salvage logging on terrestrial small mammals is fairly strong at these plots. Our observations are limited to the first growing season following logging and, thus, pertain only to short-term response. Plots for the study of fire effects were less spatially interspersed with fewer stands available for study. Thus, inference on fire effects is more limited. Additionally, all stands burned in 1987 experienced varying

levels of postfire salvage logging, confounding the effects of the fire. However, given the negligible influence of salvage observed relative to fire in 2002, we think our data reflect the effects of high severity fire and subsequent physiognomic succession rather than postfire salvage logging of our plots burned in 1987.

The immediate effects of high severity fire on small mammal species were evident in this study. High severity fire tended to simplify community composition, transitioning stands from higher species richness and lower abundance to lower species richness and elevated abundance of small mammal species. Response of individual species to high severity fire has been hypothesized to follow three broad trajectories (Quinn 1994, Fig 3.7): late seral associated species, early seral/disturbance-adapted species, and mid-seral species. Late seral species (A, Fig 3.7) require more mesic conditions with a closed canopy, a well-developed litter layer, and rotten coarse woody debris. These species become absent following fire and recolonize a site after mature/late seral conditions re-develop. In the Klamath-Siskiyou region, mid-successional species (C, Fig 3.7) would be associated with a shrub-dominated phase and an accumulating litter layer. Early successional species (B, Fig 3.7) generally are present throughout succession but increase substantially immediately following disturbance and decrease as herbs are replaced by large stature shrubs such as ceanothus, madrone, tanoak, and manzanita.

Loss of species such as voles and wood rats after fire is likely due to direct mortality from fire as well as loss of habitat via litter consumption and shrub and tree mortality. Wood rats (dusky-footed and bushy-tailed) were consistently captured in the 1987 burn and mature forest plots suggesting that 17 years after fire, vegetation conditions are adequate for wood rats, a pattern consistent with a mid-successional

associated response (curve C, Fig 3.7). Voles (Oregon, southern red-backed, and red tree) were captured only in mature forest plots, suggesting that development of habitat conditions and recolonization rates for these species are slower than those of wood rats in the dry mixed-evergreen forest of the Klamath-Siskiyou Mountains (curve A, Fig 3.7). These patterns are consistent with Pacific Northwest regional distribution patterns driven by moisture-temperature gradients (Carey and Johnson 1995). Forest floor small mammal diversity peaks in northerly mesic, low elevation forests of the Pacific Northwest (e.g. Olympic peninsula) while medium sized mammals such as wood rats and *Tamias* sp. are most numerous further south in forests with broad-leaved evergreens and higher abundance and diversity of hypogeous fungi (Carey and Johnson 1995).

High proportions of reproductive deer mice in plots burned in 2002 relative to mature forest or forest burned in 1987 support the hypothesis that deer mice rapidly colonize burned areas and are adapted to disturbance (curve B, Fig 3.7). In 2002 burn plots, increased densities of deer mice from 2004 to 2005 and colonization by pinyon mice in 2005 was consistent with a disturbance-adapted life history strategy (Verts and Carraway 1998). For deer mice, the repeat burn appeared to amplify the effect of a single fire event rather than dampening it, again reflecting the disturbance-adapted life history strategy of deer mice. The legacy effect of early seral conditions prior to the second fire event as well as high herb cover following the repeat burn provided more propagules and higher survival, respectively, for deer mice. Herb cover had a high relative importance in our modeling of deer mouse density and forbs constitute an important portion of deer mouse diets during the growing season (Carey and Johnson 1995, Verts and Carraway 1998). Additionally, high levels of coarse woody debris present in repeat burn stands

may have provided shelter during the fire event, allowing more animals to survive and recolonize the repeat burn.

Deer mice are widely distributed and known to increase after fire in many ecosystems. These include prescribed fire across North America (Ahlgren 1966, Lawrence 1966, Converse et al. 2006c, Monroe and Converse 2006) as well as high severity fire in boreal forests (Fisher and Wilkinson 2005), dry forest types (Converse et al. 2006b), sagebrush steppe (McGee 1982), and tall grass prairie (Beck and Vogl 1972). Moreover, deer mice also increase after green-tree harvest (Gashwiler 1970b, Converse et al. 2006c). Effect of repeated burning on small mammals has not been well studied, particularly in forested ecosystems. In a prairie-forest ecotone of Wisconsin, Beck and Vogl (1972) compared unburned controls with plots burned 2, 4, or 11 times in a 15 year period. Red-backed voles (*Clethrionomys gapperi*) and white-footed mice (*P. leucopus*) declined with increasing burns whereas deer mice were captured only on plots burned 11 times. In Australia, Fox (1990) studied small mammal response to recurrent fire in a sclerophyll heathland. Repeat fires, separated by 6 years, were characterized by an immediate increase in disturbance-adapted mice (*Mus musculus*, *Pseudomys gracilicaudatus*, and *P. novaehollandiae*) followed by increases in native rats (*Rattus* sp.) 14 years postfire (Fox 1990). Similar to our results, the amplitude of response to a repeat fire was greater than that to a single fire (Fox 1990).

Small mammal response to salvage logging is not well understood. A recent review (McIver and Starr 2001) found only one set of related field studies, from Israel, examining small mammal response to salvage logging (Haim and Izhaki 1994, 2000). Haim and Izhaki (1994), studied small mammal communities following fire in

unsalvaged, salvaged, and salvaged and cleared stands of Aleppo pine (*Pinus halepensis*). In their study, small mammal communities in unsalvaged stands recovered more rapidly than salvaged stands. However, logged and unlogged stands appeared to converge in community composition three years postfire. Subsequent small mammal studies combining fire and logging effects have been limited to thinning of green trees and prescribed fire (Converse et al. 2006c, Monroe and Converse 2006).

Despite a significantly larger pool of sound coarse woody debris following salvage logging, the response of deer mice, pinyon mice, and chipmunks was negligible, with a suggestion of a positive response of chipmunks. Townsend's chipmunk has been shown to preferentially use large woody debris for movement in unburned forests (Waldien et al. 2006) potentially explaining the increase we saw in logged plots. The lack of response in the three species we detected in burn 2002 stands likely is associated with the early seral nature of the stands and the species that occur there (curve B, Fig 3.7). Species associated with early seral conditions are disturbance-adapted with high reproductive rates (Table 3.2) and colonization rates of disturbed habitats. Given the higher densities of deer mice recorded in repeat burn stands, early seral small mammal species might be expected to increase following postfire salvage logging which represents a second disturbance. Changes over successional time scales require further study, particularly the potential effects of the large pulse of woody debris created by salvage logging compared to more protracted inputs in the absence of salvage. Rotten woody debris is known to provide food (hypogean fungi, invertebrates), travel corridors, and shelter to small mammals (Hayes and Stephen 1987, Carey and Johnson 1995). However, decay rates of woody debris and the dynamics of woody debris recruitment

from the snag overstory are not well known (see McIver and Ottmar 2007).

Differences in size, residence time, and decay rates between the pulse of woody debris created from salvage logging and natural recruitment as snags fall deserves further study.

Across our study, we observed an absence of species association with the four habitat metrics we analyzed (rotten and sound coarse woody debris volume, shrub mass, and herb cover). Results of past studies of small mammal association with woody debris at similar spatial scales have been mixed with some showing a lack of association for voles (Craig et al. 2006), deer mice (Smith and Maguire 2004) or chipmunks (Bowman et al. 2000b, Smith and Maguire 2004), and others showing positive associations (Carey and Johnson 1995, Fisher and Wilkinson 2005). Bowman et al. (2000a) documented positive spatial autocorrelation in four small mammal species at scales of 100-500m suggesting that the stand scale (~1-8 ha) is an appropriate scale at which to study small mammal populations. Our analysis was stand scale and not at the scale of individual pieces of CWD. Others have shown a positive relationship between rotten CWD and small mammal activity (Hayes and Stephen 1987). We found some support for positive associations between increased herb cover and deer mice in our study of response to fire and pinyon mice in response to salvage logging but the parameter estimates overlapped zero. These results agree with a number of past studies documenting associations between *Peromyscus* species and herb cover (Ahlgren 1966, Carey and Johnson 1995, Manning and Edge 2004). All three species analyzed are early seral associates to some degree and, thus, are more likely to rapidly reproduce and exhibit broader habitat tolerances. Late seral associated species might be hypothesized to show the strongest associations with habitat metrics such as rotten coarse woody debris, litter cover, etc.

*Management Implications*

Management objectives in severely burned areas often have a primary goal of rapid conifer establishment following disturbance. In once burned stands we observed a suggestive negative relationship (spearman  $r = -0.73$ ) between conifer seedling densities and high deer mouse densities (Fontaine, Donato unpubl data). Given our observation, and the previously reported link between deer mouse densities and seed predation of conifers and other plant species (Gashwiler 1970a, Tallmon et al. 2003), deer mice may exert a strong effect on vegetation dynamics following fire. Herbivory may be of particular interest in areas experiencing repeated fire, given the elevated deer mouse densities we observed. Land managers working on postfire rehabilitation in severely burned forests and particularly areas with repeated fire might anticipate greater levels of small mammal herbivory and seed predation when planning revegetation projects.

Repeated high severity fire over short intervals has notable precedent in the Pacific Northwest (e.g. Tillamook and Yacoult burns, Neiland 1958, Gray and Franklin 1997); little is known, however, about ecological responses to these events. Our study presents data describing the ecological response of small mammal communities to repeated high severity fires separated by 15 years in a region where repeated fire is within the historical range of variability. The data presented here contribute to a knowledge gap and will aid managers in forming expectations of response to future repeated fire events.

We found little effect of salvage logging on small mammal communities in the short term. The influence of the preceding fire was much larger than that of the salvage logging, the small mammal community was composed of disturbance-adapted species such as deer mice and chipmunks. Thus, land managers should not expect short-term

negative impacts of postfire salvage logging on terrestrial small mammals. However, long-term impacts of the removal of a large proportion of the dead wood and the pulse of slash and larger cull pieces of bole wood are unknown for small mammals. Our observation of a positive relationship between the volume of rotten coarse woody debris and species richness and the association of several vole species with rotten coarse woody debris (Fisher and Wilkinson 2005) suggests that removal of a large proportion of the large wood from a stand may lower the habitat suitability for certain species over longer time scales. Snag retention within salvage units and reservation of unsalvaged stands would aid in ensuring a long-term supply of dead wood at stand and watershed scales. Previous studies have shown that salvage logging reduces snag longevity (Russell et al. 2006) and compresses the window of time that large amounts of coarse woody debris are present within a stand (McIver and Ottmar 2007). Further research comparing snag and dead wood dynamics in salvage and unsalvaged stands is warranted. To the best of our knowledge, this is the first study to address the impacts of salvage logging on small mammal communities in the western United States.

## LITERATURE CITED

- Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.
- Ahlgren, C. E. 1966. Small mammals and reforestation following prescribed burning. *Journal of Forestry* **64**:614-618.
- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. *in* B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.
- Beck, A. M., and R. J. Vogl. 1972. The effects of spring burning on rodent populations in a brush prairie savanna. *Journal of Mammalogy* **53**:336-346.
- Bowman, J., G. Forbes, and T. Dilworth. 2000a. The spatial scale of variability in small-mammal populations. *Ecography* **23**:328-334.
- Bowman, J. C., D. Sleep, G. J. Forbes, and M. Edwards. 2000b. The association of small mammals with coarse woody debris at log and stand scales. *Forest Ecology and Management* **129**:119-124.
- Brown, J. K. 1974. Handbook for inventorying downed woody material. Pages 24 *in* General Technical Report GTR-INT-16. USDA Forest Service, Intermountain and Range Experiment Station, Ogden, UT.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd edition. Springer, New York.
- Carey, A. B., and M. L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth-forests. *Ecological Applications* **5**:336-352.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**:1119-1144.
- Converse, S. J., W. M. Block, and G. C. White. 2006a. Small mammal population and habitat responses to forest thinning and prescribed fire. *Forest Ecology and Management* **228**:263-273.
- Converse, S. J., G. C. White, and W. M. Block. 2006b. Small mammal responses to thinning and wildfire in ponderosa pine-dominated forests of the southwestern United States. *Journal of Wildlife Management* **70**:1711-1722.

- Converse, S. J., G. C. White, K. L. Farris, and S. Zack. 2006c. Small mammals and forest fuel reduction: National-scale responses to fire and fire surrogates. *Ecological Applications* **16**:1717-1729.
- Cook, S. F., Jr. 1959. The effects of fire on a population of small rodents. *Ecology* **40**:102-108.
- Craig, V. J., W. Klenner, M. C. Feller, and T. P. Sullivan. 2006. Relationships between deer mice and downed wood in managed forests of southern British Columbia. *Canadian Journal of Forest Research* **36**:2189-2203.
- Donato, D. C. 2007. Vegetation and fuels following high severity fire, reburn, and salvage logging in the Klamath-Siskiyou region, OR. Dissertation. Oregon State University, Corvallis, OR.
- Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2006. Post-wildfire logging hinders regeneration and increases fire risk. *Science* **311**:352.
- Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Review* **35**:51-81.
- Fox, B. J. 1990. Changes in the structure of mammal communities over successional time scales. *Oikos* **59**:321-329.
- Fox, J. F. 1983. Post-fire succession of small-mammal and bird communities. Pages 155-180 *in*.
- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. Pacific Northwest Forest and Range Experiment Station, USDA Forest Service, Portland, OR.
- Franklin, J. F., T. A. Spies, R. Van Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, D. B. Lindenmayer, M. E. Harmon, W. S. Keeton, D. C. Shaw, K. Bible, and J. Q. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* **155**:399-423.
- Gashwiler, J. S. 1967. Conifer seed survival in a western Oregon clearcut. *Ecology* **48**:431-438.
- Gashwiler, J. S. 1970a. Further study of conifer seed survival in a western Oregon clearcut. *Ecology* **5**:849-854.
- Gashwiler, J. S. 1970b. Plant and mammal changes on a clearcut in west-central Oregon. *Ecology* **51**:1018-1026.

- Gray, A. N., and J. F. Franklin. 1997. Effects of multiple fires on the structure of southwestern Washington forests. *Northwest Science* **71**:174-185.
- Haim, A., and I. Izhaki. 1994. Changes in rodent community during recovery from fire: relevance to conservation. *Biodiversity and Conservation* **3**:573-585.
- Haim, A., and I. Izhaki. 2000. The effect of different treatments on the community composition of small mammals in a post-fire pine forest. *Journal of Mediterranean Ecology* **1**:249-257.
- Harmon, M. E., and J. Sexton. 1996. Guidelines for measurements of woody detritus in forest ecosystems. Publication no. 20. *in*. United States Long Term Ecological Research Network Office, University of Washington, Seattle.
- Hayes, J. P., and P. C. Stephen. 1987. Characteristics of logs used by western red-backed voles, *Clethrionomys californicus*, and deer mice, *Peromyscus maniculatus*. *Canadian Field-Naturalist* **101**:514-504.
- Hurvich, C. M., and C. L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* **76**:297-307.
- Kotliar, N. B., S. J. Hejl, R. L. Hutto, V. A. Saab, C. P. Melcher, and M. E. McFadzen. 2002. Effects of fire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. *Studies in Avian Biology* **25**:49-64.
- Lawrence, G., E. 1966. Ecology of vertebrate animals in relation to chaparral fire in the Sierra Nevada foothills. *Ecology* **47**:278-291.
- Manning, J. A., and W. D. Edge. 2004. Small mammal survival and downed wood at multiple scales in managed forests. *Journal of Mammalogy* **85**:87-96.
- McGee, J. M. 1982. Small mammal populations in an unburned and early fire successional sagebrush community. *Journal of Range Management* **35**:177-180.
- McIver, J. D., and R. Ottmar. 2007. Fuel mass and stand structure after post-fire logging of a severely burned ponderosa pine forest in northeastern Oregon. *Forest Ecology and Management* **238**:268-279.
- McIver, J. D., and L. Starr. 2001. A literature review on the environmental effects of postfire logging. *Western Journal of Applied Forestry* **16**:159-168.
- McKelvey, K. S., and D. E. Pearson. 2001. Population estimation with sparse data: the role of estimators versus indices revisited. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **79**:1754-1765.

- Meyer, M. D., M. P. North, and D. A. Kelt. 2005. Short-term effects of fire and forest thinning on truffle abundance and consumption by *Neotamias speciosus* in the Sierra Nevada of California. *Canadian Journal of Forest Research* **35**:1061-1070.
- Monroe, M. E., and S. J. Converse. 2006. The effects of early season and late season prescribed fires on small mammals in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management* **236**:229-240.
- Morrison, M. L., editor. 2006. The northern goshawk: a technical assessment of its status, ecology, and management.
- Neiland, B. J. 1958. Forest and adjacent burn in the Tillamook burn area of northwestern Oregon. *Ecology* **39**:660-671.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* **62**:1-135.
- Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* **1**:535-545.
- Quinn, R. D. 1994. Animals, fire, and vertebrate herbivory in California chaparral and other Mediterranean-type ecosystems. *in* J. M. Moreno and W. C. Oechel, editors. *The role of fire in Mediterranean-type ecosystems*. Springer-Verlag, New York.
- R Development Core Team. 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from <http://www.R-project.org> (accessed October 2007). *in*.
- Ramsey, F. L., and D. W. Schafer. 2002. *The statistical sleuth*, 2nd edition, Duxbury, Pacific Grove, CA.
- Rosenberg, D. K., K. A. Swindle, and R. G. Anthony. 2003. Influence of prey abundance on northern spotted owl reproductive success in western Oregon. *Canadian Journal of Zoology* **81**:1715-1725.
- Russell, R. E., V. A. Saab, J. G. Dudley, and J. J. Rotella. 2006. Snag longevity in relation to wildfire and postfire salvage logging. *Forest Ecology and Management* **232**:179-187.
- Smith, T. G., and C. C. Maguire. 2004. Small-mammal relationships with down wood and antelope bitterbrush in ponderosa pine forests of central Oregon. *Forest Science* **50**:711-728.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**:353-391.

- Sullivan, T. P., R. A. Lautenschlager, and R. G. Wagner. 1999. Clearcutting and burning of northern spruce-fir forests: implications for small mammal communities. *Journal of Applied Ecology* **36**:327-344.
- Tallmon, D. A., E. S. Jules, N. J. Radke, and L. S. Mills. 2003. Of mice and men and Trillium: Cascading effects of forest fragmentation. *Ecological Applications* **13**:1193-1203.
- Taylor, A. H., and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. *Forest Ecology and Management* **111**:285-301.
- Thompson, J. R., T. A. Spies, and L. M. Ganio. 2007. Re-burn severity in managed and unmanaged vegetation in a large wildfire. *Proceedings of the National Academy of Science* **104**:10743-10748.
- USDA. 2003. Field instructions for the annual inventory of Washington, Oregon and California. Forest Inventory and Analysis Program, USDA Forest Service, PNW Research Station, Portland.
- USDA Forest Service. 2004. Biscuit Fire Recovery Project Final Environmental Impact Statement. USDA Forest Service, Pacific Northwest Region, Medford, OR.
- Verts, B. J., and L. N. Carraway. 1998. Land mammals of Oregon. University of California Press, Berkeley, CA.
- Waldien, D. L., J. P. Hayes, M. M. P. Huso, and M. M. P. Huso. 2006. Use of downed wood by Townsend's chipmunks (*Tamias townsendii*) in western Oregon. *Journal of Mammalogy* **87**:454-460.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* **313**:940-943.

Table 3.1. Summary of trapping effort and total unique individuals of small mammal species captured 2004-2005 in the Siskiyou mountains, Oregon, USA.

	2004			Repeat Burn (1987 & 2002)	2005	
	Mature forest	2-yr old burn 2002	17-yr old burn 1987		3-yr old burn: No Salvage	3-yr old burn: Salvage
Number of sites	4	4	5	4	6	7
Trap nights	1200	1300	1300	1400	1700	2000
<i>Tamias</i> sp.†	0	0	21	3	5	33
<i>Peromyscus maniculatus</i>	54	96	68	187	172	223
<i>P. truei</i>	24	0	9	0	11	9
<i>Neotoma cinerea</i>	0	2	0	0	0	0
<i>N. fuscipes</i>	3	0	2	0	0	0
<i>Clethrionomys gapperi</i>	2	0	0	0	0	0
<i>Arborimus longicaudus</i>	1	0	0	0	0	0
<i>Microtus oregoni</i>	1	0	0	0	0	0

Notes: Stands in the burn 1987 and repeat burn groups were salvage logged 1-2 years following the 1987 fire event.

†*Tamias* species include *T. townsendii* and *T. siskiyou*

Table 3.2. Mean (SE) biomass ( $\text{g ha}^{-1}$ ) and proportion of reproductive deer mice by treatment in 2004 and 2005.

	2004				2005	
	Mature forest	Burn 2002	Burn 1987	Reburn	Burn 2002 No Salvage	Burn 2002 Salvage
Biomass	510.4 (152.2)	586.0 (115.2)	661.5 (246.7)	971.6 (152)	648.7 (71.3)	993.9 (171.3)
Proportion reproductive Deer Mice	0.20 (0.05)	0.54 (0.08)	0.28 (0.08)	0.48 (0.03)	0.47 (0.06)	0.52 (0.03)

*Notes:* Reburn comprised two high severity fires with a 15 year inter-fire interval. Proportion of reproductive deer mice was significantly higher in areas burned in 2002 (burn 2002 and repeat burn):  $t_{1,10}=-2.89$ ,  $p=0.02$ ;

Table 3.3. Top-ranked (based on AIC<sub>c</sub>) models for each of five responses based on model selection results from a linear regression of small mammal densities, biomass, and species richness as a function of high severity fire, salvage logging, and habitat variables in Klamath-Siskiyou mountains, Oregon, USA 2004-2005.

	Response	Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	K	w <sub>i</sub>
Fire	Deer mouse	Density (intercept + burn 2002 + herb)	113.5	0	3	0.30
		Density (intercept + burn 2002 + herb + rotten CWD)	114.8	1.29	4	0.16
		Density (intercept + burn 2002 + herb + sound CWD)	115.1	1.57	4	0.14
	Pinyon mouse	Density (intercept + rotten CWD)	86.2	0	2	0.13
		Density (intercept)	86.9	0.06	1	0.13
		Density (intercept + shrubMass)	86.9	0.78	2	0.09
		Density (intercept + burn 2002 + shrubmass)	87.3	1.18	3	0.07
		Density (intercept + burn 2002)	87.4	1.24	2	0.07
		Density (intercept + shrubmass + rotten CWD)	87.5	1.35	3	0.07
		Chipmunk sp.	Density (intercept)	85.9	0	1
	Density (intercept + sound CWD)		87.0	1.11	2	0.13
	Density (intercept + burn 2002)		87.3	1.40	2	0.11
	Density (intercept + burn 1987)		87.4	1.56	2	0.10
	Biomass	Mass (intercept + sound CWD)	210.5	0	2	0.21
		Mass (intercept)	211.0	0.42	1	0.17
	Species richness	Species (intercept + rotten CWD)	41.5	0	2	0.23
		Species (intercept + burn 2002)	42.3	0.79	2	0.16
		Species (intercept)	43.1	1.60	1	0.10
	Salvage	Deer mouse	Density (intercept)	94.0	0	1
Density (intercept + herb)			95.1	1.16	2	0.20
Density (intercept + shrubmass)			95.6	1.64	2	0.16
Pinyon mouse		Density (intercept + herb)	50.8	0	2	0.52
Chipmunk sp.		Density (intercept)	71.1	0	1	0.32
		Density (intercept + salvage)	72.2	1.14	2	0.18
		Density (intercept + herb)	72.7	1.64	2	0.14
Biomass		Mass (intercept)	167.4	0	1	0.35
		Mass (intercept + salvage)	168.1	0.73	2	0.24
Species richness		Species (intercept + herb)	30.3	0	2	0.42

Models reported above are considered competing models within 2 AIC<sub>c</sub> units of the top-ranked model. CWD=volume of coarse woody debris (m<sup>3</sup> ha<sup>-1</sup>); herb=percent cover of herbaceous vegetation; shrubMass=mass of live shrubs (kg ha<sup>-1</sup>); K= number of estimated parameters; w<sub>i</sub>=Akaike weight

Table 3.4. Estimated relative importance values (RI), parameter estimates, and 95% confidence intervals from linear regression of disturbance history and habitat variables on small mammal densities in the Klamath-Siskiyou mountains, Oregon, USA 2004

Variable	Deer mouse		Pinyon Mouse		Chipmunk sp.		Biomass		Species Richness	
	RI	Parameter (95% CI)	RI	Parameter (95% CI)	RI	Parameter (95% CI)	RI	Parameter (95% CI)	RI	Parameter (95% CI)
Burn 1987	0.14	14.25 (1.02, 27.48)	0.17	-2.46 (-7.77, 2.85)	0.22	3.00 (-2.13, 8.13)	0.18	256.2 (-191.7, 704.0)	0.12	0.244 (-0.782, 1.27)
Burn 2002	0.98	21.94 (10.15, 33.73)	0.28	-3.91 (-8.57, 0.760)	0.25	-3.13 (-8.23, 1.98)	0.13	143.2 (-292.0, 578.4)	0.37	-0.958 (-1.98, 0.064)
CWD (rotten)	0.20	0.152 (-0.035, 0.338)	0.38	0.062 (-0.012, 0.137)	0.13	-0.002 (-0.085, 0.081)	0.14	2.18 (-4.91, 9.27)	0.49	0.016 (0.001, 0.031)
CWD (sound)	0.28	0.109 (-0.031, 0.248)	0.15	-0.033 (-0.090, 0.025)	0.26	0.038 (-0.019, 0.095)	0.44	4.16 (-0.534, 8.86)	0.14	0.002 (-0.011, 0.014)
Live shrub mass	0.11	0.842 (-1.07, 2.75)	0.34	-0.515 (-1.23, 0.197)	0.14	0.227 (-0.532, 0.986)	0.16	-40.58 (-123.3, 42.16)	0.14	-0.014 (-0.161, 0.133)
Herb cover	0.67	0.462 (0.133, 0.792)	0.12	-0.013 (-0.168, 0.141)	0.13	0.027 (-0.125, 0.179)	0.18	7.26 (-5.25, 19.77)	0.12	0.009 (-0.020, 0.038)

Parameter estimates and confidence intervals are from the top model (as determined by AICc values) containing that predictor.

CWD: coarse woody debris

Table 3.5. Estimated relative importance values (RI), parameter estimates, and 95% confidence intervals from linear regression of salvage logging and habitat variables on small mammal densities in the Klamath-Siskiyou mountains, Oregon, USA 2005

Variable	Deer mouse		Pinyon Mouse		Chipmunk sp.		Biomass		Species Richness	
	RI	Parameter (95% CI)	RI	Parameter (95% CI)	RI	Parameter (95% CI)	RI	Parameter (95% CI)	RI	Parameter (95% CI)
Salvage logging	0.09	2.87 (-17.14, 22.87)	0.12	-1.29 (-3.62, 1.05)	0.25	4.53 (-1.73, 10.80)	0.30	383.4 (-106.7, 873.4)	0.19	0.526 (-0.387, 1.44)
CWD (rotten)	0.11	-0.237 (-0.921, 0.447)	0.06	-0.004 (-0.098, 0.090)	0.09	0.061 (-0.185, 0.307)	0.08	1.02 (-18.89, 20.92)	0.14	0.026 (-0.013, 0.065)
CWD (sound)	0.09	0.016 (-0.054, 0.086)	0.09	-0.003 (-0.012, 0.005)	0.08	-0.006 (-0.031, 0.081)	0.07	-0.220 (-2.22, 1.78)	0.07	0.001 (-0.002, 0.005)
Live shrub mass	0.21	-3.11 (-7.91, 1.69)	0.16	0.666 (-0.071, 1.40)	0.16	-1.63 (-3.49, 0.236)	0.20	-76.28 (-215.3, 62.73)	0.12	-0.109 (-0.426, 0.207)
Herb cover	0.26	0.222 (-0.086, 0.531)	0.77	-0.056 (-0.097, -0.015)	0.29	-0.072 (-0.184, 0.039)	0.13	-1.99 (-11.75, 7.77)	0.66	-0.019 (-0.036, -0.003)

Parameter estimates and confidence intervals are from the top model (as determined by AICc values) containing that predictor.

CWD: coarse woody debris  
Table 3-1. Summary of trapping effort and total unique individuals of small mammal species captured 2004-2005 in the Siskiyou mountains, Oregon, USA.

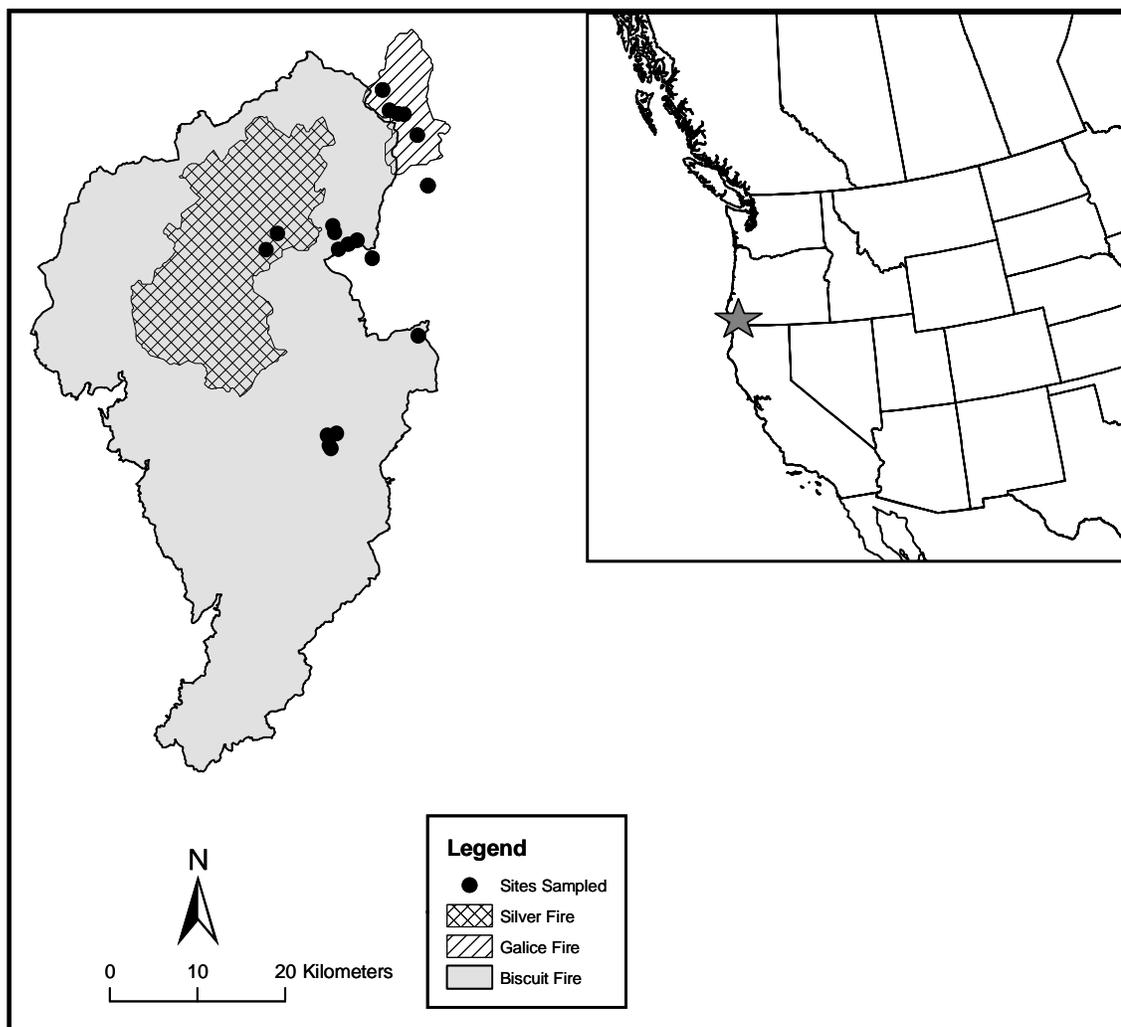


Figure 3-1. Study area in the Klamath-Siskiyou mountains of southwestern Oregon. Burned plots were located in the Biscuit (2002), Silver (1987), and Galice (1987) fires. The Biscuit Fire completely reburned the Silver Fire but did not reburn the Galice Fire.

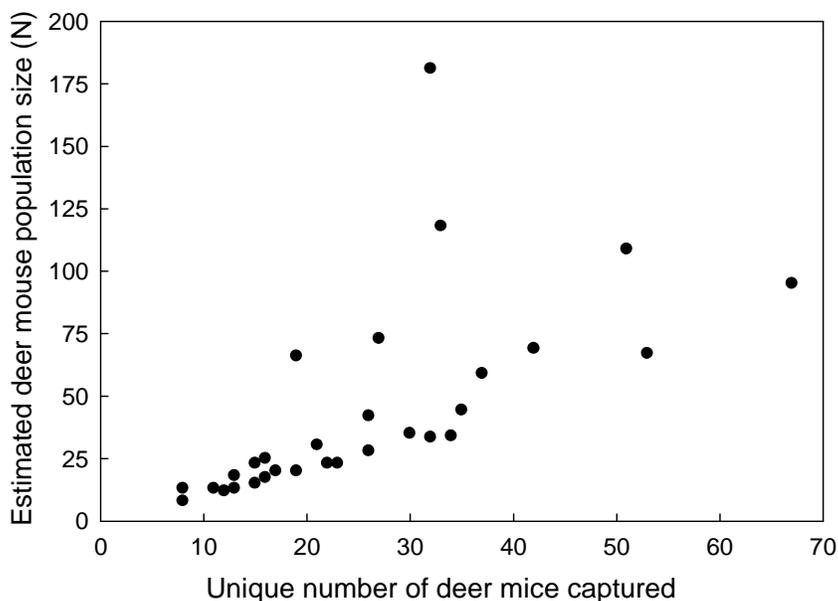
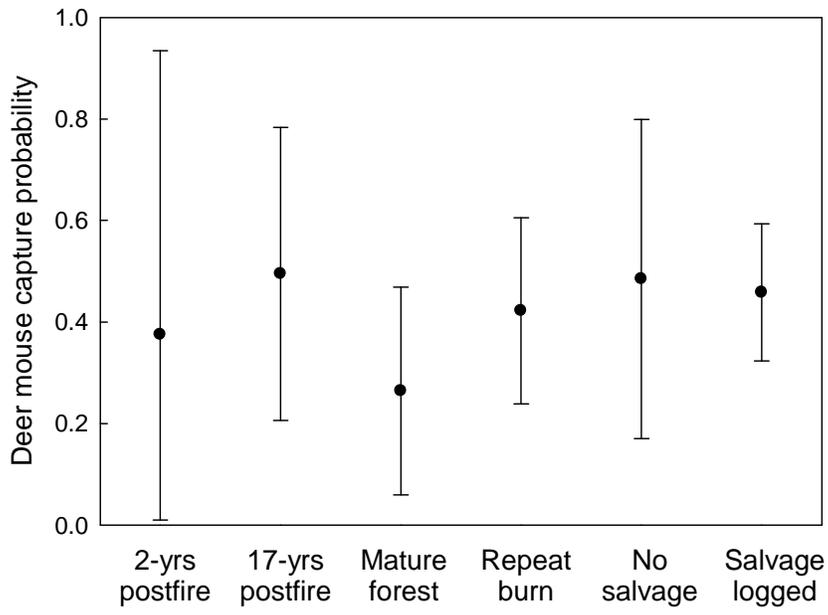


Figure 3.2. Capture probabilities (a) of deer mice by treatment (mean  $\pm$  95% confidence intervals) and (b) comparison of the number of individual deer mice captured ( $M_{t+1}$ ) and population estimates ( $\hat{N}$ ) obtained from program CAPTURE. No differences in capture probabilities among treatments were detected using a one-way ANOVA ( $F_{5,24} = 0.64, P=0.67$ ). Correlation between  $M_{t+1}$  and  $\hat{N}$  using all points pearson  $r = 0.65$  (spearman  $r=0.88$ ) and pearson  $r = 0.93$  (spearman  $r=0.95$ ) excluding the four points above the line with poor precision.

Figure 3.3. Mean ( $\pm$  95% confidence intervals) vegetation response to high severity fire: (a) basal area ( $\text{m}^2 \text{ha}^{-1}$ ) of live conifers, live hardwoods, hard snags, and soft snags (b) volume ( $\text{m}^3 \text{ha}^{-1}$ ) of rotten and coarse woody debris (CWD) and live shrub biomass ( $\text{Mg ha}^{-1}$ ) (c) percent cover of litter, bare ground, and herbs. Sample size was  $n=6$  (mature forest),  $n=14$  (2-yr old fire),  $n=9$  (17-yr old fire), and  $n=19$  (repeat burn). High severity fire converted live trees to hard snags and increased bare ground. Repeat high severity fire increased herb cover and shrub biomass relative to 2 years after a single fire.

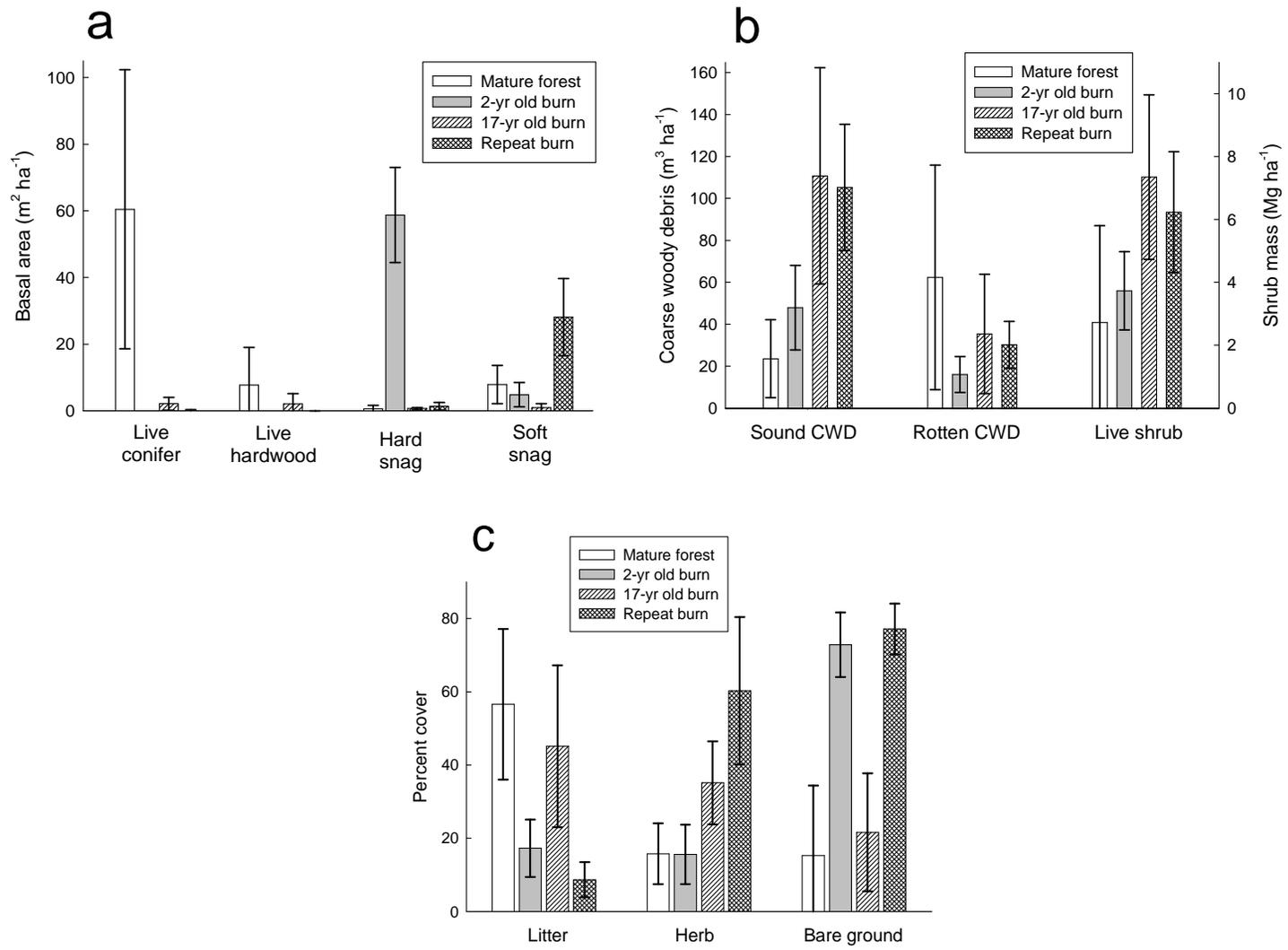


Figure 3.3

Figure 3.4. Mean ( $\pm$  95% confidence intervals) vegetation response to postfire salvage logging: (a) basal area ( $\text{m}^2 \text{ha}^{-1}$ ) of hard snags and soft snags (b) volume ( $\text{m}^3 \text{ha}^{-1}$ ) of rotten and coarse woody debris (CWD) and live shrub biomass ( $\text{Mg ha}^{-1}$ ) (c) percent cover of litter, bare ground, and herbs. Sample size was  $n=9$  (no salvage) and  $n=12$  (salvage logged). Logging removed hard snags and increased sound woody debris. Little change in mean percent cover was observed.

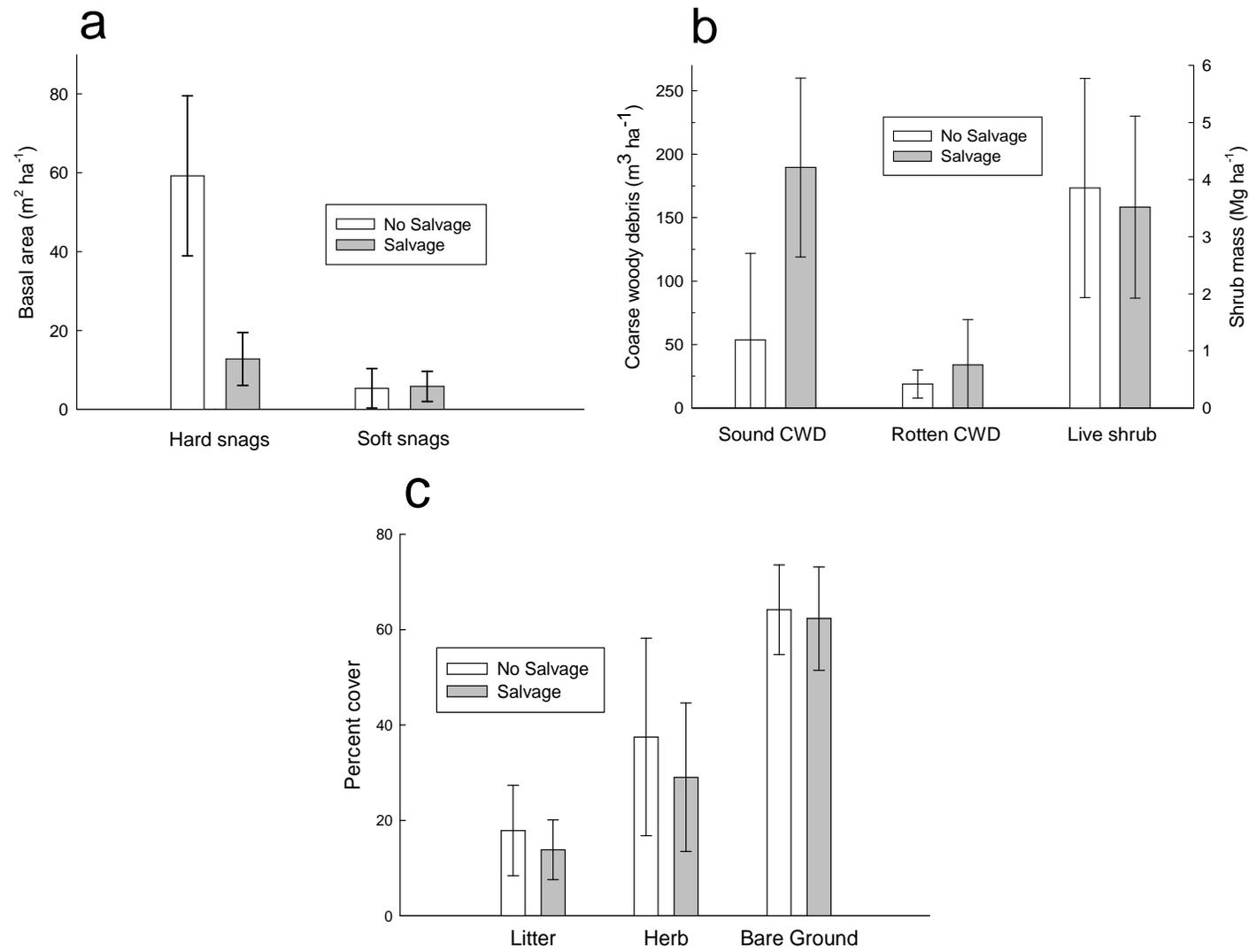


Figure 3.4

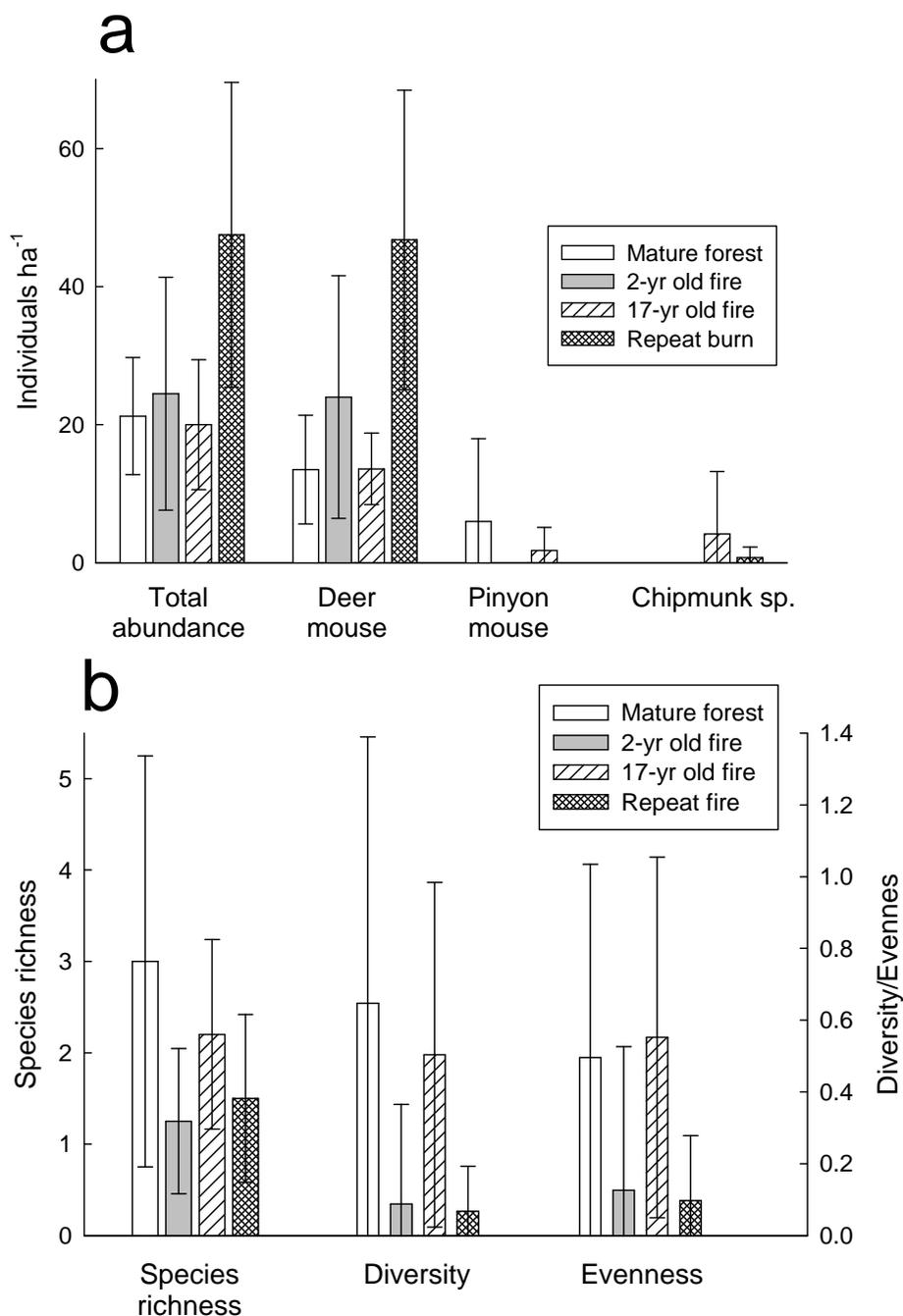


Figure 3.5 Mean ( $\pm$  95% confidence intervals) small mammal response to high severity fire: (a) densities (indiv ha<sup>-1</sup>) of all animals and individual species responses and (b) community change as measured by species richness, Shannon diversity, and evenness. Sample size was  $n=4$  (mature forest),  $n=4$  (2-yr old fire),  $n=5$  (17-yr old fire), and  $n=4$  (repeat burn). Deer mice densities were greatest in repeat burn plots. Species richness tended to be higher in plots with a longer time since fire.

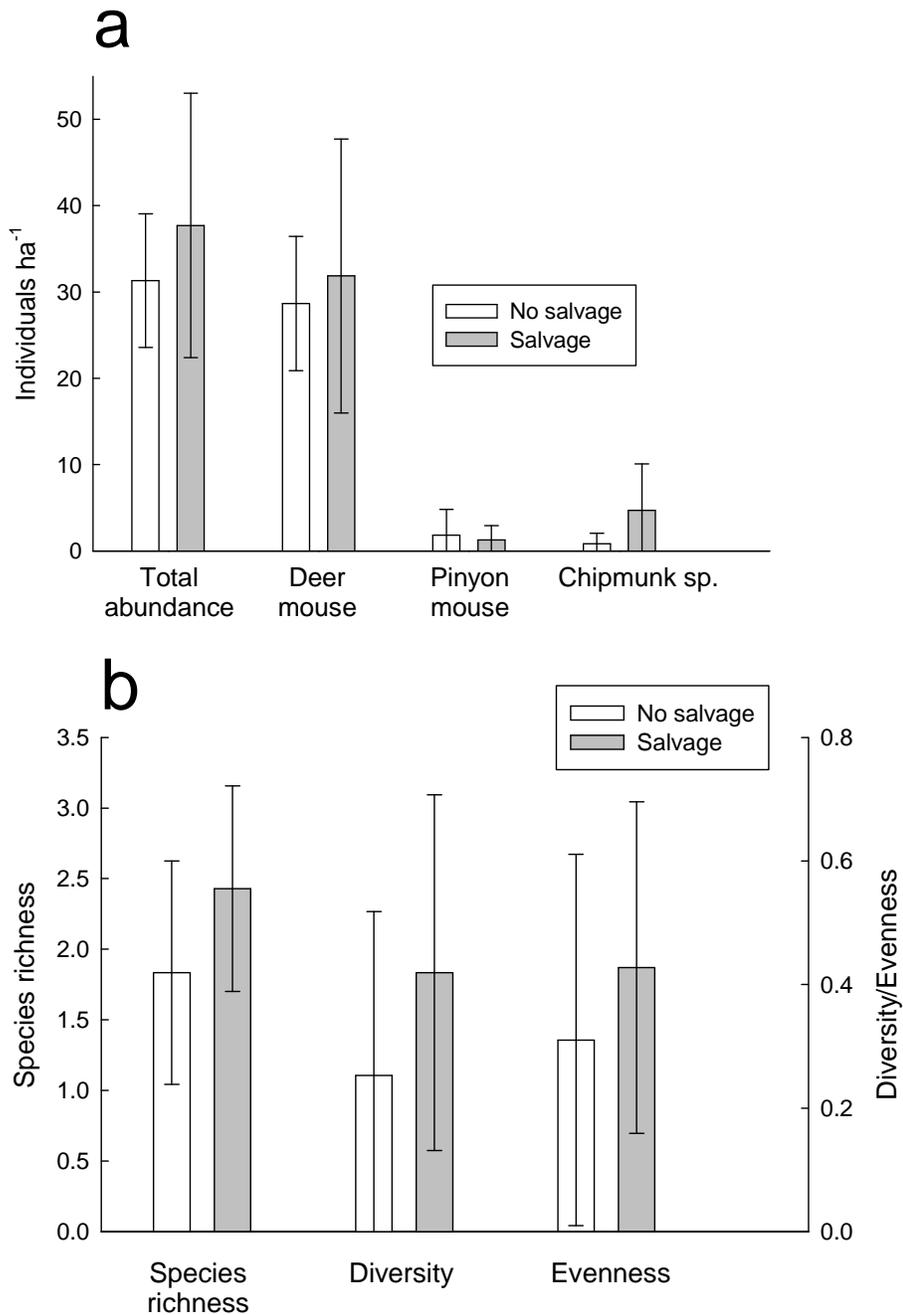


Figure 3.6. Mean ( $\pm$  95% confidence intervals) small mammal response to postfire salvage logging: (a) densities (indiv ha<sup>-1</sup>) of all animals and species responses and (b) community change as measured by species richness, Shannon diversity, and evenness. Sample size was  $n=6$  (no salvage) and  $n=7$  (salvage logged). Logging had little impact on community composition or individual species other than a slight, non-significant increase in chipmunks following logging.

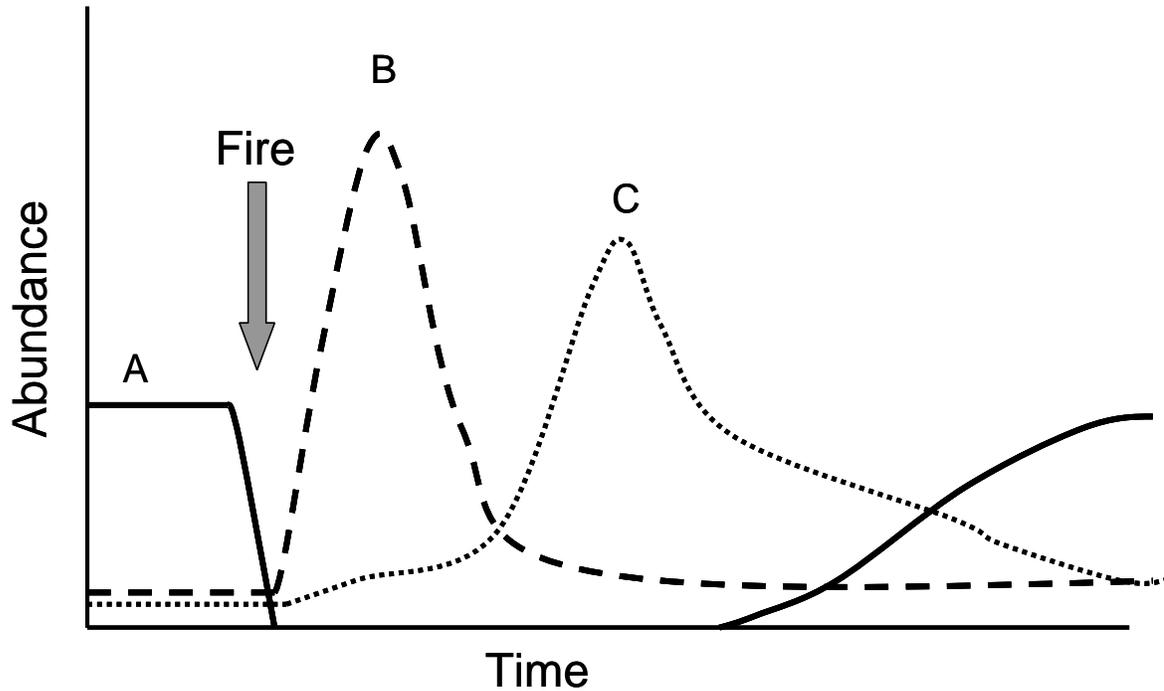


Figure 3.7. Hypothetical responses of small mammal species to high severity fire adapted from Quinn (1994). Mature/old growth associated species (A) are extirpated by fire and return once late seral conditions are achieved. Disturbance associated species (B) increase immediately after fire and decline as succession moves into a closed-canopy shrub dominated phase. Mid-successional species (C) are most common during the shrub phase of stand development.

## **CHAPTER 4: BIRD SPECIES RESPONSES TO POSTFIRE SALVAGE LOGGING IN THE SISKIYOU MOUNTAINS, OREGON, USA**

### **ABSTRACT**

High-severity fire is a common, widespread disturbance in forest ecosystems of western North America. Following high severity fire, post-fire (salvage) logging is a frequently implemented forest management practice. Considerable controversy surrounds the practice of post-fire logging; however little information on ecological responses to post-fire salvage is available to forest managers. From 2005-2006, we examined bird communities in the Klamath-Siskiyou Mountains of southwestern Oregon following post-fire logging of the 2002 Biscuit Fire, a landscape-scale (200,000-ha) mixed-severity wildfire. Logging occurred in high-severity patches; harvest units tended to be small (mean size 8 ha) with a broad range of snag retention (minimum retention of 9.5 snags >43 cm dbh per ha) . Using point counts in logged and unlogged stands, we examined changes in densities and occurrence for 17 common bird species at two spatial scales (20 ha and 2 ha) relative to two measures of salvage logging: proportion of surrounding area logged and logging intensity (proportion of basal area removed). The 20-ha scale comprised the logging unit as well as unit edges and surrounding unlogged areas, while the 2-ha scale comprised only the logging unit and not surrounding edges. At the 20-ha scale, we found a positive response in the density of shrub-associated species (house wren, lazuli bunting, black-headed grosbeak [scientific names given in Appendix A]) and edge-associated species (olive-sided flycatcher, yellow-rumped warbler) and little

evidence of negative responses, save for a reduction in density of Hammond's flycatcher. At the 2-ha scale, shrub-associates again responded positively but not edge-associates. Brown creeper responded negatively at the 2-ha scale and many species had negative but not significant estimates suggesting that, except for shrub nesting species, bird use of salvage units is associated with edges and not interior portions of salvage units. The lack of a strong negative response to salvage logging of the Biscuit Fire suggests that the small logging unit sizes relative to the burn area, as well as extensive snag retention in riparian buffers, tended to retain many bird species in the burn landscape.

## INTRODUCTION

Episodic stand-replacing disturbances are integral processes in many forest types of western North America, serving to promote and maintain biodiversity at multiple spatial scales (Agee 1993, Perry 1994). Post-fire (also known as salvage) logging is a frequently practiced management activity on many forested lands after high severity fire. Post-fire logging is often implemented with the goals of recovering economic value of fire-killed trees, funding post-fire replanting of conifers, and reducing the risk of future fire (McIver and Starr 2001). Despite the widespread practice of salvage logging, land managers have little information available to them describing ecological response to salvage logging (McIver and Ottmar 2007). Moreover, while implementing salvage logging, public land managers frequently are confronted with multiple management objectives calling for both maintenance of biodiversity as well as harvest of fire-killed trees. For example, National Forests are "to provide a framework to contribute to

sustaining native ecological systems by providing ecological conditions to support diversity of native plant and animal species in the plan area” (USDA 2005).

The role of natural disturbance in producing the spatial heterogeneity necessary for maintaining biodiversity may be altered by salvage logging. Salvage can reduce conifer regeneration (Donato et al. 2006), alter vegetation composition (Stuart et al. 1993, Rumbaitis del Rio 2006), reduce densities of cavity nesting birds (Hutto and Gallo 2006, Koivula and Schmiegelow 2007, Saab et al. 2007), and increase the severity of future fire (Thompson et al. 2007). Additionally, the impact of two disturbances--e.g. fire and timber harvest--over a short time scale (<2-3 years) has been hypothesized to alter successional trajectories of ecological systems (Stuart et al. 1993, Paine et al. 1998, Romme et al. 1998). However, salvage logging is not a dichotomous variable; harvest unit size, yarding system, time since fire, size of fire, and residual tree densities and sizes all vary widely. Salvage prescriptions have varied greatly over the last century. Historically, a high proportion of severely burned forest has been salvaged logged. For example, the Tillamook fires of the 1930s-1950s were heavily salvage logged for several years following fire with removal of virtually all fire-killed trees (Kemp 1967). Over the last 10-20 years, salvage prescriptions on publicly owned lands have trended towards higher levels of residual snags and riparian buffer strips (USDA Forest Service 2004). Despite this trend, little scientific information is available regarding the impacts of salvage logging, particularly in regard to gradients in logging intensity and extent, to assist managers developing timber salvage prescriptions (McIver and Starr 2001).

Timing, extent, and implementation of salvage logging vary widely by forest type and management objectives (Morissette et al. 2002, Lehmkuhl et al. 2003a, Hutto and

Gallo 2006, Saab et al. 2007). Despite this, most studies of avian response to salvage logging have reported salvage as a binary variable (logged vs. unlogged) at the stand level (but see Koivula and Schmiegelow 2007). However, extent (area) and intensity (amount of change per unit area) are both important measures of disturbance and predictors of ecological response (Pickett and White 1985). For example, clearcut logging (high intensity disturbance) of forest may lead to an absence of forest birds following logging but the same birds likely will persist under a thinning regime (e.g. Hagar et al. 1996, Hayes et al. 2003). However, the extent of disturbance must also be considered: a high intensity disturbance over a very small area (e.g. clearcut logging of a 1 ha patch) may not lead to a large change in a bird community whereas the same disturbance applied over a large scale (e.g. 50+ ha) likely will lead to a large change in the local bird community composition.

Our objectives were to address bird response to salvage logging in two ways. First, we examined differences in response to extent (area logged) and intensity (basal area removed) of salvage logging. Area logged was used to test whether areal extent of logging, regardless of intensity, influenced bird species occurrence; harvest intensity was used as a continuous measure of stand-level structural change (stem removal) associated with different salvage treatments. Second, we examined response to salvage at two spatial scales (2-ha and 20-ha) to examine bird use of actual salvage units (2-ha) versus the edge habitats generated by salvage logging (20-ha). Comparisons of effect estimates from mixed linear and logistic models were evaluated using 95% confidence intervals and an information theoretic approach to evaluate the strength of evidence for differing responses to logging metrics at two spatial scales.

## METHODS

### *Study Area and Fire History*

The Klamath-Siskiyou region in northwestern North America is characterized by a Mediterranean climate and a mixed severity fire regime in which fires burn every 5-75 years (Agee 1993, Taylor and Skinner 1998). The mixed severity fire regime is among the most complex and least understood ecological disturbance regimes; the combination of surface and stand-replacement fire over varying spatial and temporal scales results in a complex mosaic of plant communities, forest age structures, and successional stages on the landscape (Agee 1993).

In July 2002, at least two separate lightning strikes ignited fires in southwestern Oregon which became the 200,000 ha Biscuit Fire. Forest types in the study area are in the upper portion of the mixed evergreen zone, trending into the white fir zone (Franklin and Dyrness 1973), dominated by conifer species such as Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), and white fir (*Abies concolor*). Typical evergreen hardwoods include Pacific madrone (*Arbutus menziesii*), tanoak (*Lithocarpus densiflorus*), and canyon live-oak (*Quercus chrysolepis*) and shrubs such as manzanita (*Arctostaphylos sp.*) and snowbrush (*Ceanothus velutinus*). The landscape of the Biscuit Fire is relatively unfragmented with a large wilderness area and several large roadless areas within the fire perimeter. The rugged nature of the region and extremely dissected topography has restricted the extent of road building leading to distinct sets of road systems along ridgelines with relatively large roadless areas between road systems.

Salvage logging occurred during the fall, winter, and spring of 2004-2005 with some additional logging conducted during the winter/spring of 2005-2006. Salvage

logging consisted of handfelling followed by cable and helicopter yarding. Salvage units were designed to appear as clearcuts with residual snags (>48.8-54 cm dbh) and live trees (no live trees were harvested) retained based on plant association and wildlife habitat needs (USDA Forest Service 2004 pg. D-21). Snag retention prescriptions called for retention of 9-16 snags per hectare greater than 54 cm dbh but actual retention often exceeded these levels (USDA Forest Service 2004 pg G20-22, see results). Salvage prescriptions varied widely, ranging from clumped snag retention on the edges of logging units, resembling a small clearcut, to dispersed snags across logging units. Retained snags were often clustered in riparian buffers around streams running through logging units (USDA Forest Service 2004 pg K18-19). Harvest unit size ranged from 1-70 ha with a mean of 8 ha (Fig 4.1, Fig 2a).

Our study was conducted in areas of the Biscuit Fire selected by the US Forest Service for potential salvage logging (USDA Forest Service 2004). Sampling was conducted in 2005 and 2006. Of the post-fire logging implemented from late 2004 to early 2006, we sampled all large post-fire timber sales on the northern and eastern portions of the Biscuit Fire (Fig 4.1). Study sites were located in severely burned (overstory mortality >95%) mature to old-growth (>22.5cm DBH) Douglas-fir (*Pseudotsuga menziesii*) type conifer forests. Sampled elevations spanned 400-1400m on a full range of aspects, primarily on slopes >20°. We estimate 80-90% of all salvage logging on the Biscuit Fire occurred within this condition. We studied disturbance(s) consisting of high severity fire (>95% tree mortality) and post-fire (salvage) logging after fire (Fig 4.1). Each site was comprised of similar potential vegetation types generally dominated by Douglas-fir (Franklin and Dyrness 1973); all sites were mature to old-

growth conifer-dominated forests prior to high severity fire. At the landscape scale, we sampled the largest patches of severely burned late seral forest on the northern and eastern sides of the Biscuit Fire. Because burned sites were preexisting and not selected randomly, inference from our results may be limited to our study sites.

*Vegetation and Environmental Data.*

Vegetation and environmental data were collected at each point count station using a circular plot with a 10m radius centered on the point with the goal of characterizing vegetation strata present (ground, shrub, canopy). At the scale of the vegetation measurements, plots were randomly placed. We sampled standing trees, stumps, shrubs, and ground cover in 2005 and re-sampled shrubs and ground cover in 2006. These data allowed us to assess plant species composition of plots as well as vertical vegetation structure and their effects on bird community composition and abundance (MacArthur and MacArthur 1961). Environmental data included physiographic characteristics (elevation, slope, aspect, geographic location), ground cover (percent cover of forbs and grass, litter, bare soil, rock, wood, moss/lichen), and live and dead woody vegetation characteristics (species, height, percent cover). Within plots, each tree was identified to species and classified to the categories of live/dead, decay class 1-5 (Cline et al. 1980), diameter (dbh), and height. Shrub species were divided into two categories based on life history and growth form; species capable of re-sprouting and obtaining large stature and biomass (shrubs: 26 species) were measured separately from smaller low-stature shrubs generally less than 0.5m in height and having little secondary growth (low shrubs: 39 species). Large re-sprouting shrubs were tallied by individual, percent cover estimated by species, and the diameter and height of live and

dead stems were estimated. Low growing shrubs were identified to species and percent cover estimated.

#### *Bird Data.*

Avian point counts were conducted during days with no precipitation and light to no wind from mid-May to early-July. Point counts were conducted from just after dawn until 10:00 am, using standard point counting techniques for five minutes (Ralph et al. 1993); observers recorded all birds seen and heard and their distance using an unlimited radius. To maximize accuracy of distance estimation and proper bird identification, observers were trained extensively prior to beginning point counts, used range finders in the field, and performed double observer counts for a subset of points. Points were visited 1-2 times each year from 2005-2006. Individual points were spaced 225-250m apart and were >75m from burn edges. Points were clustered in a regular grid within large patches of severely burned forest (sites) ranging in size from ~400 to >12,000 ha in size.

#### *Data Analysis*

We analyzed the response of 17 common (i.e. sufficient number of detections for analysis) bird species to extent and intensity of salvage logging at two spatial scales (2 ha, 20 ha) using general linear mixed effects models evaluated within an information theoretic framework (Burnham and Anderson 2002). We compared means and parameter estimates and their 95% confidence intervals; lack of overlap of the mean with adjacent confidence intervals was interpreted as evidence for a statistical difference between groups while asymmetrical overlap of means (intervals overlap one mean but not the

other) was interpreted as suggestive evidence of a statistical difference between groups (Ramsey and Schafer 2002).

The two spatial scales of analysis (2-ha and 20-ha) were chosen to evaluate whether species were responding to the creation of edge habitat versus the creation of the actual logging unit itself. The finest scale of 2-ha corresponded to an 80m radius around each point. Most points with salvage logging were >80m from the edge of the unit (Fig 4.2a). The coarser scale, 20-ha, was sufficiently large (a 250 m radius) such that >80% of logged points intersected an edge (Fig 4.2c). We hypothesized that species showing consistent responses (e.g. no change in the sign of the parameter estimate) to salvage across scales were responding to the creation of the salvage unit. In contrast, we hypothesized that edge-associated species would display a positive response at the 20 ha scale and show a negative response at the 2-ha scale reflecting their use of snags at the edges of logging units.

*Quantification of salvage logging impacts.* We quantified changes in stand structure (overstory, shrub layer, ground cover) using our fine scale plot data gathered from each point count station. The fine scale of our plot measurements (0.03 ha) led us to treat salvage logging as a dichotomous variable for quantification of changes in stand structure. We also assessed the extent and intensity of salvage logging. Extent, or area logged, was calculated as the salvage logged proportion of a 250m radius circle (~20 ha) around each point using a GIS coverage of salvage unit polygons provided by the Siskiyou National Forest. Logging intensity was calculated as the proportion of total basal area removed from the same 250m radius circle. Basal area removed was estimated on a per area basis in one-hectare-size vegetation plots at point counts and other nearby

intensively measured plots (Donato et al. 2006, Donato 2008) and then multiplied by the area logged. Intensively measured plots provided reliable stand-level estimates of harvest levels due to their layout and replication, similar to the U.S. Forest Service forest inventory and analysis (FIA) program (Donato et al. 2006, Donato 2008).

*Estimation of avian densities.* Detectability of birds is well known to vary between species, observers, and habitats (Buckland et al. 2001, Allredge et al. 2007). To convert our uncorrected counts to densities (birds ha<sup>-1</sup>) at each point count, we modeled detection functions using program DISTANCE 5.0 beta 5 (Thomas 2006) for species with an adequate number of detections each year (17 species in 2005, 15 species in 2006). Following methods outlined in Buckland et al (2001), aural detections were truncated at probability of detection ~0.10 and detection functions were modeled using hazard rate, half normal, or uniform key functions with simple polynomial or cosine expansions. We first constructed appropriate cut points and then confronted the data with the three key functions each with differing covariates. Covariates allow the scale but not the shape of the detection function to vary and allow for pooling of sparse data when sample sizes are inadequate for extensive stratification (Buckland et al. 2004). Covariates were grouping variables describing salvage logging, observer, and burn patch. All model sets included models without covariates. Top models were selected on the basis of  $\Delta AICc$  and overall fit (Buckland et al. 2001, Burnham and Anderson 2002). Generally louder, large-bodied species tended to follow a uniform detection process while smaller-bodied species with higher pitched songs followed a hazard rate or half-normal detection process; detectability varied little between salvaged and unsalvaged stands (see Appendix D for additional details of analysis). Mean densities and 95%

confidence intervals for species in unsalvaged stands from 2005 and 2006 are reported for context.

*Statistical models.*

Our study design of clustered points within patches of high severity fire made it necessary to account for the lack of spatial independence among point counts within each cluster. We used hierarchical mixed regression models with penalized quasi-likelihood to determine parameter estimates for salvage logging response and two covariates. These models penalize estimated standard errors for dependence within groups making them appropriate for the analysis of clustered, spatially dependent data (see Breslow and Clayton 1993 for more details). Groups (burned patches) were allowed to vary randomly and all other variables were treated as fixed effects. Analysis was implemented in R v2.5.1 (R Development Core Team 2007) using the `glmmPQL` function in the `MASS` package (Venables and Ripley 2001). Linear mixed effects (Gaussian family) were used with density estimates at the 20 ha scale and logistic regression (binomial family) was applied to presence-absence data at the 2-ha scale. We used a presence/absence approach at the 2 ha scale in order to minimize bias caused by differences in detectability between observers, years, and salvaged/unsalvaged stands. Our 2-ha scale data set consisted of all bird detections truncated to a distance of 80m. Density estimates, corrected for detectability, were used at the 20-ha scale.

For each of the 17 species, we constructed a set of competing models describing (in addition to the burn patch random effect) the effects of two covariates (burn patch size and elevation), logging intensity, and area logged. Burn patch size, the mean area of severely burned forest within 2000m of each cluster, was a group level variable.

Elevation was used as a covariate to represent the gradient in shrub stature and plant community composition. Area logged and logging intensity were highly correlated (Pearson  $r \sim 0.91$ ) and, thus, were not included together in models. These two related measures were then utilized as separate predictors of salvage logging to test bird response to gradients in areal extent of logging, regardless of intensity, versus a similar variable that included both extent and harvest intensity. For each model set (species  $\times$  year  $\times$  scale), residual plots from the Area/Intensity + covariates model were inspected for departures from the assumptions of linear regression (homogeneity of variance, outliers, etc). Our model set contained an intercept only model, a covariate only model, and all combinations of covariates and logging intensity or area logged. Models were evaluated using an information theoretic model selection and inference framework (Burnham and Anderson 2002), in which the relative support given the data for hypotheses in the form of models was compared using Akaike's information criterion (AIC, Akaike 1973). We applied the small sample size correction (AIC<sub>c</sub>) to all AIC calculations (Hurvich and Tsai 1989). Interpretation was based on model weights ( $w_i$ ) and relative importance values of each predictor (sum of model weights containing each predictor, (Burnham and Anderson 2002)) and parameter estimates with 95% confidence intervals.

## RESULTS

### *Changes in stand structure*

Post-fire salvage prescriptions varied widely across the Biscuit Fire, ranging from complete (100%) removal of basal area to ~20% removal of basal area at the 1-hectare scale (Fig 4.2b). When logged and unlogged plots were compared in a binary fashion, salvage logging significantly reduced the basal area of hard snags created by the Biscuit

Fire but did not alter the basal area of pre-existing snags (Fig 4.3a). Small (<10cm dbh), medium (10-30cm dbh), and large snags (>30cm dbh) all showed a reduction from salvage logging with the largest change observed in the large snag category (Fig 4.3b). The shrub layer, as measured by volume ( $\text{m}^3 \text{ ha}^{-1}$ ) was not measurably affected by salvage logging (Fig 4.3c). Salvage logging increased the cover of woody detritus and reduced cover of bare ground relative to unlogged plots (Fig 4.3d). We did not observe a difference in herb and litter cover between unlogged and logged plots (Fig 4.3d).

#### *Bird response*

We sampled severely burned forests in 2005-06, 3 and 4 years after fire and <1-2 years following salvage logging. Across both years we detected 2737 individuals of 60 species. We had sufficient numbers of detections to estimate densities of 17 species in 2005 and 14 species in 2006 representing 82% of all bird detections (common and scientific names are in Appendix B). In unlogged stands, densities ranged from 0.27 (northern flicker) to 9.19 (dark-eyed junco) birds per 20 hectares, with large changes between years for some species (Table 4.1). Shrub-associated species (e.g. lazuli bunting) tended to increase from 2005 to 2006, likely in response to increased stature of regenerating shrubs following the Biscuit Fire (Table 4.1).

#### *Model selection results.*

Top models at the 20-ha spatial scale generally (19 of 31) had model weights  $\geq 0.30$  (range 0.19-0.63, Table 4.2). Area logged was part of the top model for 8 of 31 species x year combinations and logging intensity was included in 6 models (Table 4.2). Covariates were included in 17 (patch size) and 20 (elevation) models (Table 4.2). The intercept only model was the top model in 7 cases including hairy woodpecker in both

years. Relative importance values for predictors, the sum of Akaike model weights containing a parameter of interest, reflected a similar pattern. Area logged had a relative importance value  $>0.40$  in 9 of the 31 species x year combinations versus 10 times for logging intensity, 21 times for patch size, and 24 for elevation (Table 4.3). Together, this suggests that habitat factors related to burn patch size and elevation/plant community were stronger predictors of bird densities than post-fire salvage logging as measured by area and intensity.

Model selection results at the 2-ha spatial scale were generally similar in terms of predictor ranks to those at the 20-ha spatial scale (Table 4.2). The majority (17 of 29) of Akaike weights of top models were  $>0.30$  (range 0.17-0.74). Area logged was in the top model 5 times while logging intensity was in 7 models. The reversal of the count of top models containing area and intensity from 20 to 2 hectares may have been related to the increasingly dichotomous nature of area logged at 2 ha versus 20 ha. At such a fine scale, most plots were either logged or unlogged in terms of area (Fig 4.2c) but varied considerably in terms of logging intensity. Covariates were included in fewer models (patch size=8, elevation=13) and the intercept only model was selected as the top model in 12 cases. The higher frequency of selection of the intercept only model likely was a consequence of fewer observations at such a fine scale. Larger standard errors of parameter estimates also reflected the sparse nature of the fine scale data for some species, particularly larger bodied, low density species (e.g. northern flicker, Steller's jay, Fig 4.4c-d,4.5c-d).

*Species responses.*

Generally, we found little evidence for a strong (either positive or negative) response to salvage logging at the 20-ha scale as measured by area logged and harvest intensity across the bird species we examined (Fig 4.4a-b,4.5a-b). Two shrub-associated species, lazuli bunting and house wren, showed consistent positive responses to salvage logging and a third shrub-associate, black-headed grosbeak was positively associated with salvage in 2005 (Fig 4.4a, 4.5a). In addition, edge-associated species such as olive-sided flycatcher in 2005 responded positively to salvage area and salvage intensity (Fig 4.4a,4.5a). Yellow-rumped warbler also responded positively to salvage logging in 2006, particularly to area logged (Fig 4.4b). While several species had negative parameter estimates for salvage area and salvage intensity (e.g. Hammond's flycatcher, brown creeper, western wood-pewee, Fig 4.4a-b,4.5a-b), only Hammond's flycatcher had confidence intervals not overlapping zero for logging intensity in 2005 (but not area logged, suggesting a weak salvage effect, Fig 4.4a,4.5a). We also observed a suggestive positive response to salvage logging--particularly harvest intensity--in dark-eyed junco, a ground nesting and foraging species.

For burn patch size, most species had negative parameter estimates with several confidence intervals not overlapping zero (Townsend's solitaire, dark-eyed junco, house wren, lazuli bunting, yellow-rumped warbler, Fig 4.6a,4.6c). Shrub-associated species such as black-headed grosbeak, house wren, lazuli bunting, and MacGillivray's warbler showed a broad pattern of negative association with elevation while species favoring conifer-dominated stands such as brown creeper, red-breasted nuthatch, olive-sided flycatcher, Townsend's solitaire, and yellow-rumped warbler were positively associated with elevation. Based on the observed species responses to elevation, we concluded that

elevation served as an effective surrogate for an environmental gradient ranging from low, warm, moist stands with co-dominant hardwoods and vigorously resprouting hardwoods to cool, conifer dominated stands with a reduced shrub layer and few hardwoods.

At the 2 ha scale, more species had negative parameter estimates but with confidence intervals overlapping zero (Fig 4.4c-d,4.5c-d). Species such as yellow-rumped warbler (2006), olive-sided flycatcher (2005), and Steller's jay (2005) which responded positively to logging at a 20-ha scale did not demonstrate a similar pattern at 2 hectares, suggesting that these species may be associated with edges rather than the interior portions of salvage logging units (Fig 4.4,4.5). Shrub-nesting birds responded positively to both area logged and logging intensity at the 2-ha scale, congruent with patterns observed at the 20-ha scale (Fig 4.4c-d,4.5c-d). Brown creeper, a bark-foraging and cavity-nesting species, showed a negative response to area salvage logged in 2005 but not logging intensity (Fig 4.4c,4.5c). Patch size and elevation parameter values were very similar to those from the 20-ha scale but often with broader confidence intervals overlapping zero in a greater number of cases.

## DISCUSSION

### *Area and intensity of logging*

Parameter estimates for the effect of area logged and logging intensity were similar across the 17 species analyzed. This observation suggests that, within the range of intensities measured (see Fig 4.2b), birds were responding largely to the presence/absence of salvage logging. In a dry Douglas-fir and ponderosa pine (*Pinus ponderosa*) forest type in central Oregon, Cahall (2007) found similar results when

comparing moderate and high levels of salvage logging. Of the seven species found to respond to salvage logging, only one species occurred at significantly different densities between moderately and heavily salvaged stands (Cahall 2007). In a study of salvage effects on woodpeckers in boreal forests, Koivula and Schmiegelow (2007) found much smaller differences between varying levels of salvage logging than in comparisons of unlogged and salvage logged mixed-wood forests. These observations suggest that the presence or absence of postfire logging may be more important than harvest intensity. Moreover, any entry into a stand for postfire salvage, within the range of harvest intensities measured, suggests a similar response for the species examined. Similarity of response across a range of salvage logging intensities likely is a result of the focus on removal of the largest trees during salvage logging. Smaller diameter trees lose their value quickly and larger trees are prioritized for harvest regardless of overall salvage intensity. However, the results presented in this study are stand-scale results and do not consider landscape-scale dynamics such as fragmentation and overall availability of high-severity postfire habitat. Habitat availability and landscape fragmentation have been shown to influence bird species occurrence across a wide variety of forested habitat types (Cushman and McGarigal 2004, Parker et al. 2005, Betts et al. 2007).

### *Species responses*

Across both years, spatial scales, and measures of salvage (area and intensity), we found strong evidence of two species with a negative (Hammond's flycatcher, brown creeper) and six species with a positive (black-headed grosbeak, dark-eyed junco, lazuli bunting, house wren, olive-sided flycatcher, and yellow-rumped warbler) response to salvage logging. Nine species showed no significant response to salvage. Our study

presents data on several species whose response to salvage has not been previously reported (lazuli bunting, MacGillivray's warbler, Hammond's flycatcher, black-headed grosbeak, mountain quail, and Townsend's solitaire).

Positive responders at the 20 ha scale tended to be shrub and edge-associated species while at the 2-ha scale only shrub associates responded positively to salvage logging (house wren, lazuli bunting, black-headed grosbeak). Dark-eyed junco also displayed a consistent, but not always statistically significant, positive response to salvage logging; dark-eyed junco is a ground foraging and nesting species that responded positively to salvage logging in boreal mixedwood forests (Morissette et al. 2002, Stambaugh 2003) and dry interior western forests (Cahall 2007). Previous studies of salvage from boreal forest types (Morissette et al. 2002, Schwab et al. 2006) and interior Pacific Northwest forests (Cahall 2007) also have reported a positive response of shrub-associated and open habitat species to salvage logging (e.g. house wren, white-crowned sparrow [*Zonotrichia leucophrys*], white-throated sparrow [*Zonotrichia albicollis*], thick-billed fox sparrow [*Passerella iliaca megarhyncha*]). Salvage logging removes the canopy and creates open habitats favored by these species so perhaps it is not surprising to see salvage favor open-habitat type life histories. An exception was MacGillivray's warbler which had a negative but non-significant response to area logged and salvage intensity. Other species in the same genus, *Oporornis*, such as mourning warbler have shown a neutral to slightly positive response to salvage while Connecticut warbler responded negatively to salvage (Morissette et al. 2002, Stambaugh 2003). In the lower latitudes in which MacGillivray's warbler breeds relative to Connecticut and mourning

warblers, the species favors more mesic, shrub-dominated sites and riparian vegetation; the removal of the snag overstory may lessen the suitability of the habitat for this species.

The positive response of olive-sided flycatcher and yellow-rumped warbler at the 20 ha scale but neutral to negative parameter estimates of area logged and salvage intensity at the 2 ha scale suggest that these two species were utilizing the edges of salvage units rather than the actual logged area. Both species are known to be edge-associated (Altman and Sallabanks 2000). Steller's jay possessed a positive but non-significant response to area logged and salvage intensity at both spatial scales; corvids have been shown to respond positively to edge creation and habitat fragmentation (Greene et al. 1998). In addition, three other species (northern flicker, red-breasted nuthatch, Townsend's solitaire) followed a similar pattern, shifting from non-significant positive parameter estimates to non-significant negative parameter estimates at 20 ha versus 2 ha spatial scale. Townsend's solitaire is an aerial insectivore, is edge-associated (Bowen 1997), and likely has similar habitat requirements to yellow-rumped warbler and olive-sided flycatcher. Red-breasted nuthatch and northern flicker are both cavity-nesting bark gleaning/drilling foragers which utilize fire-killed trees. With respect to area logged, the parameter estimate for northern flicker changed from positive to negative moving from the 20 to 2 ha spatial scale but overlapping zero in both cases. Salvage logging of Douglas-fir/ponderosa pine forests in the northern Rocky Mountains reduced nest densities of northern flickers (Hutto and Gallo 2006, Saab et al. 2007). Salvage logging in those studies was more extensive and intensive than that measured in this study. In both years and for both area logged and salvage intensity, red-breasted nuthatch

changed from a positive to negative parameter estimate at 20 versus 2 ha. Red-breasted nuthatch is a bark-foraging cavity nesting species that relies on tree boles for its life history suggesting that it would not be as likely to utilize salvage logging units. Previous studies have reported neutral (Cahall 2007) to slightly negative (Morissette et al. 2002) response of red-breasted nuthatch to salvage logging, consistent with our observations.

Neutral responses of hairy woodpecker and mountain quail to salvage logging suggest that these two widespread, low density species may be somewhat insensitive to the fine scale of salvage logging that we measured on the Biscuit Fire. Mountain quail favors early seral habitats, possesses a large clutch size and short life span, and as a ground nesting species may be relatively insensitive to tree removal (Gutiérrez and Delehanty 1999). Hairy woodpecker, a cavity nesting and bark drilling species might be expected to respond negatively to the removal of trees. However, hairy woodpeckers are a generalist species and have been shown to be relatively insensitive to forest management, favoring edges and using reserve trees in clearcuts following live-tree harvest (Ripper et al. 2007). Hairy woodpecker displayed a neutral response to three levels of salvage logging in mixed-wood and conifer-dominated boreal forests (Koivula and Schmiegelow 2007).

Species with statistically significant negative responses to area logged and salvage intensity included brown creeper and Hammond's flycatcher. Brown creeper, a bark foraging insectivorous species that uses dead snags for nesting and foraging has been shown to decline following salvage logging (Cahall 2007). A snag-dependent species like brown creeper might be expected to exhibit heightened sensitivity to snag removal.

Hammond's flycatcher is known to respond negatively to the harvest of green trees and is an aerial insectivore that prefers foraging in shaded areas (Sedgwick 1994). A negative response to salvage logging is consistent with previous reports of the species preference for unlogged green stands with little understory (Sedgwick 1994) and a positive response to fire (Smucker et al. 2005). Additionally, we observed a consistently negative but non-significant response to area logged and salvage intensity for western wood-pewee. Western wood-pewee is a sit-and-wait foraging species preferring large trees with dead branches for foraging (Bemis and Rising 1999); in a prior study, western wood-pewee showed a significant negative response to salvage logging in Douglas-fir/ponderosa pine forests of the interior Pacific Northwest (Cahall 2007).

Most species had negative parameter estimates for the effect of burn patch size, reflecting a tendency to favor smaller sized patches of high severity fire. The mixed severity nature of the Biscuit Fire and, more generally, the Klamath-Siskiyou region, generated many smaller patches of severely burned forest rather than large contiguous patches of stand replacement fire. Edge-associated species (western wood-pewee, olive-sided flycatcher, Townsend's solitaire, and yellow-rumped warbler) all had negative estimates of burn patch size effect with confidence intervals not overlapping zero. We interpret this as evidence of species favoring spatial heterogeneity in fire severity where both surviving trees and snags are available for use by these species.

Species relationship with elevation reflected a gradient of shrub-associates at lower elevations (MacGillivray's warbler, black-headed grosbeak, lazuli bunting) and pure conifer forest associates at higher elevations (Hammond's flycatcher, brown creeper, red-breasted nuthatch, Townsend's solitaire, yellow-rumped warbler). Elevation served

as an excellent surrogate for variation in plant community composition in shrubs and hardwoods. Townsend's solitaire and Hammond's flycatcher favor stands with little to no understory component (Sedgwick 1994, Bowen 1997). The two species showing strong evidence of a negative response to salvage logging (Hammond's flycatcher, brown creeper) were increasingly prevalent at higher elevations. Thus, salvage logging at higher elevations in conifer dominated forest types appeared to be more detrimental than salvage logging at lower elevations with co-dominant conifers and hardwoods where a larger portion of the bird community is associated with non-coniferous vegetation (Hagar 2007).

#### *Study context*

Our study of bird communities 3-4 years following high severity fire and 0.5-1.5 years after salvage was comparable with previous studies of avian response to salvage logging which have typically examined bird communities 2-6 years after fire with salvage logging occurring ~1-3 years after fire (e.g. Caton 1996, Haggard and Gaines 2001, Morissette et al. 2002, Hutto and Gallo 2006, Cahall 2007, Saab et al. 2007). Exceptions include Saab et al. (2007) who studied bird communities from 2-11 years after fire and Schwab et al. (2006) who studied communities 10-12 post-fire with experimental snag removal at 11 years post-fire. Our study likely differs from previous studies in our use of salvage extent and intensity. Previous studies have reported mean unit sizes of 37 ha (Haggard and Gaines 2001), 24 ha (Hutto and Gallo 2006), and ranges of 6-70 ha (Morissette et al. 2002) and 13-112 ha (Cahall 2007). Mean size of sampled salvage units in the Biscuit Fire was 14 ha with most units irregularly shaped and experiencing a wide range of salvage intensities. This was due in large part to the complex, steep topography of the Biscuit Fire and the resulting fine grained severity mosaic and large

riparian buffers ( $\geq 30\text{m}$  on each side of streams) excluded from salvage logging by the US Forest Service (USDA Forest Service 2004). Thus, our study is at low end of salvage logging unit size.

Not only were salvage units on the Biscuit Fire smaller than those in other avian studies, they occurred in the context of a much larger burn. The Biscuit Fire's size is at the upper end of published studies examining either salvage logging effects or fire effects alone on bird species. Most previous studies examined fires  $< 10\%$  the size of the Biscuit Fire (median of 14 studies: 15,000 ha, range 1,600-275,000 ha, Bock and Lynch 1970, Murphy and Lehnhausen 1998, Haggard and Gaines 2001, Hoyt and Hannon 2002, Morissette et al. 2002, Stambaugh 2003, Smucker et al. 2005, Hutto and Gallo 2006, Schwab et al. 2006, Cahall 2007, Koivula and Schmiegelow 2007, Kotliar et al. 2007, Saab et al. 2007). The spatial extent of a fire may have implications for the response of birds to salvage logging. In such an extensive burned landscape, which occurred in a region with other recent large fire events (e.g., the Biscuit Fire reburned a 40,000 ha 1987 fire) the species pool likely is different from that following a small fire. Population sizes of fire-associated species will be substantially larger in a 200,000 ha fire versus a 2,000 or a 20,000 ha fire. The smaller the fire, the more likely that salvage logging will affect a high proportion of severely burned forest. Thus, it is not surprising that the most dramatic effects of salvage were reported by Hutto and Gallo (2006) who worked in a 1600 ha fire.

The Biscuit Fire burned in a mixed evergreen forest type characterized by a Mediterranean climatic regime (Agee 1993). Following fire, many species of broadleaved evergreen hardwoods and shrubs rapidly re-sprout or germinate from a

seedbank. For example, our lowest elevation sites possessed tanoak resprouts >2m in height 4 years after fire. Forest types of the Rocky mountains, inland Pacific Northwest, and desert southwest would not be anticipated to recover broad-leaved vegetation cover as rapidly thus, postfire bird communities in those forest types are characterized by lower overall bird densities and are composed of a higher proportion of cavity nesting and snag-utilizing species. Boreal forest types with aspen and willow possess a similar rapid recovery of their shrub layer following fire but snag longevity is much shorter due to smaller tree stature. Schieck and Song (2006), in a review of post-fire boreal bird community dynamics following fire and live tree harvest, concluded that most snags fall by 15-20 years after fire. In our study area, the mean basal area of snags from unsalvaged portions of an 18 year old fire was 72% of a 3 year old fire ( $78 \text{ m}^2 \text{ ha}^{-1}$  versus  $56.5 \text{ m}^2 \text{ ha}^{-1}$ ) and mean height of 18 year old snags was 65% that of 3 year old snags (17.7 m vs. 11.5 m; D. Donato unpubl. data). Therefore, bird community composition would be expected to reflect the standing dead wood (snag) legacy of fire for a longer period of time than in boreal forest types.

### *Management Implications*

Bird response to area logged and logging intensity was very similar, suggesting that entry into a stand produces similar responses, with little additional effect of harvest intensity across the snag retention levels we sampled (see Fig. 4.3). While wildlife responses will vary among forest types, our results and those of Cahall (2007) suggest that when evaluating the tradeoff between harvest intensity and area logged, managers might prioritize limiting spatial extent of salvage over limiting harvest intensity. This

observation may be limited to the range of snag retention we observed; increased harvest intensities above these levels may produce different responses

Within salvage units, retaining the largest snags which persist the longest will be beneficial for wildlife species (see Lehmkuhl et al. 2003a, Hutto 2006). Prompt salvage of smaller diameter trees might allow managers the flexibility to retain the largest diameter trees; salvage logging of the Biscuit Fire tended to focus on the largest diameter trees given the 2-4 years postfire that salvage was conducted.

We observed generally neutral responses of birds to salvage logging. Neutral response to salvage logging likely was a combination of small salvage units within a landscape-scale burn, large riparian buffers of snag retention, and a relatively unfragmented landscape. At a watershed scale, riparian buffers effectively served as large units of clumped snag retention. Thus when considering salvage logging and avian biodiversity, land managers may consider utilizing a similar approach at the watershed scale: small salvage units (median salvage unit size = 8 ha) with large riparian buffers serving as clumped reserve trees. Riparian reserves on the Biscuit Fire ranged from ~50-100m in width (USDA Forest Service 2004).

At the scale of the entire fire, the proportion of severely burned mature/old-growth forest within the Biscuit Fire that experienced salvage logging was much less than in past fires in the Pacific Northwest prior to the Northwest Forest Plan. Moreover, salvage logging of the Biscuit Fire occurred in a large burned landscape with a history of recent fire, relatively low levels of fragmentation, and a moderate amount of severely burned forest (~40% of the Biscuit Fire, USDA 2004). Postfire salvage logging that affects a high proportion of the severely burned forests within a burn perimeter likely will

have a larger impact on fire-associated species of birds (e.g. cavity nesters in Hutto and Gallo 2006, Saab et al 2007). Landscapes with higher levels of fragmentation and past management are likely to be more sensitive to postfire salvage logging. Where management objectives include maintenance of biodiversity, managers planning postfire salvage logging may consider reserving a large proportion of severely burned forests from entry. Retaining severely burned stands without post-fire management also ensures future opportunities for studying post-fire management in a scientifically rigorous manner over longer time scales.

## LITERATURE CITED

- Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.
- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. *in* B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.
- Allredge, M. A., T. R. Simons, and K. A. Pollock. 2007. Factors affecting aural detections of songbirds. *Ecological Applications* **17**:948-955.
- Altman, B., and R. Sallabanks. 2000. Olive-sided Flycatcher (*Contopus cooperi*), The Birds of North America Online *in* A. Poole, editor. Ithaca: Cornell Lab of Ornithology.
- Bemis, C., and J. D. Rising. 1999. Western Wood-Pewee (*Contopus sordidulus*), the birds of North America online. *in* A. Poole, editor. Ithaca: Cornell Lab of Ornithology.
- Betts, M. G., G. J. Forbes, and A. W. Diamond. 2007. Thresholds in songbird occurrence in relation to landscape structure. *Conservation Biology* **21**:1046-1058.
- Bock, C. E., and J. F. Lynch. 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. *Condor* **72**:182-189.
- Bowen, R. V. 1997. Townsend's Solitaire (*Myadestes townsendi*), the birds of North America online. *in* A. Poole, editor. Ithaca: Cornell Lab of Ornithology.
- Breslow, N. E., and D. G. Clayton. 1993. Approximate inference in Generalized Linear Mixed Models. *Journal of the American Statistical Association* **88**:9-24.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: Estimating abundance of biological populations. Oxford University Press, Oxford; New York.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas, editors. 2004. Advanced distance sampling. Oxford University Press, Oxford.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd edition. Springer, New York.
- Cahall, R. E. 2007. Influences of salvage logging on forest birds after fire in the Eastern Cascades, Oregon. Oregon State University.

- Caton, E. L. 1996. Effects of fire and salvage logging on the cavity-nesting bird community in northwestern Montana. University of Montana, Missoula, MT.
- Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *Journal of Wildlife Management* **44**:773-786.
- Cushman, S. A., and K. McGarigal. 2004. Hierarchical analysis of forest bird species-environment relationships in the Oregon Coast Range. *Ecological Applications* **14**:1090-1105.
- Donato, D. C. 2008. Vegetation and fuels following high severity fire, reburn, and salvage logging in the Klamath-Siskiyou region, OR. Dissertation. Oregon State University, Corvallis, OR.
- Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2006. Post-wildfire logging hinders regeneration and increases fire risk. *Science* **311**:352.
- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. Pacific Northwest Forest and Range Experiment Station, USDA Forest Service, Portland, OR.
- Greene, E., W. Davidson, and V. R. Muehter. 1998. Steller's Jay (*Cyanocitta stelleri*), The birds of North America online. *in* A. Poole, editor. Ithaca: Cornell Lab of Ornithology.
- Gutiérrez, R. J., and D. J. Delehanty. 1999. Mountain Quail (*Oreortyx pictus*), The Birds of North America Online *in* A. Poole, editor. Ithaca: Cornell Lab of Ornithology.
- Hagar, J. C. 2007. Wildlife species associated with non-coniferous vegetation in Pacific Northwest conifer forests: A review. *Forest Ecology and Management* **246**:108-122.
- Hagar, J. C., W. C. McComb, and W. H. Emmingham. 1996. Bird communities in commercially thinned and unthinned Douglas-fir stands of western Oregon. *Wildlife Society Bulletin* **24**:353-366.
- Haggard, M., and W. L. Gaines. 2001. Effects of stand-replacement fire and salvage logging on a cavity-nesting bird community in eastern Cascades, Washington. *Northwest Science* **75**:387-396.
- Hayes, J. P., J. M. Weikel, and M. M. P. Huso. 2003. Response of birds to thinning young Douglas-fir forests. *Ecological Applications* **13**:1222-1232.

- Hoyt, J. S., and S. J. Hannon. 2002. Habitat associations of black-backed and three-toed woodpeckers in the boreal forest of Alberta. *Canadian Journal of Forest Research* **32**:1881-1888.
- Hurvich, C. M., and C. L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* **76**:297-307.
- Hutto, R. L. 2006. Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. *Conservation Biology* **20**:984-993.
- Hutto, R. L., and S. M. Gallo. 2006. The effects of postfire salvage logging on cavity-nesting birds. *Condor* **108**:817-831.
- Kemp, J. L. 1967. *Epitaph for the giants: the story of the Tillamook Burn*. Touchstone Press, Portland, OR.
- Koivula, M. J., and F. K. A. Schmiegelow. 2007. Boreal woodpecker assemblages in recently burned forested landscapes in Alberta, Canada: Effects of post-fire harvesting and burn severity. *Forest Ecology and Management* **242**:606-618.
- Kotliar, N. B., P. L. Kennedy, and K. Ferree. 2007. Avifaunal responses to fire in southwestern montane forests along a burn severity gradient. *Ecological Applications* **17**:491-507.
- Lehmkuhl, J. F., R. L. Everett, R. Schellhaas, P. Ohlson, D. Keenum, H. Riesterer, and D. Spurbeck. 2003. Cavities in snags along a wildfire chronosequence in eastern Washington. *Journal of Wildlife Management* **67**:219-228.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* **42**:594-598.
- McIver, J. D., and R. Ottmar. 2007. Fuel mass and stand structure after post-fire logging of a severely burned ponderosa pine forest in northeastern Oregon. *Forest Ecology and Management* **238**:268-279.
- McIver, J. D., and L. Starr. 2001. A literature review on the environmental effects of postfire logging. *Western Journal of Applied Forestry* **16**:159-168.
- Morissette, J. L., T. P. Cobb, R. M. Brigham, and P. C. James. 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. *Canadian Journal of Forest Research* **32**:2169-2183.
- Murphy, E. C., and W. A. Lehnhausen. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. *Journal of Wildlife Management* **62**:1359-1372 | 1359.

- Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* **1**:535-545.
- Parker, T. H., B. M. Stansberry, C. D. Becker, and P. S. Gipson. 2005. Edge and area effects on the occurrence of migrant forest songbirds. *Conservation Biology* **19**:1157-1167.
- Perry, D. A. 1994. *Forest ecosystems*. Johns Hopkins University Press, Baltimore.
- Pickett, S. T. A., and P. S. White. 1985. *The Ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, FL.
- R Development Core Team. 2007. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. Available from <http://www.R-project.org> (accessed October 2007). *in*.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. *Handbook of field methods for monitoring landbirds*. *in* USDA Forest Service, General Technical Report PSW-GTR-144. www. Pacific Southwest Research Station, Berkeley, CA.
- Ramsey, F. L., and D. W. Schafer. 2002. *The statistical sleuth*, 2nd edition, Duxbury, Pacific Grove, CA.
- Ripper, D., J. C. Bednarz, and D. E. Varland. 2007. Landscape use by hairy woodpeckers in managed forests of northwestern Washington. *Journal of Wildlife Management* **71**:2612-2623.
- Romme, W. H., E. H. Everham, L. E. Frelich, M. A. Moritz, and R. E. Sparks. 1998. Are large, infrequent disturbances qualitatively different from small, frequent disturbances? *Ecosystems* **1**:524-534.
- Rumbaitis del Rio, C. 2006. Changes in understory composition following catastrophic windthrow and salvage logging in a subalpine forest ecosystem. *Canadian Journal of Forest Research* **36**:2943-2954.
- Saab, V. A., R. E. Russell, and J. G. Dudley. 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. *Condor* **109**:97-108.
- Schieck, J., and S. J. Song. 2006. Changes in bird communities throughout succession following fire and harvest in boreal forests of western North America: Literature review and meta-analyses. *Canadian Journal of Forest Research* **36**:1299-1318.
- Schwab, F. E., N. P. P. Simon, S. W. Stryde, and G. J. Forbes. 2006. Effects of postfire snag removal on breeding birds of western Labrador. *Journal of Wildlife Management* **70**:1464-1469.

- Sedgwick, J. A. 1994. Hammond's Flycatcher (*Empidonax hammondi*), the birds of North America online. *in* A. Poole, editor. Ithaca: Cornell Lab of Ornithology.
- Smucker, K. M., R. L. Hutto, and B. M. Steele. 2005. Changes in bird abundance after wildfire: Importance of fire severity and time since fire. *Ecological Applications* **15**:1535-1549.
- Stambaugh, C. A. 2003. Community-level response of birds to burned and salvage-logged forests. University of Alberta.
- Stuart, J. D., M. C. Grifantini, and L. Fox, III. 1993. Early successional pathways following wildfire and subsequent silvicultural treatment in Douglas-fir/hardwood forests, NW California. *Forest Science* **39**:561-572.
- Taylor, A. H., and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. *Forest Ecology and Management* **111**:285-301.
- Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B. and Marques, T.A. 2006. Distance 5.0 Beta 5. *in*. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. <http://www.ruwpa.st-and.ac.uk/distance/>.
- Thompson, J. R., T. A. Spies, and L. M. Ganio. 2007. Re-burn severity in managed and unmanaged vegetation in a large wildfire. *Proceedings of the National Academy of Science* **104**:10743-10748.
- USDA. 2005. National Forest Management Act, Planning Rule. United States Department of Agriculture.
- USDA Forest Service. 2004. Biscuit Fire Recovery Project Final Environmental Impact Statement. USDA Forest Service, Pacific Northwest Region, Medford, OR.
- Venables, W. N., and B. D. Ripley. 2001. *Modern applied statistics in Splus*. Springer-Verlag, New York, New York, USA.

Table 4.1. Mean density (standard error) of seventeen species from unlogged plots in severely burned forest of the Biscuit Fire.

Species†	Code	2005 Density (birds 20 ha <sup>-1</sup> )	2006 Density (birds 20 ha <sup>-1</sup> )
Black-headed grosbeak	BHGR	0.79 (0.24)	1.43 (0.46)
Brown creeper	BRCR	2.76 (0.60)	
Dark-eyed junco	DEJU	9.19 (1.15)	8.19 (1.28)
Hammond's flycatcher	HAFL	1.51 (0.34)	0.47 (0.26)
Hairy woodpecker	HAWO	3.34 (0.49)	2.35 (0.59)
House wren	HOWR	4.36 (0.95)	5.00 (1.21)
Lazuli bunting	LAZB	2.72 (0.80)	7.29 (1.65)
MacGillivray's warbler	MGWA	2.16 (0.46)	
Mountain quail	MOUQ	0.36 (0.09)	0.32 (0.12)
Northern flicker	NOFL	0.27 (0.09)	
Olive-sided flycatcher	OSFL	0.97 (0.18)	1.19 (0.26)
Red-breasted nuthatch	RBNU	0.94 (0.25)	0.65 (0.29)
Steller's jay	STJA	0.96 (0.23)	0.52 (0.18)
Townsend's solitaire	TOSO	2.74 (0.48)	0.98 (0.36)
Western Tanager	WETA	0.57 (0.17)	1.36 (0.30)
Western wood-pewee	WEWP	2.05 (0.37)	2.27 (0.54)
Yellow-rumped warbler	YRWA	3.59 (0.67)	1.70 (0.58)

†Scientific names are given in Appendix A.

Table 4.2. Top models based on AICc for each species by year by spatial scale combination.

Species	20-ha scale					2-ha scale				
	year	K	AICc	w <sub>i</sub>	predictors	K	AICc	w <sub>i</sub>	predictors	
BHGR	2005	5	-257.10	0.46	Intercept,Area250,psize,elev	4	62.76	0.47	Intercept,elev,psize	
	2006	4	-185.23	0.19	Intercept,elev,psize	4	50.72	0.33	Intercept,Area80,elev	
BRCR	2005	4	-30.01	0.34	Intercept,elev,psize	5	104.86	0.74	Intercept,Area80,psize,elev	
DEJU	2005	2	132.52	0.23	Intercept	3	152.16	0.17	Intercept,Intens	
	2006	5	129.97	0.27	Intercept,Intens,psize,elev	4	144.48	0.43	Intercept,Intens,psize	
HAFL	2005	4	-181.66	0.33	Intercept,Intens,elev	4	107.18	0.25	Intercept,elev,psize	
	2006	4	-184.78	0.44	Intercept,elev,psize	2	72.37	0.28	Intercept	
HAWO	2005	2	-59.53	0.20	Intercept	2	156.45	0.37	Intercept	
	2006	2	-98.15	0.27	Intercept	2	133.27	0.36	Intercept	
HOWR	2005	3	174.71	0.27	Intercept,Area250	5	121.30	0.34	Intercept,Intens,psize,elev	
	2006	4	106.98	0.49	Intercept,Intens,psize	4	152.80	0.35	Intercept,Intens,psize	
LAZB	2005	4	59.03	0.51	Intercept,Intens,elev	4	134.28	0.40	Intercept,Intens,elev	
	2006	5	96.55	0.47	Intercept,Area250,psize,elev	5	92.56	0.64	Intercept,Area80,psize,elev	
MGWA	2005	4	-104.41	0.28	Intercept,Area250,elev	4	114.09	0.38	Intercept,Area80,elev	
MOUQ	2005	4	-418.49	0.20	Intercept,Area250,psize					
	2006	2	-442.04	0.32	Intercept					
NOFL	2005	4	-422.10	0.30	Intercept,elev,psize	2	46.23	0.24	Intercept	
OSFL	2005	4	-272.12	0.34	Intercept,Area250,psize	2	110.76	0.32	Intercept	
	2006	4	-244.85	0.31	Intercept,elev,psize	2	93.99	0.38	Intercept	
RBNU	2005	4	-259.34	0.43	Intercept,elev,psize	4	69.52	0.39	Intercept,elev,psize	
	2006	4	-239.18	0.39	Intercept,elev,psize	4	66.80	0.22	Intercept,Intens,elev	
STJA	2005	2	-244.73	0.30	Intercept	2	64.05	0.32	Intercept	
	2006	4	-320.50	0.20	Intercept,Intens,elev	4	39.12	0.18	Intercept,Intens,elev	
TOSO	2005	4	-145.52	0.53	Intercept,elev,psize	4	92.77	0.50	Intercept,elev,psize	
	2006	4	-165.85	0.31	Intercept,Area250,elev	2	67.72	0.35	Intercept	
WETA	2005	2	-318.19	0.22	Intercept	2	66.85	0.24	Intercept	
	2006	4	-232.48	0.19	Intercept,elev,psize	2	81.70	0.37	Intercept	
WEWP	2005	2	-178.06	0.37	Intercept	2	116.17	0.28	Intercept	

	2006	4	-115.41	0.39	Intercept,elev,psize	2	120.57	0.28	Intercept
YRWA	2005	4	-29.29	0.29	Intercept,Intens,elev	4	138.29	0.27	Intercept,Area80,elev
	2006	5	-65.89	0.63	Intercept,Area250,psize,elev	4	118.23	0.28	Intercept,elev,psize

*Notes:* Species codes are in Table 1. Missing values are due to insufficient numbers of observations. Area250: proportion of area logged within 250m of a point count, elev: elevation (m), psize: area (ha) of severely burned forest within 2km. Area80: proportion of area logged within 80m of a point count.

Table 4.3. Relative importance values of predictors and covariates from linear mixed effects model sets.

species	year	Scale: 20 ha				Scale: 2 ha			
		Area	Intensity	patch size	elevation	Area	Intensity	patch size	elevation
BHGR	2005	0.79	0.18	0.82	0.68	0.28	0.24	0.98	0.89
	2006	0.39	0.34	0.54	0.80	0.51	0.42	0.27	0.84
BRCR	2005	0.33	0.24	0.71	0.79	0.77	0.18	0.96	0.99
DEJU	2005	0.33	0.39	0.26	0.44	0.38	0.38	0.31	0.36
	2006	0.17	0.50	0.84	0.65	0.12	0.76	0.73	0.34
HAFL	2005	0.27	0.59	0.27	0.63	0.28	0.30	0.50	0.64
	2006	0.27	0.26	0.76	0.93	0.27	0.30	0.34	0.46
HAWO	2005	0.33	0.42	0.25	0.35	0.28	0.27	0.24	0.25
	2006	0.30	0.31	0.34	0.40	0.32	0.26	0.22	0.27
HOWR	2005	0.77	0.22	0.47	0.33	0.39	0.57	0.95	0.55
	2006	0.19	0.79	0.93	0.36	0.28	0.64	0.74	0.35
LAZB	2005	0.29	0.71	0.28	1.00	0.39	0.57	0.27	0.91
	2006	0.50	0.48	0.96	1.00	0.65	0.34	0.98	1.00
MGWA	2005	0.42	0.33	0.40	0.88	0.61	0.26	0.35	0.83
MOUQ	2005	0.42	0.30	0.68	0.41	NA	NA	NA	NA
	2006	0.24	0.40	0.20	0.21	NA	NA	NA	NA
NOFL	2005	0.32	0.38	0.72	0.94	0.30	0.27	0.51	0.43
OSFL	2005	0.70	0.27	0.64	0.27	0.45	0.21	0.21	0.16
	2006	0.39	0.26	0.72	0.80	0.26	0.29	0.21	0.20
RBNU	2005	0.24	0.30	0.79	0.91	0.27	0.32	0.70	0.98
	2006	0.37	0.24	0.86	0.99	0.26	0.39	0.43	0.72
STJA	2005	0.33	0.28	0.29	0.38	0.36	0.26	0.22	0.24
	2006	0.18	0.59	0.46	0.55	0.49	0.49	0.26	0.48
TOSO	2005	0.24	0.23	0.98	1.00	0.24	0.25	0.96	1.00
	2006	0.43	0.34	0.45	1.00	0.31	0.26	0.25	0.26
WETA	2005	0.25	0.46	0.37	0.26	0.39	0.30	0.37	0.26
	2006	0.40	0.30	0.52	0.57	0.29	0.28	0.21	0.25
WEWP	2005	0.25	0.32	0.21	0.22	0.32	0.36	0.25	0.22
	2006	0.30	0.25	0.75	0.82	0.23	0.42	0.34	0.27
YRWA	2005	0.35	0.40	0.43	0.97	0.37	0.36	0.45	0.97
	2006	0.86	0.12	0.72	1.00	0.37	0.36	0.47	1.00

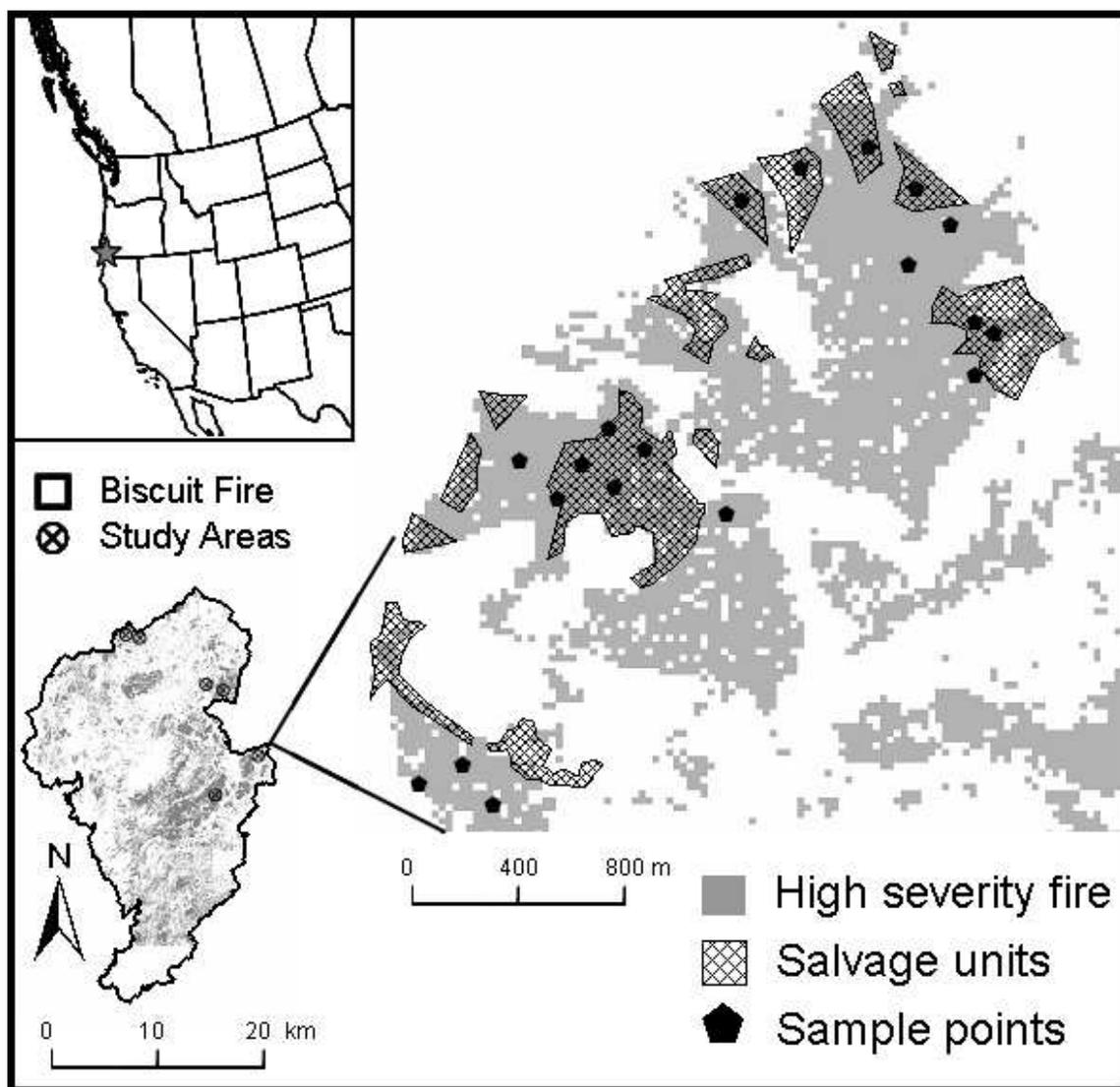


Figure 4.1. Biscuit Fire study area. Sampling points were clustered within areas of high severity within and adjacent to salvage logging units.

Figure 4.2. Histograms of (a) salvage unit sizes across the entire Biscuit Fire and units sampled in this study (b) intensity of salvage logging as measured by proportion of basal area removed (c) count of sampling points grouped by percent of area logged at 20-ha and (d) count of sampling points grouped by percent area of area logged at 2-ha. The spatial extent of salvage logging at each plot transitioned from resembling at normal distribution centered around ~50% at 20 ha to a binomial distribution of logged and unlogged plots at a 2-ha scale.

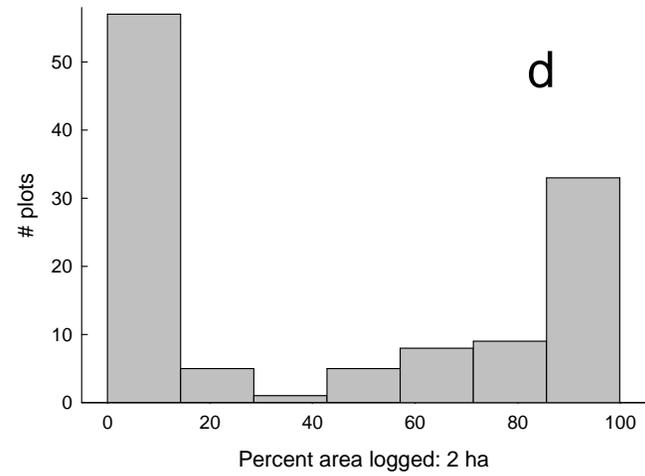
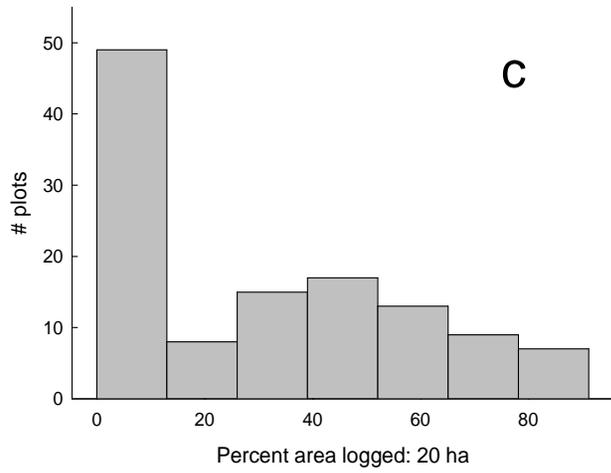
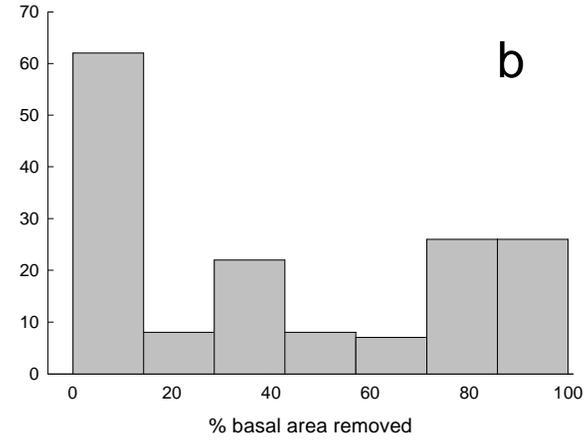
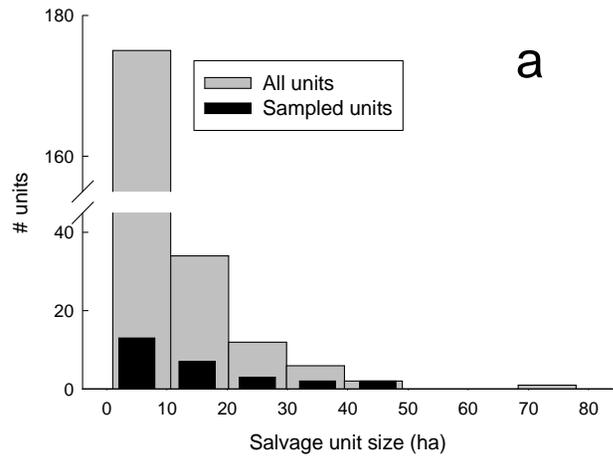


Figure 4.2

Figure 4.3. Changes in stand structure following salvage logging of the Biscuit Fire 2.5-3.5 years following fire. (a) basal area ( $\text{m}^2 \text{ha}^{-1}$ ) of fire killed sound and rotten snags in 2005 (b) trees per hectare in three diameter classes in 2005 (c) shrub volume ( $\text{m}^3 \text{ha}^{-1}$ ) in 2005 and 2006 (d) percent cover of bare ground, herbaceous plants, wood, and litter in 2005. Salvage logging reduced basal area of sound snags and density of large trees but had little effect on shrub volume and ground cover.

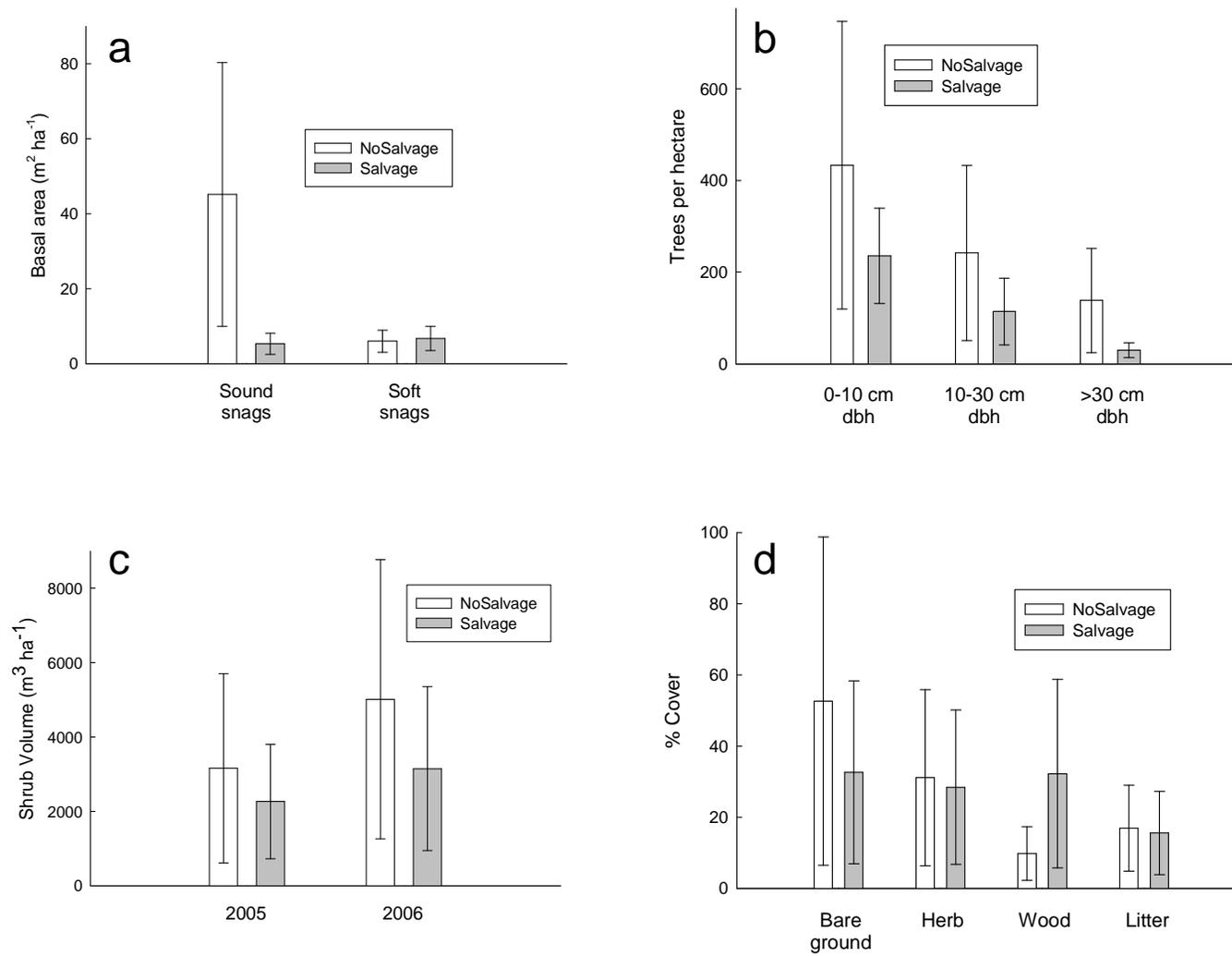
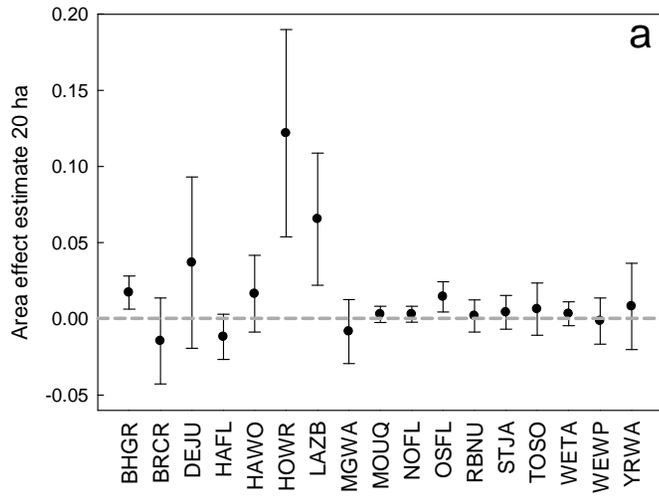
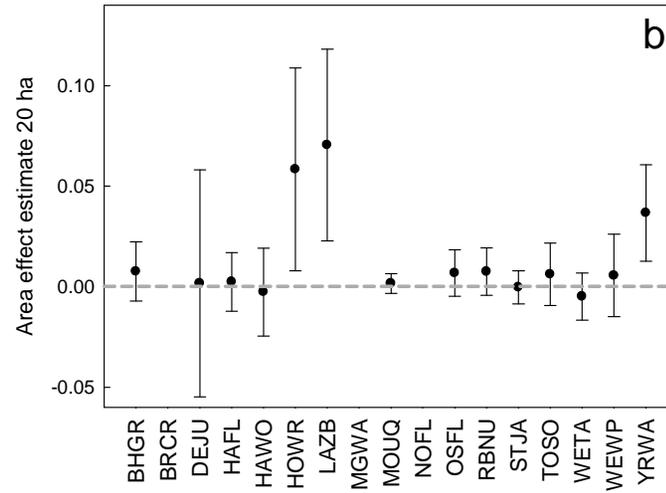


Figure 4.3

Figure 4.4. Parameter estimates and 95% confidence intervals of the effect of area logged on bird species density (a-b: 20 ha scale) and probability of occurrence (c-d: 2 ha scale) in 2005 and 2006. Confidence intervals overlapping zero indicate no effect of area logged on density (20-ha) or probability of occurrence (2-ha). Insufficient numbers of detections prevented estimation of BRCR, NOFL, and MGWA in 2006 as well as MOUQ at the 2-ha scale. Species codes are given in Table 4.1.



2005



2006

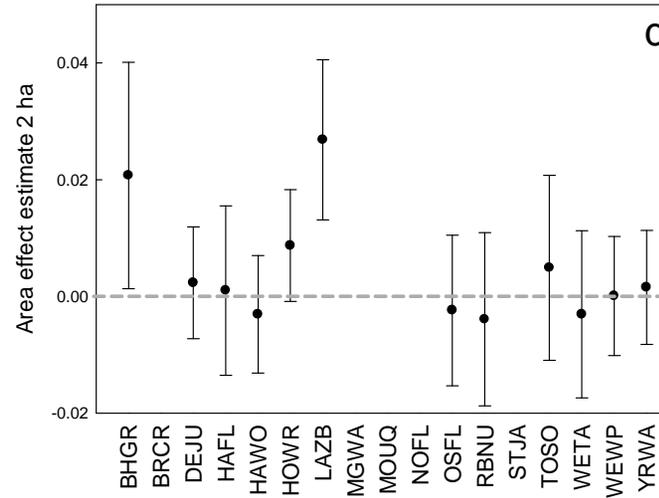
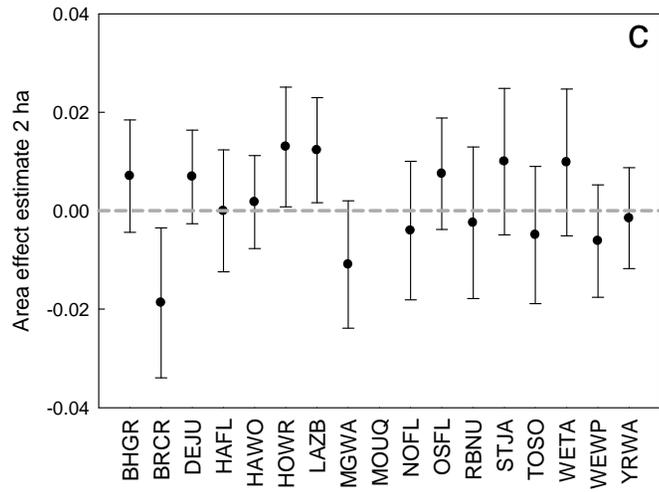
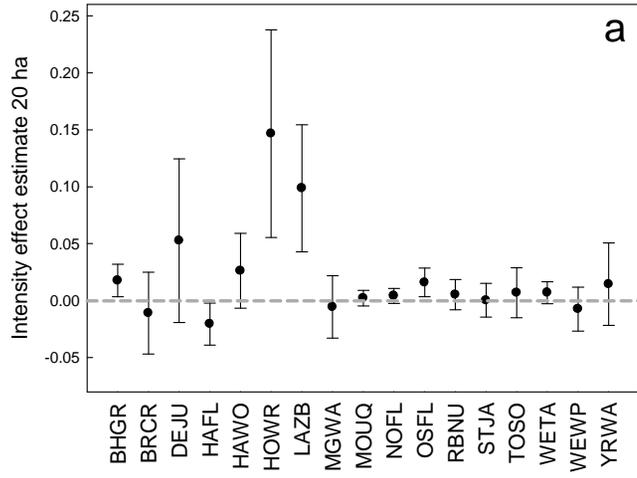
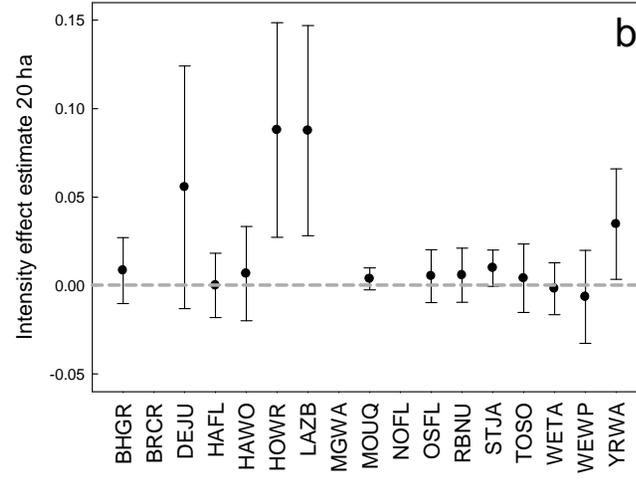


Figure 4.4

Figure 4.5. Parameter estimates and 95% confidence intervals of the effect of logging intensity (proportion of basal area removed multiplied by area logged) on bird species density (a-b: 20-ha scale) and probability of occurrence (c-d: 2-ha scale) in 2005 and 2006. Confidence intervals overlapping zero indicate no effect of logging intensity on density (20-ha) or probability of occurrence (2-ha). Insufficient numbers of detections prevented estimation of BRGR, NOFL, and MGWA in 2006 as well as MOUQ at the 2-ha scale. Species codes are given in Table 4.1.



2005



2006

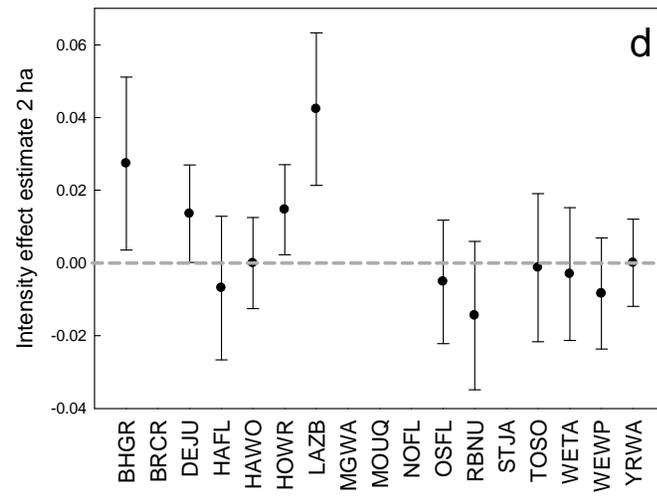
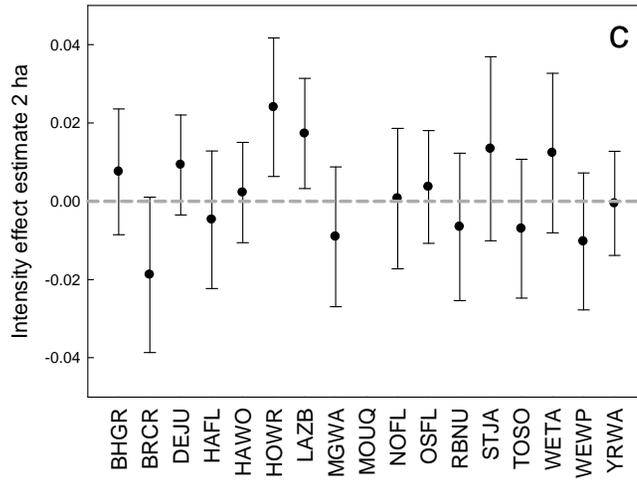
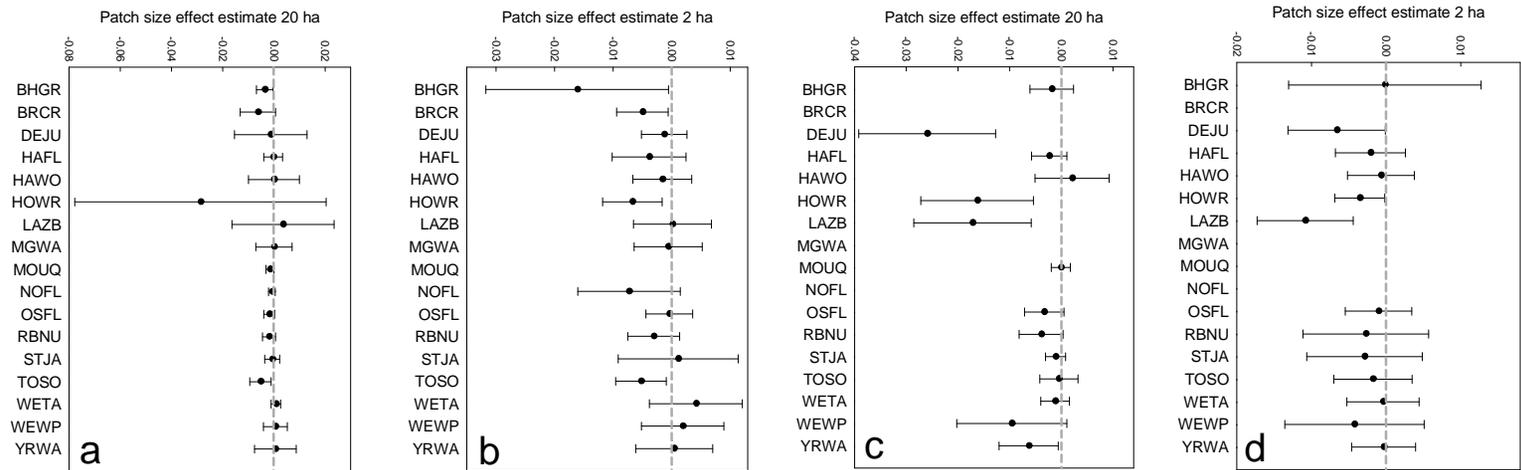


Figure 4.5

Figure 4.6. Parameter estimates and 95% confidence intervals of the effect of size of severely burned patch (estimated at a 2000 m scale, a-d) and elevation (e-f) on bird species density (20-ha scale) and probability of occurrence (2-ha scale) in 2005 and 2006. Confidence intervals overlapping zero indicate no effect of elevation or burn patch size on density (20-ha) or probability of occurrence (2-ha). Insufficient numbers of detections prevented estimation of BRGR, NOFL, and MGWA in 2006 as well as MOUQ at the 2-ha scale. Species codes are given in Table 4.1.



2005

2006

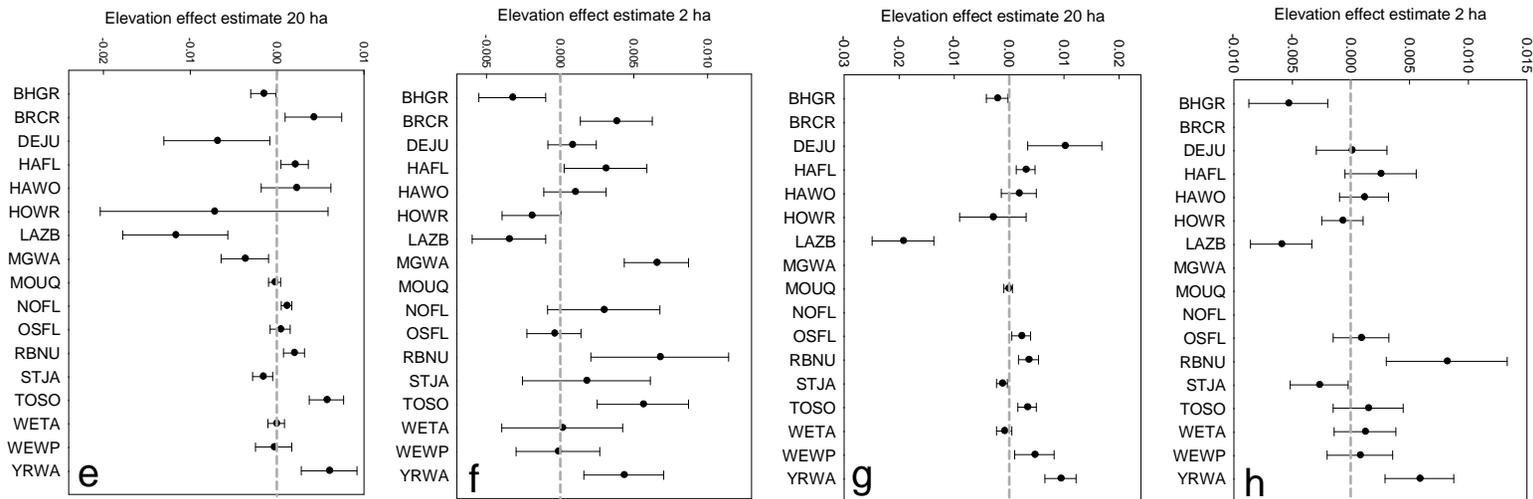


Figure 4.6

## CHAPTER 5: CONCLUSIONS

The goal of this research was to characterize the avian and small mammal communities occurring after four unique combinations of disturbances in the Klamath-Siskiyou Mountains of southwestern Oregon. By contrasting communities at differing times since a single fire with those experiencing two fires or fire plus salvage logging, we hoped to better understand the consequences of compound disturbance on vertebrate taxa. The Klamath-Siskiyou Mountains are a transitional ecoregion with broad climatic and vegetational gradients; thus, research findings from this area potentially have relevance to forested vegetation types across western North America.

Postfire ecological research from a broad range of vegetation types has consistently shown that fire is an integral process maintaining biodiversity and system function. The results of our research were congruent with this expectation. Shortly after high severity fire (2-4 years) we found lower overall densities of birds, but similar species richness as compared to unburned mature/old-growth forest. Additionally, many species of birds typically considered as forest birds were detected in severely burned stands, suggesting that high severity fire may generate important habitat for a variety of species. Species most strongly associated with high severity fire tended to be aerial insectivores (flycatchers), cavity-nesters/bark-foragers (woodpeckers, brown creeper), and shrub-nesting species (lazuli bunting, black-headed grosbeak). Species most strongly associated with mature, unburned forests were foliage gleaning species that favor mesic, closed canopy forests (hermit warbler,

hermit thrush, Pacific-slope flycatcher). Following high severity fire, small mammal communities transitioned from possessing low abundance, high species richness state to high abundance, low species richness. By 17 years after fire, small mammal communities were more similar to small mammal communities occurring in late seral stands than communities immediately following fire.

Contrary to expectations, repeated high severity fire did not reduce bird species richness. Rather, bird densities were greater in those habitats than in once-burned habitats. Broad-leaved hardwoods and shrubs, and the disturbances that mediate their abundance and structural diversity on the landscape, appear to play a major role in structuring avian communities in the Klamath-Siskiyou region. In light of these results, extended periods of early seral broadleaf dominance and short-interval, high severity fires may be important to the conservation of avian biodiversity in this region.

Postfire salvage logging created a significant pulse of woody debris. However, we observed no change in small mammal biomass or species densities in relation to salvage logging. In the short term, fire effects on small mammal communities were much larger than those of postfire salvage logging. Longer term studies of changes in small mammal and bird communities following salvage logging are needed over decades and greater time scales to fully evaluate the impacts of the management activity.

Avian response to salvage logging was examined for 17 common bird species at two spatial scales (20 ha and 2 ha) relative to two measures of salvage logging: proportion of surrounding area logged and logging intensity (basal area removed).

The 20-ha scale comprised the logging unit as well as unit edges and surrounding unlogged areas, while the 2-ha scale comprised only the logging unit and not surrounding edges. At the 20-ha scale, we found a positive response in the density of shrub-associated species (house wren, lazuli bunting, black-headed grosbeak and edge-associated species (olive-sided flycatcher, yellow-rumped warbler) and little evidence of negative responses, save for a reduction in density of Hammond's flycatcher. At the 2-ha scale, shrub-associates again responded positively, but not edge-associates. Brown creeper responded negatively at the 2-ha scale, and many species had negative but not significant estimates suggesting that, except for shrub nesting species, bird use of salvage units is associated with edges and not interior portions of salvage units. The lack of a strong negative response to salvage logging of the Biscuit Fire suggests that the small logging unit sizes relative to the burn area, as well as extensive snag retention in riparian buffers, tended to retain many bird species in the burn landscape.

The results presented here provide new information on the response of birds and small mammals to high severity fire from a region where little was previously known. Response to salvage logging of small mammals and birds is of high value for land managers working in the region given the high frequency of fires and historical prevalence of postfire salvage logging. Additionally, the response of these communities to repeated fire represent an important contribution to a sparse literature on vertebrate response to repeated high intensity disturbances and postfire salvage logging.

**BIBLIOGRAPHY**

- Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.
- Ahlgren, C. E. 1966. Small mammals and reforestation following prescribed burning. *Journal of Forestry* **64**:614-618.
- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. *in* B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.
- Allredge, M. A., T. R. Simons, and K. A. Pollock. 2007. Factors affecting aural detections of songbirds. *Ecological Applications* **17**:948-955.
- Altman, B., and R. Sallabanks. 2000. Olive-sided Flycatcher (*Contopus cooperi*), The Birds of North America Online *in* A. Poole, editor. Ithaca: Cornell Lab of Ornithology.
- Attiwill, P. M. 1994. The burning continent: Forest ecosystems and fire management in Australia. Institute of Public Affairs, West Perth, WA, Australia.
- Beck, A. M., and R. J. Vogl. 1972. The effects of spring burning on rodent populations in a brush prairie savanna. *Journal of Mammalogy* **53**:336-346.
- Bemis, C., and J. D. Rising. 1999. Western Wood-Pewee (*Contopus sordidulus*), the birds of North America online. *in* A. Poole, editor. Ithaca: Cornell Lab of Ornithology.
- Betts, M. G., G. J. Forbes, and A. W. Diamond. 2007. Thresholds in songbird occurrence in relation to landscape structure. *Conservation Biology* **21**:1046-1058.
- Bock, C. E., and W. M. Block. 2005. Fire and birds in the southwestern United States. *Studies in Avian Biology* **30**:14-32.
- Bock, C. E., and J. F. Lynch. 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. *Condor* **72**:182-189.
- Bowen, R. V. 1997. Townsend's Solitaire (*Myadestes townsendi*), the birds of North America online. *in* A. Poole, editor. Ithaca: Cornell Lab of Ornithology.
- Bowman, J., G. Forbes, and T. Dilworth. 2000a. The spatial scale of variability in small-mammal populations. *Ecography* **23**:328-334.

- Bowman, J. C., D. Sleep, G. J. Forbes, and M. Edwards. 2000b. The association of small mammals with coarse woody debris at log and stand scales. *Forest Ecology and Management* **129**:119-124.
- Brennan, L. A., R.T. Engstrom, W.E. Palmer, S.M. Hermann, G.A. Hurst, L.W. Burger, C.L. Hardy. 1998. Whither wildlife without fire? Pages 402-414 *in* transactions of the 63rd North American Wildlife and Natural Resource Conference.
- Breslow, N. E., and D. G. Clayton. 1993. Approximate inference in Generalized Linear Mixed Models. *Journal of the American Statistical Association* **88**:9-24.
- Brown, J. K. 1974. Handbook for inventorying downed woody material. Pages 24 *in* General Technical Report GTR-INT-16. USDA Forest Service, Intermountain and Range Experiment Station, Ogden, UT.
- Brown, J. K., E. D. Reinhardt, and K. A. Kramer. 2003. Coarse woody debris: managing benefits and fire hazard in the recovering forest. Pages 1-16 *in* R. M. R. Station, editor. USDA Forest Service.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: Estimating abundance of biological populations. Oxford University Press, Oxford; New York.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas, editors. 2004. Advanced distance sampling. Oxford University Press, Oxford.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd edition. Springer, New York.
- Cahall, R. E. 2007. Influences of salvage logging on forest birds after fire in the Eastern Cascades, Oregon. Oregon State University.
- Carey, A. B., and M. L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth-forests. *Ecological Applications* **5**:336-352.
- Caton, E. L. 1996. Effects of fire and salvage logging on the cavity-nesting bird community in northwestern Montana. University of Montana, Missoula, MT.
- Chapman, H. H. 1938. Birds and longleaf pine reproduction. *Journal of Forestry* **36**:1246-1247.
- Clements, F. E. 1936. Nature and structure of the climax. *The Journal of Ecology* **24**:252-284.

- Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *Journal of Wildlife Management* **44**:773-786.
- Colwell, R. K. 2006. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.0.0. *in*.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**:1119-1144.
- Converse, S. J., W. M. Block, and G. C. White. 2006a. Small mammal population and habitat responses to forest thinning and prescribed fire. *Forest Ecology and Management* **228**:263-273.
- Converse, S. J., G. C. White, and W. M. Block. 2006b. Small mammal responses to thinning and wildfire in ponderosa pine-dominated forests of the southwestern United States. *Journal of Wildlife Management* **70**:1711-1722.
- Converse, S. J., G. C. White, K. L. Farris, and S. Zack. 2006c. Small mammals and forest fuel reduction: National-scale responses to fire and fire surrogates. *Ecological Applications* **16**:1717-1729.
- Cook, S. F., Jr. 1959. The effects of fire on a population of small rodents. *Ecology* **40**:102-108.
- Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. *The Botanical Gazette* **27**:167-202.
- Craig, V. J., W. Klenner, M. C. Feller, and T. P. Sullivan. 2006. Relationships between deer mice and downed wood in managed forests of southern British Columbia. *Canadian Journal of Forest Research* **36**:2189-2203.
- Cushman, S. A., and K. McGarigal. 2004. Hierarchical analysis of forest bird species-environment relationships in the Oregon Coast Range. *Ecological Applications* **14**:1090-1105.
- Dale, V. H., C. M. Crisafulli, and F. J. Swanson. 2005. 25 years of ecological change at Mount St. Helens. *Science* **308**:961-962.
- Delitti, W., A. Ferran, L. Trabaud, and V. R. Vallejo. 2005. Effects of fire recurrence in *Quercus coccifera* L. shrublands of the Valencia Region (Spain): I. plant composition and productivity. *Plant Ecology* **177**:57-70.
- Donato, D. C. 2008. Vegetation and fuels following high severity fire, reburn, and salvage logging in the Klamath-Siskiyou region, OR. Dissertation. Oregon State University, Corvallis, OR.

- Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2006. Post-wildfire logging hinders regeneration and increases fire risk. *Science* **311**:352.
- Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* **67**:345-366.
- Engstrom, R. T., L. C. Robert, and W. W. Baker. 1984. Breeding bird populations in relation to changing forest structure following fire exclusion: A 15-year study. *Wilson Bulletin* **96**:437-450.
- Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Review* **35**:51-81.
- Foster, D. R., D. H. Knight, and J. F. Franklin. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* **1**:497-510.
- Fox, B. J. 1990. Changes in the structure of mammal communities over successional time scales. *Oikos* **59**:321-329.
- Fox, J. F. 1983. Post-fire succession of small-mammal and bird communities. Pages 155-180 *in*.
- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. Pacific Northwest Forest and Range Experiment Station, USDA Forest Service, Portland, OR.
- Franklin, J. F., T. A. Spies, R. Van Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, D. B. Lindenmayer, M. E. Harmon, W. S. Keeton, D. C. Shaw, K. Bible, and J. Q. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* **155**:399-423.
- Fule, P. Z., and D. C. Laughlin. 2007. Wildland fire effects on forest structure over an altitudinal gradient, Grand Canyon National Park, USA. *Journal of Applied Ecology* **44**:136-146.
- Gashwiler, J. S. 1967. Conifer seed survival in a western Oregon clearcut. *Ecology* **48**:431-438.
- Gashwiler, J. S. 1970a. Further study of conifer seed survival in a western Oregon clearcut. *Ecology* **5**:849-854.
- Gashwiler, J. S. 1970b. Plant and mammal changes on a clearcut in west-central Oregon. *Ecology* **51**:1018-1026.

- Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**:379-391.
- Gray, A. N., and J. F. Franklin. 1997. Effects of multiple fires on the structure of southwestern Washington forests. *Northwest Science* **71**:174-185.
- Greene, E., W. Davidson, and V. R. Muehter. 1998. Steller's Jay (*Cyanocitta stelleri*), The birds of North America online. *in* A. Poole, editor. Ithaca: Cornell Lab of Ornithology.
- Gutiérrez, R. J., and D. J. Delehanty. 1999. Mountain Quail (*Oreortyx pictus*), The Birds of North America Online *in* A. Poole, editor. Ithaca: Cornell Lab of Ornithology.
- Hagar, J. C. 2007. Wildlife species associated with non-coniferous vegetation in Pacific Northwest conifer forests: A review. *Forest Ecology and Management* **246**:108-122.
- Hagar, J. C., W. C. McComb, and W. H. Emmingham. 1996. Bird communities in commercially thinned and unthinned Douglas-fir stands of western Oregon. *Wildlife Society Bulletin* **24**:353-366.
- Haggard, M., and W. L. Gaines. 2001. Effects of stand-replacement fire and salvage logging on a cavity-nesting bird community in eastern Cascades, Washington. *Northwest Science* **75**:387-396.
- Haim, A., and I. Izhaki. 1994. Changes in rodent community during recovery from fire: relevance to conservation. *Biodiversity and Conservation* **3**:573-585.
- Haim, A., and I. Izhaki. 2000. The effect of different treatments on the community composition of small mammals in a post-fire pine forest. *Journal of Mediterranean Ecology* **1**:249-257.
- Hannon, S. J., and P. Drapeau. 2005. Bird responses to burning and logging in the boreal forest of Canada. *Studies in Avian Biology* **30**:97-115.
- Harmon, M. E., and J. Sexton. 1996. Guidelines for measurements of woody detritus in forest ecosystems. Publication no. 20. *in*. United States Long Term Ecological Research Network Office, University of Washington, Seattle.
- Hayes, J. P., and P. C. Stephen. 1987. Characteristics of logs used by western red-backed voles, *Clethrionomys californicus*, and deer mice, *Peromyscus maniculatus*. *Canadian Field-Naturalist* **101**:514-504.
- Hayes, J. P., J. M. Weikel, and M. M. P. Huso. 2003. Response of birds to thinning young Douglas-fir forests. *Ecological Applications* **13**:1222-1232.

- Herrando, S., L. s. Brotons, and S. Llacuna. 2003. Does fire increase the spatial heterogeneity of bird communities in Mediterranean landscapes? *Ibis* **145**:307-317.
- Hobbs, S. D., S. D. Tesch, P. W. Owston, R. E. Stewart, J. C. Tappeiner, and G. E. Wells, editors. 1992. Reforestation practices in Southwestern Oregon and Northern California. Forest Research Laboratory, Oregon State University, Corvallis, OR.
- Hobson, K. A., and J. Schieck. 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. *Ecological Applications* **9**:849-863.
- Holmes, R. T., J. R. E. Bonney, and S. W. Pacala. 1979. Guild structure of the Hubbard Brook bird community: A multivariate approach. *Ecology* **60**:512-520.
- Hoyt, J. S., and S. J. Hannon. 2002. Habitat associations of black-backed and three-toed woodpeckers in the boreal forest of Alberta. *Canadian Journal of Forest Research* **32**:1881-1888.
- Hurvich, C. M., and C. L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* **76**:297-307.
- Hutto, R. L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology* **9**:1041-1058.
- Hutto, R. L. 2006. Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. *Conservation Biology* **20**:984-993.
- Hutto, R. L., and S. M. Gallo. 2006. The effects of postfire salvage logging on cavity-nesting birds. *Condor* **108**:817-831.
- Jehle, G., J. A. Savidge, and N. B. Kotliar. 2006. Green-tailed Towhee response to prescribed fire in montane shrubland. *Condor* **108**:634-646.
- Johnstone, J. F. 2006. Response of boreal plant communities to variations in previous fire-free interval. *International Journal of Wildland Fire* **15**:497-508.
- Kemp, J. L. 1967. Epitaph for the giants: the story of the Tillamook Burn. Touchstone Press, Portland, OR.
- Koivula, M. J., and F. K. A. Schmiegelow. 2007. Boreal woodpecker assemblages in recently burned forested landscapes in Alberta, Canada: Effects of post-fire harvesting and burn severity. *Forest Ecology and Management* **242**:606-618.

- Kotliar, N. B., S. J. Hejl, R. L. Hutto, V. A. Saab, C. P. Melcher, and M. E. McFadzen. 2002. Effects of fire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. *Studies in Avian Biology* **25**:49-64.
- Kotliar, N. B., P. L. Kennedy, and K. Ferree. 2007. Avifaunal responses to fire in southwestern montane forests along a burn severity gradient. *Ecological Applications* **17**:491-507.
- Kruskal, J. B. 1964. Nonmetric multidimensional scaling: A numerical method. *Psychometrika* **29**:115-129.
- Lawrence, G., E. 1966. Ecology of vertebrate animals in relation to chaparral fire in the Sierra Nevada foothills. *Ecology* **47**:278-291.
- Lehmkuhl, J. F., R. L. Everett, R. Schellhaas, P. Ohlson, D. Keenum, H. Riesterer, and D. Spurbeck. 2003a. Cavities in snags along a wildfire chronosequence in eastern Washington. *Journal of Wildlife Management* **67**:219-228.
- Lehmkuhl, J. F., R. L. Everett, R. Schellhaas, P. Ohlson, D. Keenum, H. Riesterer, and D. Spurbeck. 2003b. Cavities in snags along a wildlife chronosequence in eastern Washington. *Journal of Wildlife Management* **67**:219-228.
- Lindenmayer, D. B., D. R. Foster, J. F. Franklin, M. L. Hunter, R. F. Noss, F. A. Schmiegelow, and D. Perry. 2004. Salvage harvesting policies after natural disturbance. *Science* **303**:1303.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* **39**:599-619.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* **42**:594-598.
- Manning, J. A., and W. D. Edge. 2004. Small mammal survival and downed wood at multiple scales in managed forests. *Journal of Mammalogy* **85**:87-96.
- McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.
- McCune, B., and M. J. Mefford. 2006. PC-ORD. Multivariate Analysis of Ecological Data. Version 5.04. *in*. MjM Software, Gleneden Beach, Oregon, U.S.A.
- McGee, J. M. 1982. Small mammal populations in an unburned and early fire successional sagebrush community. *Journal of Range Management* **35**:177-180.

- McIver, J. D., and R. Ottmar. 2007. Fuel mass and stand structure after post-fire logging of a severely burned ponderosa pine forest in northeastern Oregon. *Forest Ecology and Management* **238**:268-279.
- McIver, J. D., and L. Starr. 2001. A literature review on the environmental effects of postfire logging. *Western Journal of Applied Forestry* **16**:159-168.
- McKelvey, K. S., and D. E. Pearson. 2001. Population estimation with sparse data: the role of estimators versus indices revisited. *Canadian Journal of Zoology- Revue Canadienne De Zoologie* **79**:1754-1765.
- Meyer, M. D., M. P. North, and D. A. Kelt. 2005. Short-term effects of fire and forest thinning on truffle abundance and consumption by *Neotamias speciosus* in the Sierra Nevada of California. *Canadian Journal of Forest Research* **35**:1061-1070.
- Monroe, M. E., and S. J. Converse. 2006. The effects of early season and late season prescribed fires on small mammals in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management* **236**:229-240.
- Morissette, J. L., T. P. Cobb, R. M. Brigham, and P. C. James. 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. *Canadian Journal of Forest Research* **32**:2169-2183.
- Morrison, M. L., editor. 2006. *The northern goshawk: a technical assessment of its status, ecology, and management*.
- Murphy, E. C., and W. A. Lehnhausen. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. *Journal of Wildlife Management* **62**:1359-1372 | 1359.
- Neiland, B. J. 1958. Forest and adjacent burn in the Tillamook burn area of northwestern Oregon. *Ecology* **39**:660-671.
- Noss, R. F., J. F. Franklin, W. L. Baker, T. Schoennagel, and P. B. Moyle. 2006. Managing fire-prone forests in the western United States. *Frontiers in Ecology and the Environment* **4**:481-487.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* **62**:1-135.
- Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* **1**:535-545.

- Parker, K., and J. A. Wiens. 2005. Assessing recovery following environmental accidents: Environmental variation, ecological assumptions, and strategies. *Ecological Applications* **15**:2037-2051.
- Parker, T. H., B. M. Stansberry, C. D. Becker, and P. S. Gipson. 2005. Edge and area effects on the occurrence of migrant forest songbirds. *Conservation Biology* **19**:1157-1167.
- Perry, D. A. 1994. *Forest ecosystems*. Johns Hopkins University Press, Baltimore.
- Petraitis, P. S. 1989. The maintenance of species diversity by disturbance. *Quarterly Review of Biology* **64**:393-418.
- Pickett, S. T. A., and P. S. White. 1985. *The Ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, FL.
- Pyne, S. J., P. L. Andrews, and R. D. Laven. 1996. *Introduction to wildland fire*, 2nd edition. Wiley, New York.
- Quinn, R. D. 1994. Animals, fire, and vertebrate herbivory in California chaparral and other Mediterranean-type ecosystems. *in* J. M. Moreno and W. C. Oechel, editors. *The role of fire in Mediterranean-type ecosystems*. Springer-Verlag, New York.
- R Development Core Team. 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from <http://www.R-project.org> (accessed October 2007). *in*.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. *in* USDA Forest Service, General Technical Report PSW-GTR-144. www. Pacific Southwest Research Station, Berkeley, CA.
- Ramsey, F. L., and D. W. Schafer. 2002. *The statistical sleuth*, 2nd edition, Duxbury, Pacific Grove, CA.
- Raphael, M. G., M. L. Morrison, and M. P. Yoder-Williams. 1987. Breeding bird populations during twenty-five years of postfire succession in the Sierra Nevada. *Condor* **89**:614-626.
- Ripper, D., J. C. Bednarz, and D. E. Varland. 2007. Landscape use by hairy woodpeckers in managed forests of northwestern Washington. *Journal of Wildlife Management* **71**:2612-2623.
- Romme, W. H., E. H. Everham, L. E. Frelich, M. A. Moritz, and R. E. Sparks. 1998. Are large, infrequent disturbances qualitatively different from small, frequent disturbances? *Ecosystems* **1**:524-534.

- Rosenberg, D. K., K. A. Swindle, and R. G. Anthony. 2003. Influence of prey abundance on northern spotted owl reproductive success in western Oregon. *Canadian Journal of Zoology* **81**:1715-1725.
- Rumbaitis del Rio, C. 2006. Changes in understory composition following catastrophic windthrow and salvage logging in a subalpine forest ecosystem. *Canadian Journal of Forest Research* **36**:2943-2954.
- Russell, R. E., V. A. Saab, J. G. Dudley, and J. J. Rotella. 2006. Snag longevity in relation to wildfire and postfire salvage logging. *Forest Ecology and Management* **232**:179-187.
- Saab, V. A., J. Dudley, and W. L. Thompson. 2004. Factors influencing occupancy of nest cavities in recently burned forests. *Condor* **106**:20-36.
- Saab, V. A., and H. D. W. Powell. 2005. Fire and avian ecology in North America: Processes influencing pattern. *Studies in Avian Biology* **30**:1-13.
- Saab, V. A., H. D. W. Powell, N. B. Kotliar, and K. R. Newlon. 2005. Variation in fire regimes of the Rocky Mountains: Implications for avian communities and fire management. *Studies in Avian Biology* **30**:76-96.
- Saab, V. A., R. E. Russell, and J. G. Dudley. 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. *Condor* **109**:97-108.
- Schieck, J., and S. J. Song. 2006. Changes in bird communities throughout succession following fire and harvest in boreal forests of western North America: Literature review and meta-analyses. *Canadian Journal of Forest Research* **36**:1299-1318.
- Schwab, F. E., N. P. P. Simon, S. W. Stryde, and G. J. Forbes. 2006. Effects of postfire snag removal on breeding birds of western Labrador. *Journal of Wildlife Management* **70**:1464-1469.
- Seavy, N. E. 2006. Effects of disturbance on animal communities: Fire effects on birds in mixed-conifer forest. Dissertation. University of Florida, Gainesville, FL.
- Sedgwick, J. A. 1994. Hammond's Flycatcher (*Empidonax hammondii*), the birds of North America online. *in* A. Poole, editor. Ithaca: Cornell Lab of Ornithology.
- Shatford, J. P. A., D. E. Hibbs, and K. J. Puettmann. 2007. Conifer regeneration after forest fire in the Klamath-Siskiyou: How much, how soon? *Journal of Forestry* **105**:139-146.

- Smith, T. G., and C. C. Maguire. 2004. Small-mammal relationships with down wood and antelope bitterbrush in ponderosa pine forests of central Oregon. *Forest Science* **50**:711-728.
- Smucker, K. M., R. L. Hutto, and B. M. Steele. 2005. Changes in bird abundance after wildfire: Importance of fire severity and time since fire. *Ecological Applications* **15**:1535-1549.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**:353-391.
- Stambaugh, C. A. 2003. Community-level response of birds to burned and salvage-logged forests. University of Alberta.
- Stokstad, E. 2006. Salvage logging research continues to generate sparks. *Science* **311**:761.
- Stuart, J. D., M. C. Grifantini, and L. Fox, III. 1993. Early successional pathways following wildfire and subsequent silvicultural treatment in Douglas-fir/hardwood forests, NW California. *Forest Science* **39**:561-572.
- Sullivan, T. P., R. A. Lautenschlager, and R. G. Wagner. 1999. Clearcutting and burning of northern spruce-fir forests: implications for small mammal communities. *Journal of Applied Ecology* **36**:327-344.
- Swetnam, T. W., C. D. Allen, and J. L. Betancourt. 1999. Applied historical ecology: Using the past to manage for the future. *Ecological Applications* **9**:1189-1206.
- Tallmon, D. A., E. S. Jules, N. J. Radke, and L. S. Mills. 2003. Of mice and men and Trillium: Cascading effects of forest fragmentation. *Ecological Applications* **13**:1193-1203.
- Taylor, A. H., and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. *Forest Ecology and Management* **111**:285-301.
- Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B. and Marques, T.A. 2006. Distance 5.0 Beta 5. *in*. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. <http://www.ruwpa.st-and.ac.uk/distance/>.
- Thompson, J. R., T. A. Spies, and L. M. Ganio. 2007. Re-burn severity in managed and unmanaged vegetation in a large wildfire. *Proceedings of the National Academy of Science* **104**:10743-10748.

- USDA. 2003. Field instructions for the annual inventory of Washington, Oregon and California. Forest Inventory and Analysis Program, USDA Forest Service, PNW Research Station, Portland.
- USDA. 2005. National Forest Management Act, Planning Rule. United States Department of Agriculture.
- USDA Forest Service. 2004. Biscuit Fire Recovery Project Final Environmental Impact Statement. USDA Forest Service, Pacific Northwest Region, Medford, OR.
- Vandvik, V., E. Heegaard, I. E. Maren, and P. A. Aarrestad. 2005. Managing heterogeneity: the importance of grazing and environmental variation on post-fire succession in heathlands. *Journal of Applied Ecology* **42**:139-149.
- Venables, W. N., and B. D. Ripley. 2001. *Modern applied statistics in Splus*. Springer-Verlag, New York, New York, USA.
- Verts, B. J., and L. N. Carraway. 1998. *Land mammals of Oregon*. University of California Press, Berkeley, CA.
- Waldien, D. L., J. P. Hayes, M. M. P. Huso, and M. M. P. Huso. 2006. Use of downed wood by Townsend's chipmunks (*Tamias townsendii*) in western Oregon. *Journal of Mammalogy* **87**:454-460.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* **313**:940-943.
- Wiens, J. A. 1989. *The ecology of bird communities*. Cambridge University Press, Cambridge; New York.
- Wooller, R. D., and M. C. Calver. 1988. Changes in an assemblage of small birds in the understorey of dry sclerophyll forest in south-western Australis after fire. *Australian Wildlife Research* **15**:331-338.
- Zedler, P. H., C. R. Gautier, and G. S. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* **64**:809-818.

**APPENDICES**

## APPENDIX A: ESTIMATION OF AVIAN DENSITY

Comparisons of habitat types using point count data can be confounded by potential differences in detectability (Buckland et al. 2001). To account for differences in detection rates between habitats in our analyses, we truncated point counts *a posteriori* by habitat at distances corresponding to declines in detection probability. We chose this approach over estimating species-specific detection probabilities because of our focus on community level differences between treatments. Estimating detection probabilities for rare species with <50 detections can be problematic (Buckland et al. 2001) and would have removed a substantial portion of the species from our analyses. Given the assumption of a common detection process that varies primarily by sound attenuation rate, we identified cut points corresponding to similar levels of detectability among habitats, pooling across all species. Cut points were determined based on visual inspection of histograms of all detections; distances at which the cumulative percentage of detections leveled out corresponded to the distance at which probability of detection declined markedly. All four habitats sampled showed similar declines in detections around 100m, thus all data were truncated at 100m. Given the broadly similar species lists occurring in treatments and fairly even distribution of observer effort, this approach likely accounts for a large portion, but not all, of the bias due to differing detection probabilities among habitats.

We first constructed appropriate cut points and confronted the data with the two key functions and three levels of stratification. Stratification included three

levels of increasing complexity: a global detection function, a detection function with a site covariate allowing for site-level changes in the scale but not the shape of the function, or a separate detection function estimated for each site (e.g. post-stratification by site). Generally, the hazard rate key function with varying degrees of stratification was supported over the half normal key function.

Table A.1. Summary of models used to estimate bird density.

Trtmt	Year	N obs	# int	w	Model Form	Detect Func	Detect Prob (95% CI)	EDR	# param	GOF Chi-p	$\Delta$ AICc	$w_i$
NB	2004	853	8	106	Haz-Simple	cov.Site	0.47 (0.45-0.50)	73	15	0.92†	0	0.80
	2005	607	9	121	Haz-Simple	cov.Site	0.49 (0.46-0.52)	85	10	0.002 †	0	0.96
	2006	391	7	103	Half Norm-Simple	Gbl	0.67 (0.64-0.71)	84	2	0.30	0	0.41
					Haz-Simple	cov.Site	0.68 (0.64-0.72)	85	10	0.15†	0.21	0.37
					Haz-Simple	Gbl	0.73 (0.67-0.79)	88	2	0.15	1.51	0.19
B02	2004	946	9	123	Haz-Simple	cov.Site	0.56 (0.54-0.59)	92	14	0.21†	0	0.99
	2005	1474	9	146	Haz-Simple	cov.Site	0.52 (0.50-0.54)	105	21	0.82†	0	0.99
	2006	847	9	126	Haz-Simple	cov.Site	0.61 (0.59-0.64)	99	18	0.40†	0	0.99
B87	2004	374	8	126	Haz-Simple	Site	0.51 (0.41-0.61)‡	89‡	15	6/7 ns‡	0	0.99
	2005	194	8	121	Haz-Simple	cov.Site	0.38 (0.33-0.44)	75	7	0.87†	0	0.77
RB	2004	806	9	131	Haz-Simple	cov.Site	0.54 (0.52-0.57)	97	8	0.15†	0	0.81
	2005	649	8	126	Half Norm-Simple	Gbl	0.45 (0.41-0.50)	85	1	0.83	0	0.51
					Haz-Simple	Gbl	0.55 (0.49-0.62)	94	2	0.95	0.31	0.44

Note: N obs: number of bird observations; # intervals: number of distance intervals; w: truncation distance; Detect Func: detection function calculated globally (Gbl), globally using site as a covariate (cov.Site), or estimated per site (Site); Detect Prob: probability of detection; EDR: effective detection radius; # param: number of parameters in model; GOF Chi-p: p-value from a chi-square goodness of fit test;  $w_i$ : Akaike weight of model, only models with  $\Delta AICc < 2$  are reported.

† Goodness of fit tests were not possible with models using site as a covariate; p-values reported are from the Haz-Simple model with a global detection function.

‡ Values represent averages of each of the seven individually estimated detection functions. Six of seven goodness of fit tests were not significant at the 95% level.

## APPENDIX B: BIRD SPECIES LIST

Table B2. Bird species detected in the Klamath-Siskiyou mountains, 2004-2006

Common Name	Scientific Name	Species Code
Ruffed Grouse	<i>Bonasa umbellus</i>	RUGR
Sooty Grouse	<i>Dendragapus fuliginosus</i>	BLUG
Mountain Quail	<i>Oreortyx pictus</i>	MOUQ
Northern Goshawk	<i>Accipiter gentilis</i>	NOGO
Red-tailed Hawk	<i>Buteo jamaicensis</i>	RTHA
Band-tailed Pigeon	<i>Patagioenas fasciata</i>	BTPI
Mourning Dove	<i>Zenaida macroura</i>	MODO
Northern Pygmy-Owl	<i>Glaucidium gnoma</i>	NOPO
Rufous Hummingbird	<i>Selasphorus rufus</i>	RUHU
Acorn Woodpecker	<i>Melanerpes formicivorus</i>	ACWO
Red-breasted Sapsucker	<i>Sphyrapicus ruber</i>	RBSA
Downy Woodpecker	<i>Picoides pubescens</i>	DOWO
Hairy Woodpecker	<i>Picoides villosus</i>	HAWO
Northern Flicker	<i>Colaptes auratus</i>	NOFL
Pileated Woodpecker	<i>Dryocopus pileatus</i>	PIWO
Olive-sided Flycatcher	<i>Contopus cooperi</i>	OSFL
Western Wood-Pewee	<i>Contopus sordidulus</i>	WEWP
Willow Flycatcher	<i>Empidonax traillii</i>	WIFL
Hammond's Flycatcher	<i>Empidonax hammondii</i>	HAFL
Dusky Flycatcher	<i>Empidonax oberholseri</i>	DUFL
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	PSFL
Cassin's Vireo	<i>Vireo cassinii</i>	CAVI
Hutton's Vireo	<i>Vireo huttoni</i>	HUVI
Warbling Vireo	<i>Vireo gilvus</i>	WAVI
Steller's Jay	<i>Cyanocitta stelleri</i>	STJA
Western Scrub-Jay	<i>Aphelocoma californica</i>	WSJA
Common Raven	<i>Corvus corax</i>	CORA
Tree Swallow	<i>Tachycineta bicolor</i>	TACH†
Violet-green Swallow	<i>Tachycineta thalassina</i>	TACH†
Black-capped Chickadee	<i>Poecile atricapillus</i>	BCCH
Mountain Chickadee	<i>Poecile gambeli</i>	MOCH
Chestnut-backed Chickadee	<i>Poecile rufescens</i>	CBCH
Bushtit	<i>Psaltriparus minimus</i>	BUSH
Red-breasted Nuthatch	<i>Sitta canadensis</i>	RBNU
White-breasted Nuthatch	<i>Sitta carolinensis</i>	WBNU
Brown Creeper	<i>Certhia americana</i>	BRCR
Rock Wren	<i>Salpinctes obsoletus</i>	ROWR
Bewick's Wren	<i>Thryomanes bewickii</i>	BEWR
House Wren	<i>Troglodytes aedon</i>	HOWR
Winter Wren	<i>Troglodytes troglodytes</i>	WIWR
Golden-crowned Kinglet	<i>Regulus satrapa</i>	GCKI
Western Bluebird	<i>Sialia mexicana</i>	WEBL
Townsend's Solitaire	<i>Myadestes townsendi</i>	TOSO
Swainson's Thrush	<i>Catharus ustulatus</i>	SWTH

Hermit Thrush	<i>Catharus guttatus</i>	HETH
American Robin	<i>Turdus migratorius</i>	AMRO
Varied Thrush	<i>Ixoreus naevius</i>	VATH
Wrentit	<i>Chamaea fasciata</i>	WREN
Cedar Waxwing	<i>Bombycilla cedrorum</i>	CEDW
Orange-crowned Warbler	<i>Vermivora celata</i>	OCWA
Nashville Warbler	<i>Vermivora ruficapilla</i>	NAWA
Yellow-rumped Warbler	<i>Dendroica coronata</i>	YRWA
Black-throated Gray Warbler	<i>Dendroica nigrescens</i>	BTYW
Hermit Warbler	<i>Dendroica occidentalis</i>	HEWA
Macgillivray's Warbler	<i>Oporornis tolmiei</i>	MGWA
Wilson's Warbler	<i>Wilsonia pusilla</i>	WIWA
Yellow-breasted Chat	<i>Icteria virens</i>	YBCH
Western Tanager	<i>Piranga ludoviciana</i>	WETA
Green-tailed Towhee	<i>Pipilo chlorurus</i>	GTTO
Spotted Towhee	<i>Pipilo maculatus</i>	SPTO
Fox Sparrow	<i>Passerella iliaca</i>	FOSP
Song Sparrow	<i>Melospiza melodia</i>	SOSP
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	WCSP
Dark-eyed Junco	<i>Junco hyemalis</i>	DEJU
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	BHGR
Lazuli Bunting	<i>Passerina amoena</i>	LAZB
Western Meadowlark	<i>Sturnella neglecta</i>	WEME
Purple Finch	<i>Carpodacus purpureus</i>	PUFI
Red Crossbill	<i>Loxia curvirostra</i>	RECR
Pine Siskin	<i>Carduelis pinus</i>	PISI

†Swallow (*Tachycineta*) species were pooled for ordination analyses.

## APPENDIX C: SMALL MAMMAL CAPTURE PROBABILITIES

Table C.1 Capture probabilities of deer mice (*Peromyscus maniculatus*) estimated using program CAPTURE.

	2004			2005		
	Mature forest	2-yr old burn 2002	17-yr old burn 1987	Repeat Burn	3-yr old burn: No Salvage	3-yr old burn: Salvage
mean	0.26	0.37	0.49	0.36	0.48	0.46
se	0.06	0.18	0.10	0.06	0.12	0.06
range	0.11-0.42	0.06-0.69	0.11-0.72	0.17-0.54	0.14-0.85	0.30-0.71

APPENDIX D: ESTIMATION OF SPECIES DETECTION FUNCTIONS

Table D.1. Summary of detection functions used to estimate bird densities.

Species	Year	# obs	detection func	covariates	EDR	# params	AICc	GOF Chi-p†	P	P LCL	P UCL
BHGR	2005	46	Uniform-simple	gbl	127	1	181.72	0.87	0.63	0.47	0.84
	2006	23	Hazard-simple	gbl	112	2	77.60	0.38	0.55	0.37	0.79
BRCR	2005	39	Uniform-simple	gbl	76	0	142.34	0.65	1.00	1.00	1.00
DEJU	2005	177	Hazard-simple	site	81	21	47.96		0.45	0.34	0.59
	2006	91	HalfNorm-simple	site	76	16	39.35		0.47	0.41	0.55
HAFL	2005	45	Hazard-simple	gbl	98	2	189.81	0.45	0.60	0.46	0.79
	2006	18	Uniform-simple	gbl	101	0	63.99	0.41	1.00	1.00	1.00
HAWO	2005	119	HalfNorm-cosine	site	104	18	42.84		0.54	0.48	0.61
	2006	54	Hazard-cosine	gbl	104	2	203.21	0.47	0.81	0.69	0.94
HOWR	2005	92	HalfNorm-cosine	salvage	70	2	387.65	0.10	0.47	0.40	0.56
	2006	63	Hazard-simple	salvage	76	3	229.85	0.05	0.56	0.46	0.67
LAZB	2005	75	Hazard-simple	gbl	91	2	316.68	0.47	0.80	0.66	0.98
	2006	86	Uniform-simple	gbl	80	1	323.40	0.84	0.62	0.50	0.77
MGWA	2005	52	Uniform-simple	gbl	102	1	223.17	0.45	0.61	0.47	0.78
MOUQ	2005	58	Uniform-cosine	gbl	201	0	565.41	0.02	1.00	1.00	1.00
	2006	31	Uniform-cosine	gbl	201	0	319.36	0.04	1.00	1.00	1.00
NOFL	2005	53	Hazard-simple	gbl	174	2	155.58	0.34	0.75	0.62	0.91
OSFL	2005	106	Uniform-simple	gbl	151	0	349.77	0.01	1.00	1.00	1.00
	2006	71	Uniform-cosine	gbl	151	0	271.46	0.02	1.00	1.00	1.00
RBNU	2005	45	Uniform-cosine	gbl	121	0	187.56	0.78	1.00	1.00	1.00
	2006	24	Uniform-cosine	gbl	121	0	88.40	0.49	1.00	0.00	1.00
STJA	2005	48	Uniform-simple	gbl	131	1	186.61	0.43	0.66	0.48	0.91
	2006	29	Uniform-simple	gbl	161	0	113.84	0.49	1.00	1.00	1.00
TOSO	2005	110	HalfNorm-cosine	site	111	16	37.85		0.62	0.55	0.70
	2006	34	Uniform-simple	gbl	114	1	79.66	0.95	0.65	0.45	0.95

WETA	2005	34	Uniform-simple	gbl	141	0	126.45	0.59	1.00	1.00	1.00
	2006	53	Uniform-cosine	gbl	141	0	191.55	0.02	1.00	1.00	1.00
WEWP	2005	64	Uniform-cosine	gbl	111	0	213.60	0.49	1.00	1.00	1.00
	2006	58	Hazard-simple	gbl	109	2	241.77	0.20	0.81	0.71	0.94
YRWA	2005	110	HalfNorm-cosine	site	91	18	43.52		0.57	0.50	0.65
	2006	52	Uniform-cosine	gbl	104	0	179.23	0.24	1.00	1.00	1.00

Notes: Number of samples in 2005 = 201 and 2006 = 122. # obs: number of bird observations; detection func: detection function calculated globally (gbl) or with covariates (site, observer, or salvage logging); EDR: effective detection radius; # param: number of parameters in model; AICc: Akaike's information criterion adjusted for small samples size; GOF Chi-p: p-value from a chi-square goodness of fit test; P: probability of detection; P LCL: lower 95% confidence limit for probability of detection; P UCL: upper 95% confidence limit for probability of detection.

†Goodness of fit tests were not possible with models using site as a covariate.

