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The Effects of Prescribed Burning in the Spring on Avian Communities  
in the Sierra Nevada of California

A Dissertation submitted in partial satisfaction  
of the requirements for the degree of

Doctor of Philosophy

in

Biology

by

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The Dissertation of Karen Elizabeth Bagne is approved:

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ABSTRACT OF THE DISSERTATION

The Effects of Prescribed Burning in the Spring on Avian Communities  
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by

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University of California, Riverside, March 2006  
Dr. John T. Rotenberry, Chairperson

Prescribed fire is becoming an increasingly important tool in efforts to reduce the risk of severe wildfires, but little is known about its effect on natural communities. I examined short-term changes (0-6 years postfire) in avian communities following the application of low-intensity prescribed fire in the spring in the Sierra Nevada of California. The results are in three parts: avian abundance and community composition, snag populations and cavity-nesting species, and nest success for five open-cup nesting species.

Avian abundance and community composition were recorded using a strip transect. Avian communities as a whole did not change as a result of prescribed burns. Abundances of 25 species were analyzed and, of these, six responded positively to fire, six responded negatively, and the remaining 13 species showed no consistent response. Grouping species into guilds, the only effects I found more than two years after fire were increases in snag-nesting and bark-foraging species and declines in oak-associated and canopy-foraging species. Comparisons with historical data collected by Joseph Grinnell

found differences in avian communities that were hypothesized to be the result of the loss of fire since the 1910s.

Snag data was collected by following a population of random snags before and after fire as well as snags used for breeding. Snag population changes were greatest following the first introduction of fire after a long fire-free period. Snags preferred for nesting were generally of ponderosa pine (*Pinus ponderosa*), of larger diameter, and moderately decayed as compared to available snags. White fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*) were avoided. There was a small loss ( $-1.5 \text{ ha}^{-1}$ ) of snags predicted to be useable for nesting after burning. Nest success for cavity nesters was lower during the first year following fire but was not related to selected snag attributes.

Nests of Spotted Towhee (*Pipilo maculatus*), Dark-eyed Junco (*Junco hyemalis*), Black-headed Grosbeak (*Pheucticus melanocephalus*), Hutton's Vireo (*Vireo huttoni*), and Cassin's Vireo (*Vireo cassinii*) were monitored. I used Principal Components Analysis (PCA) to group variables describing nest location and used the resulting factor loadings in a logistic exposure model to evaluate nest success. Vegetation at the nest site was related to nesting success for all species except Spotted Towhee. Fire altered this relationship for Black-headed Grosbeak and Dark-eyed Junco. Nest success for Hutton's Vireo was consistently positively related to concealment, which was reduced by burning. Both vireos had higher rates of parasitism on burned plots.

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## **INTRODUCTION**

On August 5, 1949 a crew of 16 smoke jumpers moved into Mann Gulch in the Rocky Mountains of Montana to fight a wildfire. They worked in an isolated drainage towards the Missouri River creating a fire line on the steep slopes. As they climbed over a rise they found that suddenly the fire was below and racing towards them. The crew boss, Wagner “Wag” Dodge, led them up the slope then paused in the path of the fire, lit a match, and set the grass on fire. The others, thinking him insane, ignored Dodge’s cries to join him in the burned area he had just created, and ran. Dodge lay down in the ashes of his fire and survived unhurt as the main fire passed over him and roared up the hill killing all but two of the crew who narrowly escaped over the ridge (Maclean 2003).

In addition to the important lessons learned that day about firefighter safety, the incident illustrates the varied nature of fire itself. For one, the effect of fire is dependent on the intensity at which it burns. Additionally, fires of the past affect fires of the present. While often viewed as destructive, fire can also be beneficial, even life saving. It also is often feared and misunderstood.

In the Sierra Nevada of California, where this study was located, forests have been maintained by centuries of fire (Wright and Bailey 1982). The cycle of fire maintains itself as forest fuels such as pine needles, shrubs, and dead wood accumulate over time creating conditions where the forest is more likely to burn. Over time, fire creates a shifting mosaic of habitat types within the landscape. Ponderosa pine forests occur at lower elevations along the western slope. Ponderosa pine, in fact, has thick fire-resistant bark when mature, and the many old trees surviving with multiple fire scars

illustrate its survival. Historic fire regimes, which often form the basis for management practices and are of primary interest in the ecology of these forests, can only be indirectly studied. Historic accounts and photographs show largely spaced trees with a more open understory than today in many areas (Gruell 2001). The most widely cited fire regime for these forests is for frequent fire return intervals of 2 to 12 years of low intensity fires that burned the understory ((Kilgore and Taylor 1979, McKelvey et al. 1996). Others, however, have pointed out that these estimates are based on uncertain data and estimate that fires of the past had much longer fire return intervals and included a wide range of intensities (Minnich et al. 2000, Baker and Ehle 2001). Data from an unmanaged mixed-conifer forest to the south in Baja California (Minnich et al. 2000) and from an unlogged region in the Colorado Front Range (Brown et al. 1999) suggest fire return intervals of 50 years on a landscape scale. It can generally be agreed that fires have been removed from these forests for periods in excess of any of these estimates. The fire cycle was disrupted starting in the mid-1800's, at the time of the California gold rush, for various reasons including removal of Native American populations, grazing, logging, and fire suppression. Alterations of the natural fire regime have led not only to larger, more intense fires across the region but also dense forests containing large numbers of shade tolerant species and fewer ponderosa pine (Minnich et al. 1995).

In the 1970's, forest managers started to use fire to reduce fuels and thus prevent intense stand-replacing fires where, ironically, fire suppression was a contributing factor (Pyne 1984). In addition to fuels reduction, return of fire to these landscapes can be seen as the return of an important ecological element. Vegetation and wildlife have endured

on these landscapes along with fire. In ponderosa pine forests, where historically fires were relatively frequent and mainly confined to the understory, prescribed fires may more closely match historic fire regimes in intensity and frequency than current wildfires (McKelvey, Skinner et al. 1996). Prescribed fire, however, may have features that are different from natural fires of the past, particularly in timing, size, intensity, and frequency. In addition, fire is being applied to a landscape where vegetation has been unburned for long periods of time. Efforts to control the intensity of these fires reduces pyrodiversity, an important element of the natural fire regime and compromises the ability of prescribed fire to restore a natural process (Baker 1992, Martin and Sapsis 1992).

How will wildlife respond to this return of fire? Fire is variable by nature and is expected to be variable in its effect on habitats and individual species. Most studies of fire effects on avian communities refer to stand-replacing wildfires in which large continuous stands of trees are killed (Kotliar et al. 2002). Burn severity affects species response and thus response to wildfire is expected to differ from that of surface fires (Kotliar, Hejl et al. 2002). Birds are a diverse and common group whose activities are relatively visible making them ideal for this type of study. A review of avian studies in Martin and Finch (Martin and Finch 1995) revealed that, of the few studies relating birds to prescribed burns, issues of timing or frequency of burns had not been addressed. Many of these studies lack reference sites, replication, or, surprisingly, preburn data, which is one of the clear advantages of studying prescription burning. Studies of prescribed burning generally found little change or an increase in species numbers with

increases in abundance particularly for species associated with open habitats. Any effects were generally short-lived. As for areas under fire suppression for long periods, lower bird diversity and lower abundances were observed in comparison to areas with fire as a regular component (Engstrom et al. 1984, Apfelbaum and Haney 1985).

Nesting success and its relationship with the nest site is generally considered to be adaptive and under selection (Martin 1998). While nesting success can be related to a number of factors, including predator populations, food availability, and parental experience, I was particularly interested in its relationship with the nest site chosen. Predation is the major cause of nest failure in these species. As vegetation is removed through burning, nest sites will be altered and this alteration is easily measured. The interaction of birds and the suite of nest predators is complex. Various theories have been put forth to explain the patterns seen in nest-site selection and nesting success, but none have been supported consistently. Two patterns have the potential to be altered by fire. One, concealment or access to the nest, has the potential to be reduced during fire when vegetation is burned making nests more visible or accessible. A second pattern, the potential prey site hypothesis, predicts that nests that are placed in the most common nest locations will be more successful because a predator needs to search more locations before finding a nest (Martin and Roper 1988). Potentially, fire can alter the distribution and abundance of nest sites which in turn would affect search efficiency of predators. Alternatively, individuals may show plasticity in nest placement with unknown consequences to nest success. If preferred (i.e. safe) nest locations are lost, more individuals will have to use sites that are less safe. Nest placement can further be

complicated by defensive behavior of the parents (Weidenger 2002) and fluctuations in the populations of predators themselves.

I studied how prescribed fires in the spring affect birds in a ponderosa pine forest on the west slope of the Sierra Nevada at elevations ranging from 1,000 to 1,390 m (Figure a.1). I used nine 40-ha study plots where, through a prescribed burning program in the region, I could study plots of three burn histories: unburned, 0-1 year postburn and 3-6 years postburn (Figure a.2). The design is patterned after a BACI design (Before-After-Control-Impact) with replication both in the control and treatment plots (Underwood 1992). Data was collected from 2001 to 2003, but additional data for four of the study plots from 1995 to 2000 was provided by the U.S. Forest Service.

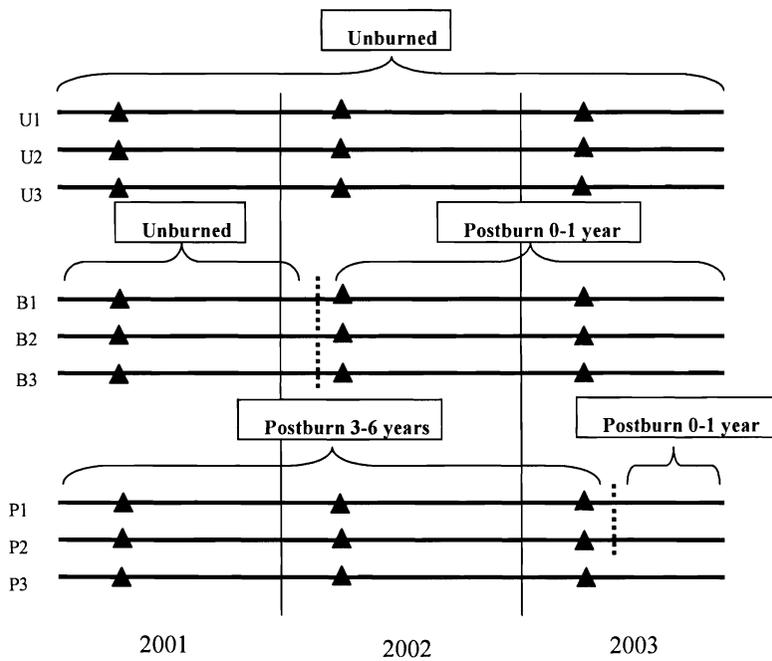
In predicting response to burning, I expected that those bird species associated with habitats or locations that were more prone to burning would be those that would respond. Because low intensity fires alter mostly understory vegetation, I expected that birds active in these zones would be the most affected. Because fires may affect populations by a variety of mechanisms, I looked at species composition, abundance of species, and reproductive consequences for individuals of a few selected species. I focused on the breeding season, which coincided with fire applications, and various aspects related to breeding ecology. The first chapter deals with composition of avian populations in response to fire and in addition takes a look at historical avian populations taken by Grinnell and Storer in the 1910's (Grinnell and Storer 1924). In the second chapter, I focus on species that depend on snags for nesting relating their selection of snags and alteration of snag populations from burning. Finally, I examine fire effects on

individuals through nest-site selection and nest success for five open-cup nesters within a landscape of burned and unburned sites. This chapter also includes data on brood parasitism rates by Brown-headed Cowbirds.

When the accident at Mann Gulch occurred, the public was outraged not only about the fatalities, but also about the fire that Wagner Dodge set, which was seen as an endangerment to the crew's escape rather than a potential savior. Prescribed fire did not come into common use until the 1970s, but despite the benefits, fire is still widely viewed exclusively as a destructive force. Ironically, Dodge died of Hodgkins disease only a few short years after his escape fire saved his life. The lessons, however, remain.

Figure a.1

**Figure a.2.** Identification of burn status for nine study plots across years. Closed triangles indicate timing of bird census and dashed lines fire applications. The period postburn 0-1 year is also referred to as immediate response to burning. Note that plot P3 is not burned again and remains designated as “Postburn 3-6 years”.



## LITERATURE CITED

- Apfelbaum, S. I. and A. Haney. 1986. Changes in bird populations during succession following fire in the Northern Great Lakes Wilderness. National Wilderness Research Conference, Fort Collins, CO, USDA Forest Service, Intermountain Research Station.
- Baker, W. L. 1992. Effects of settlement and fire suppression on landscape structure. *Ecology* 73: 1879-1887.
- Baker, W. L. and D. Ehle. 2001. Uncertainty in surface-fire history: the case of ponderosa pine forest in the western United States. *Canadian Journal of Forest Research* 31: 1205-1226.
- Brown, P. M., M. R. Kaufmann, and W. D. Shepperd. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. *Landscape Ecology* 14:513-532.
- Engstrom, R. T., R. L. Crawford 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.
- Grinnell, J. and T. Storer. 1924. *Animal Life in the Yosemite*. University of California Press, Berkeley.
- Gruell, G. E. 2001. *Fire in Sierra Nevada forests: a photographic interpretation of ecological change since 1849*. Mountain Press, Missoula.
- Kilgore, B. M. and D. Taylor. 1979. Fire history of a sequoia-mixed conifer forest. *Ecology* 60: 129-142.
- Kotliar, N. B., S. 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*.
- Macleay, J. N. 2003. *Fire and Ashes*. Henry Holt & Co., New York.
- Martin, R. E. and D. B. Sapsis. December 1992. Fires as Agents of Biodiversity: Pyrodiversity Promotes Biodiversity. Proceedings of Symposium on biodiversity of Northwestern California, Santa Rosa, CA, University of California, Wildland Resources Report.
- Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* 72: 656-670.

- Martin, T. E. and D. M. Finch, Eds. 1995. Ecology and Management of Neotropical Migratory Birds: a synthesis and review of critical issues. Oxford, Oxford University Press.
- Martin, T. E. and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *Condor* 90: 51-57.
- McKelvey, K. S., C. N. Skinner, C. R. Chang, D. C. Erman, S. J. Husari, D. J. Parsons, et al. 1996. An overview of fire in the Sierra Nevada. Sierra Nevada Ecosystem Project: final report to Congress. Davis, University of California. 2.
- Minnich, R. A., M. G. Barbour, J. H. Burk and R. F. Fernau. 1995. Sixty years fo change in Californian conifer forests of the San Bernardino mountains. *Conservation Biology* 9: 902-914.
- Minnich, R. A., M. G. Barbour, J. H. Burk and J. Sosa-Ramirez. 2000. Californian mixed-conifer forests under unmanged fire regimes in the Sierra San Pedro Martir, Baja California, Mexico. *Journal of Biogeography* 27: 105-129.
- Pyne, S. J. 1984. Introduction to wildland fire: fire management in the United States. Wiley, New York.
- Underwood, A. J. 1992. Beyond BACI: the detection of enviromental impacts on populations in the real, but variable, world. *Journal of Experimental Marine Biology and Ecology* 161: 145-178.
- Weidenger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *Journal of Animal Ecology* 71: 424-437.
- Wright, H. A. and A. W. Bailey. 1982. Fire ecology, United States and southern Canada. Wiley, New York.

## CHAPTER 1:

### CHANGES IN AVIAN POPULATIONS AND COMMUNITIES IN RESPONSE TO PRESCRIBED FIRE

**Abstract.** I examined short-term changes (0-6 years postfire) in avian abundance following low-intensity prescribed fire in a managed forest in the Sierra Nevada of California. Of 25 species analyzed, six responded positively to fire (American Robin [*Turdus migratorius*], Brown Creeper [*Certhia Americana*], Dark-eyed Junco [*Junco hyemalis*], Northern Flicker [*Colaptes auratus*], Red-breasted Nuthatch [*Sitta canadensis*], and Yellow-rumped Warbler [*Dendroica coronata*]), and six responded negatively (Acorn Woodpecker [*Melanerpes formicivorus*], Black-throated Gray Warbler [*Dendroica nigrescens*], Golden-crowned Kinglet [*Regulus satrapa*], Hermit Warbler [*Dendroica occidentalis*], Hutton's Vireo [*Vireo huttoni*], and Nashville Warbler [*Vermivora ruficapilla*]). The remaining 13 species showed no consistent response to burning. Avian communities as a whole did not change during the 3 years of the study. To further investigate community changes, I compared my abundance and fire response data with historical data collected by Joseph Grinnell in the 1910s. Differences for individual species were in the direction hypothesized if current avian communities have been altered by loss of fire, except for one species (Dark-eyed Junco) that changed significantly in the opposite direction. Grouping species into guilds, the only effects I found beyond two years after fire were increases in snag-nesting and bark-foraging species and declines in oak-associated and canopy-foraging species. Responses were generally consistent with findings of other studies, and variation was likely due to

differences in time since burning and burn severity. The small magnitude of short-term response to these types of fires should be balanced against the much larger potential for change from continued lack of fire in these ecosystems.

## **INTRODUCTION**

Alteration of fire regimes in Western forests has generally resulted in the loss of fire as an ecosystem process while increasing the risk of large severe wildfires (Kauffman 2004). Changes in fire regimes have been the result of a number of factors, including fire suppression efforts, introduced plant species, development on private lands bordering forests, logging practices, and loss of burning by Native Americans (Skinner and Chang 1996, Odion et al. 2004). Before these alterations, much of the forest was open with large widely spaced trees (Vankat and Major 1978, Minnich et al. 1995). Forest managers propose to reduce the resulting accumulation of fuels by use of prescribed fire or mechanical thinning (U.S. Healthy Forest Restoration Act). Burning, unlike thinning, also represents a return of an important ecological element to these forests, but prescribed fires may differ from fires of the past particularly within an altered landscape (McKenzie et al. 2004). Due to the specific management objectives, fuel accumulations, juxtaposition of public and private lands, and air quality issues, timing of fires is restricted to seasonal periods that can lie outside of those in which fires historically occurred. In particular, fires are set when fire intensities will be low, such as in the spring, which is concurrent with arrival of migratory birds and breeding activities. Additionally, fires of the past covered a wide range of intensities, not just low intensity

surface fires. Dissimilarities such as these, as well as lack of knowledge about wildlife populations of the past, make it difficult to predict how wildlife will respond in the modern context.

Response of a particular species to fire may be influenced by fire characteristics such as fire intensity, fire area, time of year, fire frequency, and fuel composition (Finch et al. 1997) as well as characteristics of the species such as life cycle, diet, site fidelity, and niche (Lyon et al. 2000). I note that a response, referring to changes in numbers of birds, can be the result of a number of different processes including direct mortality, population shifts, changes in reproductive success, or a combination of these effects. Reviews of the effects of severe wildfires on avian communities found that species varied in response, but in general woodpeckers and aerial foraging species were favored by burning, and foliage-gleaning species avoided burns (Kotliar et al. 2002). Unfortunately, we cannot simply extrapolate wildfire effects to prescribed fires, which differ in a number of characteristics and have had less study particularly in the West (Hejl 1994, Kotliar et al. 2002). One problem with studying the effects of fire, once an effect is found, is how to assess the meaning of this effect within the context of ecosystem processes. For instance, is the aversion of a species to a particular event to be considered cause for concern? Conversely is an increase in a population beneficial? Part of the problem is a lack of knowledge about how bird communities would be structured under a natural fire regime. At this point, we can only directly assess response within the context of a long period without fire, but we can also use historical data for information about bird abundances and communities in the past. The purpose of this study is to explore how

birds respond in the short-term (less than 6 years) to management fires used to reduce forest fuels in the Sierra Nevada, California. Response is assessed for individual species, the community, and species' guilds. In addition, I use historical data to create a frame of reference against which to compare contemporary population changes.

## **METHODS**

### **STUDY AREA AND FIRE TREATMENTS**

The study area is in a coniferous forest in the Sierra Nevada at elevations ranging from 1,000 to 1,390 meters. Sites are in Fresno County, California in the Sierra National Forest and are all within the Big Creek watershed tributary to the Kings River. Nine ~40-ha sites of mature forest that had not been recently logged were chosen. Four of these sites have been used for avian studies since 1995-1996 (K. Purcell, unpublished data). Forests are dominated by ponderosa pine (*Pinus ponderosa*) mixed with canyon live oak (*Quercus chrysolepis*), California black oak (*Quercus kelloggii*), incense cedar (*Calocedrus decurrens*), and white fir (*Abies concolor*). Sites also include riparian elements, granitic outcrops, and shrub fields dominated by white-leaf manzanita (*Arctostaphylos viscida*). Fires in the region have been regularly suppressed since the mid-1900s, but historically fires are thought to have been surface fires of mostly low severity every 2 to 12 years (Kilgore 1981, Drumm 1996), or fires of varying intensity with average return intervals of large fires every 50 years (Brown et al. 1999, Minnich et al. 2000). Excessive fuels have accumulated and, as part of a fuels reduction program begun in 1997, the area is being managed with prescribed fire by the U.S. Forest Service.

To achieve specific fuel reduction objectives, fire management plans call for multiple burn events within a 10-year period (D. MacCandliss, pers. comm.).

There are records of fires on the study sites as recently as 1947, and four sites burned in 1931 or 1932. Other sites have no written record of fires (records reach back to 1918). Three sites received controlled burn applications in April 1997, February 1998, and May 1998 prior to the initiation of the study and were designated “postburn.” Between 4 April and 11 April 2002, three additional sites had fire applied (“burn sites”). The remaining three sites (“control sites”) continued to have fire excluded. All fires were set from the ground using drip torches. Fire intensities were estimated on two of the sites burned in 2002 by rating squares of 25 x 25 meters on quantity burned within the square (0%, <50%,  $\mu$ 50%) and the intensity based on appearance such as white ash, scorching of vegetation, etc. This was done across the entire 40 hectares for these two sites.

#### **BIRD POPULATIONS**

An index of avian abundance for breeding birds was obtained for data collected in 2001 through 2003 within the period 21 April – 23 May each year. Surveys were conducted using a fixed-distance line transect method (Jarvinen and Vaisanen 1975, Verner 1985) for a total of six visits to each site during the sampling period. Each transect consisted of a permanent 1,000-meter continuous line or multiple segments surveyed over a one-hr period (3 min per 50-m segment) beginning at 07:30 PDT. All birds seen or heard were recorded as within or outside of 50 m on either side of the

walked line with care taken to avoid double-counting individuals. Surveys were delayed or repeated for inclement weather conditions such as rain, snow or wind.

The number of observers within a year varied from three to six. The same three observers conducted censuses in all 3 years with three additional observers in 2001 and one additional observer in 2002 for a total of seven different observers during the study period. All observers were trained on local birds and transect methods for two weeks prior to the counting period. Additionally, all observers passed standard hearing tests. Observers visited all sites one to two times within a year so observer was never confounded with treatment.

Use of unlimited distance counts versus counts inside the 100-meter belt was decided by examining both counts by the three observers that censused all three years noting that some variability will be due to date of the count. Unlimited counts were used because standard deviations among observers were lower for these than for restricted-width counts (SD = 19.6 per year vs. 31.6, respectively) and appeared to be due observer differences in estimating the boundaries of the belt. I considered this error to be greater than that due to counting birds off the site and/or differences in observers' abilities to hear birds at long distances. Avian abundance index data are expressed as the average number of each species counted on each transect per observer.

In addition to data from this study, I examined a dataset produced by Joseph Grinnell and Tracey Storer of bird counts in the vicinity of Yosemite National Park approximately 50 miles north of the study area. These "pencil censuses" included number of each species detected, the approximate path of the observer, and the total time

spent recording (Grinnell and Storer 1924). Locations surveyed within Yosemite Valley most closely match ours in elevation and dominant tree species. From these, censuses that occurred between mid-April and mid-May in the morning hours were selected. Three censuses done by Joseph Grinnell met these specifications: 29 April 1916, 15 May 1919, and 16 May 1919 in various locations in Yosemite Valley. A matching dataset of three hour-long censuses from unburned sites from 2001 to 2003 was created by averaging 10 censuses within two days of each date of the historic censuses.

#### **STATISTICAL ANALYSES**

Abundance (the number of birds per year per site over six visits) was analyzed for changes due to fire using repeated measures with each visit considered a repeated count on each site. Proc Genmod (SAS Institute, Inc. 2000), which uses a maximum likelihood method to fit the generalized linear model, was used for the count data with a Poisson response probability distribution and a log link function. The model included the year, the treatment (burn status), and the treatment by year interaction. Only those species with a total count greater than 10 for at least 8 of 9 possible counts (3 treatments x 3 years) were analyzed. Main effects (e.g. year) are not reported, as they are not, by themselves, relevant to the questions addressed here. Instead, four contrasts, as estimated through Generalized Estimating Equations (GEE) within the repeated measures model, were used to examine differences in abundance (Table 1.1). Recalling that three sites were burned in 2002, the first contrast specifically tested for differences between these burn sites prior to burning and unburned sites in 2001 that would indicate site differences already present.

**Table 1.1.** Null equations for contrasts based on model: total count = treatment + year + treatment\*year + intercept where treatment is U = unburned sites, B = sites burned in 2002, P = postburn sites.

Contrast	Null equation
Site differences	$B + 2001 + B*2001 + \text{intercept} = U + 2001 + U*2001 + \text{intercept}$
Immediate response	$U + 2001 + U*2001 + U + 2002 + U*2002 + U + 2003 + U*2003 + B + 2001 + B*2001 + \text{intercept} = 2(B + 2002 + B*2002 + B + 2003 + B*2003) + \text{intercept}$
Postburn sites only	$U + 2001 + U*2001 + U + 2002 + U*2002 + U + 2003 + U*2003 + B + 2001 + B*2001 + \text{intercept} = 2(P + 2001 + P*2001 + P + 2002 + P*2002 + P + 2003 + P*2003) + \text{intercept}$
Overall	$5(U + 2001 + U*2001 + U + 2002 + U*2002 + U + 2003 + U*2003 + B + 2001 + B*2001) + \text{intercept} = 4(B + 2002 + B*2002 + B + 2002 + B*2002 + P + 2001 + P*2001 + P + 2002 + P*2002 + P + 2003 + P*2003) + \text{intercept}$

The second contrast tested for an immediate effect of fire by looking for a difference between unburned sites and the three burn sites after burning in 2002 and 2003 (immediate only). The third contrast tested for differences between unburned and the three postburn sites burned previous to the study in 1997 or 1998 (postburn only). A fourth contrast combined these last two contrasts to compare all burned sites to the unburned sites, but is not considered further as it found no new effects not found by the other contrasts. In addition to the main model that included the effects of year and treatment type, I added “observer” as a variable in the model and examined main effects as well as the interaction of treatment and observer to evaluate the possibility that an observer’s detectability of a species varied with treatment. Years were analyzed separately for this analysis only, as the set of observers differed each year. These analyses are exploratory in nature and thus, despite using multiple tests, I used *P*-values of less than 0.05 to indicate a significant result (Johnson 1999).

Species abundances were pooled by nesting guilds, foraging guilds, habitat associations, and migratory status, and analyzed using the previously described generalized linear model and the contrasts (see Appendix B). Total count had to be greater than 10 birds over three years to be included. Guilds were based on information from Granholm (1974), and Beedy and Granholm (1985) as well as personal observations. For species where there was ambiguity in guild assignment, no assignment was given.

In addition to simple species richness patterns, overall bird communities were examined using Detrended Correspondence Analysis (DCA) with rare species

downweighted (Hill and Gauch 1980, Pielou 1984). DCA produces a score for each sample (i.e., site survey) that is a weighted combination of the abundance of each species in the sample; thus, the similarity of two samples' scores is indicative of the similarity of their overall species composition. Likewise, DCA produces a score for each species that is a weighted combination of its abundance in each sample. Fifty-two bird species were included (species detected only once were excluded) along with the nine sites in each year. Axes were correlated with DCA sample scores using relative Euclidean distance (McCune and Mefford 1997). Scores of both species and sites were used to interpret the ordination of the axes based on their respective characteristics. DCA was performed using PC-ORD (McCune and Mefford 1997).

Number of each species recorded per hour in 1916/1919 was compared to average count per hour of modern censuses using the generalized linear model discussed previously (without contrasts or repeated measures). Species in modern counts that were detected at a rate less than 0.096 per hour were excluded, as this would represent a single detection in the historical counts. These results were then compared to results of the previous analysis for species responding negatively or positively to fire. Specifically, if bird abundances have been affected by the loss of fire, I hypothesized that species negatively affected by fire should be more abundant in the absence of frequent fire. Conversely, I hypothesized that species positively affected will have declined in the absence of fire.

## RESULTS

Burns were mostly patchy and of low intensity leaving many unburned patches and killing few trees. On the two sites burned in 2002 where I collected fire intensity information across the site, one had ~ 49% unburned area and the other ~51% unburned. Some large blocks were unburned in areas adjacent to streams or on rock outcrops (25% and 39% of the total area respectively), but otherwise burning left an irregular pattern of small burned and unburned patches throughout the sites. The third site burned in 2002 had a similar burning pattern, but some understory trees and brush were removed prior to burning.

Seventy-eight bird species were recorded during the 3 years across all nine sites. The number of species per site ranged from 48 to 57. Three species occurred only on unburned sites: Rufous Hummingbird, Sharp-shinned Hawk, and Bewick's Wren (see Appendix B for scientific names and occurrence of species by treatment). Nine species were recorded only on burned sites following burning: Mallard, Western Kingbird, Violet-green Swallow, American Dipper, Varied Thrush, California Towhee, Bullock's Oriole, and House Finch. All these species were very rare and only occurred on one site except for Varied Thrush, which occurred on two sites (two records in 2003), and Hermit Thrush, which occurred on four sites (seven records total).

Response to burning was mixed. For all species combined, total abundance did not change after burning for all contrasts (Table 1.2, Fig. 1.1). When observer was included as a variable in the model there were significant observer effects for a few species, but there was no significant interaction between treatment and observer for any

**TABLE 1.2.** Results of contrasts for individual species with estimates from GEE models and associated *P*-value (<0.05 shown in bold). Estimates are based on contrasts from Table 1.1. Response is direction of effect in relation to burning for significant estimates.

Species	Response	Site differences		Immediate only		Postburn only	
		estimate	<i>P</i> - value	estimate	<i>P</i> - value	estimate	<i>P</i> - value
Mountain Quail	0	0.04	0.92	0.87	0.56	0.15	0.70
Anna's Hummingbird	0	<b>-0.76</b>	<b>0.01</b>	-2.34	0.18	0.32	0.40
Acorn Woodpecker	-	-0.53	0.35	-0.65	0.85	<b>1.07</b>	<b>0.04</b>
Northern Flicker	+	-0.38	0.16	<b>-2.75</b>	<b>0.02</b>	-0.09	0.75
Western Wood-0Pewee	0	0.26	0.56	0.88	0.44	0.22	0.85
Hammond's Flycatcher	0	<b>1.82</b>	<b>0.004</b>	2.45	0.67	-0.07	0.92
Pacific-slope Flycatcher	0	0.90	0.06	-0.05	0.99	-0.64	0.54
Cassin's Vireo	0	-0.07	0.87	0.03	0.99	-0.11	0.85
Hutton's Vireo	-	<b>-0.54</b>	<b>0.001</b>	-1.54	0.24	<b>0.95</b>	<b>0.008</b>
Warbling Vireo	0	0.67	0.38	1.41	0.77	1.68	0.18

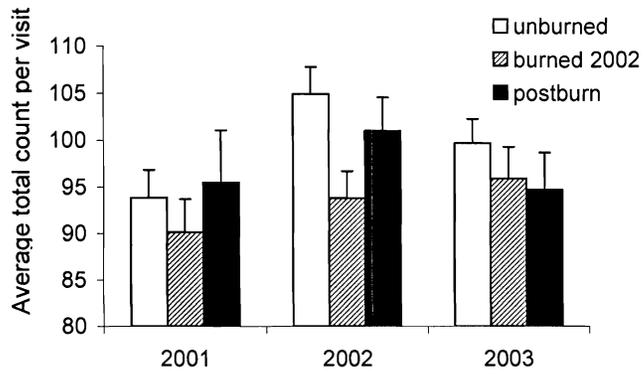
**Table 1.2** continued

Species	Response	Site differences		Immediate only		Postburn only	
		estimate	<i>P</i> - value	estimate	<i>P</i> - value	estimate	<i>P</i> - value
Steller's Jay	0	0.14	0.59	-0.59	0.64	-0.17	0.51
Red-breasted Nuthatch	+	0.25	0.54	1.17	0.58	<b>-1.35</b>	<b>0.04</b>
Brown Creeper	+	0.05	0.87	-1.50	0.59	<b>-2.03</b>	<b>&lt;0.001</b>
Golden-crowned Kinglet	-	0.20	0.77	<b>9.23</b>	<b>0.01</b>	-1.32	0.18
American Robin	+	0.22	0.47	<b>-3.27</b>	<b>0.04</b>	<b>-0.83</b>	<b>0.046</b>
Nashville Warbler	-	-0.21	0.44	-0.71	0.69	<b>1.86</b>	<b>0.001</b>
Yellow-rumped Warbler	+	0.53	0.19	1.51	0.37	<b>-1.21</b>	<b>&lt;0.001</b>
Black-throated Gray Warbler	-	0.15	0.70	-2.57	0.39	<b>2.98</b>	<b>&lt;0.001</b>
Hermit Warbler	-	0.14	0.73	<b>6.26</b>	<b>&lt;0.001</b>	0.05	0.93
Western Tanager	0	0.13	0.40	1.17	0.49	-0.08	0.90
Spotted Towhee	0	-0.26	0.32	-0.27	0.82	0.02	0.95
Dark-eyed Junco	+	-0.03	0.88	0.80	0.66	<b>-0.43</b>	<b>0.04</b>

**Table 1.2 continued**

Species	Response	Site differences		Immediate only		Postburn only	
		estimate	<i>P</i> - value	estimate	<i>P</i> - value	estimate	<i>P</i> - value
Black-headed Grosbeak	0	0.28	0.42	0.73	0.74	0.57	0.38
Brown-headed Cowbird	0	<b>-0.43</b>	<b>0.003</b>	-0.57	0.73	0.18	0.77
Purple Finch	0	-0.17	0.28	0.20	0.93	0.11	0.83
Total Abundance (all species)	0	0.01	0.91	0.37	0.28	0.09	0.07

**Figure 1.1.** Average total count of all species per observer per year (with standard errors). Treatment replicates have been combined; thus each total represents 3 separate transects. Burned plots were still unburned in 2001, but are shown separately from unburned sites.



year, indicating that observer variability was not confounded with burn status of the sites. Using the focused question approach of contrast analysis, responses to fire could be separated into immediate (0-1 year after fire) and postburn (3-6 years after fire) effects. Six species had higher abundance on burned sites, six had lower abundance, and thirteen showed no difference (Table 1.2). An immediate positive response was found for Northern Flicker and American Robin. Red-breasted Nuthatch, Brown Creeper, Yellow-rumped Warbler, and Dark-eyed Junco counts were higher on postburn sites. American Robin also had higher populations on postburn sites in addition to the immediate response. An immediate negative response was found for Golden-crowned Kinglet and Hermit Warbler. Abundances were significantly lower on postburn sites for Acorn Woodpecker, Hutton's Vireo, Nashville Warbler, and Black-throated Gray Warbler. In addition, Hutton's Vireo also had significantly different populations on burned and unburned sites before burning occurred in 2001 indicating pre-existing population differences. Mountain Quail, Anna's Hummingbird, Northern Flicker, Western Wood-Pewee, Hammond's Flycatcher, Pacific-slope Flycatcher, Cassin's Vireo, Warbling Vireo, Steller's Jay, Spotted Towhee, Black-headed Grosbeak, Brown-headed Cowbird, and Purple Finch did not show any changes consistent with response to fire.

When species were grouped by guild (54 species), contrasts showed a significant positive effect of burning in both the short- and long-term for snag nesters (Table 1.3). In addition, there was a significant positive immediate effect for short-distance migrants, and understory foragers, and positive postburn effects for aerial and bark foragers. Aerial foragers also had a significant contrast for pre-existing site differences. Canopy foragers

had a negative response both immediately and postburn. A negative immediate response only was found for ground nesters, high nesters, and long-distance migrants.

Abundances were lower on postburn sites for oak-associated species. No significant contrasts relating to burn effect were found for residents, low nesters, riparian-associated species, conifer-associated species, or open-forest associated species.

Fifty-two species were included in the DCA (Fig. 1.2). Five rare species (Blue-gray Gnatcatcher, Cedar Waxwing, Hermit Thrush, Red-tailed Hawk, and Song Sparrow) were downweighted. The DCA explained 52% of the total variance (as determined by relative Euclidean distance) with two axes explaining most of the variation.  $R^2$  values for the first and second axes were 0.576 and 0.166, respectively. Lengths of the axes were 1.32 for the first and 1.15 for the second, indicating relatively little compositional variation across all sites. Comparisons of species scores and site characteristics with the axes suggest that the first DCA axis represents a gradient from open habitats with shrubs and oaks to closed canopy forests dominated by conifers. The second DCA axis appears to represent a gradient from mesic to xeric habitats. The DCA showed that most differences were between sites and that sites with the same treatment did not group together, but rather shared some broader landscape features such as large granitic outcrops or dense stands of conifers (Fig. 1.2). Community shifts between years were mirrored, with all sites consistently declining on the first axis, which is consistent with an overall year effect in 2002.

Overall numbers of individuals per hour detected in 1916/1919 (mean = 95.3/hr) were similar to the modern censuses (mean = 98.4/hr). Conspicuous differences noted

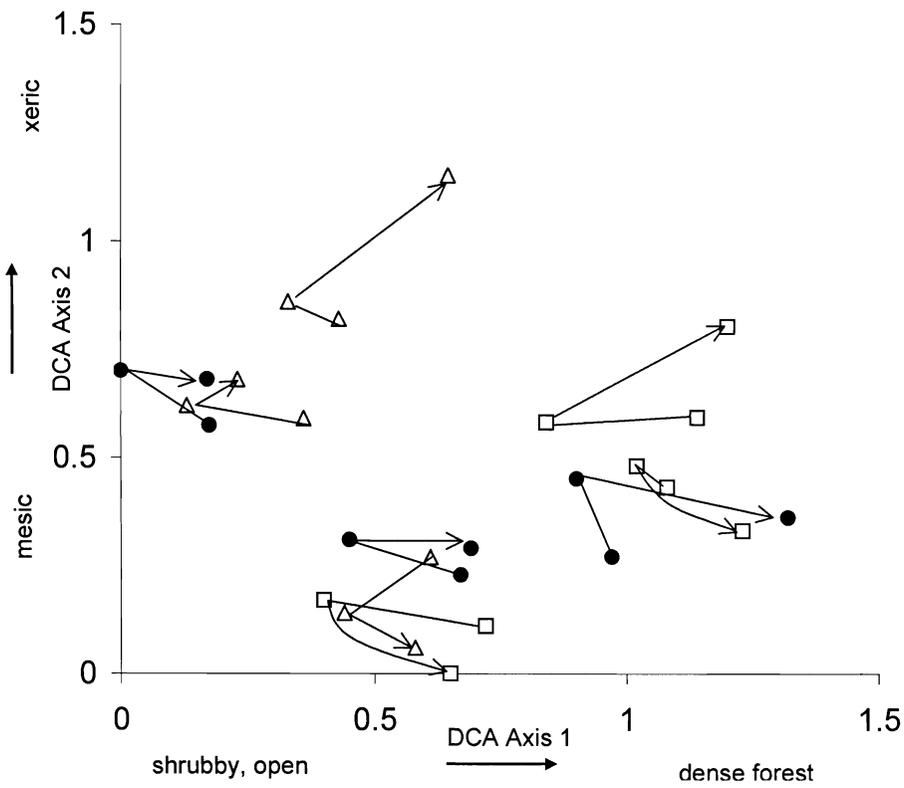
**Table 1.3.** Results of contrasts from guilds with estimates from GEE models and associated *P*-value (<0.05 shown in bold). Estimates are based on contrasts from Table 1.1 and guild classifications from Appendix B. Response is direction of effect in relation to burning for significant estimates of burn effect.

Guilds	Response	Site differences		Immediate only		Postburn only	
		estimate	<i>P</i> - value	estimate	<i>P</i> - value	estimate	<i>P</i> - value
Nesting guild							
Snag nesters	+	-0.03	0.92	<b>-3.17</b>	<b>&lt;0.001</b>	<b>-0.47</b>	<b>0.03</b>
Ground nesters	-	-0.15	0.37	<b>1.91</b>	<b>&lt;0.001</b>	0.08	0.19
High nesters	-	0.26	0.29	<b>3.99</b>	<b>0.02</b>	-0.20	0.60
Low nesters	0	0.16	0.32	-0.21	0.85	0.04	0.86
Migratory Status							
Residents	0	-0.08	0.72	0.58	0.05	-0.63	0.13
Short-distance Migrants	+	-0.05	0.74	<b>-2.37</b>	<b>&lt;0.001</b>	0.03	0.86
Long-distance Migrants	-	0.16	0.15	<b>1.73</b>	<b>0.03</b>	0.14	0.29
Habitat association							

**Table 1.3** continued

Guilds	Response	Site differences		Immediate only		Postburn only	
		estimate	<i>P</i> - value	estimate	<i>P</i> - value	estimate	<i>P</i> - value
Oak associated	-	-0.18	0.36	-0.46	0.65	<b>1.09</b>	<b>&lt;0.001</b>
Riparian associated	0	0.39	0.22	-2.59	0.06	-0.43	0.24
Conifer associated	0	0.21	0.19	1.07	0.13	- 0.46	0.09
Open associated	0	-0.11	0.43	-0.40	0.15	0.003	0.98
Foraging guild							
Aerial foraging	+	<b>0.75</b>	<b>0.01</b>	0.64	0.62	<b>-0.76</b>	<b>0.049</b>
Bark foraging	+	0.21	0.49	-1.44	0.23	<b>-1.22</b>	<b>&lt;0.001</b>
Understory foraging	+	-0.05	0.66	<b>-0.79</b>	<b>0.009</b>	-0.05	0.42
Canopy foraging	-	-0.003	0.98	<b>2.19</b>	<b>0.008</b>	<b>0.37</b>	<b>&lt;0.001</b>

**Figure 1.2.** Plot of DCA scores for sites by year for DCA axis 1 and 2 from analysis of total species counts per plot by year. Sites are shown as unburned (filled circles), burned 2002 (unfilled triangles), and postburn (unfilled squares). Consecutive years on a site are connected with arrows (2001 to 2002 to 2003). For axis one the eigenvalue is 0.13 and  $R^2 = 0.58$ . For axis two the eigenvalue is 0.06 and  $R^2 = 0.17$ .  $R^2$  is based on relative Euclidean distance.

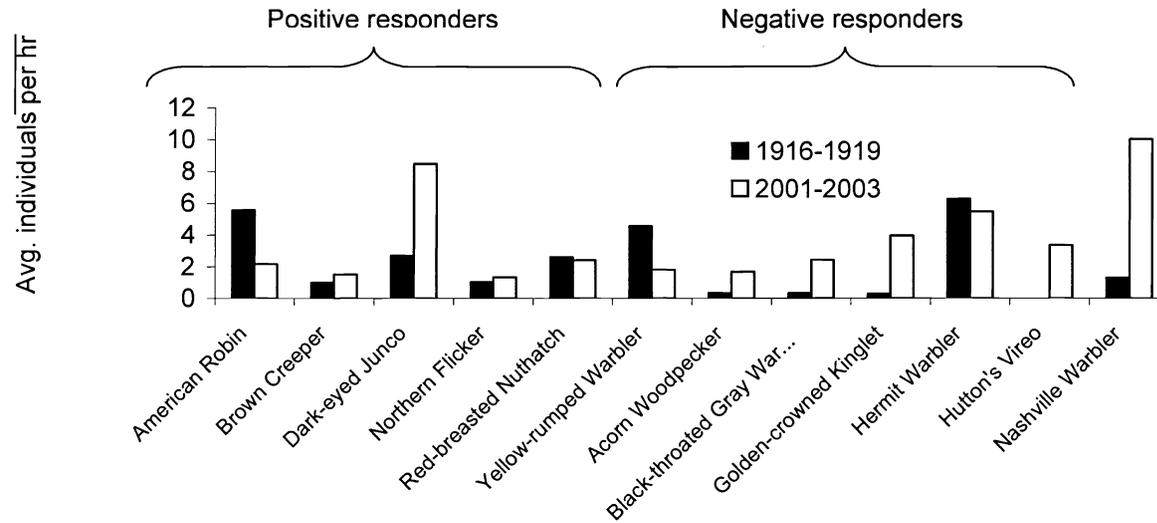


included the loss of Yellow Warbler (counted once in the current study area in 1997) and the arrival of Brown-headed Cowbirds. Comparing the 12 species I observed to respond significantly to the fire treatment to their abundances in the Grinnell dataset, six differed significantly in the direction expected based on their response to fire (Fig. 1.3). Nashville Warbler ( $\chi^2_1 = 23.02$ ,  $P < 0.001$ ), Golden-crowned Kinglet ( $\chi^2_1 = 11.32$ ,  $P < 0.001$ ), and Black-throated Gray Warbler ( $\chi^2_1 = 5.44$ ,  $P = 0.02$ ) had higher populations in the modern counts and all showed negative responses to fire. Hutton's Vireo also had a negative response to fire and was not recorded in the Grinnell dataset I used. American Robin ( $\chi^2_1 = 4.65$ ,  $P = 0.03$ ) had lower populations in the modern counts and was identified as having a positive response to fire. For Yellow-rumped Warbler, the populations were also lower, but not significantly ( $\chi^2_1 = 3.72$ ,  $P = 0.05$ ). Results for Brown Creeper ( $\chi^2_1 = 0.33$ ,  $P = 0.56$ ), Northern Flicker ( $\chi^2_1 = 0.10$ ,  $P = 0.75$ ), Red-breasted Nuthatch ( $\chi^2_1 = 0.02$ ,  $P = 0.88$ ), and Hermit Warbler ( $\chi^2_1 = 0.17$ ,  $P = 0.68$ ) suggest unchanged populations. Only Dark-eyed Junco showed a response opposite to that hypothesized: this positive responder is more abundant within a context where fires have been reduced.

## DISCUSSION

I identified a number of changes in bird abundances resulting from prescribed fires in the spring, but no overall changes in communities. Additionally, more than half the species examined did not respond to burning, indicating resilience to these types of habitat changes, although historical comparisons showed that changes might accumulate

**Figure 1.3.** Average hourly detection rate for responding species for 1916-1919 (Grinnell) and for 2001 to 2003 (unburned sites only). Responding species are those that showed a significant contrast for immediate or postburn effects. I predicted that positive responders would have high historical abundance and negative responders would have low historical abundance



over time as the result of changes that include overall reduction of fires. Grouping species into guilds, to increase sample sizes and to examine more general patterns for predicting response, again resulted in negative-responding, positive-responding, and resilient groups. I acknowledge that there was considerable overlap among the classes of guilds and, considering the multitude of factors that may affect habitat selection and suitability, it is unlikely that a single guild division is adequate to predict avian response to burning.

The fact that I were able to compare counts from before and after burning enabled us to distinguish between response to fire and pre-existing differences in abundances, perhaps due to plot-scale differences in habitat. Additionally, comparisons with unburned sites helped us to sort out annual population fluctuations that may have been the result of other factors such as weather or food abundance. Interpretation of response on postburn sites only, which lack preburn data, is more problematic as differences could also be due to site differences already present. Alternatively, response on the postburn sites could indicate differences in burn intensity or a time lag in species response to fire. Hutton's Vireo and the aerial foragers were the only responders that showed site differences before burning as well as between controls and postburn sites. For these, consistent site differences may have confounded my analysis of burning effect. Beyond these systematic differences in sites, there was considerable variation in species response to treatments on individual sites, which could be due to any number of factors (e.g. slope, past management practices, topography). Due to these inherent local differences, it is likely that my identification of responding species was conservative. It also provides a

note of caution to studies that are based on a single comparison of one burned and one unburned location.

Detectability issues are of particular concern when testing differences between treatments as changes in detectability of species between treatment types (the effect of habitat) may confound the results. Unfortunately, density estimates based on detectability functions recommend a count of >80 (Buckland et al. 2001), for which only four of my species qualify. Data collection involved distinguishing detections within and beyond only a single distance (50 m), but found that there were differences among observers indicating that this distance could not be accurately estimated. This is likely due to the relatively dense vegetation in these forests, and is exacerbated by aural detections, for which it is difficult to estimate distance (DeJong 1985), and which comprised the majority of my detections. I partially controlled for other observer differences by having observers visit all sites evenly and retaining observers over as many years as possible. For individual species I did not find that observers varied differently based on treatment. The possibility remains, however, that species differed in detectability due to differences in sound attenuation resulting from structural differences among the treatment types. England (1995) examined detectability differences between counts in chaparral of various ages since burning, finding no detectability differences based on habitat for intraspecific comparisons. In addition, he found consistent patterns in population changes for simple and adjusted counts.

While my results cannot be directly compared to studies of wildfire effects, it is likely that fire as a disturbance leads to responses that scale with fire intensity and size,

with prescribed fires such as ours at one end of the spectrum and stand-replacing wildfire at the other. Despite variation in burn severity, other studies have found results similar to mine for some species. American Robin, Northern Flicker, and Dark-eyed Junco fairly consistently show increases following wildfire (Raphael et al. 1987, Kotliar et al. 2002). However, Brown Creeper, Red-breasted Nuthatch, and Yellow-rumped Warbler show more mixed results or populations decreases, inconsistent with my findings (Granholm 1974, Raphael et al. 1987, Horton and Mannan 1988, Kotliar et al. 2002). Another study of prescribed fire in the Sierra Nevada found the same positive response for Yellow-rumped Warbler (Granholm 1974). This same study found a primarily negative response in Red-breasted Nuthatch and no pattern for Brown Creeper, but was restricted to within 2 years of burning while the positive effect I found did not occur until three to six years after fire. Thus, time since fire appears to be an important variable regulating response. Negative response to fire by Acorn Woodpecker, Nashville Warbler and Golden-crowned Kinglet were consistent with other studies (Bock and Lynch 1970, Raphael et al. 1987, Horton and Mannan 1988, Kotliar et al. 2002). Responses of the remaining three negative responders, Hermit Warbler, Black-throated Gray Warbler, and Hutton's Vireo, have been little studied, but a study of thinning in Oregon (Hayes et al. 2003) found negative impacts for these species consistent with the negative response I found to burning if burning and thinning invoke a similar reaction.

By grouping species into guilds, while acknowledging the potential problems with this approach already mentioned, I found a number of responses that may help to predict a species' response to prescribed fire. The simplest prediction is that birds associated

with habitats or locations that are more prone to burning would be those that would respond, and, with a few exceptions, I generally found this to be true. Because low intensity fires alter mostly understory vegetation, I expect that birds active in these zones will be the most affected. Understory and aerial foragers increased following fire on my sites and increased populations have been found in other studies after both wildfire (Bock and Lynch 1970, Raphael et al. 1987, Kotliar et al. 2002, Morissette et al. 2002) and prescribed fire (Woinarski 1990, Artman et al. 2001). Ground nesters had an immediate negative response to fire, but populations had apparently recovered by the third year after fire, probably in concert with the recovery of ground cover. While removal of ground cover may reduce the availability of potential nest sites in the short term, a more open understory makes foraging sites more accessible (Renwald 1977, Woinarski 1990). Low-nesting species, however, were not affected perhaps indicating the restriction of the majority of the flames to the surface. Oaks are vulnerable to burning and those species that associate with oaks were reduced on postburn sites. Higher fire frequencies in the past likely favored oak recruitment (McClaran and Bartolome 1989), so oak-associated species may not be expected to benefit from fire immediately and response to recruitment is outside the duration of this study.

Snags, while relatively combustible, are also created by fire (see Chapter 2). I found a positive response for snag nesters and bark foragers. These two guilds were similar and comprised mostly of woodpeckers and other snag-dependent species. In Ohio, repeated prescribed fires did not affect cavity nesters or bark foragers (Artman et al. 2001), but other studies have found a positive response for bark foragers (Granholm

1974, Kreisel and Stein 1999). Kotliar et al.'s review of wildfire effects (2002) found a negative response for bark gleaners. Thus availability of suitable bark foraging substrates and snags may be dependent on fire intensity or extent, and associated species will respond differently depending on disturbance level and thus severity of tree damage.

Because of the low intensity of these fires, flames seldom reach into the upper canopy or into moist locations, and thus I would expect no response for species that forage or nest there. While, as expected, species associated with riparian areas were unaffected it was interesting that I found a negative response for canopy foragers for both the immediate and postburn periods and a negative immediate response for high-nesting species. While it is possible that species nesting in the canopy may be avoiding smoke, which lingered during the time when many species are selecting nest sites, the lasting effect may be better explained by reduction in food supplies, as many of these species are also insectivorous foliage gleaners. Granholm (1974), who also found a decline in foliage-gleaning insectivores during prescribed fire, suggested this effect was due to mortality of foliage insects.

Behavioral plasticity and site fidelity have been suggested as mechanisms behind response or lack of response to disturbance (Wiens and Rotenberry 1985, Petersen 1987). Variation in the amount of plasticity a species displays might be correlated with its migratory status. The 2002 fires occurred in early April when only residents were present, but migrants arrived soon afterwards. I found that short distance migrants responded positively while long-distance migrants responded negatively to fire, but only in the short term. The positive response of short-distance migrants might be explained by

their nomadic nature, which is a quality that has been suggested to allow individuals to take advantage of resources in burned areas (Woinarski 1990). Long-distance migrants may be more restricted in habitat selection on the breeding grounds due to their limited time there, and perhaps have less tolerance for habitat changes. Residents may have the strongest site fidelity, having the most invested in the site, and thus may be more tolerant of habitat changes.

I did not find large changes in community composition related to burning nor were any species clearly restricted to burned or unburned areas. In addition, approximately half of the individual species did not show a response to fire. These results are similar to bird responses following repeated burning in Ohio where six species (four negative, two positive) out of 30 responded (Artman et al. 2001). Emlen (1970), who found little response within 5 months by birds following a prescribed fire, postulated that site fidelity might stabilize populations following disturbance if critical resources are not severely altered. My results seem to support this hypothesis for many species.

The scope of this study does not allow for testing effects longer than 6 years, or perhaps more importantly, landscape level changes. Fire is a disturbance that maintains heterogeneity in space and time and thus it is very difficult to directly monitor changes to bird populations over a large space and over many years, even if fires were not suppressed. Thus we are left to make inferences from changes at a small scale. Comparison to the 1910s data supports some of these findings and indeed argues for large-scale changes in bird abundances that may be due, at least in part, to loss of fire from the system. Beedy (1982), in the late 1970s, also compared his abundance data to

that collected by Joseph Grinnell, and found a similar species composition across an elevational gradient, but increasing populations for Golden-crowned Kinglet were identified as possibly due to fire suppression. Focusing on those species responding to applied fire, I found species that had a negative response to fire were those that have experienced overall increases in abundance. The reverse was true for positively responding species except for one species (Dark-eyed Junco) with a positive response that experienced an overall decrease in abundance. The Grinnell data indicate that the small short-term responses by birds to low intensity fire I found may accumulate over time. Despite complications such as range expansion of Brown-headed Cowbirds, global warming and habitat alterations, these findings are consistent with predictions for the effect of fire loss on bird communities. In addition, we are reminded not to expect the exact same response from fire as a single event after a long absence as when fire is an ecosystem process. Study of bird communities in the Sierra San Pedro Martir of Baja California, Mexico may give some insight into populations of these forests, but where fires are not managed.

Prescribed fire as practiced today is generally conducted on a small spatial scale. Additionally, because only about 50% of the area where fire was applied actually burned, these fires may be ineffective at restoring historical forest structures. Changes in bird populations that I found were generally within the range of population fluctuations related to other biotic and abiotic factors in the absence of fire (Appendix B). Attempts at fire exclusion will not ultimately benefit those species that have negative responses to fire, because fires cannot be suppressed indefinitely. Within this context, there is little

concern about negatively affecting populations with prescribed fire with the exception of species with extremely low populations or very restricted ranges. There does in fact also seem to be some evidence that communities may have unusually high populations of those species favored by fire exclusion. Thus decisions about implementing prescribed fire programs need to also be weighed against the consequences of continuing to try to exclude fire from these ecosystems.

## LITERATURE CITED

- Artman, V., E. Sutherland, and J. Downhower. 2001. Prescribed burning to restore mixed-oak communities in Southern Ohio: effects on breeding-bird populations. *Conservation Biology* 15:1423-1434.
- Beedy, E. C. 1982. Bird community structure in coniferous forests of Yosemite National Park, California. Ph.D. Dissertation, University of California, Davis, CA.
- Beedy, E. C., and S. L. Granholm. 1985. Discovering Sierra birds. Yosemite Natural History Association and Sequoia Natural History Association.
- 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.
- Brown, P. M., M. R. Kaufmann, and W. D. Shepperd. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. *Landscape Ecology* 14:513-532.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borghers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of animal populations. Oxford University Press, New York.
- Dieni, J. S., and S. H. Anderson. 1999. Effects of recent burning on breeding bird community structure in aspen forests. *Journal of Field Ornithology* 70:491-503.
- Drumm, M. K. 1996. Fire history in the mixed conifer series of the Kings River Adaptive Management Area, Sierra National Forest. M.S. Thesis, Humboldt State University, CA.
- Emlen, J. T. 1970. Habitat selection by birds following a forest fire. *Ecology* 51:343-345.
- England, S. A. 1995. Effects of vegetation structure and data analysis techniques on estimates of bird abundance in chaparral vegetation. Ph.D. Dissertation, University of California, Davis, CA.
- Finch, D. M., J. L. Ganey, W. Yong, R. T. Kimball, and R. Sallabanks. 1997. Effects and interactions of fire, logging, and grazing, p. 103-136. *In* W. M. Block and D. M. Finch [eds.], *Songbird ecology in Southwestern ponderosa pine forests: a*

literature review. USDA Forest Service General Technical Report RMRS-GTR-292.

- Granholm, S. L. 1982. Effects of Surface Fires on Birds and their Habitat Associations in Coniferous Forests of the Sierra Nevada, California. Ph.D. Dissertation, University of California, Davis, CA.
- Grinnell, J., and T. Storer. 1924. Animal life in the Yosemite. University of California Press, Berkeley.
- 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.
- Hejl, S. J. 1994. Human-induced changes in bird populations in coniferous forest in western North America during the past 100 years. *Studies in Avian Biology* 15:232-246.
- Hill, M. O., and H. G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetation* 42:47-58.
- Horton, S. P., and R. W. Mannan. 1988. Effects of prescribed fire on snags and cavity-nesting birds in Southeastern Arizona pine forest. *Wildlife Society Bulletin* 16:37-44.
- Impeau, L., J. L. Savard, and R. Gagnon. 1999. Comparing bird assemblages in successional black spruce stands originating from fire and logging. *Canadian Journal of Zoology* 77:1850-1860.
- Jarvinen, O., and R. A. Vaisanen. 1975. Estimating relative densities of breeding birds by the line transect method. *Oikos* 26:316-322.
- Johnson, D. H. 1999. The insignificance of statistical significance testing. *Journal of Wildlife Management* 63: 763-772.
- Kauffman, J. B. 2004. Death rides the forest: perceptions of fire, land use, and ecological restoration of western forests. *Conservation Biology* 18:878-882.
- Kotliar, N. B, S. 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.

- Lyon, L. J., M. H. Huff, E. S. Telfer, D. S. Schreiner, and J. K. Smith. 2000. Fire effects on animal populations, p. 25-34. *In* J. K. Smith [ed.], *Wildland fire in ecosystems: Effects of fire on fauna*. USDA Forest Service General Technical Report RMRS-GTR-42.
- McClaran, M. P., and J. W. Bartolome. 1989. Fire-related recruitment in stagnant *Quercus douglasii* populations. *Canadian Journal of Forest Research* 19:580-585.
- McCune, B., and M. J. Mefford. 1997. *Multivariate analysis of ecological data*, version 3.0. MjM Software, Gleneden Beach, Oregon.
- McKenzie, D., Z. Gedalof, D. L. Peterson, and P. Mote. 2004. Climatic change, wildfire, and conservation. *Conservation Biology* 18:890-902.
- Minnich, R. A., M. G. Barbour, J. H. Burk, and R. F. Fernau. 1995. Sixty years of change in Californian conifer forests of the San Bernardino Mountains. *Conservation Biology* 9:902-914.
- Minnich, R. A., M. G. Barbour, J. H. Burk, and J. Sosa-Ramirez. 2000. Californian mixed-conifer forests under unmanaged fire regimes in the Sierra San Pedro Martir, Baja California, Mexico. *Journal of Biogeography* 27:105-129.
- 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.
- Odion, D. C., E. J. Frost, J. R. Strittholt, H. Jiang, D. A. Dellasala, and M. A. Moritz. 2004. Patterns of fire severity and forest conditions in the western Klamath Mountains, California. *Conservation Biology* 18: 927-936.
- Petersen, K. L., and L. B. Best. 1987. Effects of prescribed burning on nongame birds in a sagebrush community. *Wildlife Society Bulletin* 15:317-329.
- Pielou, E. C. 1984. *The interpretation of ecological data: a primer on classification and ordination*. John Wiley & Sons, New York.
- Raphael, M. G., M. L. Morrison, and M. P. Yoder-Williams. 1987. Breeding bird population during twenty-five years of post-fire succession in the Sierra Nevada. *Condor* 89: 614-626.
- Renwald, J. D. 1977. Effect of fire on Lark Sparrow nesting densities. *Journal of Range Management* 30:283-285.

- SAS Institute, Inc. 2000. SAS/STAT User's Guide. SAS Institute, Cary, NC.
- Skinner, C. N. and C. R. Chang. 1996. Fire regimes, past and present, p.1041-1069. *In* Sierra Nevada Ecosystem Project: Final Report to Congress. Centers for Water and Wildland Resources University of California, Davis, CA.
- Vankat, J. L. and J. Major. 1978. Vegetation changes in Sequoia National Park, California. *Journal of Biogeography* 5:377-402.
- Verner, J. 1985. Assessment of counting techniques. *Current Ornithology* 2:247-302.
- Wiens, J. A., and J. T. Rotenberry. 1985. Response of breeding passerine birds to rangeland alteration in a North American shrubsteppe locality. *Journal of Applied Ecology* 22:655-668.
- Woinarski, J. C. Z. 1990. Effects of fire on the bird communities of tropical woodlands and open forest in northern Australia. *Australian Journal of Ecology* 15:1-22.

## CHAPTER 2:

### PRESCRIBED FIRE, SNAG POPULATION DYNAMICS, AND AVIAN NEST-SITE SELECTION

**Abstract.** Snags are an important resource for a wide variety of organisms, including cavity-nesting birds. I documented snag attributes before and after fire on burned and unburned plots to assess the effects of prescribed fire on snag populations in the Sierra Nevada of California. Additionally, I located and monitored snags used for nesting by avian species to examine snag selection and the consequences of that selection on productivity. There was little overall change in snag numbers, but the spatial distribution of snags was altered following burning. Snag population changes were greatest following the first introduction of fire after a long fire-free period. Snags preferred for nesting were generally of ponderosa pine (*Pinus ponderosa*), of larger diameter, and moderately decayed as compared to available snags. White fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*) were avoided. There was a small loss ( $-1.5 \text{ ha}^{-1}$ ) of snags predicted to be useable for nesting after burning. None of the selected snag attributes resulted in differences in nesting success, suggesting that nest-site selection is mainly related to physical constraints of cavity construction. There was, however, lower nest success during the first year following fire, but this effect disappeared within 3 years. I recommend protection of preferred snags, in particular large ponderosa pines, along with the continued reintroduction of fire as an ecological process.

## INTRODUCTION

Ecologists have long recognized the important role of standing dead trees, or snags, in the life cycle of a wide variety of organisms (Bull 1999). Additionally, snags have their own “life cycle,” beginning with their creation due to the death of a tree, subsequent decay, and eventually reaching termination (though not of their ecological role) by falling to the ground. Due to the nature of disease, weather, and fire, all of which are factors influencing this cycle, the transition of snags from one stage to the next is often episodic (Morrison and Raphael 1993). In addition, tree species differ in wood structure and decay pattern in ways that can also influence snag dynamics (Parks et al. 1997). Thus, snag availability for wildlife is the result of a complex of biotic and abiotic factors.

There have been numerous investigations into how bird populations interact with snag populations. As study moves beyond a simple numerical relationship between snag and bird populations, researchers are finding complex ecological relationships (Bednarz et al. 2004). The process of excavating cavities in snags by primary cavity-nesting birds forms the basis of a web that connects a wide variety of species (Martin et al. 2004). Furthermore, the choice of cavity may be influenced by competition, especially among secondary cavity nesters, and can also vary as bird populations fluctuate in abundance (Nilsson 1984). Cavity creation and snag suitability can also be influenced by the state of decay (Jackson and Jackson 2004). Additionally, fungi that promote wood decay are spread through the foraging of woodpeckers, which are further influenced by presence of prey such of bark-boring beetles, another creator of snags (Farris et al. 2004).

Stand-replacing wildfires can create large continuous stands of snags. Cavity-nesting birds can take advantage of these stands and are particularly abundant during the first years following fire (Bock and Lynch 1970, Saab et al. 2004). With wildfires increasing in severity and frequency, prescribed fire practices are gaining favor in the West as a preventative measure (Kauffman 2004), but we know less about the role of this type of fire in the snag cycle. Tree mortality following prescribed fire is generally low, is not always immediate, and is influenced by tree species, tree size, season of burn, and fire intensity (Harrington 1996). Snag loss following prescribed fire on the other hand, can be relatively high (Horton and Mannan 1988). Additionally, fall rates of snags created by prescribed fire may be higher than fall rates in the absence of fire or those following wildfire (Harrington 1996).

While a number of aspects of snag ecology have been well studied, little is known about snags within a broader ecological context (Bednarz et al. 2004). I was particularly interested in nest-site selection in cavity nesting birds within a landscape where a formerly suppressed ecological process, fire, is being returned through prescribed burning. To address these issues, I collected two sets of data; one of available snags before and after fire applications, and another of snags used by cavity nesters. The focus of this study is the immediate role of prescribed fire in the snag cycle and the use of snags for breeding by avian species in the Sierra Nevada of California. Additionally, I examined the link between the selected snag and the outcome of the nest as a means for understanding future snag suitability.

## **THE STUDY AREA**

I conducted my study in Sierra National Forest, Fresno County, California. The study area consists of nine 40-ha plots of mature coniferous forest at elevations ranging from 1,000 to 1,390 m. These forests are dominated by ponderosa pine, but other common tree species include incense cedar, white fir, sugar pine (*Pinus lambertiana*), California black oak (*Quercus kelloggii*), and canyon live oak (*Quercus chrysolepis*). The study plots experienced fires in the 1930s or 1940s, with the last wildfire in the area recorded in 1947. My experiment consisted of three treatments: (1) three unburned plots that continued to have fire excluded, (2) three similar plots that were burned in early April 2002, and (3) three plots (the “postburn” plots) that had controlled burn applications in April 1997, February 1998, and May 1998 prior to the initiation of the study, with two of these plots burned a second time in June of 2003.

## **METHODS**

### **SNAG AVAILABILITY**

Each plot contained a permanently marked 1000 m line with posts every 50 m to assist in censusing bird populations. I randomly selected one end and side of the line, and surveyed snags in a belt transect 50 m wide and of variable length. All snags greater than 20 cm diameter along the transect were marked and measured until at least 35 snags were marked. I calculated snag density (number/ha) based on the transect length of each plot. Tree species of the snag was recorded when possible and measurements included height, and dbh or diameter at breast height (at 1.32 m from ground). Classifications were made

for state of branches (size and amount of remaining branches), bark (tight to bole or loose), surface wood hardness (sound to crumbling), and overall decay class (I – V, based on Cline et al. 1980). These classifications were combined into a single summary measure of snag age or decay (higher numbers indicate greater decay). This summary measure (range 4 - 16) is hereafter referred to as “decay”. Snags known to contain bird nests that fell within the transect were included in both the random dataset and the active nest dataset described below. The snag measurements were taken before sites were burned in 2002. Snags were reassessed on all plots by September 2003.

To examine pre-existing differences in available snags before fire, I used a MANOVA with individual ANOVAs for dbh, height, and decay (PROC GLM, SAS Institute 2000). Differences in snag species composition were examined with Chi-square tests (PROC FREQ, SAS Institute 2000). These analyses were done for both individual plot differences and for differences within postburn and unburned plots.

#### **BIRD CHOICE**

Data were also obtained from snags used for breeding by cavity-nesting bird species collected as part of two studies from 1995 to 2003. Cavity-nesting species included primary cavity nesters, secondary cavity nesters, and the brown creeper (*Certhia americana*), which uses the natural “cavity” created when bark peels away from the trunk but remains attached to the bole. I collected the same measurements as those taken on the random snags, but nest snags were located throughout the entire 40-ha plots, not just within the belt transects.

I used discriminant function analysis to determine which snag characteristics best distinguished between used and available snags. Snag species was dummy-coded using incense cedar as the reference group (coded "0"), because this species is generally avoided by cavity-nesting species. Besides incense cedar, snag species included ponderosa pine, white fir, and sugar pine, and a fourth group that combined the remaining snag species used. Groups were first discriminated using a stepwise analysis (PROC STEPDISC), and then loadings of variables on canonical variates and class means were obtained using PROC DISCRIM (both programs in SAS Ver. 8.2 for personal computer, SAS Institute 2000).

Within the used snag dataset, I further examined differences in snag choice by examining the differences in choices made by individual bird species. I again used discriminant function analysis as described above with the same variables describing snags, but now creating a function that discriminated among snags selected by each bird species. Only species for which I had at least 30 nesting snags were used for this analysis.

#### **SNAG FATE AND CREATION**

Snags marked on the random transects were revisited in 2003 following burning on the treatment sites. Snags fallen, burned, or significantly altered were recorded. New snags within the transect were noted and measured. Fallen snags were removed and new snags added to create a second dataset representative of the "after" snag population.

Classifications for snag use, based on the estimated discriminant function of choice, were made using a nonparametric method. The classification is based on the Mahalanobis distance of the pooled covariance matrix (SAS Institute 2000), and the number of nearest neighbors used ( $k$ ) was varied to maximize the correct classification into the “used” snag group. Available snags were then reclassified into use and non-use groups based on this model before and after the burn applications.

#### **NEST SUCCESS**

Data on nest success was collected in the study area as part of two studies from 1995 to 2003. Nests were visited periodically (generally every 3-4 days, up to 9 days between visits), and the nest contents examined, when possible, using extension ladders and a fiber-optic scope (Purcell 1997), or an extendible video camera system. Failed nests included those lost due to abandonment, predation, weather, fire, or unknown causes. Two approaches were used to examine the relation of nest success with the snag characteristics. First, I examined the mean canonical scores of failed vs. successful nests on the choice discriminant function derived above. If birds are choosing snags that promote greater nesting success, I expect the mean of successful nests to be significantly higher than failed nests and to be associated with stronger selection (Misenhelter and Rotenberry 2000). Secondly, to account for age differences in the nests when they were found, I used a logistic-exposure model where the nest fate at each inspection interval is modeled as a binomial distribution within a logit link function using SAS PROC GENMOD (SAS Institute 2000), as suggested by Bart and Robson (1982), and refined by

Shaffer (2004) and Rotella et al. (2004). Effective sample sizes used are the number of days nests were known to survive + number of intervals where nests failed (Rotella et al. 2004). Time-dependent effects have been identified as important in nesting success (Klett and Johnson 1982). Hence, I first evaluated these effects for inclusion in later models. The linear, quadratic, and cubic effects of nest age as well as the linear and quadratic effects of day of year were considered as polynomial models (i.e. cubic effect contains linear and quadratic effect)(Grant et al. 2005). The best of these models was used in all subsequent models. I included only those snag variables identified as selected by snag nesters (diameter, ponderosa pine, white fir, and decay). I evaluated models consisting of all combinations of snag variables and the interaction of diameter with species (diameter effects differ between snag species), under the constraint that interactions could only be included in models in which their main effects occurred. To evaluate the effect of burning, I added burn status of the site (unburned, 0-1 year postburn, 3-6 year postburn) to the best of the snag variable models and alone. Because burn status changed over time and was confounded with burning, I considered year as a covariate for models that included burn status and not a time dependent effect. A model for constant survivorship (intercept only) was also included in the model set. I compared 22 models, in addition to the 11 time dependent models, using AIC (Burnham and Anderson 1998), selecting the best model from which to use the generated maximum likelihood estimates in calculating daily survival rate (DSR). Model fit was examined using the Hosmer-Lemeshow test (Hosmer and Lemeshow 1989).

## RESULTS

### SNAG AVAILABILITY

I collected information on 330 random snags. Six random snags were also known to contain active nests, and are repeated in the used dataset. Snag species included ponderosa pine (35% of total), incense cedar (32%), white fir (13%), sugar pine (10%), black oak (5%), and white alder (*Alnus rhombifolia*, 0.6%). Sixteen snags were too decayed to determine tree species. The transect area surveyed that was sufficient to find 35 to 44 random snags ranged from 1.2 to 3.7 ha (Table 2.1).

Snag characteristics differed among plots at the start of the study (Table 2.2; Wilks lambda = 0.75, F= 3.84, p < 0.001). The significant differences were found for decay (F = 6.24, p < 0.001), height (F = 3.95, p < 0.001), and dbh (F = 3.17, p = 0.002). For snag species there were overall differences among plots for ponderosa pine vs. other species ( $\chi^2_8 = 51.12$ , p < 0.001). I would expect some of these differences to be due to three of the plots being postburn. The particular snag attributes that differed were not the same for postburn and unburned plots. For the postburn plots, there were significant differences overall (Wilks lambda = 0.79, F = 3.03, p < 0.001), for decay (F = 5.16, p < 0.001), and for diameter (F = 3.27, p = 0.007), but not for height (F = 2.21, p = 0.06). For unburned plots (n = 6), there were overall differences (Wilks lambda = 0.86, F = 2.79, p = 0.01). The differences were in height (F = 7.31, p = 0.001), but not in decay (F = 0.26, p = 0.77) or diameter (F = 0.30, p = 0.74). The proportion of snags that were ponderosa pine was significantly lower on postburn plots (29.2%) compared to unburned

plots (40.9%) ( $\chi^2_1 = 4.25$ ,  $p = 0.04$ ), but despite removing this as a known source of variation, plot differences remained ( $\chi^2_7 = 14.06$ ,  $p < 0.001$ ).

### **BIRD CHOICE**

The characteristics of snags used for nesting by snag-nesting birds and unused snags differed, as did snags on burned vs. unburned plots (Table 2.2). All available information (1995 – 2003) on snags used by common snag-nesting birds was used to evaluate differences between used and available snags. Bird species recorded nesting in snags ( $n = 241$ ), in order of number of nests (from most to least), were red-breasted nuthatch (*Sitta canadensis*), brown creeper, white-headed woodpecker (*Picoides albolarvatus*), northern flicker (*Colaptes auratus*), acorn woodpecker (*Melanerpes formicivorus*), hairy woodpecker (*Picoides villosus*), downy woodpecker (*Picoides pubescens*), pileated woodpecker (*Dryocopus pileatus*), red-breasted sapsucker (*Sphyrapicus ruber*), mountain chickadee (*Parus gambeli*), northern pygmy owl (*Glaucidium gnome*), northern saw-whet owl (*Aegolius acadicus*), and great gray owl (*Strix nebulosa*). Snag species used, in order of frequency, were ponderosa pine, white fir, incense cedar, sugar pine, white alder, California black oak, and canyon live oak, which was used once.

Stepwise discriminant function analysis identified (in order of selection, with loadings [correlation between variable and canonical axis] in parenthesis) substrate diameter (0.74), ponderosa pine (0.74), white fir (-0.08), and decay (0.16) as important

**Table 2.1.** Numbers of available snags (>20cm diameter) surveyed on transects and changes following re-measurement after ~2 years on each of nine experimental plots in the Sierra Nevada, California, 2001-2003. Designation as “used” snags (used for nesting by cavity-nesting birds) is based on classification from the discriminant function model of available vs. used snags.

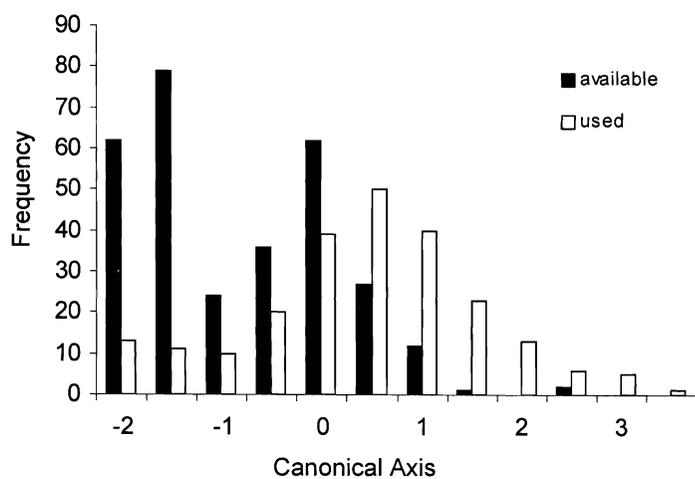
Treatment	Plot	Area surveyed (ha)	Random	Fallen	New	Change in available snags (# · ha <sup>-1</sup> )	Change in “used” snags (# · ha <sup>-1</sup> )
Unburned	U1	1.7	35	7	3	-2.4	+1.2
	U2	1.2	35	1	1	0	+0.8
	U3	3.7	37	1	2	+0.3	0
Burned 2002	B1	1.4	36	16	2	-10.0	-4.3
	B2	1.7	37	6	30	+14.1	+1.8
	B3	1.4	35	20	2	-12.9	-2.8
Burned 1997-98, again in 2003	P1	1.9	36	11	9	-1.6	-1.6
	P2	2.3	35	4	4	0	-0.9
	P3*	1.5	44	7	4	-2.0	-1.3

\*this postburn site did not have fire reapplied in 2003.

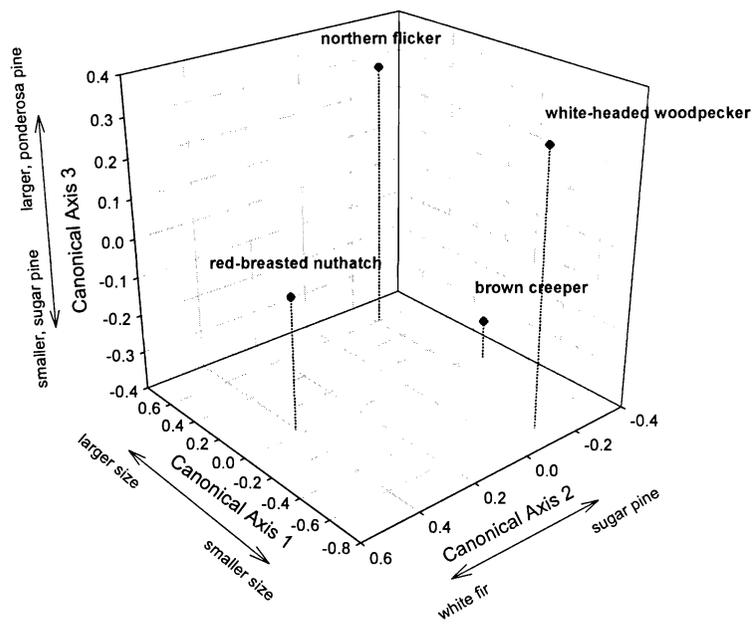
**Table 2.2.** Means (standard deviations) for snags used by cavity-nesting birds for nesting and unused snags on unburned and burned plots. Only snag species comprising at least 10% of all snags are shown here.

Attribute	Used		Unused	
	Unburned (n = 146)	Burned (n = 85)	Unburned (n = 184)	Burned (n = 103)
Height (m)	18.2 (12.0)	16.9 (12.1)	10.4 (8.0)	12.8 (8.7)
Diameter (cm)	55.6 (26.3)	46.7 (20.6)	35.7 (15.1)	32.7 (12.8)
Decay	8.5 (2.5)	8.3 (2.3)	8.5 (3.2)	6.8 (2.7)
Species (%)				
Ponderosa pine <i>(Pinus ponderosa)</i>	87.2	67.1	43.5	29.1
White fir <i>(Abies concolor)</i>	4.7	16.5	9.2	25.2
Incense cedar <i>(Calocedrus decurrens)</i>	5.4	8.2	38.6	30.1
Sugar pine <i>(Pinus lambertiana)</i>	2.7	8.2	8.7	15.5

**Figure 2.1.** Discriminant analysis of available snags from the transects vs. snags used by breeding birds. Loadings on the axis are as follows: diameter 0.74, ponderosa pine 0.74, white fir -0.08, and decay 0.16.



**Figure 2.2.** Class means for snags used by four bird species for discriminant function based on diameter, height, ponderosa pine, and white fir. Standard errors (axis1, axis 2, axis 3) are for brown creeper (0.14, 0.15, 0.16), for northern flicker (0.18, 0.13, 0.16), for red-breasted nuthatch (0.15, 0.13, 0.11), and for white-headed woodpecker (0.14, 0.10, 0.16).



for determining snag use. The model was successful at distinguishing between used and unused snags (Wilks lambda = 0.70  $F = 55.31$ ,  $p < 0.001$ ; Figure 2.1). Dummy variables for white fir and ponderosa pine were important, but the other two dummy variables, sugar pine and other species, were not significant in determining snag use. This resulted in these species being included with the reference species, incense cedar, in analyses with the reduced variable set. Increased diameter and ponderosa pine were associated with greater probability of use, as were snags with less decay. Compared with ponderosa pine, all other species were avoided, with white fir being particularly discriminated against.

The discriminant function for distinguishing snags used by four bird species successfully distinguished among snags used for nesting by northern flickers, red-breasted nuthatches, white-headed woodpeckers, and brown creepers (Table 2.3, Figure 2.2; Wilks lambda = 0.76,  $F = 4.2$ ,  $p < 0.001$ ). The selected variables, in order of selection, were snag height, white fir, ponderosa pine, and snag diameter (Table 2.4). These same variables, except snag height, were also important in the previously described overall choice model, and thus variation among species with respect to height may be responsible for it not being in the bird choice model. The first canonical axis was associated with greater height and diameter, and separated northern flicker and white-headed woodpecker (Table 2.4). The second canonical axis was mainly associated with red-breasted nuthatch's use of smaller snags and white fir. Lastly, the third canonical axis was associated with ponderosa pine snags and separated northern flicker and white-headed woodpecker (the latter with a stronger association with ponderosa pine), from the other two species. In sum, northern flicker used tall, large-diameter ponderosa pine

**Table 2.3.** Mean, standard deviations, and range of characteristics of snags used by snag nesting bird species in the Sierra Nevada, California, 1995-2003. Diameter is measured at 1.32 m and the decay index increases as the snag is more decayed.

Species	Number of nests	Diameter (cm)		Height (m)		Decay		%	
		Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Ponderosa Pine	White Fir
Red- Breasted	66	48.6 ± 2.9	14 - 120	17.4 ±	1.4 - 66.1	8.4 ± 0.3	5 - 14	73	21
Nuthatch ( <i>Sitta Canadensis</i> )				1.5					
Brown creeper ( <i>Certhia americana</i> )	53	51.5 ± 3.6	15 - 135	18.9 ±	1.7 - 48.3	8.6 ± 0.4	4 - 14	71	5
				1.8					
Northern flicker ( <i>Colaptes auratus</i> )	31	67.4 ±	29 - 120	23.0 ±	4.2 - 49.8	8.2 ±	4 - 13	88	6
		4.1		2.1		0.37			
White-head Woodpecker ( <i>Picoides albolarvatus</i> )	31	42.2 ± 3.7	19 - 92	9.7 ±	1.4 - 35.1	8.6 ± 0.6	4 - 16	87	0
				1.6					

**Table 2.4.** Loadings (correlation of variables with canonical variates) for total canonical structure describing differences among bird species with respect to snag characteristics selected in a stepwise discriminant function analysis, for the Sierra Nevada, California, 1995-2003. Means for the species on the axes follow.

Variables	Canonical Axis 1	Canonical Axis 2	Canonical Axis 3
<b>Snags</b>			
Diameter	0.82	-0.31	0.28
Height	0.91	-0.14	-0.38
Ponderosa pine	-0.01	-0.16	0.72
White fir	0.23	0.83	-0.32
<b>Birds</b>			
Red-breasted nuthatch	0.04	0.40	-0.05
Brown creeper	-0.03	-0.30	-0.29
Northern flicker	0.62	-0.22	0.31
White-head Woodpecker	-0.66	-0.12	0.30

snags, white-headed woodpecker used small short snags, and red-breasted nuthatch used relatively more white fir. Brown creeper, which utilized tall snags of a variety of species, was associated with negative values on axes two and three, the axes associated with white fir and ponderosa pine, respectively (Table 2.4).

#### **SNAG FATE AND CREATION**

Following fire, existing snags fell ( $n = 73$  out of 330 prefire snags) and new ones were created ( $n = 57$ ). Greatest turnover occurred on plots burned for the first time (Figure 2.3). For snags predicted to be used the changes were small, but there was a net loss of "used" snags on all burned plots except one (Table 2.1).

Even though few snags fell, those that did tended to be larger than average diameter on burned plots (Table 2.5). The species of snags vulnerable to falling differed between burned and unburned plots. Ponderosa pines were more vulnerable, but on unburned plots the remaining snags that fell were white fir and sugar pine, although sample size was small. Incense cedar snags were vulnerable to burning, but none fell on unburned plots.

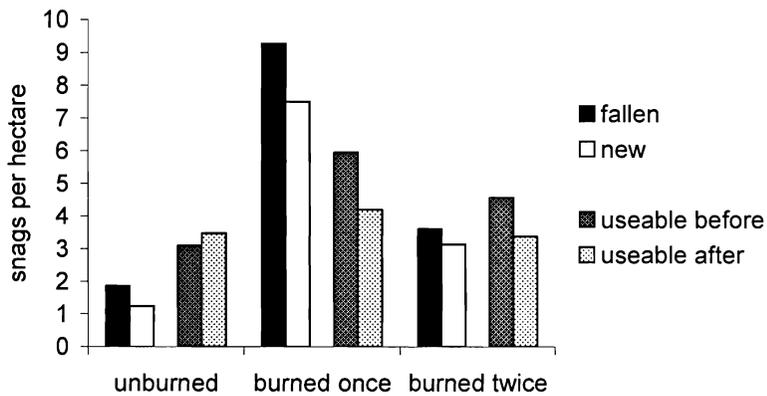
New snags were dominated by ponderosa pine, with a large number of these from a single burned site (B2) where the transect included a stand infested by bark beetles following burning (~20 of 25 new ponderosa pines). On unburned plots there were few new snags and half of these were sugar pine, although sample size was small. The newly created snags were of slightly smaller average diameter (7 of 9 sites) than random snags,

**Table 2.5.** Average (SD) attributes and percent of tree species comprising snags leaving or entering the sample on unburned plots and following prescribed fire. For decay (range 4-16) higher values indicate greater decay and new snags by definition are undecayed.

Snag Status	Attribute	Unburned Plots*	Burned Plots
Fallen or burned		N = 17	N = 56
	height (m)	14.0 (8.1)	12.5 (9.9)
	diameter (cm)	30.2 (8.0)	42.7 (20.2)
	decay	8.0 (3.0)	8.7 (3.4)
	ponderosa pine	64.7	66.1
	white fir	17.7	3.6
	incense cedar	0	23.2
	sugar pine	17.7	3.6
	other	0	3.6
New		N = 10	N = 47
	height (m)	17.8 (6.9)	17.1 (8.8)
	diameter (cm)	33.7 (11.7)	30.4 (10.0)
	ponderosa pine	30	70.2
	white fir	20	2.1
	incense cedar	0	19.2
	sugar pine	50	4.3
	other	0	4.3

\*Unburned includes one previously burned site not burned during the study

**Figure 2.3.** Changes in available snags assessed within transects in 2001 and in 2003 after treatments in the Sierra Nevada, California. “Unburned” are untreated between assessments and includes the three plots unburned throughout the study and an additional plot burned in 1997 that was not burned again. “Burned once” includes three plots burned in 2002. “Burned twice” includes two plots burned in 1998 that were reburned in 2003 before snags were reassessed. Useable snags are based on classification by the discriminant function based on snag selection by cavity nesting species (Fig. 2.1).



with size being similar between new snags on unburned plots and on burned plots (Table 2.5).

The discriminant function for bird use of snags was used to classify available snags. A  $k$  (number of nearest neighbors) of two was chosen for classification as this maximized correct classification of the used group (93% correct for used, 76% correct for unused). That the proportion of correct classifications for unused is less than that for used is expected, as that category contains snags that are suitable but that have not yet been used. It further implies that suitable snags as a whole may not be a limiting resource (although cavities may still be). There were differences between plots in numbers of snags predicted to be “useable” and fate of these snags varied (Table 2.1, Figure 2.3). Before burning, 19% and 28% of snags were predicted to be suitable for use for unburned plots and plots burned in 2002, respectively. In the absence of fire, 11% (2) of useable snags fell. For plots burned once, 60% (17) of the useable snags fell. For the postburn sites, 24% (27) were predicted to be useable and 26% (7) of these fell after burning on two sites (the third site was not burned again and one useable snag fell).

#### **NEST SUCCESS**

Nest outcome was determined for 204 nests (71 red-breasted nuthatches, 53 brown creepers, 32 white-headed woodpeckers, 21 northern flickers, 11 acorn woodpeckers, 7 hairy woodpeckers, 2 red-breasted sapsuckers, 2 mountain chickadees, 1 downy woodpecker, 1 pileated woodpecker, 1 great gray owl, 1 northern pygmy owl, and 1 northern saw-whet owl). Apparent nest success was 41% for all nests combined. For

unburned plots (n = 133), 19% of nests were lost to depredation and 16% were lost from unknown causes. Depredation rates were 22% on postburn plots (n = 58) with 13% unknown. There was a 31% depredation rate on plots within 1 year following fire with 15% unknown, though I only found 13 nests after burning. Using the canonical scores for nests on the snag choice function, I did not find differences between the means of successful and failed nests (0.79 and 0.59 respectively,  $t = -1.22$  for unequal variances,  $p = 0.23$ ). The mean of selected nesting snags was 0.74 and was  $-0.58$  for unused snags.

A smaller subset of 39 red-breasted nuthatches, 39 brown creepers, 19 white-headed woodpeckers, 6 hairy woodpeckers, 5 northern flicker, 2 red-breasted sapsucker, 1 downy woodpecker, 1 pileated woodpecker, 1 great gray owl, and 1 mountain chickadee nests were used within the logistic-exposure model. Only nests from 2001 to 2003 were used (effective sample size = 2,665). A total of 30 models were evaluated. Age of the nest improved the nest success models with best model including the quadratic polynomial of nest age and day of year (Table 2.6). This model fit the data well ( $X^2_8 = 8.99$ ,  $p = 0.34$ ). I then included these effects in all other models even though this reduced the dataset by 14 nests (effective sample size = 2,512), because age could not be estimated. The best model subsequently was for year with burn status (Table 2.7). For the subset of models that only included selected snag variables, the best model was for white fir though many of the other single snag variables were competing. Though there were many competing models, because year and burn status occurred in 6 of 10 top models, and because the role of fire was of central interest, I selected the year and burn status model to examine further (Figure 2.4). The selected model was a good fit for the

**Table 2.6.** Model selection results for logistic-exposure model for effect of time dependent variables on survival of nests in the Sierra Nevada, California, 2001-2003. Only those models with  $\Delta\text{AIC} < 2$  are shown, plus the global model (8 models total). The quadratic and cubic functions of nest age were considered with the lower order effects. The quadratic function of day of year was considered with lower order effects.  $K$  is number of parameters including error term and  $w_i$  is the normalized model weight.

Model	Log likelihood	$K$	$\Delta\text{AIC}$	$w_i$
AGE + AGE <sup>2</sup> + DAY	-135.9	4	0	0.27
AGE + AGE <sup>2</sup>	-137.1	3	0.38	0.22
AGE + AGE <sup>2</sup> + AGE <sup>3</sup> + DAY + DAY <sup>2</sup>	-135.9	5	1.97	0.10
AGE + AGE <sup>2</sup> + AGE <sup>3</sup> + DAY	-135.9	5	1.97	0.10
(Global) AGE + AGE <sup>2</sup> + AGE <sup>3</sup> + DAY + DAY <sup>2</sup>	-135.9	6	3.94	0.04

**Table 2.7.** Model selection results for logistic-exposure model for survival of nests. All models include the effects of age (linear and quadratic functions) and day of year (See Table 2.6). Only those models with  $\Delta\text{AIC} < 2$  are shown, plus the global model and a reduced global model with only snag variables (22 models total). Parameters were included individually and in combinations including interactions, but interactions only in conjunction with their main effects. “DAY” is day of year and “BURN” is burn status of the plots.  $K$  is number of parameters including error term and  $w_i$  is the normalized model weight. The constant model had a  $\Delta\text{AIC} = 2.83$ .

Model	Log likelihood	$K$	$\Delta\text{AIC}$	$w_i$
AGE + AGE <sup>2</sup> + DAY + YEAR + BURN	-131.8	8	0	0.12
AGE + AGE <sup>2</sup> + DAY + YEAR + BURN + WHITE FIR	-131.0	9	0.37	0.10
AGE + AGE <sup>2</sup> + DAY + YEAR + BURN + DIAMETER	-131.1	9	0.60	0.09
AGE + AGE <sup>2</sup> + DAY + YEAR + BURN + DECAY	-131.1	9	0.64	0.09
AGE + AGE <sup>2</sup> + DAY + WHITE FIR	-135.3	5	1.00	0.08
AGE + AGE <sup>2</sup> + DAY + YEAR + BURN + DIAMETER + DECAY	-130.5	10	1.32	0.06
AGE + AGE <sup>2</sup> + DAY + YEAR + BURN + PONDEROSA PINE	-131.5	9	1.33	0.06
AGE + AGE <sup>2</sup> + DAY + DECAY	-135.5	5	1.34	0.06

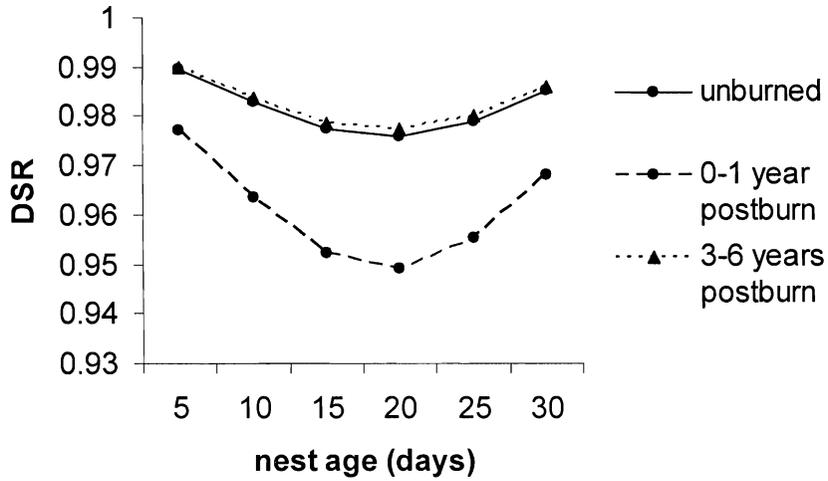
Table 2.7. continued

Model	Log likelihood	<i>K</i>	$\Delta$ AIC	$w_i$
AGE + AGE <sup>2</sup> + DAY + PONDEROSA PINE	-135.6	5	1.67	0.05
AGE + AGE <sup>2</sup> + DAY + DIAMETER	-135.8	5	1.98	0.04
(Global - all variables) AGE + AGE <sup>2</sup> + DAY + YEAR + BURN + DIAMETER + PONDEROSA PINE + WHITE FIR + PONDEROSA PINE*DIAMETER + WHITE FIR*DIAMETER + DECAY	-128.0	12	4.32	0.01
(Global - snag variables only) AGE + AGE <sup>2</sup> + DAY + DIAMETER + PONDEROSA PINE + WHITE FIR + PONDEROSA PINE*DIAMETER + WHITE FIR*DIAMETER + DECAY	-133.4	7	7.29	0.003

**Table 2.8.** Parameter estimates for selected logistic-exposure model for nest age, day of year, year, and treatment effects on nest success intervals.

Variable	Coefficient	SE
Intercept	6.76	1.80
Nest age	-0.16	0.07
Nest age <sup>2</sup>	0.004	0.002
Day of year	-0.01	0.01
0-1 year after burning vs. unburned	-0.77	0.57
3-6 years after burning vs. unburned	0.07	0.41
2001 vs. 2003	0.01	0.45
2002 vs. 2003	0.93	0.48

**Figure 2.4.** Daily survival rate (DSR) for cavity-nesting birds (all snag species combined) as estimated for May 23, 2003 in the Sierra Nevada, California, based on parameter estimates from the selected AIC model that included linear and quadratic effects of age, day of year, year, and burn status.



data ( $\chi^2_8 = 11.9$ ,  $p = 0.16$ ). Model results indicated that daily survival rate was lower 0-1 years after burning while at the same time survival rate was lowest in the middle of the nesting cycle (Table 2.8, Figure 2.4). In addition, nest survival was lower in 2001 compared to 2003 and higher in 2002 compared to 2003 (Table 2.8).

## DISCUSSION

Whereas snag selection by cavity-nesting birds was consistent among plots, there was variability among plots, and the differences in availability of snags was somewhat mirrored by use. For example, even though ponderosa pine was consistently selected, the proportion used was smaller when there was less ponderosa pine available, indicating that low availability limited selection (Table 2.1). These differences in availability among plots before fire were likely due to a variety of factors including topography, microclimate, or past logging practices.

I found that specific snag types were selected for nesting. Relative to available snags, cavity-nesting species selected large ponderosa pine snags, although even very small snags (6 of 226 were < 20 cm, minimum = 14 cm) were used on occasion. Selection of larger snags for nesting is consistent with other studies (Horton and Mannan 1988, Ganey and Votja 2004, Blewett and Marzluff 2005). Additionally, preference for particular snag species has been found in other studies, including ponderosa pine and Douglas fir (*Pseudotsuga menziesii*) (Bevis and Martin 1999) (Ganey and Vojta 2004), and aspen (*Populus tremuloides*) (Conway and Martin 1993, Martin et al. 2004), the latter a species that does not occur in my study area. Greater use of ponderosa pines for cavity

construction is thought to be due to the relatively greater proportion of sapwood, which decays more readily, as compared to other conifer species (Parks et al. 1997).

Interestingly, the avoided species, white fir and incense cedar, have been favored by the loss of fire in the Sierra Nevada (Vankat and Major 1978). Unfortunately, ponderosa pine has been found to be declining in this forest type, probably because fire suppression inhibits seed germination (Roy and Vankat 1999). Used snags also differed among bird species, particularly with regard to size and snag species. Red-breasted nuthatch utilized relatively more white fir. White fir heartwood and sapwood is easily decayed (Parks et al. 1997), and thus the wood can be more easily excavated by this weak excavator.

Northern flickers and white-headed woodpeckers both selected the largest snags, though white-headed woodpeckers were distinguished from the other species by their use of shorter snags and less preference for ponderosa pine. Brown creepers also used a variety of species. Because of their nesting habits, thickness and condition of the bark would be more important to brown creepers than the interior condition of the snag.

Fire's role in snag population dynamics is a complex one. Other studies have found increased use of snags in the first years following wildfire (Linder and Anderson 1998, Saab et al. 2004). I found that in the first years following prescribed burning, snags were created and lost, but the average densities changed little. Other studies have reported an overall loss of snags during prescribed burning (Horton and Mannan 1988, Randall-Parker and Miller 2002). Initial burning of plots after a long period of fire exclusion seemed to result in the greatest turnover in snags, with lower turnover after the second burn. This trend likely results because those snags that are most vulnerable are

removed during the first burn, leaving more resistant ones behind. Alternatively, there may be differences in fire intensity between fire applications. Most snags lost were ponderosa pine and/or of larger than average diameter, a finding consistent with Horton and Mannan (1988). Because these are preferred snags, it is not surprising that I found proportionally more useable snags lost after fire, though generally the numbers/ha were small (average  $-1.5 \text{ ha}^{-1}$ ). One plot experienced a large increase in number of snags (all ponderosa pine) due to attack by bark beetles. Whereas it is likely that the infestation was related to burning, a single patch of snags, regardless of the number of snags within the patch, will benefit birds only within a limited area. On the other two sites burned for the first time, there was an overall loss of total snags and useable snags. Thus while overall numbers of useable snags changed little, the spatial distribution of these snags was altered and, presumably, the availability of snags for individual birds. In addition, snags created through insect outbreaks are sometimes removed for forest management purposes and so, despite the potential benefits, are additionally vulnerable to loss from the system.

While greater numbers of snags may result in larger populations of cavity nesting birds, other aspects may be more important in determining bird populations. Within this study area I found greater populations of cavity-nesting species on both the recently burned plots and on the older burn plots, indicating that burning has positive and lasting effects on these species beyond the loss or creation of useable snags for nesting (K. Bagne and K. Purcell, unpubl. data).

Despite the strong and consistent preference for particular types of snags, these preferences were not strongly related to nesting success. The effects of time were important particularly the age of the nest. The lowest daily survival rate corresponds with the mean hatching age for these species at around 20 days (Fig. 2.4). There was some support for a negative effect of nesting in white fir, which was generally avoided for nesting, but there was more support for time and burn status, which were included in almost all of the top models. It is likely that preference is related to physical suitability of the snag for excavation and cavity creation. Once created, nests may then be equally likely to be depredated. Hooge et al. (1999) suggested that cavity construction of acorn woodpeckers were constrained by characteristics of trees available and the species' excavation abilities. Interior decay and ease of excavation are important and are related to tree species, size, and tree hardness (Parks et al. 1997, Schepps et al. 1999). It may be the case, however, that snag attributes, while not affecting success of the entire nest, are related to clutch size or productivity. I did not test these effects, but rather the loss of entire nests, which is mostly the result of predation.

While snag attributes did not appear to be important to nest success, I did find lower nest success in the period within one year following fire compared to unburned areas or areas burned 3 to 6 years previously. Based on daily survival rates, a nest on an unburned plot in 2003 would have a 64% chance of surviving 30 days whereas a nest on a recently burned plot would have a 38% chance of surviving 30 days. After wildfire, Saab et al. (2004) found that snag characteristics were relatively unimportant in predicting cavity occupancy. Occupancy was best predicted by time since fire, and was

greatest in the first four years after fire and declined over time. They suggest that this effect was caused by reduction in nest predators immediately following wildfire and the subsequent recovery of the predator populations (Saab et al. 2004). My finding of reduced nest success immediately following prescribed fire on a smaller scale is more suggestive of an increased risk of predation. As there were also increased numbers of cavity-nesting species (though not necessarily of nests) on burned plots, it seems likely they were attracted by foraging opportunities. If this increase translates to more nesting, site fidelity (Beheler et al. 2003) or inability to assess local predator populations (Filliater 1994) may explain the apparent maladaptive response to increased predation risk.

Despite the patchy distribution and the dynamic nature of snag populations, researchers and forest managers have created guidelines for recommended density of snags for wildlife (Balda 1975, Raphael and White 1984, Brawn et al. 1987). Balda (1975) recommended 6.7 snags/ha for maximum density of cavity nesters. I found an average of 19.6 snags/ha (>20cm) across all sites, with 25% greater than 40 cm diameter, but only an average of 2.5 snags/ha had characteristics chosen by snag nesting species. I agree with others who have criticized the snags/acre approach (Morrison and Raphael 1993, Zack and Laudenslayer 2002), and instead emphasize the process of snag selection as well as dynamics of snag populations. Furthermore, characteristics such as decay or height, will change over time, hence altering suitability. Forest management strategies that affect tree species composition, tree mortality, and tree size will affect snag-nesting species. My results suggest that forest managers can improve availability of useable snags by retaining large trees (both living and dead), and preferred species (ponderosa

pine in my area). As these trees are among the most commercially valuable tree species, they can be vulnerable to removal. On the other hand, fire creates open forest floor that promotes recruitment of ponderosa pine (Moir et al. 1997). Prescribed fire efforts, while playing a role in snag population dynamics, do not seem to threaten snag populations in the short term and in the long term may increase recruitment of preferred species such as ponderosa pines.

## LITERATURE CITED

- Balda, R. P. 1975. The relationship of secondary cavity nesters to snag densities in western coniferous forests, U.S. Forest Service, Southwest Region, Wildlife Habitat Technical Bulletin.
- Bart, J. and D. S. Robson. 1982. Estimating survivorship when the subjects are visited periodically. *Ecology* 63:1078-1090.
- Bednarz, J. C., D. Ripper, and P. M. Radley. 2004. Emerging concepts and research directions in the study of cavity-nesting birds: keystone ecological processes. *Condor* 106:1-4.
- Beheler, A. S., O. E. Rhodes, Jr. and H. P. Weeks, Jr. 2003. Breeding site and mate fidelity in eastern phoebes (*Sayornis phoebe*) in Indiana. *Auk* 120: 990-999.
- Bevis, K. R., and S. K. Martin. 2002. Habitat preferences of primary cavity excavators in Washington's East Cascades. Pages 207-221 in W. F. Laudenslayer, Jr., P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle, technical coordinators. Proceedings on the symposium on the ecology and management of coarse woody debris in Western forests. U.S. Forest Service General Technical Report PSW-GTR-181.
- Blewett, C. M. and J. M. Marzluff. 2005. Effects of urban sprawl on snags and the abundance and productivity of cavity-nesting birds. *Condor* 107:678-693.
- 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.
- Brawn, J. D., W. J. Boeklen, and R. P. Balda. 1987. Investigations of density interactions among breeding birds in ponderosa pine forest: correlative and experimental evidence. *Oecologia* 72:348-357.
- Bull, E. L. 2002. The value of coarse woody debris to vertebrates in the Pacific Northwest. Pages 171-178 in W. F. Laudenslayer, Jr., P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle, technical coordinators. Proceedings on the symposium on the ecology and management of coarse woody debris in Western forests. U.S. Forest Service General Technical Report PSW-GTR-181.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer, New York.

- Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in douglas-fir forest, western Oregon. *Journal of Wildlife Management* 44:773-786.
- Conway, C. J., and T. E. Martin. 1993. Habitat suitability for Williamson's Sapsuckers in mixed conifer forests. *Journal of Wildlife Management* 57:322-328.
- Farris, K. L., E. O. Garton, P. J. Heglund, S. Zack, and P. J. Shea. 2002. Woodpecker foraging and the successional decay of ponderosa pine. Pages 237-246 *in* W. F. Laudenslayer, Jr., P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle, technical coordinators. Proceedings on the symposium on the ecology and management of coarse woody debris in Western forests. U.S. Forest Service General Technical Report PSW-GTR-181.
- Farris, K. L., M. J. Huss, and S. Zack. 2004. The role of foraging woodpeckers in the decomposition of ponderosa pine snags. *Condor* 106:50-59.
- Filliater, T. S., R. Breitwisch, and P.M. Nealen. 1994. Predation on northern cardinal nests: does nest choice matter. *Condor* 96:761-768.
- Ganey, J. L., and S. C. Vojta. 2004. Characteristics of snags containing excavated cavities in Northern Arizona mixed-conifer and ponderosa pine forests. *Forest Ecology and Management* 199:323-332.
- Grant, T. A., T. L. Shaffer, E. M. Madden, and P. J. Pietz. 2005. Time-specific variation in passerine nest survival; new insights into old questions. *Auk* 122:661-672.
- Harrington, M. G. 1996. Fall rates of prescribed fire-killed ponderosa pine. U.S. Forest Service Research Paper, INT-RP-489.
- Hooge, P. N., M. T. Stanback, and W. D. Koenig. 1999. Nest-site selection in the acorn woodpecker. *Auk* 116:45-54.
- Horton, S. P., and R. W. Mannan. 1988. Effects of prescribed fire on snags and cavity-nesting birds in Southeastern Arizona pine forest. *Wildlife Society Bulletin* 16:37-44.
- Hosmer, D. W., Jr. and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons, New York.
- Jackson, J. A., and B. J. S. Jackson. 2004. Ecological relationships between fungi and woodpecker cavity sites. *Condor* 106:37-49.

- Kauffman, J. B. 2004. Death rides the forest: perceptions of fire, land use, and ecological restoration of Western forests. *Conservation Biology* 18:878-882.
- Linder, K. A., and S. H. Anderson. 1998. Nesting habitat of Lewis' woodpeckers in Southeastern Wyoming. *Journal of Field Ornithology* 69:109-116.
- Martin, K., K. E. H. Aitken, and K. L. Wiebe. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. *Condor* 106:5-19.
- Misenhelter, M. D., and J. T. Rotenberry. 2000. Choices and consequences of habitat occupancy and nest site selection in sage sparrows. *Ecology* 81:2892-2901.
- Moir, W. H. , B. Geils, M. A. Benoit, and D. Scurlock. 1997. Ecology of Southwestern ponderosa pine forests. Pages 3-27 *in* W. M Block and D. M. Finch, technical editors. *Songbird ecology in Southwestern ponderosa pine forest; a literature review*. U.S. Forest Service General Technical Report RM-GTR-292.
- Morrison, M. L., and M. G. Raphael. 1993. Modeling the dynamics of snags. *Ecological Applications* 3:322-330.
- Nilsson, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. *Ornis Scandinavica* 15:167-175.
- Parks, C. G., D. A. Conklin, L. Bednar, and H. Maffei. 1997. Field guide for the identification of snags and logs in the interior Columbia River Basin. U.S. Forest Service Research Paper, PNW-RP-515.
- Purcell, K. L. 1997. Use of a fiberscope for examining cavity nests. *Journal of Field Ornithology* 68:283-286.
- Randall-Parker, T., and R. Miller. 2002. Effects of prescribed fire in ponderosa pine on key wildlife habitat components: preliminary results and a method for monitoring. Pages 823-834 *in* W. F. Laudenslayer, Jr., P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle, technical coordinators. *Proceedings on the symposium on the ecology and management of coarse woody debris in Western forests*. U.S. Forest Service General Technical Report PSW-GTR-181.
- Raphael, M. G., and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. *Wildlife Monographs* 86:1-66.

- Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* 27:1-19.
- Roy, D. G, and J. L. Vankat. 1999. Reversal of human-induced vegetation changes in Sequoia National Park, California. *Canadian Journal of Forest Research* 29:399-412.
- Saab, V. A., J. Dudley, and W. L. Thompson. 2004. Factors influencing occupancy of nest cavities in recently burned forests. *Condor* 106: 20-36.
- SAS Institute, Inc. 2000. SAS/STAT User's Guide. SAS Institute, Cary, NC.
- Schepps, J., S. Lohr, and T. E. Martin. 1999. Does tree hardness influence nest-tree selection by primary cavity nesters? *Auk* 116:658-665.
- Shaffer, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121: 526-540.
- Vankat, J. L., and J. Major. 1978. Vegetation changes in Sequoia National Park, California. *Journal of Biogeography* 5:377-402.
- Zack, S., T. L. George, and W. F. Laudenslayer, Jr. 2002. Are there snags in the system? Comparing cavity use among nesting birds in "snag-rich" and "snag-poor" Eastside pine forests. Pages 207-221 *in* W. F. Laudenslayer, Jr., P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle, technical coordinators. Proceedings on the symposium on the ecology and management of coarse woody debris in Western forests. U.S. Forest Service General Technical Report PSW-GTR-181.

### CHAPTER 3:

#### THE EFFECT OF PRESCRIBED FIRE ON THE RELATIONSHIP BETWEEN NEST SITES AND NESTING SUCCESS

**Abstract.** I located and monitored nests of five species of open cup-nesting passerines in the Sierra Nevada of California on 9 plots with 3 prescribed fire treatment histories: unburned, 0-1 year postburn, and 3-6 years postburn. Vegetation data were collected from 0.04-ha circles centered on each nest and on random points taken before and after burning. I used Principal Component Analysis of data collected from random points before burning to summarize dimensions of variation in the vegetation, then scored random points after fire and nest sites onto these new dimensions. I then used the resulting component scores to look for evidence of nest-site preferences, and in a logistic exposure model to evaluate nest success with relation to nest-site habitat and burn treatment. All species except Spotted Towhee (*Pipilo maculatus*) showed some relationship between nest-site habitat and nesting success. This relationship was altered by fire for Dark-eyed Junco (*Junco hymelis*) and Black-headed Grosbeak (*Pheucticus melanocephalus*). Dark-eyed Junco nests on unburned plots were most successful when associated with open oak forests, but on plots burned within 1 year success was best in closed conifer forests. Success of Black-headed Grosbeak nests was related to nest height with lower nests more successful on unburned plots, but taller nests were more successful on plots 0-1 year postburn. Hutton's Vireo (*Vireo huttoni*) success was associated with increasing concealment and success was also lower following burning,

and this appeared to be due to nests being less concealed on burned sites. Both Hutton's and Cassin's vireos (*Vireo cassinii*) had higher rates of parasitism on burned plots, but Hutton's Vireo was particularly susceptible with rates of 33.3% with no fire, 58.3% 0-1 years after fire, and 61.5% 3-6 years after fire. I suggest that species that were associated with burned vegetation suffered higher predation, because nests or parental behavior was more visible. Similarly, that rates of parasitism of vireos by Brown-headed Cowbirds (*Molothrus ater*) were high on burned sites regardless of time since fire further suggests that visually-orienting predators may have increased search efficiency on burned sites.

## INTRODUCTION

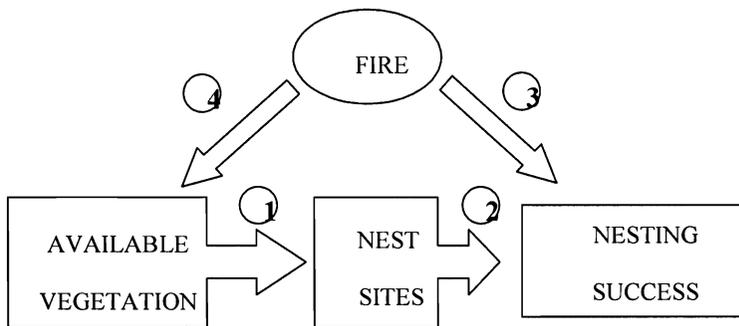
Adaptive nest-site selection in birds consists of a pattern of both coarse- and fine-scale habitat preference that results in greater nesting success and/or productivity at the preferred sites (Clark and Shutler 1999). Nesting success in passerines is generally limited by predation and thus nests should be placed in habitats and at specific sites where they are less accessible to predators (Martin 1993). Diverse predator communities (Filliater et al. 1994), variation in parental behavior at the nest (Weidenger 2002), microclimate preferences (Morton 2002), site fidelity (Misenhelter and Rotenberry 2000), and predator behavior (With 1994, Howlett and Stutchbury 1996) complicate the issue of identifying advantageous nest sites. Additionally, studies of habitat selection commonly assume that habitats are constant when they are in fact changing as a result of either natural (e.g., plant community succession) or anthropogenic (e.g., prescribed fire) processes. These processes may then alter nest selection by altering vegetation and thus

availability of nest sites, including the availability of those that are preferred (Jones et al. 2001). Altered vegetation may also affect nest predators by affecting search efficiency of predators or foraging costs (Schmidt et al. 2001). Finally, these processes may also affect predator populations directly through mortality or availability alternate food resources (Best 1979, Jones, DeBruyn et al. 2001).

Fire is a significant agent of habitat change in many regions including the Sierra Nevada of California (Skinner and Chang 1996). The accumulation of fuel through decades of fire suppression has prompted the adoption of prescribed fire as a management tool to reduce the risk of severe wildfires. Prescribed fires differ, however, from historical natural wildfires in that they are applied during moist periods, particularly in spring, to minimize potential negative impacts. This period also coincides with breeding of most avian species. Because of the nature of these fires, vegetation and potentially nest sites will be particularly affected in the understory, and thus I predicted that bird species that nest in this layer would exhibit changes in nest success and/or changes in nest-site selection in response to prescribed burning.

The relationship between nesting success and the nest site sets the foundation for examining the effect of any habitat alteration. First, does nest-site selection occur? Then, does the selected nest site have any effect on predation risk? Fire may affect this relationship through two pathways (Figure 3.1). The effect of fire may be direct if, for instance, predator populations change, or it may affect nesting success through alteration of vegetation. I examined nest-site selection and predation as well as the influence

**Figure 3.1.** Diagram of the relationship between nest sites and predation risk, as measured through nesting success, and the potential influence of fire. Predation is the primary cause of total nest failure. Numbers refer to questions addressed in the text. 1. Is there selection? 2. Does vegetation affected nesting success? 3. Does fire directly influence nesting success? 4. Does fire alter the relationship between nest sites and nesting success?



of prescribed fire applied in the spring in ponderosa pine forest in the Sierra Nevada, California. I targeted five species that commonly nest in the understory and that varied with respect to life histories, nest placements, and parental nest defense behaviors. In addition to predation, I examined the effect of prescribed fire on brood parasitism rates.

## **METHODS**

### **STUDY AREA**

The study took place in Sierra National Forest on the west slope of the Sierra Nevada, California, approximately 80 km east of Fresno, California. Forests are dominated by ponderosa pine (*Pinus ponderosa*) mixed with canyon live oak (*Quercus chrysolepis*), California black oak (*Quercus kelloggii*), incense cedar (*Calocedrus decurrens*), and white fir (*Abies concolor*). The study area also contains riparian elements, granitic outcrops, and shrub fields dominated by white-leaf manzanita (*Arctostaphylos viscida*). Mountain misery (*Chamaebatia foliolosa*) is the dominant ground-cover species. Fires in the region have been regularly suppressed since the mid-1900s, but historically fires are thought to have been surface fires of mostly low severity every 2 to 12 years (Kilgore 1981, Drumm 1996), or fires of varying intensity with average return intervals of large fires every 50 years (Brown et al. 1999, Minnich et al. 2000). Prescribed fires are applied in the area as part of a fuels reduction program conducted by the U.S. Forest Service.

The study area consisted of nine 40-hectare plots. Elevation ranged from 1,000 to 1,390 m. These plots had experienced fires of unknown severities in the 1930s or 1940s,

with the last fire in the area recorded in 1947. Three sites (the “postburn” sites) had controlled burn applications in April 1997, February 1998, and May 1998 prior to the initiation of the study in 2001. Two of these postburn plots were burned a second time in June of 2003 with the third plot not burned for a second time. In early April 2002, three additional sites were burned from April 4 to April 11, though I focused nest-searching effort on only two of these plots. The remaining three unburned sites continued to have fire excluded for the duration of the study. Fire intensities were estimated on two of the sites burned in 2002 by rating 25 x 25-m squares on quantity burned within the square (0%, < 50%, ≥ 50%) and physical evidence such as white ash, scorching of vegetation, etc. This was done across the entire 40 hectares for each of these two sites.

#### **HABITAT VARIABLES**

A variety of measurements were used to quantify structure and composition of vegetation available for breeding birds. Measurements were confined to a 0.04-ha circle centered on random point, or on or below the nest. Vegetative cover, logs and trees were measured in the circle generally following the sampling protocol created by the National Breeding Biology Research and Monitoring Database (BBIRD) (<http://pica.wru.umt.edu/bbird>). To obtain estimates of vegetative cover, the species of plant was recorded as “hits” on a 2m pole every 0.5 m for 10 m in each of the four cardinal directions (James and Shugart 1970). Logs that were greater than 23 cm in diameter and 1.0 m in length in the circle were recorded in the circle. I also recorded all trees in the circle and classified them by diameter at breast height (dbh, 3cm minimum).

These were compiled into the number of small stems (dbh = 3 - 7.9 cm), medium stems (8 – 36 cm), and large trees (dbh > 36 cm). Stems of shrub species were counted when greater than 3-cm dbh, a size only reached when mature. Using the tree data, I calculated the ratio of oak species to conifers as this tends to be an important difference in habitat association among bird species. Additionally, I calculated the ratio of ponderosa pine to the shade-tolerant incense cedar and white fir. Because of their shade-tolerance, white fir and incense cedar tend to increase during periods of fire suppression, whereas ponderosa tends to decrease. Canopy cover surrounding each point was taken using a densiometer facing each cardinal direction from the center.

Approximately 35 randomly located points were surveyed on each of 4 plots from 1996 to 1999 before fire. Two of these plots were then burned in 2002 and the same random locations re-measured, along with a measure of the percentage of the 0.04-ha circle that was burned. I used these data, before and after burning, to determine how available habitat changed. Values before and after were compared using *t*-tests.

Variables related to structure and composition of habitat were then subjected to a Principal Components Analysis (PCA) to describe independent patterns of covariation among habitat variables. In addition to the practical aspect of reducing the number of variables for use in subsequent analyses, I expected to identify groups of correlated variables that represented true biological relationships, because composition and structure are related to features such as light availability or soils. Variables with many missing values were excluded, but I used means for missing data points for variables with only a few data points missing. Variables that were ratios or that had large spread were log

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transformed using  $\log_{10}(x + 0.01)$  to better approximate the normal distribution. I used varimax rotation to optimize PC factor loadings (Tabachnick and Fidell 1996). Ultimately, I used the number of snags, the number of small stems (dbh < 8cm), the percent cover of mountain misery, the number of large trees (dbh > 32cm), the number of perennial species recorded in the point intercept, the number of stems of white-leaf manzanita (*Arctostaphylos viscida*)(log transformed), the average percent of open sky (from canopy cover), ratio of oak species to conifer species (log transformed), and the ratio of ponderosa pine to white fir and incense cedar (log transformed). The ratio of ponderosa pine to white fir and incense cedar, in addition to providing information about conifer species composition, was related to past burn history and forest density as white fir and incense cedar are shade tolerant and have likely benefited from previous decades of fire suppression. I chose to retain factors with eigenvalues >1 and refer to the principal components that summarize the habitat from the random points as simply the habitat variables.

Burned random points were scored onto the PC-derived habitat variables based on random points surveyed before fire, then compared to the random scores using a *t*-test to examine differences among the habitat variables produced by prescribed burning. Only points that were > 50% burned were used for this test. In addition, I also used a correlation analysis on burned random plots to see if any of the habitat variables represented a gradient of burning by correlating the percentage of the 0.04-ha circle that was burned with each of the habitat variables from the PCA.

## NESTS

Five focal species were chosen based on my ability to collect sufficient data and because of their placement of nests within vegetation strata most likely to be affected by fire. These species were Dark-eyed Junco (*Junco hyemalis*) and Spotted Towhee (*Pipilo maculatus*) which both nest on the ground, Black-headed Grosbeak (*Pheucticus melanocephalus*), which commonly nests in shrubs, Hutton's Vireo (*Vireo huttoni*) which generally nest in shrubs or low in trees, and the similar Cassin's Vireo (*Vireo cassinii*) which generally nests low in trees. Nests were checked every three to four days.

Contents were examined on most nest checks, but when possible nests were not approached after confirming them still active so as to minimize disturbance. Age of the nest was estimated by extrapolating from laying and back-dating from fledging dates, or from nestling age based on assessment of chick development. Almost all nests could be accessed through a variety of techniques: mirrors, ladders, extendible video camera systems, and tree climbing. Presence of Brown-headed Cowbird eggs or nestlings was noted. Nest success was defined as fledging at least one nestling. A nest that appeared undisturbed on the final nest check that was within 3 days of fledging was considered successful. Fledglings were located when possible to confirm success.

The same habitat variables as taken for the random points were measured at each nest location. Each nest was scored onto the dimensions of habitat variation represented by the PCA of the random points. I also measured concealment of the nest and nest height. Concealment was taken as percent cover of a 25-cm radius area surrounding the

nest from each cardinal direction, plus above and below at 1m away (BBIRD protocol). These measures were combined with nest monitoring data for the following analysis.

#### **NEST-SITE SELECTION, NESTING SUCCESS, AND FIRE**

The analysis was done in steps to address specific questions about nest-site selection and nest success (Figure 3.1). Fire may also cause direct mortality to nests, but is not considered here (Appendix A). First, selection was considered by comparing the PCA-derived scores from vegetation surrounding the random points with vegetation scores from nest sites for each species using a stepwise Discriminant Function Analysis (DFA). Variables retained were considered to be selected by the species.

For each of the questions related to nesting success, I used a logistic-exposure model in PROC GENMOD (SAS Institute 2000) as developed by Shaffer (Shaffer 2004) to examine success of the exposed intervals (i.e. time periods of observation when predation could occur) as related to habitat variables, nest variables, and the prescribed fire applications. Because predation is the primary cause of loss of entire nests, nesting success is essentially a measure of predation risk. Parasitism was ignored and fate was for the nest regardless of contents to focus on predation risk. Parasitism is considered further below. Variables were considered to be affecting nesting success if p-values were  $\geq 0.05$  for type III contrasts (i.e. controlling for the effects of the other variables). While they were not one of my primary questions, before proceeding with the analysis of nesting success, I looked at time-dependent effects which have been found to influence nesting success in other studies and may confuse subsequent analyses (Grant et al. 2005).

I considered the linear, quadratic, and cubic effects of nest age as well as the linear and quadratic effects of day of year (Grant et al. 2005). Time variables that potentially were related to success ( $p < 0.15$ ) were retained in all subsequent models with the restriction that models with higher order effects included all lower order effects as well.

Before considering the effects of fire, I examined the effect of the nest site (including habitat and nest variables) on success. Scores from the PCA habitat variables, concealment, and nest height (except for ground nests) were examined. Next, to answer the question if burning has some direct effect on nest success unrelated to the nest site, I ran an analysis with only the burn history. Burn history grouped nests by location into three categories. One group was “unburned”, which included the three plots unburned throughout the study and the three plots to be burned in 2002, but before they were actually burned. Nests from these later three plots after burning were subsequently placed in the second group, “0-1 year postburn”. Nests from the three plots burned in 1997-1998 constituted a third group, “3-6 years postburn”. There were a few nests on this last group of plots that were burned a second time in 2003 and these were placed into the previous “0-1 year postburn” category. Year is a potentially confounding factor and was always included with burn history.

Finally, if the above analyses indicated that nest success was potentially related to any nest-site variable ( $p < 0.15$ ), I combined those variables with burn history to examine the specific relationship between burning, the nest site, and nesting success. Indicated nest-site variables were included with burn history, year, and their interaction with burn history. This interaction assessed if the relationship between the nest site and nest

success differed as a result of the prescribed fire treatment. Models that indicated a significant relationship with nesting success were used to calculate daily survival rates (DSR) to illustrate the nature of the relationship.

### **PARASITISM**

I considered parasitism rates by Brown-headed Cowbirds for the Hutton's Vireo and the Cassin's Vireo, which are typical host species. Since Brown-headed Cowbirds do not arrive until after some individuals have begun nesting, particularly the resident Hutton's Vireos, I excluded earlier nests. The earliest date for a cowbird egg in a nest was 13 April though this date was unusual and generally cowbird eggs were not found until May. I chose this earlier date to calculate the most conservative estimate as this would increase the number of nests considered to be potentially parasitized. A logistic regression (PROC LOGISTIC in SAS) was used to model incidence of parasitism with respect to burning, and habitat and nest variables.

### **RESULTS**

Burns were patchy, leaving many unburned areas throughout, but particularly in riparian areas and rocky outcrops. On the two sites burned in 2002 where I collected fire intensity information across the site, one had ~49% unburned area and the other ~51% unburned. Some large blocks were unburned in areas adjacent to streams or on rock outcrops (25% and 39% of the total area respectively), but otherwise burning left an irregular pattern of small burned and unburned patches throughout the sites. Vegetation

changed little as a result of burning with only litter depth (cm), canopy cover (1 - open canopy), density of mature manzanita stems, and the number of logs ( $\text{ha}^{-1}$ ) being reduced though only significantly for litter depth ( $t_{206} = -4.32$ ,  $p < 0.001$ ). Live trees in all size classes increased, although this was probably an effect of time between measurements (up to 6 years) rather than from burning (Table 3.1). Few nests were active during burning and these nests are not considered further (Appendix A).

Three principal components had eigenvalues  $> 1$  and were retained as habitat variables; together they explained 56% of the total variation in the vegetation dataset (Table 3.2). The first principal component (PC1) was associated with increasing cover of mountain misery (the primary ground cover), dominance of ponderosa pine, and more mature manzanita vs. dominance of white fir and incense cedar, and more large trees. Thus, this axis is associated with changing vertical structure, shifting from more understory structure (negative scores) to more overstory structure (positive scores). The second principal component (PC2) represents a gradient from oak dominance and open canopy (negative scores) to increasing conifer dominance, closed canopy, and perennial plant diversity (positive scores). PC2 was thus associated with canopy and species composition. The third principal component (PC3) was associated increasing numbers of snags and small stems, and decreasing perennial diversity. This axis was associated with the densification of the forest, culminating in a thicket of small stems where trees were dying and fewer species survived. Habitat variables represented by these components were not related to burning in the  $t$ -tests (all  $p$ -values  $> 0.10$ ), nor were any correlated with the amount of area burned in the 0.04 ha circle (all  $p$ -values  $> 0.10$ ).

**Table 3.1.** Forest structure and densities for logs and live stems( $\text{ha}^{-1}$ ) before and after fire for random points. Variables are measured on 0.04-ha circles taken at 138 points before burning (1996-1999) and 70 points after (2002). Logs are  $>8$  cm diameter and  $>1.0$  m in length.

	Before burning		After burning	
	Mean	SE	Mean	SE
<u>Structure</u>				
Percent open canopy cover	19.2	1.3	24.4	2.7
Litter depth (cm)	7.2	0.3	5.0	0.4
<u>Density (<math>\text{ha}^{-1}</math>)</u>				
Number of logs	109	8.2	99	10.8
Number of mature manzanita stems	323	46.9	314	58.5
<u>Live Trees</u>				
3 cm – 7.9 cm	637	75.8	760	90.3
8 cm – 35.9 cm	625	45.3	815	72.1
$>36$ cm	73	4.8	90	7.8
Total	1335	110.0	1665	150.0

**TABLE 3.2.** Factor loadings for Principal Components Analysis (PCA) for random points before burning. Three principal components (eigenvalues > 1) were retained and were rotated using varimax rotation. Large trees are those with dbh > 32 cm. White leaf manzanita includes only those with stems >3 cm and small stems are > 3cm and < 8 cm diameter. Loadings greater than 0.40 are shown in bold. Names below each component are based on interpretation of loadings.

variables	Component		
	I	II	III
	Vertical structure	Canopy Composition	Densification
Number of snags	-0.15	-0.37	<b>0.73</b>
Log <sub>10</sub> (number of manzanita stems)	<b>-0.65</b>	0.31	0.19
Average percent open sky	0.24	<b>0.68</b>	-0.16
Number of perennial species	0.004	<b>-0.43</b>	<b>-0.49</b>
Log <sub>10</sub> (number of small stems)	0.09	-0.06	<b>0.81</b>
Log <sub>10</sub> (ratio ponderosa pine to fir and cedar)	<b>-0.58</b>	<b>0.78</b>	-0.01
Log <sub>10</sub> (ratio oak to conifer)	-0.03	0.37	-0.07
Number of large trees	<b>-0.65</b>	0.15	0.02
Percent cover of mountain misery	<b>0.72</b>	0.03	-0.12
Percent total variance	26.0	16.9	12.8

## **SPOTTED TOWHEE**

Sixty-eight Spotted Towhee nests were found from 2001 to 2003, all but two on the ground. Selection was apparent for PC1 (vertical structure, Wilks' lambda = 0.91  $p < 0.001$ ) and PC3 (densification, Wilks' lambda = 0.86  $p < 0.001$ ), in which Spotted Towhees nested at points with greater understory structure and less densification than was randomly available. In the logistic-exposure model I was able to use nest observation intervals for 66 nests for an effective sample size of 698. Nest age effects up to the cubic effect were related to nest success and thus the linear, quadratic, and cubic effects were included in all subsequent analyses (Appendix D). Concealment was the only vegetation variable related to nesting success ( $p = 0.10$ ) and success did not vary between plots of different burn history (Appendix E). There was also no indication of an interaction effect between concealment and burn history. Thus, only concealment was related to success, but this was only a weak relationship.

## **DARK-EYED JUNCO**

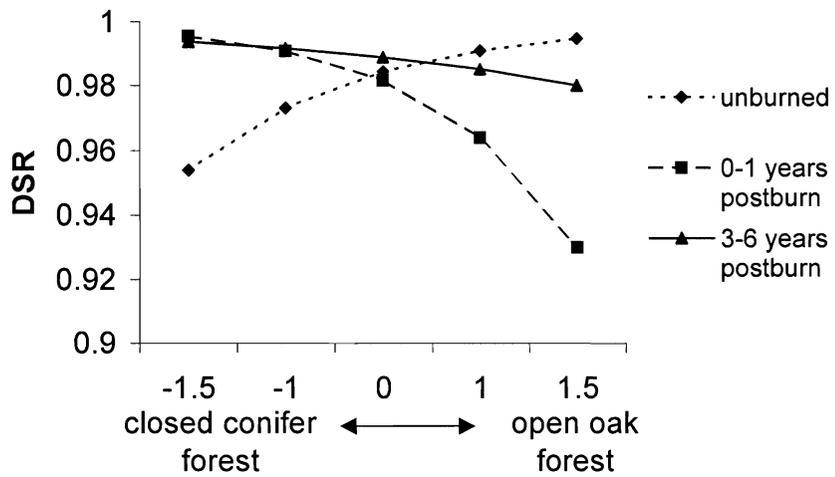
Data were collected on 77 Dark-eyed Junco nests, all of which were on the ground. Effective sample size for logistic exposure models was 937. Selection was significant for PC1 (vertical structure, Wilks' lambda = 0.79  $p < 0.001$ ) and PC3 (densification, Wilks' lambda = 0.74  $p < 0.001$ ), with Dark-eyed Juncos choosing nest sites with more upper canopy structure and less densification than was available. No time dependent effects were related to success (Appendix D). PC2 (canopy composition) was indicated as possible influencing nest success ( $p = 0.08$ ), but success

did not vary between burn histories (all p-values > 0.20) (Appendix E). When combined, there was a significant relationship between PC2 (canopy composition) and the burn history (Appendix E). Success was higher in surrounding vegetation that included more oak and open canopy on unburned plots, whereas it was higher plots 0-1 year postburn when surrounding vegetation included more conifers and closed canopy (Figure 3.2). Successful nests generally had lower values on PC2, which is associated with closed conifer forest (Table 3.3). For a nest surrounded by closed canopy forest (PC2 = -1.0) the probability of surviving the entire nest cycle is 45% for unburned, 82% for 0-1 year postburn, and 87% for 3-6 years postburn.

#### **BLACK-HEADED GROSBEAK**

A total of 70 nests of Black-headed Grosbeak was found with 79% placed in white-leaf manzanita. Selection was significant for PC1 (vertical structure, Wilks' lambda = 0.90  $p < 0.001$ ) and PC3 (densification, Wilks' lambda = 0.87  $p < 0.001$ ), and grosbeaks chose nests sites with more understory structure and less densification. Time-dependent effects were important for nest age (linear, quadratic, and cubic effects; Appendix D), and these effects were included in all subsequent analyses. Nesting success was somewhat related to nest height, but was unrelated to burn history. When combined with the interaction, however, there was a significant effect of burn history and the interaction of burn history and nest height, and nest height alone was no longer related (Appendix E). Nest heights were generally similar except for failed nests on plots 3-6 years postburn (Table 3.3). Daily survival rates decreased with nest height except on plots burned within 1 year

**Figure 3.2.** Daily survival rates (DSR) for Dark-eyed Junco in 2003 as calculated from parameter estimates from logistic exposure model including year, burn history, PC2 (canopy composition) and its interaction with burning.

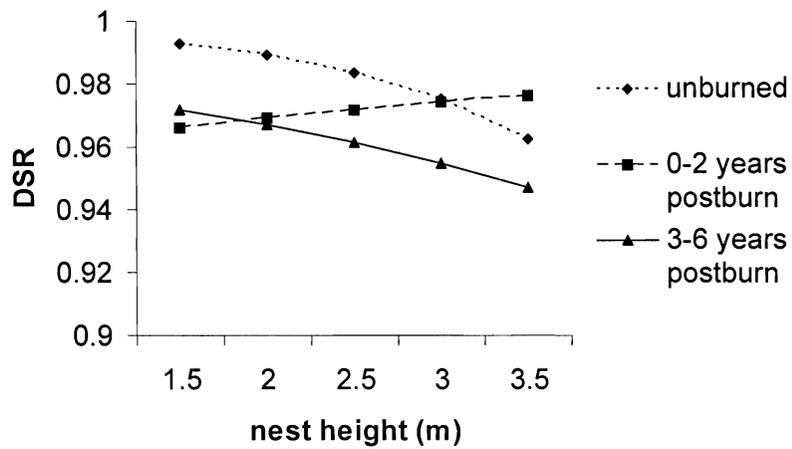


**Table 3.3.** Means (se) for failed and successful nests for variables significantly related to nesting success in logistic exposure models. Only significant variables are shown except for Hutton's Vireo where only concealment was significant when the effect of burn history was removed. No significant variables were found for Spotted Towhee.

	Failed		Successful*	
	n	Mean (se)	n	Mean (se)
Dark-eyed Junco				
PC2 (canopy composition) unburned	12	-0.5 (0.2)	6	-0.3 (0.2)
PC2 (canopy composition) postburn 0-1 year	7	0.5 (0.2)	3	-0.8 (0.3)
PC2 (canopy composition) postburn 3-6 years	16	0.2 (0.1)	25	-0.09 (0.2)
Black-headed Grosbeak				
Nest height unburned	20	4.0 (0.8)	11	2.2 (0.1)
Nest height postburn 0-1 year	8	2.6 (0.3)	12	2.8 (0.3)
Nest height postburn 3-6 years	11	4.0 (1.2)	8	2.1 (0.3)
Hutton's Vireo				
Concealment unburned	17	45.2 (3.7)	16	54.2 (4.3)
Concealment postburn 0-1 year	21	47.0 (3.0)	9	44.0 (6.1)
Concealment postburn 3-6 years	18	46.4 (3.4)	10	51.4 (4.0)
Cassin's Vireo				
PC2	52	-0.4 (0.1)	29	-0.06 (0.1)
PC3	52	-0.6 (0.1)	29	-0.27 (0.1)
Concealment	52	24.1 (2.6)	29	28.8 (2.3)

\* Successful includes nests that only fledge cowbirds

**Figure 3.3.** Daily survival rates (DSR) for Black-headed Grosbeak in 2003 as calculated from parameter estimates from logistic exposure model including nest age (linear, quadratic, and cubic effects), year, burn history, nest height, and its interaction with burning.



where higher nests had better success (Fig. 3.3). Based on these values, a nest on an unburned plot had a 74% chance of surviving the entire nesting period, whereas the chance of surviving is 43% and 41% on sites 0-1 year postburn and 3-6 years postburn, respectively.

#### **HUTTON'S VIREO**

There was a total of 91 nests of Hutton's Vireo with 42% were placed in canyon live-oak and 36% in white-leaf manzanita. Seventy-nine nests were used in the logistic exposure model yielding an effective sample size of 1,378. Selection was only significant along PC3 (densification, Wilks' lambda = 0.87  $p < 0.001$ ). Nest sites with more understory structure and less densification were chosen. Time-dependent effects were not strongly apparent, but the quadratic and cubic effects of nest age met the screening criteria ( $p < 0.15$ ), and, along with the linear effect, were retained in subsequent analyses (Appendix D). Concealment was the only vegetation variable related to success, and burn history alone was significant (Appendix E). When combined with the interaction of concealment and burn history, burn history was no longer important and only concealment was still significant ( $p = 0.05$ ), revealing that differences in success among plots of different burn histories was most likely due to differences in concealment. The mean concealment values were for highest for unburned and lowest for 0-1 year postburn plus lower for failed nests (Table 3.3). Daily survival rates increased with increasing concealment with the effect becoming more pronounced as nests aged (Figure

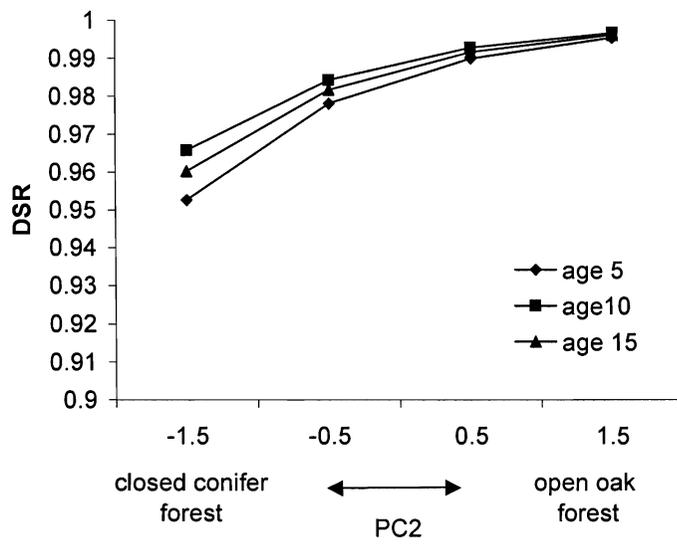
3.4). Based on these rates, the probability of surviving the entire nest cycle is 41% for a nest 40% concealed and 72% for a nest 80% concealed.

Parasitism rates for Hutton's Vireos were high with highest overall rates on burned plots. Rates were 58.3% (n = 19) for 0-1 year postburn and 61.5% (n = 21) for 3-6 years postburn as compared to 33.3% (n = 66) on unburned sites. On three occasions vireo young fledged along with cowbirds.

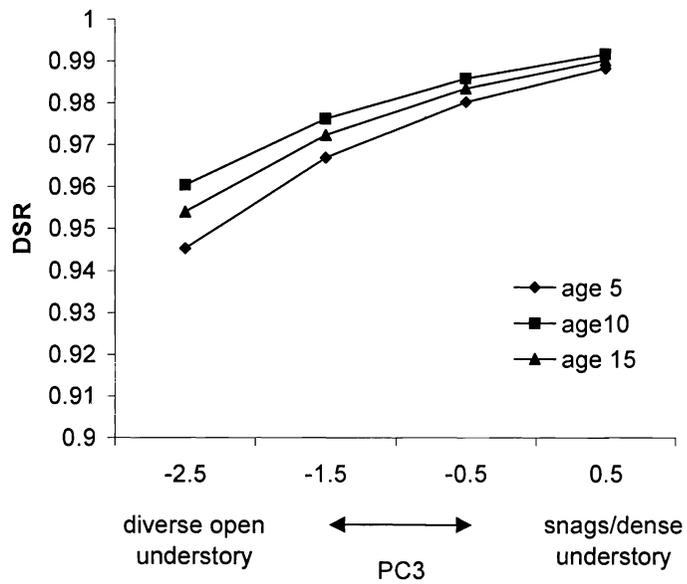
#### **CASSIN'S VIREO**

For Cassin's Vireo, 81 nests were found with 40% placed in incense cedar, 26% in California black oak, and 25% in canyon live oak. Selection occurred with respect to PC1 (vertical structure, Wilks' lambda = 0.78 p < 0.001), PC2 (canopy composition, Wilks' lambda = 0.76 p < 0.001), and PC3 (densification, Wilks' lambda = 0.86 p < 0.001). Cassin's Vireos chose nest sites with more upper canopy structure, more closed conifer forest, and less densification. Time dependent effects were important for nest age (linear, quadratic, and cubic effects), and these effects were included in all subsequent analyses (Appendix D). Nesting success varied with respect to PC2 (canopy composition), PC3 (densification), and concealment (Appendix E). Burn history alone was not significant, and when combined with vegetation variables, there were no significant interactions and the same vegetation variables remained important. Daily survival rates increased with age and greater amounts of oak dominated open forests and with more densification in the understory (Fig. 3.5 and 3.6).

**Figure 3.5.** Daily survival rates (DSR) for Cassin's Vireo for PC2 (vertical structure) as calculated from parameter estimates from logistic exposure model including nest age (linear, quadratic, and cubic effects), PC1 (vertical structure), PC2 (canopy composition), PC3 (densification), nest height, and concealment. Only PC2 and age are varied and means were used for all other variables.



**Figure 3.6.** Daily survival rates (DSR) for Cassin's Vireo for PC3 (densification) as calculated from parameter estimates from logistic exposure model including nest age (linear, quadratic, and cubic effects), PC1 (vertical structure), PC2 (canopy composition), PC3 (densification), nest height, and concealment. Only PC3 and age are varied and means were used for all other variables.



Parasitism rates for Cassin's Vireos were high, particularly on burned sites. Rates were 50% (n = 6) on 0-1 year postburn and 40.9% (n = 31) on 3-6 years postburn, but only 14.8% (n = 81) on unburned sites. Only in one case were Cassin's Vireos thought to have fledged vireo young along with cowbirds.

#### **BROWN-HEADED COWBIRD**

Forty-five percent (n = 58) of parasitized nests successfully fledged Brown-headed Cowbirds. This rate was essentially the same between Hutton's Vireo (44%) and Cassin's Vireo (45%). A logistic regression model of relationship between probability of parasitism and vegetation attributes (3 habitat variables from the PCA, concealment, and nest height) for both vireo species (n = 158) fit the data well according to the Hosmer and Lemeshow test ( $\chi^2_8 = 6.42$ ,  $p > 0.60$ ), but only PC1 (vertical structure) showed any relationship to cowbird parasitism ( $\chi^2_1 = 3.10$ ,  $p = 0.08$ ).

#### **DISCUSSION**

All species showed some selection for nest sites. In addition, nest sites were related to the risk of predation for all but the Spotted Towhee. Fire altered these relationships to the point of switching which nest sites incurred a greater probability of success for Dark-eyed Juncos and Black-headed Grosbeaks (Table 3.4). These effects were primarily found less than 3 years after burning. In addition, prescribed fires increased brood parasitism, an effect that was not reduced with time since burning.

With respect to vegetation, these prescribed fires only resulted in a reduction of litter on the forest floor and were not enough to offset the continued densification of the forest. Total density of trees > 3 cm was 1,900 stems ha<sup>-1</sup>, the majority < 36 cm. Data from the 1930's for mixed conifer forests in the San Bernardino Mountains recorded an average of 250 stems ha<sup>-1</sup> (> 12 cm) (Minnich et al.1995). Though the west slope of the Sierra Nevada receives more rainfall, species composition is similar and differences are dramatic. With respect to vegetation, these prescribed fires only resulted in a reduction of litter on the forest floor and were not enough to offset the continued densification of the forest. Total density of trees > 3 cm was 1,900 stems ha<sup>-1</sup>, the majority < 36 cm. Data from the 1930's for mixed conifer forests in the San Bernardino Mountains recorded an average of 250 stems ha<sup>-1</sup> (> 12 cm) (Minnich et al.1995). Though repeated burning is planned in these areas, which will probably reduce fuels further, it seems unlikely that fires of this low intensity will reduce tree densities significantly. Regardless of the magnitude of vegetation changes, nesting success was affected by burning.

All species demonstrated some degree of non-random nest-site selection, and always for lower values of PC3 (less densification). PC1 (vertical structure) was selected by all species except Hutton's Vireo and varied by species. This may be because Hutton's Vireos build their nests in shrubs as well as in trees, a range that covers this entire gradient,. Only Cassin's Vireos selected nest sites with respect to the PC2 axis (canopy composition). While selection covered a broad range of variation related to vegetation, a narrower range of vegetation was associated with success (Table 3.4).

Vegetation surrounding nests was related to nesting success for all but one species, the Spotted Towhee, though often only a single nest site variable was important. Samples sizes were lowest for the Spotted Towhee of the five species examined, so the lack of significance may be a result of relatively less statistical power. For Hutton's Vireo, Black-headed Grosbeak and Dark-eyed Junco, the relationship between vegetation and nesting success was influenced by fire. For Hutton's Vireo, whereas fire did not alter the positive relationship between concealment and nesting success, it is likely responsible for the reduction in concealment seen on burned sites, which subsequently resulted in lower nesting success on burned sites. Hutton's Vireos, as well as other species, were observed nesting in substrates that were burned. Thus, cover may be reduced because scorched leaves are not as concealing or because dead leaves were gradually falling to the ground leaving the nest progressively more exposed. The effect was most evident on sites 0-1 year postburn and thus it appears that, in this case, vegetation may recover over a short time so that concealment, and thus nesting success, is no longer affected after 2 or more years. Alternatively, if lower concealment is caused by the use of burned substrates, Hutton's Vireos may no longer use these sites after 1 year.

Black-headed Grosbeaks generally nested fairly low in manzanita, but nested in trees on occasion. Nest success generally improved when nests were lower, which may be related to their accessibility and/or visibility to avian predators. For recently burned areas, nests that were taller were more likely to succeed, which may be related to reduction in cover for the lowest level of the forest where fire was most likely to burn.

**Table 3.4.** Summary of nest-site selection and nesting success results. Nesting success was evaluated in three steps: vegetation, burning and a combined analysis that included interactions. All significant ( $p \leq 0.05$ ) variables are shown with variables that passed screening ( $p > 0.15$ ) and were used in later analyses in parentheses. Age is age of the nest in days from first egg laid. See Appendices D and E for statistical values.

Species	Selection	Time	Vegetation Only	Burning Only	Vegetation*Burnin g
Spotted	PC1, PC2,	Age			
Towhee	PC3	Age2 Age3			
Dark-eyed Junco	PC1, PC2, PC3		(PC2)		PC2*burning
Black-headed Grosbeak	PC1, PC3	Age, Age2 Age3	Nest height		Burning, Nest height*burning
Hutton's Vireo	PC3	(Age) (Age2) (Age3)	Concealment	Burning	(Concealment)
Cassin's Vireo	PC1, PC2, PC3	Age, Age2 (Age3)	PC2, PC3, concealment		PC2, PC3, concealment

For Dark-eyed Junco, nesting success was better where canopy was more open and oak dominated when unburned, but this relationship switched when sites were burned. Litter and other forest fuels dry out faster in more open forest areas so these areas would perhaps be more prone to burning. Junco nests on later burns were relatively unrelated to this factor.

The interaction of predation risk and vegetation was altered by fire. One possible explanation is that fire affected the searching efficiency of predators and certain nest types become more vulnerable. Either nests are more vulnerable, because they are in areas more altered by fire and thus more visible or accessible, or there is relatively less of a particular vegetation type to search (i.e. fewer potential nest sites; Martin 1993). An alternative may be that a diverse assemblage of predators collectively covers all vegetation types and only particular predators were affected by fire thus making certain vegetation types (associated with those predators) more vulnerable. On the other hand, I did not find that vegetation along any of the PCs was affected by burning, but recall that the vegetation is considered in only a restricted area and inclusion of multiple variables may weaken relationships when only a few of the variables that compose the PC are affected.

Cassin's Vireos, although similar to Hutton's Vireos in many aspects, were relatively unaffected by fire, which is probably related to differences in nest sites. They are often more closely associated with more mesic conditions and uncommonly used manzanita, which is prone to burning, for nesting. Both Cassin's and Hutton's Vireos showed a positive effect of concealment though only Hutton's Vireo used nests with

lower concealment on burned sites, again possibly related to Cassin's Vireos preference for less flammable vegetation (Table 3.3). The question of why Hutton's Vireo would use burned substrates when unburned are available is unanswered.

Cowbirds have arrived in the Sierra Nevada only in the past 70 years (Rothstein et al. 1980). Hutton's Vireo has generally been considered an uncommon host, because of its well-concealed nests (Davis 1995). Whereas I also found Hutton's Vireo nests to be well concealed in the immediate vicinity around the nest, a third of nests were parasitized on unburned plots and the rate increased with burning. It is interesting that Hutton's Vireo had higher rates of parasitism than Cassin's Vireo. Cassin's Vireos should be more conspicuous as their nests are less concealed (Appendix C) and they sing more from the nest (personal observation), but cowbirds may concentrate on Hutton's Vireo because Hutton's Vireo are more common at this elevation. Huttons' Vireos and Brown-headed Cowbirds also co-occur over a wider range, as Cassin's Vireo generally breeds at higher elevations where cowbirds do not occur. Survey data did not indicate that populations of Brown-headed Cowbirds were altered by burning (Chapter 1); thus, increased levels of brood parasitism after burning suggest that parental activities may be more visible and nests more easily found. Probability of parasitism has been found to increase with reduction in concealment (Budnik et al. 2001) and cowbirds use visual clues to locate nests (Wiley 1988). This further supports the idea that parental activities and or nests are becoming more obvious in fire-prone vegetation whether the consequence is predation of the nest or brood parasitism. This pattern is worrisome for Hutton's Vireo in that the effect was particularly pronounced on burned sites where success was already reduced.

Accounting for nests that were not depredated but only fledged cowbirds, 27% of Hutton's Vireos were successful on plots 0-1 postburn and 21% on plots 3-6 years postburn (apparent success rates). Additionally, brood parasitism rates appear to have increased considerably since 1997 when estimates from this same study area were 25% for Cassin's Vireo and 9% for Hutton's Vireo (Purcell and Verner 1999). I did not find any instances of parasitism of Black-headed Grosbeak, though they are a host in other regions (Hill 1995).

My result, that context of the nest was important to nesting success and parasitism rates, has close parallels to studies identifying the importance of landscape factors in determining nest success in a variety of habitats (Donovan et al. 1997, Tewksbury et al. 1998, Peak et al. 2004). Generally, this is an extension of the issue of scale and the hierarchical selection of habitat by birds. Specifically, landscape factors may be more important in determining predator populations than microhabitat surrounding the nest and thus may be better predictors of nesting success. A study of nesting success in Song Sparrows (*Melospiza melodia*) found a result similar to mine in comparing grazed and ungrazed pastures where nest-site locations associated with success differed between pastures (Chase 2002).

Also noteworthy is that a number of the factors, while relating to nest placement, were not significantly associated with nest outcome particularly when burning was not considered. This is actually a fairly common result among nest studies and has stimulated a number of hypotheses. One is that a diverse predator group can locate nests based on a variety of cues leading to unpredictability of predation risk as a whole

(Filliater et al. 1994). Secondly, if most birds make optimal choices then, in the absence of manipulating habitats, all selected nest locations are about the same with respect to predation risk (Schmidt and Whelan 1999). Thirdly, spatial and temporal variation in selection pressures may weaken the link between choice and consequence obscuring patterns (Clark and Shutler 1999, Misenhelter and Rotenberry 2000) or favoring plasticity (Martin 1998, Chase 2002). For these data, a diverse predator community may be responsible for the pattern we see if fire caused changes in searching ability or densities of only particular predators, thus revealing patterns that relate nest-site selection to nest success for this group. That choices are basically optimal in the absence of manipulation was only supported for some species. And finally, spatial and temporal variability, like that caused by burning, while revealing patterns, may in the long term obscure optimal choices or favor plasticity. This seems particularly relevant to Dark-eyed Junco and Black-headed Grosbeak for which safe nesting sites varied with burn history. The relation of nesting success to nest-site selection may then best be studied in the context of a variety of locations or within a changing landscape.

## LITERATURE CITED

- Best, L. B. 1979. Effects of Fire on a Field Sparrow Population. *The American Midland Naturalist* 101: 434-442.
- Brown, P. M., M. R. Kaufmann, and W. D. Shepperd. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. *Landscape Ecology* 14:513-532.
- Budnik, J. M., D. E. Burhans, M. R. Ryan and F. R. Thompson III. 2001. Nest desertion and apparent nest protection behavior by Bell's Vireos in response to cowbird parasitism. *Condor* 103: 639-643.
- Chase, M. K. 2002. Nest site selection and nest success in a song sparrow population: the significance of spatial variation. *Condor* 104:103-116.
- Clark, R. G. and D. Shutler. 1999. Avian habitat selection: pattern from process in nest-site use by ducks? *Ecology* 80: 272-287.
- Davis, J. N. 1995. Hutton's Vireo (*Vireo huttoni*). *The Birds of North America*. Washington, D.C., The Academy of Natural Sciences and the American Ornithologists' Union. No. 189.
- Donovan, R. M., P. W. Jones, E. M. Annand and F. R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78: 2064-2075.
- Drumm, M. K. 1996. Fire history in the mixed conifer series of the Kings River Adaptive Management Area, Sierra National Forest. *Natural Resources*. Arcata, Humboldt State University:30.
- Filliater, T. S., R. Breitwisch and P. M. Nealen. 1994. Predation on Northern Cardinal nests: does choice of a nest site matter? *Condor* 96.
- Grant, T. A., T. L. Shaffer, E. M. Madden, and P. J. Pietz. 2005. Time-specific variation in passerine nest survival; new insights into old questions. *Auk* 122:661-672.
- Hill, G. E. 1988. Age, plumage brightness, territory quality, and reproductive success in the Black-headed Grosbeak. *Condor* 90: 379-388.
- Hill, G. E. 1995. Black-headed Grosbeak (*Pheucticus melanocephalus*). *The Birds of North America*. Washington, D.C., The Academy of Natural Sciences and the American Ornithologists' Union. No. 143.

- Howlett, J. S. and B. J. Stutchbury. 1996. Nest concealment and predation in Hooded Warblers: experimental removal of nest cover. *Auk* 113: 1-9.
- James, F. C. and H. H. Shugart Jr. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24: 727-736.
- Jones, J., R. D. DeBruyn, J. J. Barg and R. J. Robertson. 2001. Assessing the effects of natural disturbance on a neotropical migrant songbird. *Ecology* 82: 2628-2635.
- Kilgore, B. M. 1981. Fire in ecosystem distribution and structure: western forests and scrublands. Proceedings of the conference on fire regimes and ecosystem properties. Honolulu, HI, USDA Forest Service. GTR-WO-26.
- Martin, T. E. 1993. Nest predation and nest sites: new perspectives on old patterns. *BioScience* 43: 523-532.
- Minnich, R. A., M. G. Barbour, J. H. Burk and R. F. Fernau. 1995. Sixty years of change in Californian conifer forests of the San Bernardino Mountains. *Conservation Biology* 9:902-914.
- Minnich, R. A., M. G. Barbour, J. H. Burk and J. Sosa-Ramirez. 2000. Californian mixed-conifer forests under unmanaged fire regimes in the Sierra San Pedro Martir, Baja California, Mexico. *Journal of Biogeography* 27: 105-129.
- Misenhelter, M. D. and J. T. Rotenberry. 2000. Choices and consequences of habitat occupancy and nest site selection in sage sparrows. *Ecology* 81: 2892-2901.
- Morton, M. L. 2002. The Mountain White-crowned Sparrow: migration and reproduction at high altitude. *Studies in Avian Biology* 24.
- Peak, R. G., F. R. Thompson III and T. L. Shaffer. 2004. Factors affecting songbird nest survival in riparian forests in a midwestern agricultural landscape. *Auk* 121: 726-737.
- Purcell, K. L. and J. Verner. 1999. Research and management of the Brown-headed Cowbird in Western landscapes. Abundance and rates of brood parasitism by Brown-headed Cowbirds over an elevational gradient in the southern Sierra Nevada, Cooper Ornithological Society. 18: 97-103.
- Rothstein, S. I., J. Verner and E. Stevens. 1980. Range expansion and diurnal changes in dispersion of the Brown-headed Cowbird in the Sierra Nevada. *Auk* 97: 253-267.
- SAS Institute, I. 2000. SAS/STAT User's Guide. SAS Institute, Cary, NC.

- Schmidt, K. A., J. R. Gohenn and R. Naumann. 2001. Incidental nest predation in songbirds: behavioral indicators detect ecological scales and processes. *Ecology* 82: 2937-2947.
- Schmidt, K. A. and C. J. Whelan. 1999. Nest placement and mortality: is nest predation a random event in space and time? *Condor* 101:916-920.
- Shaffer, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121: 526-540.
- Skinner, C. N. and C.-r. Chang. 1996. Fire regimes, past and present. Sierra Nevada Ecosystem Project: Final Report to Congress. University of California Davis, Centers for Water and Wildland Resources. 2: 1041-1069.
- Tabachnick, B. G. and L. S. Fidell. 1996. *Using Multivariate Statistics*. HarperCollins, New York.
- Tewksbury, J. J., S. J. Hejl and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* 79: 2890-2903.
- Weidenger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *Journal of Animal Ecology* 71: 424-437.
- Wiley, J. W. 1988. Host selection by the Shiny Cowbird. *Condor* 90:289-303.
- With, K. A. 1994. The hazards of nesting near shrubs for a grassland bird, the McCown's Longspur. *Condor* 96: 1009-1019.

## CONCLUSION

As expected, I found that avian species varied in their response to burning. When examining the effect of burning on avian abundance, some species responded positively, some negatively, and nearly half had no response. Specific snag types were preferred for nesting for cavity-nesting species and open-cup nesters preferred particular vegetation structures or compositions. Response to fire also varied by species when measured via nesting success, though I found no species that had significantly higher success on burned sites. The interaction of fire, nest-site selection, and nesting success proved to be complex.

Through coordination with the U.S. Forest Service, fire was applied to all but one plot as planned. Variation in precipitation and temperature resulted in fires set earlier than most breeding in 2002 and later than most breeding in 2003. Fire was applied using drip torches and generally took 1 to 2 days to complete, though areas of active burning remained for weeks. Despite this, I was able to observe the fires firsthand and was able to enter these areas immediately following fire to continue with the data collection. Because of the timing of fires, few nests were active during burning. The fate of these nests is listed in Appendix A. While it is not surprising that some nests were spared considering the patchy nature of the fires, vegetation burned in very close proximity to a few nests with nestlings that survived.

American Robin, Northern Flicker, Brown Creeper, Red-breasted Nuthatch, and Yellow-rumped Warbler had higher abundances following prescribed fire. Dark-eyed Junco also had higher abundance on burned plots, but nesting success for this species was

**Comment [F1]:** Try talking about each of the target species and combining results too.

**Comment [K2]:** skip recap?

not altered by fire. Attractiveness may have been unrelated to nesting success, or any benefits from nesting on burned areas were reduced by competition with conspecifics. I found that short distance migrants responded positively. Additionally, understory, bark, and aerial foragers increased following fire. This is a common result of fire studies and it has been proposed that the removal of vegetation by fire or attraction of insects to stressed trees increases food availability for these species (Kotliar et al. 2002). While I found snag nesters increased in abundance, they actually had lower nesting success immediately following burning, which was also the time period during which suitable nest snags were at the most risk.

A negative response to fire was found for Acorn Woodpecker, Nashville Warbler and Golden-crowned Kinglet, Hermit Warbler, Black-throated Gray Warbler, and Hutton's Vireo. Ground nesters had an immediate negative response to fire, but populations had apparently recovered by the third year after fire. One ground nesting species, Dark-eyed Junco, showed a short-term effect of fire on nesting success. Another ground-nester, Spotted Towhee, showed no effect on nesting success. Long-distance migrants responded negatively to fire, but only in the short term. Those species that associate with oaks were reduced on postburn sites. While oaks recover well after fire, this did not occur within the limited time of my study. I found a negative response for canopy foragers for both the immediate and postburn periods and a negative immediate response for high-nesting species. Because, I did not expect high canopy nesting species to be impacted by fire and because nest-searching time was limited, I did not monitor nests of these species. The lasting effect may be best explained by reduction in food

supplies, as many of these species are also insectivorous foliage gleaners. Granholm (Granholm 1974), who also found a decline in foliage-gleaning insectivores during prescribed fire, suggested this effect was due to mortality of foliage insects. As previously mentioned, nesting success for cavity-nesting species was lower in the first year following fire though their abundance was higher both 0-1 year postburn and 3-6 years postburn. There was a small net loss of snags preferred for nesting ( $\sim 1.5 \text{ ha}^{-1}$ ), but this did not appear to deter breeding cavity nesters. Hutton's Vireo not only had reduced abundance on burned sites, but also had lower nest success on burned plots. One explanation is that individuals leave burned areas following reduced success. While this was not directly tested, it is consistent with my result that abundance differences were not found until 3-6 years postburn while nest success differences emerged in the first year following fire.

I did not find large changes in community composition related to burning nor were any species clearly restricted to burned or unburned areas. In addition, approximately half of the individual species did not show a response to fire. In light of nest success results, it is interesting that the abundance of Steller's Jay, an important nest predator, and Brown-headed Cowbird, a brood parasite, were not affected by burning though both predation and parasitism had some increases. I was somewhat surprised to find that the abundance of low-nesting species was similar between burned and unburned sites though nest success was affected for three of these species. Another species, Cassin's Vireo, had no changes in nesting success despite its tendency to nest low and its similarity to Hutton's Vireo who suffered lower reproductive success. These results are

similar to bird responses following repeated burning in Ohio where six species (four negative, two positive) out of 30 responded (Artman et al. 2001). Emlen (1970), who found little response within 5 months by birds following a prescribed fire, postulated that site fidelity might stabilize populations following disturbance if critical resources are not severely altered. My results seem to support this hypothesis for many species.

Fire severity and time since fire are two factors known to be important in predicting change after fire (Smucker et al. 2005). While my results are consistent with some studies, they are different for others, an effect that seems related to the severity of the fires studied as discussed in Chapter 1. My results more closely matched those from other prescribed burns though this varied by species. An important factor in determining response seems to be not only general location of nesting (such as nest height) or foraging preferences, but also how prone the particular vegetation used was to burning and how quickly it recovers. While this hypothesis was suggested by the nest success data, it may also explain the species-specific variation in population response with fire severity. Examining the specific nesting relationships, fire effect seems to be mostly related to loss of cover in fire-prone vegetation. Nesting success was only altered for species who build nests in areas prone to fire that do not recover quickly such as mature shrubs. Additionally, consequences of merely nesting within a burned area were only found for Black-headed Grosbeaks and cavity nesting species as a group. This does not explain all the results, because canopy-foraging species were affected even though this habitat is relatively unaffected by these types of fires.

Another interesting result is that many of the effects of the nest site were clearer when burning effects were added and thus alteration of the vegetation, in some ways, may be revealing the relationship between nest sites and nesting success. I suggest that the effect of burning is primarily related to visually-oriented predators which are better able to detect nests and parental behavior where fire has reduced available cover. This is supported by the finding that rates of parasitism increased while abundance of brood parasites, which use visual clues to find nests, did not. Since nest sites were examined as groups of correlated variables measured in close proximity to the nest ( $\leq 11.3$  m), it was hard to tell if the effect was related to alteration of potential prey sites and thus searching efficiency. I hope to examine the mechanisms behind this alteration in the link between nest success and nest-site selection in the future.

Fire is a disturbance that maintains heterogeneity in space and time, and thus it is very difficult to directly monitor changes to bird populations over a large space and over many years, even if fires were not suppressed. Results of this study indicate that burn history of the plot matters and indicates that effects on a broader scale than the nest-site are important. For instance, while I found that the choice of snag for nesting did not affect nesting success, success was lower on recently burned areas. Additionally, the relationship between nest success and nest site was altered when the nest was located in areas of different burn histories.

In general, the strongest effects were found for areas that had been burned less than 2 years. Vegetation re-grows and thus alteration lessens with time. Some effects that lasted beyond 2 years were somewhat surprising such as the reduction of canopy

foraging species and the effects on nesting success. I was unable, however, to look at effects beyond 6 years following burning.

While cowbird parasitism is often associated with disturbance, it is usually associated with livestock use and residential areas (Airolo 1986). Pack stations can also be a source of cowbirds in more remote forest areas though none occur in this study area (Verner and Ritter 1983). Though the study area is approximately 5 km from any significant human habitation, this food source in addition to dispersed cattle grazing on Forest Service lands may allow for cowbird populations to invade. Cattle arrival dates have been associated with parasitism risk and cattle arrive relatively early at this elevation (Purcell and Verner 1999). In addition to the finding of high parasitism rates in an area that would not generally be considered highly suitable for cowbirds, I found that cowbird parasitism increased following prescribed fire. Because abundance data did not show an increase in numbers of cowbirds, it seems likely that nests and/or nesting activities became more visible. Additionally, the effect lasted 3-6 years postburn.

Though I was primarily interested in ecology of fire-adapted ecosystems, I was also able to make observations about the effect of spring prescribed fire on vegetation. The first application of fire did not greatly affect vegetation and in fact was not even enough to offset ongoing densification. This may be why so many species did not respond to fire. It seems we have only just begun to reduce the accumulated fuels and reverse structural changes in these forests, but we cannot ignore the fact that without fuel reduction efforts, wildfires will be more intense and cover broader areas. Thus attempts at fire exclusion will not ultimately benefit those species that have negative responses to

fire. In addition, the landscape where study is conducted is altered. Estimates of tree densities were very high (1,665 trees ha<sup>-1</sup> >3cm) exceeding historical estimates (Minnich et al. 1995) by an order of magnitude. For birds, fire exclusion may support unusually high populations of those species favored by dense forest structure (Chapter 1). Recently arrived species such as invasive plants and the Brown-headed Cowbird may create additional effects of fire not present during historic fire periods (Chapter 3). Prescribed fire did not affect species or habitats uniformly, so in predicting effects we need to consider factors such as preferred vegetation and its flammability, potential predators and their search strategies, and timing of burning in relation to breeding activities. While these prescribed fires may have different attributes than natural fires, their continued use for forest management justifies investigating their impacts and allows us to examine how species respond to disturbance within a replicated study design. In addition, altering vegetation reveals ecological patterns and gives us insight into the relationship between species and habitat in a context of change.

## LITERATURE CITED

- Airola, D. A. 1986. Brown-headed cowbird parasitism and habitat disturbance in the Sierra Nevada. *Journal of Wildlife Management* 50: 571-575.
- Artman, V., E. Sutherland and J. Downhower. 2001. Prescribed burning to restore mixed-oak communities in Southern Ohio: effects on breeding-bird populations. *Conservation Biology* 15: 1423-1434.
- Emlen, J. T. 1970. Habitat Selection by Birds following a Forest Fire. *Ecology* 51: 343-345.
- Granholm, S. L. 1974. Effects of Surface Fires on Birds and their Habitat Associations in Coniferous Forests of the Sierra Nevada, California. Department of Zoology, University of California, Davis:130.
- Kotliar, N. B., S. 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*.
- Purcell, K. L. and J. Verner. 1999. Research and management of the Brown-headed Cowbird in Western landscapes. Abundance and rates of brood parasitism by Brown-headed Cowbirds over an elevational gradient in the southern Sierra Nevada, Cooper Ornithological Society. 18: 97-103.
- 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.
- Verner, J. and L. V. Ritter. 1983. Current status of the Brown-headed Cowbird in the Sierra National Forest. *Auk* 100: 355-368.

**Appendix A.** Direct losses of nests recorded during prescribed burns on five plots. These are only nests that were active during burning. Failure includes those lost in fire, and nests of Northern Flicker and Red-breasted Sapsucker were not monitored through the nest cycle. Burns occurred on 4 April 2002, 11 April 2002, 9 April 2002, 10 June 2003, and 20 June 2003.

	Number of nests	Number failed	Number destroyed by fire
Brown Creeper	1	1	1
Red-breasted Nuthatch	1	0	0
Northern Flicker	3	?	0
White-headed Woodpecker	1	0	0
Red-breasted Sapsucker	2	?	0
Spotted Towhee	2	1	1
Dark-eyed Junco	3	1	2
Black-headed Grosbeak	3	0	0
Hutton's Vireo	6	4	0
Cassin's Vireo	1	0	0
<b>TOTAL</b>	<b>23</b>	<b>~7</b>	<b>4</b>

**Appendix B.** Species list of common and scientific names with presence by treatment, and guild assignment. Guilds are assigned for species with total counts > 10 over all years.

Common name	Scientific name	Presence by treatment <sup>a</sup>	Nesting guild <sup>b</sup>	Migratory status <sup>c</sup>	Habitat association <sup>d</sup>	Foraging guild <sup>e</sup>
Mallard	<i>Anas platyrhynchos</i>	Ba				
Sharp-shinned Hawk	<i>Accipiter striatus</i>	U				
Cooper's Hawk	<i>Accipiter cooperii</i>	all				
Red-tailed Hawk	<i>Buteo jamaicensis</i>	all				
Mountain Quail	<i>Oreotyx pictus</i>	all	GN	RS	PA	UF
Band-tailed Pigeon	<i>Columba fasciata</i>	all	LN	SD	OA	CF
Mourning Dove	<i>Zenaida macroura</i>	all	NA	RS	PA	UF
Northern Pygmy-Owl	<i>Glaucidium gnoma</i>	U, P				
White-throated Swift	<i>Aeronautes saxatalis</i>	all	NA	LD	PA	AF
Anna's Hummingbird	<i>Calypte anna</i>	all	NA	SD	NA	UF
Calliope Hummingbird	<i>Stellula calliope</i>	U, P				

**Appendix B.** continued

Common name	Scientific name	Presence by treatment <sup>a</sup>	Nesting guild <sup>b</sup>	Migratory status <sup>c</sup>	Habitat association <sup>d</sup>	Foraging guild <sup>e</sup>
Rufous Hummingbird	<i>Selasphorus rufus</i>	U				
Belted Kingfisher	<i>Ceryle alcyon</i>	all	NA	SD	RA	NA
Acorn Woodpecker	<i>Melanerpes formicivorus</i>	all	SN	RC	OA	CF
Red-breasted Sapsucker	<i>Sphyrapicus ruber</i>	U, Bb, P	SN	NA	RA	BF
Downy Woodpecker	<i>Picoides pubescens</i>	all	SN	RS	RA	BF
Hairy Woodpecker	<i>Picoides villosus</i>	all	SN	RS	CA	BF
White-headed Woodpecker	<i>Picoides albolarvatus</i>	all	SN	RS	CA	BF
Northern Flicker	<i>Colaptes auratus</i>	all	SN	SD	PA	UF
Pileated Woodpecker	<i>Dryocopus pileatus</i>	all	SN	RS	CA	BF
Olive-sided Flycatcher	<i>Contopus cooperi</i>	all	HN	LD	PA	AF
Western Wood-Pewee	<i>Contopus sordidulus</i>	all	HN	LD	OA	AF
Hammond's Flycatcher	<i>Empidonax hammondii</i>	all	HN	LD	CA	AF

Appendix B. continued

Common name	Scientific name	Presence by treatment <sup>a</sup>	Nesting guild <sup>b</sup>	Migratory status <sup>c</sup>	Habitat association <sup>d</sup>	Foraging guild <sup>e</sup>
Dusky Flycatcher	<i>Empidonax oberholseri</i>	all	LN	LD	PA	AF
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	all	LN	LD	RA	AF
Black Phoebe	<i>Sayornis nigricans</i>	all	NA	NA	RA	AF
Western Kingbird	<i>Tyrannus verticalis</i>	P				
Cassin's Vireo	<i>Vireo cassinii</i>	all	LN	LD	RA	CF
Hutton's Vireo	<i>Vireo huttoni</i>	all	LN	RS	OA	CF
Warbling Vireo	<i>Vireo gilvus</i>	all	HN	LD	OA	CF
Steller's Jay	<i>Cyanocitta stelleri</i>	all	LN	RS	CA	NA
Western Scrub-Jay	<i>Aphelocoma californica</i>	all				
Common Raven	<i>Corvus corax</i>	all	HN	RS	NA	NA
Violet-green Swallow	<i>Tachycineta thalassina</i>	Ba				
Mountain Chickadee	<i>Poecile gambeli</i>	all	SN	RS	CA	CF

Appendix B. continued

Common name	Scientific name	Presence by treatment <sup>a</sup>	Nesting guild <sup>b</sup>	Migratory status <sup>c</sup>	Habitat association <sup>d</sup>	Foraging guild <sup>e</sup>
Bushtit	<i>Psaltriparus minimus</i>	all	LN	RS	NA	NA
Red-breasted Nuthatch	<i>Sitta canadensis</i>	all	SN	RS	CA	BF
Brown Creeper	<i>Certhia americana</i>	all	SN	RS	CA	BF
House Wren	<i>Troglodytes aedon</i>	Bba, P				
Bewick's Wren	<i>Thryomanes bewickii</i>	U				
Winter Wren	<i>Troglodytes troglodytes</i>	all	NA	RS	RA	UF
American Dipper	<i>Cinclus mexicanus</i>	P				
Golden-crowned Kinglet	<i>Regulus satrapa</i>	all	HN	RS	CA	CF
Ruby-crowned Kinglet	<i>Regulus calendula</i>	all	NA	LD	NA	CF
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	Bba				
Townsend's Solitaire	<i>Myadestes townsendi</i>	all	LN	SD	PA	NA
Hermit Thrush	<i>Catharus guttatus</i>	all*	LN	LD	CA	UF

**Appendix B.** continued

Common name	Scientific name	Presence by treatment <sup>a</sup>	Nesting guild <sup>b</sup>	Migratory status <sup>c</sup>	Habitat association <sup>d</sup>	Foraging guild <sup>e</sup>
American Robin	<i>Turdus migratorius</i>	all	LN	SD	RA	UF
Varied Thrush	<i>Ixoreus naevius</i>	Ba, P				
Wrentit	<i>Chamaea fasciata</i>	all	LN	RS	NA	UF
Cedar Waxwing	<i>Bombycilla cedrorum</i>	U, Ba, P	NA	SD	NA	NA
Orange-crowned Warbler	<i>Vermivora celata</i>	all	NA	LD	RA	CF
Nashville Warbler	<i>Vermivora ruficapilla</i>	all	GN	LD	OA	CF
Yellow-rumped Warbler	<i>Dendroica coronata</i>	all	HN	LD	CA	CF
Black-throated Gray Warbler	<i>Dendroica nigrescens</i>	all	LN	LD	OA	CF

<sup>a</sup>U = unburned sites, Bx = sites burned during study (x = b for before burning in 2001 and x = a for after burning 2002/03), P = postburn sites (burned previous to study)

<sup>b</sup>Nesting guilds: SN = snag nesting, GN = ground nesting, LN = low nesting, HN = high nesting

<sup>c</sup>Migratory status: LD = long distance migrant, SD = short-distance migrant, RS = resident

<sup>d</sup>Habitat associations: CA = conifer associated, OA = oak associated, RA = riparian associated, PA = open forest associated

<sup>e</sup>Foraging guilds: AF = aerial foraging, CF = canopy foraging, UF=understory foraging, BF = bark foraging, NA = no assignment

**Appendix C.** Means  $\pm$  se for nest site variables on sites with different burn histories for all years. Variables are measured in a 0.04 ha circle around the nest.

	Spotted Towhee			Dark-eyed Junco			Black-headed Grosbeak		
	Unburned	0-1 year postburn	3-6 years postburn	Unburned	0-1 year postburn	3-6 years postburn	Unburned	0-1 year postburn	3-6 years postburn
n	23	17	28	20	10	47	31	20	19
Large Trees	2.9 $\pm$ 0.4	2.6 $\pm$ 0.6	4.0 $\pm$ 0.4	3.9 $\pm$ 0.7	5.4 $\pm$ 1.0	4.5 $\pm$ 0.4	1.9 $\pm$ 0.3	1.0 $\pm$ 0.3	1.8 $\pm$ 0.6
Number of white leaf manzanita stems	31.2 $\pm$ 10.2	6.8 $\pm$ 2.7	2.1 $\pm$ 1.0	0.1 $\pm$ 0.1	3 $\pm$ 2.8	0.3 $\pm$ 0.3	40.4 $\pm$ 8.0	62.8 $\pm$ 20.8	17.2 $\pm$ 6.8
Average percent open sky	31.8 $\pm$ 3.5	36.1 $\pm$ 3.7	36.3 $\pm$ 3.6	16.3 $\pm$ 2.9	19.4 $\pm$ 4.7	25.6 $\pm$ 2.8	21.3 $\pm$ 3.4	23.1 $\pm$ 4.5	27.8 $\pm$ 5.6
Number of perennial species	5.9 $\pm$ 0.4	6.1 $\pm$ 0.8	6.2 $\pm$ 0.5	7.6 $\pm$ 0.5	5.3 $\pm$ 0.8	6.0 $\pm$ 0.3	6.5 $\pm$ 0.4	6.2 $\pm$ 0.5	7.4 $\pm$ 0.6
Number of snags	4.9 $\pm$ 1.3	6.7 $\pm$ 1.4	10.9 $\pm$ 2.4	3.2 $\pm$ 1.2	17.5 $\pm$ 4.5	9.6 $\pm$ 1.5	3.1 $\pm$ 1.0	11.1 $\pm$ 3.7	17.0 $\pm$ 5.6
Number of small stems	48.0 $\pm$ 10.3	22.6 $\pm$ 3.7	16.5 $\pm$ 3.2	16.4 $\pm$ 0.4	25.3 $\pm$ 6.7	13.7 $\pm$ 3.7	53.6 $\pm$ 6.5	76.8 $\pm$ 19.5	54.2 $\pm$ 12.6
Ratio pine to fir and cedar	6.1 $\pm$ 3.3	4.8 $\pm$ 2.8	3.6 $\pm$ 2.2	1.5 $\pm$ 0.8	1.0 $\pm$ 0.4	0.8 $\pm$ 0.2	5.4 $\pm$ 1.6	7.1 $\pm$ 4.1	7.2 $\pm$ 3.5
Ratio oak to conifers	0.5 $\pm$ 0.2	0.85 $\pm$ 0.21	0.59 $\pm$ 0.08	0.6 $\pm$ 0.1	0.58 $\pm$ 0.14	0.62 $\pm$ 0.06	1.1 $\pm$ 0.5	2.3 $\pm$ 1.0	1.2 $\pm$ 0.3
Percent cover mountain misery	68.5 $\pm$ 5.7	8.4 $\pm$ 2.3	7.0 $\pm$ 1.6	20.1 $\pm$ 6.3	36.1 $\pm$ 12.2	30.9 $\pm$ 3.7	51.5 $\pm$ 5.9	53.0 $\pm$ 6.9	45.4 $\pm$ 7.7
Nest height	--	--	--	--	--	--	2.9 $\pm$ 0.3	2.7 $\pm$ 1.8	3.2 $\pm$ 0.7
Concealment	86.8 $\pm$ 2.3	89.0 $\pm$ 3.0	89.8 $\pm$ 1.8	77.7 $\pm$ 4.6	80.8 $\pm$ 6.2	89.6 $\pm$ 1.6	60.6 $\pm$ 3.2	61.4 $\pm$ 4.6	65.3 $\pm$ 3.6

Appendix C. continued

	Hutton's Vireo			Cassin's Vireo			Random Points	
	Unburned	0-1 year postburn	3-6 years postburn	Unburned	0-1 year postburn	3-6 years postburn	Unburned	0-1 year postburn
n	33	30	28	39	7	35	138	70
Large Trees	4.1 ± 0.6	3.1 ± 0.4	3.8 ± 0.4	5.1 ± 0.5	4.3 ± 1.2	5.7 ± 0.4	2.9 ± 0.2	3.6 ± 0.3
Number of white leaf manzanita stems	10.9 ± 2.9	14.0 ± 2.9	0.4 ± 0.2	2.8 ± 1.2	2.1 ± 1.8	0.4 ± 0.3	12.9 ± 1.9	12.5 ± 2.3
Average percent open sky	15.7 ± 2.3	17.0 ± 2.9	14.4 ± 2.2	12.2 ± 1.9	19.1 ± 5.8	9.3 ± 1.5	19.2 ± 1.3	24.4 ± 2.7
Number of perennial species	6.2 ± 0.4	5.3 ± 0.5	6.6 ± 0.4	6.4 ± 0.4	4.9 ± 1.0	5.2 ± 0.3	4.9 ± 0.2	5.1 ± 0.2
Number of snags	5.0 ± 1.5	23.8 ± 4.9	8.0 ± 1.3	8.4 ± 2.2	13.1 ± 3.9	12.7 ± 2.0	11.2 ± 1.7	24.7 ± 3.3
Number of small stems	28.3 ± 3.6	39.8 ± 5.0	14.2 ± 2.1	21.4 ± 2.6	20.9 ± 4.5	14.1 ± 1.7	38.5 ± 2.8	42.9 ± 3.9
Ratio ponderosa pine to fir and cedar	6.0 ± 2.1	3.5 ± 1.3	0.3 ± 0.1	2.4 ± 1.0	1.7 ± 0.8	0.2 ± 0.1	3.8 ± 0.8	2.0 ± 0.4
Ratio oak to conifers	0.4 ± 0.1	0.6 ± 0.1	0.8 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.6 ± 0.1	1.2 ± 0.5	1.4 ± 0.7
Percent cover mountain misery	50.1 ± 6.1	39.9 ± 5.9	48.2 ± 2.6	19.8 ± 4.6	41.4 ± 12.0	14.4 ± 4.4	39.5 ± 2.5	41.7 ± 3.7
Nest height	5.3 ± 0.8	5.1 ± 0.6	8.5 ± 0.8	5.1 ± 0.6	4.2 ± 1.1	5.0 ± 0.5	--	--
Concealment	49.6 ± 2.9	46.1 ± 2.7	48.2 ± 2.6	28.6 ± 2.2	18.8 ± 2.7	22.8 ± 2.0	--	--

**Appendix D.** Relationship between nest age and date based on logistic-exposure model. Age is age of the nest in days from the first egg laid and date is day of year. *P*-values < 0.15 are shown in bold (the screening criterion).

	Spotted Towhee		Dark-eyed Junco		Black-headed Grosbeak		Hutton's Vireo		Cassin's Vireo	
	<i>X</i> <sup>2</sup>	<i>p</i>	<i>X</i> <sup>2</sup>	<i>p</i>	<i>X</i> <sup>2</sup>	<i>p</i>	<i>X</i> <sup>2</sup>	<i>p</i>	<i>X</i> <sup>2</sup>	<i>p</i>
Age	<b>22.23</b>	<b>&lt; 0.001</b>	0.46	0.50	<b>4.62</b>	<b>0.03</b>	1.48	0.22	<b>5.89</b>	<b>0.02</b>
Age <sup>2</sup>	<b>26.36</b>	<b>&lt; 0.001</b>	1.20	0.27	<b>7.76</b>	<b>0.01</b>	<b>2.24</b>	<b>0.13</b>	<b>3.83</b>	<b>0.05</b>
Age <sup>3</sup>	<b>27.24</b>	<b>&lt; 0.001</b>	1.44	0.23	<b>9.53</b>	<b>0.002</b>	<b>2.40</b>	<b>0.12</b>	<b>2.57</b>	<b>0.11</b>
Date	0.18	0.67	0.68	0.41	0.46	0.50	0.61	0.43	1.58	0.21
Date <sup>2</sup>	0.11	0.73	0.72	0.40	0.46	0.50	0.72	0.40	1.37	0.24

**Appendix E.** Relationship between nest success and burning. Statistics are from type III contrasts from logistic exposure model. Models were run sequentially starting with vegetation alone then burning alone. Year is used as a covariate with burning, but is not reported. Lastly vegetation variables with  $p \leq 0.10$  were combined with burning to look at interaction effects (note that specific interactions vary by species). Vegetation is from PCA plus concealment and nest height for non-ground nesters. Linear, quadratic, and cubic effects of age are included for all species except Dark-eyed Junco for which no time dependent effects were included. P-values < 0.05 are shown in bold.

	Spotted Towhee						Dark-eyed Junco						Black-headed Grosbeak					
	<u>vegetation</u>		<u>burning</u>		<u>combined</u>		<u>vegetation</u>		<u>burning</u>		<u>combined</u>		<u>vegetation</u>		<u>burning</u>		<u>combined</u>	
	$X^2$	$p$	$X^2$	$p$	$X^2$	$p$	$X^2$	$p$	$X^2$	$p$	$X^2$	$p$	$X^2$	$p$	$X^2$	$p$	$X^2$	$p$
PC1 (vertical structure)	0.00	0.96					0.65	0.42					1.03	0.31				
PC2 (canopy composition)	0.02	0.90					3.04	0.08			0.65	0.42	1.23	0.27				
PC3 (densification)	0.59	0.44					0.35	0.56					1.16	0.28				
Concealment	2.69	0.10			2.21	0.14	1.99	0.15					0.44	0.51				
Nest height	-	-					-	-					3.80	0.05			2.32	0.13
Burn history			0.37	0.42	2.12	0.35			2.54	0.28	2.19	0.33			2.31	0.31	<b>6.86</b>	<b>0.03</b>
Burn *concealment					1.98	0.37												
Burn*PC2											<b>8.45</b>	<b>0.01</b>						
Burn*nest height															<b>6.24</b>	<b>0.04</b>		

Appendix E. continued

	Hutton's Vireo						Cassin's Vireo					
	<u>vegetation</u>		<u>burning</u>		<u>combined</u>		<u>vegetation</u>		<u>burning</u>		<u>combined*</u>	
	$X^2$	$p$	$X^2$	$p$	$X^2$	$p$	$X^2$	$p$	$X^2$	$p$	$X^2$	$p$
PC1 (vertical structure)	0.00	0.98					0.53	0.47				
PC2 (canopy composition)	1.12	0.29					<b>7.51</b>	<b>0.01</b>			0.35	0.56
PC3 (densification)	0.30	0.59					<b>5.26</b>	<b>0.02</b>			<b>6.67</b>	<b>0.01</b>
Concealment	<b>5.66</b>	<b>0.02</b>			5.72	0.06	<b>5.46</b>	<b>0.02</b>			<b>9.85</b>	<b>0.002</b>
Nest height	0.01	0.91					1.73	0.19				
Burn history			5.72	0.06	0.55	0.76			0.09	0.93	1.87	0.39
Burn* concealment					0.06	0.97					0.32	0.57
Burn*PC2											1.13	0.29
Burn*PC3											0.36	0.55

\*burn sites 0-1 year postburn and 3-6 years postburn had to be combined for this species because of small sample size