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Black-backed Woodpecker MIS Surveys on Sierra Nevada National Forests: 2010 Annual Report

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Above: A male Black-backed excavating a nest cavity. Photo by Joseph Leibrecht.

Table of Contents

Table of Contents, continued.

List of Tables

List of Figures

List of Figures, continued.

List of Figures, continued.

Summary

The Black-backed Woodpecker (*Picoides arcticus*) was recently selected by the Pacific Southwest Region of the USDA Forest Service as a Management Indicator Species (MIS) for snags in burned forests across the ten Sierra Nevada national forest units in the Pacific Southwest Region: Eldorado, Inyo, Lassen, Modoc, Plumas, Sequoia, Sierra, Stanislaus, Tahoe, and the Lake Tahoe Basin Management Unit. In 2008 The Institute for Bird Populations collaborated with Region personnel on a pilot study that developed and field-tested survey procedures and collected preliminary information on Black-backed Woodpecker distribution across Sierra Nevada national forests (Siegel et al. 2008). We used the findings from the 2008 pilot study to inform the design of a long-term MIS monitoring program for Black-backed Woodpecker across ten national forest units of the Sierra Nevada, which we implemented in 2009 and continued in 2010. The primary goal of the program is to monitor trends in the amount of recently burned forest on the study area's ten national forests that is occupied by Black-backed Woodpecker, so that Forest Service personnel can evaluate the likely effects of forest plan implementation on Black-backed Woodpecker populations. Additional goals are to better understand Black-backed Woodpecker abundance, distribution, and habitat associations across the Sierra Nevada, to develop information that can inform effective conservation of Black-backed Woodpecker in the Sierra Nevada, and to collect information on other bird species utilizing burned forests.

During the 2010 field season, we used passive and broadcast surveys to assess Black-backed Woodpecker occupancy at 860 survey stations arrayed across 49 recent fire areas (1-10 years post-fire) throughout our study area, adding to the 899 survey stations in 51 fire areas visited in the 2009 field season. A total of 545 stations were visited in both years, providing for direct year-to-year comparisons of results. We also collected on-the-ground habitat data at each survey station, and collected additional habitat data from existing GIS sources. In addition, we conducted passive point counts for other bird species at 420 of the Black-backed Woodpecker survey stations.

In 2010 we detected Black-backed Woodpeckers at 132 survey stations distributed across 29 of the 49 fire areas we surveyed, including fire areas on nine of the ten national forest units in our

study area—the only forest where we did not detect the species was Sierra NF, where our random sample yielded only one fire area to survey. We detected Black-backed Woodpeckers on both the west and east sides of the Sierra crest, and across nearly the full latitudinal range of our study area.

Prior to formal analysis, we examined the distribution of stations with detections and without detections (non-detection stations) in relation to environmental covariates expected to influence Black-backed Woodpecker occupancy rates. Specifically, we examined habitat type (California Wildlife Habitat Relationships [CWHR] classification), elevation, pre-fire canopy cover, number of years since fire, fire-induced change in canopy cover, and latitude. For our formal Black-backed Woodpecker occupancy analysis, we used a novel hierarchical modeling approach that incorporated separate but linked models for the observation (detection) and state (occupancy) processes. Additionally, the state process was split into two hierarchical levels, to separately model whether a fire was occupied (fire-level occupancy) and whether survey stations within a fire were occupied (station-level occupancy). For each occupancy probability model, we defined a logit-linear model that included covariates examined or derived as part of our data exploration. Fire-level covariates included fire age, while station-level covariates included latitude, snag basal area, change in percent canopy cover, and elevation adjusted for latitude (residuals of a regression of latitude on elevation). For our detection probability model we defined a logit-linear model that included indicator variables to account for variation in detection probability associated with count duration (2- vs. 3-minute interval), count type (passive vs. broadcast survey interval), and seasonality (Julian day).

Mean occupancy probability for stations surveyed was 0.227 during 2009 (95% credible interval: 0.209 – 0.248) and 0.231 during 2010 (95% credible interval: 0.199 – 0.271). Assuming that our sample was representative of habitat yielded by all fires in the study area that burned in the 10 years prior, we estimate that approximately 61,696 ha (i.e., 22.7%) of the 271,788 ha of burned forest on the ten national forest units within our sampling frame was occupied by Black-backed Woodpeckers in 2009 (or a range based on the 95% credible interval of 71,921 – 93,610 ha), and approximately 58,367 ha (i.e., 23.1%) of the 252,673 ha of burned forest was occupied in 2010 (95% credible interval: 50,282 – 68,474 ha).

These occupancy estimates indicate no significant differences in Black-backed Woodpecker occurrence in the sampled areas between 2009 and 2010. While the mean occupancy probability for 2009 provided above (0.227) is slightly lower than the 2009 value indicated in previous work (0.253; Siegel et al. 2010), the 95% credible intervals fully overlap and the slight difference in means is due to refined estimates of detectability resulting from an extra year's data. While a higher proportion of sampled fires were estimated to be occupied in 2010 than 2009, this difference is likely due to the random selection of fires, as fires that were surveyed in both years showed no difference in average occupancy probability. Moreover, a logit-linear model that included survey year as a covariate of fire occupancy found no significant relationship for that model term. Consequently, we conclude that the proportion of fires occupied in the study region by Black-backed Woodpeckers, as well as the proportion of area within each fire utilized by woodpeckers, remained stable between 2009 and 2010.

Our logit-linear model for occupancy probability suggested strong spatial variation in Black-backed Woodpecker occurrence related primarily to elevation (more common at higher elevations within the range of elevations we surveyed), fire age (more common in recent fire areas), and canopy cover change (more common in higher severity fires with greater canopy cover change). Our findings with respect to fire age are in general agreement with published data from other studies conducted elsewhere in the Black-backed Woodpecker range that find the species to be most common within a few years of a high-severity fire. Our finding of the importance of canopy cover change is consistent with the suggestion elsewhere that severe fires are necessary to kill enough trees to provide foraging and nesting resources for the woodpeckers. The importance of this factor was less apparent in the previous year's analyses.

Count duration, seasonality, and, especially, count type (passive versus broadcast) had marked effects on detection probability. Sampling in 2010 consisted of 11-minute passive surveys (with 5 intervals) and 6-minute broadcast surveys (with 3 intervals). Our estimate of overall probability of detection during a broadcast survey on its own was 0.755 (95% credible interval: 0.549 – 0.900); when combined with a passive survey it increased to 0.873 (95% credible interval: 0.707 – 0.932). Our estimates of detection probability indicate that using just passive 2-

min point count intervals, an observer would need 28 intervals to achieve a 95% probability of detecting one or more Black-backed Woodpeckers at a survey station.

We also used the combined 2009 and 2010 dataset to explore the potential impact of post-fire salvage logging on Black-backed Woodpecker occupancy. In contrast to previously published findings from elsewhere in the species' range, we found occupancy not to be affected by salvage logging status, at least after accounting for measured differences in snag basal area. This result suggests that salvage logging may reduce Black-backed Woodpecker occupancy probability to the extent that it reduces snag basal area, but the fact of salvage logging having occurred *per se* does not appear to reduce occupancy rates. Black-backed Woodpeckers were detected at 25% of salvaged stations, whereas they were detected at only 20% of unsalvaged stations. The relationship between salvage logging and Black-backed Woodpecker occupancy deserves further exploration.

In addition to Black-backed Woodpeckers, our passive point counts combined across both years yielded detections of 118 other bird species within the fire areas. The five most frequently detected species were Mountain Chickadee (*Poecile gambeli,* 455 detections), Dark-eyed Junco (*Junco hyemalis*; 417 detections), Western Wood-Pewee (*Contopus sordidulus*, 426 detections), Western Tanager (*Piranga ludoviciana*; 429 detections), and Steller's Jay (*Cyanocitta stelleri*, 423 detections); these and dozens of additional species were detected frequently enough to facilitate analysis of the effects of fire severity and fire age on bird assemblages in post-fire forest stands. Preliminary results for a multi-species hierarchical occupancy model analyzing community dynamics suggest that overall bird richness increases and then decreases as post-fire stands age during the ten years after a fire, leading to greatest richness at middle-aged stands (i.e., around 5 years post-fire). This fire-age effect is likely due to the existence of considerable underlying turnover in species composition, with certain species favoring young burns and other species favoring older burns. Additionally, richness was highest at stations with intermediate levels of fire severity (as measured by percent canopy cover change), suggesting that fire areas with a heterogeneous mix of burned trees and live trees may support the greatest diversity of bird species as fires age.

In the coming months we aim to formalize results presented here and submit two manuscripts for publication in peer-reviewed journals. The first manuscript will present our analyses exploring the relationship between Black-backed Woodpecker occupancy and post-fire salvage logging. The second manuscript will focus on the multi-species analysis, and will document the dynamic process through which bird species composition is determined and changes in post-fire areas.

We are pleased to have recently completed our 2011 field season—the third year of full-scale Black-backed Woodpecker MIS monitoring on greater Sierra Nevada national forests. This third year of sampling will allow us to model for the first time the colonization and extinction probabilities of stations over time, thus allowing more direct inference on the underlying dynamics in woodpecker occurrence.

Introduction

The Black-backed Woodpecker (*Picoides arcticus*) was recently selected by the Pacific Southwest Region of the USDA Forest Service as a Management Indicator Species (MIS) for snags in burned forests across the ten Sierra Nevada national forest units in the Pacific Southwest Region: Eldorado, Inyo, Lassen, Modoc, Plumas, Sequoia, Sierra, Stanislaus, Tahoe, and the Lake Tahoe Basin Management Unit (USDA Forest Service 2007a, 2007b). The MIS approach identifies species whose population changes are believed to indicate the effects of management activities (USDA Forest Service 2007a). The habitat needs of MIS are to be considered in the establishment of forest plan objectives for important wildlife and fish habitat, and as forest plans are implemented through individual projects, Forest Service managers are to assess their effects on MIS habitat (USDA Forest Service 2007a). Additionally, MIS population monitoring is used to assess the outcomes of forest plan implementation, since it is impossible to monitor the status or population trend of all species (USDA Forest Service 2007a). Population monitoring is thus an integral component of the MIS approach.

Black-backed Woodpecker throughout the Sierra Nevada is not well-monitored by other multi-species, regional monitoring programs. Two large-scale, annual bird monitoring programs, the Breeding Bird Survey (BBS; Sauer et al. 2008) and the Monitoring Avian Productivity and Survivorship Program (MAPS; DeSante et al. 2008), detect Black-backed Woodpecker throughout the region in small numbers, but due in part to the ephemeral nature of the species' preferred habitat, neither program yields data that are adequate for regional MIS monitoring. Although Black-backed Woodpecker was detected on 13 Sierra Nevada BBS routes on or adjacent to Sierra Nevada national forests between 1991 and 2006 (Sauer et al. 2008), the data are too sparse for estimating the species' regional population trend (Sauer et al. 2008). Black-backed Woodpeckers were captured at five of 29 MAPS stations that operated in the Sierra Nevada physiographic province (including MAPS stations operating on national forests, national parks and private lands), but only rarely; overall just 0.023 adults and 0.005 young were captured per 600 net-hours in the region (Siegel and Kaschube 2007). These data are insufficient for estimating population trends and adult survival rates, or for calculating meaningful productivity indices.

Most of what is known about Black-backed Woodpecker ecology and population dynamics comes from elsewhere in the species' range. Black-backed Woodpeckers occur in conifer forests from western Alaska to northern Saskatchewan and central Labrador, south to southeastern British Columbia, central California, northwestern Wyoming, southwestern South Dakota, central Saskatchewan, northern Minnesota, southeastern Ontario, and northern New England (NatureServe 2007; Fig 1a). Outside of the breeding season, individuals may move to areas south of the breeding range, with occasional large irruptions (Dixon et al. 2000). In California, Black-backed Woodpeckers occur from the Siskiyou Mountains, Mount Shasta, and Warner Mountains south through the Cascade Range and the Sierra Nevada to Tulare County (California Department of Fish and Game 2005; Fig. 1b).

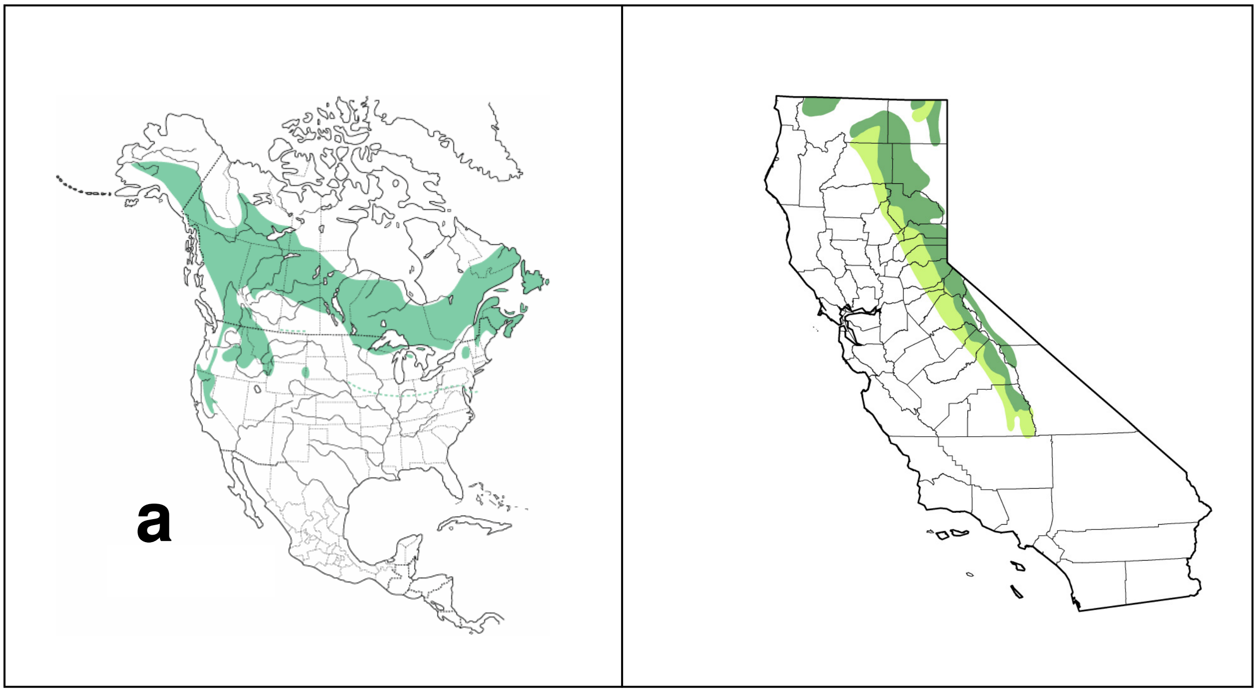

Figure 1. Distribution of Black-backed Woodpecker across (a) North America (figure from Dixon et al. 2000) and (b) California (figure from California Department of Fish and Game 2005). In part (b), light green indicates winter range, dark green indicates year-round range, though CDFG personnel have more recently indicated they are unable to find evidence for the altitudinal migration suggested by the map.

Although Black-backed Woodpecker can be found in unburned forest stands throughout its range, the species appears to be most abundant in stands of recently fire-killed snags (Hutto

1995, Kotliar et al. 2002, Smucker et al. 2005). Black-backed Woodpeckers foraging in burned forests feed primarily on wood-boring beetle larvae (Villard and Beninger 1993, Murphy and Lehnhausen 1998, Powell 2000), although some studies have also reported or inferred foraging on bark beetle larvae (Lester 1980, Goggans et al. 1988). Although bark beetles and wood-boring beetles share important life-history characteristics (both spend a prolonged portion of their life-cycle as larvae inside dead or dying trees) they also exhibit differences that may be important in their ecological interactions with Black-backed Woodpeckers. Bark beetles are small (generally <6 mm in length), numerous, often able to attack live trees, and generally remain as larvae in bark less than a year before emerging as adults (Powell 2000). In contrast, wood-boring beetles have much larger larvae (up to 50 mm long), are less numerous, and can remain as larvae in dead wood for up to three years (Powell 2000). Additionally, most wood-boring beetles are unable to attack living trees, and concentrate heavily in fire-killed wood, which some genera have been shown to find by sensing smoke or heat (reviewed in Powell 2000). Black-backed Woodpecker preference for wood-boring beetles could thus either drive or result from the species' proclivity to forage and nest in or near forest stands that have recently burned.

Although Black-backed Woodpecker shows a strong association with burned stands of conifer forest, the species is not closely tied to any particular tree species or forest type. Studies from different parts of its range report preferential foraging on Lodgepole Pine (*Pinus contorta*; Bull et al. 1986, Goggans et al. 1989), spruce (*Picea* sp.; Villard 1994, Murphy and Lehnhausen 1998), White Pine (*Pinus strobus*; Villard and Beninger 1993), and in California, Red Fir (*Abies magnifica*; Raphael and White 1984).

In 2008 The Institute for Bird Populations collaborated with Region personnel on a pilot study that developed and field-tested survey procedures and collected preliminary information on Black-backed Woodpecker distribution across Sierra Nevada national forests (Siegel et al. 2008). We used the findings from the 2008 pilot study to inform the design a long-term MIS monitoring program for Black-backed Woodpecker across ten national forest units of the Sierra Nevada. The primary goal of the program is to monitor trends in the amount of recently burned forest on the study area's ten national forests that is occupied by Black-backed Woodpecker, so that Forest

Service personnel can evaluate the likely effects of forest plan implementation on Black-backed Woodpecker populations. Additional goals are to better understand Black-backed Woodpecker abundance, distribution, and habitat associations across the Sierra Nevada, to develop information that can inform effective conservation of Black-backed Woodpecker in the Sierra Nevada, and to collect information on other bird species utilizing burned forests. The Institute for Bird Populations collaborated with the Forest Service to launch the first season of full-scale MIS monitoring for Black-backed Woodpecker in 2009 (Saracco et al. 2011, Siegel et al. 2010), based on finding and recommendations in Siegel et al. (2008).

In 2010 we continued Sierra-wide MIS monitoring for Black-backed Woodpeckers. Here we detail the results of this second year of full-scale MIS monitoring in recently burned forest stands.

Methods

Sample Design

We used the GIS data layer VegBurnSeverity08_1.mdb (obtained from http://www.fs.fed.us/r5/rsl/clearinghouse/gis-download), which indicates fire boundaries and fire severity of fires throughout California, to extract data for all fires that occurred between 2001 and 2010 and that included at least 50 ha of conifer forest that burned at mid-severity and/or high-severity on one or more of the ten national forest units in our study area. In a few cases we were unable to determine in advance whether individual fire areas included burned conifer forest; these information gaps were resolved with site visits, after which the fire area was either included in the sampling frame, or discarded.

These selection criteria yielded 65 fire areas, to which we assigned a random priority order. Selected fires included both a portion of the fires that were previously sampled in 2009, and fires that would be new to the survey. Our intention was to survey the first 50 fire areas on the list in

2010, but if that proved impossible, we would discard fire areas according the priority order, to avoid biasing the sample.

Data Collection

All data collection procedures remained consistent with protocol established for the 2009 field season, unless noted otherwise.

Establishing survey stations. The fire areas we selected varied greatly in size, from 107 ha (2001 White Fire on Stanislaus NF) to 61,261 ha (2002 McNally Fire on Sequoia NF). At the smaller fire areas, a 2-person team could easily saturate the fire area with survey effort in a single morning; however saturating the larger fire areas with survey effort could require weeks of work. We limited survey effort to what could be achieved by a 2-person team in one day, generally surveys at about 20 survey stations.

For fires that we did not previously survey in 2009, we determined where within the fire area to place our survey stations by using GIS to randomly select a ‘survey target point’ somewhere within the perimeter of each fire area, and indicating that point on field maps given to field crews. Crews were instructed to establish their survey stations as close to the survey target point as possible, using the following rules:

> 1 – If trails or roads passed through the fire area, survey stations were placed along them, such that the point along the road and trail network that was closest to the survey target point AND lay within low- mid- or high-severity burned conifer forest was included within a contiguous array of survey stations, spaced 250 m apart. Survey stations that were placed along a road were offset 50 m from the actual road in a randomly selected direction, unless only one side of the road was accessible (due to cliffs, for example) or only one side of a road was burned.

2 – If no trails or roads bisected the fire area, crews established an array of evenly spaced (250 m between stations) off-trail survey stations, as close to the target survey point as reasonably possible, without compromising safety or requiring additional days of hiking to access.

At the larger fire areas we thus sampled only a fraction of the total land area, but that fraction was randomly selected, within reasonable accommodations for accessibility and safety.

For fire areas that were previously surveyed in 2009, we simply used the same survey stations that were established by our field crews in 2009, using the placement rules described above. On rare occasions where survey stations established in 2009 were inaccessible due to changes in the landscape, later-lingering snowpack, etc., substitute stations were established as close as possible to the previous stations following the previously described rules.

Broadcast surveys. At each survey station we conducted a 6-min broadcast survey to elicit responses from Black-backed Woodpeckers. We used FoxPro ZR2 digital game callers to broadcast electronic recordings of Black-backed Woodpecker vocalizations and drumming. The electronic recording we broadcast was obtained from The Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology (G.A. Keller, recordist), and included the *scream-rattle-snarl* vocalization, *pik* calls, and territorial drumming.

We began the 6-min broadcast survey (Fig. 2) at each survey station by broadcasting the recording of Black-backed Woodpecker vocalizations and drumming for approximately 30 seconds at a standardized volume, and then quietly listening and watching for Black-backed Woodpeckers until two minutes had elapsed (including the 30-second broadcast period). At two minutes into the survey we again broadcasted the 30-second recording, and then quietly listened and watched until a total of four minutes had elapsed since the beginning of the survey, at which point we repeated the sequence of broadcasting and listening one more time, yielding three 2-min survey intervals. When Black-backed Woodpeckers were detected, we recorded their initial distance and bearing from the observer, whether species identification was confirmed visually, age (adult or juvenile) and sex (male, female, or unknown) of each bird, and whether the individual performed territorial drumming or vocalized. Black-backed Woodpecker surveys generally began within 10 min of official local sunrise, and were always completed by 3.5 h after sunrise.

Passive surveys and multi-species point counts. At approximately half (420 of 860) of the survey stations (generally every second station), we *preceded* the broadcast survey with an 11-min passive point count to count all birds of any species (including Black-backed Woodpecker). The 11-min point count consisted of a 3-min interval immediately followed by four 2-min intervals (Fig. 2). The 11-min point count represents an increase in passive survey time from the 2009 season, where only 5-min point counts were used. However this increase in passive survey length was counter-balanced by eliminating the 3-min passive woodpecker survey we previously conducted at survey stations where multi-species point counts were not conducted. This change reflects analyses of the 2009 data (Siegel et al. 2010), which revealed that the 3-min passive survey added very little to overall Black-backed Woodpecker detection probability. Point counts were divided into five intervals to yield additional information for assessing detection probability of Black-backed Woodpecker and other species detected during the counts. Observers estimated the horizontal distance, to the nearest meter, to each bird detected. Estimating distance to each bird provides additional information for estimating detection probability, in a distance sampling framework (Buckland et al. 2001). The observers also recorded whether each bird ever produced its territorial song during the point count. Additional details of the point count methodology are provided in Siegel et al. (2009).

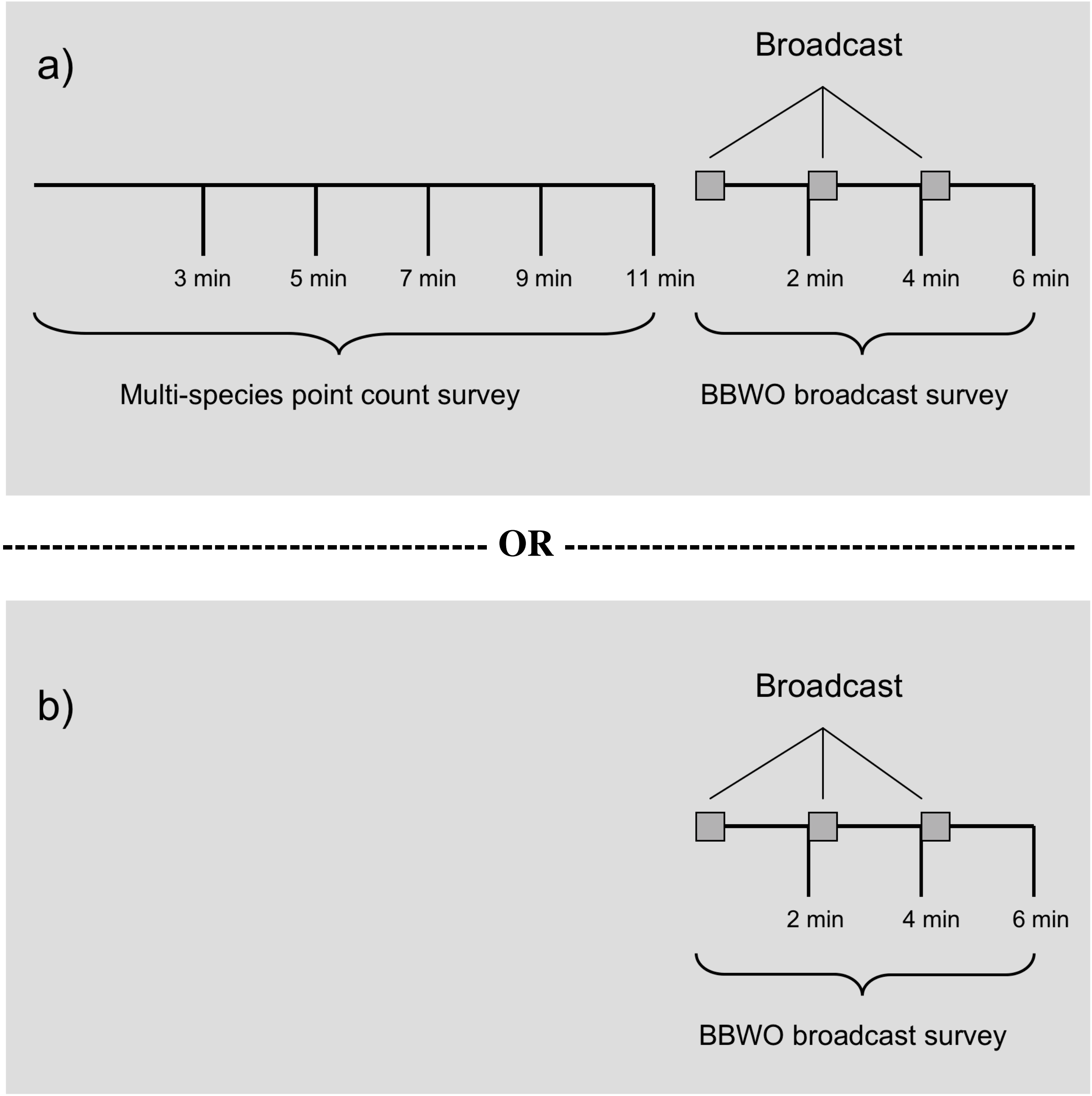

Figure 2. Schematic diagram of our survey methodology for detecting Black-backed Woodpeckers. Dark gray squares indicate period of actively broadcasting Black-backed Woodpecker drumming and vocalizations; black line segments indicate periods of passive observation. Observers alternated between method (a) and method (b) at successive survey stations.

Habitat and other ancillary data. After completing point counts and broadcast surveys each day, observers returned to the survey stations to collected cursory habitat data. In addition to recording UTM coordinates, they classified the habitat within a 50-m radius plot centered on the survey station, according to the California Wildlife Habitat Relationships (CWHR) habitat classification system (California Department of Fish and Game 2005). They also characterized the abundance and size of snags within the plot, estimated basal area of snags and live trees using a 10 BAF timber-cruising crutch, recorded the dominant pre-fire habitat type, and used CWHR-defined categories to classify the dominant tree size (including snags) and amount of remaining live canopy cover. Additional details of the methods for collecting habitat data are provided in Siegel et al. 2010.

Data Analysis

Exploratory analyses. Prior to formal modeling, we examined the distribution of stations with Black-backed Woodpecker detections and those without detections (non-detection stations) in relation to environmental covariates that we expected to influence Black-backed Woodpecker occupancy rates. Our preconceptions of important predictors of woodpecker occupancy were based on our own field experience and analyses from our 2009 surveys, as well as on previous research conducted on the species (Hanson and North 2008, Hutto 2008, Tremblay et al. 2009). We expected woodpecker occupancy to be influenced by fire age (higher occupancy in more recently burned areas), fire severity (higher occupancy in more severely burned areas), and pre- and post-fire habitat characteristics. Because habitat type is closely allied with elevation, we also examined the relationship between detections and elevation. In addition, based on our 2009 analysis, it appeared that there was also a geographic gradient in woodpecker distribution, with occupancy being more common in the northern latitudes of the study area than in the southern latitudes. Specific variables we examined included:

- California Wildlife Habitat Relationships (CWHR) classification (Mayer and Laudenslayer 1988), as determined on the ground by our crew.

- Elevation, collected in the field from GPS and USGS topographic maps but formalized from intersecting GPS points with a 30-m resolution California DEM (Gesch 2003, 2007).
- Basal area of snags (standing dead trees) recorded at the survey station based on the Bitterlich variable plot method (see Mueller-Dombois and Ellenberg 1974 for detail). There were a small number of survey stations (n=34) with missing snag basal area counts. These missing values were filled in with the mean basal area of all stations. There was additionally statistical evidence that basal area measurements may have been collected differently across survey years, although measurements were consistent within survey year. For this reason, snag basal area measurements were binned into four equal quantiles within each survey year, and these quantile bins were used for modeling. Quantile bins can be interpreted as counts of: none, low, medium, and high snag basal area.
- Pre-fire % tree cover calculated from 100-m resolution California Multi-source Land Cover Data (http://frap.cdf.ca.gov/data/frapgisdata/download.asp?spatialdist=1&rec=fveg02_2). We calculated this variable using Hawth's Tools (Beyer 2004) in ArcGIS (Ver. 9.2, Environmental Systems Research Institute, Redlands, CA) by averaging midpoints of the % tree cover variable (WHRDENSITY) at 100 m buffers around survey stations.
- Number of years since fire (range = 1 to 10 years).
- Change in percent canopy cover (a measure of burn severity) based on satellite derived relativized difference normalized burn ratio score RdNBR (Miller et al. 2009). Values of *cc* were summarized at 90-m^2 resolution by averaging 30-m^2 values from GIS layers provided by the US Forest Service (J. D. Miller) using the 'raster' package in R (http://cran.r-project.org/web/packages/raster/vignettes/Raster.pdf). See Fig. 3 for an example map showing percent canopy cover change values for the Gondola fire surveyed in 2009.
- Latitude (in decimal degrees) recorded from USGS topographic maps.
- Status of post-fire salvage logging at survey sites, as derived from the Forest ACtivity Tracking System (FACTS) database (http://www.fs.fed.us/r5/rsl/clearinghouse/gis-download.shtml). Survey points were queried for intersection, at a 50-m buffer, with accomplished forest activities that indicated post-fire salvage logging (codes 4113, 4114, 4230 and 4231, verified by J. Sherlock, US Forest Service), resulting in a binary variable representing the presence or absence of salvage logging in the immediate vicinity of survey

points. Long “snake-like” spatial polygons following roads or trails indicating post-fire hazard removal (pers. comm. J. Sherlock, US Forest Service) were excluded.

- Survey year (2009 versus 2010). In a multi-year survey, year-to-year changes in occupancy status are of obvious interest and, thus, these differences were explored thoroughly (see further *Results: Year-to-year differences*). In our final model, however, survey year was not included as a covariate of occupancy as the parameter did not end up contributing positively to overall model fit.

We examined the distribution of stations with detections and non-detection stations in relation to these predictor variables using bean plots, which we generated using the 'beanplot' package (Kampstra 2008) in R (R Development Core Team 2009). Bean plots facilitate comparison of distributions of data points by simultaneously displaying the data along with normal density traces of the data.

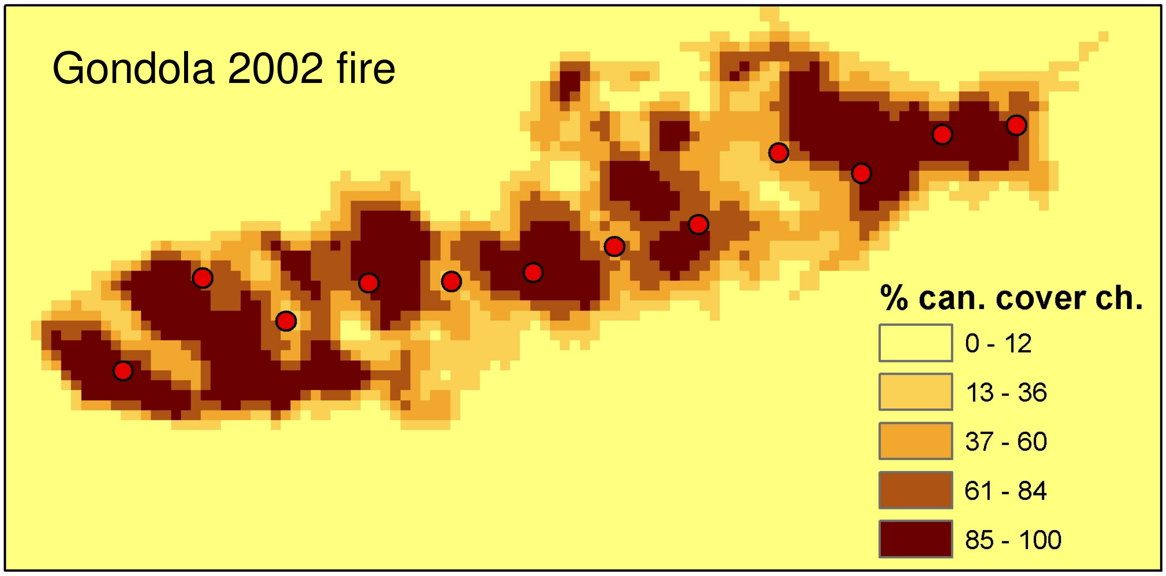

Figure 3. Example map of change in percent canopy cover values based on satellite derived relativized difference normalized burn ratio score RdNBR (Miller et al. 2009) for the Gondola fire surveyed in 2009. Values were summarized at 90-m^2 resolution by averaging 30-m^2 values from GIS layers.

Occupancy modeling. Occupancy models allow the estimation of the true presence (or occupancy) of a species at a location, unbiased by false absences. As survey data inherently contain an unknown quantity of false absences (i.e., non-detections when the species was truly present), it is critical that occurrence data collected by surveys be interpreted only after accounting for false absences. The framework presented here builds off the framework in the 2009 MIS report (Siegel et al. 2010) and subsequently published by Saracco et al. (2011).

We developed a model based on $i = 1,\ldots,N$ survey stations, $j = 1,\ldots,M$ fire areas, and $k = 1,\ldots,K$ survey intervals, combined across both survey years. Since occurrence status of woodpeckers could change between years at the same survey point, points and fires visited in both years were modeled unique to survey year, such that the occupancy status of a specific point in 2010 was independent of the occupancy status at that point in 2009 (but dependent on site- and fire-specific covariates that remain the same across years, see below). While this is potentially an invalid assumption, two years of survey data were insufficient to parameterize a model that would incorporate prior status into occupancy estimation. We hope to implement such a model following the completion of our 2011 field season.

In 2009 we surveyed $N_{2009} = 899$ stations within $M_{2009} = 51$ fire areas with (up to) $K_{2009} = 5$ intervals (1-2 passive survey intervals and 1-3 call broadcast survey intervals). In 2010 we surveyed $N_{2010} = 860$ stations within $M_{2010} = 49$ fire areas with (up to) $K_{2010} = 8$ intervals (0-5 passive survey intervals and 1-3 call broadcast survey intervals). Combined, our model had $N = 1759$ stations surveyed across both years (consisting of 1214 uniquely located points) within $M = 100$ fires across both years (consisting of 67 unique fires), with up to $K = 8$ survey intervals.

Based on a hierarchical modeling framework (Royle and Dorazio 2008), we developed separate but linked models for the observation (detection) and state (occupancy) processes. Building off of our 2009 analysis, the state process was further subdivided into two hierarchical levels separating the processes that determine whether a fire is occupied (more accurately, the portion of a fire surveyed by all points), and the processes that determine whether a point is occupied. This separation of fire-level and point-level occupancy processes better describe the heterogeneity of the system and the observed dynamics of woodpecker occupancy.

We modeled detections, $y(i, j, k)$, conditional on occupancy, $z(i, j)$, such that:

$$y(i,j,k) \mid z(i,j) \sim \text{Bern}(z(i,j) \cdot p_{ijk})$$

where $y(i, j, k) = 1$ if at least one Black-backed Woodpecker was observed at station i in fire area j during sampling interval k_i and $y(i, j, k) = 0$ otherwise; and $z(i,j)$ represents the true occupancy state of the station, such that $z(i,j) = 1$ if one or more woodpeckers were at the station and $z(i,j) = 0$ if no woodpecker was present. The probability of detecting at least one individual at an occupied station i in fire area j and interval k (i.e., $\Pr(y(i,j,k) = 1 \mid z(i,j) = 1)$) is a Bernoulli trial with success (i.e., detection) probability $p_{ijk} \times 1 = p_{ijk}$. The model assumes that the probability of identifying an unoccupied station as being occupied (i.e., $\Pr(y(i,j,k) = 1 \mid z(i,j) = 0)$ is a Bernoulli trial with probability $p_{ijk} \times 0 = 0$.

The data for this model, our observations $y(i, j, k)$, thus consisted of encounter histories for each station. In 2009, our field protocol consisted of what might be called a 'double' removal design (Farnsworth et al. 2002), such that only the first interval of encounter was recorded for the passive count intervals, and the count was discontinued following a detection on the broadcast count intervals. In 2010, a full detection history recording all detections or non-detections was recorded for all 5 passive survey intervals, while the removal design (i.e., discontinuing counts following the initial broadcast-based detection) was used for playback intervals. This level of detail resulted in 128 possible detection histories for 2010 alone, the results of which are summarized in Table 1.

We modeled the point-level latent occupancy state indicator variable, $z(i,j)$, as:

$$z(i,j) \sim \text{Bern}(w(j) \cdot \psi_{ij}),$$

such that ψ_{ij} is the Bernoulli probability of station i at fire j being occupied by at least one Black-backed Woodpecker. This is modified by the fire-level latent occupancy state indicator variable, $w(j)$, which is further modeled as:

$$w(j) \sim \mathrm{Bern}(\omega_j),$$

such that ω_j is the Bernoulli probability that fire *j* is occupied by at least one Black-backed Woodpecker.

We defined a logit-linear model to relate each Bernoulli-distributed probability to covariates selected *a priori* as important in influencing occupancy rates (see *Exploratory analyses*, above). First, ω_j, or fire-level occupancy, was modeled as a function of a random fire area effect independent of year (fire_j) and the fire age ($\mathrm{fire.age}_j$):

$$\mathrm{logit}(\omega_j) = \mathrm{fire}_j + \gamma_1 \mathrm{fire.age}_j,$$

where $\mathrm{fire.age}_i$ is the number of years since fire for fire area *j* (variable was normalized prior to analysis).

Second, ψ_{ij}, or point-level occupancy, was modeled as a function of four *a priori* selected covariates, such that:

$$\mathrm{logit}(\psi_{ij}) = \beta_0 + \beta_1 \mathrm{latitude}_{ij} + \beta_2 \mathrm{elev.res}_{ij} + \beta_3 \mathrm{snag.ba}_{ij} + \beta_4 \mathrm{cc}_{ij},$$

where $\mathrm{latitude}_{ij}$ is the (standardized) latitude in decimal degrees for survey station *i*, $\mathrm{elev.res}_{ij}$ is the residuals from a regression of elevation on latitude (see *Results: Exploratory Analyses for details*), $\mathrm{snag.ba}_{ij}$ is the quantile binned basal area of snags at survey station *i* (see *Methods: Exploratory Analyses* for detail), and cc_{ij} is the percent canopy cover change from pre-fire to post-fire at survey station *i*.

Table 1. Encounter history frequencies (numbers of survey stations) in the 2009 and 2010 Black-backed Woodpecker survey data. For passive surveys, the total number of survey intervals that one or more Black-backed Woodpeckers were detected in is listed (in 2009, a removal model was used for passive surveys, such that woodpecker detections were not recorded after an initial detection; in 2010, detections in all survey intervals were recorded). For playback survey capture histories, ones indicate detections, zeros indicate non-detections, and NAs indicate missing data (by design, see text for detail). Overall, Black-backed Woodpeckers were detected at 167 of the 899 stations that we surveyed in 2009 and at 132 of the 860 stations that we surveyed in 2010.

Year	Number of passive detections	Playback History			Frequency
		Interval 1	*Interval 2*	*Interval 3*	
2009	0	0	0	0	730
	0	0	0	1	31
	0	0	1	NA	37
	0	1	NA	NA	56
	1	0	0	0	12
	1	0	0	1	1
	1	0	1	NA	5
	1	1	NA	NA	27
2010	0	0	0	0	728
	0	0	0	1	38
	0	0	1	NA	26
	0	1	NA	NA	40
	1	0	0	0	3
	1	0	0	1	0
	1	0	1	NA	3
	1	1	NA	NA	7
	2	0	0	0	1
	2	0	0	1	0
	2	0	1	NA	0
	2	1	NA	NA	0
	3	0	0	0	2
	3	0	0	1	0
	3	0	1	NA	1
	3	1	NA	NA	4
	4	0	0	0	0
	4	0	0	1	0
	4	0	1	NA	1
	4	1	NA	NA	2
	5	0	0	0	0
	5	0	0	1	0
	5	0	1	NA	0
	5	1	NA	NA	1

Finally, we defined a logit-linear model for detection probability p_{ijk}:

$$\text{logit}(p_{ijk}) = \alpha_0 + \alpha_1 \text{effort}_k + \alpha_2 \text{type}_k + \alpha_3 \text{jday}_{ij}$$

where the variable effort_k represents interval length effort, such that $\text{effort}_k = 1$ if the interval length was 3 min (i.e., just the first passive-count interval; $k = 1$), and zero otherwise; type_k represents an indicator variable to denote whether the count interval was a passive survey ($\text{type}_k = 0$) or a call broadcast survey ($\text{type}_k = 1$); and jday_{ij} represents the Julian day (1 = January 1st, then normalized for model fit) of each survey to account for suspected seasonal differences in detectability.

We implemented a Bayesian analysis of the model using Markov chain Monte Carlo (MCMC) methods (Gilks et al. 1996) in the software package WinBUGS (Spiegelhalter et al. 2003). We used vague prior distributions for all model parameters. For all covariate effects in the model we used Norm(0, 0.001) priors. We assigned a prior of Norm(0, $1/\sigma_f^2$) for the random site effect (fire_j) in the model for ω_j, and a prior of Unif(0,10) for the variance parameter σ_f. For the intercepts of the p and ψ models, we defined priors for inverse-logit transformed parameters using Unif(0, 1). We conducted the WinBUGS analysis from R (R Development Core Team 2009) using the R2WinBUGS package (Sturtz et al. 2005). We provide WinBUGS model code in Appendix 1.

Results

Scope of Survey Work Completed

In 2010 we completed surveys fully to protocol at 49 fire areas (Table 2), including broadcast surveys and habitat assessments at 860 survey stations and passive, multi-species point counts at 420 of those stations. All surveys were conducted between 9 May and 18 July, 2010. Combined with data collected in 2009, we now have broadcast surveys and habitat assessments data at 1214 unique survey points within 67 fire areas, of which 545 survey points were surveyed in both years. We provide summary information about fire areas surveyed in 2010 in Table 2.

Black-backed Woodpecker Detections

In 2010 we detected Black-backed Woodpeckers at 132 survey stations (Table 2) distributed across 29 of the 49 fire areas we surveyed (Figs. 4-7). We detected Black-backed Woodpeckers on nine of the ten national forest units in our study area—the only forest where we did not detect the species was Sierra NF, where our random sample yielded only one fire area (the North Fork fire area; Fig. 6) to survey. Black-backed Woodpeckers were not detected in the North Fork fire area in 2009 either. As was the case in 2009, we detected Black-backed Woodpeckers on both the west and east sides of the Sierra crest, and across nearly the full latitudinal range of our study area, including the most northerly fire area we surveyed (the Fletcher fire area on the Modoc NF, which spans the California – Oregon border; Fig. 4), and the third most southerly fire area we surveyed (the Vista fire area on the Sequoia NF; Fig. 7). We provide UTM coordinates of all survey stations and maps indicating locations where Black-backed Woodpeckers were detected at: http://birdpop.org/Sierra/bbwo_results.htm.

Table 2. Summary information for each fire area surveyed during our 2009 or 2010 field season of Black-backed Woodpecker MIS monitoring on Sierra Nevada national forests.

Primary national forest	Fire name	Year of fire	Burned area (ha)	Dominant pre-fire habitat[1]	No. stations surveyed (2009)	No. stations surveyed (2010)
Eldorado	Freds	2004	1,814	Sierra Mixed Conifer	20	0
Eldorado	Plum	2002	417	Sierra Mixed Conifer	12	12
Eldorado	Power	2004	5,538	Sierra Mixed Conifer	20	20
Eldorado	Star	2001	4,979	Sierra Mixed Conifer	0	20
Inyo	Azusa	2000	164	Pinyon-Juniper	8	0
Inyo	Birch	2002	1,117	Pinyon-Juniper	19	0
Inyo	Crater	2001	1,118	Jeffrey Pine	20	20
Inyo	Dexter	2003	1,022	Jeffrey Pine	16	16
Inyo	Inyo Complex	2007	7,574	Ponderosa Pine	16	0
Inyo	Mclaughlin	2001	939	Jeffrey Pine	0	13
Inyo	Sawmill 2000	2000	144	Ponderosa Pine	5	0
Lassen	Brown	2009	684	Sierra Mixed Conifer	0	20
Lassen	Cone	2002	703	Eastside Pine	21	0
Lassen	Cub	2008	6,093	Sierra Mixed Conifer	0	20
Lassen	Onion 2	2008	1,067	White Fir	0	20
Lassen	Peterson Complex	2008	1,161	Eastside Pine	20	20
Lassen	Sugar Loaf	2009	3,127	Sierra Mixed Conifer	0	21
Modoc	Bell	2001	1,260	Juniper	20	20
Modoc	Bell West	1999	773	Eastside Pine	21	0
Modoc	Blue	2001	13,329	Eastside Pine	20	20
Modoc	Fletcher	2007	916	Ponderosa Pine	19	17
Modoc	High	2006	421	Eastside Pine	0	19
Plumas	Antelope Complex	2007	9,297	Eastside Pine	21	21
Plumas	Belden	2008	224	Mixed Hardwood-Conifer	0	13
Plumas	Boulder Complex	2006	1,475	Eastside Pine	20	20
Plumas	Bucks	1999	11,325	Sierra Mixed Conifer	20	0
Plumas	Devils Gap	1999	612	Sierra Mixed Conifer	20	0
Plumas	Frey	2008	9,664	Sierra Mixed Conifer	0	20

Table 2, continued.

Plumas	Horton 2	1999	1,637	Sierra Mixed Conifer	20	0
Plumas	Lookout	1999	1,009	Sierra Mixed Conifer	21	0
Plumas	Moonlight	2007	18,864	Eastside Pine	20	20
Plumas	Pidgeon	1999	1,859	Sierra Mixed Conifer	18	0
Plumas	Rich	2008	2,360	Sierra Mixed Conifer	21	21
Plumas	Scotch	2008	9,664	Sierra Mixed Conifer	21	21
Plumas	Storrie	2000	21,117	Red Fir	15	0
Plumas	Stream	2001	1,507	Eastside Pine	20	20
Sequoia	Albanita	2003	958	Jeffrey Pine	21	21
Sequoia	Broder Beck	2006	1,457	Jeffrey Pine	0	20
Sequoia	Clover	2008	6,088	Jeffrey Pine	0	20
Sequoia	Crag 2004	2004	364	Jeffrey Pine	19	0
Sequoia	Crag 2005	2005	611	Jeffrey Pine	21	20
Sequoia	Deep	2004	1,305	Ponderosa Pine	11	11
Sequoia	Granite	2009	607	Jeffrey Pine	0	20
Sequoia	Hooker	2003	1,004	Jeffrey Pine	20	16
Sequoia	Lion	2009	1,075	Red Fir	0	20
Sequoia	Manter	2000	22,450	Pinyon-Juniper	21	20
Sequoia	McNally	2002	61,261	Sierra Mixed Conifer	19	17
Sequoia	Piute 2008	2008	13,516	Jeffrey Pine	20	19
Sequoia	Vista	2007	180	Red Fir	19	19
Sierra	North Fork	2001	1,614	Sierra Mixed Conifer	20	13
Stanislaus	Hiram	1999	1,144	Jeffrey Pine	10	0
Stanislaus	Kibbie	2003	1,501	Sierra Mixed Conifer	21	0
Stanislaus	Knight	2009	2,140	Sierra Mixed Conifer	0	19
Stanislaus	Mountain	2003	1,747	Red Fir	0	12
Stanislaus	Mud	2003	1,803	Red Fir	21	20
Stanislaus	Whit	2003	438	Red Fir	20	0
Stanislaus	White	2001	107	Sierra Mixed Conifer	8	8
Tahoe	Bassetts	2006	1,006	Sierra Mixed Conifer	18	18
Tahoe	Fall	2008	584	Sierra Mixed Conifer	10	10
Tahoe	Gap	2001	574	Sierra Mixed Conifer	0	20
Tahoe	Government	2008	7,784	Sierra Mixed Conifer	19	19
Tahoe	Harding	2005	616	Ponderosa Pine	21	21

Table 2, continued.

Tahoe	Peavine	2008	192	Sierra Mixed Conifer	16	0
Tahoe	Treasure	2001	143	Eastside Pine	10	10
Tahoe Basin	Angora	2007	1,146	Sierra Mixed Conifer	19	12
Tahoe Basin	Gondola	2002	165	Red Fir	12	12
Tahoe Basin	Showers	2002	125	Eastside Pine	9	9

[1] Habitat classifications follow California Habitat Relationships (CWHR; California Department of Fish and Game 2005), and indicate the primary pre-fire habitat at the greatest number of survey stations in a particular fire area, based on our own on-the-ground assessments.

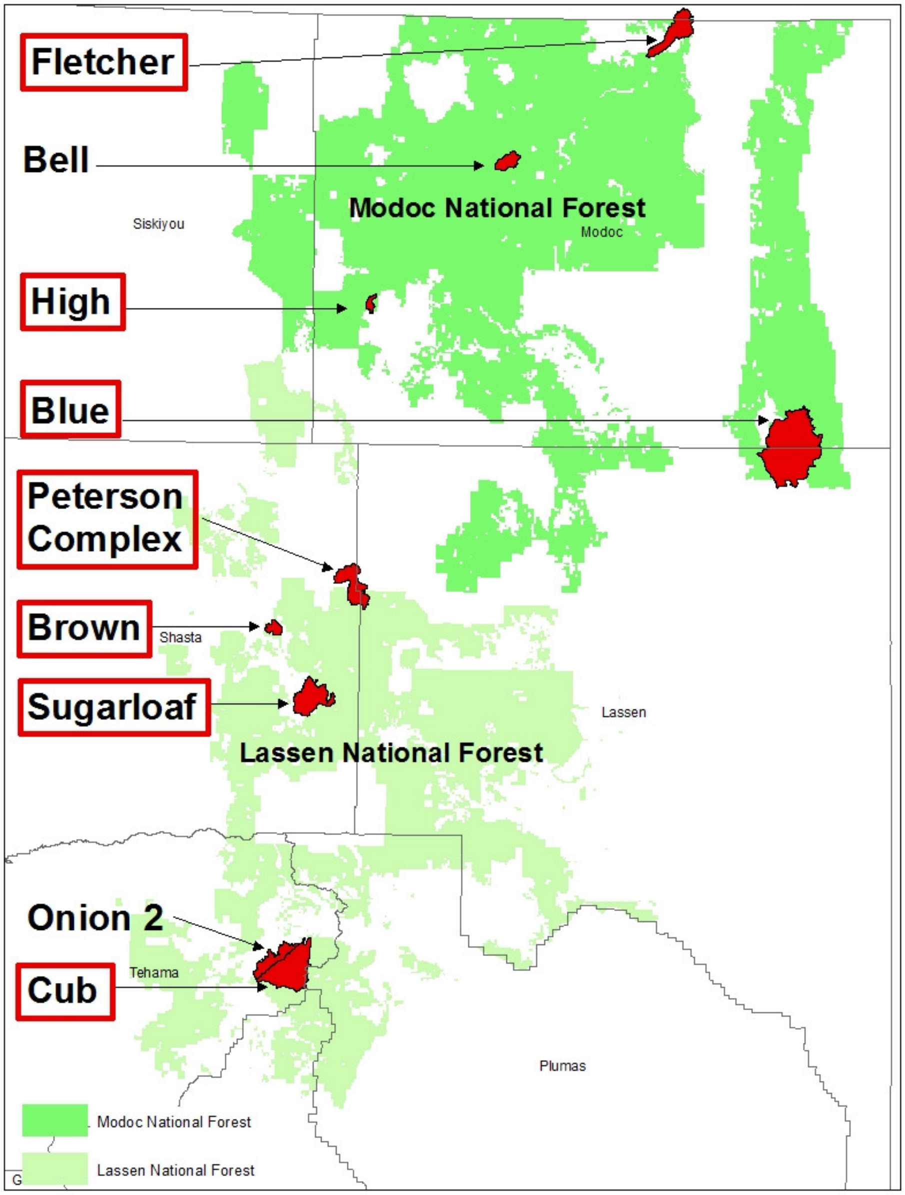

Figure 4. Fire areas (red shading) on the Modoc and Lassen National Forests that we surveyed for Black-backed Woodpeckers during the 2010 Black-backed Woodpecker MIS monitoring field season. Names of fire areas where Black-backed Woodpeckers were detected are enclosed in red boxes. Fire area names without red boxes indicate that no Black-backed Woodpeckers were detected; note that lack of detection does not necessarily mean Black-backed Woodpeckers were absent (see text for discussion of detection probability during this survey).

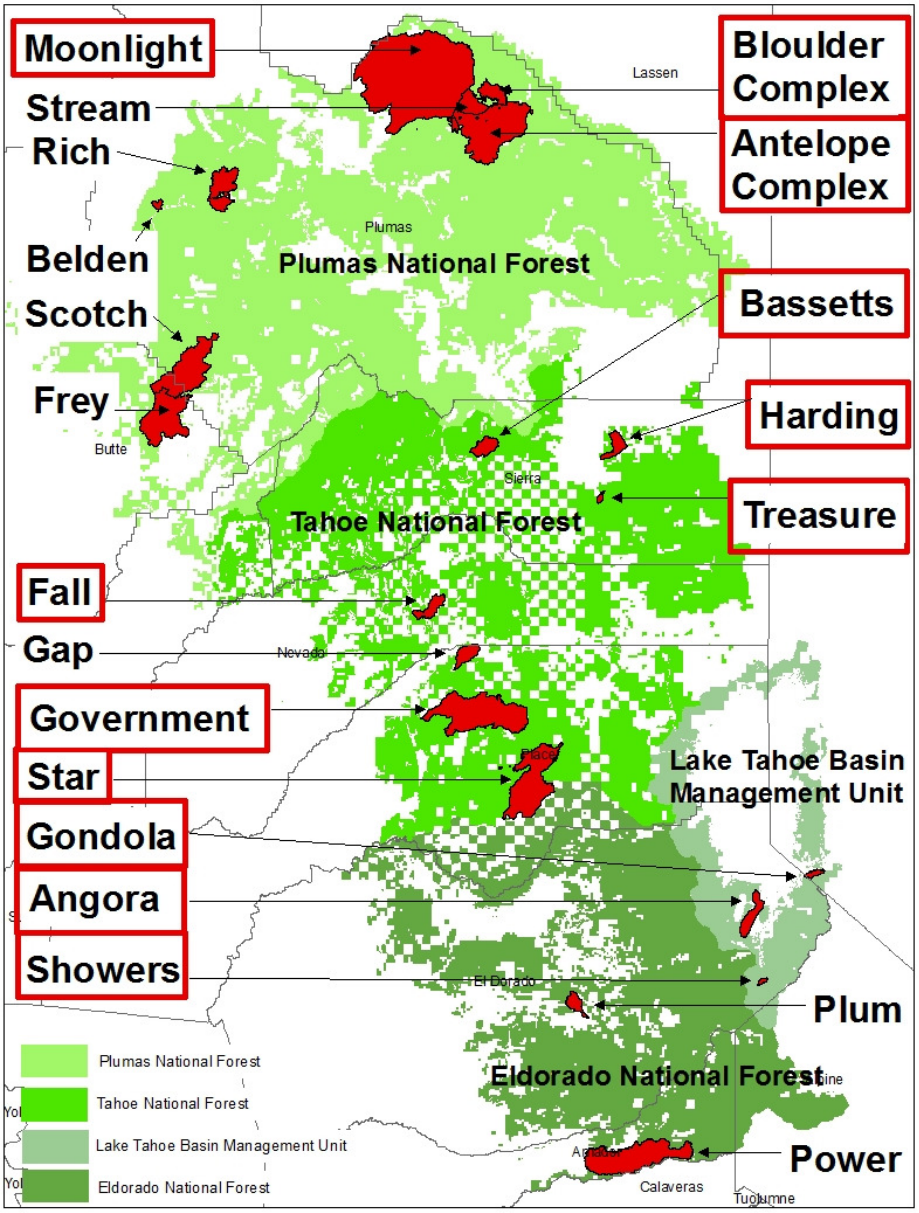

Figure 5. Fire areas (red shading) on the Plumas, Tahoe, and Eldorado National Forests and the Lake Tahoe Basin Management Unit that we surveyed for Black-backed Woodpeckers during the 2010 Black-backed Woodpecker MIS monitoring field season. Names of fire areas where Black-backed Woodpeckers were detected are enclosed in red boxes. Fire area names without red boxes indicate that no Black-backed Woodpeckers were detected; note that lack of detection does not necessarily mean Black-backed Woodpeckers were absent (see text for discussion of detection probability during this survey).

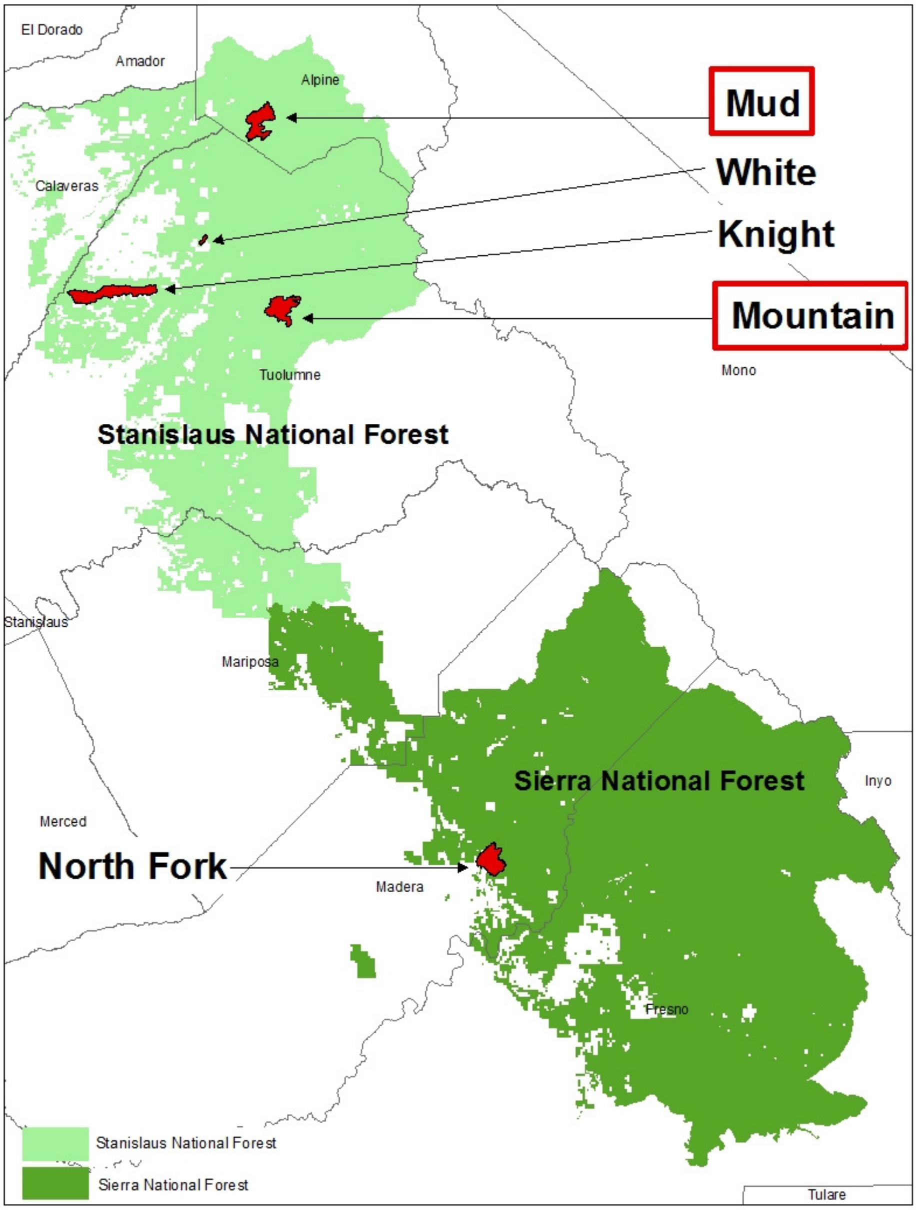

Figure 6. Fire areas (red shading) on the Stanislaus and Sierra National Forests that were surveyed for Black-backed Woodpeckers during the 2010 Black-backed Woodpecker MIS monitoring field season. Names of fire areas where Black-backed Woodpeckers were detected are enclosed in red boxes. Fire area names without red boxes indicate that no Black-backed Woodpeckers were detected; note that lack of detection does not necessarily mean Black-backed Woodpeckers were absent (see text discussion of detection probability during this survey).

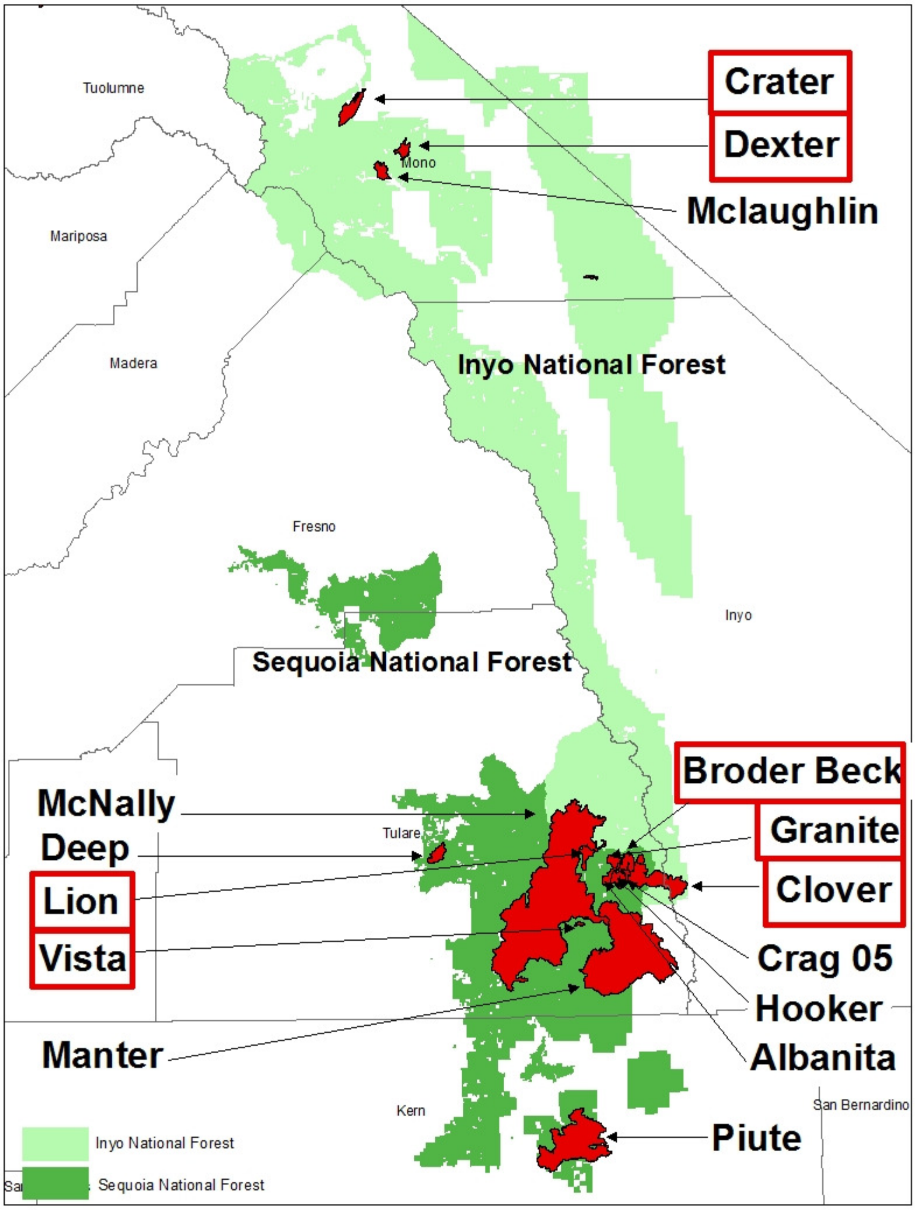

Figure 7. Fire areas (red shading) on the Inyo and Sequoia National Forests that were surveyed for Black-backed Woodpeckers during the 2010 Black-backed Woodpecker MIS monitoring field season. Names of fire areas where Black-backed Woodpeckers were detected are enclosed in red boxes. Fire area names without red boxes indicate that no Black-backed Woodpeckers were detected; note that lack of detection does not necessarily mean Black-backed Woodpeckers were absent (see text discussion of detection probability during this survey).

Exploratory Analyses

Black-backed Woodpecker detections during the 2010 survey varied somewhat by major habitat type (Fig. 8). Of six major habitat types sampled by ≥ 50 stations, Sierra Mixed Conifer (SMC) had the lowest percentage of stations with detections (7%), followed by Ponderosa Pine (PPN; 11%), Jeffrey Pine (JPN; 18%), White Fir (WFR; 19%), Eastside Pine (EPN; 21%), and Red Fir (26%). Although only 31 points classified as Lodgepole Pine (LPN) were surveyed in 2010, they had the greatest percentage of detections (35%).

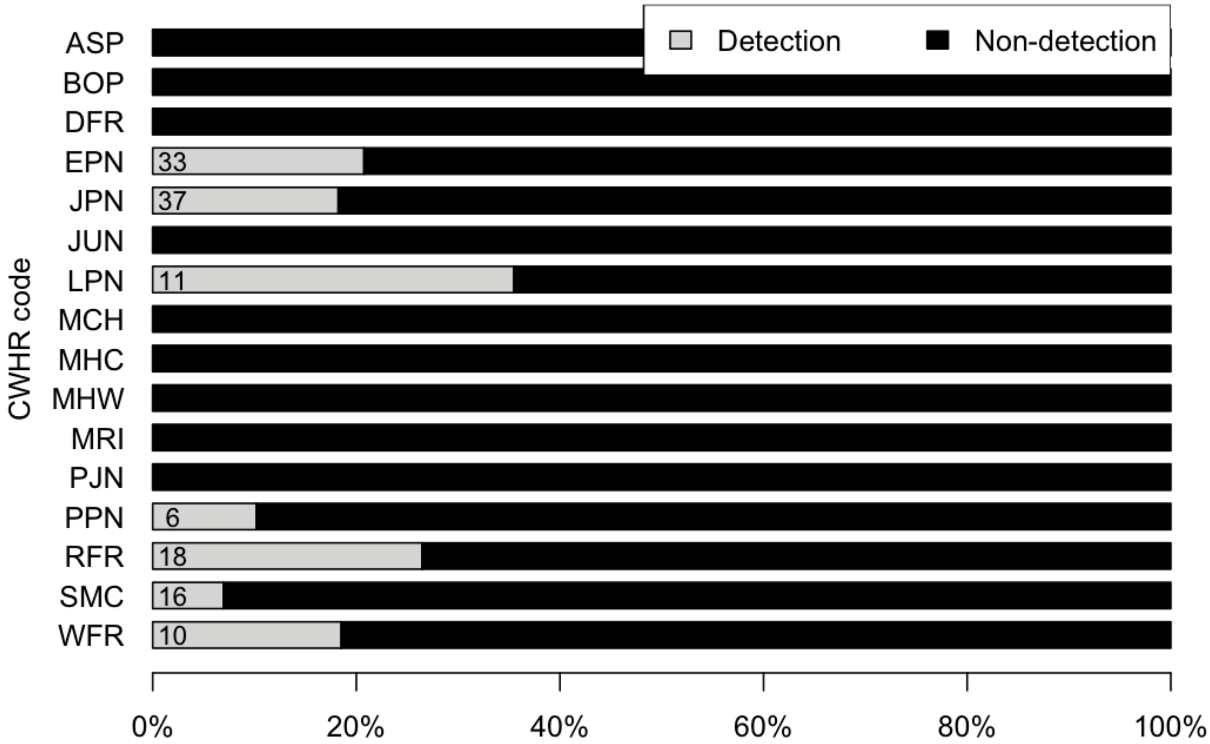

Figure 8. Percentage of stations with detections and without detections (non-detections) by major habitat type for 860 stations surveyed during 2010. Numbers within bars represent the number of points with detections. Y-axis labels are as follows: ASP = Aspen, BOP = Blue Oak-Foothill Pine, DFR = Douglas Fir, EPN = Eastside Pine, JPN = Jeffrey Pine, JUN = Juniper, LPN = Lodgepole Pine, MCH = Mixed Chaparral, MHC = Mixed Hardwood/Conifer, MHW = Mixed Hardwood, MRI = Montane Riparian, PJN = Pinyon-Juniper, PPN = Ponderosa Pine, RFR = Red Fir, SMC = Sierra Mixed Conifer, and WFR = White Fir.

Some of the habitat-related variation in detections might be explained by elevation (Fig. 9). For example, in habitats at elevations representing the low end of the elevation gradient, such as

Ponderosa Pine, Eastside Pine, and White Fir, Black-backed Woodpecker detections tended to occur at the higher stations sampled. In contrast, woodpecker detections in higher elevation habitats such as Red Fir, Jeffrey Pine and Lodgepole Pine tended to occur at the lower-elevation survey stations. Detections in Sierra Mixed Conifer (another relatively low-elevation habitat), however, do not hold to this pattern.

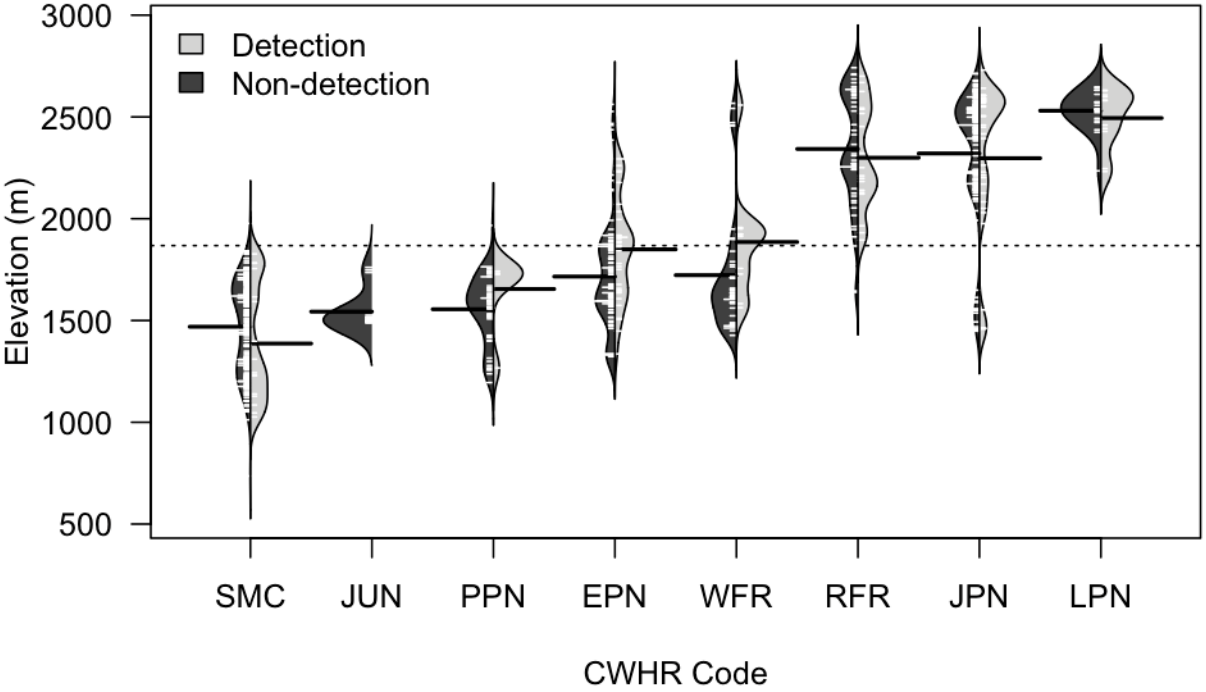

Figure 9. Bean plots showing the elevational (m) distribution of non-detection stations (left density traces in black) and detection stations (right density traces in gray) by major habitat type (California Wildlife Habitat Relationships [CWHR] classification). The dashed line shows the overall mean elevation of stations that were surveyed in 2010. Bold black lines show means for non-detections (left) and detections (right) for each habitat type. Data points are represented by thin white lines. See Figure 8 caption for key to CWHR codes.

Overall, detections occurred most frequently at the middle elevations that were surveyed (Fig. 10). The potential importance of elevation in explaining detections (and occupancy), however, was somewhat complicated by a strong negative correlation between elevation and latitude (Fig. 11). That is, the more southerly fire areas we surveyed tended to be at higher elevations, and the more northerly fire areas we surveyed were at lower elevations.

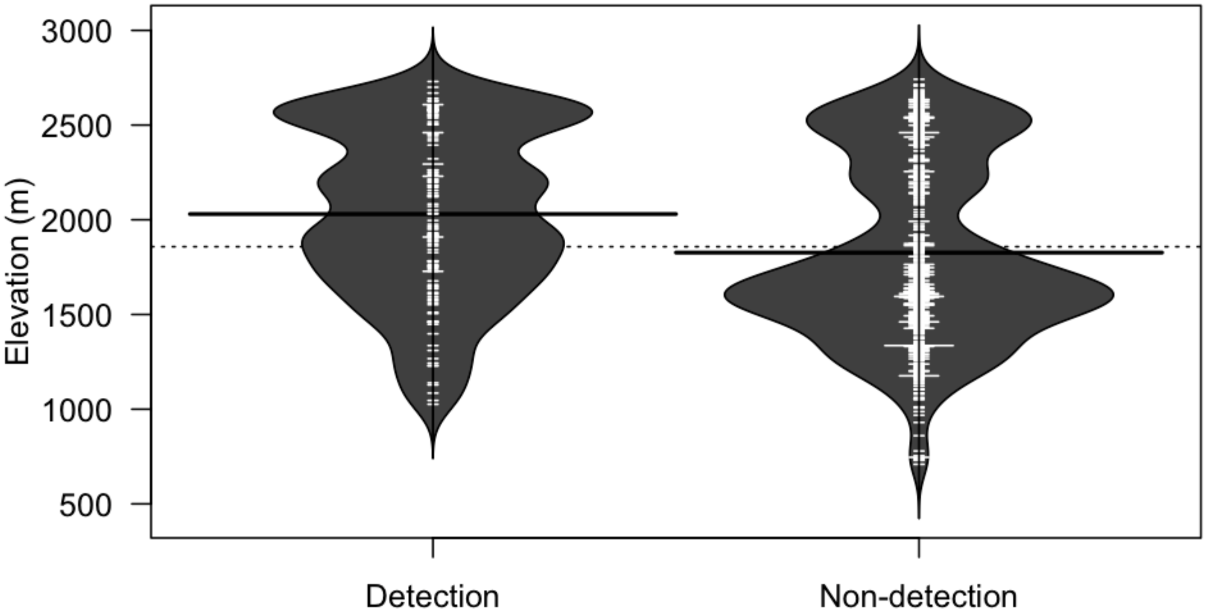

Figure 10. Elevational distribution (m) of detections and non-detections for stations surveyed for Black-backed Woodpeckers in 2010. There was not much difference in the mean elevations for stations with detections and those without (solid black lines); however, detections were generally clustered around the middle elevations, while a preponderance of non-detections were at lower elevations (below the dashed line, which represents the overall mean for both detection and non-detection stations).

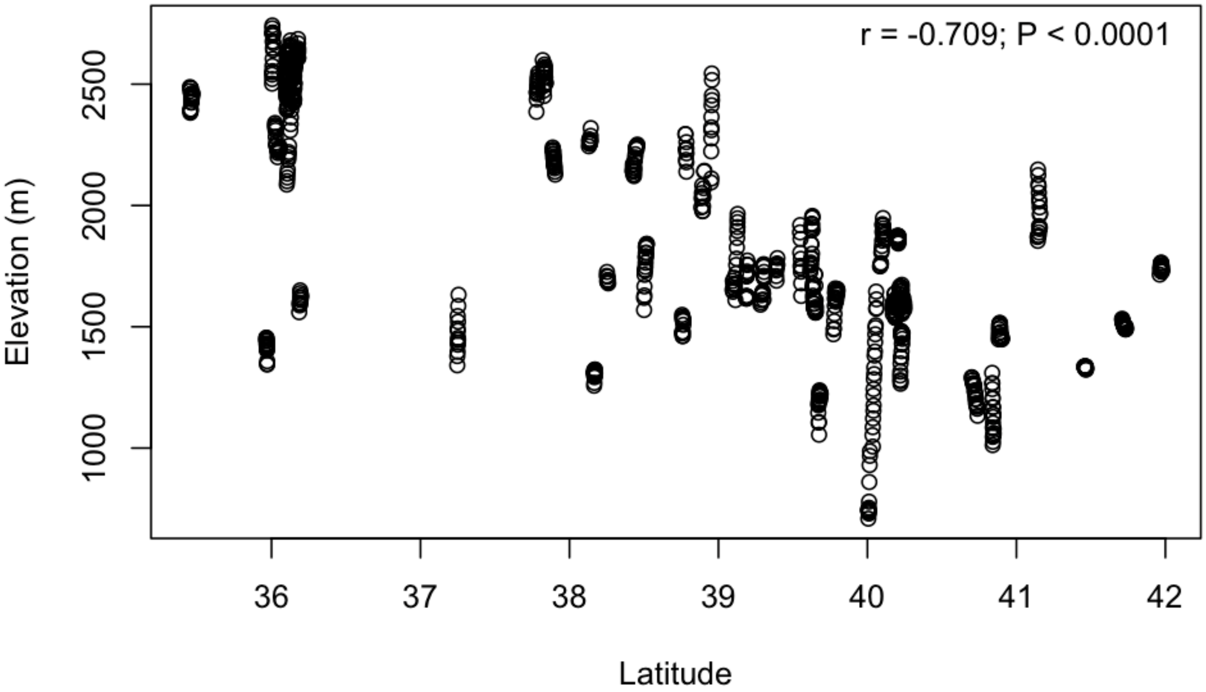

Figure 11. Correlation between elevation (m) and latitude (degrees) for sites surveyed for Black-backed Woodpeckers in 2010 was strong and negative.

In 2009 we also found a latitudinal gradient in detections, with detections more common at higher latitude fire areas, however in 2010 this pattern was not apparent (Fig 12). Nevertheless, because of the strong correlation between latitude and elevation, and apparent relationships between detections and both of these variables, we regressed elevation on latitude and used residuals from this regression as our elevation covariate in the occupancy model (below). This resolves the issue of collinearity between these two variables in the linear model (Graham 2003); the elevation variable considered here can thus be interpreted as 'elevation effects after controlling for latitude effects'. Detections tended to occur at higher elevations for any given latitude (Fig. 13).

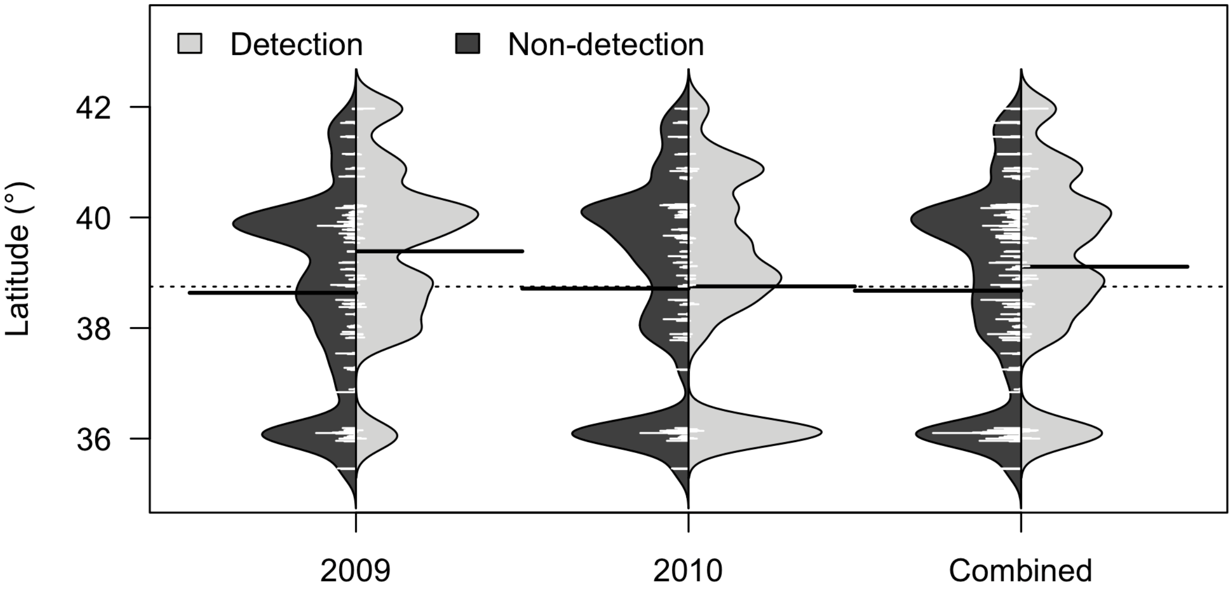

Figure 12. Latitudinal distribution of detections and non-detections for stations surveyed for Black-backed Woodpeckers in 2009, 2010, and both year combined. The dashed line in the bean plot shows the overall mean latitude of survey stations, and the solid black lines indicate the mean station latitude for each group (detection and non-detection) in each year. The 'beans' (shaded regions) in the plot are normal density traces of the data; individual data points are represented by white bars within the beans.

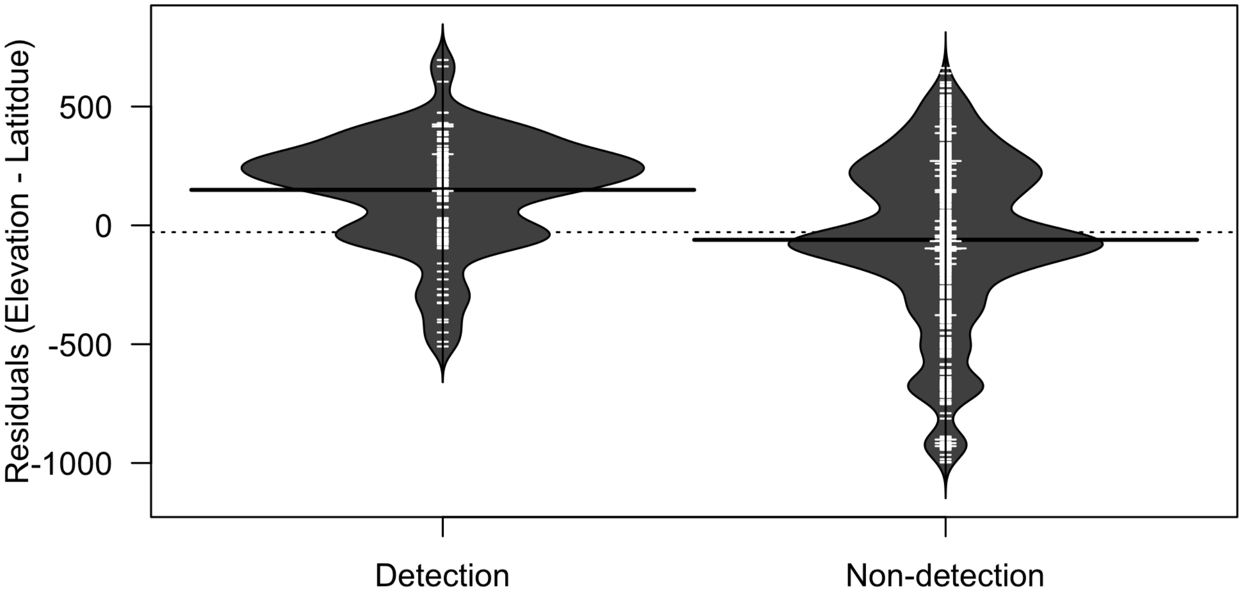

Figure 13. Bean plot showing the distributions of detections and non-detections in relation to residuals from a regression of elevation on latitude. The y-axis scale represents meters below (negative values) or above (positive values) the mean elevation surveyed at a given latitude.

There seemed to be some evidence of a relationship between Black-backed Woodpecker detections and each of the remaining predictor variables considered except pre-fire canopy cover (Fig. 14). Because of the lack of relationship between pre-fire canopy cover and detections, we did not consider this variable in our linear model for occupancy probability (below).

Occupancy Modeling

Because detectability is imperfect, inference about occupancy probability of woodpeckers must be based on models that consider both the detection (observations) and occupancy (partially observed state) processes. Here we summarize model results for occupancy and detection probabilities.

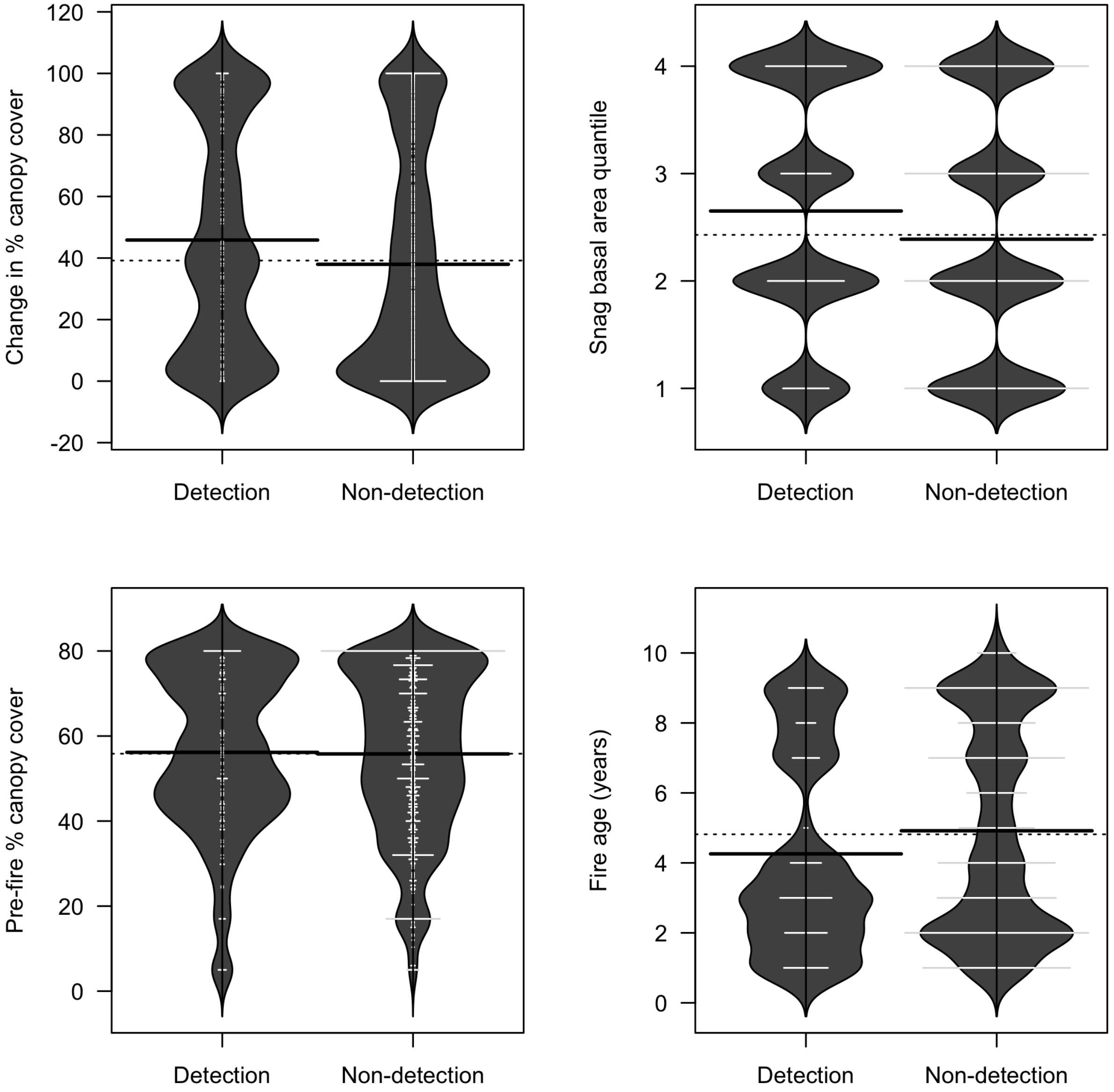

Figure 14. Bean plots for remaining variables considered in exploratory analyses. Survey stations with Black-backed Woodpecker detections averaged greater fire-induced change in canopy cover, greater snag basal area, and fewer years since fire than survey stations where Black-backed Woodpecker was not detected. However we did not detect any effect of pre-fire percent canopy cover.

Occupancy Probability. Mean occupancy probability for stations surveyed during 2010 was 0.231 (95% credible interval: 0.199 – 0.271) which overlaps closely with an updated mean occupancy probability for 2009 of 0.227 (95% CI: 0.209 – 0.248). While this mean occupancy probability for 2009 (0.227) is slightly lower than the 2009 value indicated in previous work (0.253; Siegel et al. 2010), the 95% credible intervals fully overlap and the slight difference in mean is due to refined estimates of detectability resulting from an extra year's data. Assuming that our sample was representative of woodpecker habitat yielded by fire areas that burned between 1999 and 2009, we estimate that approximately 58,367 ha (i.e., 23.1%) of the 252,673 ha of burned forest on the ten national forest units within our sampling frame were occupied by Black-backed Woodpeckers in 2010 (or a range based on the 95% credible interval of 50,282 – 68,474 ha) compared to an updated estimate of 61,696 ha (95% CI: 56,804 – 67,403 ha) out of 271,788 ha occupied in 2009. Table 3 summarizes detections and predicted occupancy probabilities for each fire area surveyed in 2009 and 2010.

Table 3. Summary of Black-backed Woodpecker detections and posterior distributions of both fire-level (ω) and average station-level ($\bar{\psi}$) predictions of occupancy probability for all fire areas surveyed during 2009 and 2010.

Fire name	2009 Detects. (# stns)	2010 Detects. (# stns)	2009 predicted fire-level occupancy probability $(\omega_{2009})^1$	2010 predicted fire-level occupancy probability (ω_{2010})	2009 predicted station-level occupancy probability $(\bar{\psi}_{2009})^2$	2010 predicted station-level occupancy probability $(\bar{\psi}_{2010})$
Albanita	1 (21)	0 (21)	0.59 (0.05-0.99)	0.4 (0.02-0.96)	0.11 (0.05-0.24)	0 (0-0)
Angora	13 (19)	7 (12)	0.97 (0.69-1)	0.94 (0.45-1)	0.74 (0.68-0.84)	0.62 (0.58-0.75)
Antelope Complex	9 (21)	2 (21)	0.97 (0.7-1)	0.94 (0.49-1)	0.52 (0.43-0.67)	0.24 (0.1-0.43)
Azusa	0 (8)	'-	0.08 (0-0.77)	-	0 (0-0)	-
Bassetts	7 (18)	7 (18)	0.97 (0.69-1)	0.93 (0.44-1)	0.44 (0.39-0.56)	0.45 (0.39-0.56)
Belden	-	0 (13)	-	0.56 (0-1)	-	0 (0-0.08)
Bell	0 (20)	0 (20)	0.05 (0-0.49)	0.03 (0-0.27)	0 (0-0)	0 (0-0)
Bell West	1 (21)	-	0.83 (0.11-1)	-	0.1 (0.05-0.19)	-
Birch	0 (19)	'-	0.09 (0-0.73)	-	0 (0-0)	-
Blue	5 (20)	5 (20)	0.94 (0.53-1)	0.88 (0.27-1)	0.4 (0.25-0.6)	0.38 (0.25-0.55)
Boulder Complex	9 (20)	1 (20)	0.97 (0.68-1)	0.93 (0.43-1)	0.5 (0.45-0.6)	0.13 (0.05-0.25)
Broder Beck	-	7 (20)	-	0.91 (0.26-1)	-	0.42 (0.35-0.55)
Brown	-	7 (20)	-	0.94 (0.38-1)	-	0.37 (0.35-0.45)
Bucks	0 (20)	-	0.07 (0-0.67)	-	0 (0-0)	-
Clover	-	7 (20)	-	0.93 (0.33-1)	-	0.39 (0.35-0.5)

Table 3. cont.

Cone	5 (21)	-	0.87 (0.17-1)	-	0.35 (0.24-0.52)	-
Crag 2004	4 (19)	-	0.89 (0.21-1)	-	0.29 (0.21-0.42)	-
Crag 2005	0 (21)	0 (20)	0.09 (0-0.63)	0.04 (0-0.38)	0 (0-0)	0 (0-0)
Crater	8 (20)	3 (20)	0.94 (0.57-1)	0.89 (0.31-1)	0.47 (0.4-0.6)	0.26 (0.15-0.45)
Cub	-	3 (20)	-	0.93 (0.37-1)	-	0.18 (0.15-0.3)
Deep	0 (11)	0 (11)	0.31 (0-1)	0.25 (0-1)	0 (0-0)	0 (0-0)
Devils Gap	0 (20)	'-	0.06 (0-0.6)	-	0 (0-0)	-
Dexter	6 (16)	1 (16)	0.95 (0.59-1)	0.9 (0.34-1)	0.48 (0.38-0.63)	0.27 (0.06-0.5)
Fall	0 (10)	1 (10)	0.91 (0.22-1)	0.86 (0.1-1)	0.05 (0-0.2)	0.15 (0.1-0.3)
Fletcher	15 (19)	5 (17)	0.97 (0.73-1)	0.94 (0.52-1)	0.83 (0.79-0.95)	0.49 (0.29-0.71)
Freds	0 (20)	-	0.11 (0-0.82)	-	0 (0-0)	-
Frey	-	0 (20)	-	0.44 (0-1)	-	0 (0-0.05)
Gap	-	0 (20)	-	0.07 (0-0.66)	-	0 (0-0)
Gondola	6 (12)	4 (12)	0.95 (0.58-1)	0.9 (0.33-1)	0.65 (0.5-0.83)	0.51 (0.33-0.75)
Government	1 (19)	3 (19)	0.97 (0.72-1)	0.95 (0.5-1)	0.09 (0.05-0.21)	0.2 (0.16-0.32)
Granite	-	6 (20)	-	0.94 (0.38-1)	-	0.36 (0.3-0.5)
Harding	7 (21)	2 (21)	0.96 (0.63-1)	0.92 (0.39-1)	0.38 (0.33-0.48)	0.16 (0.1-0.29)
High	'-	1 (19)	-	0.91 (0.26-1)	-	0.09 (0.05-0.21)
Hiram	0 (10)	-	0.07 (0-0.72)	-	0 (0-0)	-
Hooker	0 (20)	0 (16)	0.07 (0-0.6)	0.04 (0-0.35)	0 (0-0)	0 (0-0)
Horton 2	7 (20)	-	0.83 (0.11-1)	-	0.43 (0.35-0.55)	-
Inyo Complex	0 (16)	-	0.17 (0-0.93)	-	0 (0-0)	-
Kibbie	6 (21)	-	0.88 (0.2-1)	-	0.33 (0.29-0.43)	-
Knight	-	0 (19)	-	0.53 (0-1)	-	0.01 (0-0.11)
Lion	-	7 (20)	-	0.94 (0.38-1)	-	0.41 (0.35-0.55)
Lookout	0 (21)	-	0.06 (0-0.69)	-	0 (0-0)	-
Manter	0 (21)	0 (20)	0.05 (0-0.5)	0.03 (0-0.27)	0 (0-0)	0 (0-0)
Mclaughlin	'-	0 (13)	-	0.07 (0-0.65)	-	0 (0-0)
McNally	0 (19)	0 (17)	0.18 (0-1)	0.14 (0-1)	0 (0-0)	0 (0-0)
Moonlight	11 (20)	5 (20)	0.97 (0.67-1)	0.94 (0.44-1)	0.58 (0.55-0.65)	0.29 (0.25-0.4)
Mountain	-	1 (12)	-	0.87 (0.18-1)	-	0.22 (0.08-0.42)
Mud	10 (21)	12 (20)	0.95 (0.57-1)	0.9 (0.32-1)	0.52 (0.48-0.62)	0.68 (0.6-0.8)
North Fork	0 (20)	0 (13)	0.11 (0-0.99)	0.08 (0-0.98)	0 (0-0)	0 (0-0)
Onion 2	-	0 (20)	-	0.18 (0-0.99)	-	0 (0-0)
Peavine	0 (16)	'-	0.46 (0-1)	-	0.01 (0-0.06)	-
Peterson Comp.	9 (20)	7 (20)	0.97 (0.73-1)	0.95 (0.51-1)	0.48 (0.45-0.55)	0.38 (0.35-0.5)
Pidgen	0 (18)	-	0.06 (0-0.64)	-	0 (0-0)	-
Piute 2008	0 (20)	0 (19)	0.12 (0-0.7)	0.06 (0-0.45)	0 (0-0)	0 (0-0)
Plum	0 (12)	0 (12)	0.14 (0-1)	0.1 (0-0.99)	0 (0-0)	0 (0-0)
Power	1 (20)	0 (20)	0.63 (0.06-1)	0.46 (0.02-1)	0.09 (0.05-0.2)	0.01 (0-0.1)
Rich	1 (21)	1 (21)	0.97 (0.71-1)	0.95 (0.49-1)	0.09 (0.05-0.19)	0.07 (0.05-0.14)
Sawmill 2000	0 (5)	-	0.11 (0-0.98)	-	0 (0-0)	-
Scotch	3 (21)	0 (21)	0.72 (0.08-1)	0.58 (0.03-1)	0.19 (0.14-0.33)	0.02 (0-0.14)
Showers	3 (9)	6 (9)	0.95 (0.56-1)	0.9 (0.32-1)	0.44 (0.33-0.67)	0.74 (0.67-0.89)
Star	-	6 (20)	-	0.84 (0.13-1)	-	0.35 (0.3-0.45)
Storrie	4 (15)	-	0.84 (0.13-1)	-	0.38 (0.27-0.57)	-
Stream	0 (20)	0 (20)	0.05 (0-0.51)	0.03 (0-0.3)	0 (0-0)	0 (0-0)
Sugar Loaf	-	3 (21)	-	0.94 (0.39-1)	-	0.18 (0.14-0.29)

Table 3. cont.

Treasure	2 (10)	4 (10)	0.94 (0.57-1)	0.89 (0.29-1)	0.25 (0.2-0.4)	0.45 (0.4-0.6)
Vista	9 (19)	8 (19)	0.97 (0.69-1)	0.94 (0.47-1)	0.52 (0.47-0.63)	0.49 (0.42-0.63)
Whit	6 (20)	-	0.88 (0.2-1)	-	0.34 (0.3-0.45)	-
White	0 (8)	0 (8)	0.1 (0-0.95)	0.07 (0-0.86)	0 (0-0)	0 (0-0)
Total	**169 (899)**	**132 (860)**	**0.59 (0.55-0.63)**	**0.74 (0.69-0.81)**	**0.23 (0.21-0.25)**	**0.23 (0.20-0.27)**

[1] ω represents the probability that the surveyed portion of a fire contains at least one Black-backed woodpecker. Numbers within parentheses are 5% credible intervals around the posterior mean.

[2] $\overline{\psi}$ represents the average probability within a fire that any one station contains at least one woodpecker.

While there appeared to be some year-to-year differences in Black-backed Woodpecker occupancy, particularly in the average probability that a fire was occupied by at least one woodpecker (ω, Table 3), these apparent differences appear to be determined to be the result of sampling a different subset of available fires and not due to significant changes in woodpecker occupancy over the two sampling years. For more information, see *Results: Year-to-Year Differences.*

Three of the five covariates included in either occupancy model appeared to be important predictors of occupancy probability (fire.age$_j$, elev.res$_{ij}$, and cc$_{ij}$; Table 4). Standardized regression coefficients (Table 4) and plots showing predicted occupancy probability across observed covariate values (Fig. 15), show elev.res$_{ij}$ (i.e., elevation adjusted for latitude) to have had the strongest effect on point-level occupancy probability (ψ), followed by change in canopy cover, cc$_{ij}$. Fire age (fire.age$_{ij}$) also had a very strong effect on fire-level occupancy probability (ω). Mean predicted occupancy probability was higher for stations at higher elevations (for a given latitude), for stations with greater changes in percent canopy cover post-fire, and for stations in more recent fire areas. Standardized regression coefficients for latitude$_{ij}$ and snag.ba$_{ij}$ were relatively small in magnitude and 95% credible intervals included zero in both cases, suggesting they were of minor importance in affecting patterns of occupancy. In both cases, however, coefficients were positive, supporting (albeit weakly) the hypothesis that Black-backed Woodpecker occurrence is more likely in the northern part of the Sierra and in areas with more standing snags. In addition, although the increase in predicted occupancy probability across the range of snag.ba$_{ij}$ values was relatively small when considered across all fire ages (Fig. 15), high snag basal area may be especially important in maintaining viability of woodpecker habitat in older fire areas. For example, snag basal area was relatively high for stations where detections occurred compared to stations of non-detections in older fire areas (6-10 years old); but was similar for detection and non-detection stations in younger (1-5 years old) fire areas (Fig. 16). It should also be noted that while the selection of covariates has remained the same between the current analysis and the 2009-only analysis, the results have changed slightly. Previously, latitude was found to be a significant covariate while canopy cover change was not. Latitude initially appeared to have a strong relationship with Black-backed Woodpecker occupancy based on 2009 data, but this relationship was not apparent in the 2010 data (Fig. 12). The diminished effect of latitude in the model likely reflects the detection of Black-backed Woodpeckers at several new and/or previously unsurveyed fire areas on Sequoia NF in 2010 (Broder Beck, Clover, Granite, and Lion; see Table 2 and Figure 7). With added information and continued sampling, it is likely that our ability to discern the true underlying characteristics guiding Black-backed Woodpecker occupancy will only continue to increase.

Table 4. Posterior summaries (means, standard deviations [sd], and credible interval boundaries [lower and upper 95%]) for intercepts and regression coefficients from the occupancy and detectability models as applied to 2009-2010 survey data. See *Methods: Data Analysis: Occupancy Modeling* for variable definitions.

Parameter	mean	sd	lower 95%	upper 95%
Fire-level occupancy probability				
σ_f (variance of random fire effect)	+7.59	1.72	+3.80	+9.92
γ_1 (fire.age$_j$ effect)	-3.49	1.51	-6.69	-0.89
Station-level occupancy probability				
β_0	-0.99	0.16	-1.30	-0.67
β_1 (latitude$_{ij}$ effect)	+0.10	0.09	-0.07	+0.29
β_2 (elev.res$_{ij}$ effect)	+0.78	0.12	+0.54	+1.03
β_3 (snag.ba$_{ij}$ effect)	+0.03	0.07	-0.11	+0.17
β_4 (cc$_{ij}$ effect)	+0.32	0.09	+0.15	+0.50
Detection probability				
α_0	-2.17	0.16	-2.50	-1.86
α_1 (effort$_k$ effect)	+0.81	0.21	+0.40	+1.22
α_2 (type$_k$ effect)	+1.65	0.18	+1.31	+2.01
α_3 (jday$_{ij}$ effect)	-0.18	0.10	-0.37	+0.01

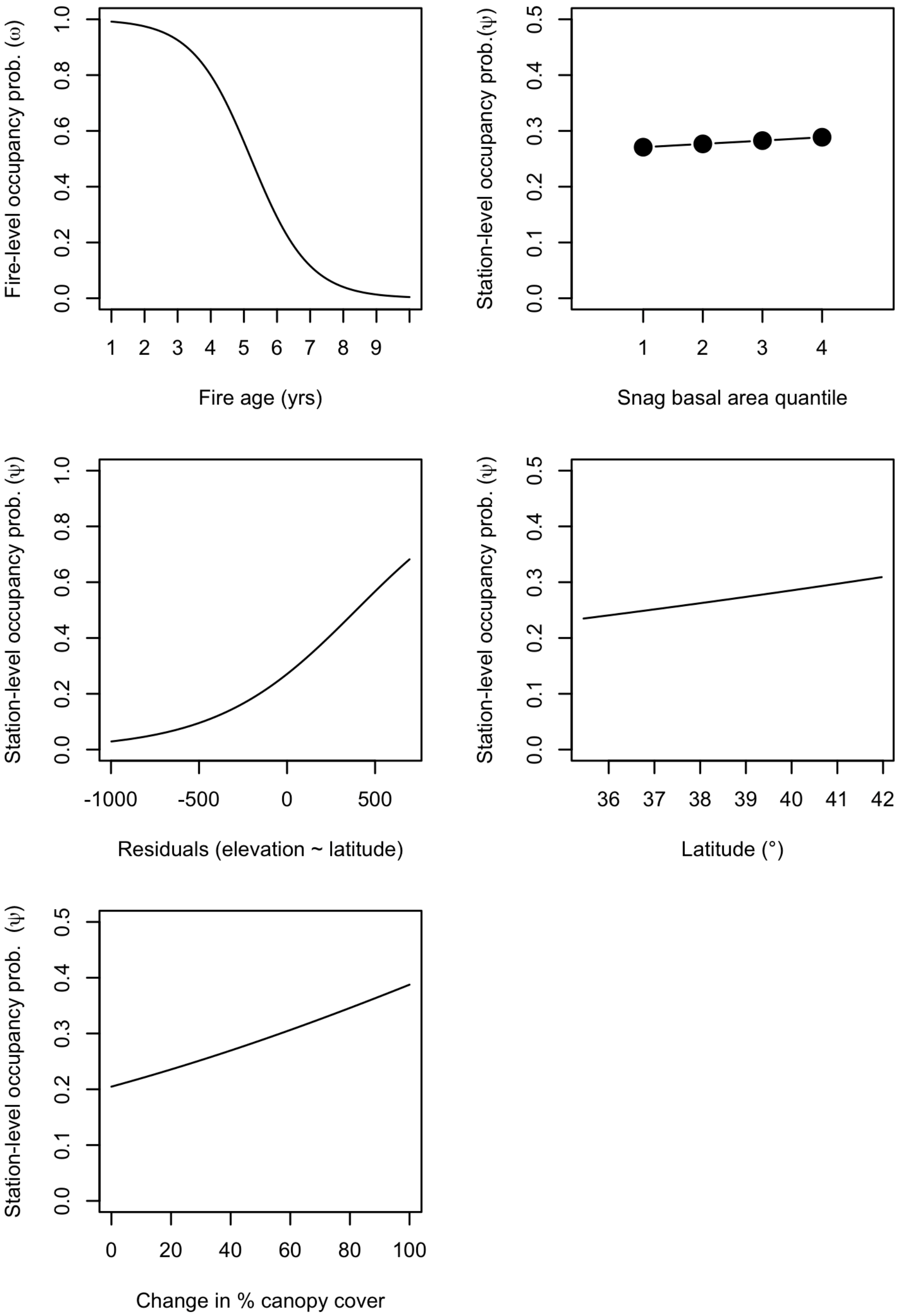

Figure 15. Predicted occupancy probability for covariates included in the hierarchical occupancy model based on application of model to 2009 and 2010 survey data. See *Methods: Data Analysis: Occupancy Modeling* for variable definitions.

Figure 16. Bean plots showing the distributions of non-detections (left sides of beans in dark gray) versus detections (right sides in light gray) for recent (1-5 year-old) fire areas and older (6-10 year-old) fire areas. Shaded regions show density traces of the data; the individual data points are represented by line segments. Means are indicated by bold black lines. The mean difference in snag basal area quantile between stations with detections and those without detections was much greater for older fire areas than for newer fire areas.

Detection Probability

Both effort_k (interval duration) and, especially, survey type_k (passive v. broadcast interval) were important in affecting detection probability (Table 4). Julian day was found to have a negative relationship with detectability, indicating that Black-backed Woodpeckers were harder to detect later in the survey season. The parameter for Julian day overlapped zero, however, indicating that Julian day was not a significant factor in affecting detection in our surveys (Table 4). Our estimated detection probability for the 2-minute passive count interval was just 0.103 (95% credible interval: 0.076 – 0.134), and for the 3-minute passive interval 0.205 (95% credible interval: 0.109 – 0.345). Combined, a 5-minute passive count with a 3-min interval followed by a 2-min interval would have a detection probability of 0.286 (95% credible interval: 0.177 –

0.433). We estimated the detection probability for a single call broadcast interval to be: 0.374 (95% credible interval: 0.233 – 0.536). Combined, our 5 passive intervals and 3 playback intervals in 2010 had an estimated probability of detection per-station of 0.873 (95% CI: 0.707 – 0.932), while our 2 passive intervals and 3 playback intervals in 2009 had an estimated probability of detection per station of 0.825 (95% CI: 0.629 – 0.943).

Our survey objectives did not include meeting any particular detection probability threshold. Nevertheless, we note that in some instances, land managers could need to determine with a known level of certainty whether Black-backed Woodpeckers are present in a project area. Our estimates of detection probability indicate that using just passive point counts would fail to efficiently detect Black-backed Woodpeckers (Fig. 17). A total of 28 2-minute passive survey intervals would be necessary to achieve greater than 95% certainty in the presence or absence of a woodpecker at a site. In contrast, using broadcast surveys would yield a greater than 95% certainty in occurrence status after 7 2-minute survey intervals (Fig. 17). Using the two methods together in sequence allows the collection of multispecies occurrence data while simultaneously providing a high degree of certainty in Black-backed Woodpecker occupancy (Fig. 17).

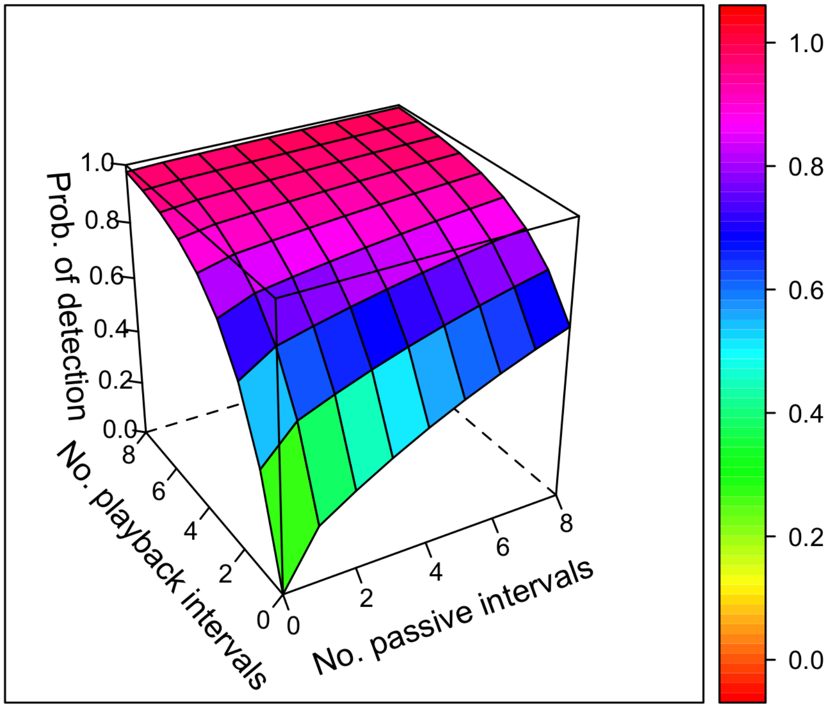

Figure 17. Relationship between number of survey intervals and probability of detecting one or more Black-backed Woodpeckers at an occupied survey station using either passive surveys or broadcast surveys. Nodes on the three-dimensional surface show the cumulative probability of detection given various combinations of passive and playback survey intervals. Probabilities are calculated given an initial 3-minute passive interval followed by additional 2-minute passive intervals, while all playback intervals are 2 minutes.

Year-to-Year Differences in Occupancy

Of major interest in the analysis of the 2009 and 2010 data together was to test whether Black-backed Woodpecker occupancy rates changed significantly over the two years, indicating year-to-year fluctuations in population size and/or meta-population dynamics occurring at the yearly level. Initial summary statistics suggested this might be the case. The percentage of fires with detections increased in 2010 from 55% to 59%, while the percentage of stations with detections decreased in 2010 from 18% to 15%.

To better understand the year-to-year changes in Black-backed Woodpecker occurrence patterns, a separate occupancy model was built from that presented previously (see *Methods: Occupancy*

Modeling) with the slight modification that a covariate for survey year (year_j) was added to the fire-level occupancy probability model, such that:

$$\text{logit}(\omega_j) = \text{fire}_j + \gamma_1 \text{fire.age}_j + \gamma_2 \text{year}_j \ .$$

All other aspects of this model and its specifications were identical to those presented in *Methods*.

The year-based occupancy model indicated that there was no significant effect of year on the probability of Black-backed Woodpecker occupancy. While the posterior mean of the parameter was positive (0.691) indicating that fire-level occupancy was greater in 2010 than 2009 (consistent with the trend based on naïve detections), the 95% credible interval of this parameter (-1.799 – 3.195) crossed zero and showed a very high degree of uncertainty. This suggests that the model had difficulty fitting the parameter due to its failure to improve model fit.

Much of the apparent difference in Black-backed Woodpecker occupancy between years is likely due to the different selection of fires sampled. While the estimated true proportion of occupied fires appears to have increased from 2009 to 2010 when looking at each year's sample of fires individually, when only looking at the subset of fires that were sampled in both years, there is no significant difference between the estimated true proportion of occupied fires in 2009 versus 2010 (Fig. 18).

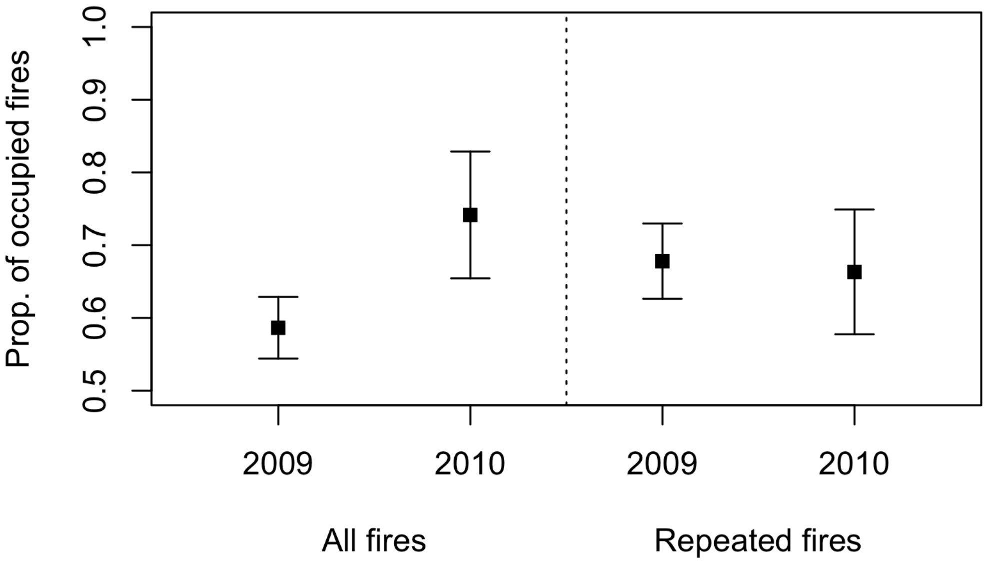

Figure 18. Estimated proportion of truly occupied fires, by year, for (left) all sampled fires and (right) only those fires sampled in both survey years. The proportion of occupied fires was directly estimated within the occupancy model framework as a derived quantity. Squares represent the posterior means and bars are 95% credible intervals.

Exploratory Analysis of Impacts of Salvage Logging

With the 2010 monitoring data in hand, we are interested in furthering our understanding of Black-backed Woodpecker dynamics in burned forests in the Sierra. One goal is to build understanding of the role of post-fire salvage logging on woodpecker occupancy. It has been previously suggested (Hanson and North 2008) that Black-backed Woodpeckers are restricted to foraging in high-severity burns without logging and are not found in burns subject to salvage logging. Due to a randomized sampling strategy that included post-fire areas both with and without salvage logging, our data provide a new opportunity to test this hypothesis.

The presence of post-fire salvage logging within 50 m of survey stations was determined from the FACTS database (see *Methods: Data Analysis*) and defined by the binary variable salvage_{ij}. Approximately 12% of stations in 2009 (106/899) and 9% of stations in 2010 (74/860) were within 50 m of salvage logging operations. Although salvage logging occurs up to multiple years post-fire, there is only one surveyed fire with three affected stations where salvage logging occurred in between Black-backed Woodpecker monitoring in 2009 and 2010 (affecting stations MOON.HP05, MOON.HP06, and MOON.HP07). Of those three sites, HP05 had no detections in 2009 but a detection post-salvage in 2010, HP06 had no detections in either year, and HP07 had detections in both years. Overall, across both years, Black-backed Woodpeckers were detected at approximately 20% of unsalvaged stations (265 of 1314 stations) and 25% of salvaged stations (36 of 144 stations), suggesting that Black-backed Woodpecker occurrence might not be negatively associated with salvage logging.

To further explore this association, we ran an additional modified version of our primary occupancy model (see *Methods: Occupancy Modeling*) with the addition of the salvage logging indicator variable, such that:

$$\text{logit}(\psi_{ij}) = \beta_0 + \beta_1\text{latitude}_{ij} + \beta_2\text{elev.res}_{ij} + \beta_3\text{snag.ba}_{ij} + \beta_4\text{cc}_{ij} + \beta_5\text{salvage}_{ij}$$

This allowed the assessment of the effects of salvage logging independent of other habitat-based variables like snag basal area and fire severity.

The model results indicate that whether survey areas had been salvage logged had little to no independent effect on the probability of occupancy of survey stations by Black-backed Woodpeckers, once other variables including snag basal area were taken into account. The model estimated the parameter (β_5) to be -0.106 (95% credible interval: -0.713 – 0.494), which suggests post-fire logging marginally decreased occupancy probability but since the 95% credible interval is so large, and includes zero, it is highly uncertain what effect, if any, post-fire logging had on occupancy probability. It is clear that some areas subject to post-fire logging do contain woodpeckers (Fig. 19) and that post-fire logging does not fully preclude woodpeckers from occupying burned areas. However, since salvage logging is inter-correlated with measures of snag basal area (since basal area measurements were taken at the time of survey, post-logging), the capacity of the current analysis to detect the full effects of salvage logging on Black-backed Woodpecker occupancy may be limited (Fig. 20).

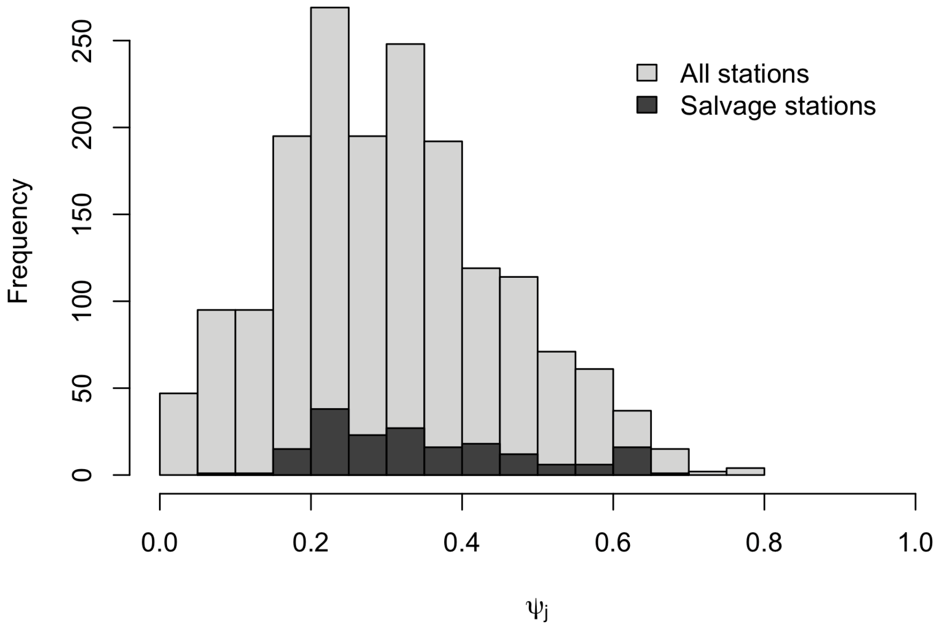

Figure 19. Overlaid histograms of the estimated probability of occupancy by Black-backed Woodpeckers (x-axis) for all survey stations (light gray) and for stations with salvage logging (dark gray). As illustrated, stations with salvage logging varied in occupancy probability, largely following the distributional pattern evident for all stations.

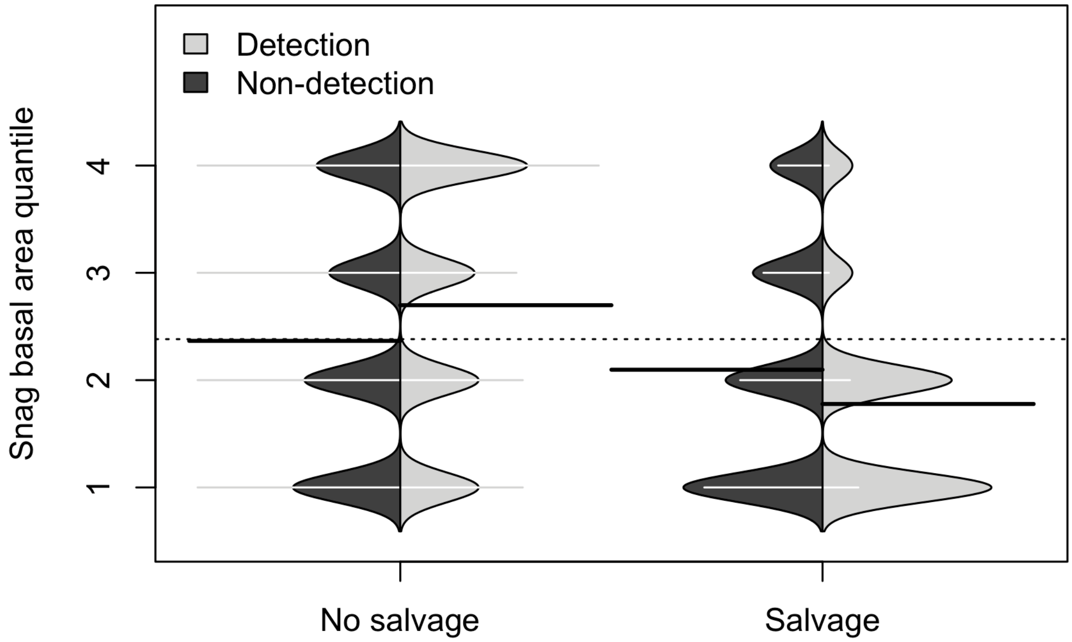

Figure 20. Beanplot showing patterns of detections and non-detections by snag basal area quantile for sites with (right) and without (left) post-fire salvage logging. At sites without salvage logging, woodpecker detections were biased towards sites with greater snag basal area, while at sites with salvage logging, woodpeckers detections were biased in the opposite direction – toward sites with lower snag basal area.

Multi-species Occupancy Dynamics in Burned Areas

Background and Methodology

In addition to Black-backed Woodpecker, our 465 passive point counts in 2009 and 420 passive point counts in 2010 yielded detections of 118 other bird species within the fire areas. The five most frequently detected species were Mountain Chickadee (*Poecile gambeli*, 455 detections), Western Tanager (*Piranga ludoviciana*, 429 detections), Western Wood-Pewee (*Contopus sordidulus*, 426 detections), Steller's Jay (*Cyanocitta stelleri*, 423 detections), and Dark-eyed Junco (*Junco hyemalis*, 417 detections).

To explore the effects of fire severity and fire age on bird assemblages in post-fire forest stands, we built a multi-species hierarchical occupancy model. Similar to the occupancy model presented for the main analysis (see *Methods: Occupancy Modeling*), the multi-species framework builds an occupancy model individually for each species but draws estimated parameters for each species (e.g., $\alpha_{n,i}$, $\beta_{m,i}$) from higher, hierarchical distributions governed by simple hyper-parameters (i.e., a mean and variance). Specifically, the multi-species modeling framework presented here builds off Dorazio and Royle (2005), Dorazio et al. (2006), and Kéry and Royle (2008) and was recently used to analyze the impact of burned forests on bird communities by Russell et al. (2009). The strength of these models is that they estimate the probability of occupancy of every species without *a priori* assumptions of how species should co-occur, allowing estimation of community descriptors (e.g., species richness) that can only be estimated when data for all species are available (Zipkin et al. 2009).

While the Black-backed Woodpecker model contained a hierarchical level separating fire-level and station-level occupancy, this extra level of modeling was eliminated in our multi-species model and replaced with a hierarchical level connecting all species. Consequently, in this context, observed detections, $y(i,j,k)$, represent detections for species 1…i…119, at site 1…j...885, during survey segment 1…k…5. With this in mind, the we similarly modeled detections, $y(i,j,k)$, conditional on occupancy, $z(i,j)$, such that:

$$y(i,j,k) \mid z(i,j) \sim \text{Bern}(z(i,j) \cdot p_{ijk})$$

where $y(i, j, k) = 1$ if at least one individual of species *i* was observed at station *j* during sampling interval *k* and $y(i, j, k) = 0$ otherwise; and $z(i, j)$ represents the true occupancy state of the station for species *i*. We modeled the latent occupancy state indicator variable, $z(i, j)$, as:

$$z(i, j) \sim \mathrm{Bern}(\psi_{ij}),$$

such that ψ_{ij} is the Bernoulli probability of species *i* occupying station *j*.

Again, we defined a logit-linear model to relate each Bernoulli-distributed probability to covariates selected *a priori* as important in influencing occupancy rates for all species. First, ψ_{ij}, or occupancy at each station in each year, was modeled as a function of four *a priori* selected covariates, such that:

$$\mathrm{logit}(\psi_{ij}) = \beta_{0,i} + \beta_{1,i}\mathrm{latitude}_{ij} + \beta_{2,i}\mathrm{elev.res}_{ij} + \beta_{3,i}\mathrm{elev.res}_{ij}^{2} + \beta_{4,i}\mathrm{fire.age}_{ij} + \beta_{5,i}\mathrm{snag.ba}_{ij},$$

where all variables are as described previously (see *Methods: Occupancy Modeling*), with the exception of the squared term of elevation residuals, as many bird species have narrower elevational ranges than the full scale sampled here. Second, we defined a logit-linear model for detection probability p_{ijk}:

$$\mathrm{logit}(p_{ijk}) = \alpha_{0,i} + \alpha_{1}\mathrm{effort}_{k} + \alpha_{2,i}\mathrm{year}_{j} + \alpha_{3,i}\mathrm{jday}_{jk}$$

where the variable effort_k represents interval length effort, such that $\mathrm{effort}_k = 1$ if the interval length was 3 min (i.e., just the first count interval; $k = 1$), and zero otherwise; year_j represents the survey year (2009 = 0; 2010 = 1) to account for differences in detectability between survey years; and jday_{jk} represents the normalized Julian day on which the survey took place, to account for seasonal differences in detectability.

In comparing the multi-species model to the single-species woodpecker model, it is important to note that here, each species *i* has independently estimated parameters $\alpha_{0,i}$ … $\alpha_{3,i}$ and $\beta_{0,1}$ … $\beta_{5,i}$. Critically, these species-specific parameter values are drawn from hyper-distributions with uninformative priors, such that:

$$\alpha_{n,i} \sim \text{Normal}(\mu_n, \tau_n) \text{ and } \beta_{m,i} \sim \text{Normal}(\mu_m, \tau_m),$$

for 1…*n*…3 detectability parameters and 1…*m*…5 occupancy parameters, where μ is the mean and τ is the precision of normal distribution.

Results

Table 5 lists the average occupancy probability and average detection probability for each of the 119 observed species.

Table 5. Numbers of each bird species detected during 885 passive point counts conducted in conjunction with Black-backed Woodpecker surveys across 67 fire areas surveyed in 2009 and 2010.

Common name	Scientific name	No. of detections	Predicted occupancy probability ($\bar{\psi}_i$)	Predicted detection probability($\bar{p}_i$)
Mountain Quail	*Oreortyx pictus*	289	0.432	0.658
California Quail	*Callipepla californica*	18	0.019	0.600
Chukar	*Alectoris chukar*	2	0.002	0.571
Sooty Grouse	*Dendragapus fuliginosus*	9	0.011	0.562
Turkey Vulture	*Cathartes aura*	1	0.001	0.381
Osprey	*Pandion haliaetus*	8	0.007	0.643
Bald Eagle	*Haliaeetus leucocephalus*	3	0.002	0.771
Sharp-shinned Hawk	*Accipiter striatus*	1	0.001	0.542
Cooper's Hawk	*Accipiter cooperii*	1	0.001	0.381
Red-shouldered Hawk	*Buteo lineatus*	2	0.002	0.405
Red-tailed Hawk	*Buteo jamaicensis*	17	0.010	0.612
American Kestrel	*Falco sparverius*	12	0.013	0.407
Prairie Falcon	*Falco mexicanus*	1	0.001	0.384
Killdeer	*Charadrius vociferus*	5	0.004	0.734
Band-tailed Pigeon	*Patagioenas fasciata*	7	0.008	0.593
Mourning Dove	*Zenaida macroura*	110	0.097	0.544
Western Screech-Owl	*Megascops kennicottii*	2	0.002	0.338
Great Horned Owl	*Bubo virginianus*	3	0.003	0.490
Northern Pygmy-Owl	*Glaucidium gnoma*	9	0.007	0.545

Table 5. continued

Common Nighthawk	*Chordeiles minor*	5	0.003	0.448
Common Poorwill	*Phalaenoptilus nuttallii*	2	0.002	0.478
Anna's Hummingbird	*Calypte anna*	23	0.026	0.285
Costa's Hummingbird	*Calypte costae*	4	0.004	0.442
Calliope Hummingbird	*Stellula calliope*	10	0.018	0.220
Rufous Hummingbird	*Selasphorus rufus*	4	0.006	0.331
Lewis's Woodpecker	*Melanerpes lewis*	4	0.004	0.623
Acorn Woodpecker	*Melanerpes formicivorus*	24	0.006	0.392
Williamson's Sapsucker	*Sphyrapicus thyroideus*	3	0.003	0.374
Red-breasted Sapsucker	*Sphyrapicus ruber*	55	0.075	0.219
Downy Woodpecker	*Picoides pubescens*	3	0.002	0.399
Hairy Woodpecker	*Picoides villosus*	213	0.379	0.453
White-headed Woodpecker	*Picoides albolarvatus*	96	0.148	0.480
Black-backed Woodpecker	*Picoides arcticus*	47	0.053	0.603
Northern Flicker	*Colaptes auratus*	219	0.353	0.385
Pileated Woodpecker	*Dryocopus pileatus*	17	0.019	0.525
Olive-sided Flycatcher	*Contopus cooperi*	281	0.431	0.743
Western Wood-Pewee	*Contopus sordidulus*	426	0.502	0.774
Hammond's Flycatcher	*Empidonax hammondii*	24	0.022	0.699
Gray Flycatcher	*Empidonax wrightii*	35	0.017	0.823
Dusky Flycatcher	*Empidonax oberholseri*	216	0.326	0.623
Pacific-slope Flycatcher	*Empidonax difficilis*	11	0.008	0.520
Black Phoebe	*Sayornis nigricans*	4	0.002	0.316
Ash-throated Flycatcher	*Myiarchus cinerascens*	6	0.003	0.438
Western Kingbird	*Tyrannus verticalis*	3	0.003	0.432
Cassin's Vireo	*Vireo cassinii*	101	0.109	0.653
Hutton's Vireo	*Vireo huttoni*	4	0.004	0.596
Warbling Vireo	*Vireo gilvus*	94	0.114	0.662
Gray Jay	*Perisoreus canadensis*	1	0.001	0.394
Steller's Jay	*Cyanocitta stelleri*	423	0.517	0.576
Western Scrub-Jay	*Aphelocoma californica*	11	0.013	0.433
Pinyon Jay	*Gymnorhinus cyanocephalus*	12	0.008	0.605
Black-billed Magpie	*Pica hudsonia*	6	0.005	0.615
Clark's Nutcracker	*Nucifraga columbiana*	74	0.028	0.642
Common Raven	*Corvus corax*	53	0.062	0.387
Tree Swallow	*Tachycineta bicolor*	15	0.012	0.542
Violet-green Swallow	*Tachycineta thalassina*	20	0.018	0.462
Cliff Swallow	*Petrochelidon pyrrhonota*	1	0.001	0.545
Mountain Chickadee	*Poecile gambeli*	455	0.527	0.702
Chestnut-backed Chickadee	*Poecile rufescens*	2	0.002	0.566
Oak Titmouse	*Baeolophus inornatus*	2	0.001	0.399
Juniper Titmouse	*Baeolophus ridgwayi*	5	0.004	0.563
Bushtit	*Psaltriparus minimus*	6	0.008	0.314
Red-breasted Nuthatch	*Sitta canadensis*	309	0.389	0.669
White-breasted Nuthatch	*Sitta carolinensis*	98	0.117	0.398
Pygmy Nuthatch	*Sitta pygmaea*	37	0.057	0.322
Brown Creeper	*Certhia americana*	189	0.311	0.605

Table 5. continued

Rock Wren	*Salpinctes obsoletus*	52	0.053	0.556
Canyon Wren	*Catherpes mexicanus*	2	0.002	0.407
Bewick's Wren	*Thryomanes bewickii*	8	0.007	0.624
House Wren	*Troglodytes aedon*	172	0.172	0.767
Pacific Wren	*Troglodytes hiemalis*	1	0.001	0.389
Golden-crowned Kinglet	*Regulus satrapa*	21	0.038	0.336
Ruby-crowned Kinglet	*Regulus calendula*	3	0.002	0.471
Western Bluebird	*Sialia mexicana*	35	0.051	0.433
Mountain Bluebird	*Sialia currucoides*	98	0.107	0.567
Townsend's Solitaire	*Myadestes townsendi*	124	0.169	0.419
Hermit Thrush	*Catharus guttatus*	30	0.030	0.673
American Robin	*Turdus migratorius*	321	0.297	0.604
Wrentit	*Chamaea fasciata*	8	0.003	0.405
European Starling	*Sturnus vulgaris*	8	0.006	0.659
Orange-crowned Warbler	*Vermivora celata*	23	0.024	0.590
Nashville Warbler	*Vermivora ruficapilla*	50	0.035	0.714
Yellow Warbler	*Dendroica petechia*	30	0.022	0.644
Yellow-rumped Warbler	*Dendroica coronata*	274	0.334	0.698
Black-throated Gray Warbler	*Dendroica nigrescens*	9	0.005	0.481
Townsend's Warbler	*Dendroica townsendi*	1	0.001	0.402
Hermit Warbler	*Dendroica occidentalis*	49	0.055	0.607
MacGillivray's Warbler	*Oporornis tolmiei*	119	0.153	0.712
Common Yellowthroat	*Geothlypis trichas*	1	0.001	0.546
Wilson's Warbler	*Wilsonia pusilla*	9	0.009	0.345
Green-tailed Towhee	*Pipilo chlorurus*	185	0.209	0.664
Spotted Towhee	*Pipilo maculatus*	159	0.137	0.665
Chipping Sparrow	*Spizella passerina*	155	0.151	0.666
Brewer's Sparrow	*Spizella breweri*	42	0.025	0.744
Black-chinned Sparrow	*Spizella atrogularis*	2	0.001	0.549
Vesper Sparrow	*Pooecetes gramineus*	8	0.007	0.647
Lark Sparrow	*Chondestes grammacus*	5	0.006	0.536
Black-throated Sparrow	*Amphispiza bilineata*	8	0.007	0.533
Sage Sparrow	*Amphispiza belli*	5	0.004	0.574
Fox Sparrow	*Passerella iliaca*	305	0.394	0.806
Song Sparrow	*Melospiza melodia*	17	0.015	0.463
Lincoln's Sparrow	*Melospiza lincolnii*	25	0.033	0.650
Dark-Eyed Junco	*Junco hyemalis*	417	0.525	0.617
Western Tanager	*Piranga ludoviciana*	429	0.509	0.738
Black-headed Grosbeak	*Pheucticus melanocephalus*	132	0.089	0.649
Lazuli Bunting	*Passerina amoena*	173	0.196	0.770
Red-winged Blackbird	*Agelaius phoeniceus*	9	0.006	0.830
Western Meadowlark	*Sturnella neglecta*	23	0.021	0.612
Brewer's Blackbird	*Euphagus cyanocephalus*	30	0.023	0.650
Brown-headed Cowbird	*Molothrus ater*	56	0.054	0.369
Bullock's Oriole	*Icterus bullockii*	4	0.004	0.425
Purple Finch	*Carpodacus purpureus*	37	0.028	0.684
Cassin's Finch	*Carpodacus cassinii*	164	0.196	0.489

Table 5. continued

House Finch	*Carpodacus mexicanus*	22	0.022	0.713
Red Crossbill	*Loxia curvirostra*	12	0.015	0.382
Pine Siskin	*Spinus pinus*	29	0.038	0.378
Lesser Goldfinch	*Spinus psaltria*	29	0.023	0.500
Lawrence's Goldfinch	*Spinus lawrencei*	1	0.001	0.740
Evening Grosbeak	*Coco. vespertinus*	12	0.019	0.302

Of main interest are the factors that influence species richness at a survey station. Figure 21 illustrates how the estimated true bird species richness at each survey station relates to a number of factors. Many of these factors individually have significant explanatory relationships with total species richness at a station. Together, in a multiple linear regression analysis, we tested all explanatory variables illustrated in Figure 21 including quadratic terms for elevation, fire age, and canopy cover change. The resulting general linear model found significant (Wald scores: $P < 0.05$) effects for latitude (coefficient ± st. error: 0.26 ± 0.10), fire age (linear and quadratic effects: 0.40 ± 0.10; -0.55 ± 0.14), and change in canopy cover (linear and quadratic effects: 0.045 ± 0.011; -0.00054 ± 0.00011). Altogether, these results suggest that avian species richness is greatest at higher latitudes, at intermediate fire ages, and at sites where burn severity (as indicated by change in percent canopy cover) is intermediate. It should be noted, however, that overall fit for this general linear model is quite poor (adjusted R^2: 0.06), indicating a very large amount of residual variance in species richness, as is evident in Figure 21.

The overall apparent stability of species richness at sites given varying fire ages and fire severities (Fig. 21) belies a large degree of hidden, underlying turnover in species composition. This can be better appreciated when looking at how the multi-species occupancy model predicts individual species to respond to selected covariates of occupancy (Fig. 22). For instance, species can be divided into those that increase in occupancy as fires age and those that decrease (Fig. 22). Overall, 41 species decline in occupancy probability as fires age, and 78 species increase in occupancy probability. Of the 8 woodpecker species observed during surveys, three declined in occupancy probability as fire age increased (Black-backed Woodpecker, Downy Woodpecker, and Hairy Woodpecker), and five increased in occupancy probability in areas with greater snag basal area (Black-backed Woodpecker, Downy Woodpecker, Hairy Woodpecker, Acorn Woodpecker, and White-headed Woodpecker). The three species that did not increase with increased snag basal area (Williamson's Sapsucker, Red-breasted Sapsucker, Pileated Woodpecker) are all species generally associated with mature, live forests.

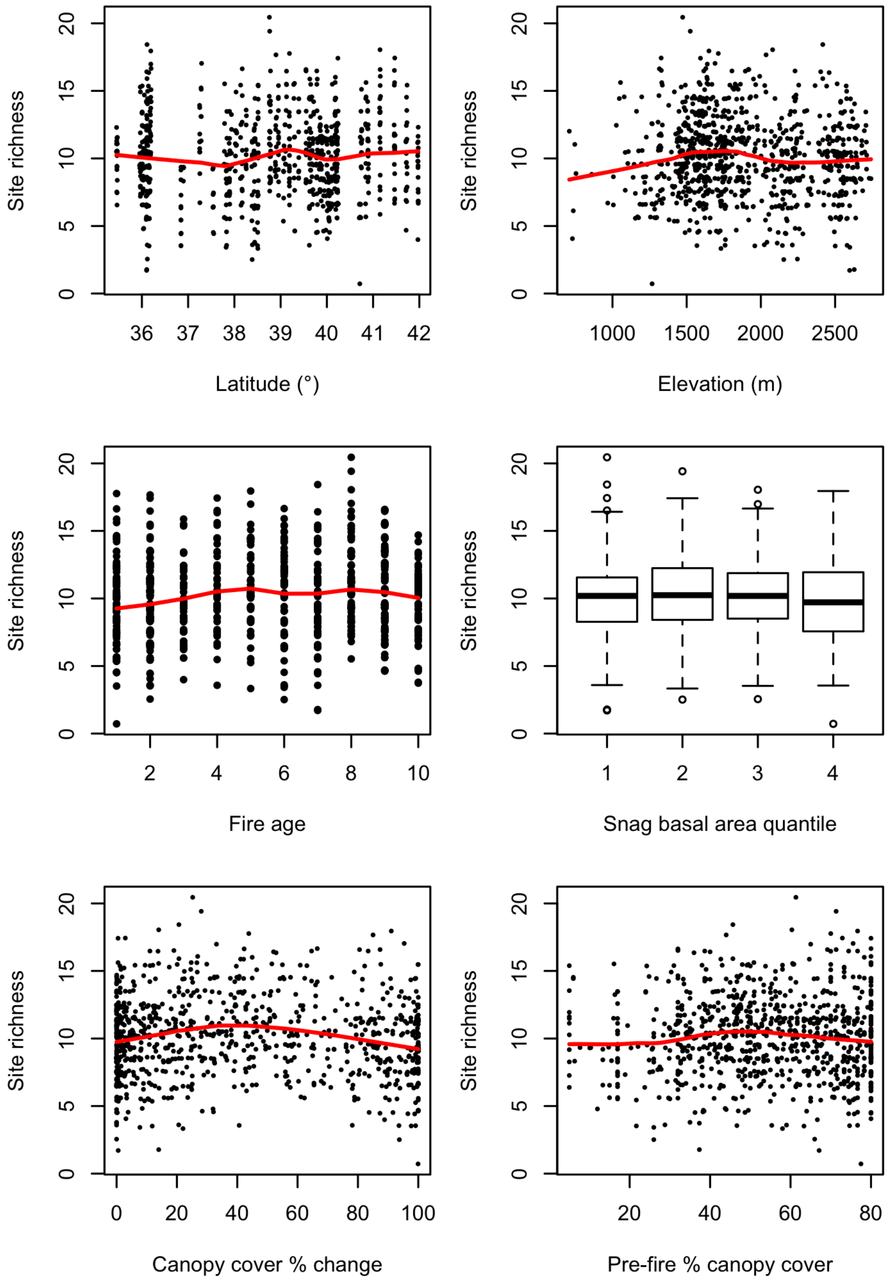

Figure 21. Plots of total estimated bird species richness at each survey station versus six explanatory variables. In all cases (excluding snag basal area quantile, which is ordinal), the red line is a general additive model spline showing the non-linear relationship between each variable and richness.

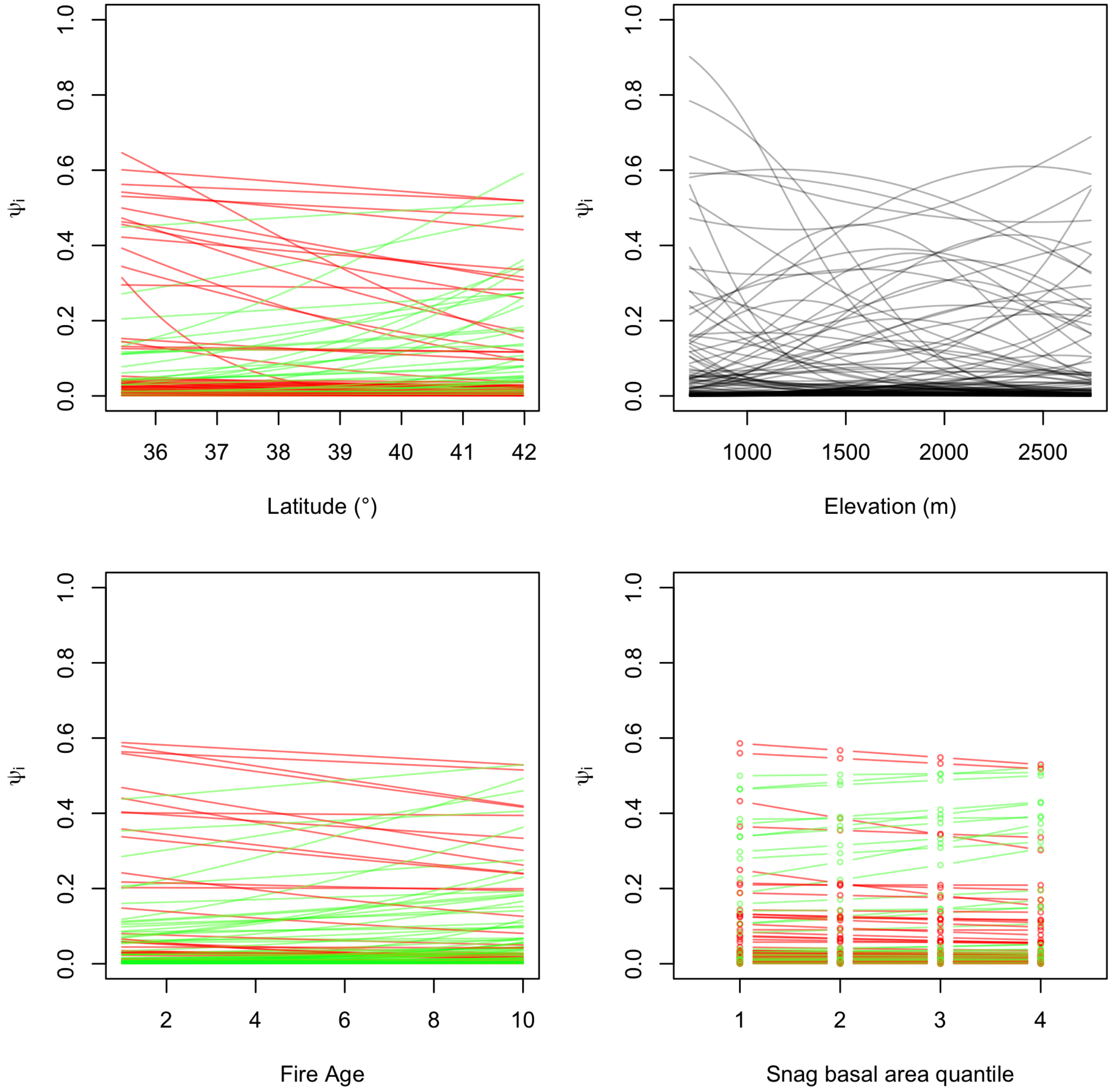

Figure 22. Plots showing the modeled relationship between occupancy (ψ) and four different covariates for each of 119 species, as derived from the multi-species occupancy model. In each chase, the plots show one line for each species, describing the species-specific modeled relationship. For latitude, fire age, and snag quantile, the lines are colored green if occupancy increases with increasing x-axis variables, and red if occupancy decreases with increasing x-axis variables.

Discussion

Black-backed Woodpecker Habitat Occupancy

Our two years of surveys confirm that Black-backed Woodpeckers are infrequent but widely distributed across recent fires areas on the ten national forests in our study area. Across 2009 and 2010, Black-backed Woodpeckers appeared to occupy a stable and unchanging proportion of burned forest. Of the 271,788 ha of burned forest in our 2009 sampling frame, we estimate that approximately 22.7% (61,696 ha; 95% credible interval = 56,803 – 76,403 ha) were occupied by Black-backed Woodpeckers in 2009 and 23.1% (58,367 of 252,673 ha; 95% credible interval = 50,282 – 68,474 ha) were occupied in 2010. The slightly lower estimate of occupancy probability for 2009 compared to estimates reported in previous work (Siegel et al. 2010) is due to more accurate estimates of detectability resulting from an extra year's worth of detection data and a revised estimate of burned hectares that excluded non-forest service lands. These quantities are only estimates, but will provide useful benchmarks for assessing future changes in Black-backed Woodpecker habitat and occupied areas in the Sierra Nevada. In particular, the proportion of occupied habitat (i.e., ~23%) could be used to assess long-term changes in woodpecker occurrence, assuming available habitat is defined consistently over time.

Year-to-Year Differences in Occupancy

Our results indicate that Black-backed Woodpecker occupancy rates were highly stable between 2009 and 2010. The estimated proportion of occupied area in our study area only differed by 0.4% between 2009 and 2010, and occupancy modeling found no significant relationship between the probability of occupancy and survey year. We did find that Black-backed Woodpeckers occupied a greater proportion of sampled fires in 2010 than in 2009 (73.5% versus 58.7%; Figure 18); however, these differences were due to a differing selection of sampled fires in each year. For only those fires that were sampled in both years, the proportion of occupied fires was slightly greater in 2009 than in 2010 (68.0% versus 65.8%). Considering that all sampled fires aged one year from 2009 to 2010 and that occupancy decreases as fire areas age, we would expect a slight decrease in overall fire occupancy for fires sampled both in 2009 and

2010. Thus, we conclude that overall occupancy rates for Black-backed Woodpeckers remained stable from 2009 to 2010.

Given that Black-backed Woodpeckers appeared to occupy constant proportions of available habitat across the two sample years, the greatest changes in Black-backed Woodpecker density or populations may relate directly to the amount of available habitat. Between 2009 and 2010, 12 fires aged out of our study selection (i.e., they aged from 10 years to 11 years, thus qualifying for exclusion), while 5 new fires that burned in 2009 entered into the selection. Overall, the number of fires in the study selection declined from 72 to 65, and the total area of potential habitat on Forest Service land declined from 271,788 ha to 252,673 ha. Consequently, while occupancy within the sample remained constant, we estimate the total occupied area within the sampling frame to have declined. Since we do not know how Black-backed Woodpecker occupancy changed in areas excluded from the study (e.g., green forest), it is unknown whether this constitutes a population decline, or if woodpeckers simply moved from burned forests to green forest.

In terms of covariates of Black-backed Woodpecker occupancy, we found generally consistent results between our previous analyses of 2009 results (Siegel et al. 2010; Saracco et al. 2011) and the results obtained from looking at both 2009 and 2010 data. As a measure of confidence, no modeled relationships changed in sign between the two years (i.e., switched from indicating a factor increased occupancy to indicating the factor decreased occupancy). Several factors shifted in the strength of their relationship to occupancy, however. Based on 2009-only results, latitude and snag basal area were found to have significant positive relationships with occupancy. In the new analysis, both covariates are still positively related to occupancy, but they are no longer considered significant (95% credible intervals cross zero). For latitude, this is likely caused by the discovery in 2010 of Black-backed Woodpeckers in several fires in the southernmost section of the study area (Figure 7), thus weakening the positive relationship between latitude and occupancy. Comparisons of snag basal area are complicated by a change in snag basal area was measured in the model, from a continuous measure to quartiles. Additionally, snag basal area is just one of two burn severity measures used in the occupancy model, the other being percent canopy cover change. Canopy cover change was not a significant covariate in the 2009 analysis, but was found to be significant in this analysis. To the extent that canopy cover change and snag basal area both indicate burn severity, they may compete for "power" in the occupancy model.

The strength of continued monitoring, however, lies in the increased potential for statistical inference. With each year of sampling, our ability to discern "true" relationships between Black-backed Woodpecker presence and habitat and environmental covariates increases. Additionally, multi-year monitoring allows increased ability to measure year-to-year population and occupancy dynamics. Beginning with the analysis of 2011 monitoring data, we will be able to build a "multi-season" occupancy model (MacKenzie et al. 2003) that estimates not only occupancy, but also extinction and colonization probabilities. For example, for stations that were sampled in both 2009 and 2010, 41 had non-detections in 2009 but detections in 2010 (apparent colonizations) and 88 had detections in 2009 but non-detections in 2010 (apparent extinctions). With increased years of sampling, we can better estimate what factors are driving these colonization-extinction dynamics.

Black-backed Woodpecker Detection Probability

Our detection probability estimates indicate that broadcast surveys are necessary to determine reliably whether Black-backed Woodpeckers are present at a site. Passive point counts aid in detection and also collect multi-species data thus providing additional value. In 2010 we increased the number of passive point count intervals at each survey station from 2 to 5, thus increasing the total probability of detecting a Black-backed Woodpecker during passive surveys from 28.6% to 48.4%. However, given the diminishing marginal returns in increased passive survey intervals, there may be justification for reducing the number of intervals from 5 to, for example, 3, which would only decrease probability of passive survey detection to 35.9%. Combined with playback surveys, a reduction in passive survey time such as this would not effectively reduce total probability of woodpecker detection at a site (from 87.3% to 84.3%).

Black-backed Woodpecker Occupancy and Post-fire Salvage Logging

Pilot analyses indicate that after accounting for differences in snag basal area, the status of salvage logging at a survey station may not be a significant determinant of Black-backed Woodpecker occupancy. This is in contrast to previously published findings (Hanson and North 2008). Certainly, multiple areas in our study area subject to salvage logging were found to be used by Black-backed Woodpeckers (Figure 19).

However, it remains unclear from the current analysis how salvage logging interacts with measured snag basal area to influence woodpecker occupancy. In un-logged areas, Black-backed Woodpeckers are detected more frequently in stands with higher snag basal areas yet in logged areas, they are detected more frequently in stands with lower snag basal area (Figure 20). This result is not obviously intuitive, but may result from the preference of logging operations for large snags. For example, an area dominated by large snags before logging could have lower snag basal area after logging than an area dominated by smaller snags before logging. As Black-backed Woodpeckers appear to favor areas with larger snags, if they remain in the same areas for a year or two after logging, then this pattern could arise.

Clearly the effect of salvage logging on Black-backed Woodpecker occupancy is complex. We hope to continue and expand this analysis for incorporation into a manuscript to be published in a peer-reviewed journal.

Multi-species Analyses

Our preliminary analyses suggest that bird communities change in a complex manner in the decade immediately post-fire. While species richness remains relatively constant, there appears to be a change in the composition of the bird community over the ensuing decade, with certain bird species benefiting and other species negatively affected (Figure 22). This leads to a slight but statistically significant increase in species richness at middle-aged burns (Figure 21). From a management perspective, it will be useful to know which species benefit or are hindered, and how the groupings relate to overall forest and fire management goals. In the context of Black-backed Woodpecker management, it will be helpful to know which species might benefit from or be harmed by post-fire management that is tailored to the habitat needs of Black-backed Woodpeckers. Additionally, given the heterogeneity in richness (Figure 21), there are clearly many other factors determining bird species richness at sites, beyond the factors modeled in this analysis. In further analyses and an eventual manuscript for a peer-reviewed journal, we hope to expand our model to better understand the habitat-level factors determining bird species richness in post-fire communities as well as to quantify how the communities change over time.

Future Directions for this Project

We are pleased to have recently completed our 2011 field season—the third year of full-scale Black-backed Woodpecker MIS monitoring on greater Sierra Nevada national forests. Multiple years of data will allow more accurate assessments of whether the amount and proportion of burned forest habitat occupied by Black-backed Woodpeckers are stable, increasing, or decreasing. In addition to continued explorations of salvage logging effects and post-fire bird communities, we also recently completed our first field season of Black-backed Woodpecker telemetry work. This research will greatly aid in our estimates of population size and our understanding of foraging ecology in burned areas of Sierra Nevada national forests.

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