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**Sierra Nevada Bird Observatory**

## **Black-backed Woodpecker MIS Surveys on Sierra Nevada National Forests: 2011 Annual Report**

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Photo by Monica Bond

Above: A male Black-backed Woodpecker delivers food to its nest.

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## Summary

The Black-backed Woodpecker (*Picoides arcticus*) was 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 have now implemented annually since 2009. 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 Woodpeckers, 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 and interpret information on other bird species utilizing burned forests.

During the 2011 field season, we used passive and broadcast surveys to assess Black-backed Woodpecker occupancy at 895 survey points arrayed across 50 recent fire areas (1-10 years post-fire) throughout our study area, yielding a total of 1315 unique survey points located within 73 fire areas that we have surveyed at least once between 2009-2011. A total of 964 points were visited in at least two years, providing direct year-to-year comparisons of results. We also collected on-the-ground habitat data at each survey point, and collected additional habitat data from remote-sensed GIS sources. In addition, we conducted passive point counts for other bird species at approximately half of the Black-backed Woodpecker survey points.

In 2011 we detected Black-backed Woodpeckers at 148 survey points distributed across 24 of the 50 fire areas we surveyed, including fire areas on all ten national forest units in our study area. 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.

Results were divided across three separate analyses, beginning with an exploration of annual changes in Black-backed Woodpecker occurrence within our sampling frame. To assess these changes, we used a 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 points within a fire were occupied (point-level occupancy). For each occupancy probability model, we defined a logit-linear model that included covariates that we deemed important based on previous years' analyses. Fire age was the only fire-level covariate, while point-level covariates included latitude, snag density, burn severity, pre-fire canopy cover, and elevation. Detectability was modeled as a function of survey interval duration (2- vs. 3-minute), count type (passive vs. broadcast survey), and seasonality (day of year). Each survey year was modeled separately, providing independent but comparable models of true occurrence within each year's sampling frame.

Mean occupancy probability for points surveyed in 2011 was 0.205 (95% credible interval: 0.18 – 0.24), which overlaps with estimates for 2009 (mean: 0.25; 95% CI: 0.22-0.31) and 2010 (mean: 0.19; 95% CI: 0.17 – 0.21). These results suggest, however, that occupancy was lower in 2010 but potentially rebounded in 2011. 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 58,443 ha of the 233,774 ha of burned forest on the ten national forest units within our sampling frame was occupied by Black-backed Woodpeckers in 2009 (95% CI: 51,430 – 72,470 ha), approximately 41,024 ha of the 215,915 ha of burned forest was occupied in 2010 (95% CI: 36,707 – 45,342 ha), and approximately 37,183 ha of the 181,381 ha of burned forest was occupied in 2011 (95% CI: 32,649 – 45,531).

Our second analysis used data from all three survey years (2009-2011) to explore occurrence dynamics over time, specifically the probabilities of colonization and extinction of Black-backed Woodpeckers at survey points. Our top models of colonization and extinction, as compared using the Akaike Information Criterion (AIC), strongly indicated that different parameters governed colonization dynamics versus extinction dynamics. The average probability of colonization by Black-backed Woodpeckers at a previously unoccupied point in any given year was modeled to be 7%, while the average probability that an occupied site would go extinct was 57%. The probability of extinction had no clear covariate relationships, with weak support distributed across multiple variables. The strongest relationship between a covariate and extinction was a negative relationship between extinction probability and pre-fire canopy cover – extinction occurred less frequently at survey points with greater pre-fire canopy cover. Colonization, however, had very strong relationships to two covariates. Colonization was more likely at early post-fire points and at points with higher densities of snags. At the youngest sites (1 year post-fire) with the greatest density of snags (~250 snags per hectare), the probability that an unoccupied point would become occupied the next year was greater than 60%.

Our third analysis focused on other bird species occupying recently burned forests. In addition to Black-backed Woodpeckers, our passive point counts combined across three years yielded detections of 127 other bird species within the fire areas. We used these data to support a multi-species hierarchical occupancy model analyzing community dynamics in relation to post-fire forest stand environmental characteristics. We looked at estimated bird species richness in relation to fire age, burn severity, and pre-fire canopy cover. We also looked at how these trends may differ by nesting guild. Overall species richness increased with fire age, decreased with burn severity, and increased with pre-fire canopy cover. Canopy nesting species followed these general trends, but had no significant trend with fire age. Shrub and ground nesting species, however, also increased in richness with fire age and pre-fire canopy cover, but also increased with burn severity. Cavity nesting species showed no overall richness relationship with burn severity, but increased significantly with fire age and decreased with pre-fire canopy cover. These trends, as well as species-specific analyses of environmental covariate relationships, confirm that post-fire bird species response is both individualistic and, in aggregate, generalizable by nesting guild.



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 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. The second manuscript will focus on colonization and extinction dynamics in Black-backed Woodpeckers and the differential effects of environmental covariates on each.

Shortly, we will begin our 2012 field season—the fourth year of full-scale Black-backed Woodpecker MIS monitoring on greater Sierra Nevada national forests. This fourth year of sampling will allow us to continue to track the amount of recently burned forest on the study area's ten national forests that is occupied by Black-backed Woodpeckers, and to refine models of colonization and extinction probabilities of points over time, thus allowing more direct inference on the underlying dynamics in woodpecker occurrence.

## Introduction

The Black-backed Woodpecker (*Picoides arcticus*) is designated 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 Woodpeckers are most abundant in stands of recently fire-killed snags (Hutto 1995, Kotliar et al. 2002, Smucker et al. 2005), although the species can be found in unburned forest stands throughout its range. 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). 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) but 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 to conduct 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 initiate an annual MIS monitoring program beginning in 2009 (Siegel et al. 2010 and 2011, Saracco et al. 2011, Tingley et al. in prep), based on findings and recommendations in Siegel et al. (2008).

In 2011 we continued Sierra-wide MIS monitoring for Black-backed Woodpeckers. Here we detail the results of this third year of MIS monitoring in recently burned forest stands.

## Methods

### Sample Design

We used the GIS data layer VegBurnSeverity10\_1.mdb (obtained from <http://www.fs.fed.us/r5/rsi/clearinghouse/gis-download>), which indicates fire boundaries and fire severity of fires throughout California, to extract data for all fires that occurred between 2002 and 2011 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.

These selection criteria yielded 68 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/or 2010, and fires that would be new to the survey. Our intention was to survey the first 50 fire areas on the list in 2011, 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 utilized during the 2010 field season, unless noted otherwise.

*Establishing survey points.* 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 points.

For fires that we did not previously survey in 2009 or 2010, we determined where within the fire area to place our survey points 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 points as close to the survey target point as possible, using the following rules:

1 – If trails or roads passed through the fire area, survey points 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 points, spaced 250 m apart. Survey points 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 points) off-trail survey points, 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.

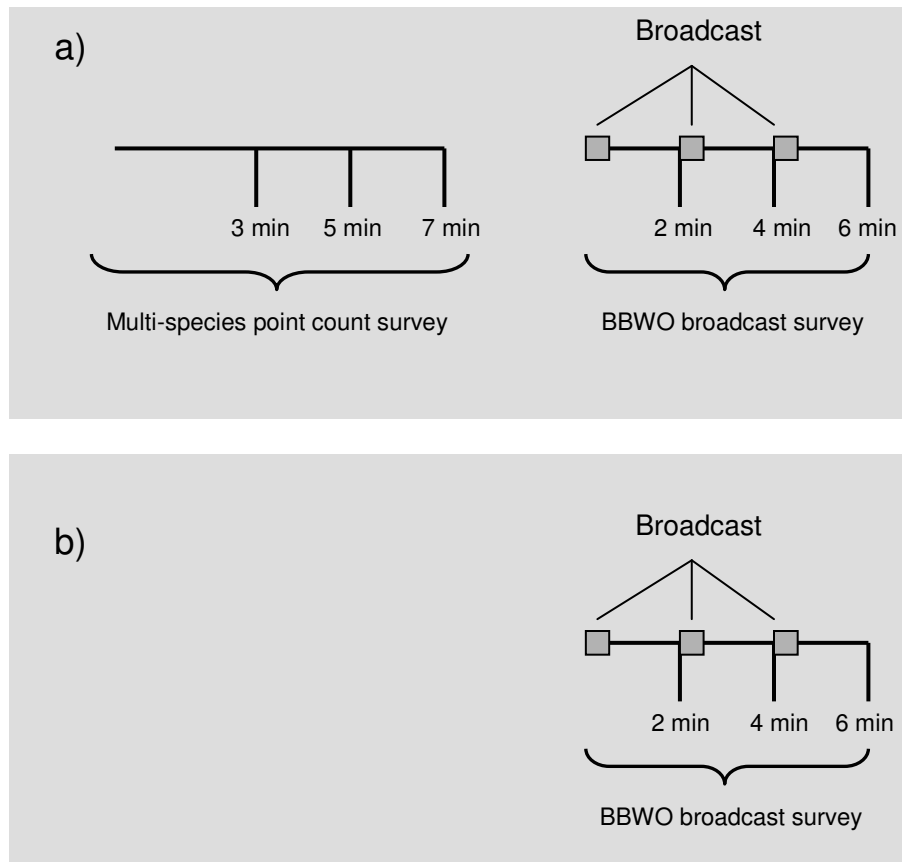
For fire areas that were previously surveyed in 2009 or 2010, we simply used the same survey points that were established previously by our field crews, using the placement rules described above. On rare occasions where survey points established previously were inaccessible due to changes in the landscape, later-lingering snowpack, etc., substitute points were established as close as possible to the previous points following the previously described rules.

*Broadcast surveys.* At each survey point 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. 1) at each survey point 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 (443 of 895) of the survey points (generally every second point), we *preceded* the broadcast survey with a 7-min passive point count to count all birds of any species (including Black-backed Woodpecker). The 7-min point count consisted of a 3-min interval immediately followed by two 2-min intervals (Fig. 1). Division of the count into discrete detection intervals yields information for assessing detection probability of Black-backed Woodpeckers. The 7-min point count represents a decrease in passive survey time from the 2010 season, when 11-min point counts with five discrete temporal intervals were used. This change reflects analyses of the 2010 data (Siegel et al. 2011), which revealed that additional intervals beyond the first 7 minutes added relatively little to overall Black-backed Woodpecker detection probability. 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. (2010).



**Figure 1.** 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 both passive and broadcast (a) and broadcast-only (b) methods at successive survey points.

*Habitat and other ancillary data.* After completing point counts and broadcast surveys each day, observers returned to the survey points to collect cursory habitat data. In addition to recording UTM coordinates, they classified the habitat within a 50-m radius plot centered on the survey point, 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

*Goals and analysis structure.* Based on previous analyses of the MIS data (Siegel et al. 2010 and 2011, Saracco et al. 2011, Tingley et al. in prep), our analytical goals for the 2011 data were more specific than in previous years, with less exploratory analysis. Here, our analysis focuses on answering three questions:

- (1) What is the overall proportion of fires and points in the sampling frame occupied in 2011 and how does this compare to previous years?
- (2) What are the probabilities of colonization and extinction at sites, and how have they changed over time and with site-specific environmental factors?
- (3) What can we learn about overall bird community composition and structure at recently burned sites?

Question 1 builds extensively on previous work, provides a model for future annual assessments, and is the central question that this monitoring program was implemented to answer. Question 2 requires development of a new model which, given 3 or more years of data, allows a greater understanding of the dynamics underlying changes in Black-backed Woodpecker occurrence. Goal 3 builds upon the 2010 analysis (Siegel et al. 2011) to further explore post-fire bird communities via hierarchical multi-species models. Descriptions of the modeling methods used in addressing each of these questions follow this section.

Based on previous modeling work with the 2009 and 2010 MIS monitoring data, we examined the relationship between occupancy and occupancy dynamics with the following environmental and site characteristics:

- Latitude (in decimal degrees) recorded from USGS topographic maps.
- 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 2007, Gesch et al. 2002). In models we used the residuals of a regression of elevation on latitude, thereby



controlling for the downslope bias in elevational ranges as latitude increases (Saracco et al. 2011, Siegel et al. 2011).

- Density of snags (standing dead trees) recorded at the survey point. Snag counts were conducted immediately after completing woodpecker surveys at burned sites and consisted of counting all snags of different size classes (10-30, 30-60, and >60 cm dbh) within 50 m of each survey point. Size-specific snag counts were aggregated in the field into different categories ( $\leq 5$ , 6-15, 16-30, 31-50, 51-100, >100), which were converted to numerical quantities (1, 5, 16, 31, 51, 100, respectively) for analysis. Counts across all three size classes were summed and snag density (snags/ha) was calculated.
- Density of live trees recorded at the survey point. Live tree density was calculated from vegetation survey data using the same methods as snag density.
- 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](http://frap.cdf.ca.gov/data/frapgisdata/download.asp?spatialdist=1&rec=fveg02_2)). We calculated this variable by averaging midpoints of the % tree cover variable (WHRDENSITY) at 100 m buffers around survey points.
- 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<sup>2</sup> resolution by averaging 30-m<sup>2</sup> 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>).

*Modeling annual occupancy.* 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 on the framework developed in the 2009 and 2010 MIS reports (Siegel et al. 2010, 2011) and published by Saracco et al. (2011). The model presented here is different from that presented in the 2010 MIS report (Siegel et al. 2011) because, given 3 (or more) years of sampling, combining all data into one model is not advantageous. A dynamic occupancy modeling framework (MacKenzie et al. 2003) allows

the annual modeling of occupancy within one model, but that framework prioritizes the modeling of colonization and extinction probabilities, leaving annual occupancy solely as a derived parameter. As a derived parameter, one cannot explicitly model relationships between occupancy and other factors, such as environmental or point-specific covariates. Thus, we prefer not to use dynamic occupancy models for direct inference on annual changes in occupancy. While we present a dynamic occupancy analysis here (see *Modeling dynamic occupancy*), for consistency in occurrence estimates across yearly reports, we also present results of single-year occupancy models for each of the three years of monitoring that have now been completed. The drawback of this method is that covariate relationships will be modeled independently for each year, which will result in different occurrence estimates than if all years were pooled into a single model. However, combined with modeling of occurrence dynamics, we believe this to be a strong framework for the analysis of trends over time.

Our annual model of occurrence was based from data on  $i = 1, \dots, N$  survey points,  $j = 1, \dots, M$  fire areas, and  $k = 1, \dots, K$  survey intervals, with values for  $N$ ,  $M$ , and  $K$ , unique to survey year. For the three years of monitoring, these values were: 899, 860, and 895 for  $N$  points in 2009, 2010, and 2011, respectively; 51, 49, and 50 for  $M$  fire areas; and 5, 9, and 6 for  $K$  survey intervals (combined passive surveys with 3 broadcast surveys).

The observational data for our model consisted of encounter histories for each survey point. 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 and 2011, a full detection history recording all detections or non-detections was recorded for all passive survey intervals, while the removal design (i.e., discontinuing counts following the initial broadcast-based detection) was used for broadcast intervals. This sampling framework resulted in 32 possible detection histories for 2011, the results of which are summarized in Table 1. Tables of encounter histories for previous years can be found in previous annual reports (Siegel et al. 2010, 2011).

**Table 1.** Encounter history frequencies (numbers of survey points) in the 2011 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 (passive surveys were only conducted at approximately half of points). For broadcast 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 148 of the 895 points that we surveyed in 2011.

Number of passive detections	Broadcast History			Frequency
	Interval 1	Interval 2	Interval 3	
-	0	0	0	385
-	0	0	1	11
-	0	1	NA	23
-	1	NA	NA	33
0	0	0	0	362
0	0	0	1	11
0	0	1	NA	13
0	1	NA	NA	23
1	0	0	0	5
1	0	0	1	1
1	0	1	NA	2
1	1	NA	NA	3
2	0	0	0	5
2	0	0	1	1
2	0	1	NA	0
2	1	NA	NA	6
3	0	0	0	2
3	0	0	1	1
3	0	1	NA	1
3	1	NA	NA	6

To model annual occupancy, we used a hierarchical modeling framework (Royle and Dorazio 2008) to build separate but linked models for the observation (detection) and state (occupancy) processes. With the exception of input data (i.e., each year was a separate model, instead of combining years into one model), our occupancy model structure identically followed that described in the 2010 analysis (Siegel et al., 2011). This structure is interesting as it subdivided the state (i.e., true occurrence) observation 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.

For each year of data, the same set of covariates was used for the modeling of occupancy (both fire-level and point-level) and detectability. Detectability was modeled as a function of survey interval duration (3-minute or 2-minute), survey type (passive or broadcast), and day of year. Fire-level occupancy was modeled as a function of fire age but was also allowed a random fire-level effect (Saracco et al., 2011). Point-level occupancy was modeled as a function of latitude, elevation, snag density, pre-fire canopy cover, and burn severity (see *Goals and analysis structure*, above).

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 point effect (fire<sub>j</sub>) in the model for  $\omega_j$ , and a prior of Unif(0,10) for the variance parameter  $\sigma_f$ . For the intercepts of the  $p$  and  $\psi$  models, we defined priors for inverse-logit transformed parameters using Unif(0, 1). We conducted the WinBUGS analysis from R (R Development Core Team 2011) using the R2WinBUGS package (Sturtz et al. 2005). Further details of model structure and parameterization, are provided in our 2010 analysis (Siegel et al. 2011).

*Modeling dynamic occupancy.* Detectability, initial occupancy, colonization and extinction of Black-backed Woodpeckers at survey points over time were modeled using a dynamic occupancy framework (MacKenzie et al. 2003). In this framework, initial occupancy ( $\psi_0$ ) is modeled for all survey points in the first year of sampling (here, 2009), and then the occurrence status is allowed to change between years according to an estimated probability of colonization ( $\gamma$ ) or extinction ( $\epsilon$ ). Thus, the probability of occupancy at time  $t$  is dependent on both the initial occupancy probability as well as the probability (combined  $\gamma$  and  $\epsilon$ ) that the point has transitioned states from time 0 to time  $t$ .

In this framework,  $\psi$  has a slightly different interpretation from the previous analysis (*Modeling annual occupancy*). First, as the focus was on colonization and extinction dynamics, occupancy was modeled only at the point level (i.e., no fire-level occupancy) and occurrence at neighboring

points within the same fire were assumed to be independent (i.e., no random effect of fire). Second, in a dynamic framework, average occupancy for year  $t$  is based upon the total number of points that are surveyed across all years, not the total number of points that were actually surveyed in year  $t$ . In other words, the dynamic framework estimates occupancy in any year across all 1315 survey points, not the 850-900 that were actually visited in any given survey season. Thus, occupancy estimates derived from a dynamic analysis will not have a straightforward interpretation similar to those from the annual analysis. Comparing occupancy estimates across the two model frameworks should not be done without realizing that average occupancy estimates from a dynamic model will always be lower due to the larger sampling frame.

Dynamic occupancy modeling was conducted in a likelihood-based framework, whereby different competing models were built and their relative strength was measured using the Akaike Information Criterion (AIC; Burnham and Anderson 2002). In this model selection framework, competing models are built using all possible combinations of *a priori* selected variables. Since four variables can be parameterized ( $p$ ,  $\psi_0$ ,  $\gamma$  and  $\epsilon$ ), this can lead to an untenable number of competing models. Thus, we used a two-step process, through which the best parameterization for  $p$  and  $\psi_0$  was determined by AIC, and then that single parameterization was used for all competing models of  $\gamma$  and  $\epsilon$ . Similar to the previous analysis, for detectability we investigated the effect of interval duration, survey type and day of year. For initial occupancy, we only investigated the effect of elevation (including quadratic effects) and latitude. Combined, these factors resulted in 56 competing models which were combined with null (i.e., random) model parameterizations for colonization and extinction. All 56 models were run and the best supported model was selected as the one with the lowest AIC.

Following selection of the best supported parameterization for detectability and initial occupancy, this parameterization was used to compare differently parameterized models of colonization and extinction. We tested the effects of snag density, fire age, burn severity, and pre-fire canopy cover as potential covariates for both colonization and extinction. Including models with multiple covariates, this resulted in 256 uniquely parameterized competing models, each with the same initial occupancy and detectability covariates, but with different colonization

and extinction covariates. Support within the data for each model was determined through comparisons of AIC.

All models were run in R version 2.14 (R Core Development Team 2011) using the package ‘unmarked’ (Fiske and Chandler 2011).

*Modeling community occupancy.* Building on the analysis of the 2010 data (Siegel et al. 2011), we built a multi-species hierarchical occupancy model to explore the effects of environmental variables on bird assemblages in post-fire forest stands. Similar to the occupancy model presented for the main analysis (see *Modeling annual occupancy*), the multi-species framework builds an occupancy model individually for each species but draws estimated parameters for each species (e.g., beta-parameters for occupancy covariates) from higher, hierarchical distributions governed by simple hyper-parameters (i.e., a mean and variance). Specifically, the multi-species modeling framework presented here builds on 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 point-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  $1 \dots i \dots 120$ , at survey point  $1 \dots j \dots 1173$ , during survey interval  $1 \dots k \dots 5$ . With this in mind, the we similarly modeled detections,  $y(i,j,k)$ , conditional on occupancy,  $z(i,j)$ , such that detection was a Bernoulli distributed outcome of the product of the true occupancy ( $z$ ) and the probability of detecting species  $i$  at point  $j$  on survey interval  $k$ . We modeled the latent occupancy state indicator variable,  $z(i,j)$ , as a Bernoulli-distributed random variable with a probability of species  $i$  occupying point  $j$  of  $\psi_{ij}$ .

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,  $\psi_{ij}$ , or occupancy at each point in each year, was modeled as a function of six *a priori* selected covariates: elevation (including quadratic term), fire age, snag density, live tree density, % shrub coverage, and burn severity (all variable as described previously). Second, we defined a logit-linear model for detection probability  $p_{ijk}$ , based on similar covariates as our annual model for Black-backed Woodpeckers: survey duration, and day of year.

In comparing the multi-species model to the single-species Black-backed Woodpecker model, it is important to note that here, each species  $i$  has independently estimated parameters  $\alpha_{0,i} \dots \alpha_{2,i}$  and  $\beta_{0,i} \dots \beta_{7,i}$ . 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  $1 \dots n \dots 2$  detectability parameters and  $1 \dots m \dots 7$  occupancy parameters, where  $\mu$  is the mean and  $\tau$  is the precision of a normal distribution.

## **Results**

### Scope of Survey Work Completed

In 2011 we completed surveys fully to protocol at 50 fire areas (Table 2), including broadcast surveys and habitat assessments at 895 survey points and passive, multi-species point counts at 443 of those points. All surveys were conducted between 13 May and 10 July, 2011. Combined with data collected in 2009 and 2010, we now have broadcast surveys and habitat assessments data at 1315 unique survey points within 73 fire areas. We provide summary information about fire areas surveyed once or more between 2009 and 2011 in Table 2.

### Black-backed Woodpecker Detections

In 2011 we detected Black-backed Woodpeckers at 148 survey points distributed across 24 of the 50 fire areas we surveyed (Figs. 2-4). We detected Black-backed Woodpeckers on all ten of the national forest units in our study area. As was the case in previous years, 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. 2), and the second most southerly fire area we surveyed (the Vista fire area on the Sequoia NF; Fig. 5). We provide UTM coordinates and survey history of all survey points on an interactive, online map at: <http://www.birdpop.net/index.php/viewmaps?catid=2&id=10:bbwomap>.



**Table 2.** Summary information for each fire area surveyed once or more during the 2009 – 2011 field seasons of Black-backed Woodpecker MIS monitoring on Sierra Nevada national forests.

Primary national forest	Fire name	Year of fire	Burned area (ha) <sup>1</sup>	Dominant pre-fire habitat <sup>2</sup>	No. points surveyed (2009)	No. points surveyed (2010)	No. points surveyed (2011)
Eldorado	Freds	2004	1,814	Sierra Mixed Conifer	20	0	19
Eldorado	Plum	2002	417	Sierra Mixed Conifer	12	12	12
Eldorado	Power	2004	5,538	Sierra Mixed Conifer	20	20	20
Eldorado	Star	2001	4,979	Sierra Mixed Conifer	0	20	20
Inyo	Azusa	2000	164	Pinyon-Juniper	8	0	0
Inyo	Birch	2002	1,117	Pinyon-Juniper	19	0	0
Inyo	Crater	2001	1,118	Jeffrey Pine	20	20	20
Inyo	Dexter	2003	1,022	Jeffrey Pine	16	16	0
Inyo	Inyo Complex	2007	7,574	Ponderosa Pine	16	0	0
Inyo	Mclaughlin	2001	939	Jeffrey Pine	0	13	13
Inyo	Sawmill '00	2000	144	Ponderosa Pine	5	0	0
Inyo	Sawmill '06	2006	2,452	Pinyon-Juniper	0	0	19
Inyo	Summit	2003	2,474	Jeffrey Pine	0	0	16
Lassen	Brown	2009	684	Sierra Mixed Conifer	0	20	20
Lassen	Cone	2002	703	Jeffrey Pine	21	0	21
Lassen	Cub	2008	6,093	Sierra Mixed Conifer	0	20	20
Lassen	Onion 2	2008	1,067	Sierra Mixed Conifer	0	20	20
Lassen	Peterson Complex	2008	1,161	Eastside Pine	20	20	20
Lassen	Sugarloaf	2009	3,127	Sierra Mixed Conifer	0	21	21
Modoc	Bell	2001	1,260	Juniper	20	20	20
Modoc	Bell West	1999	773	Eastside Pine	21	0	0
Modoc	Blue	2001	13,329	Eastside Pine	20	20	20
Modoc	Fletcher	2007	916	Ponderosa Pine	19	17	19
Modoc	High	2006	421	Eastside Pine	0	19	19
Plumas	Antelope Complex	2007	9,297	Eastside Pine	21	21	21
Plumas	Belden	2008	224	Mixed Hardwood-Conifer	0	13	13

Table 2. Continued.

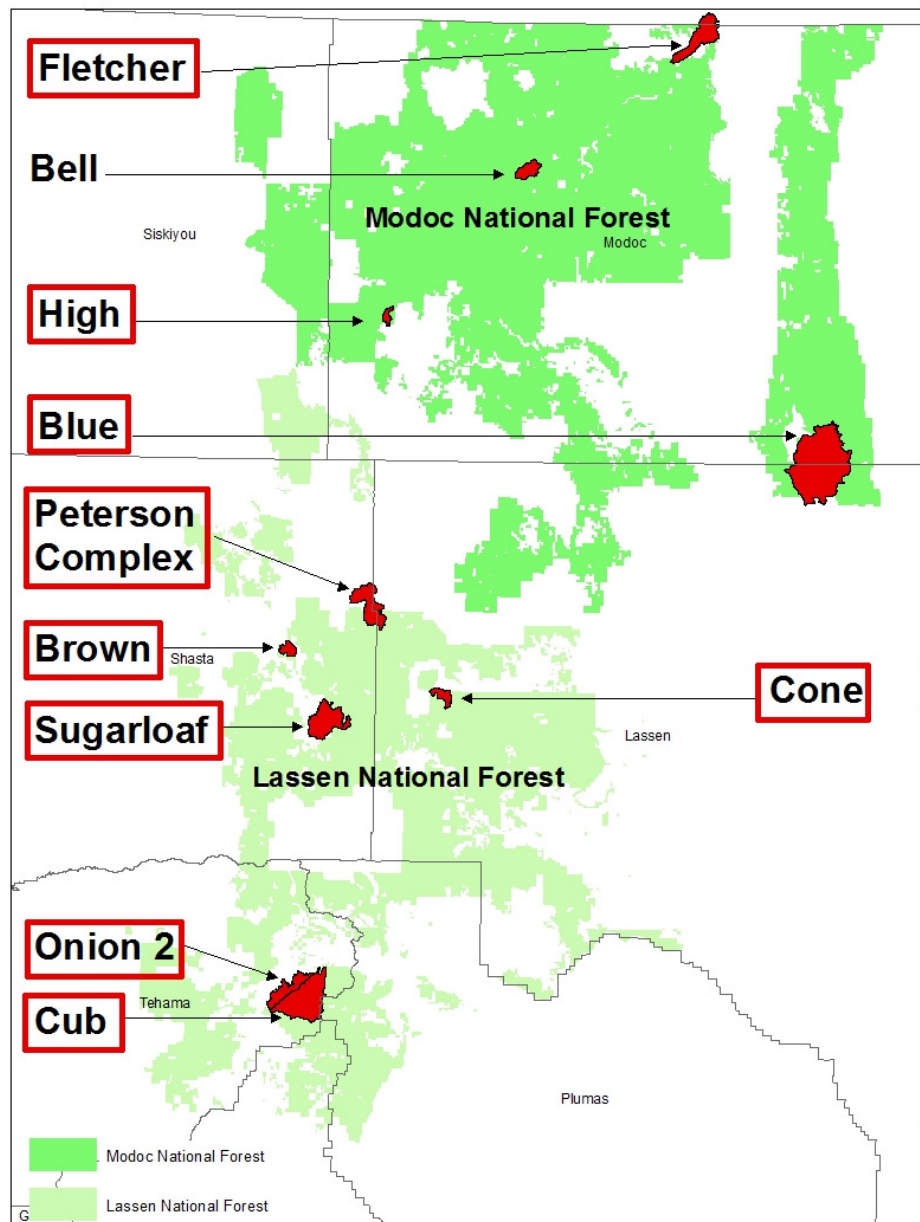
Plumas	Boulder Complex	2006	1,475	Eastside Pine	20	20	0
Plumas	Bucks	1999	11,325	Sierra Mixed Conifer	20	0	0
Plumas	Devils Gap	1999	612	Sierra Mixed Conifer	20	0	0
Plumas	Fox	2008	1,007	Sierra Mixed Conifer	0	0	18
Plumas	Frey	2008	4,406	Sierra Mixed Conifer	0	20	18
Plumas	Horton 2	1999	1,637	Sierra Mixed Conifer	20	0	0
Plumas	Lookout	1999	1,009	Sierra Mixed Conifer	21	0	0
Plumas	Moonlight	2007	18,864	Eastside Pine	20	20	20
Plumas	Pidgen	1999	1,859	Sierra Mixed Conifer	18	0	0
Plumas	Rich	2008	2,360	Sierra Mixed Conifer	21	21	0
Plumas	Scotch	2008	5,647	Sierra Mixed Conifer	21	21	0
Plumas	Silver	2009	140	Sierra Mixed Conifer	0	0	11
Plumas	Storrie	2000	21,117	Red Fir	15	0	0
Plumas	Stream	2001	1,507	Eastside Pine	20	20	15
Sequoia	Albanita	2003	958	Jeffrey Pine	21	21	21
Sequoia	Broder Beck	2006	1,457	Jeffrey Pine	0	20	20
Sequoia	Clover	2008	6,088	Jeffrey Pine	0	20	20
Sequoia	Crag '04	2004	364	Jeffrey Pine	19	0	18
Sequoia	Crag '05	2005	611	Jeffrey Pine	21	20	21
Sequoia	Deep	2004	1,305	Sierra Mixed Conifer	11	11	11
Sequoia	granite	2009	607	Jeffrey Pine	0	20	20
Sequoia	Highway	2001	1,384	Mixed Hardwood-Conifer	0	0	20
Sequoia	Hooker	2003	1,004	Jeffrey Pine	20	16	20
Sequoia	Lion	2009	1,075	Red Fir	0	20	20
Sequoia	Manter	2000	22,450	Pinyon-Juniper	21	20	0
Sequoia	Mcnally	2002	61,261	Sierra Mixed Conifer	19	17	16
Sequoia	Piute '08	2008	13,516	Jeffrey Pine	20	19	0
Sequoia	Vista	2007	180	Red Fir	19	19	19
Sierra	North Fork	2001	1,614	Sierra Mixed Conifer	20	13	8
Sierra	Oliver	2008	1,099	Sierra Mixed Conifer	0	0	17

**Table 2.** Continued.

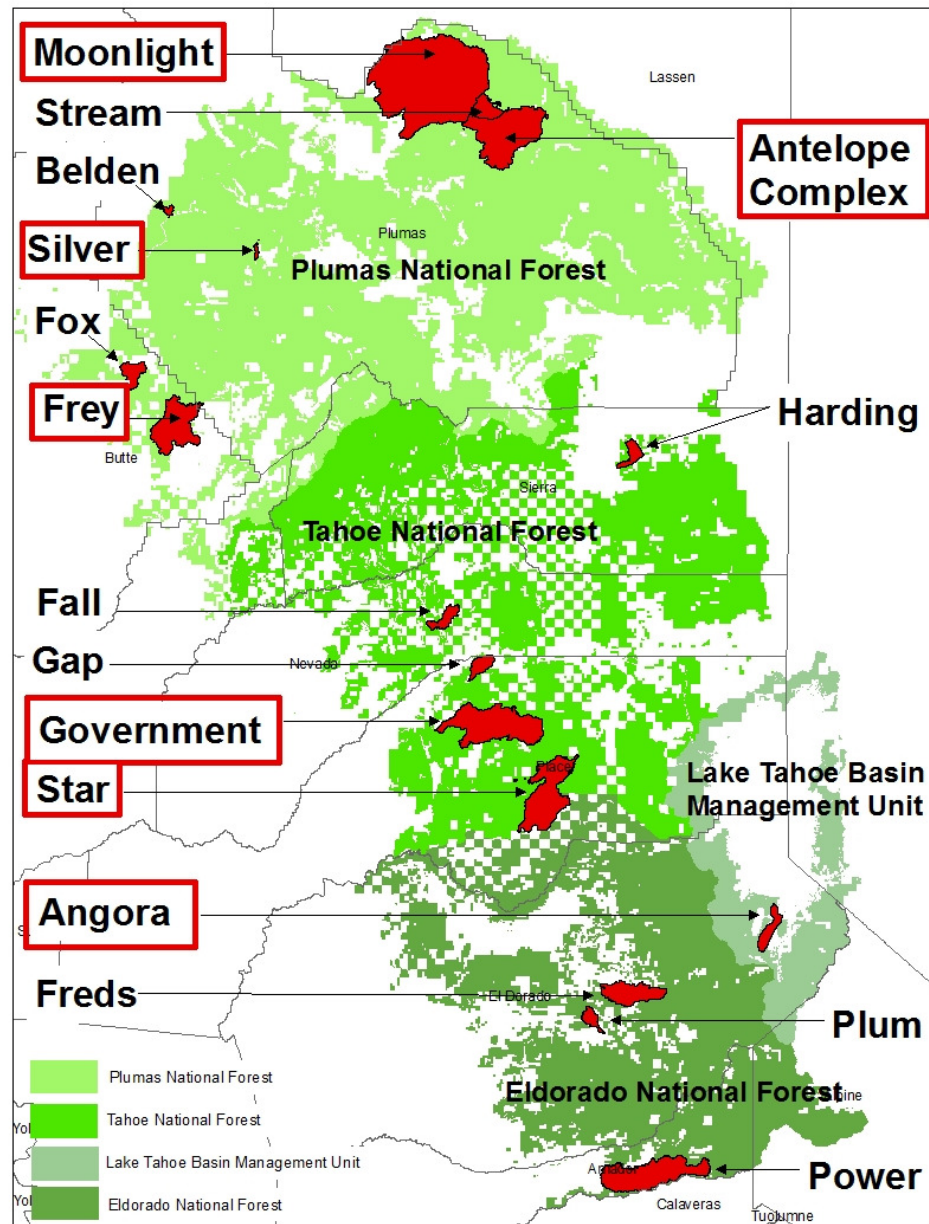
Stanislaus	Hiram	1999	1,144	Jeffrey Pine	10	0	0
Stanislaus	Kibbie	2003	1,501	Sierra Mixed Conifer	21	0	21
Stanislaus	Knight	2009	2,140	Sierra Mixed Conifer	0	19	19
Stanislaus	Mountain	2003	1,747	Red Fir	0	12	12
Stanislaus	Mud	2003	1,803	Red Fir	21	20	21
Stanislaus	Whit	2003	438	Red Fir	20	0	20
Stanislaus	White	2001	107	Sierra Mixed Conifer	8	8	8
Tahoe	Bassetts	2006	1,006	Sierra Mixed Conifer	18	18	0
Tahoe	Fall	2008	584	Sierra Mixed Conifer	10	10	10
Tahoe	Gap	2001	574	Sierra Mixed Conifer	0	20	19
Tahoe	Government	2008	7,784	Sierra Mixed Conifer	19	19	19
Tahoe	Harding	2005	616	Ponderosa Pine	21	21	21
Tahoe	Peavine	2008	192	Sierra Mixed Conifer	16	0	0
Tahoe	Treasure	2001	143	Eastside Pine	10	10	0
Tahoe Basin	Angora	2007	1,146	Sierra Mixed Conifer	19	12	19
Tahoe Basin	Gondola	2002	165	Red Fir	12	12	0
Tahoe Basin	Showers	2002	125	Eastside Pine	9	9	0

<sup>1</sup>Burned area represents only the total area of the fire within National Forest boundaries.

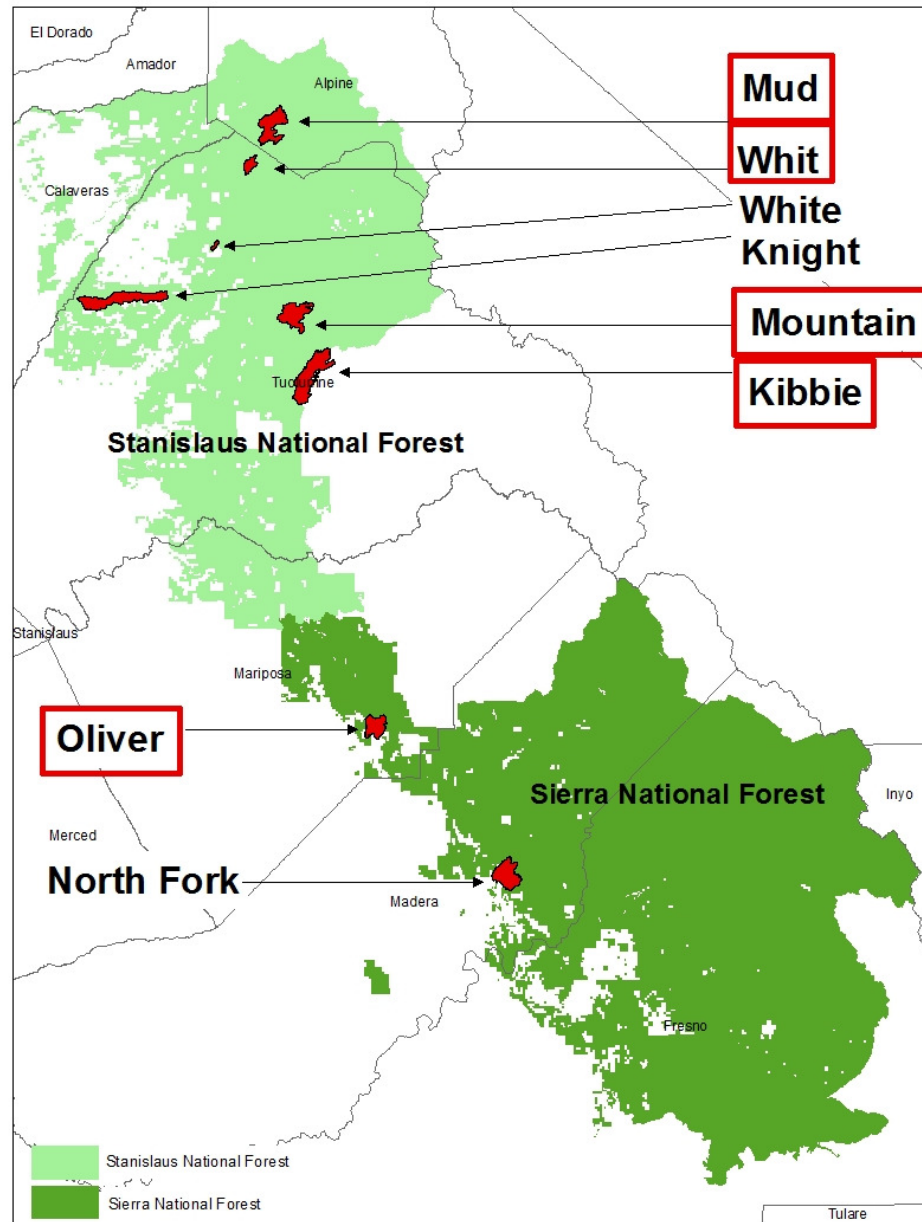
<sup>2</sup>Habitat classifications follow California Habitat Relationships (CWHR; California Department of Fish and Game 2005), and indicate the primary pre-fire habitat at the greatest number of survey points in a particular fire area, based on our own on-the-ground assessments.



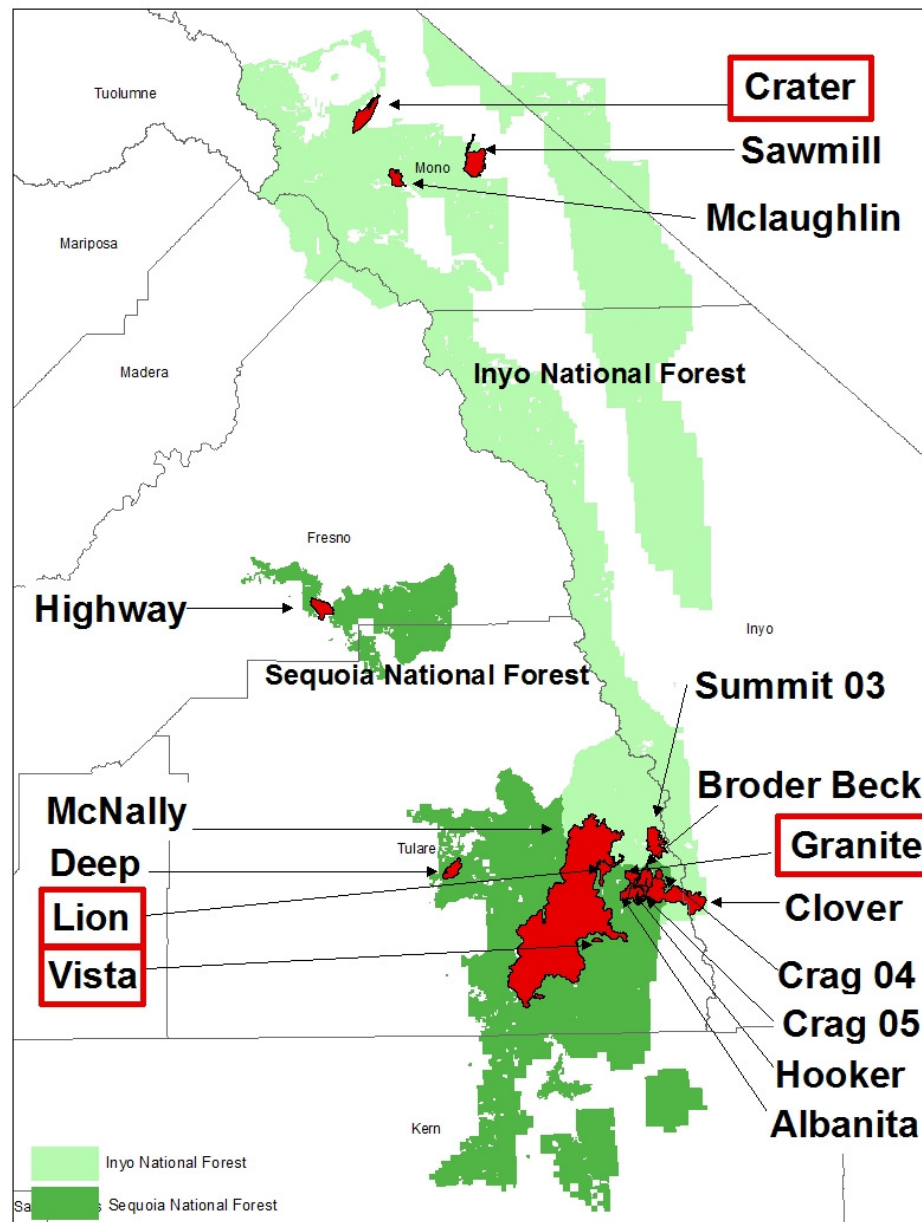
**Figure 2.** Fire areas (red shading) on the Modoc and Lassen National Forests that we surveyed for Black-backed Woodpeckers during the 2011 Black-backed Woodpecker MIS monitoring field season. Names of fire areas where Black-backed Woodpeckers were detected are enclosed in red boxes. Fire area names 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 3.** 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 2011 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 4.** Fire areas (red shading) on the Stanislaus and Sierra National Forests that were surveyed for Black-backed Woodpeckers during the 2011 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).



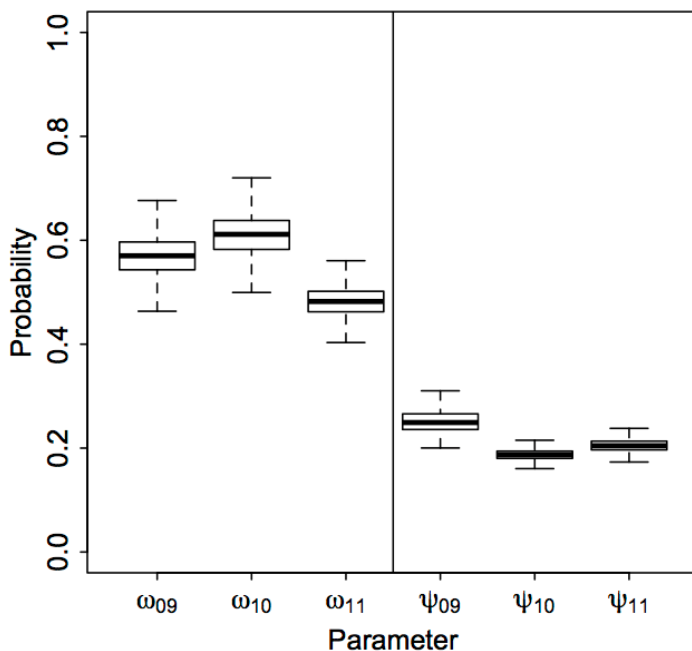
**Figure 5.** Fire areas (red shading) on the Inyo and Sequoia National Forests that were surveyed for Black-backed Woodpeckers during the 2011 Black-backed Woodpecker MIS monitoring field season. Names of fire areas where Black-backed Woodpeckers were detected are enclosed in red boxes. Fire area names 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).



### Analysis of Annual Occupancy

Mean occupancy probability for points surveyed during 2011 was 0.205 (95% credible interval: 0.18 – 0.24), which overlaps with both estimates for 2009 (95% CI: 0.22 – 0.31) and 2010 (95% CI: 0.17 – 0.21) (Figure 6). The mean value for 2009 (0.25) is very close to previous estimates (0.25, Siegel et al. 2010; 0.23, Siegel et al., 2011), while the mean value for 2010 (0.19) is lower than previously modeled (0.23, Siegel et al. 2011), although confidence intervals overlap.

Changing model structures will result in slightly different estimates of occupancy (see *Discussion*). Assuming that our sample was representative of woodpecker habitat yielded by fire areas that burned between 1999 and 2010, we estimate that approximately 37,183 ha (i.e., 20.5%) of the 181,381 ha of burned forest on the ten national forest units within our sampling frame were occupied by Black-backed Woodpeckers in 2011 (or a range based on the 95% credible interval of 32,649 – 43,531 ha) compared to an estimate of 58,443 ha (95% CI: 51,430 – 72,470 ha) of 233,774 ha occupied in 2009 and 41,024 ha (95% CI: 36,706 – 45,342 ha) of 215,915 ha occupied in 2010. Table 3 summarizes detections and predicted occupancy probabilities for each fire area surveyed in 2009 through 2011.



**Figure 6.** Mean probability of fire-level ( $\omega$ ) and point-level ( $\psi$ ) occupancy for Black-backed Woodpeckers as modeled from individual year-based hierarchical models. Plots show median (bold line), interquartile range (box) and 95% quantile range (whiskers) of posterior distribution of modeled parameters.



**Table 3.** Summary of Black-backed Woodpecker detections and posterior distributions of both fire-level ( $\omega$ ) and average point-level ( $\psi$ ) predictions of occupancy probability for all fire areas surveyed during 2009 - 2011.

Fire name	2009 Detects. (# stns)	2010 Detects. (# stns)	2011 Detects. (# stns)	$\omega_{2009}$	$\omega_{2010}$	$\omega_{2011}$	$\psi_{2009}$	$\psi_{2010}$	$\psi_{2011}$
Albanita	21 (1)	21 (0)	21 (0)	0.84	0.12	0.13	0.10	0.00	0.00
Angora	19 (13)	12 (7)	19 (13)	0.90	0.89	0.87	0.78	0.61	0.73
Antelope Complex	21 (9)	21 (2)	21 (6)	0.90	0.89	0.86	0.62	0.23	0.41
Azusa	8 (0)	-	-	0.12	-	-	0.00	-	-
Bassetts	18 (7)	18 (7)	-	0.89	0.88	-	0.48	0.44	-
Belden	-	13 (0)	13 (0)	-	0.61	0.18	-	0.00	0.00
Bell	20 (0)	20 (0)	20 (0)	0.11	0.10	0.11	0.00	0.00	0.00
Bell West	21 (1)	-	-	0.77	-	-	0.15	-	-
Birch	19 (0)	-	-	0.13	-	-	0.00	-	-
Blue	20 (5)	20 (5)	20 (5)	0.81	0.78	0.79	0.59	0.32	0.34
Boulder Complex	20 (9)	20 (1)	-	0.88	0.88	-	0.54	0.09	-
Broder Beck	-	20 (7)	20 (0)	-	0.87	0.16	-	0.41	0.00
Brown	-	20 (7)	20 (14)	-	0.92	0.88	-	0.37	0.75
Bucks	20 (0)	-	-	0.09	-	-	0.00	-	-
Clover	-	20 (7)	20 (0)	-	0.91	0.19	-	0.42	0.00
Cone	21 (5)	-	21 (6)	0.82	-	0.81	0.47	-	0.36
Crag 04	19 (4)	-	18 (0)	0.86	-	0.14	0.29	-	0.00
Crag 05	21 (0)	20 (0)	21 (0)	0.19	0.16	0.16	0.00	0.00	0.00
Crater	20 (8)	20 (3)	20 (7)	0.81	0.77	0.79	0.48	0.20	0.39
Cub	-	20 (3)	20 (3)	-	0.91	0.88	-	0.17	0.25
Deep	11 (0)	11 (0)	11 (0)	0.49	0.30	0.15	0.00	0.00	0.00
Devils Gap	20 (0)	-	-	0.09	-	-	0.00	-	-
Dexter	16 (6)	16 (1)	-	0.84	0.82	-	0.53	0.19	-
Fall	10 (0)	10 (1)	10 (0)	0.42	0.91	0.19	0.02	0.16	0.00
Fletcher	19 (15)	17 (5)	19 (8)	0.90	0.90	0.86	0.90	0.40	0.53
Fox	-	-	18 (0)	-	-	0.18	-	-	0.00
Freds	20 (0)	-	19 (0)	0.17	-	0.14	0.00	-	0.00
Frey	-	20 (0)	18 (0)	-	0.49	0.18	-	0.00	0.00
Gap	-	20 (0)	19 (0)	-	0.10	0.11	-	0.00	0.00
Gondola	12 (6)	12 (4)	-	0.83	0.80	-	0.74	0.43	-
Govnmt.	19 (1)	19 (3)	19 (4)	0.91	0.91	0.88	0.10	0.20	0.31
Granite	-	20 (6)	20 (10)	-	0.92	0.88	-	0.37	0.53
Harding	21 (7)	21 (2)	21 (0)	0.87	0.86	0.14	0.41	0.14	0.00
High	-	19 (1)	19 (5)	-	0.87	0.86	-	0.07	0.36
Highway	-	-	20 (0)	-	-	0.11	-	-	0.00
Hiram	10 (0)	-	-	0.10	-	-	0.00	-	-

Hooker	20 (0)	16 (0)	20 (0)	0.14	0.12	0.13	0.00	0.00	0.00
Horton 2	20 (7)	-	-	0.77	-	-	0.51	-	-
Inyo Complex	16 (0)	-	-	0.26	-	-	0.00	-	-
Kibbie	21 (6)	-	21 (3)	0.85	-	0.81	0.33	-	0.21
Knight	-	19 (0)	19 (0)	-	0.61	0.20	-	0.01	0.00
Lion	-	20 (7)	20 (2)	-	0.92	0.88	-	0.41	0.15
Lookout	21 (0)	-	-	0.10	-	-	0.00	-	-
Manter	21 (0)	20 (0)	-	0.14	0.08	-	0.00	0.00	-
McLaughlin	-	13 (0)	13 (1)	-	0.10	0.79	-	0.00	0.13
McNally	19 (0)	17 (0)	16 (0)	0.35	0.23	0.12	0.00	0.00	0.00
Moonlight	20 (11)	20 (5)	20 (11)	0.90	0.90	0.86	0.61	0.28	0.61
Mountain	-	12 (1)	12 (3)	-	0.82	0.82	-	0.21	0.32
Mud	21 (10)	20 (12)	21 (8)	0.85	0.81	0.82	0.54	0.65	0.44
North Fork	20 (0)	13 (0)	8 (0)	0.25	0.17	0.12	0.00	0.00	0.00
Oliver	-	-	17 (6)	-	-	0.87	-	-	0.43
Onion 2	-	20 (0)	20 (0)	-	0.30	0.18	-	0.00	0.00
Peavine	16 (0)	-	-	0.54	-	-	0.01	-	-
Peterson Complex	20 (9)	20 (7)	20 (14)	0.92	0.91	0.87	0.51	0.37	0.74
Pidgen	18 (0)	-	-	0.09	-	-	0.00	-	-
Piute 08	20 (0)	19 (0)	-	0.37	0.23	-	0.00	0.00	-
Plum	12 (0)	12 (0)	12 (0)	0.29	0.22	0.12	0.00	0.00	0.00
Power	20 (1)	20 (0)	20 (0)	0.86	0.18	0.13	0.10	0.00	0.00
Rich	21 (1)	21 (1)	-	0.91	0.91	-	0.12	0.08	-
Sawmill 00	5 (0)	-	-	0.17	-	-	0.01	-	-
Sawmill 06	-	-	19 (0)	-	-	0.16	-	-	0.00
Scotch	21 (3)	21 (0)	-	0.91	0.29	-	0.22	0.01	-
Showers	9 (3)	9 (6)	-	0.82	0.79	-	0.52	0.72	-
Silver	-	-	11 (7)	-	-	0.88	-	-	0.68
Star	-	20 (6)	20 (1)	-	0.77	0.79	-	0.35	0.18
Storrie	15 (4)	-	-	0.80	-	-	0.48	-	-
Stream	20 (0)	20 (0)	15 (0)	0.11	0.09	0.11	0.00	0.00	0.00
Sugarloaf	-	21 (3)	21 (2)	-	0.92	0.88	-	0.17	0.29
Summit	-	-	16 (0)	-	-	0.14	-	-	0.00
Treasure	10 (2)	10 (4)	-	0.80	0.77	-	0.29	0.42	-
Vista	19 (9)	19 (8)	19 (2)	0.90	0.90	0.86	0.52	0.50	0.17
Whit	20 (6)	-	20 (7)	0.84	-	0.82	0.36	-	0.41
White	8 (0)	8 (0)	8 (0)	0.23	0.20	0.12	0.00	0.01	0.00
Total	899 (169)	860 (132)	895 (148)	0.57 (0.49 - 0.65)	0.61 (0.53 - 0.69)	0.48 (0.42 - 0.54)	0.25 (0.22 - 0.31)	0.19 (0.17 - 0.21)	0.21 (0.18 - 0.24)

Models of annual occupancy show changes in the total estimated proportion of (sampled) fire areas being occupied by at least one Black-backed Woodpecker in different years (Table 3). The proportion of occupied fire areas ( $\omega$ ) in 2009 and 2010 appears to have been relatively stable (0.60 and 0.65, respectively, with overlapping confidence intervals), while the proportion in 2011 is significantly lower (0.48, 95% CI: 0.48 – 0.50). Given that different fires were sampled in different years, the interpretation of this statistic is ambiguous. For example, there is only one fire (Harding, which burned in 2005) where Black-backed Woodpeckers were detected in 2009 and 2010 but were not detected in 2011 (Table 3). Therefore, a decline in the proportion of occupied fires could simply be the result of having randomly selected more unoccupied fires. Actual changes in colonization or extinction are best understood through dynamic occupancy models (see next section).

Although covariate relationships were not a primary subject of interest, we compared modeled covariate relationships with occupancy and detectability for each of the three annual occupancy models (Table 4). Covariate signs showed general consistency across years – there were no significant covariate relationships that switched signs across years. The strength of covariate relationships differed from year to year, with particularly low covariate strengths in 2011. Given that the ability of models to fit covariate relationships is a function of data quantity, the observation that covariates did not show consistent strength in single-year analyses should not reflect upon the true strength of covariate relationships (which are best determined from combined, multi-season analyses, see *Analysis of Dynamic Occupancy*).

**Table 4.** Posterior summaries (means and 95% credible intervals) for intercepts and regression coefficients for single-year occupancy models as applied to 2009-2011 survey data.

Parameter	Year		
Fire level occupancy probability	2009	2010	2011
$\sigma_f$ (variance of random fire effect)	6.5 (0.93 - 9.87)	6.34 (1.05 - 9.85)	6.2 (0.57 - 9.86)
$\gamma_1$ (fire age)	-2.76 (-6.58 - -0.14)	-3.23 (-7.42 - -0.39)	-1.83 (-5.15 - 0.44)
Point-level occupancy probability			
$\beta_0$	-1.01 (-1.37 - -0.61)	-1.17 (-1.47 - -0.86)	-0.45 (-0.76 - -0.11)
$\beta_1$ (latitude)	0.54 (0.17 - 1.01)	-0.26 (-0.53 - 0.00)	0.22 (-0.06 - 0.52)
$\beta_2$ (elevation)	1.20 (0.70 - 1.91)	0.81 (0.45 - 1.16)	-0.07 (-0.37 - 0.24)
$\beta_3$ (snag density)	0.08 (-0.18 - 0.32)	0.29 (0.00 - 0.60)	0.10 (-0.15 - 0.36)
$\beta_4$ (burn severity)	0.37 (0.06 - 0.72)	0.21 (-0.05 - 0.47)	0.20 (-0.09 - 0.49)
$\beta_5$ (pre-fire canopy cover)	0.06 (-0.22 - 0.33)	0.35 (0.06 - 0.63)	0.22 (-0.03 - 0.48)
Detection probability			
$\alpha_0$	-3.45 (-4.41 - -2.65)	-1.57 (-1.89 - -1.25)	-1.2 (-1.58 - -0.83)
$\alpha_1$ (interval duration)	1.94 (1.11 - 2.91)	0.72 (0.14 - 1.31)	0.09 (-0.51 - 0.68)
$\alpha_2$ (survey type)	2.83 (2.03 - 3.77)	1.05 (0.65 - 1.47)	0.67 (0.22 - 1.12)
$\alpha_3$ (day of year)	-0.24 (-0.54 - 0.06)	-0.16 (-0.41 - 0.08)	0.01 (-0.21 - 0.22)

### Analysis of Dynamic Occupancy

Of the 1315 survey points, 965 (73%) were surveyed in more than one year and 350 (27%) were surveyed in all three years. Of those points that were surveyed in more than one year, 84 showed apparent colonizations (i.e., not detected in one year, detected in subsequent), 130 showed apparent extinctions, and 42 showed mixed detection histories (i.e., the apparent occurrence status changed each year). This degree of apparent occurrence change at revisited points (19% of all points) facilitated the building of dynamic occupancy models focused on the estimation of point-specific colonization and extinction probabilities.

Of the 56 model parameterizations of detectability and initial occupancy, strong support was limited to 4 models within 2 AIC units of each other (Table 5). The best supported model was also the model with all possible covariates, so this “full” model was used as the base parameterization for comparing colonization and extinction models.

**Table 5.** Top 5 models comparing different combinations of detectability ( $p$ ) and occupancy ( $\psi_0$ ) covariates. Table shows the number of estimated parameters (K), AIC score, the difference in AIC score from a model and the top model ( $\Delta_i$ ), and the AIC model weight ( $w_i$ ) which expresses general weight of evidence in support of a specific model relative to all tested models.

$p$ covariates	$\psi_0$ covariates	K	AIC	$\Delta_i$	$w_i$
duration, survey type, day of year	elevation, elevation <sup>2</sup> , latitude	10	1698.5	0.00	0.28
duration, survey type	elevation, elevation <sup>2</sup>	8	1699.0	0.53	0.22
duration, survey type, day of year	elevation, elevation <sup>2</sup>	9	1699.2	0.71	0.20
duration, survey type	elevation, elevation <sup>2</sup> , latitude	9	1699.4	0.90	0.18
duration, survey type, day of year	elevation	8	1702.8	4.32	0.03

In comparison, model support for colonization and extinction models was broadly distributed across many similar candidate models (Table 6). Twelve models were within 2 AIC units of each other, an index often used to delineate models with “substantial support” (Burnham and Anderson 2002).

**Table 6.** Top models ( $\Delta_i < 2$ ) comparing different combinations of colonization and extinction covariates.

Colonization covariates	Extinction covariates	K	AIC	$\Delta_i$	$w_i$
snag density, fire age	pre-fire cc	13	1684.6	0.00	0.05
snag density, fire age	fire age, pre-fire cc	14	1685.0	0.33	0.04
snag density, fire age	-	12	1685.2	0.54	0.04
snag density, fire age, pre-fire cc	-	13	1685.4	0.71	0.03
snag density, fire age	burn severity, pre-fire cc	14	1685.4	0.77	0.03
snag density, fire age	fire age, burn severity, pre-fire cc	15	1685.6	0.94	0.03
snag density, fire age	fire age	13	1686.2	1.56	0.02
snag density, fire age, pre-fire cc	pre-fire cc	14	1686.2	1.57	0.02
snag density, fire age	burn severity	13	1686.3	1.62	0.02
snag density, fire age, pre-fire cc	burn severity	14	1686.3	1.65	0.02
snag density, fire age, burn severity	pre-fire cc	14	1686.4	1.75	0.02
snag density, fire age, pre-fire cc	fire age	14	1686.5	1.85	0.02
snag density, fire age	snag density, pre-fire cc	14	1686.6	2.00	0.02

Although there is no single clear “top model” for colonization and extinction models, there is general consistency in support for certain variables. For instance, all top models within 2 AIC units included both snag density and fire age as colonization covariates, while there was greater uncertainty with regard to important variables for extinction covariates (Table 6). Indeed, the 3<sup>rd</sup>

and 4<sup>th</sup> ranked extinction models were “null” models where extinction was essentially a random process with a fixed probability.

The differences between colonization and extinction are clearly shown by the cumulative AIC weight (“relative importance” or  $w_+(j)$ ; Burnham and Anderson 2002) in support of different covariates for colonization and extinction (Table 7). Both snag density and fire age have nearly full, universal support as covariates of colonization, while burn severity and pre-fire canopy cover have lower support ( $< 0.5$ ). There is essentially no support ( $< 0.01$ ) for models that had colonization as a random process at a fixed probability. In comparison, the cumulative weights for covariates of extinction showed much more widespread, ambiguous support. The only variable that had strong support ( $> 0.5$ ) was pre-fire canopy cover, which was included in the top two best-supported models (Table 6). These data show that colonization dynamics are strongly predicted by two factors (snag density and fire age), while extinction dynamics are moderately or poorly predicted by many factors.

**Table 7.** Cumulative AIC weights in support of individual covariates in compared models for both colonization and extinction probabilities.

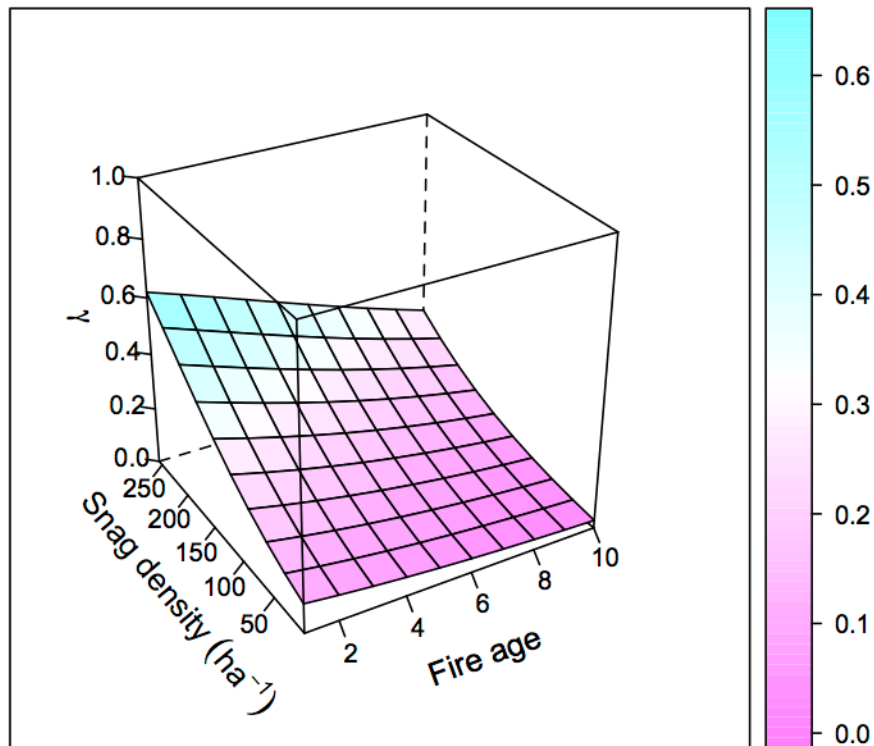
	Colonization $w_+(j)$	Extinction $w_+(j)$
Null (random)	0.00	0.13
Snag density	0.89	0.29
Fire age	0.90	0.42
Burn severity	0.30	0.41
Pre-fire canopy cover	0.42	0.54

Of critical interest is the sign and magnitude of covariate relationships to probabilities of colonization and extinction (Table 8). Based on the top AIC-ranked model (Table 6), while average probability of colonization is low (7%), the probability of colonization significantly increases with snag density but decreases with fire age.

**Table 8.** Covariate parameter estimates, standard errors, and significance for the best supported colonization-extinction model.

Parameter	Covariate	Estimate	Std. Error	<i>P</i>
Detectability	Intercept	-1.25	0.15	< 0.001
-	Interval length	0.80	0.20	< 0.001
-	Survey type	0.69	0.21	0.001
-	Day of year	-0.18	0.11	0.096
Initial occupancy	Intercept	-2.31	0.26	< 0.001
-	Elevation	1.94	0.57	0.001
-	Elevation <sup>2</sup>	-1.05	0.46	0.022
-	Latitude	0.36	0.17	0.038
Colonization	Intercept	-2.56	0.28	< 0.001
-	Snag density	0.38	0.13	0.003
-	Fire age	-0.47	0.20	0.020
Extinction	Intercept	0.29	0.43	0.492
-	Pre-fire canopy cover	-0.54	0.35	0.127

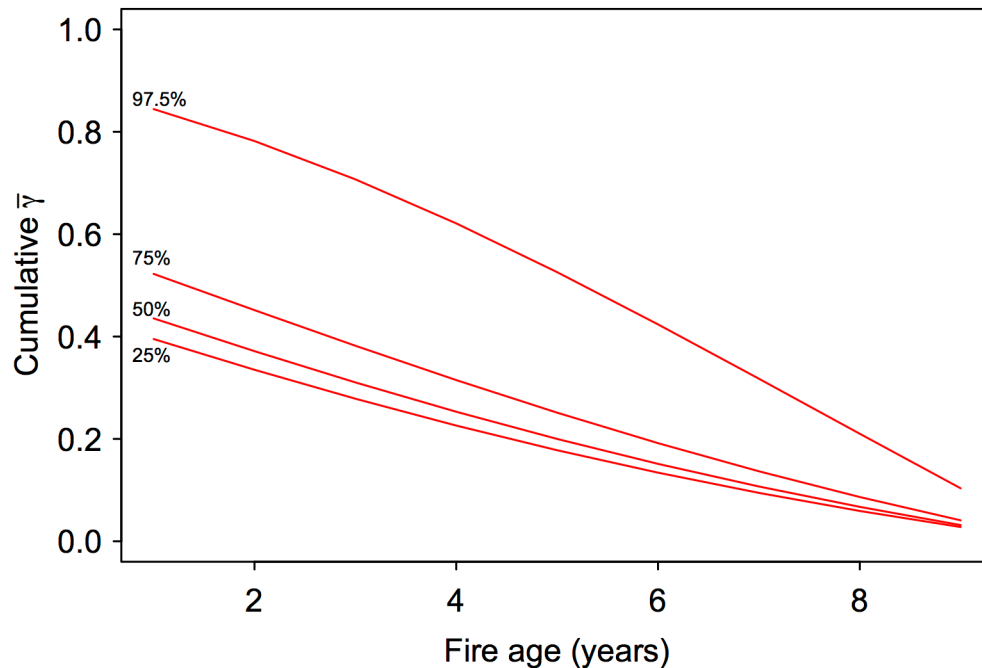
Over the range of values for which snag density and fire age were observed in the Sierra Nevada, the probability of colonization was only ever greater than 50% for points less than or equal to 4-years post-fire and only at the points with the highest snag densities (~ >200 snags per ha) (Figure 7). On average, after 3-years post-fire, the probability of an unoccupied point being colonized by Black-backed Woodpeckers in any subsequent year drops below 10%. However, cumulatively, the probability that an average point (snag density ~16 snags/ha) that is unoccupied at 1-year post fire will become colonized in any year over the next 9 years is over 40% (Figure 8). This assumes that the density of snags at a point is constant and does not change over time – an assumption we know is invalid, as snags may increase in the first few years as trees continue to die but eventually will decrease with time as they decay and fall. Consequently, the true probability that a point unoccupied in year  $i$  will become colonized at some time between year  $i+1$  and 10 will be lower than modeled here.



**Figure 7.** The modeled relationship between the probability of colonization ( $\gamma$ ), the snag density at a point, and the number of years post-fire.

While colonization probability decreases with time, the best supported model indicates that extinction probability is time-insensitive (although there is marginal support for extinction varying with fire age across all compared models; Table 7) but decreases with higher levels of pre-fire canopy cover. In other words, at points where pre-fire forest conditions were denser, Black-backed Woodpeckers were more likely to persist post-fire. The strength of this forest density relationship appears stronger than the relationship between extinction and snag density (Table 7).

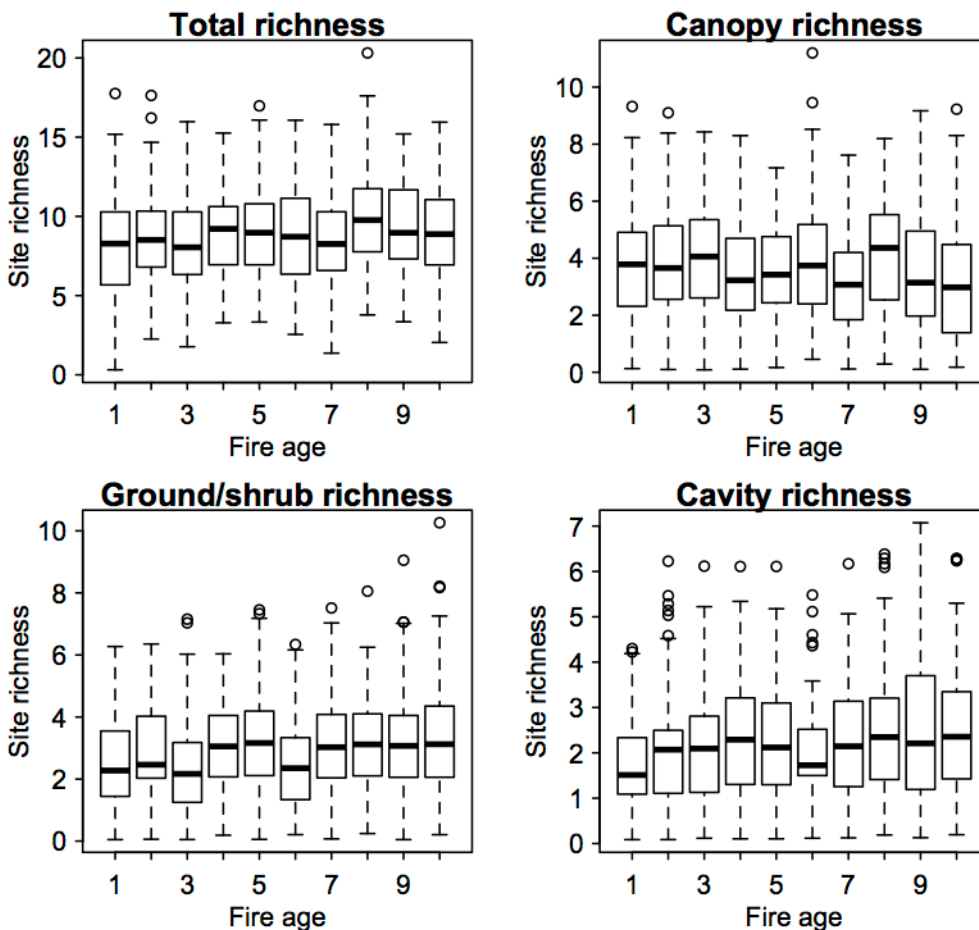




**Figure 8.** The modeled relationship between fire age and the average cumulative probability of colonization for four levels of snag density. Given an unoccupied point  $i$ -years post-fire (i.e., x-axis: fire age), the y-axis is the probability that that point will be colonized in any subsequent year, from  $i+1$  to 10. Chosen snag densities represent the 2.5<sup>th</sup> and 25<sup>th</sup> (3.8 snag/ha), 50<sup>th</sup> (16.5 snag/ha), 75<sup>th</sup> (42 snag/ha), and 97.5<sup>th</sup> (137 snag/ha) percentiles of snag densities observed at plots. Graph assumes that snag densities are constant over time.

### Analysis of Multispecies Occupancy

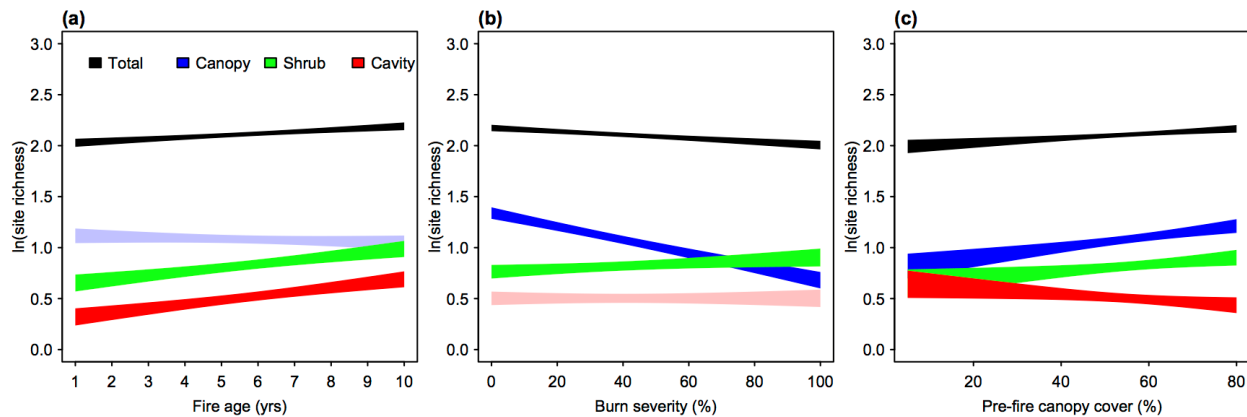
A total of 127 bird species have been detected during passive bird surveys at Black-backed Woodpecker points (Appendix I). In 2011, seven new species were detected on point counts that had not previously been detected: American Crow, Blue-gray Gnatcatcher, California Towhee, Cliff Swallow, Mallard, Purple Martin, and White-crowned Sparrow. Following on the analysis of the 2010 data (Siegel et al. 2011), our goal was to explore the factors that affected species richness at the point level while using hierarchical occupancy models to account for the species that may have been present at points but went undetected. We grouped all species into one of three categories – canopy nester, shrub or ground nester, and cavity nester – based on Saab and Powell (2005), and used these classifications to look at how different nesting guilds of birds differentially respond to early post-fire conditions.



**Figure 9.** Estimated total richness and richness of nesting guilds by fire age. Barplots show median (line), interquartile range (box), 95% interquartile range (whiskers) and outliers (circles).

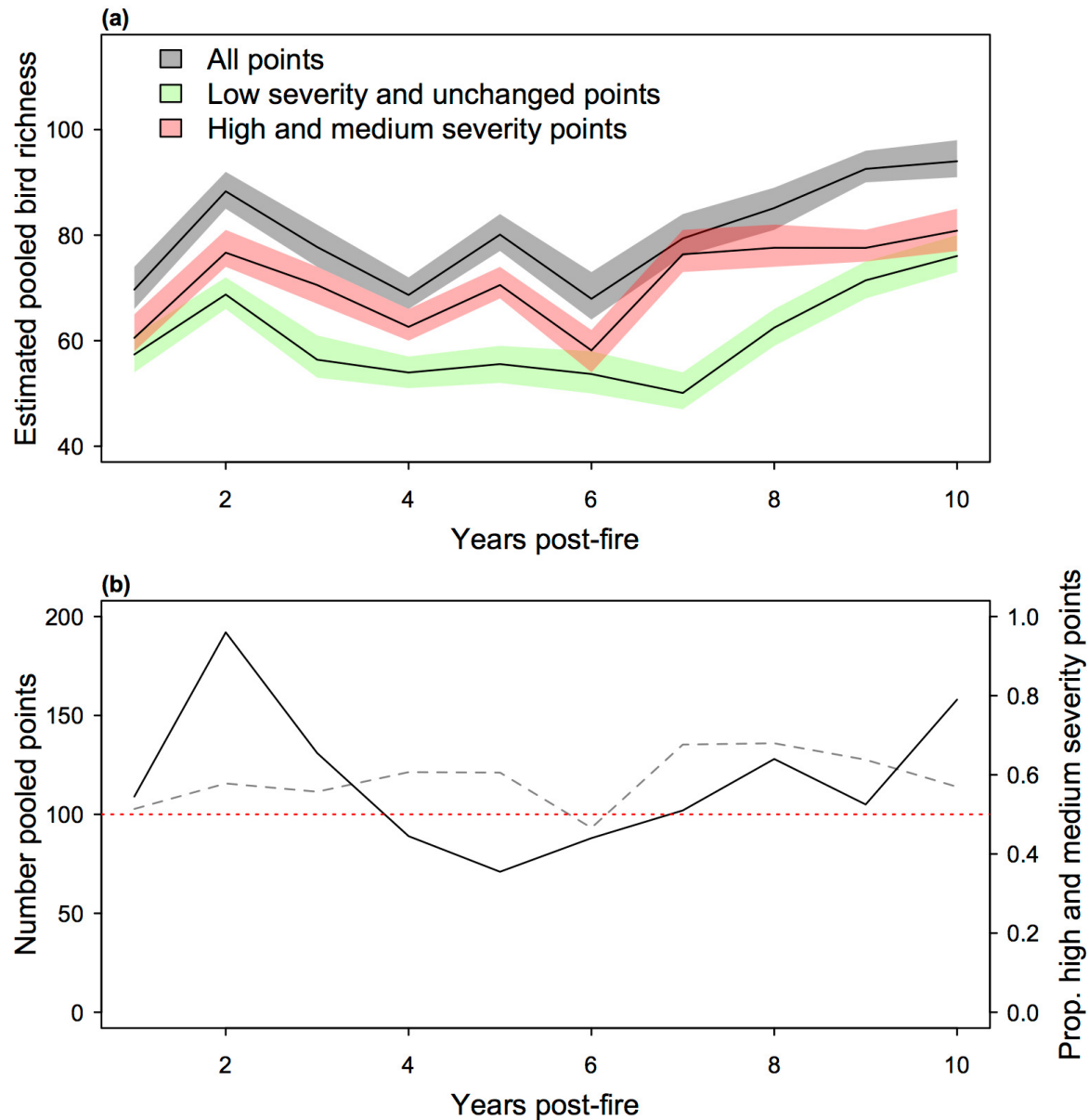
In general, species richness, regardless of nesting guild, showed a high degree of variation across sites (Figure 9). Canopy nesters were generally the most abundant species at points, followed by ground and shrub nesters, and then cavity nesters. There were, however, several statistically significant relationships between estimated total richness and estimated richness of nesting guilds with environmental covariates (Figure 10). Total richness increased with time since fire, decreased with burn severity, and increased with the percentage of pre-fire canopy cover (Figure 10). The responses of particular nesting guilds, however, did not always follow this pattern. Canopy nesters showed no significant relationship to fire age, but decreased greatly with burn severity and increased with percentage of pre-fire canopy cover. By comparison, shrub and ground nesters responded positively to all three environmental traits: time since fire, burn severity and pre-fire canopy cover. Lastly, cavity nesters increased with time since fire, showed

no statistical response to burn severity, and were the only guild to show a negative response to pre-fire canopy cover.



**Figure 10.** Modeled relationships between fire age (a), burn severity (b), and pre-fire canopy cover (c) and the log of estimated species richness at a point. Statistical tests were general linear models testing all three environmental variables together, with each richness response variable weighted by the standard deviation of posterior estimates. Non-significant relationships ( $p < 0.05$ ) are shown as faded colors (b and c, only) and lines show 95% confidence intervals.

We also parameterized the multi-species occupancy model to estimate the total number of species that were ever recorded at all fires of each age class. We additionally estimated this pooled richness for survey points that were all of equal-aged fires and also of the same burn severity class ('high' severity pools medium and high severity points, 'low' severity pools low and unchanged points). In analyzing this pooled richness, several trends are evident (Figure 11a). First, regardless of burn severity, older sites held a larger pool of species than earlier post-fire sites. Second, in general, high severity fires held larger pools of species than low severity fires. This is in contrast to the point-specific trend in richness with burn severity (Figure 10), which showed that total richness decreased with burn severity. Together, these two results suggest that while an individual high severity survey point may contain fewer species than an individual low severity survey point, all high severity points together hold a greater diversity of species than all low severity points pooled together. Third, the relative difference between richness estimates (Figure 11a) illustrates similarity between pooled communities. For example, at year 7, the high severity species pool contains almost all species in the total species pool, while in year 10, both high severity points and low severity points have approximately equal numbers of unique species.

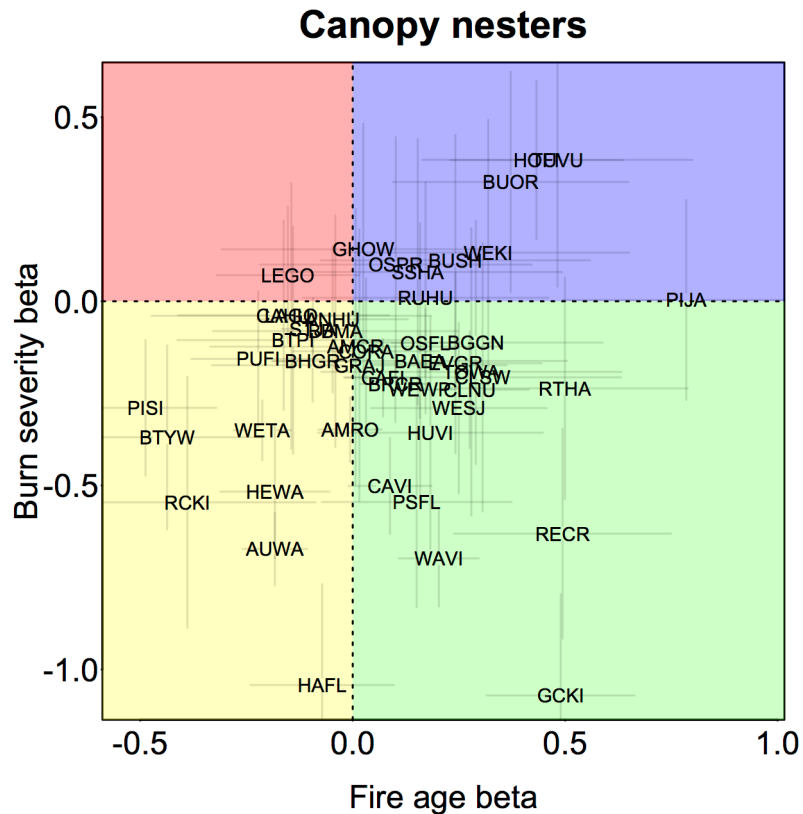


**Figure 11.** (a) Estimated pooled richness across all survey points of a similar post-fire age and point-specific burn severity class. Dark lines show posterior means and shading shows 95% credible intervals. (b) Inequality in sampling frequency as illustrated by the total number of points within fires of different ages (black solid line) and by the proportion of points within each age class that are classified as high or medium burn severity (gray dashed line). Burn severity sampling has been slightly skewed away from even (red dotted line) and toward higher severity points.

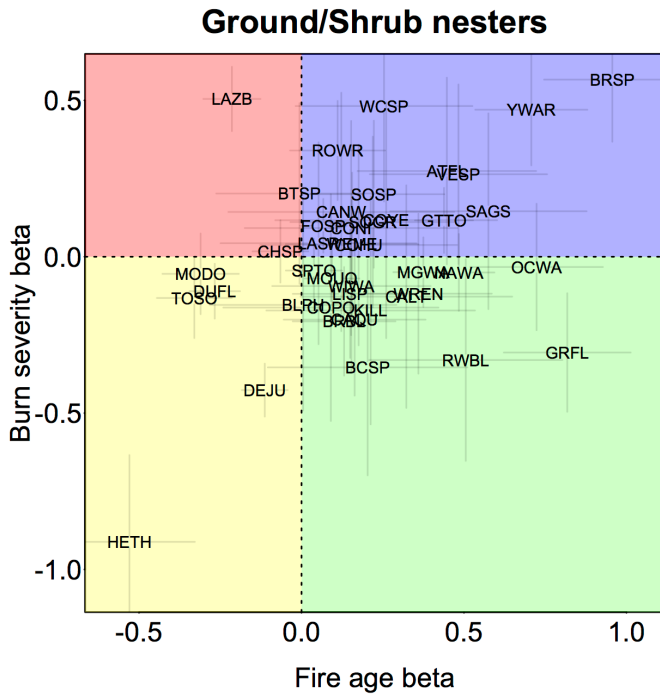
The validity of these trends, however, is highly subject to the evenness of sampling in the underlying data. While the selection of fires is a random sample, it is not a perfectly balanced design. Thus, combining 2009-2011, there are unequal numbers of survey points within each post-fire age class (Figure 11b). Additionally, while points are approximately equally distributed

across burn severities, there is a slight bias toward high severity points (including mid-severity points; Figure 11b). Since the total number of species detected is a product of total effort, there is the potential for these imbalances to influence the apparent trends in the pooled richness analysis (Figure 11a). Consequently, until this is accounted for, the interpretation of these results (Figure 11a, only) is not definitive.

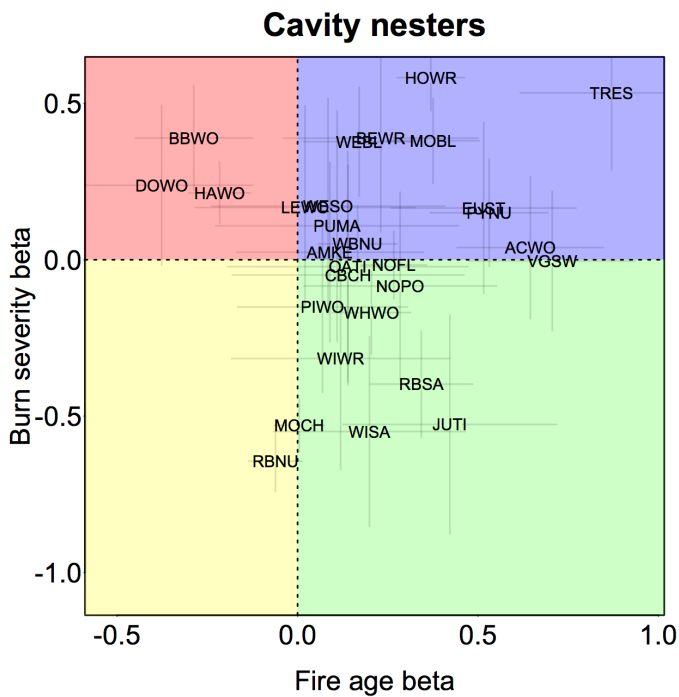
Estimated richness at survey points is the cumulative result of individual species occurrences. Differences in ecology and use of early post-fire forests can be explored through the analysis of individual  $\beta$  parameters for different environmental covariates. For example, we hypothesized that species would respond differently to fire age and burn severity by nesting guild. The differences between these guilds are evident (Figures 12-14). Canopy nesters showed species-specific responses to fire age, but trended towards avoiding high severity points (Figure 12). In comparison, ground and shrub nesters showed species-specific responses to burn severity, but with few exceptions (e.g., early post-fire colonizers like Lazuli Bunting, Mourning Dove, Dusky Flycatcher, and Townsend's Solitaire) trended toward preferring older fires (Figure 13). Finally, cavity nesters showed strongly differential responses between several primary excavators (Black-backed Woodpecker, Downy Woodpecker, and Hairy Woodpecker) which prefer high severity, early post-fire sites, and secondary excavators (e.g., wrens, parids, and swallows) which occur more in older fires (Figure 14). While the larger patterns in Figures 12-14 mirror the aggregate statistical trends discussed previously (Figure 10), the species-specific plots provides a richer understanding of how individual species either support or diverge from these larger trends.



**Figure 12.** Plots of  $\beta$  parameter values for fire age and burn severity covariates for canopy nesting species. Positive fire age  $\beta$  (green and blue zone) means the species occurs more frequently in older fires, while negative (red and yellow zone) means the species occurs more in younger fires. Positive burn severity  $\beta$  (red and blue zone) means the species occurs more in high severity points, while negative (yellow and green zone) means the species occurs more in low severity points. Species are identified through 4-letter codes (see Appendix I).



**Figure 13.** Plots of  $\beta$  parameter values for fire age and burn severity covariates for ground and shrub nesting species. Interpretation follows Figure 12.



**Figure 14.** Plots of  $\beta$  parameter values for fire age and burn severity covariates for cavity nesting species. Interpretation follows Figure 12.

## **Discussion**

### Black-backed Woodpecker Annual Occupancy

Our three years of surveys confirm that Black-backed Woodpeckers are infrequent but widely distributed across recent fire areas on the ten national forests in our study area. Based on three years of data, from 2009 to 2011, Black-backed Woodpeckers appeared to occupy a relatively stable proportion of burned forest. Point estimates of the percentage of occupied survey points within each year's sampling frame varied from 25% in 2009 and 19% in 2010 to 21% in 2011. Applied to the total amount of burned forest within each year's sampling frame, this results in 58,443 occupied hectares in 2009, 41,024 occupied hectares in 2010, and 37,183 occupied hectares in 2011. 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.

Of particular interest is whether Black-backed Woodpecker occupancy within sampled fires in our study region is significantly changing from year to year. Based on the results of annual occupancy models, the total proportion of occupied points in 2010 was significantly lower than in 2009, indicating a drop in occupancy. In 2011, the proportion of occupied sites was not statistically different from that in 2010, and 95% confidence intervals overlap with estimates from 2009. Consequently, while total occupancy appears to have dropped from 2009 to 2010, it also appears to have increased in 2011 when it was indistinguishable from 2009 levels.

Year-specific estimates of the proportion of occupied points presented here differ slightly from those presented previously. Specifically, in our previous report (Siegel et al. 2011), the total proportion of occupied sites in 2009 and 2010 were estimated to be approximately equal (~23%). Whereas the first report (Siegel et al. 2010) estimated that the total proportion of occupied sites was 25%, essentially identical to what is presented here. In these cases, differences in estimates of occupancy derive from differences in model parameterization. In the 2010 analysis (Siegel et al. 2011), both years were combined into one model. While this may have provided a refined estimate of detectability (improving inference), non-independence among survey points visited in both years may have artificially caused occupancy estimates to converge (biasing inference).



In comparison, while the current model of annual occupancy has an extra hierarchical (i.e., fire-level) level of occupancy, both the current model of 2009 occupancy as well as the original model (Siegel et al. 2010) are based on only the 2009 data, and thus their estimates of occupancy are nearly identical. Although single-year models used here and originally (Siegel et al. 2010) may have looser covariate relationships, we believe that for long-term monitoring, single-season models will provide an unbiased method for comparing estimates of total occupancy over time, particularly when combined with analyses of dynamic occupancy which model all years at once.

### Black-backed Woodpecker Dynamic Occupancy

Our presentation of an analysis of dynamic occupancy represents the first such analysis for this monitoring project and is the result of collecting greater than 2 years of survey data at a sufficient number of survey points. Given continued collection of survey data, including revisiting a large number of points surveyed in previous years, we will have a greater ability to understand the dynamic changes in occupancy over time, particularly with regard to the probability of colonization and extinction.

Our results from 3 years of data indicate strong differences between colonization and extinction dynamics for occurrence of Black-backed Woodpeckers in burned forests. Average colonization probability (defined here as the probability of a single survey point becoming occupied by woodpeckers given that it was previously unoccupied ) was quite low (7.2%) while average extinction probability was much higher (57.3%). The probability of a site being colonized was strongly positively associated with snag density and strongly negatively associated with fire age. By comparison, no single factor was as strongly associated with extinction, with a negative association with pre-fire canopy coverage garnering the strongest support.

The differences between the relative frequency of colonization versus extinction as well as the strength of covariate relationships of colonization versus extinction lead to novel insight on the drivers behind changes in Black-backed Woodpecker occurrence. Based on previous work (e.g., Siegel et al. 2011, Saracco et al. 2011), we tend to think of occurrence as being limited by fire age and snag density. This leads to the assumption that an occupied site may go extinct because

the site has aged to a certain point, and that the critical age at which a site goes extinct depends on habitat quality characteristics, such as snag density.

Our results, however, question this general framework. Since extinction probability was weakly supported by any of the hypothesized factors (including fire age, etc.), extinction may best be considered a relatively likely event, but essentially a random one. That does not mean that other factors that were not investigated to impact extinction probability (e.g., post-fire management actions that change habitat) do not have an effect on extinction, but that extinction appears to occur with no strong relationship to the investigated covariates. By contrast, colonization (after fires are greater than 1 year old) is a relatively unlikely event, but one which is strongly associated with both fire age and snag density. Despite being unlikely, since overall occupancy is only around 20 to 25% (see previous section), colonization is a relatively common occurrence. For example, given an overall occupancy of 20% and modeled average probabilities of colonization and extinction, assuming all sites have average covariate values, we would expect 11.5% of all sites (regardless of occupancy status) to go extinct in a given year and 5.8% of all sites to become colonized. Colonization after one year post-fire, consequently, is an important dynamic strongly influencing overall occupancy. If management actions were to be taken aimed at increasing overall occupancy, these results would suggest that colonization should be targeted rather than extinction, presumably through the retention of early post-fire stands with high snag densities.

The major limitation of the dynamic occupancy analysis is the scale at which the study is conducted. We sought to explain patterns of occurrence change at individual points. Based on knowledge of Black-backed Woodpecker home range sizes in Californian burned forests (e.g., Siegel et al. 2012), it is likely that individual breeding woodpeckers have home ranges that could potentially span more than 1 survey point within a fire. Consequently, analyses of occurrence dynamics at this scale will likely have upwardly biased estimates of both colonization and extinction resulting from year-to-year heterogeneity in occupied home ranges within fires. While the spatial scale of our analysis may pick up meaningful environmental relationships that correlate with intra-fire occurrence dynamics (e.g., why an individual woodpecker may move its

home range within a fire over several years as the post-fire habitat changes), this analysis will also yield unavoidable extra “noise.”

In the present study, this potential bias was unavoidable because of the still limited spatial and temporal scale of sampling after 3 years. If, for example, occupancy dynamics were explored at the scale of the individual fire instead of the survey point, then our sample size would drop from 1315 (points) to 73 (fires) and critically, the number of occurrence changes (e.g., apparent colonizations or extinctions) would drop from 256 (19.5% of points) to 9 (12% of fires). With each extra year of sampling, however, both the number of fires sampled increases and also additional repeat sampling at sites will result in higher percentages of fires with occurrence changes. Consequently, given continued monitoring of Black-backed Woodpecker occurrence with the current sampling scheme, an analysis of dynamic occupancy at the fire-level should become a viable option within a few years.

Until a dynamic model at the fire-level can be used, analyses of dynamic occupancy at the point level will have to consider the potential effects of intra-fire occupancy heterogeneity. If this bias were a serious problem, then we would expect the percentage of points with apparent occurrence changes to be much greater than the percentage of fires with apparent occurrence changes. For instance, if a woodpecker moved from one end of a 20-point transect to the other over two years, at least two points would have apparent occurrence changes (one extinction and one colonization), while the fire would have a constant occurrence status (occupied). At a minimum, consequently, this would artificially increase the number of apparent occurrence changes by 10% (2 out of 20 points) per occupied fire, and if individual woodpeckers are detected at greater than one point per fire (also a possibility given home range sizes), then it could upwardly bias the percentage of apparent occurrence changes by up to 100%. In our study frame, the conservative estimate (10% upward bias) would result in an apparent occurrence change rate at the point level of 21.4%. However, our observed apparent occurrence change rate was only 19.5%. Therefore, if occurrence dynamics at the point level are biased by the small spatial scale of sampling relative to the home range of the individual animal, then this bias is, at most, limited to certain sites and not widespread among fires. This is reinforced by a much higher modeled probability of extinction (0.57) relative to the probability of colonization (0.07); woodpeckers shifting

occurrence intra-fire over time would equally inflate both parameters. For this reason, the maximum possible bias would inflate both rates by 0.07, which would mean that all observed colonizations were the result of intra-fire movement. This is a highly unlikely situation, particularly given the strong modeled relationship between colonization and fire age, which has biological meaning yet would not be expected if colonizations resulted from intra-fire movements (e.g., there is little a priori support for why Black-backed Woodpeckers would shift home ranges more within new post-fire sites than old post-fire sites). Consequently, we conclude that if our dynamic occupancy results are biased by the spatial scale with which we analyze occupancy, then this bias has a small effect relative to our overall results.

#### Multi-species Occupancy within Post-fire Forests

Our analyses strongly support the notion that bird communities change in a complex manner in the decade immediately post-fire. Community change is not just limited to changes over time (fire age), but richness and species composition also have strong relationships to burn severity and pre-fire habitat. This was shown strongly by different nesting guilds which showed divergent richness relationships to different environmental factors (Figure 10). Each group – canopy nesters, shrub nesters, and cavity nesters – exhibited unique richness relationships to the combination of fire age, burn severity, and pre-fire canopy cover. In particular, two variables had different fundamental relationships for different groups; canopy nesters decreased with increasing burn severity while ground and shrub nesters increased, and cavity nesters decreased with increasing pre-fire canopy cover while both canopy and ground and shrub nesters increased. While these statistical relationships mostly agree with a priori notions of habitat needs for different nesting guilds, the results highlight that no single set of post-fire conditions will be beneficial to all members of post-fire bird communities. Rather, post-fire communities at the scale of a survey point will be determined by fine-scale habitat and structural features defined by the intersection of fire age, burn severity, pre-fire vegetation, and presumably other topographical and environmental features.

Relationships between occurrence and environmental factors are, however, a species-specific trait. Even within nesting guilds, there was considerable species-specific heterogeneity with regard to relationships to environmental covariates. For instance, cavity nesters showed no

statistical response as a group to burn severity, yet it is clear (Figure 14) that this is partly due to the difference between cavity nesters that primarily use dead wood for nesting (e.g., Black-backed Woodpecker, House Wren, Mountain Bluebird) and cavity nesters that often use live wood for nesting (e.g., Mountain Chickadee, Red-breasted Nuthatch). Similarly, some species found (perhaps rarely) in burned forests are likely individual birds returning to territories that were more suitable to the species pre-fire. Such species are identified by strong occupancy relationships to the first years post-fire and low burn severity. Hermit Thrush is a particularly good example (“HETH” in Figure 13), as it is a species commonly found in dense forest and in this study was the species with the strongest relationship to young fires. Other examples would be Ruby-crowned Kinglet, Hermit Warbler, Western Tanager, and Yellow-rumped Warbler. It is likely these forest species persist in post-fire landscapes for a breeding season or two but eventually move to more suitable habitats.

Analyses of entire bird communities also allow different species to be grouped based on similar occupancy relationships to environmental covariates. For example, species can be identified that have similar occupancy relationships to habitat as Black-backed Woodpeckers. Consequently, if management actions are taken to increase or conserve Black-backed Woodpecker occurrence in burned landscapes, then species with similar environmental-occurrence relationships are also likely to benefit. After grouping species only by relationships to fire age and burn severity (Figures 12-14), Black-backed Woodpeckers appear to be different from most other observed species. There are only four other species that, as modeled, occurred preferentially in early post-fire habitats with high burn severity: Lesser Goldfinch, Lazuli Bunting, Downy Woodpecker and Hairy Woodpecker (although Lesser Goldfinch and Downy Woodpecker occurred at less than 5% of survey points). Many more species occur at high burn severity sites starting several years post-fire, however, and these include the majority of ground and shrub nesters as well as many cavity nesters. Secondary cavity nesters, such as swallows, bluebirds, and wrens, are particularly associated with severe burns, but only after nest cavities have been created, presumably by the pioneering cavity-excavating species such as the Black-backed Woodpecker. Consequently, fires that create preferred conditions for Black-backed Woodpeckers in the early post-fire years will likely result in increased nesting sites for secondary cavity nesters in successive years.

### Future Directions for this Project

We have now completed three years of full-scale Black-backed Woodpecker MIS monitoring on greater Sierra Nevada national forests. We also recently completed our first field season of Black-backed Woodpecker telemetry in 2011 (Siegel et al. 2012). Taken together, these studies are yielding substantial new information and insight into the ecology, distribution, and abundance of Black-backed Woodpeckers in burned forests of California, and into the ecology and community dynamics of other bird species that use recent post-fire forest stands. Our findings will help land managers meet the habitat needs of birds in this unique and relatively little-studied habitat. In addition to continuing to track trends in Black-backed Woodpecker occupancy across burned forests of the greater Sierra Nevada, in the near future we will also continue to refine and publish our findings with respect to the effects of post-fire snag removal on Black-backed Woodpecker occupancy; dynamic occupancy of Black-backed Woodpeckers, including colonization and extinction processes; Black-backed Woodpecker home range size and foraging ecology; and multi-species occupancy analyses of birds in post-fire forests. Additionally, a few more years of data collection will enable modeling of fire-level (rather than point-level) Black-backed Woodpecker occupancy dynamics, including fire-level colonization and extinction processes, across our study area. Multiple years of data will also allow more accurate assessments of whether the amount and proportion of burned forest habitat occupied by Black-backed Woodpeckers are stable, increasing, or decreasing.

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## Appendix I.

List of all bird species identified during Black-backed Woodpecker passive surveys.

Common Name	Scientific Name	Family	4-Letter Code
Mountain Quail	<i>Oreortyx pictus</i>	Odontophoridae	MOUQ
California Quail	<i>Callipepla californica</i>	Odontophoridae	CAQU
Sooty Grouse	<i>Dendragapus fuliginosus</i>	Phasianidae	SOGR
Turkey Vulture	<i>Cathartes aura</i>	Cathartidae	TUVU
Osprey	<i>Pandion haliaetus</i>	Pandionidae	OSPR
Bald Eagle	<i>Haliaeetus leucocephalus</i>	Accipitridae	BAEA
Sharp-shinned Hawk	<i>Accipiter striatus</i>	Accipitridae	SSHA
Red-tailed Hawk	<i>Buteo jamaicensis</i>	Accipitridae	RTHA
American Kestrel	<i>Falco sparverius</i>	Falconidae	AMKE
Killdeer	<i>Charadrius vociferus</i>	Charadriidae	KILL
Band-tailed Pigeon	<i>Patagioenas fasciata</i>	Columbidae	BTPI
Mourning Dove	<i>Zenaida macroura</i>	Columbidae	MODO
Western Screech-Owl	<i>Megascops kennicottii</i>	Strigidae	WESO
Great Horned Owl	<i>Bubo virginianus</i>	Strigidae	GHOW
Northern Pygmy-Owl	<i>Glaucidium gnoma</i>	Strigidae	NOPO
Common Nighthawk	<i>Chordeiles minor</i>	Caprimulgidae	CONI
Common Poorwill	<i>Phalaenoptilus nuttallii</i>	Caprimulgidae	COPO
Anna's Hummingbird	<i>Calypte anna</i>	Trochilidae	ANHU
Costa's Hummingbird	<i>Calypte costae</i>	Trochilidae	COHU
Calliope Hummingbird	<i>Stellula calliope</i>	Trochilidae	CAHU
Rufous Hummingbird	<i>Selasphorus rufus</i>	Trochilidae	RUHU
Lewis's Woodpecker	<i>Melanerpes lewis</i>	Picidae	LEWO
Acorn Woodpecker	<i>Melanerpes formicivorus</i>	Picidae	ACWO
Williamson's Sapsucker	<i>Sphyrapicus thyroideus</i>	Picidae	WISA
Red-breasted Sapsucker	<i>Sphyrapicus ruber</i>	Picidae	RBSA
Downy Woodpecker	<i>Picoides pubescens</i>	Picidae	DOWO
Hairy Woodpecker	<i>Picoides villosus</i>	Picidae	HAWO
White-headed Woodpecker	<i>Picoides albolarvatus</i>	Picidae	WHWO
Black-backed Woodpecker	<i>Picoides arcticus</i>	Picidae	BBWO
Northern Flicker	<i>Colaptes auratus</i>	Picidae	NOFL
Pileated Woodpecker	<i>Dryocopus pileatus</i>	Picidae	PIWO
Olive-sided Flycatcher	<i>Contopus cooperi</i>	Tyrannidae	OSFL
Western Wood-Pewee	<i>Contopus sordidulus</i>	Tyrannidae	WEWP
Hammond's Flycatcher	<i>Empidonax hammondi</i>	Tyrannidae	HAFL
Gray Flycatcher	<i>Empidonax wrightii</i>	Tyrannidae	GRFL
Dusky Flycatcher	<i>Empidonax oberholseri</i>	Tyrannidae	DUFL
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	Tyrannidae	PSFL
Black Phoebe	<i>Sayornis nigricans</i>	Tyrannidae	BLPH

Common Name	Scientific Name	Family	4-Letter Code
Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>	Tyrannidae	ATFL
Western Kingbird	<i>Tyrannus verticalis</i>	Tyrannidae	WEKI
Cassin's Vireo	<i>Vireo cassinii</i>	Vireonidae	CAVI
Hutton's Vireo	<i>Vireo huttoni</i>	Vireonidae	HUVI
Warbling Vireo	<i>Vireo gilvus</i>	Vireonidae	WAVI
Gray Jay	<i>Perisoreus canadensis</i>	Corvidae	GRAJ
Steller's Jay	<i>Cyanocitta stelleri</i>	Corvidae	STJA
Western Scrub-Jay	<i>Aphelocoma californica</i>	Corvidae	WESJ
Pinyon Jay	<i>Gymnorhinus cyanocephalus</i>	Corvidae	PIJA
Black-billed Magpie	<i>Pica hudsonia</i>	Corvidae	BBMA
Clark's Nutcracker	<i>Nucifraga columbiana</i>	Corvidae	CLNU
American Crow	<i>Corvus brachyrhynchos</i>	Corvidae	AMCR
Common Raven	<i>Corvus corax</i>	Corvidae	CORA
Purple Martin	<i>Progne subis</i>	Hirundinidae	PUMA
Tree Swallow	<i>Tachycineta bicolor</i>	Hirundinidae	TRES
Violet-green Swallow	<i>Tachycineta thalassina</i>	Hirundinidae	VGSW
Cliff Swallow	<i>Petrochelidon pyrrhonota</i>	Hirundinidae	CLSW
Mountain Chickadee	<i>Poecile gambeli</i>	Paridae	MOCH
Chestnut-backed Chickadee	<i>Poecile rufescens</i>	Paridae	CBCH
Oak Titmouse	<i>Baeolophus inornatus</i>	Paridae	OATI
Juniper Titmouse	<i>Baeolophus ridgwayi</i>	Paridae	JUTI
Bushtit	<i>Psaltiriparus minimus</i>	Aegithalidae	BUSH
Red-breasted Nuthatch	<i>Sitta canadensis</i>	Sittidae	RBNU
White-breasted Nuthatch	<i>Sitta carolinensis</i>	Sittidae	WBNU
Pygmy Nuthatch	<i>Sitta pygmaea</i>	Sittidae	PYNU
Brown Creeper	<i>Certhia americana</i>	Certhiidae	BRCR
Rock Wren	<i>Salpinctes obsoletus</i>	Troglodytidae	ROWR
Canyon Wren	<i>Catherpes mexicanus</i>	Troglodytidae	CANW
Bewick's Wren	<i>Thryomanes bewickii</i>	Troglodytidae	BEWR
House Wren	<i>Troglodytes aedon</i>	Troglodytidae	HOWR
Winter Wren	<i>Troglodytes hiemalis</i>	Troglodytidae	WIWR
Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	Poliophtilidae	BGGN
Golden-crowned Kinglet	<i>Regulus satrapa</i>	Regulidae	GCKI
Ruby-crowned Kinglet	<i>Regulus calendula</i>	Regulidae	RCKI
Western Bluebird	<i>Sialia mexicana</i>	Turdidae	WEBL
Mountain Bluebird	<i>Sialia currucoides</i>	Turdidae	MOBL
Townsend's Solitaire	<i>Myadestes townsendi</i>	Turdidae	TOSO
Hermit Thrush	<i>Catharus guttatus</i>	Turdidae	HETH
American Robin	<i>Turdus migratorius</i>	Turdidae	AMRO
Wrentit	<i>Chamaea fasciata</i>	Timaliidae	WREN
European Starling	<i>Sturnus vulgaris</i>	Sturnidae	EUST

Common Name	Scientific Name	Family	4-Letter Code
Orange-crowned Warbler	<i>Oreothlypis celata</i>	Parulidae	OCWA
Nashville Warbler	<i>Oreothlypis ruficapilla</i>	Parulidae	NAWA
Yellow Warbler	<i>Setophaga petechia</i>	Parulidae	YWAR
Yellow-rumped Warbler	<i>Setophaga coronata</i>	Parulidae	AUWA
Black-throated Gray Warbler	<i>Setophaga nigrescens</i>	Parulidae	BTYW
Townsend's Warbler	<i>Setophaga townsendi</i>	Parulidae	TOWA
Hermit Warbler	<i>Setophaga occidentalis</i>	Parulidae	HEWA
MacGillivray's Warbler	<i>Geothlypis tolmiei</i>	Parulidae	MGWA
Common Yellowthroat	<i>Geothlypis trichas</i>	Parulidae	COYE
Wilson's Warbler	<i>Cardellina pusilla</i>	Parulidae	WIWA
Green-tailed Towhee	<i>Pipilo chlorurus</i>	Emberizidae	GTTO
Spotted Towhee	<i>Pipilo maculatus</i>	Emberizidae	SPTO
California Towhee	<i>Melospiza crissalis</i>	Emberizidae	CALT
Chipping Sparrow	<i>Spizella passerina</i>	Emberizidae	CHSP
Brewer's Sparrow	<i>Spizella breweri</i>	Emberizidae	BRSP
Black-chinned Sparrow	<i>Spizella atrogularis</i>	Emberizidae	BCSP
Vesper Sparrow	<i>Pooecetes gramineus</i>	Emberizidae	VESP
Lark Sparrow	<i>Chondestes grammacus</i>	Emberizidae	LASP
Black-throated Sparrow	<i>Amphispiza bilineata</i>	Emberizidae	BTSP
Sage Sparrow	<i>Amphispiza belli</i>	Emberizidae	SAGS
Fox Sparrow	<i>Passerella iliaca</i>	Emberizidae	FOSP
Song Sparrow	<i>Melospiza melodia</i>	Emberizidae	SOSP
Lincoln's Sparrow	<i>Melospiza lincolni</i>	Emberizidae	LISP
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	Emberizidae	WCSP
Dark-Eyed Junco	<i>Junco hyemalis</i>	Emberizidae	DEJU
Western Tanager	<i>Piranga ludoviciana</i>	Cardinalidae	WETA
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	Cardinalidae	BHGR
Lazuli Bunting	<i>Passerina amoena</i>	Cardinalidae	LAZB
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	Icteridae	RWBL
Western Meadowlark	<i>Sturnella neglecta</i>	Icteridae	WEME
Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	Icteridae	BRBL
Brown-headed Cowbird	<i>Molothrus ater</i>	Icteridae	BHCO
Bullock's Oriole	<i>Icterus bullockii</i>	Icteridae	BUOR
Purple Finch	<i>Carpodacus purpureus</i>	Fringillidae	PUFI
Cassin's Finch	<i>Carpodacus cassinii</i>	Fringillidae	CAFI
House Finch	<i>Carpodacus mexicanus</i>	Fringillidae	HOFI
Red Crossbill	<i>Loxia curvirostra</i>	Fringillidae	RECR
Pine Siskin	<i>Spinus pinus</i>	Fringillidae	PISI
Lesser Goldfinch	<i>Spinus psaltria</i>	Fringillidae	LEGO
Lawrence's Goldfinch	<i>Spinus lawrencei</i>	Fringillidae	LAGO
Evening Grosbeak	<i>Coccothraustes vespertinus</i>	Fringillidae	EVGR

