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Black-backed Woodpecker MIS Surveys on Sierra Nevada National Forests: 2015 Annual Report

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Black-backed Woodpecker.
Original artwork by Lynn Schofield.

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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 5 personnel to develop and field-tested survey procedures and collected preliminary information on Black-backed Woodpecker distribution across Sierra Nevada National Forests. We used the findings from our 2008 pilot study to design 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 2015 field season, we used passive and broadcast surveys to assess Black-backed Woodpecker occupancy at 969 survey points arrayed across 50 recent fire areas (1-10 years post-fire) throughout our study area. Combined with data collected during 2009 - 2014, we now have broadcast surveys and habitat assessment data at 1993 unique survey points within 105 fire areas. We also collected on-the-ground habitat data at each survey point, and collated 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 2015 we detected Black-backed Woodpeckers at 193 survey points distributed across 31 of the 50 fire areas we surveyed, including fire areas on nine of the ten National Forest units in our

study area (all units except Eldorado National Forest). We detected Black-backed Woodpeckers across nearly the full latitudinal range of our study area.

Results were produced by 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 (or at least the portion of it we sampled) 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 2015 was 0.22 (95% credible interval: 0.21 – 0.23), which is significantly higher than the previous two years but within the historical range of variation. Mean fire occupancy (i.e., the proportion of occupied fires) was also relatively high in 2015 (0.65, 95% CI: 0.62-0.70) compared to 2014 (mean = 0.52), but was within the range of variation seen in prior years.

At this time there is no significant evidence of a temporal trend in occupancy rates during the seven years (2009-2015) we have been monitoring Black-backed Woodpeckers on National Forests in California, or of a broad-scale change in the species' distribution in California. Although there was a two-year decline in point-level occupancy from 2013-2014, resulting in a previously-reported marginal ($P = 0.13$) negative trend, this trend was no longer apparent after including the 2015 surveys. Additionally, the proportion of occupied fires has remained largely constant. Black-backed Woodpeckers remain present across their historic range in California.

Our second analysis used data from all seven survey years (2009-2015) to explore occurrence dynamics over time, specifically the probabilities of colonization and extinction of Black-backed Woodpeckers at survey points and fires. Our top models of point-level 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 less than 15%, while the average probabilities that an occupied site would go extinct in any given year was ranged from 50 to 90%. The probability of extinction had no clear covariate relationships, with moderate support for negative relationships with increased burn severity and pre-fire canopy cover – extinction occurred less frequently at survey points with greater burn severity and 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.

Although little is known about dispersal dynamics in Black-backed Woodpeckers, the birds in our greater Sierra Nevada study area may frequently have the potential to colonize younger post-fire forests, as adequately large fires burn throughout the region during most years. So, for a woodpecker hatched at a 6-year old fire area, whether or not it moves to a newer fire area may not be determined by the characteristics of the site it currently occupies, but rather by whether there is a better, more recently burned site nearby to colonize. Thus extinction may not be a function of just the currently occupied habitat patch, but also a consequence of the proximity to desirable colonization options and the capacity to find them. Further work is needed to test this hypothesis, perhaps by marking individual birds and following their movements across multiple years.

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).

Although the 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). Research in burned forests of California indicates that the overall abundance of fire-killed trees, rather than the presence of any particular tree species, is among the more important predictors of Black-backed Woodpecker occupancy (Saracco et al. 2011) and home-range size (Tingley et al. 2014).

In 2008 The Institute for Bird Populations collaborated with Region personnel to develop and field-test 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 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.

In 2015 we continued Sierra-wide MIS monitoring for Black-backed Woodpeckers. Here we detail the results of this seventh year of MIS monitoring in recently burned forest stands.

Methods

Sample Design

We used the GIS data layer VegBurnSeverity15_1.mdb (available from http://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=STELPRDB5327833), which indicates fire boundaries and fire severity of fires throughout California, to extract data for all fires that occurred between 2004 and 2014 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.

We assigned fire areas that met our selection criteria, including fires that were sampled in previous years and fires that were new to the survey, to a random priority order. Our intention was to survey the first 50 fire areas on the list in 2014, 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 previous several field seasons (e.g., Siegel et al. 2014b, 2015).

Establishing survey points. The fire areas we selected varied in size, from 140 ha (2009 Silver Fire on Plumas NF) to 93,023 ha (2013 Rim Fire on Stanislaus 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 had not previously surveyed, 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 had been surveyed previously, 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, *kek* 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 349 of the survey points (generally every second point along each transect), 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. 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 methods are provided in Siegel et al. (2010).

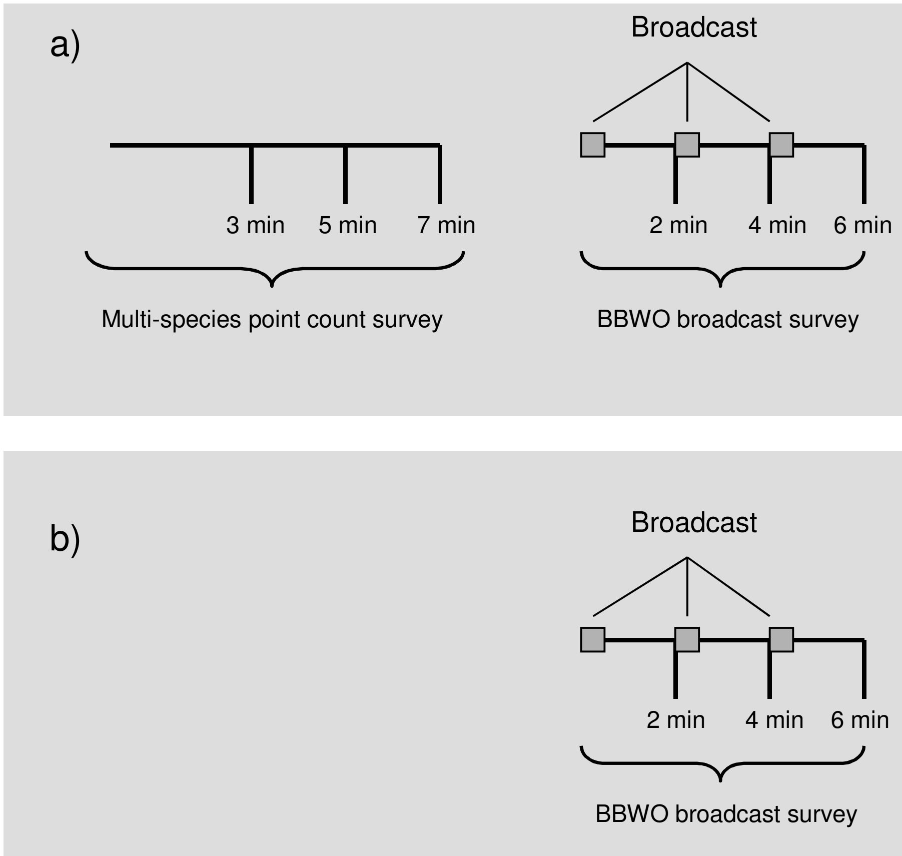

Figure 1. Schematic diagram of our survey methodology for detecting Black-backed Woodpeckers. Dark gray squares indicate period of actively broadcasting Black-backed Woodpecker drumming and vocalizations; black line segments indicate periods of passive observation. Observers alternated between both passive 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 and collected 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. 2015), our analytical goals for the 2015 data centered on formalizing analyses begun in 2011 to capitalize on the extended time-series of monitoring data. Specifically, our analysis focuses on answering two questions:

(1) What is the overall proportion of fires and points in the sampling frame occupied in 2015 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?

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 allows a greater understanding of the dynamics underlying changes in Black-backed Woodpecker occurrence. Descriptions of the methods used in addressing each of these questions follow this section.

Based on previous modeling work with the 2009-2014 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 (≤5, 6-15, 16-30, 31-50, 51-100, >100), which were converted to numerical quantities (1, 6, 16, 31, 51, 101, 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-sw-fveg_download.php). 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^2 resolution by averaging 30-m^2 values from GIS layers provided by the US Forest Service (J. D. Miller) using the 'raster' package in R (Hijmans and Etten 2012).

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 survey data be interpreted only after accounting for false absences. The framework presented here builds on the framework developed in the 2011 MIS report (Siegel et al. 2012) and published by Saracco et al. (2011) and Tingley et al. (2016). As presented in prior reports (Siegel et al. 2012, 2014a, b, 2015), given 3 (or more) years of sampling, combining all data into one model is not advantageous due to pseudoreplication of treating yearly surveys at the same sites as independent occurrence samples. A dynamic occupancy modeling framework (MacKenzie et al. 2003) allows the annual modeling of occupancy within one model, and avoids pseudoreplication, but that framework prioritizes the modeling of colonization and extinction probabilities, leaving annual occupancy solely as a derived parameter. When occupancy is a derived parameter, one cannot explicitly model relationships between it and other factors, such as environmental 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 seven years of monitoring that have now been completed. The drawback of using multiple single-year occupancy models is that covariate relationships will be modeled independently for each year, yielding different occupancy estimates than if all years were pooled into a single model. However, combined with modeling of occupancy dynamics, we believe this to be a strong framework for the analysis of trends over time.

Our annual model of occupancy was based from data on $i = 1,\ldots,N$ survey points, $j = 1,\ldots,M$ fire areas, and $k = 1,\ldots,K$ survey intervals, with values for N, M, and K, unique to survey year. For the seven years of monitoring, these values were: 899, 860, 895, 953, 1008, 976, and 969 for N points in 2009, 2010, 2011, 2012, 2013, 2014, and 2015, respectively; 51, 49, 50, 52, 53, 51 and 50 for M fire areas; and 5, 9, 6, 6, 6, 6, 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 - 2015, 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 2015, 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, 2012, 2014a, b, 2015).

Table 1. Encounter history frequencies (numbers of survey points) in the 2015 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 193 of the 969 points that we surveyed in 2016.

Number of passive detections	Broadcast History			Frequency
	Interval 1	*Interval 2*	*Interval 3*	
-	0	0	0	506
-	0	0	1	19
-	0	1	NA	38
-	1	NA	NA	57
0	0	0	0	270
0	0	0	1	10
0	0	1	NA	11
0	1	NA	NA	23
1	0	0	0	2
1	0	0	1	2
1	0	1	NA	4
1	1	NA	NA	5
2	0	0	0	3
2	0	0	1	0
2	0	1	NA	0
2	1	NA	NA	6
3	0	0	0	0
3	0	0	1	1
3	0	1	NA	0
3	1	NA	NA	12

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. Our occupancy model structure identically followed that described in the 2011 analysis (Siegel et al. 2012). This structure subdivides 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 JAGS (Plummer 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$_j$) in the model for ω_j, and a prior of Unif(0,10) for the variance parameter σ_f. For the intercepts of the *p* and ψ models, we defined priors for inverse-logit transformed parameters using Unif(0, 1). We conducted the JAGS analysis from R (R Development Core Team 2012) using the R2jags package (Su and Yajima 2014). Further details of model structure and parameterization, are provided in our previous analyses (Siegel et al. 2011, 2012, 2014a, b, 2015).

Modeling point-level 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 (ψ_0) is modeled for all survey points in the first year of sampling, and then the occurrence status is allowed to change between years according to an estimated probability of colonization (γ) or extinction (ε). Thus, the probability of occupancy at time *t* is dependent on both the initial occupancy probability as well as the probability (combined γ and ε) that the point has transitioned states from time 0 to time *t*.

In this framework, ψ 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 1993 survey points, not the ~850-1000 that were actually visited in any given survey season. As occupancy estimates are always proportions, the occupancy estimates derived from the two analyses will always be different due to different denominators within the occupancy proportions. Thus, care needs be taken when comparing occupancy estimates derived from the two analyses.

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, ψ_0, γ, and ε), 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 ψ_0 was determined by AIC, and then that single parameterization was used for all competing models of γ and ε. 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 48 competing models which were combined with null (i.e., random) model parameterizations for colonization and extinction. All 48 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 (snags per ha, as estimated from counts within a 50-m radius of survey points), fire age, burn severity (as measured by the % change in canopy cover following fire, Miller at al. 2009), and pre-fire canopy cover (%) as potential covariates for both colonization and extinction. Including all additive combinations of these 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 (Arnold 2010) and the calculation of summed model weights (Burnham & Anderson 2002). Model averaging over all models in the candidate set (Burnham & Anderson 2002), following the guidelines of Arnold (2010), was used to provide predictive inference on relationships between model parameters and covariates. All models were run in R version 3.2.2 (R Core Team 2015) using the 'colext()' function from the package 'unmarked' (Fiske and Chandler 2011).

Results

Scope of Survey Work Completed

In 2015 we completed surveys fully to protocol at 50 fire areas across 9 of the 10 National Forests (Table 2; no fires were selected within Eldorado due to low availability within the sampling window), including broadcast surveys and habitat assessments at 969 survey points and passive, multi-species point counts at 349 of those points. All surveys were conducted between 8 May and 30 June, 2015 and surveyed fires encompassed nearly the full latitudinal range of the surveyed National Forests. Combined with data collected during 2009-2014 we now have broadcast surveys and habitat assessment data at 1993 unique survey points within 105 fire areas. We provide summary information about fire areas surveyed once or more between 2009 and 2015 in Table 2.

Black-backed Woodpecker Detections

In 2015 we detected Black-backed Woodpeckers at 193 survey points distributed across 31 of the 50 fire areas we surveyed (Figs. 2-4). We detected Black-backed Woodpeckers at one or more fires at 8 of 10 National Forest units in our study area. The only Forest without detections were Eldorado, where no surveys were conducted, and Inyo, where only the Sawmill (2006) fire was surveyed. Black-backed Woodpeckers have not been detected at fires on Inyo National Forest in either 2014 or 2015 as part of MIS surveys. As was the case in previous years, we detected Black-backed Woodpeckers across nearly the full latitudinal range of our study area, including the most northerly fire area we surveyed (the Barry Point 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.org/pages/blackBackedWoodpeckerMap.php

Table 2. Summary information for each fire area surveyed once or more during the 2009 – 2015 field seasons of Black-backed Woodpecker MIS monitoring on Sierra Nevada National Forests.

Primary National Forest	Fire name	Year of fire	Burned area (ha)[1]	Dominant pre-fire habitat[2]	No. points (2009)	No. points (2010)	No. points (2011)	No. points (2012)	No. points (2013)	No. points (2014)	No. points (2015)
Eldorado	Freds	2004	1814	Sierra Mixed Conifer	20	0	19	20	20	20	0
Eldorado	Plum	2002	417	Sierra Mixed Conifer	12	12	12	13	0	0	0
Eldorado	Power	2004	5538	Sierra Mixed Conifer	20	20	20	20	20	20	0
Eldorado	Star	2001	4979	Sierra Mixed Conifer	0	20	20	0	0	0	0
Inyo	Azusa	2000	164	Pinyon-Juniper	8	0	0	0	0	0	0
Inyo	Birch	2002	1117	Pinyon-Juniper	19	0	0	0	0	0	0
Inyo	Crater	2001	1118	Jeffrey Pine	20	20	20	0	0	0	0
Inyo	Dexter	2003	1022	Jeffrey Pine	16	16	0	16	16	0	0
Inyo	Inyo Complex	2007	7574	Ponderosa Pine	16	0	0	0	0	0	0
Inyo	Mclaughlin	2001	939	Jeffrey Pine	0	13	13	0	0	0	0
Inyo	Sawmill 00	2000	144	Ponderosa Pine	5	0	0	0	0	0	0
Inyo	Sawmill 06	2006	2452	Pinyon-Juniper	0	0	19	0	20	0	20
Inyo	Sherwin	2008	146	Sierra Mixed Conifer	0	0	0	0	13	13	0
Inyo	Summit	2003	2474	Jeffrey Pine	0	0	16	0	16	0	0
Lassen	Bald	2014	15819	Eastside Pine	0	0	0	0	0	0	20
Lassen	Brown	2009	684	Sierra Mixed Conifer	0	20	20	20	19	20	20
Lassen	Cone	2002	703	Jeffrey Pine	21	0	21	0	0	0	0
Lassen	Corral	2008	1952	Eastside Pine	0	0	0	20	20	20	20
Lassen	Cub	2008	6093	Sierra Mixed Conifer	0	20	20	15	20	20	21
Lassen	Eiler	2014	12947	Sierra Mixed Conifer	0	0	0	0	0	0	20
Lassen	Onion 2	2008	1067	Sierra Mixed Conifer	0	20	20	20	20	20	20
Lassen	Peterson Complex	2008	1161	Eastside Pine	20	20	20	20	20	20	20
Lassen	Reading	2012	4504	Sierra Mixed Conifer	0	0	0	0	20	20	20
Lassen	Straylor	2004	996	Eastside Pine	0	0	0	20	20	20	0
Lassen	Sugar Loaf	2009	3127	Sierra Mixed Conifer	0	21	21	21	21	21	20
Modoc	Barry Point	2012	6740	Eastside Pine	0	0	0	0	20	20	20

Primary National Forest	Fire name	Year of fire	Burned area (ha)[1]	Dominant pre-fire habitat[2]	No. points (2009)	No. points (2010)	No. points (2011)	No. points (2012)	No. points (2013)	No. points (2014)	No. points (2015)
Modoc	Bell	2001	1260	Juniper	20	20	20	0	0	0	0
Modoc	Bell West	1999	773	Eastside Pine	21	0	0	0	0	0	0
Modoc	Blue	2001	13329	Eastside Pine	20	20	20	0	0	0	0
Modoc	Cougar	2011	749	Ponderosa Pine	0	0	0	20	0	20	20
Modoc	Fletcher	2007	916	Eastside Pine	19	17	19	20	20	20	0
Modoc	High	2006	421	Eastside Pine	0	19	19	19	0	19	0
Plumas	Antelope Complex	2007	9297	Sierra Mixed Conifer	21	21	21	21	21	21	20
Plumas	Belden	2008	224	Mixed Hardwood-Conifer	0	13	13	13	13	13	13
Plumas	Boulder Complex	2006	1475	Eastside Pine	20	20	0	0	20	20	0
Plumas	Bucks	1999	11325	Sierra Mixed Conifer	20	0	0	0	0	0	0
Plumas	Chips	2012	26957	Sierra Mixed Conifer	0	0	0	0	20	20	20
Plumas	Cold	2008	2327	Sierra Mixed Conifer	0	0	0	19	19	19	0
Plumas	Devils Gap	1999	612	Sierra Mixed Conifer	20	0	0	0	0	0	0
Plumas	Fox	2008	1007	Mixed Hardwood-Conifer	0	0	18	0	20	18	20
Plumas	Frey	2008	4406	Sierra Mixed Conifer	0	20	18	0	20	20	0
Plumas	Grease	2006	163	Eastside Pine	0	0	0	17	17	17	0
Plumas	Horton 2	1999	1637	Sierra Mixed Conifer	20	0	0	0	0	0	0
Plumas	Lookout	1999	1009	Sierra Mixed Conifer	21	0	0	0	0	0	0
Plumas	Moonlight	2007	18864	Eastside Pine	20	20	20	20	0	20	20
Plumas	Peak	2012	314	Eastside Pine	0	0	0	0	0	0	20
Plumas	Pidgen	1999	1859	Sierra Mixed Conifer	18	0	0	0	0	0	0
Plumas	Pit	2008	9142	Sierra Mixed Conifer	0	0	0	20	20	0	20
Plumas	Rich	2008	2360	Sierra Mixed Conifer	21	21	0	21	0	20	21
Plumas	Scotch	2008	5647	Sierra Mixed Conifer	21	21	0	21	20	21	21
Plumas	Silver	2009	140	Sierra Mixed Conifer	0	0	11	11	11	11	11
Plumas	Storrie	2000	21117	Red Fir	15	0	0	0	0	0	0
Plumas	Stream	2001	1507	Eastside Pine	20	20	15	0	0	0	0
Sequoia	Albanita	2003	958	Jeffrey Pine	21	21	21	21	21	0	0

Primary National Forest	Fire name	Year of fire	Burned area (ha)[1]	Dominant pre-fire habitat[2]	No. points (2009)	No. points (2010)	No. points (2011)	No. points (2012)	No. points (2013)	No. points (2014)	No. points (2015)
Sequoia	Broder Beck	2006	1457	Sierra Mixed Conifer	0	20	20	20	20	20	20
Sequoia	Clover	2008	6088	Jeffrey Pine	0	20	20	20	0	0	0
Sequoia	Comb	2005	480	Sierra Mixed Conifer	0	0	0	20	20	21	0
Sequoia	Cooney	2003	841	Sierra Mixed Conifer	0	0	0	20	20	0	0
Sequoia	Crag 04	2004	364	Jeffrey Pine	19	0	18	19	19	0	0
Sequoia	Crag 05	2005	611	Jeffrey Pine	21	20	21	21	21	21	20
Sequoia	Deep	2004	1305	Sierra Mixed Conifer	11	11	11	11	11	11	0
Sequoia	Fish	2013	824	Sierra Mixed Conifer	0	0	0	0	0	20	19
Sequoia	George	2012	720	Jeffrey Pine	0	0	0	0	20	20	20
Sequoia	Granite	2009	607	Sierra Mixed Conifer	0	20	20	0	20	20	20
Sequoia	Highway	2001	1384	Mixed Hardwood-Conifer	0	0	20	0	0	0	0
Sequoia	Hooker	2003	1004	Jeffrey Pine	20	16	20	20	0	0	0
Sequoia	Lion	2009	1075	Lodgepole Pine	0	20	20	20	20	0	20
Sequoia	Lion 11	2011	7993	Sierra Mixed Conifer	0	0	0	20	0	20	20
Sequoia	Manter	2000	22450	Pinyon-Juniper	21	20	0	0	0	0	0
Sequoia	McNally	2002	61261	Sierra Mixed Conifer	19	17	16	17	0	0	0
Sequoia	Piute 08	2008	13516	Sierra Mixed Conifer	20	19	0	0	20	20	20
Sequoia	Sheep	2010	2428	Sierra Mixed Conifer	0	0	0	20	20	21	0
Sequoia	Shotgun	2009	403	Sierra Mixed Conifer	0	0	0	16	0	0	15
Sequoia	Soda	2014	420	Sierra Mixed Conifer	0	0	0	0	0	0	20
Sequoia	Tamarack	2006	1911	Sierra Mixed Conifer	0	0	0	20	20	19	20
Sequoia	Vista	2007	180	Red Fir	19	19	19	19	0	19	19
Sierra	Aspen	2013	9236	Sierra Mixed Conifer	0	0	0	0	0	20	20
Sierra	Bear	2012	397	Sierra Mixed Conifer	0	0	0	0	20	20	20
Sierra	French	2014	5617	Sierra Mixed Conifer	0	0	0	0	0	0	20
Sierra	Motor	2011	2038	Blue Oak - Foothill Pine	0	0	0	24	0	0	0
Sierra	North Fork	2001	1614	Sierra Mixed Conifer	20	13	8	0	0	0	0
Sierra	Oliver	2008	1099	Sierra Mixed Conifer	0	0	17	0	15	0	20

Primary National Forest	Fire name	Year of fire	Burned area (ha)[1]	Dominant pre-fire habitat[2]	No. points (2009)	No. points (2010)	No. points (2011)	No. points (2012)	No. points (2013)	No. points (2014)	No. points (2015)
Sierra	Tehipite	2008	3112	Sierra Mixed Conifer	0	0	0	21	21	0	20
Stanislaus	Dome Rock	2008	392	Sierra Mixed Conifer	0	0	0	0	0	19	19
Stanislaus	Hiram	1999	1144	Jeffrey Pine	10	0	0	0	0	0	0
Stanislaus	Kibbie	2003	1501	Sierra Mixed Conifer	21	0	21	21	21	0	0
Stanislaus	Knight	2009	2140	Sierra Mixed Conifer	0	19	19	19	19	19	19
Stanislaus	Mountain	2003	1747	Red Fir	0	12	12	9	0	0	0
Stanislaus	Mud	2003	1803	Red Fir	21	20	21	21	21	0	0
Stanislaus	Power 13	2013	438	Mixed Hardwood-Conifer	0	0	0	0	0	0	20
Stanislaus	Ramsey	2012	476	Sierra Mixed Conifer	0	0	0	0	20	20	20
Stanislaus	Rim	2013	93023	Sierra Mixed Conifer	0	0	0	0	0	20	20
Stanislaus	Whit	2003	438	Sierra Mixed Conifer	20	0	20	19	19	0	0
Stanislaus	White	2001	107	Sierra Mixed Conifer	8	8	8	0	0	0	0
Tahoe	American	2013	10891	Sierra Mixed Conifer	0	0	0	0	0	20	0
Tahoe	Bassetts	2006	1006	Sierra Mixed Conifer	18	18	0	19	17	17	17
Tahoe	Fall	2008	584	Sierra Mixed Conifer	10	10	10	10	19	18	19
Tahoe	Gap	2001	574	Sierra Mixed Conifer	0	20	19	0	0	0	0
Tahoe	Government	2008	7784	Sierra Mixed Conifer	19	19	19	0	19	19	19
Tahoe	Harding	2005	616	Eastside Pine	21	21	21	20	20	21	21
Tahoe	Peavine	2008	192	Sierra Mixed Conifer	16	0	0	0	0	0	16
Tahoe	Treasure	2001	143	Eastside Pine	10	10	0	0	0	0	0
Tahoe Basin	Angora	2007	1146	Sierra Mixed Conifer	19	12	19	19	19	18	19
Tahoe Basin	Gondola	2002	165	Red Fir	12	12	0	12	0	0	0
Tahoe Basin	Showers	2002	125	Sierra Mixed Conifer	9	9	0	8	0	0	0

[1]Burned area represents only the total area of the fire within National Forest boundaries.

[2]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.

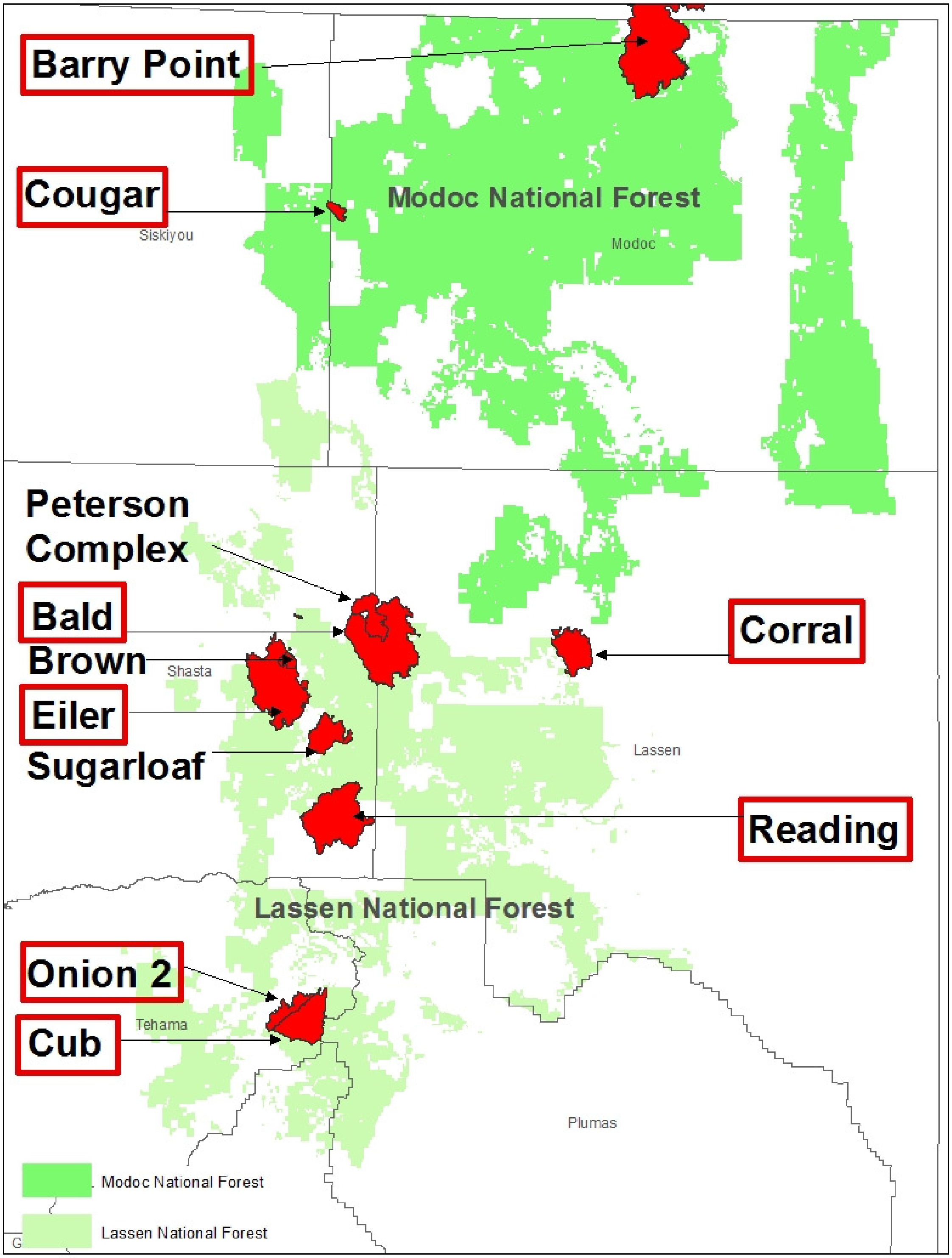

Figure 2. Fire areas (red shading) on the Modoc and Lassen National Forests that we surveyed for Black-backed Woodpeckers during the 2015 Black-backed Woodpecker MIS monitoring field season. Names of fire areas where Black-backed Woodpeckers were detected are enclosed in red boxes. Fire area names without 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).

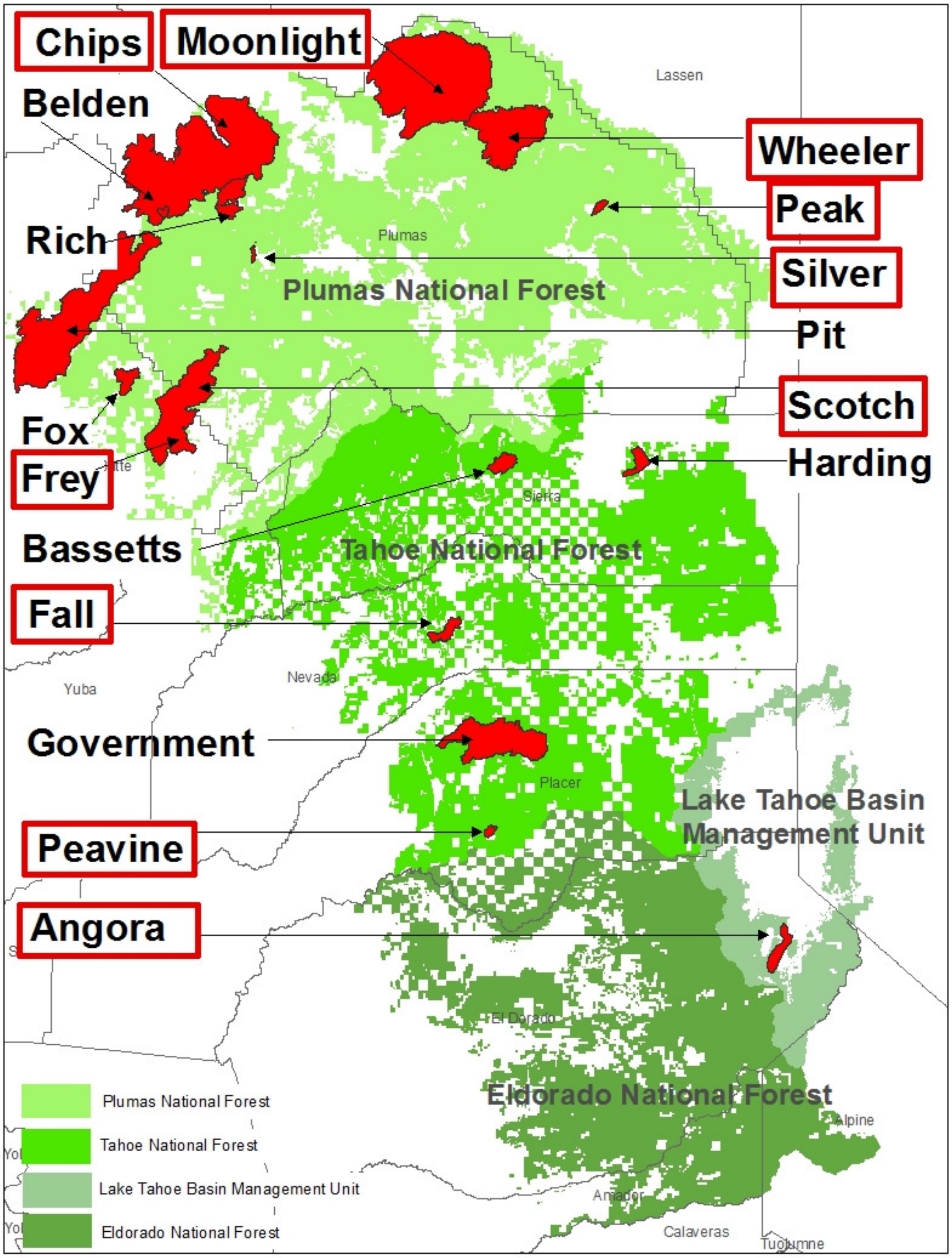

Figure 3. Fire areas (red shading) on the Plumas, Tahoe, and Eldorado National Forests and the Lake Tahoe Basin Management Unit that we surveyed for Black-backed Woodpeckers during the 2015 Black-backed Woodpecker MIS monitoring field season. Names of fire areas where Black-backed Woodpeckers were detected 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).

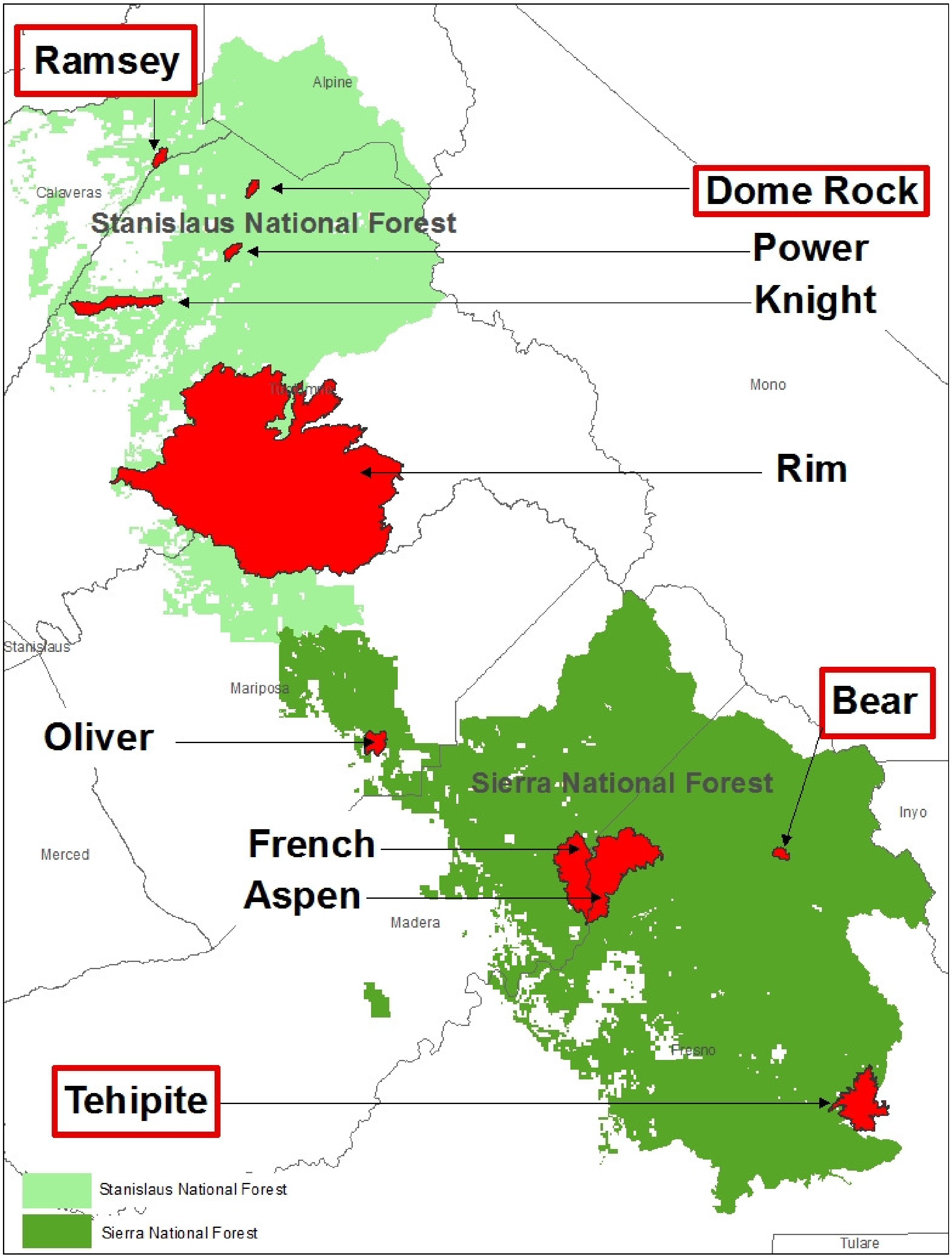

Figure 4. Fire areas (red shading) on the Stanislaus and Sierra National Forests that were surveyed for Black-backed Woodpeckers during the 2015 Black-backed Woodpecker MIS monitoring field season. Names of fire areas where Black-backed Woodpeckers were detected are enclosed in red boxes. Fire area names 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).

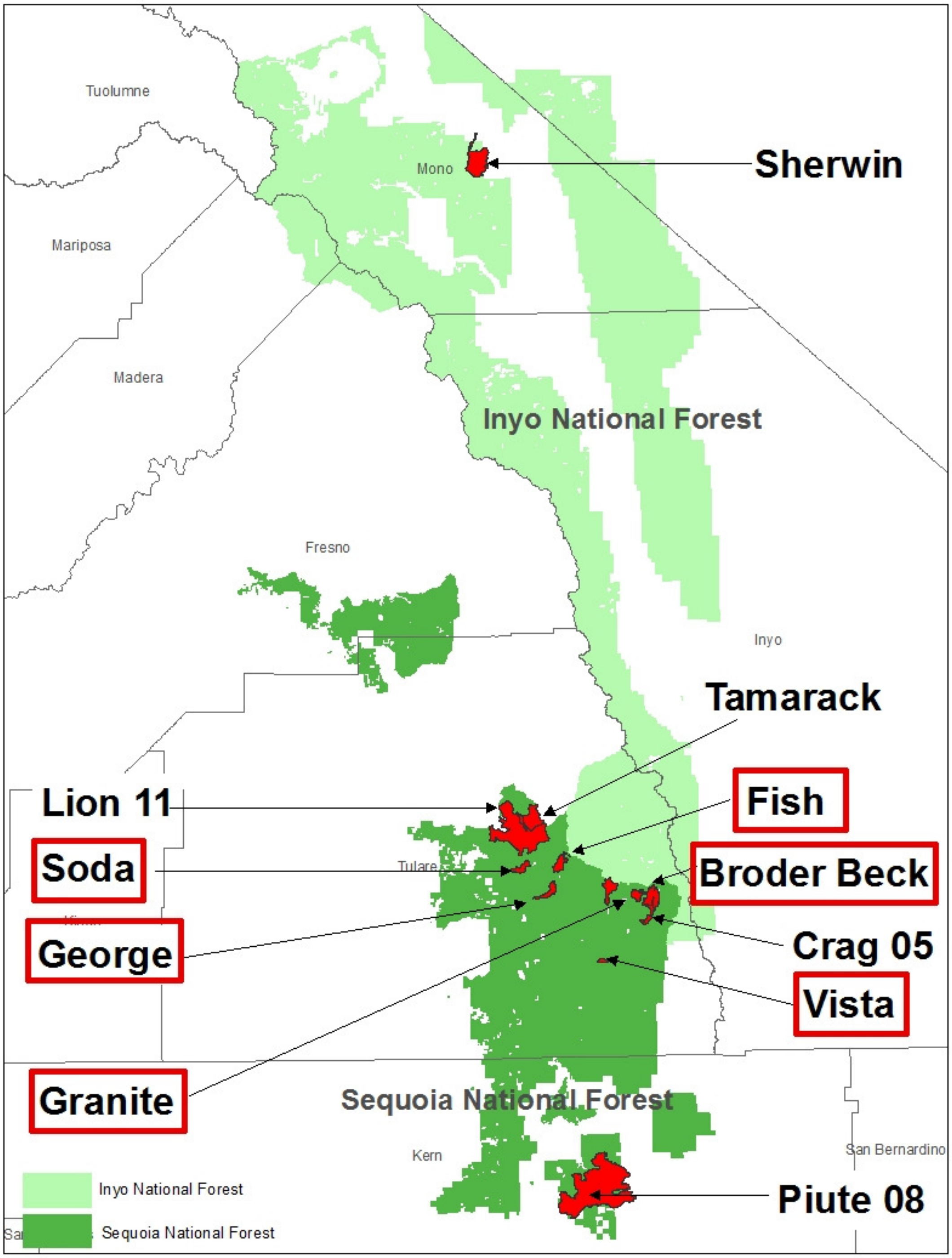

Figure 5. Fire areas (red shading) on the Inyo and Sequoia National Forests that were surveyed for Black-backed Woodpeckers during the 2015 Black-backed Woodpecker MIS monitoring field season. Names of fire areas where Black-backed Woodpeckers were detected are enclosed in red boxes. Fire area names 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 in 2015 was 0.22 (95% credible interval: 0.21 – 0.23), which is consistent with previous years and significantly higher than the previous two years (Figure 6). Table 3 summarizes detections and Table 4 summarizes predicted occupancy probabilities for each fire area surveyed in 2009 through 2015.

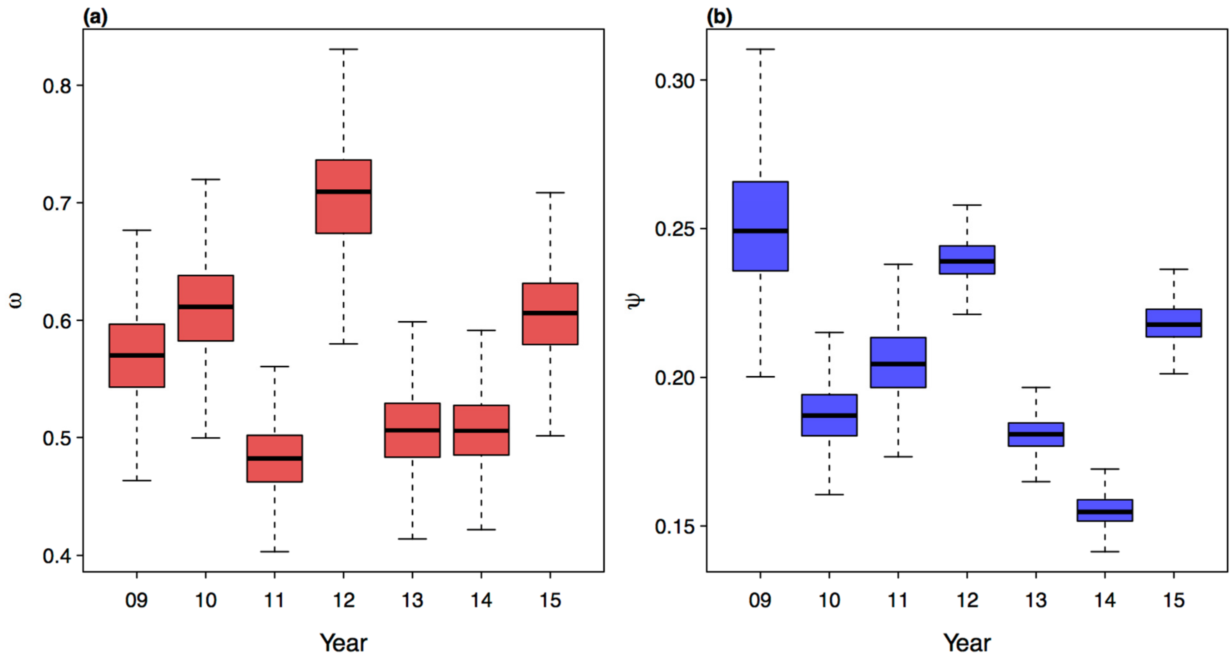

Figure 6. Mean probability of a) fire-level (ω) and b) point-level (ψ) occupancy for Black-backed Woodpeckers as modeled from individual year-based hierarchical models. Plots show median (bold line), 50% (box) and 95% (whiskers) Bayesian credible intervals of posterior distribution of modeled parameters.

Table 3. Summary of Black-backed Woodpecker positive detections (detects.) at surveyed stations (# stns) for each fire area visited during 2009 - 2015.

Fire name	2009 Detects. (# stns)	2010 Detects. (# stns)	2011 Detects. (# stns)	2012 Detects. (# stns)	2013 Detects. (# stns)	2014 Detects. (# stns)	2015 Detects. (# stns)
Albanita	1 (21)	0 (21)	0 (21)	6 (21)	0 (21)	-	-
American	-	-	-	-	-	0 (20)	-
Antelope Complex	9 (21)	2 (21)	6 (21)	8 (21)	4 (21)	2 (21)	6 (20)
Angora	13 (19)	7 (12)	13 (19)	13 (19)	13 (19)	9 (18)	3 (19)
Aspen	-	-	-	-	-	6 (20)	0 (20)
Azusa	0 (8)	-	-	-	-	-	-
Bald	-	-	-	-	-	-	6 (20)
Barry Point	-	-	-	-	17 (20)	15 (20)	14 (20)
Bassetts	7 (18)	7 (18)	-	5 (19)	2 (17)	1 (17)	0 (17)
Bear	-	-	-	-	15 (20)	11 (20)	3 (20)
Belden	-	0 (13)	0 (13)	0 (13)	0 (13)	0 (13)	0 (13)
Bell	0 (20)	0 (20)	0 (20)	-	-	-	-
Bell West	1 (21)	-	-	-	-	-	-
Birch	0 (19)	-	-	-	-	-	-
Blue	5 (20)	5 (20)	5 (20)	-	-	-	-
Boulder Complex	9 (20)	1 (20)	-	-	1 (20)	0 (20)	-
Broder Beck	-	7 (20)	0 (20)	2 (20)	3 (20)	5 (20)	5 (20)
Brown	-	7 (20)	14 (20)	10 (20)	2 (19)	0 (20)	1 (20)
Bucks	0 (20)	-	-	-	-	-	-
Chips	-	-	-	-	1 (20)	5 (20)	4 (20)
Clover	-	7 (20)	0 (20)	1 (20)	-	-	-
Cold	-	-	-	11 (19)	11 (19)	7 (19)	-
Comb	-	-	-	0 (20)	0 (20)	0 (21)	-
Cone	5 (21)	-	6 (21)	-	-	-	-
Cooney	-	-	-	1 (20)	0 (20)	-	-
Corral	-	-	-	10 (20)	7 (20)	2 (20)	2 (20)
Cougar	-	-	-	13 (20)	-	9 (20)	8 (20)
Crag 04	4 (19)	-	0 (18)	1 (19)	0 (19)	-	-
Crag 05	0 (21)	0 (20)	0 (21)	0 (21)	0 (21)	0 (21)	0 (20)
Crater	8 (20)	3 (20)	7 (20)	-	-	-	-
Cub	-	3 (20)	3 (20)	1 (15)	5 (20)	5 (20)	3 (21)
Deep	0 (11)	0 (11)	0 (11)	0 (11)	0 (11)	0 (11)	-
Devils Gap	0 (20)	-	-	-	-	-	-
Dexter	6 (16)	1 (16)	-	7 (16)	0 (16)	-	-
Dome Rock	-	-	-	-	-	6 (19)	2 (19)
Eiler	-	-	-	-	-	-	13 (20)
Fall	0 (10)	1 (10)	0 (10)	1 (10)	4 (19)	4 (18)	3 (19)

Fire name	2009 Detects. (# stns)	2010 Detects. (# stns)	2011 Detects. (# stns)	2012 Detects. (# stns)	2013 Detects. (# stns)	2014 Detects. (# stns)	2015 Detects. (# stns)
Fish	-	-	-	-	-	7 (20)	14 (19)
Fletcher	15 (19)	5 (17)	8 (19)	10 (20)	0 (20)	0 (20)	-
Fox	-	-	0 (18)	-	0 (20)	0 (18)	0 (20)
Freds	0 (20)	-	0 (19)	0 (20)	0 (20)	0 (20)	-
French	-	-	-	-	-	-	0 (20)
Frey	-	0 (20)	0 (18)	-	0 (20)	0 (20)	-
Gap	-	0 (20)	0 (19)	-	-	-	-
George	-	-	-	-	2 (20)	1 (20)	6 (20)
Gondola	6 (12)	4 (12)	-	2 (12)	-	-	-
Government	1 (19)	3 (19)	4 (19)	-	6 (19)	3 (19)	0 (19)
Granite	-	6 (20)	10 (20)	-	10 (20)	10 (20)	12 (20)
Grease	-	-	-	0 (17)	0 (17)	0 (17)	-
Harding	7 (21)	2 (21)	0 (21)	0 (20)	0 (20)	0 (21)	0 (21)
High	-	1 (19)	5 (19)	11 (19)	-	1 (19)	-
Highway	-	-	0 (20)	-	-	-	-
Hiram	0 (10)	-	-	-	-	-	-
Hooker	0 (20)	0 (16)	0 (20)	0 (20)	-	-	-
Horton 2	7 (20)	-	-	-	-	-	-
Inyo Complex	0 (16)	-	-	-	-	-	-
Kibbie	6 (21)	-	3 (21)	5 (21)	0 (21)	-	-
Knight	-	0 (19)	0 (19)	0 (19)	0 (19)	0 (19)	0 (19)
Lion 11	-	-	-	4 (20)	-	0 (20)	1 (20)
Lion	-	7 (20)	2 (20)	6 (20)	7 (20)	-	10 (20)
Lookout	0 (21)	-	-	-	-	-	-
Manter	0 (21)	0 (20)	-	-	-	-	-
Mclaughlin	-	0 (13)	1 (13)	-	-	-	-
McNally	0 (19)	0 (17)	0 (16)	0 (17)	-	-	-
Moonlight	11 (20)	5 (20)	11 (20)	11 (20)	-	4 (20)	4 (20)
Motor	-	-	-	0 (24)	-	-	-
Mountain	-	1 (12)	3 (12)	4 (9)	-	-	-
Mud	10 (21)	12 (20)	8 (21)	8 (21)	9 (21)	-	-
North Fork	0 (20)	0 (13)	0 (8)	-	-	-	-
Oliver	-	-	6 (17)	-	0 (15)	-	0 (20)
Onion 2	-	0 (20)	0 (20)	1 (20)	0 (20)	0 (20)	2 (20)
Peak	-	-	-	-	-	-	17 (20)
Peavine	0 (16)	-	-	-	-	-	1 (16)
Peterson Complex	9 (20)	7 (20)	14 (20)	3 (20)	0 (20)	0 (20)	0 (20)
Piute 08	0 (20)	0 (19)	-	-	0 (20)	0 (20)	0 (20)
Pidgen	0 (18)	-	-	-	-	-	-
Pit	-	-	-	2 (20)	0 (20)	-	0 (20)

Fire name	2009 Detects. (# stns)	2010 Detects. (# stns)	2011 Detects. (# stns)	2012 Detects. (# stns)	2013 Detects. (# stns)	2014 Detects. (# stns)	2015 Detects. (# stns)
Plum	0 (12)	0 (12)	0 (12)	0 (13)	-	-	-
Power 13	-	-	-	-	-	-	0 (20)
Power	1 (20)	0 (20)	0 (20)	2 (20)	0 (20)	0 (20)	-
Ramsey	-	-	-	-	8 (20)	10 (20)	3 (20)
Reading	-	-	-	-	12 (20)	8 (20)	15 (20)
Rich	1 (21)	1 (21)	-	6 (21)	-	0 (20)	4 (21)
Rim	-	-	-	-	-	0 (20)	0 (20)
Sawmill 06	-	-	0 (19)	-	0 (20)	-	0 (20)
Sawmill 00	0 (5)	-	-	-	-	-	-
Scotch	3 (21)	0 (21)	-	1 (21)	2 (20)	1 (21)	1 (21)
Sheep	-	-	-	1 (20)	0 (20)	0 (21)	-
Sherwin	-	-	-	-	4 (13)	0 (13)	-
Shotgun	-	-	-	3 (16)	-	-	0 (15)
Showers	3 (9)	6 (9)	-	4 (8)	-	-	-
Silver	-	-	7 (11)	6 (11)	5 (11)	1 (11)	3 (11)
Soda	-	-	-	-	-	-	4 (20)
Star	-	6 (20)	1 (20)	-	-	-	-
Storrie	4 (15)	-	-	-	-	-	-
Straylor	-	-	-	1 (20)	0 (20)	0 (20)	-
Stream	0 (20)	0 (20)	0 (15)	-	-	-	-
Sugar Loaf	-	3 (21)	2 (21)	0 (21)	0 (21)	0 (21)	0 (20)
Summit	-	-	0 (16)	-	0 (16)	-	-
Tamarack	-	-	-	3 (20)	0 (20)	0 (19)	0 (20)
Tehipite	-	-	-	9 (21)	11 (21)	-	17 (20)
Treasure	2 (10)	4 (10)	-	-	-	-	-
Vista	9 (19)	8 (19)	2 (19)	5 (19)	-	5 (19)	6 (19)
White	0 (8)	0 (8)	0 (8)	-	-	-	-
Whit	6 (20)	-	7 (20)	9 (19)	4 (19)	-	-
Total	169 (899)	132 (860)	148 (895)	207 (953)	165 (1008)	138 (976)	193 (969)

Table 4. Summary of Black-backed Woodpecker posterior distributions of both fire-level (ω) and average point-level (ψ) predictions of occupancy probability for all fire areas surveyed during 2009 - 2015.

Fire name	ω_{2009}	ω_{2010}	ω_{2011}	ω_{2012}	ω_{2013}	ω_{2014}	ω_{2015}	ψ_{2009}	ψ_{2010}	ψ_{2011}	ψ_{2012}	ψ_{2013}	ψ_{2014}	ψ_{2015}
Albanita	0.84	0.12	0.13	0.84	0.04	-	-	0.10	0.00	0.00	0.30	0.00	-	-
American	-	-	-	-	-	0.28	-	-	-	-	-	-	0.00	-
Antelope Complex	0.90	0.89	0.86	0.86	0.83	0.82	0.83	0.62	0.23	0.41	0.42	0.26	0.13	0.34
Angora	0.90	0.89	0.87	0.86	0.83	0.82	0.83	0.78	0.61	0.73	0.70	0.71	0.54	0.19
Aspen	-	-	-	-	-	0.93	0.33	-	-	-	-	-	0.32	0.00
Azusa	0.12	-	-	-	-	-	-	0.00	-	-	-	-	-	-
Bald	-	-	-	-	-	-	0.91	-	-	-	-	-	-	0.34
Barry Point	-	-	-	-	0.96	0.92	0.89	-	-	-	-	0.86	0.76	0.74
Bassetts	0.89	0.88	-	0.85	0.79	0.80	0.10	0.48	0.44	-	0.30	0.16	0.09	0.00
Bear	-	-	-	-	0.96	0.92	0.89	-	-	-	-	0.78	0.59	0.19
Belden	-	0.61	0.18	0.28	0.49	0.34	0.36	-	0.00	0.00	0.00	0.00	0.00	0.00
Bell	0.11	0.10	0.11	-	-	-	-	0.00	0.00	0.00	-	-	-	-
Bell West	0.77	-	-	-	-	-	-	0.15	-	-	-	-	-	-
Birch	0.13	-	-	-	-	-	-	0.00	-	-	-	-	-	-
Blue	0.81	0.78	0.79	-	-	-	-	0.59	0.32	0.34	-	-	-	-
Boulder Complex	0.88	0.88	-	-	0.79	0.10	-	0.54	0.09	-	-	0.09	0.00	-
Broder Beck	-	0.87	0.16	0.85	0.80	0.79	0.82	-	0.41	0.00	0.12	0.21	0.28	0.29
Brown	-	0.92	0.88	0.86	0.90	0.19	0.86	-	0.37	0.75	0.52	0.12	0.00	0.07
Bucks	0.09	-	-	-	-	-	-	0.00	-	-	-	-	-	-
Chips	-	-	-	-	0.96	0.92	0.89	-	-	-	-	0.07	0.27	0.24
Clover	-	0.91	0.19	0.86	-	-	-	-	0.42	0.00	0.08	-	-	-
Cold	-	-	-	0.86	0.87	0.84	-	-	-	-	0.62	0.61	0.39	-
Comb	-	-	-	0.21	0.09	0.10	-	-	-	-	0.00	0.00	0.00	-
Cone	0.82	-	0.81	-	-	-	-	0.47	-	0.36	-	-	-	-
Cooney	-	-	-	0.84	0.04	-	-	-	-	-	0.07	0.00	-	-
Corral	-	-	-	0.86	0.87	0.84	0.84	-	-	-	0.56	0.42	0.17	0.18
Cougar	-	-	-	0.86	-	0.90	0.88	-	-	-	0.68	-	0.46	0.44
Crag 04	0.86	-	0.14	0.85	0.06	-	-	0.29	-	0.00	0.07	0.00	-	-
Crag 05	0.19	0.16	0.16	0.15	0.08	0.08	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Crater	0.81	0.77	0.79	-	-	-	-	0.48	0.20	0.39	-	-	-	-
Cub	-	0.91	0.88	0.86	0.86	0.85	0.84	-	0.17	0.25	0.11	0.27	0.27	0.19
Deep	0.49	0.30	0.15	0.40	0.14	0.15	-	0.00	0.00	0.00	0.00	0.00	0.00	-
Devils Gap	0.09	-	-	-	-	-	-	0.00	-	-	-	-	-	-
Dexter	0.84	0.82	-	0.85	0.04	-	-	0.53	0.19	-	0.47	0.00	-	-
Dome Rock	-	-	-	-	-	0.85	0.84	-	-	-	-	-	0.40	0.15
Eiler	-	-	-	-	-	-	0.91	-	-	-	-	-	-	0.70
Fall	0.42	0.91	0.19	0.86	0.86	0.84	0.84	0.02	0.16	0.00	0.14	0.23	0.23	0.21
Fish	-	-	-	-	-	0.93	0.90	-	-	-	-	-	0.37	0.75

Fire name	ω_{2009}	ω_{2010}	ω_{2011}	ω_{2012}	ω_{2013}	ω_{2014}	ω_{2015}	ψ_{2009}	ψ_{2010}	ψ_{2011}	ψ_{2012}	ψ_{2013}	ψ_{2014}	ψ_{2015}
Fletcher	0.90	0.90	0.86	0.86	0.14	0.12	-	0.90	0.40	0.53	0.56	0.00	0.00	-
Fox	-	-	0.18	-	0.45	0.28	0.24	-	-	0.00	-	0.00	0.00	0.00
Freds	0.17	-	0.14	0.14	0.06	0.08	-	0.00	-	0.00	0.00	0.00	0.00	-
French	-	-	-	-	-	-	0.20	-	-	-	-	-	-	0.00
Frey	-	0.49	0.18	-	0.38	0.21	-	-	0.00	0.00	-	0.00	0.00	-
Gap	-	0.10	0.11	-	-	-	-	-	0.00	0.00	-	-	-	-
George	-	-	-	-	0.96	0.91	0.89	-	-	-	-	0.11	0.06	0.31
Gondola	0.83	0.80	-	0.84	-	-	-	0.74	0.43	-	0.25	-	-	-
Government	0.91	0.91	0.88	-	0.87	0.84	0.13	0.10	0.20	0.31	-	0.34	0.20	0.00
Granite	-	0.92	0.88	-	0.90	0.87	0.86	-	0.37	0.53	-	0.54	0.52	0.62
Grease	-	-	-	0.15	0.11	0.10	-	-	-	-	0.00	0.00	0.00	-
Harding	0.87	0.86	0.14	0.14	0.09	0.09	0.10	0.41	0.14	0.00	0.00	0.00	0.00	0.00
High	-	0.87	0.86	0.85	-	0.80	-	-	0.07	0.36	0.60	-	0.08	-
Highway	-	-	0.11	-	-	-	-	-	-	0.00	-	-	-	-
Hiram	0.10	-	-	-	-	-	-	0.00	-	-	-	-	-	-
Hooker	0.14	0.12	0.13	0.14	-	-	-	0.00	0.00	0.00	0.00	-	-	-
Horton 2	0.77	-	-	-	-	-	-	0.51	-	-	-	-	-	-
Inyo Complex	0.26	-	-	-	-	-	-	0.00	-	-	-	-	-	-
Kibbie	0.85	-	0.81	0.84	0.05	-	-	0.33	-	0.21	0.27	0.00	-	-
Knight	-	0.61	0.20	0.24	0.44	0.22	0.27	-	0.01	0.00	0.00	0.00	0.00	0.00
Lion 11	-	-	-	0.87	-	0.21	0.87	-	-	-	0.21	-	0.00	0.06
Lion	-	0.92	0.88	0.87	0.90	-	0.85	-	0.41	0.15	0.32	0.39	-	0.53
Lookout	0.10	-	-	-	-	-	-	0.00	-	-	-	-	-	-
Manter	0.14	0.08	-	-	-	-	-	0.00	0.00	-	-	-	-	-
Mclaughlin	-	0.10	0.79	-	-	-	-	-	0.00	0.13	-	-	-	-
McNally	0.35	0.23	0.12	0.37	-	-	-	0.00	0.00	0.00	0.00	-	-	-
Moonlight	0.90	0.90	0.86	0.86	-	0.82	0.83	0.61	0.28	0.61	0.58	-	0.25	0.24
Motor	-	-	-	0.39	-	-	-	-	-	-	0.00	-	-	-
Mountain	-	0.82	0.82	0.84	-	-	-	-	0.21	0.32	0.46	-	-	-
Mud	0.85	0.81	0.82	0.85	0.68	-	-	0.54	0.65	0.44	0.42	0.47	-	-
North Fork	0.25	0.17	0.12	-	-	-	-	0.00	0.00	0.00	-	-	-	-
Oliver	-	-	0.87	-	0.44	-	0.16	-	-	0.43	-	0.00	-	0.00
Onion 2	-	0.30	0.18	0.86	0.23	0.16	0.84	-	0.00	0.00	0.08	0.00	0.00	0.12
Peak	-	-	-	-	-	-	0.89	-	-	-	-	-	-	0.86
Peavine	0.54	-	-	-	-	-	0.84	0.01	-	-	-	-	-	0.07
Peterson Complex	0.92	0.91	0.87	0.86	0.19	0.15	0.12	0.51	0.37	0.74	0.20	0.00	0.00	0.00
Piute 08	0.37	0.23	-	-	0.18	0.15	0.13	0.00	0.00	-	-	0.00	0.00	0.00
Pidgen	0.09	-	-	-	-	-	-	0.00	-	-	-	-	-	-
Pit	-	-	-	0.86	0.45	-	0.23	-	-	-	0.11	0.00	-	0.00
Plum	0.29	0.22	0.12	0.23	-	-	-	0.00	0.00	0.00	0.00	-	-	-

Fire name	ω_{2009}	ω_{2010}	ω_{2011}	ω_{2012}	ω_{2013}	ω_{2014}	ω_{2015}	ψ_{2009}	ψ_{2010}	ψ_{2011}	ψ_{2012}	ψ_{2013}	ψ_{2014}	ψ_{2015}
Power 13	-	-	-	-	-	-	0.30	-	-	-	-	-	-	0.00
Power	0.86	0.18	0.13	0.85	0.06	0.07	-	0.10	0.00	0.00	0.12	0.00	0.00	-
Ramsey	-	-	-	-	0.96	0.92	0.89	-	-	-	-	0.43	0.54	0.18
Reading	-	-	-	-	0.96	0.91	0.89	-	-	-	-	0.62	0.42	0.77
Rich	0.91	0.91	-	0.86	-	0.15	0.84	0.12	0.08	-	0.31	-	0.00	0.22
Rim	-	-	-	-	-	0.26	0.19	-	-	-	-	-	0.00	0.00
Sawmill 06	-	-	0.16	-	0.11	-	0.10	-	-	0.00	-	0.00	-	0.00
Sawmill 00	0.17	-	-	-	-	-	-	0.01	-	-	-	-	-	-
Scotch	0.91	0.29	-	0.86	0.86	0.85	0.84	0.22	0.01	-	0.09	0.12	0.05	0.08
Sheep	-	-	-	0.86	0.41	0.27	-	-	-	-	0.06	0.00	0.00	-
Sherwin	-	-	-	-	0.87	0.15	-	-	-	-	-	0.45	0.00	-
Shotgun	-	-	-	0.86	-	-	0.14	-	-	-	0.20	-	-	0.00
Showers	0.82	0.79	-	0.84	-	-	-	0.52	0.72	-	0.55	-	-	-
Silver	-	-	0.88	0.87	0.90	0.87	0.85	-	-	0.68	0.56	0.46	0.10	0.28
Soda	-	-	-	-	-	-	0.91	-	-	-	-	-	-	0.21
Star	-	0.77	0.79	-	-	-	-	-	0.35	0.18	-	-	-	-
Storrie	0.80	-	-	-	-	-	-	0.48	-	-	-	-	-	-
Straylor	-	-	-	0.85	0.06	0.07	-	-	-	-	0.13	0.00	0.00	-
Stream	0.11	0.09	0.11	-	-	-	-	0.00	0.00	0.00	-	-	-	-
Sugar Loaf	-	0.92	0.88	0.15	0.23	0.18	0.16	-	0.17	0.29	0.00	0.00	0.00	0.00
Summit	-	-	0.14	-	0.04	-	-	-	-	0.00	-	0.00	-	-
Tamarack	-	-	-	0.85	0.11	0.10	0.11	-	-	-	0.16	0.00	0.00	0.00
Tehipite	-	-	-	0.86	0.87	-	0.84	-	-	-	0.44	0.55	-	0.86
Treasure	0.80	0.77	-	-	-	-	-	0.29	0.42	-	-	-	-	-
Vista	0.90	0.90	0.86	0.85	-	0.82	0.83	0.52	0.50	0.17	0.29	-	0.31	0.36
White	0.23	0.20	0.12	-	-	-	-	0.00	0.01	0.00	-	-	-	-
Whit	0.84	-	0.82	0.84	0.67	-	-	0.36	-	0.41	0.49	0.28	-	-
Mean (95% CI)	0.60 (0.55, 0.67)	0.65 (0.59, 0.71)	0.48 (0.48, 0.50)	0.78 (0.75, 0.83)	0.52 (0.47, 0.58)	0.52 (0.44, 0.57)	0.65 (0.62, 0.70)	0.25 (0.22, 0.31)	0.19 (0.17, 0.21)	0.21 (0.18, 0.24)	0.24 (0.23, 0.26)	0.18 (0.17, 0.20)	0.16 (0.15, 0.17)	0.22 (0.21, 0.23)

Models of annual occupancy show changes in the total estimated proportion of (sampled) fire areas occupied by at least one Black-backed Woodpecker in different years (Tables 3, 4). The proportion of occupied fire areas (ω) 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 was significantly lower (0.48). This proportion then increased significantly in 2012 (0.78) and dropped again to approximately 2011-levels in 2013 (0.52, 95% CI: 0.47 – 0.58). In 2014, the proportion of occupied fires remained nearly the same as in 2013 (0.52, 95% CI: 0.44 – 0.57). In 2015, the proportion of occupied fires again rose to levels similar to 2009 and 2010 (0.65, 95% CI: 0.62 – 0.70)

With seven years of data we can assess the presence of linear trends over time through evaluation of the posterior estimates of mean annual point-level and fire-level occupancy. Accounting for uncertainty, there was a weak, non-significant negative linear trend in point-level occupancy from 2009 to 2015 (mean ± se: -0.0069 ± 0.0064; $P = 0.33$). Additionally, there was no linear trend in fire-level occupancy (mean ± se: -0.0028 ± 0.0157; $P = 0.87$).

We compared modeled covariate relationships with occupancy and detectability for each of the seven annual occupancy models (Table 5). Covariate signs showed general consistency across years, with 2015 showing similar parameter magnitudes and posteriors as in previous years. Elevation and snag density remain the strongest two predictors of Black-backed Woodpecker occurrence at the point level. Burn severity continues to have a weak and non-significant relationship to occurrence, likely due to the inclusion of snag density (which is strongly correlated with burn severity), and perhaps also related to a possible confounding with post-fire salvage efforts that may disproportionately target high-severity burned areas. Although burn severity has largely had a positive relationship to occurrence over the seven years, in 2015 the parameter had a negative and non-significant mean. The role of pre-fire canopy cover remains similarly uncertain. In 2015, similar to previous years, the parameter mean has been negative (i.e., lower occupancy with higher pre-fire canopy cover), but insignificant. Of the seven years, the parameter has been significantly negative twice, and significantly positive once (Table 5). Pre-fire canopy cover likely also interacts with snag density, which could lead to the switching in directions over years. Unlike the two previous years, the effect of fire age on fire-level occupancy was not significant. However, we note that in years with low overall occupancy, this parameter is significant. Given the high overall occupancy in 2015, the parameter was negative but not significant. Of the factors affecting detectability, survey type (i.e., passive versus broadcast) remains the only covariate which is significant across all 7 years (broadcast has a higher detection rate than passive).

Table 5. Posterior summaries (means and 95% credible intervals) for intercepts and regression coefficients for single-year occupancy models as applied to 2009-2015 survey data. Parameters with 95% credible intervals that do not cross 0 are bolded.

Parameter	Year						
Fire level occupancy probability	2009	2010	2011	2012	2013	2014	2015
σ_f (variance of random fire effect)	6.5 (0.93, 9.87)	6.34 (1.05, 9.85)	6.2 (0.57, 9.86)	6.4 (0.89, 9.86)	6.2 (0.45, 9.88)	6.3 (0.97, 9.86)	6.6 (0.94 – 9.88)
γ_1 (fire age)	**-2.76** (-6.58, -0.14)	**-3.23** (-7.42, -0.39)	-1.83 (-5.15, 0.44)	-0.49 (-3.77, 2.49)	**-5.81** (-11.9, -1.35)	**-3.23** (-7.67, -0.38)	-2.04 (-5.76, 0.60)
Point-level occupancy probability							
β_0	**-1.01** (-1.37, -0.61)	**-1.17** (-1.47, -0.86)	**-0.45** (-0.76, -0.11)	**-0.97** (-1.19, -0.77)	**-1.01** (-1.33, -0.70)	**-0.98** (-1.25, -0.71)	**-0.80** (-1.03, -0.57)
β_1 (latitude)	**0.54** (0.17, 1.01)	-0.26 (-0.53, 0.00)	0.22 (-0.06, 0.52)	**0.53** (0.34, 0.73)	-0.06 (-0.33, 0.21)	-0.01 (-0.24, 0.22)	0.18 (-0.05, 0.41)
β_2 (elevation)	**1.20** (0.70, 1.91)	**0.81** (0.45, 1.16)	-0.07 (-0.37, 0.24)	**0.53** (0.27, 0.80)	**1.00** (0.60, 1.41)	**0.54** (0.20, 0.90)	**0.77** (0.48, 1.07)
β_3 (snag density)	0.08 (-0.18, 0.32)	**0.29** (0.00, 0.60)	0.10 (-0.15, 0.36)	**0.36** (0.18, 0.54)	**0.45** (0.23, 0.70)	**0.40** (0.12, 0.68)	**0.84** (0.56, 1.13)
β_4 (burn severity)	**0.37** (0.06, 0.72)	0.21 (-0.05, 0.47)	0.20 (-0.09, 0.49)	0.03 (-0.18, 0.22)	**0.25** (0.00, 0.50)	0.12 (-0.12, 0.36)	-0.04 (-0.27, 0.17)
β_5 (pre-fire canopy cover)	0.06 (-0.22, 0.33)	**0.35** (0.06, 0.63)	0.22 (-0.03, 0.48)	**-0.21** (-0.41, -0.01)	-0.31 (-0.31, 0.24)	**-0.28** (-0.55, -0.02)	-0.06 (-0.27, 0.18)
Detection probability							
α_0	**-3.45** (-4.41, -2.65)	**-1.57** (-1.89, -1.25)	**-1.2** (-1.58, -0.83)	**-0.94** (-1.24, -0.63)	**-1.33** (-1.71, -0.97)	**-1.12** (-1.59, -0.77)	-0.96 (-1.33, -0.62)
α_1 (interval duration)	**1.94** (1.11, 2.91)	**0.72** (0.14, 1.31)	0.09 (-0.51, 0.68)	0.25 (-0.25, 0.75)	0.23 (-0.39, 0.84)	0.44 (-0.22, 1.09)	0.21 (-0.39, 0.80)
α_2 (survey type)	**2.83** (2.03, 3.77)	**1.05** (0.65, 1.47)	**0.67** (0.22, 1.12)	**0.92** (0.53, 1.30)	**1.37** (0.92, 1.83)	**1.30** (0.78, 1.83)	**1.09** (0.65, 1.54)
α_3 (day of year)	-0.24 (-0.54, 0.06)	-0.16 (-0.41, 0.08)	0.01 (-0.21, 0.22)	0.07 (-0.11, 0.26)	0.03 (-0.20, 0.26)	**0.43** (0.15, 0.72)	0.23 (-0.01, 0.47)

Analysis of Dynamic Occupancy

Of the 1,993 individual points surveyed across 105 fires, 1,552 points (78%) have been surveyed in more than one year and 101 points (5%) have been surveyed in all seven years. Of those points that were surveyed in more than one year, 528 (27%) showed apparent colonizations, (i.e. non-detection in one year followed by detection in another year) and 530 (44%) showed apparent extinctions. In total, 609 points (31%) showed some degree of apparent change in occurrence status over the 7 years, although this proportion rose drastically for points surveyed in more years. For example, 47% of points visited in 6 years and 59% of points visited in 7 years showed at least one apparent change in occurrence status.

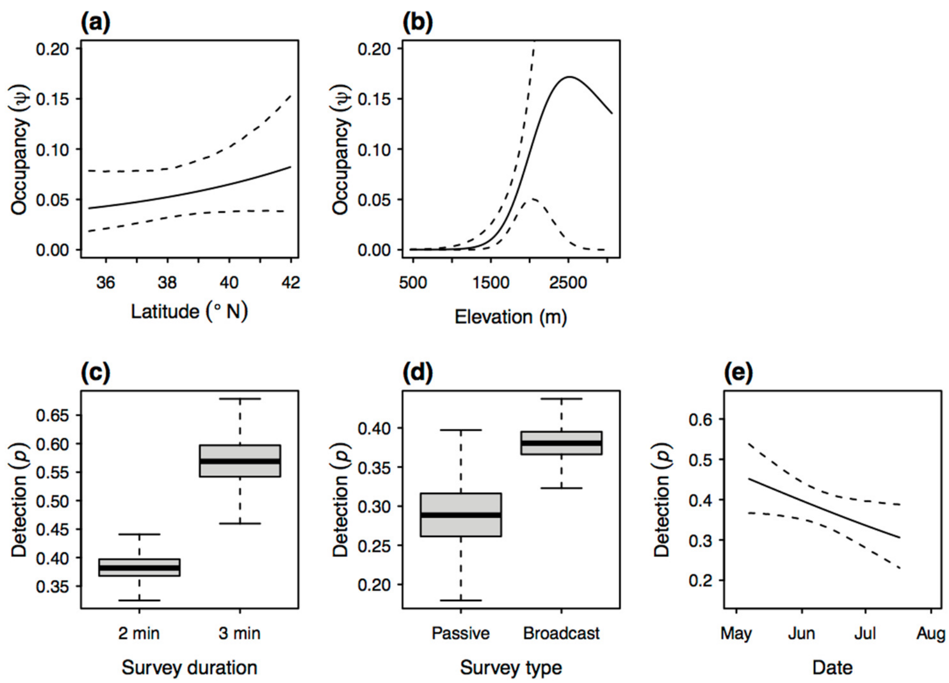

Figure 7. Model-averaged covariate relationships for occupancy (a, b) and detection (c – e) probabilities. Mean covariate relationships are depicted by a solid black line (a, b, e) or a bold horizontal line (c, d). Dotted black lines indicate 95% confidence intervals on relationships, estimated from parametric bootstrapping of model-averaged covariate and intercept means and standard errors. In the case of elevation (b), model-averaging was only conducted on the subset of models containing both linear and quadratic terms.

Our analysis of seven years of data exploring 48 model parameterizations of detectability and initial occupancy resulted in strong support for three similar models, which together represented over 68% of the total AIC model weight. These three models fall within 2 AIC units of each other, an index often used to delineate models with "substantial support" (Burnham and Anderson 2002). The top model selected (AIC weight = 0.28; AIC = 3288) retained all covariates for detectability (i.e., survey type, survey duration, Julian day) and retained elevation (including quadratic term) for initial occupancy.

Model-averaged predictions holding other variables constant showed that detectability per survey interval varied from about 0.2 – 0.7, with detectability higher during 3-minute survey intervals compared to 2-minute intervals, during broadcast surveys when compared to passive surveys, and earlier in the season (Figure 7c-e). Initial occupancy was low (generally < 0.2) but increased weakly with latitude and strongly with elevation (Figure 7a-b). The selection of two initial occupancy (i.e., linear and quadratic terms on elevation) and three detectability covariates was used for all subsequent models of colonization and extinction.

Table 6. Top models ($\Delta_i < 2$) comparing different combinations of colonization and extinction covariates for point-level changes in occupancy.

Colonization covariates	Extinction covariates	K	AIC	Δ_i	w_i
Snag density + fire age	Burn severity + canopy cover	13	3228.4	0.00	0.08
Snag density + fire age	Burn severity	12	3228.4	0.05	0.08
Snag density + fire age	-	11	3228.9	0.48	0.06
Snag density + fire age	Canopy cover	12	3229.4	1.04	0.05
Snag density + fire age	Burn severity + fire age	13	3230.2	1.84	0.03
Snag density + fire age + canopy cover	Burn severity	13	3230.3	1.93	0.03
Snag density + fire age + canopy cover	Burn severity + canopy cover	14	3230.3	1.94	0.03
Snag density + fire age + burn severity	Burn severity + canopy cover	14	3230.3	1.95	0.03
Snag density + fire age	Burn severity + canopy cover + fire age	14	3230.3	1.96	0.03
Snag density + fire age	Burn severity + canopy cover + snag density	14	3230.4	1.98	0.03
Snag density + fire age	Snag density	12	3230.4	1.99	0.03

Model support for colonization and extinction models was broadly distributed across many similar candidate models (Table 6). Eleven models were within 2 AIC units of each other and together comprised over 48% of the total AIC model weight. Although there was no single "top model" for colonization and extinction models, there was general consistency in support for certain variables. All top models within 2 AIC units included both snag density and fire age as colonization covariates. There was greater uncertainty with regard to important variables for extinction covariates (Table 6). Of the covariates tested for extinction, burn severity (% change in canopy cover) was included in 8 of the 11 models within 2 AIC units, while pre-fire canopy cover (%) was included in 6 of the 11 models. The covariates selected were very similar to those selected previously using fewer years of data (Siegel et al. 2012, 2014a, b, 2015).

The cumulative AIC weight in support of the tested variables shows strong differences in support for colonization versus extinction covariates (Table 7). Both snag density and fire age have full, universal support as covariates of colonization, while other variables had little support (< 0.5). There was very low 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, with the strongest providing moderate support (> 0.6) for burn severity (Table 7). Twelve percent of AIC weight supported models where extinction occurred randomly at a fixed probability.

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

Covariate	Colonization relative importance score	Extinction relative importance score
Snag density	1.00	0.29
Fire age	1.00	0.28
Burn severity	0.30	0.55
Pre-fire canopy cover	0.28	0.47

The sign and magnitude of covariate relationships to probabilities of colonization and extinction link our results to environmental features. Model averaged results show relatively low average probabilities of colonization (< 0.15) and high probabilities of local extinction (0.5 – 0.9) at points from year to year. Colonization probability, however, strongly increased with snag density and decreased with fire age (Figure 8a-b). Extinction probability showed no significant relationships, but parameter estimates indicate that extinction probability may decrease with burn severity and extent of pre-fire canopy cover.

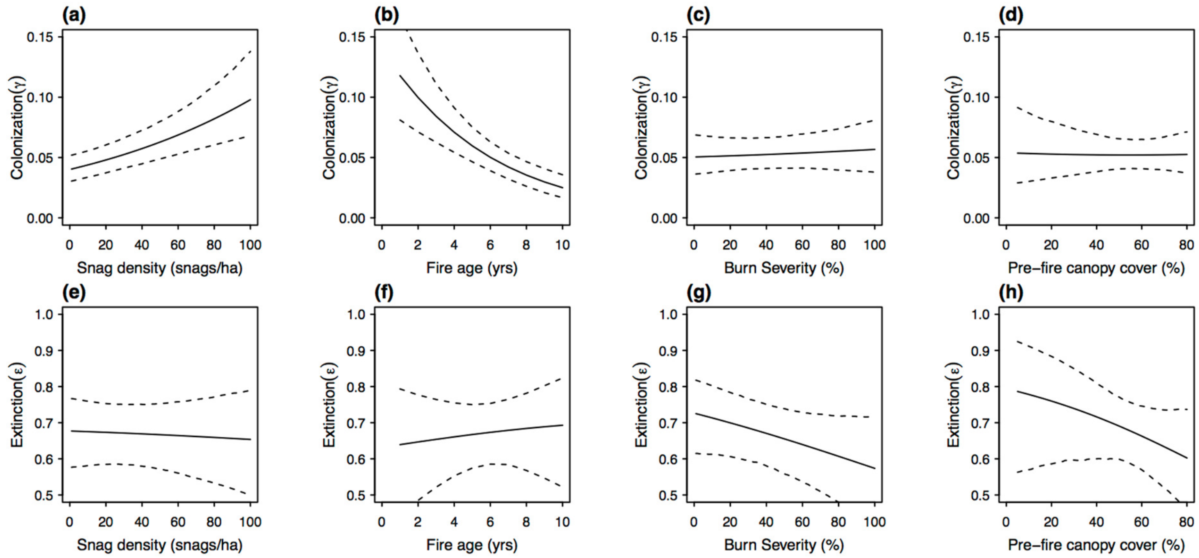

Figure 8. Modeled relationships between *a priori* covariates and probabilities of colonization (a-d) and local extinction (e-h). Plots show model-averaged mean covariate relationships (solid black line) and 95% confidence interval for slopes (dotted black line). Confidence intervals were estimated through parametric bootstrapping of model-averaged covariate and intercept means and standard errors.

Discussion

Black-backed Woodpecker Annual Occupancy

Our seventh year of surveys indicate that Black-backed Woodpeckers continue to be widely distributed across recent fire areas on the National Forests in our study area. The only National Forests where we did not detect Black-backed Woodpeckers in 2015 were Eldorado National Forest, where we did not conduct any surveys, and Inyo National Forest, where our random sample drew only a single fire. The proportion of occupied fires was well within the range of historic variation for our study, and showed a significant increase over the previous two years (2013-2014). Point estimates of the percentage of occupied survey points within each year's sampling frame have varied across years: 25% in 2009, 19% in 2010, 21% in 2011, 24% in 2012, 18% in 2013, 16% in 2014, and most recently, 22% in 2015. The estimated percentage of occupied fires within the sampling frame has shown greater changes: 60% in 2009, 65% in 2010, 48% in 2011, 78% in 2012, 52% in both 2013 and 2014, and 65% in 2015. With seven years of data, there is no evidence for a linear temporal trend in either fire-level or point-level occupancy by Black-backed Woodpeckers. Although the distribution of the species appears to change slightly from year to year, Black-backed Woodpeckers remain present across their historic range in California.

Black-backed Woodpecker Dynamic Occupancy

Our results from 7 years of data indicate strong differences between colonization and extinction dynamics 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 subsequent to the fire) was quite low (5.3%), while average extinction probability was much higher (70%). Despite being low, the probability of a site being colonized was strongly positively associated with snag density and strongly negatively associated with fire age. Thus, early post-fire sites with high snag densities have a relatively higher probability of being colonized than other sites. By comparison, no single factor was strongly associated with extinction, with a moderate negative association with burn severity (i.e., more severe fires make extinction less likely) and pre-fire canopy cover (i.e. more trees pre-fire make extinction less likely). Inferential trends over multiple years of repeating this analysis with increasing amounts of data suggest that the relationships between burn severity and pre-fire canopy cover with extinction probability are likely important (i.e., real) and may become increasingly apparent with additional years of data. Previous analyses of occupancy dynamics (Siegel et al. 2012, 2014a, b) have indicated extinction was purely random.

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 analyses limited to modeling occupancy (e.g., Siegel et al. 2011, Saracco et al. 2011, Tingley et al. 2016, Table 5), we tend to think of occurrence as being limited predominantly 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, suggest that the mechanistic pathway is actually the opposite. Extinction appears to be a relatively likely event, but one with relatively weak controls (e.g., burn severity). That does not mean that other factors that were not investigated (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 point-level occupancy is only around 16 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 14% of all points to go extinct in a given year and 4% of all points to become colonized. Colonization after one year post-fire, consequently, is an important dynamic strongly influencing the observed distribution on a landscape. If management actions were to be taken aimed at increasing overall occupancy, these results suggest that colonization should be targeted rather than extinction, presumably through the retention of early post-fire stands with high snag densities.

The importance of colonization as a driver of occurrence dynamics for Black-backed Woodpeckers in burned forests suggests a sort-of “grass is always greener” scenario, or more accurately, a “trees are always blacker” one. Although little is known about dispersal dynamics in Black-backed Woodpeckers, the birds in our greater Sierra Nevada study area may frequently have the potential to colonize younger post-fire forests, as adequately large fires burn throughout the region during most years. So, for a woodpecker hatched in a 6-year old fire area, whether or not it moves to a newer fire area may not be determined by the characteristics of the site it currently occupies, but rather by whether there is a better, more recently burned site nearby to colonize. Thus extinction may not only be a function of the currently occupied patch, but also a consequence of the proximity to desirable colonization options and the capacity to find them. Further work is needed to test this hypothesis, perhaps involving marking individual birds and following their movements across multiple years.

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