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Research Paper

Occurrence patterns of Black-backed Woodpeckers in green forest of the Sierra Nevada Mountains, California, USA.

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ABSTRACT. Black-backed Woodpeckers (*Picoides arcticus*) are a rare habitat specialist typically found in moderate and high severity burned forest throughout its range. It also inhabits green forest but little is known about occurrence and habitat use patterns outside of burned areas, especially in the Sierra Nevada of California, USA. We used point count and playback surveys to detect Black-backed Woodpeckers during 2011 – 2013 on 460 transects on 10 national forest units. We defined green forest as areas that had not burned at moderate or high severity since 1991 and were more than 2 km from areas burned at moderate or high severity within the previous eight years (n = 386 transects). We used occupancy models to examine green forest habitat associations and found positive relationships with elevation, latitude, northern aspects, number of snags, tree diameter, lodgepole pine (*Pinus contorta*) forest, and a negative relationship with slope. Estimated occupancy in green forest was higher than previously understood (0.21). In addition site colonization and extinction probability in green forest were low (0.05 and 0.19, respectively) and suggest that many of the individuals detected in green forest were not just actively dispersing across the landscape in search of burned areas, but were occupying relatively stable home ranges. The association with high elevation and lodgepole pine forest may increase their exposure to climate change as these elevation forest types are predicted to decrease in extent over the next century. Although density is high in burned forest, green forest covers significantly more area in the Sierra Nevada and should be considered in efforts to conserve this rare species.

Tendance dans l'occurrence du Pic à dos noir dans les forêts vertes de la Sierra Nevada, Californie, États-Unis

RÉSUMÉ. Le Pic à dos noir (*Picoides arcticus*) est un spécialiste rare qui fréquente les forêts modérément à fortement brûlées dans l'ensemble de son aire de répartition. Il s'observe également dans les forêts vertes, mais les tendances dans l'occurrence et l'utilisation de l'habitat à l'extérieur des secteurs brûlés, tout particulièrement dans la Sierra Nevada, aux États-Unis, sont très peu connues. Nous avons effectué des dénombrements par points d'écoute et à l'aide d'enregistrements sonores pour détecter le Pic à dos noir le long de 460 transects situés dans 10 unités de forêts nationales, en 2011-2013. Selon notre définition, une forêt verte n'a pas brûlé de modérément à sévèrement depuis 1991 et est localisée à plus de 2 km de secteurs qui ont brûlé de modérément à sévèrement au cours des huit années précédentes (n = 386 transects). Nous avons utilisé des modèles de présence pour examiner les associations avec les forêts vertes et avons trouvé une relation positive avec l'altitude, la latitude, l'orientation vers le nord, le nombre de chicots, le diamètre des arbres et les forêts de Pin tordu (*Pinus contorta*), ainsi qu'une relation négative avec la pente. L'occurrence estimée dans les forêts vertes était plus élevée que ce qu'on croyait auparavant (0,21). De plus, les probabilités de colonisation et de disparition dans les forêts vertes étaient faibles (0,05 et 0,19, respectivement), et semblent indiquer que bon nombre des individus détectés dans les forêts vertes n'étaient pas simplement en train chercher des secteurs brûlés dans le paysage, mais occupaient plutôt des domaines vitaux stables. Cette association avec les secteurs en haute altitude et les forêts de Pin tordu pourrait augmenter la vulnérabilité de l'espèce aux changements climatiques, étant donné que, selon les prédictions, l'étendue de ce type de forêts en altitude se contractera au cours du prochain siècle. Bien que la densité du Pic à dos noir soit élevée dans les forêts brûlées, les forêts vertes occupent une superficie beaucoup plus grande dans la Sierra Nevada et, de ce fait, devraient recevoir une attention particulière dans les efforts de conservation voués à cette espèce rare.

Key Words: *forest management; habitat specialist; occupancy modeling; Picoides arcticus; secondary habitat*

INTRODUCTION

Conservation of special status species includes identifying and focusing on primary habitats, the environmental conditions that are tied to their highest likelihood of occurrence, rather than secondary habitats where a species occurs at lower density (Goble et al. 2012). This process allows land managers and conservationists to prioritize specific locations for protection where maximum benefits can be achieved with limited conservation resources. In some cases secondary habitats may also be important for long-term population viability (Howe et al. 1991, Aldridge and Boyce 2007). Secondary habitat can offer refugia especially if primary habitat is reduced in quantity or quality (Nielsen et al. 2006). However, because many species of conservation concern are rare even in primary habitat, identifying and managing secondary habitat can be a challenge.

Regional monitoring programs provide data for multiple species and create opportunities to inform species conservation decisions where otherwise no data would have been available (Geupel et al. 2011). Though such monitoring programs may not be specifically

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designed for evaluating population abundance and distribution for certain species, modern occupancy modeling methods have been developed that account for imperfect detectability, thus making it possible to reliably estimate species distributions and habitat associations even in some cases for rare and inconspicuous species (MacKenzie et al. 2006). Occupancy modeling can also account and correct for detectability.

In western North America, the challenge of managing primary and secondary habitats to conserve a bird population is exemplified by the Black-backed Woodpecker (*Picoides arcticus*). The Black-backed Woodpecker is considered a habitat specialist. Throughout its range, it occurs at highest densities in conifer forests that have recently burned (within 1-5 years) at high severity (Murphy and Lehnhausen 1998, Hutto 2008, Saracco et al. 2011). In western North America, especially in the Sierra Nevada and Rocky Mountain ranges, research and management has primarily focused on burned forest habitat (Dixon and Saab 2000, U.S. Forest Service 2007, Hutto 2008, Saracco et al. 2011, Bond et al. 2012). Their status and occurrence patterns in Sierra Nevada green forest are unknown, although small numbers of nesting pairs have been documented outside of areas that recently burned at moderate or high severity (Raphael and White 1984). The importance of this secondary habitat may be underappreciated by researchers and managers working to conserve this rare species at the southern extent of its range (Odion and Hanson 2013).

In the absence of a regional population estimate and a clear understanding of the relative importance of burned forest (primary habitat) and green forest (secondary habitat), there is increasing debate regarding the level of protection Black-backed Woodpeckers should receive (Hanson and Cummings 2010, Hanson et al. 2012). The species was recently considered for listing as threatened or endangered in California (California Department of Fish and Game 2012) and the California population is currently being considered for listing under the United States Endangered Species Act (Federal Register 2013).

In the Sierra Nevada occupancy in burned forest approaches 0.60; with strong positive associations with elevation, northern latitudes, and high fire severities that produce high snag density (Siegel et al. 2012). Occupancy in green forest is unknown, but many assume it to be near zero (Hanson and Cummings 2010, Hanson et al. 2012). Given that there is vastly more green forest than burned forest, even a low density population of Black-backed Woodpeckers in green forest may be important to conservation of this species in the region.

Understanding the habitat associations of Black-backed Woodpecker in green forest is an important step to developing management guidelines for the species. Their habitat associations in green forest of western North America, and especially the Sierra Nevada are poorly known. In eastern Canadian boreal forest, they are associated with late seral characteristics including large amounts of downed wood and snags (Tremblay et al. 2009), and large diameter trees and snags (Hoyt and Hannon 2002, Tremblay et al. 2010). Similarly, in the Cascade Mountains of Oregon, Black-backed Woodpeckers nested in mature and over-mature lodgepole pine stands with an abundance of snags and beetle-infested trees (Goggans et al. 1989). They have also nested in forests with mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the Black Hills of South Dakota (Bonnot et al. 2009).

Beyond the importance of conserving a single species, protection of Black-backed Woodpeckers may have broader implications to the cavity nesting wildlife community in North American conifer forests. Woodpeckers are often considered keystone species for their role in excavating cavities used by many other wildlife species (Martin and Eadie 1999, Virkkala 2006, Tarbill 2010). Black-backed Woodpeckers may play a unique role among primary cavity excavators in that they are known to excavate cavities in less decayed snags than other woodpecker species (Raphael and White 1984, Seavy et al. 2012) and rarely reuse cavities from year to year (Saab et al. 2004). Thus, they are able to produce cavities that may be used by other species for several decades in forest where existing decayed snags are lacking. This may be important for allowing cavity nesting species to exploit ephemeral food resources, such as bark and wood-boring beetle outbreaks (e.g., Norris and Martin 2010). It has been suggested they play a keystone role for the cavity nesting wildlife community in eastern boreal forest (Tremblay et al. 2009, 2010), and burned forest of the Sierra Nevada (Tarbill 2010).

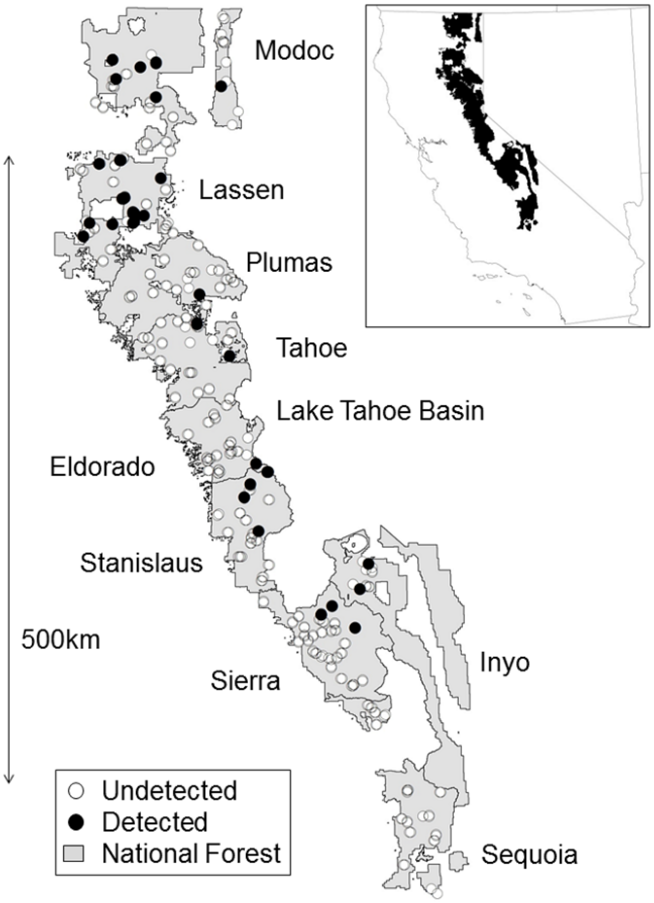
To begin to address the knowledge gap in Black-backed Woodpecker distribution and habitat requirements in western North American forests and help guide management of this potential keystone species, we used data from a Sierra Nevada avian monitoring program to investigate their occurrence in green forests of the Sierra Nevada. Using an occupancy modeling framework, our objectives were to (1) identify the important habitat types and attributes to guide management of this species across its range in California, (2) use multiyear dynamic models to estimate occupancy in green forest, (3) use extinction and colonization probabilities to infer the persistence of birds on occupied sites, and (4) summarize information on Black-backed Woodpecker nests encountered in Sierra Nevada green forest.

METHODS

Study area

Our study area included nine national forests and the Lake Tahoe Basin Management Unit in the Sierra Nevada forest planning area in California, USA (Fig. 1; U.S. Forest Service 2004*a*). This area extends from the southern Cascade and Warner Mountains in Modoc National Forest to Sequoia National Forest at the southern extreme of Black-backed Woodpecker range. Maximum elevations across this region are significantly higher in the southern Sierra vs. the northern Sierra and southern Cascade Mountains (4200 m in the south vs. 2900 m in the north). Precipitation patterns are Mediterranean with the vast majority occurring from November to March. Precipitation increases with elevation and substantially higher amounts fall on the western slope compared with the rain-shadowed eastern slope. Conifer forest is the dominant land cover with ponderosa pine (*Pinus ponderosa*) types dominant at lower elevations; mixed conifer forests comprising ponderosa pine, white fir (*Abies concolor*), sugar pine (P. lambertiana), Douglas fir (*Pseudotsuga menzeisii*), and incense cedar (*Calocedrus decurrens*) are dominant at intermediate elevations; and white fir, red fir (*A. magnifica*), Jeffrey pine (*P. jeffreyi*), and lodgepole pine (P. contorta) are dominant at higher elevations.

Fig. 1. Study area and survey locations in green forest across the Sierra Nevada region of California, USA. Black-backed Woodpecker (*Picoides arcticus*) surveys were conducted between 2011 and 2013 and transects with and without detections are illustrated. Names of national forests and units within the Sierra Nevada forest planning area are shown.



Before ~1940, fire was common in the Sierra Nevada with short fire return intervals (5-20 years) in mixed conifer and lower elevation east and west-side pine-dominated forests; longer intervals (15-60 years) occurred in higher elevation red fir and lodgepole pine forest (Stephens et al. 2007). Since ~1940, fire suppression efforts have led to a significant decline in area burned annually across the Sierra Nevada, but recent evidence has shown that when fires currently burn, they are larger and burn at higher severity than in the beginning of the previous century (Miller et al. 2009*a*). A sample of the California Fire Return Interval Departure GIS layer (Safford and Van de Water 2013, U.S. Forest Service 2013) at our survey locations show that approximately 21% of the study area has burned in the last 70 years, and on average each location has gone more than four fire return intervals without burning. High-elevation red fir and lodgepole pine forests have a lower departure from their historic (pre-Euro-American settlement) fire return interval than low and middle-elevation mixed conifer and pine-dominated forest (Mallek et al. 2013). Thus, they may be closer to their presettlement forest structure.

Sample design

We recorded all Black-backed Woodpeckers detected at sampling locations established for a bioregional monitoring project that was not originally designed for monitoring this species, but rather for four other avian forest and chaparral management indicator species (Roberts et al. 2011). Sample locations ranged in elevation from 1005 to 2737 m and latitudes from 35.3929° to 41.9401°, and were limited to areas within 1 km of accessible roads or trails and slopes less than 35%. We assembled a vegetation layer of 35 different California Wildlife Habitat Relationship (CWHR) land cover types (U.S. Forest Service 2004*b*). We then eliminated nonforest and nonmontane habitat types including grassland, sagebrush, riparian, foothill chaparral, oak woodland, subalpine, barren, and juniper. These stratifications reduced our sampling frame to 1,505,500 ha.

Sample locations were selected using a generalized random-tessellation stratified (GRTS) sampling protocol (Stevens and Olsen 2004, Theobald et al. 2007). The set of potential sampling locations was built from a tessellation generated in ArcGIS (Ver. 9.2, Environmental Systems Research Institute, Redlands, California, USA), consisting of a grid of 1 km^2 cells with a random origin covering the entire study area. We used the GRTS algorithm to select survey locations with equal weight across the entire study area, which consisted of 13,976 1 km^2 cells, resulting in the placement of locations proportional to the amount and spatial distribution of all forested and chaparral habitats within our sampling frame. At each location we established two transects in adjacent 1 km grid cells consisting of four point count stations at 250 m in the cardinal directions from a fifth point in the center. This resulted in a sample of 2300 points on 460 transects distributed as 230 spatially balanced pairs.

Defining green forest

To evaluate occurrence patterns in green forest we removed sampling locations associated with their primary burned forest habitat. We used Spatial Analyst in ArcGIS (Ver. 10.1, Environmental Systems Research Institute, Redlands, California, USA) to calculate the distance from each transect to the nearest patch burned at moderate or high severity within the previous eight years for each of the three years we sampled for Black-backed Woodpecker (2011-2013). We accessed composite burn index fire severity information from the California Vegetation Burn Severity GIS layer (U.S. Forest Service 2012) and used the definitions of moderate and high severity described by Miller et al. (2009*b*). We removed transects where the average distance to the nearest moderate or high severity fire patch for the five point count stations was less than 2 km. We also removed all transects with at least one point occurring directly within a patch that had burned at moderate or high severity since 1990. We included locations within areas that had burned more than 20 years prior since that is well beyond the time that Black-backed Woodpeckers are known to occupy those habitats (Dixon and Saab 2000, Saracco et al. 2011). We feel this definition gives us a conservative sample of the Black-backed Woodpecker population in green forest. Any individuals detected more than 2 km from recently burned patches or within older fire areas are best classified as green forest birds. Removing these locations reduced our sample from 460 transects to the 386 we have defined as green forest.

Survey methods

At each of the five point count stations within a transect we conducted a standardized unlimited distance 5 min point count survey (Ralph et al. 1995). At each station a single observer estimated the distance to the location of each individual bird they detected (hereafter "passive surveys"). Following the five passive surveys, at the center point of each transect only, we conducted a 5 min playback survey for Hairy Woodpecker (*Picoides villosus*) and Mountain Quail (*Oreortyx pictus*), and a 6 min playback survey for Black-backed Woodpecker. We conducted surveys for the two other species as part of the protocol for the regional monitoring program for which these sampling locations were established. Black-backed Woodpecker survey duration was 6 min, with a series of three 25 sec playbacks followed by 95 sec of listening and watching. Playbacks included the scream-rattle-snarl and pik calls and territorial drumming sounds (recording by G. A. Keller, Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology). Playbacks were broadcast at a standardized volume (90 db) using FOXPRO® ZR2 digital game callers (FOXPRO Inc., Lewistown, Pennsylvania, USA). Playback surveys have been shown to significantly increase detection probability for this species compared to individual passive point count surveys (Saracco et al. 2011). Playback surveys were only conducted once per transect visit after all passive point count surveys were completed to avoid influencing detection probability on passive surveys via individuals drawn toward the broadcast from large distances away. Based on our field observations, the approximate range at which human observers can hear the playback calls is 200 m, but highly variable depending on topography and vegetation. There were three transects where the only Black-backed Woodpecker detections were during a Hairy Woodpecker/Mountain Quail playback survey, and none were detected during the passive surveys or Black-backed Woodpecker playbacks. Because of our relatively small sample of Black-backed Woodpecker detections, we included those data in our analysis to better inform our models.

All observers underwent an intensive, three-week training period focused on bird identification prior to conducting surveys. Surveys were conducted between local sunrise and 1000 h from 13 May to 15 July in 2011 to 2013. Surveys did not occur in inclement weather that could reduce detectability, e.g., high wind, rain, or dense fog. In each year, at least 96% of transects were surveyed, and 93% were visited in all three years. The remaining 7% were visited in two out of the three years. Of the transects visited in all three years, 48% received two visits in 2011, 80% in 2012, and 62% in 2013, with the remainder receiving a single visit. Variable survey effort was accounted for in our occupancy modeling framework described below.

Habitat association variables

We assigned a CWHR habitat type to each of the point count locations using a GIS framework (Mayer and Laudenslayer 1988, U.S. Forest Service 2004*b*), and then selected the CWHR type representing the largest number of points in each transect. To reduce the number of predictor variables in the occupancy model we combined the full list of 14 different CWHR types into the following six categories with similar vegetation structure and composition; Sierra mixed conifer (includes ponderosa pine, Douglas fir, and pine-hardwood types), eastside pine (includes Jeffrey pine), white fir, red fir, lodgepole pine, and all remaining nonforest types, including grassland, chaparral, juniper, and sagebrush, were combined into "other." We used a statewide digital elevation model in GIS to assess elevation (as a residual of regression with latitude to remove correlation), percent slope, and solar radiation index (SRI), which is a linear representation of aspect (Keating et al. 2007).

At each point we quantified forest structural conditions within a 50 m radius plot (0.79 ha) centered at each point count station. We made ocular estimates of percent cover of trees > 5 m in height, measured basal area using a 10 factor Basal Area Factor key gauge (converted to per hectare scale), average diameter of the largest trees in the plot, and counted number of snags > 10 cm in diameter. To create transect-scale habitat covariates for occupancy models we averaged the tree cover, basal area, and largest tree diameter at breast height (dbh) values from the five points on each transect. To characterize snag resources, we calculated the maximum snag count from among the five points rather than average. We used the maximum snag count because woodpeckers are readily able to travel the 250 meters between points and thus averaging across the five points would not describe these resources as the birds might perceive them.

Nest surveys

To document breeding activity by Black-backed Woodpeckers, we recorded information for 19 nests found in green forest. Nests were found incidentally by trained field technicians during the May to July survey period during avian point count monitoring in the Sierra Nevada from 2004 to 2013. In 2012 we instructed field crews to follow any individual they observed to find nests as time allowed. In all other years, nests were from chance encounters with far greater survey effort in the northern Sierra. For each nest, we recorded the nest tree condition (snag or live tree), nest tree species, CWHR habitat type, and for nine nests we recorded tree or snag dbh.

Statistical analysis

To evaluate the distribution and habitat associations of Black-backed Woodpecker in Sierra Nevada green forest we used occupancy models (MacKenzie et al. 2006). Occupancy models correct occurrence data for imperfections in the detection process, variable sampling efforts across time and space, and can include covariates on both probability of detection and occurrence by assessing the history of detections across multiple visits to the same survey sites.

We assembled detection histories for each transect by combining all detections from the five passive point counts during a single transect visit, and considered this as a separate survey event from the playback surveys that were done only at the center point. We visited each transect up to twice per year, for a maximum of K = 4 survey events (2 passive, 2 playback) per year per transect. For all models we included survey type (passive or playback) as a covariate of detection probability.

To answer the questions posed, and because of the relatively small sample of detections, we built three separate occupancy models. First we used two single-season models to determine occupancy associations by (1) forest type and (2) habitat structure and physiography. We separated these into separate analyses because of the correlation between habitat types and the physiographic variables. We estimated occupancy and site turnover rates across the three years of our study period with a multiseason dynamic occupancy model.

To evaluate forest type and habitat associations we used a static single-season occupancy model where each site was defined as a transect-year combination, thus "stacking" the yearly detection histories at all surveyed transects to achieve a larger effective sample size (hereafter referred to as the "static habitat association model"). By using this design, we were able to include a larger number of habitat covariates for model selection and avoid problems associated with poor model fit experienced with our full set of covariates using the multiseason occupancy model. The total sample size for this dataset is n = 1135 sites (transect/year combinations) with 377 transects visited in 2011, 386 in 2012, and 372 in 2013. This effectively triples the sample size for examining the relationships between environmental variables and occupancy. Replicating the sites for each survey year in this manner does have the potential to underestimate error in model coefficients due to pseudo-replication, but we feel this method is preferable to the multiseason dynamic model because sites with potentially higher quality habitat are likely to be occupied across more years than lower quality sites and thus will contribute more to identifying clear habitat associations with these sparse data (McClure and Hill 2012). In the multiyear dynamic formulation a site that is occupied only one year, i.e., a potentially lower quality habitat, will have as much influence on the occupancy-habitat relationship as sites that are occupied consistently across years.

In the static habitat association model, we included a large set of covariates on occupancy including; latitude (degrees), the residual of elevation regressed against latitude, slope, SRI, and distance from moderate or high severity fire patches within eight previous years, measured from the center point of the transect. We also included forest structure covariates: percent tree cover of trees > 5 m tall, tree basal area, largest tree dbh, and maximum number of snags per hectare. We verified that none of these variables were correlated at higher than R > 0.55. All covariates were standardized prior to analysis, and we also included squared values of slope, tree cover, basal area, tree dbh, and snags to account for potential associations with intermediate or extreme values of these covariates. We selected a final model starting with a complete model including all 14 variables listed above via removal of the variable with lowest significance in a stepwise fashion until the AIC value (Akaike Information Criterion) ceased to improve (Burnham and Anderson 2002).

We initially included forest type (as a 6-level factor) in the static habitat association model but the model performed poorly and thus we eliminated this categorical variable from the stepwise model selection process. This was not surprising because topographical variables such as elevation, latitude, slope, and aspect are among the primary drivers of the distribution patterns of these broad forest types in the Sierra Nevada. Thus, we analyzed a separate static model using the same data structure with only the six broad forest types (hereafter referred to as the "static forest type model").

The second goal of our occupancy analysis was to evaluate the proportion of area occupied by Black-backed Woodpecker over the three years in our study area. We used a multiseason dynamic model (hereafter referred to as the "dynamic model"), which includes probabilities of transect colonization and extinction between seasons, in our case, years. The time intervals between secondary survey events (within a single season) were up to six weeks, while the time interval between primary survey events was one year. We included the occupancy covariates identified from the lowest AIC value static habitat association model, because with our relatively low number of Black-backed Woodpecker detections we sought to avoid overparameterization of the model.

All models were analyzed using R version 3.0 statistical software and the package "unmarked" (Fiske and Chandler 2011, R Core Team 2013). All counts were converted to detection/nondetection (1 or 0). Both occupancy and probability of detection were defined by logit-linear models. Probability of detection in all models was evaluated as a function of an intercept term, and a covariate for survey type, passive [0] or playback [1]. We defined the model for occupancy probability as the logit-transformed probability of occupancy in relation to the covariates listed above. In the dynamic occupancy model, colonization logit(γ_i) and extinction logit(ε_i) were assumed to be constants because we did not have enough observation data to accommodate more covariates.

We plotted the relationships between occupancy and covariates included in the final static habitat association model using the "predict" function in unmarked, by deriving predicted occupancy estimates from a range of values for the variable of interest and setting all other variables to mean values, except for elevation. We plotted the elevation residual at the third quartile value to produce a figure that shows the occupancy relationship at levels not truncated by extremely low predicted occupancy values. We plot all results as estimates with 95% confidence intervals (CIs).

We derived annual occupancy estimates from the dynamic model using the "smoothed" estimator in the R package "unmarked" and generated standard errors for occupancy estimates using 1000 nonparametric bootstraps (Weir et al. 2009, Kery and Chandler 2012). Turnover probability was calculated from the dynamic occupancy model colonization and extinction parameters and the derived occupancy estimates as described in Weir et al. (2009). We followed the approach of Kery and Chandler (2012), where the probability of a transect changing from occupied to unoccupied or vice versa between years is a function of the colonization probability in the previous year, the extinction probability in the previous year, and the proportion of unoccupied sites in the previous year. We report the two yearly turnover probabilities and estimated 95% CIs using standard error estimates from 1000 parametric bootstraps (Kery and Chandler 2012).

RESULTS

We detected Black-backed Woodpeckers on 75 of 386 (naïve transect detection rate = 19%) transects visited across the three years of our study (Fig. 1). We detected them on 27 of 373 (7%) transects surveyed in 2011, 38 of 373 (10%) surveyed in 2012, and 35 of 372 (9%) surveyed in 2013. They were detected in more than one year at 22 of the 75 (31%) green forest transects with detections.

The final static habitat association model contained seven covariates on occupancy: latitude, elevation, slope, SRI, maximum number of snags, snags^2, and largest tree dbh. The strongest associations were with physiographic variables: high elevations, northern latitudes, and low slopes (Table 1, Fig. 2). Very few detections were recorded below -200 m standardized elevation (approximately 1500 m elevation in the north and 1800 m in the south), and none south of 37.2° latitude. Slightly weaker associations were apparent with moderate to high snag densities, large diameter trees, and more northerly aspects (Figs. 2, 3).

Table 1. Black-backed Woodpecker occupancy model coefficient estimates (β), standard errors, and p-values derived from the static habitat association model in which each year-transect combination was considered a separate sampling unit.

	β	SE	P(>|z|)
Detection probability (*p*)			
Intercept	-0.95	0.19	< 0.001
Survey Type	-0.17	0.20	0.378
Occupancy (ψ)			
Intercept	-2.46	0.24	< 0.001
Latitude (degrees)	0.80	0.19	< 0.001
Elevation*latitude residuals	1.34	0.21	< 0.001
Solar radiation index (SRI)	-0.28	0.17	0.093
Slope	-0.97	0.18	< 0.001
Maximum snags per ha	0.78	0.22	0.001
Maximum snags per ha^2	-0.37	0.14	0.007
Maximum dbh (cm)	0.39	0.17	0.018

Fig. 2. Model-predicted associations between Black-backed Woodpecker (*Picoides arcticus*) occupancy and four topographical covariates. Predicted occupancy was calculated for a range of values of the plotted variable while holding all other model covariates at their mean values, except for elevation, which was set at the third quartile value (because of a highly positive relationship). Transects where Black-backed Woodpeckers were detected received a predicted occupancy value of 1.0.

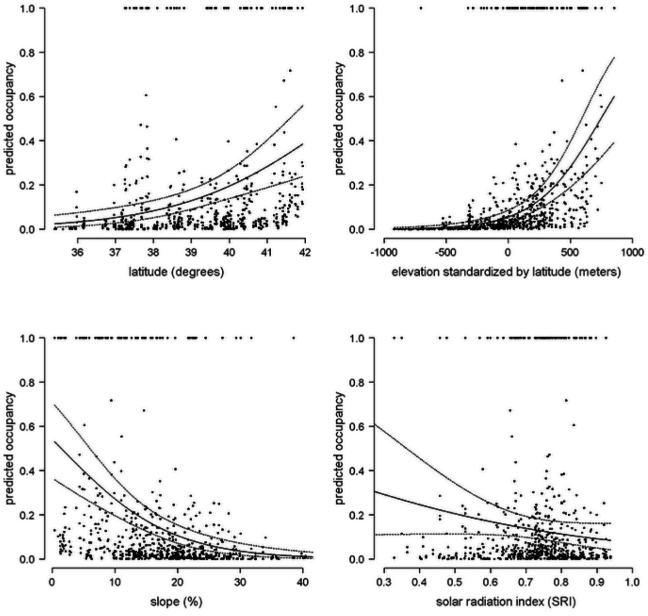
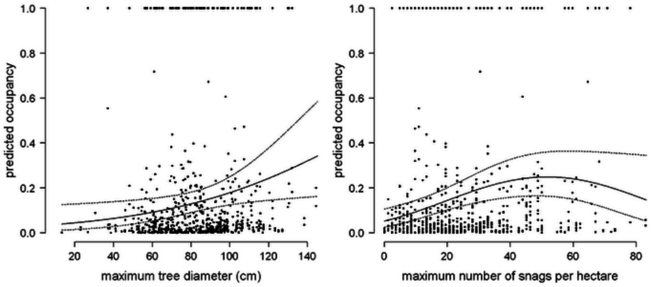


Fig. 3. Model-predicted associations between Black-backed Woodpecker (*Picoides arcticus*) occupancy and two vegetation structure covariates. Predicted occupancy was calculated for a range of values of the plotted variable while holding all other model covariates at their mean values, except for elevation which was set at the third quartile value (because of a highly positive relationship). Transects where Black-backed Woodpeckers were detected received a predicted occupancy value of 1.0.



The static forest type model showed that Black-backed Woodpecker occupancy was highest in the high elevation forest types, especially lodgepole pine (0.37), followed by red fir (0.23), white fir (0.20), and eastside-Jeffery pine (0.17; Fig. 4). Occupancy in lower elevation forest types including Sierra mixed conifer and other habitats was < 0.05.

Estimates of occupancy from the dynamic model was 0.21 in 2011 (95% CI: 0.11 0.31), in 2012 it was 0.20 (95% CI: 0.12 0.28), and in 2013 it was 0.19 (95% CI: 0.10 0.27). Colonization probability was 0.04, and extinction probability was 0.19 (Fig. 5). The probability of a transect changing from occupied to unoccupied or vice versa (turnover rate) from 2011 to 2012 was 0.13 (95% CI: 0.04 0.23) and from 2012 to 2013, it was 0.14 (95% CI: 0.05 0.24).

Fig. 4. Model estimates of Black-backed Woodpecker (*Picoides arcticus*) occupancy across six green forest types. Estimated occupancy values were derived from the static forest type model including only forest type and no other covariates on occupancy. "Other" refers to nonconiferous forest and other nonforest habitats.

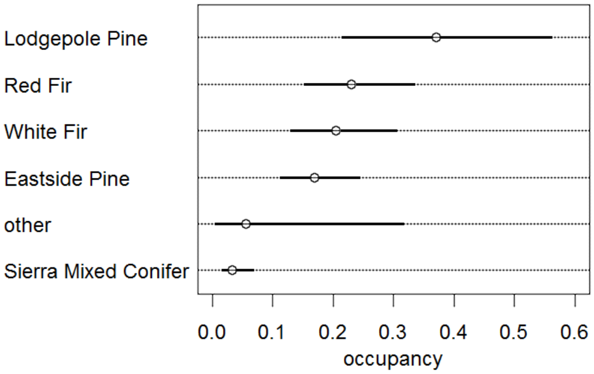
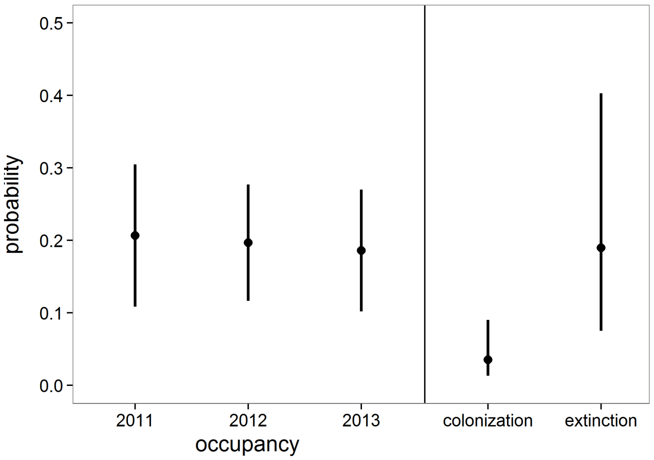


Fig. 5. Annual occupancy estimates and colonization and extinction probabilities for Black-backed Woodpeckers (*Picoides arcticus*) in green forest. Vertical lines bounding each point indicate 95% confidence intervals.



Transect level detection probability in the dynamic model for passive surveys was 0.20 (95% CI: 0.15 0.27) and 0.16 for the playback surveys (95% CI: 0.12 0.22). The combined detection probability for both survey types was 0.33 (95% CI: 0.25 0.43).

We found 19 nests in green forest between 2004 and 2013 at either the incubation or nestling stage. Nests were found across the entire study area, including east and west of the Sierra crest, the southern Cascades, the Modoc plateau and the southern Sierra. Two of the 19 nests occurred in the same tree (different cavity) in consecutive years. Nests ranged in elevation from 1524 to 2521 m. Five different tree species were utilized and 12 of the 19 nests were in dead trees. Lodgepole pine was the most frequently used (n = 5), followed by aspen (*Populus tremuloides,* n = 4), red fir (n = 3), Jeffrey pine (n = 3), whitebark pine (*Pinus albicaulis*, n = 1), and three unidentified tree species. Six of the seven live tree nests were in lodgepole or Jeffrey pine that had no visible evidence of decay. Seventy-nine percent of nests were found in lodgepole pine, red fir, or eastside pine habitat types. For the nine nests we recorded tree dbh, the average was 47 cm ± 1.8 SE (range 24 83 cm).

DISCUSSION

This study provides new information on the occupancy and habitat associations of a rare habitat specialist outside of its primary habitat across the Sierra Nevada region. Our findings suggest that Black-backed Woodpecker occurrence in green forest is far greater than has been suggested by others (Odion and Hanson 2013), though it is still much lower than what has been reported in burned forest in this region (Seigel et al. 2012), a pattern that is consistent with findings for the species elsewhere in its range (Goggans et al. 1989, Trebmlay et al. 2009, Rota 2013). Their distribution in green forest varies based on forest type, physiographic parameters, and habitat conditions, some of which follow patterns found in burned forest in the region. Conservation strategies for Black-backed Woodpecker, especially because they are rare and potentially a keystone species, should consider its green forest habitat in the Sierra Nevada and throughout its extensive range.

Black-backed Woodpecker affinity for lodgepole pine is consistent with descriptions of this species' distribution in green forest in California in the early part of the 20th century (Grinnell and Miller 1944) and in the Cascades region of Oregon (Goggans et al. 1989). Lodgepole pine occurs in association with meadow edges from the mid to upper elevations and as a distinct habitat type above 1800 m in the north and 2400 m in the south (Mayer and Laudenslayer 1988). Overall lodgepole pine forest occupies a relatively small proportion of forested habitat in the Sierra Nevada.

Occupancy was relatively high in other high-elevation conifer types, including red and white fir, that occupy a larger proportion of forested habitat in the Sierra Nevada than lodgepole pine. Occupancy estimates in each of these forest types was higher than our overall estimate. This was due to very low occupancy in Sierra mixed conifer forest types, which dominate the study area. Saracco et al. (2011) found similar occupancy patterns in burned lodgepole pine and red fir forest in the Sierra Nevada, although our results suggest their habitat selection may be more restricted in green forest. For example, Saracco et al (2011) detected Black-backed Woodpeckers at a far higher percentage of burned Sierra mixed conifer and ponderosa pine point count stations compared to what we found in green forest. In fact, we had no detections in ponderosa pine forest types across the three years of our study.

When we examined habitat associations beyond forest type, we found variation in green forest occupancy patterns at the transect scale was best explained by physiographic variables rather than habitat structure. Similarly, in burned forests of the Sierra Nevada, among the strongest predictors of occupancy were positive associations with elevation and latitude (Saracco et al. 2011). We detected very few individuals below 1700 m in the north and 1900 m in the south or below 37.2° latitude. This relationship with latitude is likely the result of the southern portion of our study area representing the southern extent of their North American range as ample high elevation fir and lodgepole pine habitat exists in the southern Sierra (Mayer and Laudenslayer 1988).

The association between habitat structure and occupancy was not as strong as associations with elevation, latitude, and lodgepole pine forest, but we did find an association with areas that contained larger trees and patches of high snag density. In a preliminary analysis, we had included the average number of snags from all five sampling locations for each transect, instead of the maximum, and found no relationship with occupancy. Considering the patchy nature of snags and a reconsideration of the species' natural history, we decided to include the maximum snag count from any of the five sampling locations in the static habitat association model instead of average snag count. Because maximum snag count was a significant predictor of occupancy it suggests that current guidelines that call for retention of an average of 9.9 snags per hectare (4 per acre; U.S. Forest Service 2004*a*) may not be appropriate for maintaining habitat for Black-backed Woodpeckers in green forest. In our models, there was a positive association with patches of high snag density, with transect scale high counts averaging 27 per hectare (11 per acre).

Dense patches of snags, unevenly distributed on the landscape, likely those created through wood-boring beetle outbreaks, may be far more important than an even distribution of suitable nesting trees across a territory. Other researchers have found associations with late seral characteristics in green forest, including high snag densities (Goggans et al. 1989, Setterington et al. 2000, Tremblay et al. 2009, 2010). Further study of the composition and distribution of dead and dying trees within their home ranges and a more detailed evaluation of their habitat associations would help fine tune management recommendations for their green forest habitat.

One hypothesis explaining Black-backed Woodpecker occurrence in green forest is that the majority of individuals detected were not within established territories, but rather were actively dispersing or seeking out new suitable burned habitat. Movement through the green forest matrix would be expected because burned habitat is only suitable for the species for a limited time (Saab et al. 2007, Saracco et al. 2011), and usually in isolated patches across the landscape. Black-backed Woodpeckers are known for their strong association with an abundance of wood-boring beetles, especially following fire (Dixon and Saab 2000). Thus, we consider our 4% colonization, 19% extinction, and 14% total turnover estimates in green forest to be low for a species adapted to exploiting irruptive food resources. Siegel et al. (2012) estimated yearly point-scale rates of colonization and extinction in burned forest in the Sierra Nevada at 7% and 57%. Indeed we would expect point-scale turnover rates would be biased higher than for the transect scale (Hanski 1998). High colonization rates in recent (1-3 years) fires and high extinction rates in older (5-8 years) fires would be expected as individuals colonize new habitat and then abandon it as habitat quality declines rapidly 6-8 years postfire (Saab et al. 2007, Nappi and Drapeau 2009, Saracco et al. 2011).

Though it is important to consider the limitations outlined above, our findings suggest that Black-backed Woodpecker occupancy may be more stable over time in green forest than in burned forest, and at a minimum, along with our sample of nests, provides strong evidence that their presence in green forest is not characterized by dispersal of birds from one burn to another. We advise caution in interpreting habitat quality in burned and green forest solely based on presence of nests and occupancy values. In the Black Hills of South Dakota, population growth rates in recently burned areas were positive compared to negative growth rates in mountain pine beetle-infested green forest (Rota 2013). However, the author suggested beetle-infested forest may buffer population declines when burned forest is unavailable. Further study of productivity, home range size, finer scale habitat selection, and foraging ecology of green forest-nesting individuals is needed to guide conservation efforts for the species.

Black-backed Woodpeckers' role as a keystone cavity creator in burned forest of the Sierra Nevada is distinguished by their ability to excavate cavities in recently fire-killed trees (Tarbill 2010, Seavy et al. 2012). In burned forest, a number of species showed preference for utilizing Black-backed Woodpecker nest cavities (Tarbill 2010). Even though Black-backed Woodpeckers are far less common than Hairy and White-headed Woodpeckers (*Picoides albolarvatus*) across most of the Sierra Nevada, their role as a keystone cavity creator may extend beyond burned forest and they may create cavities preferred by some species in green forest as well. Unique among the conifer dwelling Sierra Nevada woodpecker species, we found a substantial portion of green forest nests excavated in live trees. Similarly, in the Cascades, 66% of nests in beetle-infested lodgepole pine stands were in live trees (Goggans et al. 1989). This pattern of excavating cavities in live conifer trees may have several important ecological implications. First, they may create cavities where snag resources are limited. Second, live trees in which cavities are excavated may be of greater long-term value as a cavity resource because they tend to stand much longer than the already decaying snags where other woodpeckers prefer to excavate (Bagne et al. 2008, Edworthy et al. 2012). Finally, at each of the live tree cavities we found, the bark had been removed from the area immediately below the cavity and resin wells had been excavated causing sap to weep down the tree bole, a behavior that has been reported for the species elsewhere in its range (Dixon and Saab 2000). Woodpeckers in the southern Cascade Mountains, including Black-backed Woodpecker, have been shown to carry fungus and bacteria on their bills associated with wood decay (Farris et al. 2004). By targeting live trees, inflicting substantial wounds, and potentially introducing pathogens, Black-backed Woodpeckers may play an important role in creating snag resources in green forest.

Occupancy methods are robust to variation in detection probability related to survey type or effort and thus can correct for false absences and imbalances in survey efforts in both space and time (MacKenzie et al. 2006). Despite the robust methods used in the occupancy framework, the estimates produced are limited by field methodology and data quantity (MacKenzie and Royle 2005). Because we conducted this research in the context of a multispecies monitoring program, we were not able to allocate extra field effort toward increasing our detections of Black-backed Woodpeckers, such as conducting extra playback surveys (Saracco et al. 2011) or extending survey length (Ibarzabal and Desmeules 2006). In eastern Canada, detection probability in burned vs. unburned forest varied, with significantly longer time until detection in mature unburned forest (Ibarzabal and Desmeules 2006). Our occupancy methodology did not account specifically for habitat induced variation in detection probability, but uncertainty is captured in confidence intervals. We likely could have improved confidence in occupancy estimates, and colonization and extinction rates by conducting additional visits or longer playback surveys. The decision on how to allocate limited resources, including the trade-offs between more visits versus greater spatial coverage is one that researchers should carefully evaluate when designing a study (Bailey et al. 2007). We feel that our analysis provides meaningful estimates to assess the green forest distribution of Black-backed Woodpecker on National Forest in the Sierra Nevada and is an example of how large-scale avian monitoring programs, can answer questions beyond their primary scope (Geupel et al. 2011, Hutto 2005).

Conservation and management implications

Threats to Black-backed Woodpecker populations in burned forest include salvage logging, fire suppression, and prefire reduction of forest fuels that reduces tree densities in future burned areas (Hutto 1995, Hoyt and Hannon 2002, Hutto 2008, Saab et al. 2009). Threats in green forests are rarely discussed and little studied, but may include salvage logging of beetle-killed stands (Bonnot et al. 2009), fuel-wood cutting, low snag retention rates (Tremblay et al. 2010), and potentially climate change.

Some conservation threats, including reduction of forest fuels and salvage logging, may be consistent across burned and green forest habitat, but climate change may have opposite effects. Climate change models predict large increases in burn severity and area burned in the Sierra Nevada (Miller and Urban 1999). These predicted changes should increase burned forest habitat for Black-backed Woodpeckers (Bond et al. 2012, Malleck et al. 2013). At the same time, climate models predict a significant reduction in high-elevation lodgepole pine and red fir forests by the end of the century (Lenihan et al. 2008). Especially in the northern Sierra Nevada, where maximum elevations are lower, the distribution of these forests may become reduced as they are pushed off the top of the mountain (Lenihan et al. 2008). In the southern Sierra Nevada, high elevation lodgepole pine and red fir forest may persist longer as the higher maximum elevations provide space for these habitats to move upslope. Although we found more Black-backed Woodpeckers in the northern Sierra Nevada national forests, the southern forests and national parks may harbor the majority of suitable green forest types preferred by this species by the latter half of this century (Stralberg et al. 2009). Today, the southern Sierra has considerable lodgepole pine and red fir forest yet Black-backed Woodpeckers have higher occupancy at northerly latitudes suggesting they may not readily expand their range south. With increasing effects of climate change, we may find the geographically isolated Sierra population stuck between a rock (declining habitat in north) and a hard place (southern extent of range).

We recommend secondary habitats should not be ignored in conservation planning for Black-backed Woodpeckers in the Sierra Nevada and likely elsewhere. In a broader sense, traditional approaches of focusing on primary habitat for rare species may need to be reassessed in the face of rapidly changing conditions that result in large shifts in the climate envelopes of species and their preferred habitats, changes in disturbance regimes, as well as other increasing threats.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/671

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