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AVIAN COMMUNITY USE AND OCCUPANCY OF CALIFORNIA OAK SAVANNA

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Abstract. California oak savanna is a habitat of sparse tree canopy that extends from northern Baja California to southern British Columbia and is under threat from land-use pressures such as conversion to agriculture, overgrazing, urban development, and fire suppression. Bird-conservation plans have been drafted for the region's oak woodlands. Yet it is unclear whether birds use California oak savanna at different frequencies than they do neighboring oak habitats. In the foothills of the central and northern Sierra Nevada, California, we explored patterns of avian community structure and habitat occupancy in four habitats: blue oak (*Quercus douglasii*) savanna with a well-developed grass and forb layer, blue oak savanna with a well-developed shrub layer, and two habitats with a denser canopy, blue oak woodland, and montane hardwood. Additionally, we assessed the effect of habitat characteristics on avian community structure and occupancy. Avian communities were uniquely grouped among the four habitats. Five species of management and conservation concern—the Western Kingbird (*Tyrannus verticalis*), Western Bluebird (*Sialia mexicana*), Lark Sparrow (*Chondestes grammacus*), Western Meadowlark (*Sturnella neglecta*), and Bullock's Oriole (*Icterus bullockii*)—were predicted to occupy oak savanna habitats at frequencies higher than in oak woodland or montane hardwood. Shrub cover was the most influential habitat characteristic shaping the avian community and was negatively associated with occupancy of the five savanna-affiliated birds. The distinctive structure and occupancy patterns observed for species of concern in California oak savanna suggest that birds perceive this as unique habitat, highlighting the need for its conservation.

Key words: *blue oak, habitat relationships,* Quercus douglasii*, Sierra Nevada, shrub*

Uso y Ocupación de la Comunidad de Aves de la Sabana de Roble de California

Resumen. La sabana de roble de California es un hábitat de copas de árboles dispersos que se extiende desde el norte de Baja California hasta el sur de la Columbia Británica y está bajo amenaza por presiones de uso del suelo como conversión a agricultura, sobrepastoreo, desarrollo urbano y supresión de fuego. Los planes de conservación de aves han sido elaborados para los bosques de roble de la región. Sin embargo, no está claro si las aves usan las sabanas de roble de California con una frecuencia diferente a la de los hábitats de roble vecinos. En las faldas del centro y norte de Sierra Nevada, California, exploramos los patrones de la estructura de la comunidad de aves y de la ocupación de hábitat en cuatro ambientes: sabana de *Quercus douglasii* con una capa bien desarrollada de pastos y herbáceas, sabana de *Quercus douglasii* con una capa bien desarrollada de arbustos, y dos ambientes con un dosel más denso, bosques de *Quercus douglasii* y bosque montano. Adicionalmente, evaluamos el efecto de las características del hábitat en la estructura y ocupación de la comunidad de aves. Las comunidades de aves fueron agrupadas inequívocamente entre los cuatro ambientes. Predijimos que cinco especies con estatus de preocupación de manejo y de conservación—*Tyrannus verticalis*, *Sialia mexicana*, *Chondestes grammacus*, *Sturnella neglecta* y *Icterus bullockii*—ocuparían los hábitat de sabana de roble en mayor frecuencia que los de bosque de roble o bosque montano. La cobertura de arbustos fue la característica de hábitat más influyente modelando la comunidad de aves y estuvo negativamente asociada con la ocupación de cinco aves afiliadas a la sabana. La estructura distintiva y los patrones de ocupación observados para las especies de interés en la sabana de roble de California sugieren que las aves lo perciben como un ambiente único, subrayando la necesidad de su conservación.

INTRODUCTION

Savanna, a habitat of sparse trees and grassland situated in temperate, tropical, and montane regions, is one of the most imperiled biomes on the planet (Hoekstra et al. 2005). Savanna habitats are unique because the vegetative structure combines aspects of open grasslands and woodlands with denser canopy and it is maintained by periodic disturbances such as fire or grazing (Anderson et al. 1999). Without disturbance, the vegetative structure of savanna becomes more similar to shrubland,

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woodland, or forest (Rogers et al. 2008, Sirami et al. 2009). In North America, oak savanna historically occurred throughout the Midwest and in the foothills and adjacent valley bottoms of the West (McPherson 1997). However, with Euro-American settlement came land-cover changes and increasingly intense land use in the form of agriculture, livestock grazing, and urban and suburban development, which has dramatically reduced the extent of oak savanna. In the North American Midwest (Nuzzo 1986) and Pacific Northwest (Christy and Alverson 2011, Dunwiddie et al. 2011), oak savanna has been nearly extirpated from the landscape. The story is similar, though not as bleak, in California where 60% of the state's historic oak savanna and woodland remains (Thomas 1997). These changes in land cover likely alter habitat quality for species best adapted to a sparse canopy (Brawn et al. 2001).

California oak savanna is a broad classification describing floristically unique savanna communities ranging from northern Baja California to southern British Columbia (McPherson 1997). These savanna communities are located primarily in the foothills and adjacent valley bottoms of three mountain regions: the western Sierra Nevada and eastern California Coast Ranges (blue oak savanna, *Quercus douglasii*), southern California mountains (Engelmann oak savanna, *Q. engelmannii*), and northern California and Cascade Range (Oregon white oak savanna, *Q. garryana*, McPherson 1997, Allen-Diaz et al. 1999). Furthermore, on the floor of the Central Valley, valley oak (*Q. lobata*) savannas are interspersed within agricultural and developed areas (Allen-Diaz et al. 1999). California oak savanna and woodlands constitute the dominant hardwood habitats within their range (Bartolome 1987).

Conservation plans have been drafted for birds that use oak woodland habitats (California Partners in Flight 2002). Additionally, there are numerous descriptive studies of birds in California oak habitats (e.g., Block 1989, Tietje and Vreeland 1997). Yet oak savanna, which is classified as having canopy cover of 5–30% and a well-developed grass and forb layer, is structurally different from oak woodland (>30% tree canopy cover, Allen-Diaz et al. 1999), and quantitative analysis of the avian community associated with this habitat has been limited (Verner 1980, Michael and Tietje 2008, Altman 2011). Thus it is unclear whether birds use California oak savanna at frequencies different from those of neighboring oak habitats. This refinement of knowledge is important for management and conservation because California oak habitats and several birds breeding in them are under threat (California Partners in Flight 2002).

Our goal was to quantify avian community structure and habitat occupancy of oak-dominated habitats situated along gradients of canopy cover maintained by elevation and aspect in the foothills of the central and northern Sierra Nevada. More specifically, we had four objectives. First, we examined patterns of avian community structure in oak-dominated habitats of the Sierra Nevada foothills. We predicted bird communities of savannas would be different from those of woodland and montane hardwood habitats, in part because of differences in canopy cover of trees. Second, we assessed the effect of habitat characteristics on the structure of the avian community in the oak-dominated habitats. We identified five habitat characteristics that we hypothesized should influence the structure of the avian community: cover of hardwoods, shrubs, conifers, and herbaceous material, and tree size. Third, we quantified occupancy patterns of species of management and conservation concern by type of oak habitat. Fourth, we evaluated the relationship of bird species predicted to occupy savanna habitats in high frequencies with habitat characteristics. We designed these analyses to provide information for management of birds associated with oak savanna in the Sierra Nevada foothills.

METHODS

STUDY AREA AND SAMPLING DESIGN

Our study encompassed both public and private lands in foothills of the northern Sierra Nevada in Tehama County and of the central Sierra in Yuba and Nevada counties, California. The northern region in Tehama County, the "northern study area," totaled 37 265 ha and included three separate areas: the Tehama Wildlife Area (18 965 ha), managed by the California Department of Fish and Game (CDFG), Dye Creek Preserve (15 190 ha), managed by The Nature Conservancy, and 3110 ha of the Lassen National Forest managed by the United States Forest Service. The region of the central Sierra, the "southern study area," totaled 7695 ha and consisted of three properties: the Spenceville (4635 ha) and Daugherty Hill (1020 ha) Wildlife Areas managed by the CDFG as well as the Sierra Foothill Research and Extension Center (2310 ha) managed by the University of California. The climate of the Sierra Nevada foothills is Mediterranean and characterized by hot dry summers and cool wet winters. Annual precipitation averages 50 to 75 cm, and elevations in our study sites ranged from 93 to 950 m.

The Sierra Nevada foothills support a diverse mosaic of habitats shaped by stark changes in elevation, slope, aspect, microclimate, and edaphic attributes as well as historic and current land use (e.g., grazing, fire, and logging). Trees in the study areas include blue oak, interior live oak (*Q. wislizenii*), canyon live oak (*Q. chrysolepis*), California black oak (*Q. kelloggii*), California scrub oak (*Q. berberidifolia*), valley oak, gray pine (*Pinus sabiniana*), ponderosa pine (*P. ponderosa*), and California buckeye (*Aesculus californica*). Shrubs include buckbrush (*Ceanothus cuneatus*), poison oak (*Toxicodendron diversilobum*), whiteleaf manzanita (*Arctostaphylos viscida*), chaparral coffeeberry (*Rhamnus tomentella*), and toyon (*Heteromeles arbutifolia*). The herbaceous layer is dominated by annual grasses and forbs.

We randomly generated 3000 polygons of 500 m^2 within the boundaries of our study areas. The polygons encompassed the range of five abiotic attributes that influence the area's vegetation: precipitation, temperature, slope, aspect, and geologic substrate. The CDFG generated the GIS maps of these attributes. We randomly selected 60 of the 3000 polygons and plotted the centroid of each. At each of the 60 centroids, we plotted three sample points spaced 250 m apart in an equilateral triangle (i.e., triplet), centered on the centroid (Fig. 1) for a total of 180 sample points. At each of these, we recorded habitat characteristics and birds by point counts. We averaged the data for each sample point of a triplet to represent the sample plot. We surveyed 29 sample plots in the northern study area and 31 in the southern study area (Fig. 1). Two sample plots in the northern study area were in chaparral, not oak habitat, so we excluded them from further analysis. The distance between sample points of neighboring plots ranged from 325 to 1200 m. To explore patterns of spatial autocorrelation among sample plots, we fit semivariograms of the residuals of the occupancy estimates for three bird species, which we chose as indicators of the oak habitats of our study area (Legendre and Fortin 1989): the Lark Sparrow (*Chondestes grammacus*), Spotted Towhee (*Pipilo maculatus*), and White-breasted Nuthatch (*Sitta carolinensis*). We chose these because these species are associated with open, shrubby, and woodland areas, respectively, encompassing the range of vegetation in our study area. We did not find any pattern of spatial autocorrelation of the occupancy estimates for each species among the sample plots so considered data from the 58 plots as independent.

HABITAT CHARACTERISTICS

To measure habitat characteristics in the field, we used a modification of the circular-plot method (James and Shugart 1970). We subdivided a circle of radius 100 m around each sample point into three 120° sections (1–120°, 121–240°, and 241–360°) then established one circular plot of radius 15 m within each section. From each sample point, within each

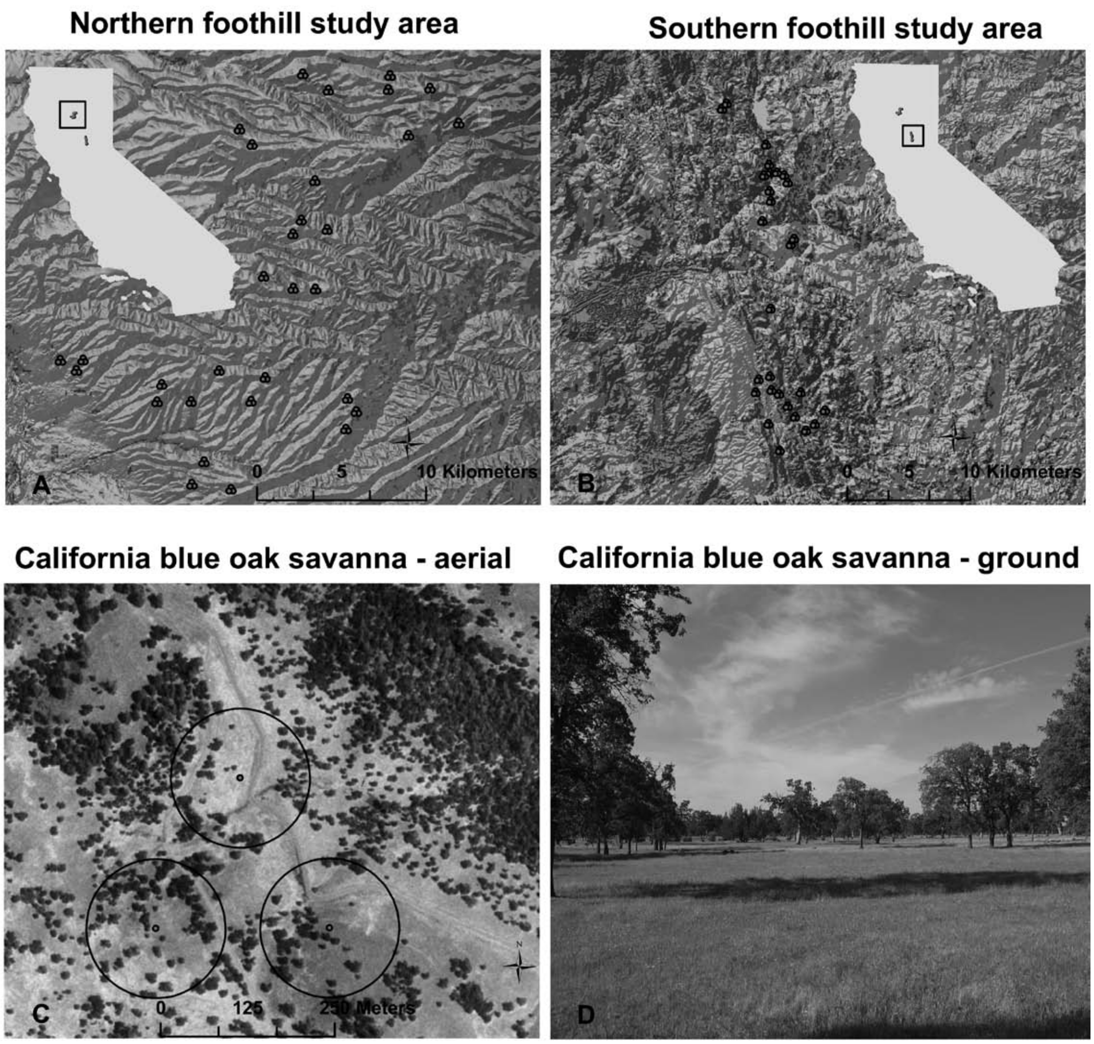

FIGURE 1. Locations of two clusters of 60 sample plots in the foothills of the Sierra Nevada, California. (A) Northern study area; (B) southern study area. (C) Aerial photograph of blue oak savanna with illustrating design of a sample plot with the three sample points used for all bird and habitat surveys. (D) Photo of California blue oak (*Quercus douglasii*) savanna in the northern study area, Tehama County.

120° section, we determined the locations of the smaller circular plots with a random compass bearing and random distance between 20 and 80 m. We used the distance of 20 to 80 m so that the circular plots would be completely within the 100-m radius. Within each circular plot, we identified all live trees ≥10 cm in diameter at breast height (dbh) to species and recorded the trees' dbh. We averaged the dbh of the trees in the three smaller circular plots to generate a mean for each sample point. We measured cover of live vegetation of trees (>2 m above the ground), shrubs (0.5–2.0 m), and the herbaceous layer (<0.5 m) at 25 points within each of the three circular plots, using a sighting tube held vertically at eye level. At the center of each circular plot, we placed eight 15-m transects that radiated out, spaced 45° apart. We recorded three readings through the sighting tube at 5-m intervals along each transect, totaling 24 readings per circular plot. The 25th reading was taken at the center of the circular plot. We held the sighting tube facing up to record a hit of trees or tall shrubs, down to record a hit of shorter shrubs and the herbaceous layer at each of the 25 locations along a transect. We measured each hit of tree and shrub by species but recorded hits in the herbaceous layer material by life form (e.g., grass or forb). Thus we recorded readings through the sighting tube at 75 locations per sample point. We averaged data from the 75 readings to come up with percent values of cover of all hardwood species (hardwood cover), all conifer species (conifer cover), all shrub species (shrub cover), and herbaceous material (herbaceous cover) per sample point. Thus our data represent three levels of sampling, (1) the sample plot (broadest level, describing the averaged data for the three sample points), (2) sample point (refers to the individual points where we sampled birds and habitat characteristics), and (3) circular plot (three plots around a sample point in which we measured habitat characteristics).

Prior to analysis, we classified habitats on the basis of vegetation-classification systems for the Sierra Nevada (Mayer and Laudenslayer 1988, Allen-Diaz and Holzman 1991, Sawyer and Keeler-Wolf 1995). To do so, we visually explored the two-dimensional distribution of sample plots, based on their habitat characteristics, using a nonmetric multidimensional scaling ordination (Carr 1997). We computed a Bray–Curtis dissimilarity index of five habitat characteristics (hardwood, conifer, shrub, and herbaceous cover, and the average dbh of trees). We log-transformed all variables and constructed a rank-dissimilarity matrix from the Bray–Curtis index (Clarke and Green 1988), from which we calculated the ordination (Carr 1997). We used the Bray–Curtis measure because it is designed to quantify dissimilarity of habitat characteristics and species along environmental gradients (McCune et al. 2002). To group sample plots on the basis of habitat characteristics, we used a hierarchical cluster analysis (Clarke and Gorley 2006) of the Bray–Curtis dissimilarity measure (McCune et al. 2002). Four habitat types were grouped, in which >85% of the similarity of habitat characteristics within a group were shared (Fig. 2). Axis 1 captured a gradient of shrub cover, axis two a gradient of tree-canopy cover (Fig. 2).

Additionally, prior to classifying habitats, we used a Kruskal–Wallis test to quantify differences in the five habitat characteristics among the four habitats. When the results of the Kruskal–Wallis tests were significant, we used a nonparametric multiple-comparisons procedure, based on relative contrast effects, in nparcomp (Konietschke 2011) in the R statistical software package (R Development Core Team 2012). We used a Bonferroni adjustment for pairwise comparisons of habitats ($\alpha = 0.05/6 = 0.008$). We classified two habitats as oak savanna (tree-canopy cover 5–30%, Table 1, Allen-Diaz et al. 1999). The distinction between the two was a difference in shrub cover (Table 1). Thus we classified these habitats as oak savanna-grass and oak savanna-shrub, with 23 and 13 sample plots, respectively (Fig. 2). In addition to oak savanna, the two other habitat types we classified for our study were oak woodland (>30% tree-canopy cover) and montane hardwood (>30% tree-canopy cover and a well-developed shrub layer; Mayer and Laudenslayer 1988, Sawyer and Keeler-Wolf 1995), which were represented in 9 and 12 sample plots, respectively (Fig. 2).

AVIAN POINT COUNTS AND SAMPLE-PLOT OCCUPANCY

To characterize the community of breeding birds, from late March to mid-June 2004 we did a 10-min point count within a fixed radius of 100 m at each sample point (Ralph et al. 1993). We surveyed each sample point three times, separated by approximately two weeks. To distribute observer variability (Ralph et al. 1995), five individuals performed all counts and rotated among sample points. We counted from 10 min after sunrise and continued for 3 to 3.5 hr, permitting surveys at six to nine sample points (i.e., two or three plots) per day. We counted only birds detected within the 100-m radius. Before data analysis, we constructed species-accumulation curves within each habitat. After the three visits, there was very little evidence of additional species accumulation in any habitat, so we were confident our survey effort sufficiently characterized the avian community of our study area.

To reduce bias due to variation in species' detectability, we calculated the probability of a sample plot being occupied, psi (ψ), adjusted for detection probability $p(.)$, in the program Presence (Hines 2006). We fit a single-season, single-species model to estimate probabilities of occupancy specific to a sample plot by using the history of detection and nondetection of birds that commonly use oak-dominated habitats of the Sierra Nevada foothills (MacKenzie et al. 2006). We fit the null model, in which the probability of occupancy of a sample plot and detection probability were held constant, $[\psi(.),p(.)]$, for 32 bird species (Table 2). This resulted in unique derived parameter estimates for each species' probability of occupying the sample plot. We used the sample-plot-specific estimate of a species' occupancy as the response variable in all univariate and multivariate analyses. Species that were either too common (e.g.,

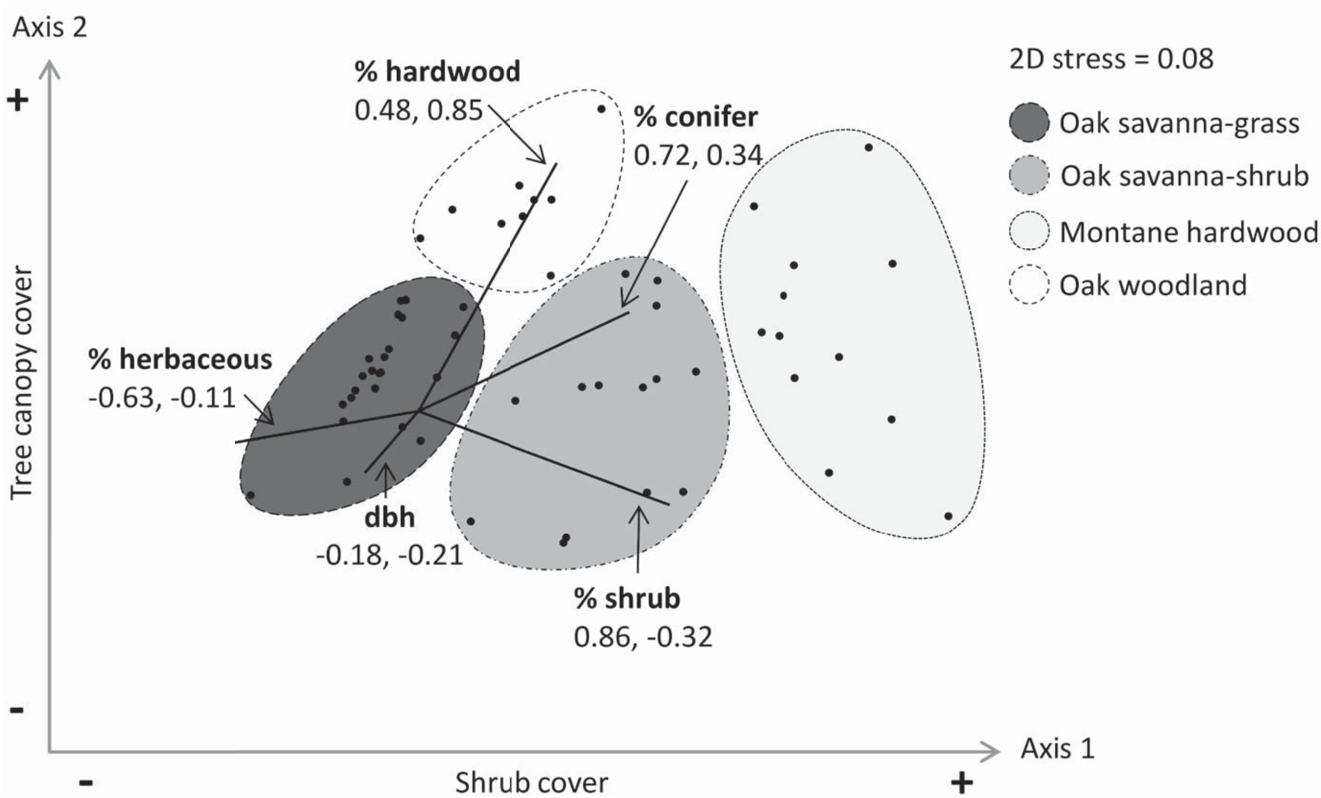

FIGURE 2. Two-dimensional plot for nonmetric multidimensional scaling ordination of resemblance matrix (Bray–Curtis, log-transformed habitat data) for sample plots in the Sierra Nevada foothills. Sample plots are organized by five habitat characteristics: cover of hardwoods, of conifers, of shrubs, and of herbaceous vegetation, and the average diameter at breast height of trees within each sample plot. Lines indicate directionality of correlations of habitat characteristics with the two axes. Numbers following a habitat characteristic are Spearman's ρ correlations with axis 1 (first number) and 2 (second number). Circles around points are groupings independently determined by hierarchical cluster analysis (group average, >85% similarity).

Acorn Woodpecker, *Melanerpes formicivorus*) or too rare (e.g., Yellow-billed Magpie, *Pica nuttalli*) were not included in this analysis because the common birds were predicted to occupy all sample plots and the estimates for rarer birds were unreliable (MacKenzie and Royle 2005). We considered only those species whose detection probability exceeded 0.2 because inferring occupancy patterns of species with low detection probabilities is not recommended (Table 2, MacKenzie et al. 2006).

STATISTICAL ANALYSIS

For our first objective, we explored patterns of avian community structure among the oak habitats of our study area. To do so, we used a nonmetric multidimensional scaling ordination of the between-plot rank-dissimilarity matrix (Carr 1997) on the square-root-transformed estimate of species occupancy, following methods similar to our habitat-classification analysis. To test for differences in the avian community by habitat, we used an analysis of similarities test (ANOSIM, Carr 1997). We computed a Bray–Curtis dissimilarity index on the square-root-transformed estimate of species occupancy, from which we computed the ANOSIM. The ANOSIM uses a Monte Carlo permutation test of observed data to evaluate whether rank dissimilarities within habitats were less dissimilar than among habitats. We used 999 Monte Carlo permutations to generate the ANOSIM R test statistic. ANOSIM R values generally range from zero to one. A value of zero

TABLE 1. Mean value of average diameter at breast height (dbh) of all trees measured at a sample plot, and percent cover of hardwoods, conifers, shrubs, and herbaceous vegetation in four habitats in the foothills of the central and northern Sierra Nevada. Variables with same superscript do not differ significantly by habitat (Kruskal–Wallis test with nonparametric multiple comparisons procedure based on relative contrasts effects, type Tukey, with Bonferroni adjusted P: 0.05/6 = 0.008).

Variable	Oak savanna–grass	Oak savanna–shrub	Montane hardwood	Oak woodland
dbh (cm)	13.17	9.74	11.15	10.50
% Hardwood	20.03^{A}	24.24^{A}	48.80^{B}	58.73^{B}
% Conifer	0.20^{A}	1.18^{B}	8.55^{C}	2.44^{B}
% Shrub	0.09^{A}	10.38^{B}	31.75^{C}	0.44^{A}
% Herbaceous	69.55^{A}	56.63^{B}	37.82^{C}	62.76^{AB}

TABLE 2. Naïve (raw) detection rate and null detection probability $p(.)$ for 32 species of birds in the Sierra Nevada foothills. Birds selected because they are either species of conservation concern or were detected in oak savanna.

English name	Scientific name	Code	Detection rate	$p(.)$
American Kestrel	*Falco sparverius*	AMKE	0.07	0.21
California Quail[a,b]	*Callipepla californica*	CAQU	0.40	0.29
Mourning Dove[c]	*Zenaida macroura*	MODO	0.38	0.32
Anna's Hummingbird[c]	*Calypte anna*	ANHU	0.59	0.39
Nuttall's Woodpecker[a,c]	*Picoides nuttallii*	NUWO	0.47	0.23
Pacific-slope Flycatcher[c]	*Empidonax difficilis*	PSFL	0.07	0.38
Ash-throated Flycatcher[a]	*Myiarchus cinerascens*	ATFL	0.91	0.78
Western Kingbird[c]	*Tyrannus verticalis*	WEKI	0.31	0.41
Hutton's Vireo[a,c]	*Vireo huttoni*	HUVI	0.28	0.26
Western Scrub-Jay[a,c]	*Aphelocoma californica*	WESJ	0.66	0.38
Tree Swallow[c]	*Tachycineta bicolor*	TRES	0.24	0.24
Bushtit[c]	*Psaltriparus minimus*	BUSH	0.71	0.43
White-breasted Nuthatch[a,c]	*Sitta carolinensis*	WBNU	0.86	0.62
Rock Wren[c]	*Salpinctes obsoletus*	ROWR	0.14	0.30
Bewick's Wren[a,c,d]	*Thryomanes bewickii*	BEWR	0.48	0.39
House Wren[c]	*Troglodytes aedon*	HOWR	0.45	0.36
Blue-gray Gnatcatcher[a,c,d]	*Polioptila caerulea*	BGGN	0.40	0.31
Western Bluebird[a,c]	*Sialia mexicana*	WEBL	0.55	0.38
American Robin[c]	*Turdus migratorius*	AMRO	0.64	0.35
Wrentit[b,c]	*Chamaea fasciata*	WREN	0.24	0.53
European Starling[a,c]	*Sturnus vulgaris*	EUST	0.48	0.33
Orange-crowned Warbler[c]	*Oreothlypis celata*	OCWA	0.40	0.44
Nashville Warbler[c]	*Oreothlypis ruficapilla*	NAWA	0.12	0.24
Black-throated Gray Warbler[c]	*Setophaga nigrescens*	BTYW	0.29	0.21
Spotted Towhee[c]	*Pipilo maculatus*	SPTO	0.40	0.59
California Towhee[a,b,c]	*Melozone crissalis*	CALT	0.21	0.33
Chipping Sparrow[c]	*Spizella passerina*	CHSP	0.64	0.39
Lark Sparrow[a,c]	*Chondestes grammacus*	LASP	0.67	0.59
Western Meadowlark[c,d]	*Sturnella neglecta*	WEME	0.33	0.66
Brown-headed Cowbird[c]	*Molothrus ater*	BHCO	0.22	0.23
Bullock's Oriole[c]	*Icterus bullockii*	BUOR	0.16	0.47
House Finch[c]	*Haemorhous mexicanus*	HOFI	0.54	0.41

[a]Focal species of California Oak Woodland Conservation Plan (California Partners in Flight 2002).
[b]Focal species of Coastal Scrub and Chaparral Bird Conservation Plan (California Partners in Flight 2004).
[c]Focal species of Sierra Nevada Bird Conservation Plan (Siegel and DeSante 1999).
[d]Focal species of Grassland Bird Conservation Plan (California Partners in Flight 2000).

indicates the avian communities are identical, whereas a value of one indicates the avian communities of the habitats are completely different. We used a Bonferroni adjustment for pairwise comparisons among habitats ($\alpha = 0.05/6 = 0.008$). We completed the nonmetric multidimensional scaling, cluster analysis, and ANOSIM with the statistical software package PRIMER (version 5.2; Clarke and Warwick 2001).

For our second objective, we assessed the effect of habitat characteristics on the structure of the avian community among the habitats studied. We used the four cover variables measured in the field because we hypothesized differences in physical structure and the invertebrate community of these habitat characteristics would likely affect birds' habitat use (Table 1). We also hypothesized that tree size (i.e., dbh) should indicate a sparse cover of trees. Thus we included average dbh as a descriptor variable (Table 1).

We ran a canonical correspondence analysis of the estimate of species occupancy at the 58 sample plots in the main matrix with the five habitat characteristics as descriptor variables in the second matrix. We used a canonical correspondence analysis because the method is appropriate for understanding relationships of community composition to descriptor variables (ter Braak 1986), which in our case were the habitat characteristics. We first log-transformed the five habitat characteristic variables in the second matrix, then standardized the row (sample plots) and column (bird-occupancy estimates) scores by centering and normalizing to a mean of zero and a standard deviation of one. We scaled ordination scores to optimize columns, which were the estimate of species occupancy in the main matrix by sample plot. To test whether the avian community of the Sierra Nevada foothills was more strongly related to any of the five habitat characteristics than expected by chance, we applied a Monte Carlo permutation procedure (999 randomized runs). For the canonical correspondence analysis, we used the statistical software package PC-ORD (version 5, Gleneden Beach, OR; McCune et al. 2002).

For our third objective, we quantified predicted occupancy patterns of species of management and conservation concern by the four habitats. We used a Kruskal–Wallis test, with habitat type as the treatment, following methods similar to our habitat-classification analysis.

For our fourth objective, we explored the relationship between bird species predicted to occupy savanna habitats at high frequencies with habitat characteristics. Our purpose with this analysis was to generate information on relationships of savanna birds with characteristics of oak savanna. By means of the Kruskal–Wallis test, we identified five species that used oak savanna more frequently than other habitats: the Western Kingbird (*Tyrannus verticalis*), Western Bluebird (*Sialia mexicana*), Lark Sparrow, Western Meadowlark (*Sturnella neglecta*), and Bullock's Oriole (*Icterus bullockii*). These we categorize as oak savanna affiliates. We included cover of hardwoods, shrubs, and the herbaceous layer and the average dbh of trees as response variables, using a rationale similar to that of the canonical correspondence analysis. We calculated ψ as a function of each of the four habitat characteristics for each bird. We modeled detection probability as constant $p(.)$ or as the full identity-design matrix p(survey), where the probability of detection varied by survey visit. We determined the best supported of the two scenarios for detection probability and used this in all models for each bird species. We assessed models' fit to the data by a goodness-of-fit bootstrap test, using 1000 bootstraps on the best-supported model of a set (MacKenzie and Bailey 2004). We fit models by using the program PRESENCE (Hines 2006).

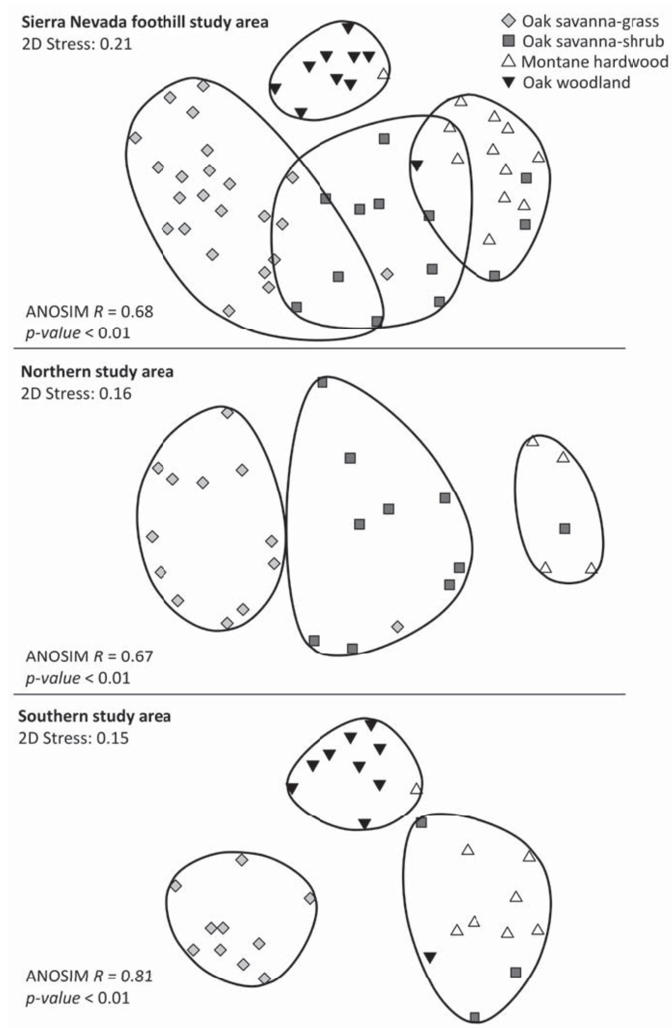

FIGURE 3. Two dimensional, nonmetric multidimensional scaling ordination plot of resemblance matrix (Bray–Curtis, square-root-transformed estimates of relative bird occupancy) for (A) sample plots by four habitats at the scale of the entire study area in the Sierra Nevada foothills and at the scale of the two smaller, separate study areas, (B) the northern study area in Tehama and Butte counties, and the (C) southern study area in Yuba and Nevada counties. Stress indexes are a measure of fit between the resemblance matrix and the two-dimensional representation of the similarity matrix (0.10 to 0.20 = good fit). Circles around points are groupings independently determined by hierarchical cluster analysis (group average, >85% dissimilarity). ANOSIM R values represent results of a one-way test of similarities indicating differences in avian communities by habitat. Higher values of ANOSIM R indicate increased dissimilarities of the avian communities.

RESULTS

FACTORS AFFECTING AVIAN COMMUNITY STRUCTURE

Strong differences in avian community structure by habitat were apparent in the nonmetric multidimensional scaling ordination and revealed by the ANOSIM analysis across the entire study area (ANOSIM $R = 0.68$, $P < 0.01$) and in both the northern and southern study areas (ANOSIM $R = 0.67$ and 0.81, $P < 0.01$, respectively, Fig. 3, Table 3). Across the study area, the hierarchical cluster analysis identified four groupings at the 85% similarity level, roughly corresponding to the four habitats of our study area (Fig. 3). In all ordinations, axis 1 characterized a gradient of shrub cover, whereas axis 2 captured a gradient of tree-canopy cover.

TABLE 3. *Analysis of similarities (ANOSIM) matrices of avian communities among four habitats. We performed an ANOSIM for the entire study area as whole and the northern and the southern study areas separately. Numbers below the diagonals are ANOSIM R values, those above are P-values.* ANOSIM *R* values generally range from zero to one. A value of zero indicates identical avian communities whereas a value of one indicates completely different avian communities. Pairwise comparisons of habitats were evaluated with a Bonferroni adjusted *P*-value of 0.05/6 = 0.008.

Study area and habitat	Oak savanna-grass	Oak savanna-shrub	Montane hardwood	Oak woodland
Sierra Nevada study area				
Oak savanna-grass	—	<0.01	<0.01	<0.01
Oak savanna-shrub	0.64	—	<0.01	<0.01
Montane hardwood	0.93	0.32	—	<0.01
Oak woodland	0.67	0.61	0.72	—
Northern study area[a]				
Oak savanna-grass	—	<0.01	<0.01	—
Oak savanna-shrub	0.59	—	<0.01	—
Montane hardwood	0.98	0.41	—	—
Oak woodland	—	—	—	—
Southern study area				
Oak savanna-grass	—	<0.01	<0.01	<0.01
Oak savanna-shrub	0.95	—	0.21	<0.01
Montane hardwood	0.99	0.13	—	<0.01
Oak woodland	0.88	0.68	0.67	—

[a]Oak woodland was not present in northern study area.

In the canonical correspondence analysis, 19% of the explained variance was in axis 1, while 6% was explained in axis 2 (Fig. 4). The Monte Carlo test (999 permutations) indicated that the habitat characteristics had an effect on avian community structure larger than expected by chance ($P < 0.01$). Of the five habitat characteristics, three were positively correlated with axis 1 while two were negatively correlated (Fig. 4). All habitat characteristics were positively correlated with axis 2 (Fig. 4). Shrub cover had the highest correlation with axis 1 ($r = 0.79$, $P < 0.01$), implying that this was the strongest habitat characteristic shaping the structure of the avian community (Fig. 4). The average dbh and herbaceous cover were negatively correlated with axis 1 and approximately defined a "savanna" gradient (Fig. 4).

AVIAN OCCUPANCY PATTERNS

In addition to the five oak savanna affiliates, we identified several other birds predicted to occupy oak savanna at higher frequencies than the other habitats, though not significantly so: the American Kestrel (*Falco sparverius*), Mourning Dove (*Zenaida macroura*), Rock Wren (*Salpinctes obsoletus*), European Starling (*Sturnus vulgaris*), and House Finch (*Haemorhous mexicanus*). Six species, the White-tailed Kite (*Elanus leucurus*), Rufous-crowned Sparrow (*Aimophila ruficeps*, southern study area), Grasshopper Sparrow (*Ammodramus savannarum*), Yellow-billed Magpie, Phainopepla (*Phainopepla nitens*, southern study area), and Lawrence's Goldfinch (*Spinus lawrencei*) were uncommon during our study, so we did not analyze their occupancy by sample plot. Yet these species were detected only in oak savanna–grass or oak savanna–shrub (Phainopepla) habitats. The Western Scrub-Jay (*Aphelocoma californica*), Bewick's Wren (*Thryomanes bewickii*), Wrentit (*Chamaea fasciata*), Orange-crowned Warbler (*Oreothlypis celata*), California Towhee (*Pipilo crissalis*), and Spotted Towhee were predicted to occupy oak savanna–shrub and montane hardwood at significantly higher frequencies than oak savanna–grass and oak woodland (Table 4). The only species predicted to occupy oak woodland at frequencies significantly higher than the other habitats was the Brown-headed Cowbird (*Molothrus ater, Table 4)*.

The five oak savanna affiliates were all negatively related to hardwood and shrub cover and positively related to herbaceous cover and average tree dbh (Table 5, Fig. 5). Hardwood cover was selected as the habitat characteristic most strongly influencing sample-plot occupancy by the Western Bluebird and Lark Sparrow, whereas, shrub cover was the most influential for explaining Western Meadowlark occupancy. Occupancy by the Western Kingbird and Bullock's Oriole was best explained by herbaceous cover and the average tree dbh, respectively (Table 5).

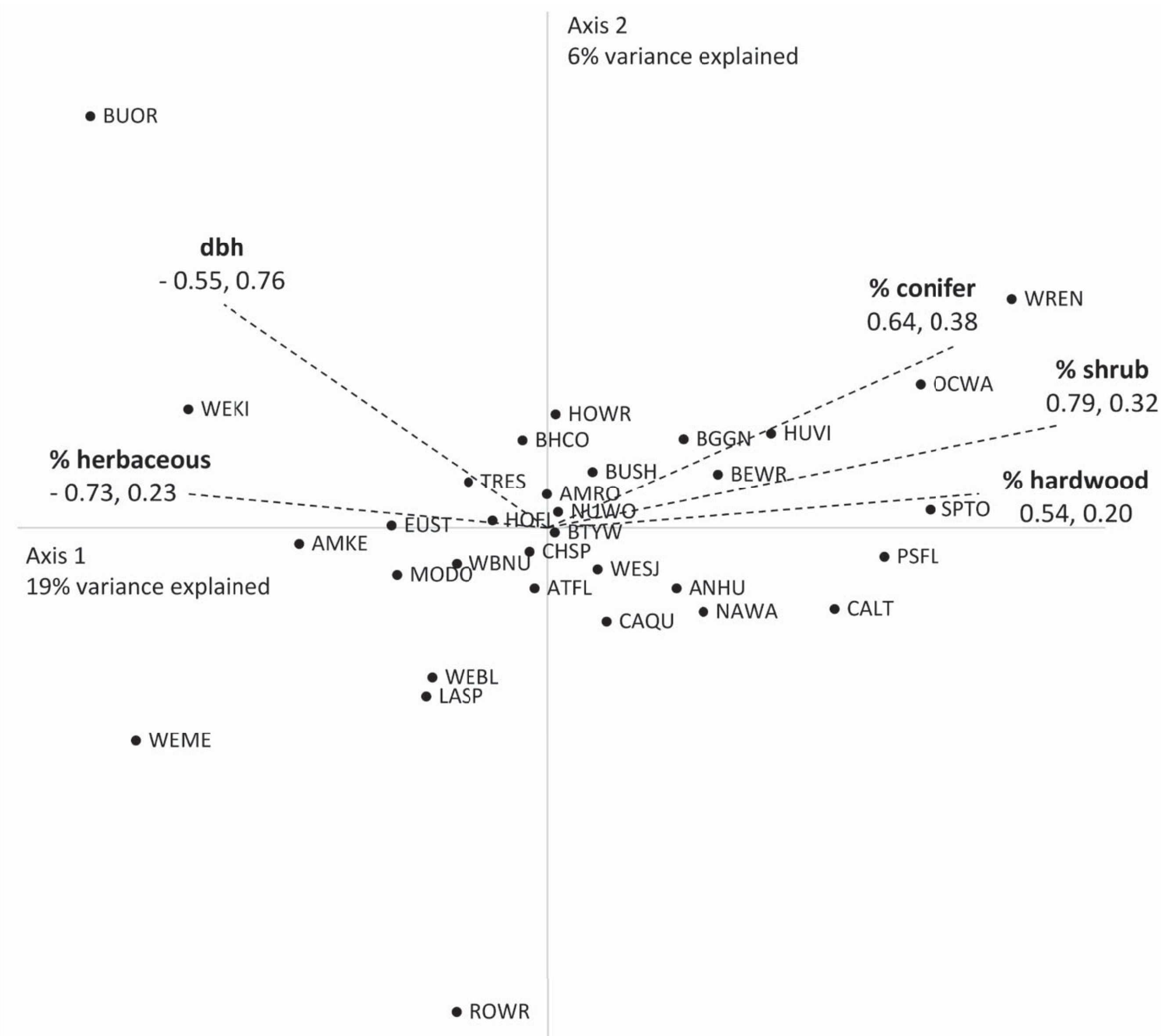

FIGURE 4. Two-dimensional canonical correspondence analysis of patterns of occupancy of sample plots predicted for 32 bird species relative to five habitat characteristics: hardwood, conifer, shrub, and herbaceous cover, and the average diameter at breast height of trees (dbh). Dotted lines represent intra-set correlations of habitat characteristics with axis 1 (first number) and 2 (second number) (ter Braak 1986). See Table 2 for definitions of four-letter codes.

DISCUSSION

Our findings of strong differences in avian communities by habitat as well as in the *occupancy patterns of several species of management and conservation concern suggest that* California oak savanna supports an assemblage of breeding birds distinct from communities in other oak habitats. We found that heterogeneity in shrub cover most strongly influences the avian communities of oak habitats of the Sierra Nevada foothills. Shrub-dominated habitats support diverse avian communities, and some species of management and conservation concern in California oak habitats are strongly associated with shrub cover (California Partners in Flight 2002). However, California oak savanna is distinct because of habitat characteristics such as expansive grasslands and open groves of large trees, which are critical for several breeding birds and are not found in other habitat types. Our results illuminate the need for careful management of shrub cover for California oak savanna to be maintained as important bird habitat.

TABLE 4. Average derived occupancy estimate (ψ) for 32 bird species by four habitats in the Sierra Nevada foothills. Species with same superscript letter do not differ significantly by habitat (Kruskal–Wallis test with nonparametric multiple comparisons procedure based on relative contrasts effects, type Tukey, with Bonferroni adjusted *P*-value: 0.05/6 = 0.008).

Species	Oak savanna–grass	Oak savanna–shrub	Montane hardwood	Oak woodland
American Kestrel	0.15	0.21	0.07	0.07
California Quail	0.59	0.71	0.68	0.50
Mourning Dove	0.69	0.50	0.47	0.43
Anna's Hummingbird	0.67^{A}	0.92^{B}	0.88^{AB}	0.74^{AB}
Nuttall's Woodpecker	0.86	0.87	0.86	0.90
Pacific-slope Flycatcher	0.07	0.10	0.19	0.02
Ash-throated Flycatcher	0.98	1	0.89	0.96
Western Kingbird	0.73^{A}	0.25^{B}	0.12^{B}	0.12^{B}
Hutton's Vireo	0.36^{A}	0.32^{A}	0.82^{B}	0.49^{AB}
Western Scrub-jay	0.82^{A}	1^{B}	0.98^{B}	0.71^{A}
Tree Swallow	0.48	0.43	0.38	0.41
Bushtit	0.77^{A}	0.90^{B}	1^{B}	0.91^{B}
White-breasted Nuthatch	1^{A}	0.71^{B}	1^{A}	0.87^{AB}
Rock Wren	0.32	0.22	0.09	0.09
Bewick's Wren	0.44^{A}	0.94^{B}	0.88^{B}	0.36^{A}
House Wren	0.64	0.57	0.78	0.45
Blue-gray Gnatcatcher	0.44^{A}	0.74^{B}	0.78^{B}	0.54^{AB}
Western Bluebird	0.90^{A}	0.86^{A}	0.46^{B}	0.53^{B}
American Robin	0.92	0.83	0.93	0.85
Wrentit	0.04^{A}	0.33^{BC}	0.76^{C}	0.14^{AB}
European Starling	0.90^{A}	0.54^{B}	0.51^{B}	0.65^{AB}
Orange-crowned Warbler	0.21^{A}	0.60^{B}	0.93^{B}	0.40^{A}
Nashville Warbler	0.19	0.31	0.26	0.11
Black-throated Gray Warbler	0.82	0.76	0.84	0.78
Spotted Towhee	0.14^{A}	0.71^{B}	0.93^{B}	0.15^{A}
California Towhee	0.15^{A}	0.52^{B}	0.49^{B}	0.12^{A}
Chipping Sparrow	0.88	0.78	0.80	0.81
Lark Sparrow	0.93^{A}	0.94^{A}	0.46^{B}	0.35^{B}
Western Meadowlark	0.79^{A}	0.10^{B}	0.02^{B}	0.02^{B}
Brown-headed Cowbird	0.35^{B}	0.25^{B}	0.44^{B}	0.77^{A}
Bullock's Oriole	0.41^{A}	0.03^{B}	0.03^{B}	0.03^{B}
House Finch	0.73^{A}	0.84^{A}	0.67^{AB}	0.39^{B}

Since Euro-American settlement, California oak savanna has undergone structural and compositional changes (Allen-Diaz et al. 1999). Fire suppression leads to encroachment of shrubs and trees, affecting birds associated with savanna (Purcell and Stephens 2006). Another concern is the reduction of blue oak through lack of recruitment of seedlings (Mensing 1992). Factors influencing recruitment include changes in land use (Dunwiddie et al. 2011), overgrazing and foraging by livestock (Sampson and Jesperson 1963) and wild herbivores (*Rooney 2001)*, and competitive exclusion by aggressive non-native plant species (Keeley et al. 2003). While we did not study the effects of fire suppression or lack of oak recruitment directly, our results documented strong differences in the avian community among habitats that differ in characteristics known to be affected by the aforementioned factors. Thus further reduction, or successional changes, of California oak savanna will likely result in lower habitat quality for birds associated with a sparse canopy.

Our finding that shrub cover is the most influential habitat characteristic shaping avian communities in our study region is paralleled by other studies in similar systems. In the American Midwest, bird species richness was highest in oak savanna with shrub cover (Grundel and Pavlovic

TABLE 5. Model-selection rankings for occupancy (ψ) of five bird species as a function of four habitat characteristics hypothesized to influence habitat use.

Species and model	ΔAIC_c[a]	w_i[b]	K[c]	Beta ψ[d]
Western Kingbird				
ψ(herbaceous),*p*(survey)	0	0.95	5	+
ψ(hardwood),*p*(survey)	6.09	0.04	5	–
ψ(shrub),*p*(survey)	10.10	0.01	5	–
ψ(dbh),*p*(survey)	11.03	0	5	+
ψ(.),*p*(survey)	20.81	0	4	
Western Bluebird				
ψ(hardwood),*p*(.)	0	1	3	–
ψ(shrub),*p*(.)	11.52	0	3	–
ψ(herbaceous),*p*(.)	15.95	0	3	+[e]
ψ(.),*p*(.)	15.78	0	2	
ψ(dbh),*p*(.)	18.01	0	3	+[e]
Lark Sparrow				
ψ(hardwood),*p*(.)	0	0.95	3	–
ψ(shrub),*p*(.)	6.35	0.04	3	–
ψ(.),*p*(.)	11.38	0	2	
ψ(herbaceous),*p*(.)	11.94	0	3	+
ψ(dbh),*p*(.)	13.53	0	3	+[e]
Western Meadowlark				
ψ(shrub),*p*(.)	0	0.92	3	–
ψ(hardwood),*p*(.)	4.82	0.08	3	–
ψ(herbaceous),*p*(.)	15.73	0	3	+
ψ(dbh),*p*(.)	17.63	0	3	+
ψ(.),*p*(.)	18.68	0	2	
Bullock's Oriole[f]				
ψ(dbh),*p*(.)	0	1	3	+
ψ(shrub),*p*(.)	24.31	0	3	–[e]
ψ(hardwood),*p*(.)	26.71	0	3	–
ψ(.),*p*(.)	34.71	0	2	

[a]Measure of a model's importance, corrected for sample size, relative to the best model; values <2 indicate a competitive model.
[b]AIC_c model weight.
[c]Number of parameters included in model
[d]Direction of occupancy coefficient direction for univariate models.
[e]Coefficient estimate overlaps zero thus indicating less model support.
[f]Percent herbaceous cover not displayed for Bullock's Oriole because model failed to converge.

2007). In an oak savanna mosaic in Wisconsin, shrub-associated birds occupy habitats that are different in tree-canopy cover but not in shrub cover (Wood et al. 2011). In Illinois, 11 of 31 bird species were more common in restored oak savanna than in closed-canopy forest (Brawn 2006). Some species, such as the Summer Tanager (*Piranga rubra*), appear to respond to differences in tree-canopy cover while others, such as the Indigo Bunting (*Passerina cyanea*) and Northern Bobwhite (*Colinus virginianus*), respond to differences in shrub cover between restored oak savanna and closed forest. In an African savanna, Sirami et al. (2009) attributed large changes in the savanna avian community to shrub encroachment, and, without management, several bird species disappear locally.

We extend the findings from Africa (Sirami et al. 2009) and the American Midwest (Brawn 2006, Grundel and Pavlovic 2007, Wood et al. 2011) to the foothills of the Sierra Nevada. Our results suggest avian communities of California oak savanna will be altered by shrub encroachment. As in other savannas elsewhere, in California oak savanna we found there appear to be thresholds for occupancy of savanna-affiliated birds based on tree, shrub, and herbaceous cover. Even with modest encroachment of shrubs and trees, occupancy of savanna-affiliated birds declines greatly. For example, in our study area, shrub encroachment reduces nesting habitat for the Western Kingbird and Western Bluebird, which require open areas with little shrub cover (Purcell and Stephens 2006). In areas of extremely high shrub density, local extirpation of these and other shrub-sensitive species is likely (Altman 2011). These results illuminate the need for shrub encroachment to be managed for California oak savanna to be maintained as important bird habitat.

A central goal for management of California oak habitats is to "prioritize … a diversity of oak woodland types" (California Partners in Flight 2002). Yet the lack of information about the avian community of California oak savanna has left a critical gap in knowledge regarding conservation of this subset of oak habitat. Our results highlight that birds breeding in the Sierra Nevada perceive oak savanna as unique habitat. Furthermore, we identified how species of management and conservation concern affiliated with oak savanna respond to characteristics of the oak habitats of the Sierra Nevada foothills. Our findings suggest that conservation and management of the region's oak habitats should explicitly include California oak savanna with a sparse canopy and grass- and forb-dominated understory.

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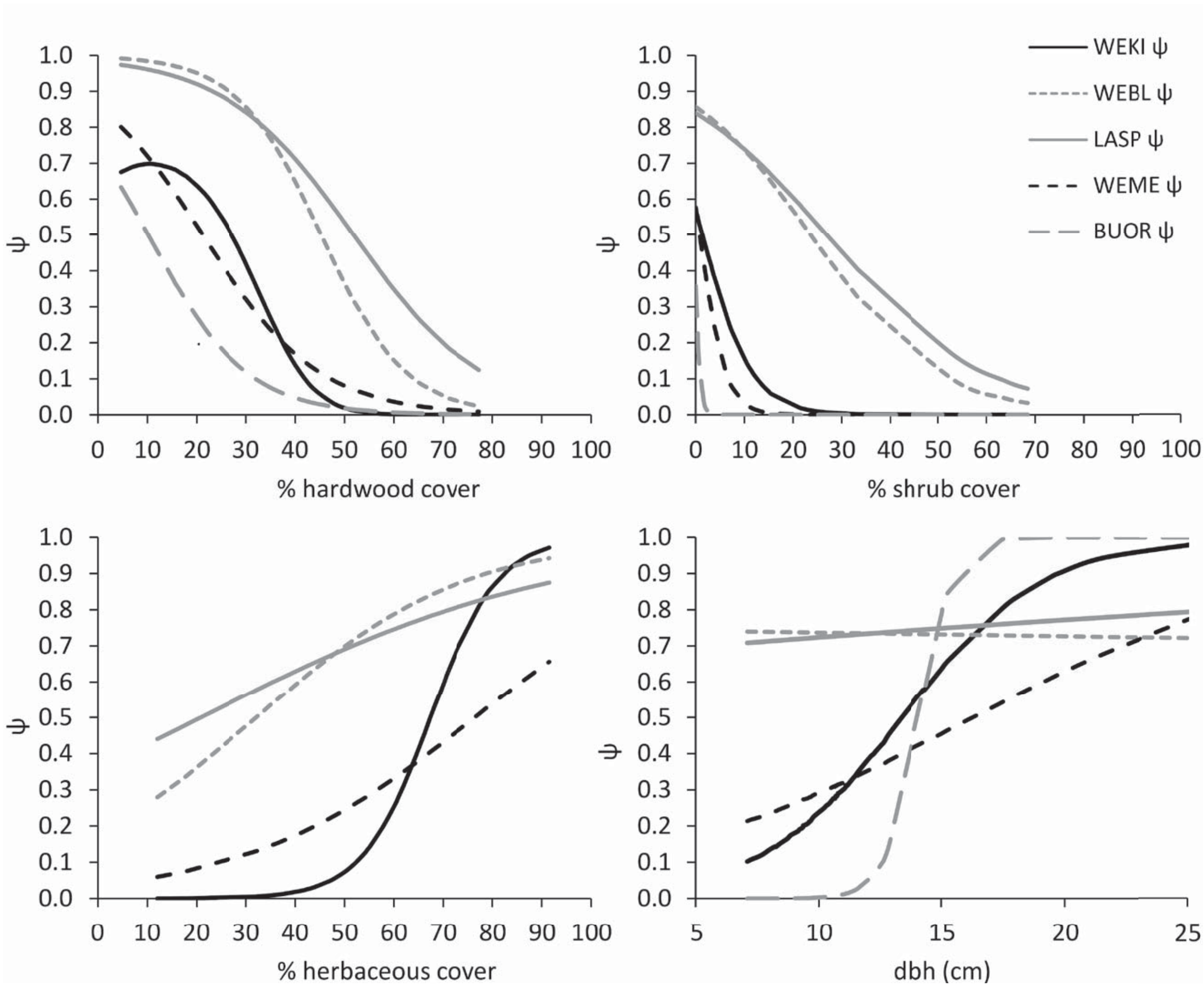

FIGURE 5. Relationships of predicted occupancy (ψ) for five bird species with four habitat characteristics. See Table 2 for definitions of four-letter codes. Bullock's Oriole not displayed for herbaceous cover because the model failed to converge.

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