

BIRD ASSEMBLAGES IN PATCHY WOODLANDS: MODELING THE EFFECTS OF EDGE AND MATRIX HABITATS

THOMAS D. SISK,¹ NICK M. HADDAD,² AND PAUL R. EHRLICH

*Center for Conservation Biology, Department of Biological Sciences, Stanford University,
Stanford, California 94305 USA*

Abstract. As habitats become more fragmented, understanding landscape-level effects on habitat quality becomes increasingly important. These effects include factors intrinsic to the habitat fragments, such as vegetation cover and structure, and extrinsic factors, such as the modifying influences of surrounding (matrix) habitats. We develop a spatial model, the Effective Area Model (EAM), that predicts the effects of matrix habitats on species abundances in habitat patches. Model predictions are based on two sets of parameters: measures of species abundances at various distances from habitat edges (“edge responses”) and measures of the size and shape of the habitat fragments. We test model predictions for bird assemblages occupying fragmented habitats in central coastal California. Predictions of the relative abundances of birds, based on results from previous studies at nearby sites, are made for six small (<3 ha) patches of oak woodland habitat, three surrounded by grassland and three surrounded by chaparral. Results from field studies of these patches show significant differences between the two groups, indicating that the type of habitat surrounding a patch influences the composition and structure of the bird assemblage it supports. The rank order of species abundances correlated more closely with predictions of the EAM than with those of a null model that did not account for edge and matrix effects. The EAM is an improvement over models that do not account for the influence of surrounding habitats on the distribution and abundance of animals in small habitat patches, and over those that assume a consistent response, for a given species or taxon, at all types of edges. This approach may prove useful in attempts to understand and predict the effects of habitat fragmentation and restoration on the organization of animal assemblages.

Key words: *bird assemblages; California; edge effects; habitat fragmentation; landscape heterogeneity; matrix habitats; population density; spatial modeling.*

INTRODUCTION

Conservation science has focused intensely on the implications of habitat fragmentation and the increasing isolation of the remaining patches (Diamond 1975, Simberloff and Abele 1976, Terborgh 1976, Ambuel and Temple 1983, Harris 1984, Robinson et al. 1992, Herkert 1994, Robinson et al. 1995). This attention is appropriate: in many areas, agriculture and development have made a patchwork out of previously continuous native habitat, creating landscape mosaics composed of open fields, secondary vegetation, and patches of remnant habitat (Wilcox and Murphy 1985, Wilcove et al. 1986, Franklin and Forman 1987, Saunders et al. 1987). Despite interest in the ability of these patches to sustain viable populations of native species, relatively little work has focused on the effects of the modified environment surrounding the remnant patches (Andr n 1992, Pearson 1993, Mills 1995).

Manuscript received 22 January 1996; revised 7 January 1997; accepted 15 January 1997; final version received 5 February 1997.

¹ Present address: Environmental Sciences, Northern Arizona University, Flagstaff, Arizona 86011-5694 USA.

² Present address: Institute of Ecology, University of Georgia, Athens, Georgia 30602-2202 USA.

Studies of animal assemblages in patches have focused on the importance of patch area and distance from sources of potential colonists. Species diversity in these habitat patches is known to depend, in part, on rates of immigration and emigration (MacArthur and Wilson 1967, Diamond and May 1977, Fahrig 1994), as well as on vegetational, topographic, and microclimatic diversity (Galli et al. 1976, Wilcove et al. 1986, Wiens 1989, Fraver 1994). Research on habitat patches in isolation from the surrounding landscape, however, has highlighted the shortcomings of applied island biogeography (Simberloff and Abele 1976, Saunders et al. 1991, Wiens 1994). Increasingly, ecologists are focusing on population dynamics and community structure in heterogeneous environments (Danielson 1992, Pulliam et al. 1992, McKelvey et al. 1993) and examining environmental influences from outside the patch, including the availability of resources, and exposure to sun and wind (Ranney et al. 1981, Saunders et al. 1991, Matlack 1993). These studies are becoming increasingly relevant as animal populations and natural resources are managed as complex and continuously changing landscapes (Reichman and Pulliam 1996).

One framework for understanding the effects of landscape heterogeneity on individual species is to study

their response to habitat edges (Giles 1978, Dasmann 1981, Harris 1988, Reese and Ratti 1988, Noss 1991). Studies of edge effects constitute some of the earliest attempts by ecologists to understand ecological processes at the landscape scale (e.g., Leopold 1933, Lay 1938). Many studies have shown that certain species reach their highest or lowest abundances at particular habitat edges (e.g., Kendeigh 1944, Johnston 1947, Whitcomb et al. 1981, Kroodsma 1984, Lynch and Whigham 1984). Species that are encountered more commonly near the edge are often termed "edge species" (e.g., Johnson 1975, Giles 1978, Reese and Ratti 1988), and those whose densities are low near the edge are considered to be habitat-interior species (e.g., Brittingham and Temple 1983, Wilcove et al. 1986, Thompson 1993). A more quantitative approach to understanding how species respond to habitat edges involves measurement of a species-specific edge response (Noss 1991, Sisk 1992), defined as the pattern of change in population density at incremental distances from the habitat edge. Despite broad recognition of the influence of edges on insular biota, consideration of edge effects has not been demonstrated to be particularly useful in attempts to understand the organization of animal assemblages in heterogeneous landscapes. A quantitative, predictive approach is needed before the concept can be effectively applied to solve problems of reserve design and management.

Here we develop an empirically based spatial model that incorporates patch size and shape, composition of matrix habitats, and species-specific edge responses to predict the organization of animal assemblages occupying heterogeneous landscapes. Field tests are used to evaluate the model and to compare it with a null model that does not take into account the effects of edge and matrix habitats. Drawing on the models and our empirical results, we address two related questions: (1) how does the habitat surrounding a given patch influence the composition and organization of the bird assemblage it supports; and (2) how consistent are the population-level responses of birds at different edges of similar types?

We hypothesize that similar patches, surrounded by habitats that differ in vegetation structure and species composition, will support different bird assemblages, while patches surrounded by the same habitat will support similar bird assemblages. To test this hypothesis, we compare the avian assemblages in isolated patches of oak woodland habitat surrounded by one of two habitat types—grassland or chaparral. These two matrix habitats are expansive and continuous in the study areas, broken only by the oak patches. If bird assemblages in oak patches are not influenced by the matrix habitat, then the assemblages occupying patches surrounded by different matrix habitats would be expected to differ no more than those surrounded by the same matrix habitat.

The Effective Area Model

Ecologists and wildlife managers have often assumed that animals will show consistent, characteristic patterns of habitat selection at edges, even when the adjoining habitat differs in vegetation structure and/or species composition. Implicit in this assumption is the idea that edges of all types share some intrinsic qualities, and that their influence on the distribution of organisms and the composition of assemblages is similar. There is little evidence to support these views. Very few studies have measured population-level responses of organisms at even one type of edge, making it impossible to determine whether the response detected is characteristic of the species' response to edges in general. Studies that have measured edge responses for entire assemblages or communities find considerable variation among species (Noss 1991, Sisk and Margules 1993). Some occur in greater abundance near edges (hereafter called "edge-exploiters"), some are less abundant or absent ("edge-avoiders"), and some species are equally abundant at the edge and in the interior of a habitat patch ("edge-neutral").

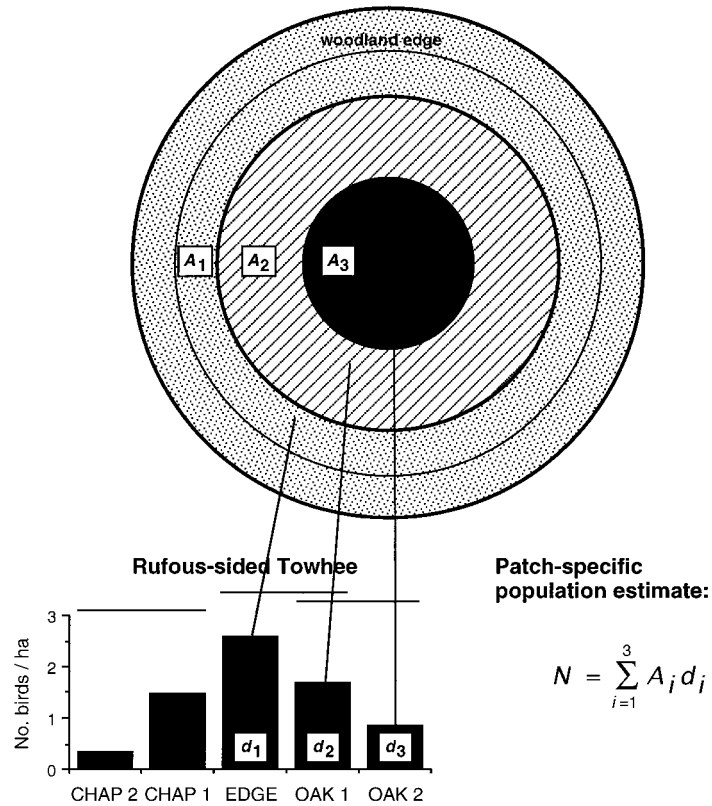
To test the consistency of the responses of individual species to edges and thus the influence of matrix habitat on animal abundances in habitat patches, we developed an empirically based spatial model that we call the Effective Area Model (EAM). The EAM requires two types of input: the edge response of each species, and a landscape map. The edge responses are determined for each species from independent field data, and described by a plot of abundance against distance from the edge (see Fig. 1 for an example). Landscape maps characterize the size, shape, and habitat type of each patch in the study area and the matrix habitat(s) surrounding them.

The EAM predicts species abundances in a habitat fragment by projecting density estimates from the edge response curves onto digitized maps of each of the habitat patches. Each patch is divided into subregions based on distance from the edge. The boundaries of these subregions correspond to the distance intervals used for field surveys of species abundances, which are used to define species-specific edge responses. Multiplying the area of each subregion by the corresponding estimate of population density, and then summing the products for all subregions, gives a predicted population size for the species in a particular patch (Fig. 1). Model predictions can be represented by the equation

$$\text{number of individuals} = \sum_1^n A_i d_i$$

where A_i is the area of the patch that is contained within subregion i , d_i is the density estimate for subregion i , and n is the number of subregions in the patch. This approach relaxes assumptions of previous "core-area" models that employed a fixed edge effect for all species

FIG. 1. Schematic representation of the Effective Area Model. The edge response measured for each species (here represented by the bar graph for the Rufous-sided Towhee) is used to estimate population density in different subregions of a particular habitat patch. Subregions are defined according to their distance from the habitat edge; in this example CHAP designates chaparral habitat, and OAK designates oak woodland. Summing the predictions for each subregion gives an abundance estimate for the patch.



when predicting animal abundances in habitat fragments (Temple 1986, Temple and Cary 1988, Laurance and Yensen 1991). The EAM incorporates variability in edge effects among species and among different edge types (i.e., where patches are embedded in different matrix habitats).

Several practical considerations influence how the EAM is applied. The resolution of the edge responses determines the spatial resolution of the model. The layout of transects and selection of survey techniques should be scaled to the life history characteristics (e.g., territory size, vagility) of the taxa being studied. Logistic and methodological limitations often constrain sampling designs somewhat, but the flexibility in quantifying edge responses allows the EAM to be applied to animals operating at different spatial scales.

We characterize species-specific edge responses and develop the EAM using discrete distance intervals. A different approach involves fitting a continuous weighting function to the field data, and applying this equation to the landscape maps. We explored both approaches, and found the discrete model to be most appropriate. Identification of a continuous function describing edge responses is theoretically satisfying, but in this case it was not defensible. Even the “best fits” smoothed actual responses considerably, and discrimination between first and higher order functions was seldom straightforward. The discrete approach employs field

data directly in the weighting procedure, and can be readily applied by managers (Sisk and Margules 1993).

To test the accuracy of this model, we used it to predict the relative abundances of breeding birds in the small patches of oak woodland described above. Small patches were chosen because they have a high proportion of edge relative to the area of interior habitat. This dictates that edge responses will have a large influence on the predictions of species abundances in each patch, providing a robust test of the generality of the empirically derived edge responses and the ability of the EAM to model the influence of matrix habitats on bird assemblages. Edge responses were determined for all breeding bird species in a previous study.

A second set of predictions was made using a null model based on the assumption that oak woodland habitat within each of the focal patches was homogeneous and unaffected by the matrix habitat. These predictions were generated using estimates of bird abundances in the interior of large tracts of oak woodland habitat (Sisk and Margules 1993). The area of the small woodland patches was multiplied by the mean density of each bird species in interior oak woodland. The products are the predicted abundances of each species in each habitat patch, disregarding edge and matrix effects. This represents a typical approach to estimating species abundances based on habitat associations, and is used here as a benchmark against which the EAM is compared.

FIELD METHODS

Study system

The foothills of the Santa Cruz Mountains in central coastal California support a landscape characterized by a mix of grassland, chaparral, and oak woodland habitats. Frequently, these habitats form abrupt edges. From an initial pool of 20 potential sites identified from aerial photographs, six suitable oak woodland patches were selected in San Mateo County: three that are surrounded by chaparral at the Jasper Ridge Biological Preserve, and three that are surrounded by grassland in adjacent foothills. No two patches in the same landscape were separated by <200 m or >500 m, and the two landscapes were ~4 km apart. Landscape composition precluded the selection of sites that were distributed randomly in space—patches surrounded by chaparral were closer to each other than they were to patches surrounded by grassland. This could confound comparisons between the two matrix types; however, it is inconsequential to the primary objective of the field study: comparison of the predictions of both the EAM and null model with the actual bird assemblages.

The selected patches had similar areas (mean \pm 1 SD = 1.62 \pm 0.25 ha), edge:area ratios (370 \pm 45 m/ha), and spatial configurations. Each was a discrete patch completely surrounded by either chaparral or grassland. Through the site selection process, we controlled (to the extent possible) for habitat structure and understory vegetation. However, the oak woodland component of the two landscapes differed slightly, as the understory of each patch included some species common to the surrounding habitat. All of the patches are part of the same range of foothills, and are close enough together to suggest that they draw from the same pool of potential bird species. All species treated in the EAM are abundant in suitable habitats throughout the region. The oak woodland patches, and the chaparral shrubland and nonnative grasslands surrounding them, are typical of the Santa Cruz Mountains (Munz 1959).

Measuring microclimate variables

Microclimatic measurements were taken prior to bird surveys on eight occasions to quantify the abiotic factors that may influence habitat selection by birds, allowing us to compare site characteristics for the different habitat patches. Measurements were taken at 10-m intervals along transects perpendicular to the edge, beginning at the center of the oak woodland patch and continuing 30 m into the matrix habitat. Air temperature was measured at 1 m above ground level with a digital thermometer (Keithley 872). Light intensity was measured at 2 m above ground level with a video light meter (FCL-150, Shepard Video, New York, New York). Relative humidity was measured at 1 m above the ground using a wet-bulb/dry-bulb sling psychrometer.

Bird surveys

Edge responses, the basic input data for the EAM, were determined for all common breeding birds in an earlier study at nearby sites (Sisk and Margules 1993). Transects were established perpendicular to edges between oak woodland and chaparral, and between oak woodland and grassland. Unlike the current study, the relatively straight edges separated large (>100 ha), continuous tracts of oak woodland from chaparral or grassland. Birds were surveyed repeatedly at 36 fixed points along eight parallel transects. Density estimates (variable circular plot method [Reynolds et al. 1980, DeSante 1981]) were determined for all species at the edge and at points 100 and 200 m into the oak woodland, chaparral, and grassland habitats. These distance intervals were selected after consideration of life history characteristics and methodological limitations. We believe these intervals are appropriate for characterizing the edge responses of many passerine birds, whose territory sizes typically are \geq 1 ha, and whose vagility makes finer scale resolution of edge responses problematic. Sampling units were circles with radii of 35–50 m, depending on species, so smaller intervals would have resulted in an unacceptable number of double counts. Some species, such as hummingbirds, may be responding to edges at a finer scale, but methodological constraints precluded greater resolution. For descriptive purposes, we classified all bird species as being either edge-exploiters, edge-avoiders, or edge-neutral at each edge type (see Table 1 for summary). All input data, for both the EAM and null models, consisted of density estimates from the species-specific edge responses.

Birds were surveyed in the oak woodland patches during the 1991 breeding season, blind to the predictions of the model. A single observer (N. M. Haddad), who was not involved in the modeling effort, conducted 60 point counts at each of the six oak woodland patches over 15 site visits between 5 April and 17 May. Within each patch, four survey points were established such that each point was 15 m from the edge and at least 80 m from any other point, thus minimizing double-counting. Precise locations were mapped for each individual located by site or sound. Territorial males were distinguished from other individuals and used to identify the species breeding in or near each patch (Franzreb 1981). Surveys occurred between 0.5 h before and 3 h after sunrise. No surveys took place on days that were rainy or unusually windy.

Analysis

To determine the effect of matrix habitats on bird assemblages in the oak woodland patches, we examined differences in species richness, diversity (Shannon's index), and species composition among patches. We calculated coefficients of dissimilarity among bird assemblages in each patch, then made pairwise compar-

TABLE 1. Edge responses and rank orders of bird abundances based on two sets of model predictions and field surveys.

Species	Chaparral matrix				Grassland matrix			
	Edge response	EAM	Null	Field	Edge response	EAM	Null	Field
CAQU	neutral	20	21	15	exploiter	4	11	4
MODO	neutral	13	13	12	exploiter	15	8	7
ALHU	avoider	22	22	16	not present			
ANHU	avoider	4	7	10	neutral	5	7	10
NUWO	exploiter	14	14	22	exploiter	16	21	14
NOFL	exploiter	21	22	16	exploiter	25	14	18
ATFL	exploiter	16	22	16	exploiter	10	14	17
WWPW	avoider	24	17	22	neutral	26	25	23
VGSW	not present				exploiter	20	23	23
SCJA	exploiter	3	15	1	neutral	9	19	1
COBU	avoider	18	2	5	exploiter	2	22	6
BEWR	neutral	2	4	13	neutral	6	14	11
BGGN	neutral	7	5	7	neutral	8	2	12
WEBL	not present				neutral	19	13	21
NOMO	not present				exploiter	18	24	8
CATH	neutral	14	19	7	not present			
WREN	exploiter	5	16	7	exploiter	7	25	23
PLTI	neutral	8	9	3	avoider	14	1	5
CBCH	avoider	12	1	11	avoider	17	12	23
WBNU	exploiter	23	20	22	exploiter	23	17	16
EUST	not present				neutral	24	3	3
HUVI	exploiter	6	8	14	neutral	22	6	21
OCWA	neutral	19	11	2	avoider	21	8	18
RSTO	exploiter	1	5	5	neutral	11	10	9
CATO	exploiter	9	18	16	exploiter	3	5	2
DEJU	avoider	10	3	4	exploiter	1	3	18
PUFI	neutral	11	12	16	exploiter	13	17	15
LEGO	neutral	17	10	16	neutral	12	20	12

Notes: Definitions: Edge responses—empirically derived classification of effects of habitat edges on species abundance; EAM—Effective Area Model; Null—null model that does not take edge or matrix habitat into account; Field—results of 15 surveys in oak woodland patches surrounded by either grassland or chaparral. Species are identified by their American Ornithologists' Union abbreviations (see Appendix).

isons using the chord distance method (Able and Noon 1976, Ludwig and Reynolds 1988). We used cluster analysis to compare coefficients of dissimilarity and to identify similarities in avian assemblages occupying different patches. The cluster algorithm identifies the most similar patches, groups them, and then repeats the process until cluster distances are determined for all patches or groups of patches (Ludwig and Reynolds 1988). Euclidean distances between patches reflect the degree of similarity among bird assemblages occupying each patch, and serve as measures of the influence of matrix habitats on species composition.

To compare the predictions of the EAM and the null model with field results, we ranked species according to their relative abundance in each landscape. The available empirical data permitted ranking of 26 species in the grassland-oak woodland landscape and 24 species in the chaparral-oak woodland landscape. We used the independent predictions generated by the EAM and null models to rank species according to their expected relative abundances, given the assumptions for each model. We then tested these expected rank orders for correlation with the rank order obtained from the field surveys using Kendall's τ as a test statistic (Sokal and Rohlf 1981).

Finally, to identify some of the population-level differences underlying the observed differences in bird

assemblages, we examined the abundances of individual species in the two patch types. Inspection of survey results revealed dramatic differences for many species. To quantify differences among patches surrounded by different matrix habitats, we computed *t* statistics, following square-root transformation of point counts to correct for truncation of normal distributions caused by frequent counts of zero for many species (Sokal and Rohlf 1981). Significance tests of these results must be viewed with caution, however, because the patches are not spatially independent replicates: patches surrounded by the same matrix habitat were closer to each other than they were to other patches, introducing the possibility of spatial autocorrelation. Nevertheless, the results provide a more detailed perspective on the differences in the organization of bird assemblages in each patch, and they identify species thought to be most and least affected by edge and matrix habitats.

RESULTS

Microclimate

The most dramatic changes in environmental conditions in both patch types occurred within 25 m of the habitat edge (Fig. 2). Trends in the values for microclimatic variables from the center to the edge of the oak woodland patches did not differ significantly be-

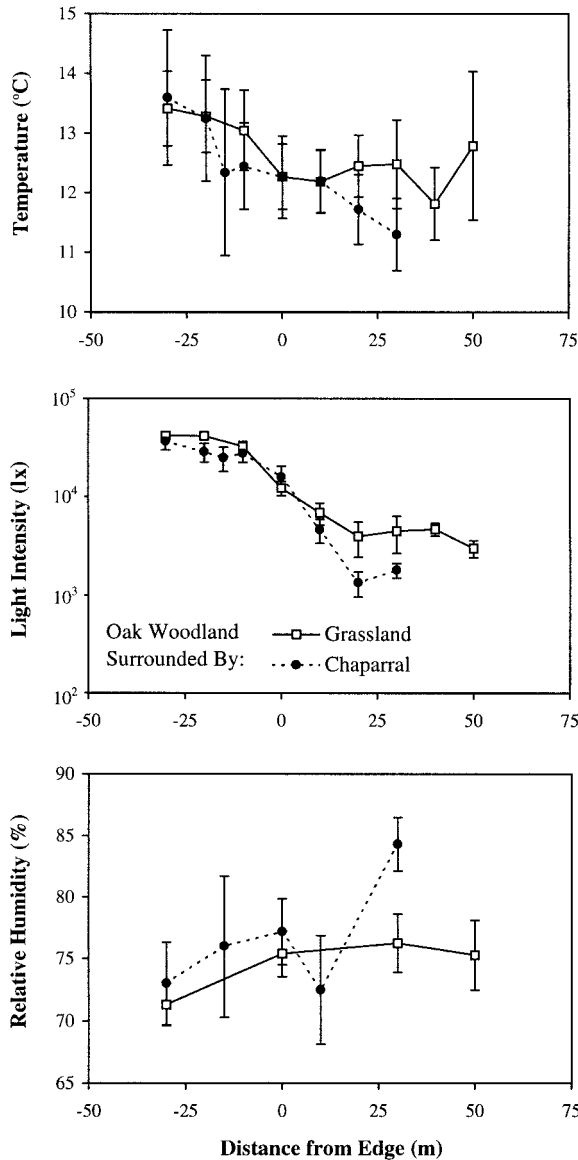


FIG. 2. Microclimatic variation across edges between oak woodland patches and two different matrix habitats, chaparral and grassland. Positive values indicate the distance from an edge into oak woodland; negative numbers indicate the distance into the matrix habitat. Bars represent standard errors of the means.

tween the two landscapes, with the exception of relative humidity, which was higher in patches surrounded by chaparral ($t = 2.63$; $P < 0.05$). Otherwise, mean rates for all variables were similar.

Bird assemblages

In the oak woodland patches surrounded by chaparral, 439 individuals representing 26 species were counted with an average (mean \pm 1 SD) of 20 ± 1.7 species in each patch. In the patches surrounded by grassland, 1189 individuals representing 44 species were detected, with an average of 32 ± 3.2 species in

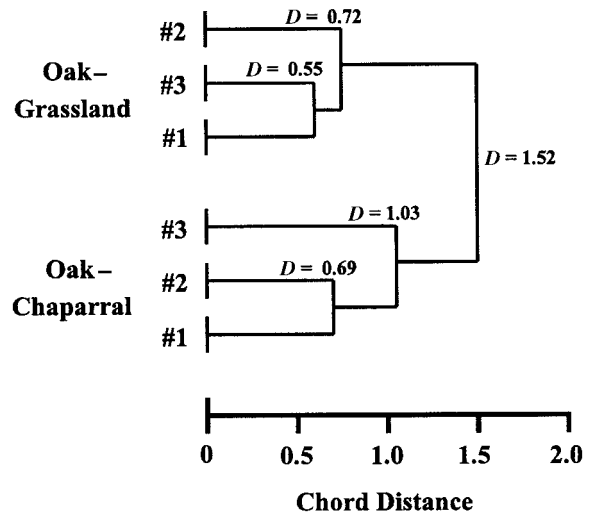


FIG. 3. Dendrogram showing the relationships among six oak woodland patches, three surrounded by grassland and three surrounded by chaparral, based on the similarity of their bird assemblages. D = Euclidean distance between patches or groups of patches (chord distance method).

each patch. Mean values for Shannon's index were 2.51 ± 0.07 in the patches surrounded by chaparral, and 2.90 ± 0.11 in patches surrounded by grassland. Both the number of species ($t = 2.13$; $P < 0.01$) and Shannon's index ($t = 2.13$; $P < 0.01$) differed significantly between patches surrounded by different matrices.

Indices of dissimilarity also show consistent differences among patches surrounded by different matrix habitats. The cluster analysis illustrates these differences by grouping the most similar patches (Fig. 3). Without exception, patches with the same matrix habitat formed closer groupings than patches with different matrices. The greatest Euclidean distance between patches surrounded by the same matrix habitat is shorter than the smallest distance between patches surrounded by different matrices (Fig. 3). However, no cluster distance was close to zero (the value signifying perfect overlap of species assemblages), indicating heterogeneity in species composition among like patches.

Testing model predictions

The primary objective of this study was to compare the accuracy of the EAM against a null model that ignored the effects of edge and matrix habitats. First, we examined the predictions of the EAM for patches surrounded by different matrix habitats to evaluate the model's sensitivity to the different responses recorded for many species at the different edge types. The rank order of species abundance predicted by the EAM for the patches surrounded by grassland showed no correlation with predictions for patches surrounded by chaparral (Kendall's $\tau = 0.090$; $P > 0.50$), suggesting that the variation in responses should have a profound effect on bird assemblages in the two landscapes. This was consistent with results from field surveys showing

TABLE 2. Correlation of actual and predicted rank orders of abundance for breeding birds occupying small patches of oak woodland habitat surrounded by different matrix habitats.

Habitat type	Number of species	EAM vs. survey results		Null model vs. survey results	
		τ	P	τ	P
Oak woodland islands in matrix of chaparral	24	0.393	<0.01	0.342	<0.05
Oak woodland islands in matrix of grassland	26	0.282	<0.05	0.228	>0.10

Note: Predictions of the Effective Area Model (EAM), developed in this paper, and those of a null model based on patch area alone are presented; τ = Kendall's coefficient of rank correlation (Sokal and Rohlf 1981).

significant differences in both species composition and relative abundances (Table 1).

For the three oak woodland patches surrounded by chaparral, results from both the EAM and the null model were significantly correlated with the rank order of species abundance detected in the field surveys. However, the EAM's predictions fit the empirical data better (Kendall's τ = 0.393; n = 24; P < 0.01) than do those

of the null model (τ = 0.342; n = 24; P < 0.05) (Table 2).

The EAM predictions for the oak woodland islands surrounded by grassland were also correlated with results from field surveys (τ = 0.285; n = 26; P < 0.05), whereas those of the null model were not significantly correlated with field data (τ = 0.228; n = 26; P > 0.10). Here, the EAM predictions were much more accurate than those of the null model, although the predictive ability of both techniques was lower for these patches than for those surrounded by chaparral.

Species-level comparisons

Comparison of the abundances of individual species in the two landscapes highlights the great disparity between bird assemblages in the otherwise similar oak woodland patches. Of the 26 species found in the patches surrounded by chaparral, 4 were absent from similar patches surrounded by grassland: Steller's Jay, Chestnut-backed Chickadee, Wrentit, and Anna's Hummingbird (Table 3; scientific names of all species are given in the Appendix). Half of the species (22/44) present in the oak woodland patches surrounded by grassland were not observed in the patches surrounded by chaparral, including three of the seven most abundant species: European Starling, Northern Mockingbird, and Red-winged Blackbird. Thirty-four species were sufficiently common to test the null hypothesis that their abundances did not differ among oak woodland patches surrounded by different matrix habitats. For 16 species (47%), this hypothesis was rejected (Table 3), significantly more than would be expected by chance alone (expected: $34 \times 0.05 = 1.7$; $\chi^2 = 49.96$ with 1 df; P < 0.001).

DISCUSSION

The influence of chaparral and grassland habitats on bird assemblages in oak woodland patches adds to a growing literature documenting the pervasive effects of matrix habitats on animal distributions in fragmented landscapes (e.g., Szaro and Jakle 1985, Pearson 1993, Fahrig 1994, Mills 1995). Patches surrounded by the same matrix habitat supported bird assemblages that were much more similar than patches surrounded by different habitats, both in species composition and in relative abundance. One source of the similarity among patches was the contribution, from both matrix habitats, of characteristic habitat specialists that were also en-

TABLE 3. Bird species in small patches of oak woodland and mean number of observations per survey (n = 15) in six oak woodland patches, three surrounded by grassland and three surrounded by chaparral.

Species	Chaparral matrix			Grassland matrix			t	P <
	1	2	3	1	2	3		
CAQU	0.2	0.0	0.1	2.3	0.5	1.2	3.18	0.05
MOD0	0.3	0.2	0.1	1.5	0.7	1.1	4.76	0.01
ANHU	0.3	0.1	0.9	0.4	0.6	1.3	1.13	NS
ACWO	0.0	0.0	0.0	1.1	0.5	0.3	5.49	0.01
NUWO	0.0	0.0	0.0	0.2	0.4	0.3	10.06	0.01
NOFL	0.1	0.0	0.0	0.0	0.1	0.1	0.53	NS
ATFL	0.0	0.1	0.0	0.1	0.1	0.1	2.61	0.10
WEFL	0.2	0.1	0.3	0.1	0.0	0.1	1.5	NS
STJA	1.1	0.9	0.0	0.0	0.0	0.0	1.99	NS
SCJA	3.2	1.1	0.9	2.0	1.5	1.8	0.22	NS
COBU	0.1	0.2	1.3	0.9	2.4	0.2	0.85	NS
BEWR	0.3	0.1	0.1	0.8	0.3	0.1	1.52	NS
BGGN	0.0	0.2	1.1	0.9	0.3	0.0	0.03	NS
AMRO	0.0	0.0	0.0	0.1	0.1	0.2	5.09	0.01
NOMO	0.0	0.0	0.0	0.3	0.5	1.2	5.21	0.01
CATH	0.7	0.4	0.5	0.1	0.3	0.0	2.41	0.10
CEDW	0.0	0.0	0.0	5.7	4.0	1.6	5.74	0.01
WREN	0.5	0.7	0.1	0.0	0.0	0.0	3.47	0.05
PLTI	0.5	1.1	0.9	1.5	0.7	1.7	1.43	NS
CBCH	0.6	0.1	0.1	0.0	0.0	0.0	2.5	0.10
WBNU	0.0	0.0	0.0	0.1	0.1	0.3	4.27	0.05
EUST	0.0	0.0	0.0	1.1	0.6	2.5	4.8	0.01
HUVI	0.1	0.0	0.3	0.1	0.0	0.0	1.18	NS
OCWA	0.7	0.5	2.8	0.1	0.1	0.0	2.55	0.10
TOWA	0.0	0.4	0.0	0.4	0.0	0.4	0.71	NS
YRWA	0.0	0.0	0.0	1.4	2.6	2.1	11.29	0.01
WIWA	0.3	0.3	0.3	0.2	0.3	0.6	0.63	NS
WETA	0.0	0.0	0.0	0.1	0.1	0.3	5.07	0.01
RSTO	0.9	0.2	0.5	0.9	0.7	0.3	0.53	NS
CATO	0.0	0.1	0.0	1.5	1.7	1.7	9.17	0.01
GCSP	0.3	0.2	0.0	4.3	1.9	2.5	4.99	0.01
DEJU	0.3	0.9	0.7	0.0	0.2	0.0	3.13	0.05
RWBL	0.0	0.0	0.0	2.7	0.3	1.5	3.67	0.05
BHCO	0.0	0.0	0.0	0.2	0.4	0.0	1.92	NS
PUFI	0.0	0.0	0.1	0.0	0.2	0.4	1.33	NS

Note: Differences in mean abundance for patches surrounded by different matrix habitats were compared with t tests for species detected more than five times. Species are identified by their American Ornithologists' Union abbreviations (see Appendix).

countered in oak woodland patches, presumably due to their proximity to their preferred habitats. Examples include the California Thrasher in chaparral and the California Quail in grassland. In addition, several oak woodland species were absent in patches surrounded by one matrix type and common in those surrounded by the other, and many more were present at different levels of abundance in patches surrounded by different matrix habitats (Table 3).

The observed differences between the bird assemblages might have resulted from factors intrinsic to the individual patches or from the effects of the surrounding habitats. The proximity of the six oak woodland islands studied (all were within 5 km of each other) and the local commonness of the species included in the analyses suggest that all patches drew from the same regional pool of bird species. Vegetation composition and structure were similar in all oak woodland patches, and microclimatic measurements showed similar trends for all variables within the patches and across the oak woodland–matrix edges (Fig. 2). Together, these results indicate that factors intrinsic to the patches were not driving the observed patterns of bird abundance, and that matrix habitats influenced within-patch habitat quality.

Many of these matrix effects are manifested as edge effects. Studies of animal abundances in heterogeneous landscapes have documented consistent trends in abundance near edges (Noss 1991, Sisk and Margules 1993, Mills 1995), and support the idea that different portions of a habitat patch may be of disparate value to many bird species, depending on distance from the edge. Species that utilize both patch and matrix habitats are likely to be more abundant near edges, and therefore relatively common in small patches with high edge-to-area ratios. In contrast, edge-avoiding species may find little or no suitable habitat in patches where the influence of the edge reaches the center of the patch.

Results from this study demonstrate that these factors do play an important role in determining the organization of bird assemblages in patchy habitats, and that these effects can be quantified and used in a predictive framework. The area of a habitat patch that is suitable for a particular species is a function of the organism's sensitivity to edge effects, and the size and shape of the patch. The EAM offers a tool for predicting the effective habitat area for multiple species in heterogeneous landscapes.

The agreement between the predictions of the EAM and results of field surveys in each group of patches indicates that knowledge of species-specific edge responses can provide a reasonably good prediction of how each species will respond in landscapes of differing composition and spatial structure. When the EAM was applied to the study landscapes, the predicted relative abundances of bird species occupying the two groups of habitat patches differed significantly, reflecting the model's sensitivity to variations in population-

level responses to the different edge types. A species' response to edges between grassland and oak woodland often differs greatly from its response to edges between oak woodland and chaparral, but its response to different grassland–woodland edges appears to be relatively consistent.

The incorporation of empirically derived edge responses for each species into a predictive model gives the EAM several advantages over earlier habitat-based models of edge effects. First, it considers all members of the assemblage, not only the habitat-interior or edge-avoiding species that are the focus of most models dealing with fragmented habitats (Temple 1986, Temple and Cary 1988). The EAM can be used to predict the densities of species of special concern, as well as other species likely to influence their abundance, such as competitors, prey species, or predators. Secondly, the EAM treats edge responses as functions that change with distance from the edge. Some models treat the edge response as a constant, even though the effects of the mechanisms underlying it (e.g., changes in vegetation and microclimate, interactions with species from matrix habitats) generally decline with distance from the edge (Wilcove et al. 1986, Laurance and Yensen 1991). Most importantly, the model considers in its predictions the variation in edge responses among species and edge types. This study demonstrates that an understanding of the variation in the responses of different species to habitat edges is important when attempting to predict animal abundance in patchy habitats and heterogeneous landscapes.

APPLICATION TO MANAGEMENT

The EAM's consideration of factors external to the patch itself permits a more realistic approach for modeling habitat suitability in heterogeneous landscapes, and provides a tool for assessing the possible effects of alternative management options on many species, over large areas (Sisk and Margules 1993). In cases of habitat fragmentation and restoration, for example, these factors may dominate, leading to very different bird assemblages in similarly isolated patches of the same habitat type (Burgess and Sharpe 1981, Wiens 1989).

The EAM may also prove useful as a "front end" to other landscape models, including demographic models that operate in spatially explicit landscapes (e.g., Pulliam et al. 1992, McKelvey et al. 1993). These models typically treat individual patches as homogeneous areas of equally suitable habitat, and incorporate variability in habitat quality only among different patches. The EAM approach allows within-patch habitat quality to vary based on the composition of matrix habitat, the amount of edge, and species-specific responses to those edges. Ongoing work integrating the EAM approach with one such spatially explicit demographic model indicates that, in highly fragmented

landscapes, the model is sensitive to relatively subtle edge responses (T. D. Sisk, *unpublished data*).

Even when managers lack the resources for detailed investigation and population modeling, the EAM provides managers with a tool for considering the surrounding matrix and the effects of habitat edges. Land management decisions often hinge on issues related to boundary management, such as the delineation of timber, grazing, and reserve areas. In fragmented habitats, where management activities are common and often intensive, consideration of spatial effects becomes critical. Conservation and resource planning will benefit from tractable, management-oriented modeling approaches that incorporate the effects of edge and matrix habitats on animal distribution and abundance.

ACKNOWLEDGMENTS

We thank the Santa Clara Valley chapter of the Audubon Society and the A. W. Mellon Foundation for financial support of this project, and the staff of the Jasper Ridge Biological Preserve for cooperation on logistics. The comments of B. Danielson, G. C. Daily, R. Dial, A. E. Launer, B. R. Noon, H. R. Pulliam, J. Roughgarden, J. R. Sauer, K. R. Switky, P. M. Vitousek, S. E. Weiss, D. Woodward, and an anonymous reviewer substantially improved the manuscript.

LITERATURE CITED

- Able, K. P., and B. R. Noon. 1976. Avian community structure along elevational gradients in the northeastern United States. *Oecologia* **26**:275–294.
- Ambuel, B., and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* **64**:1057–1068.
- Andr n, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* **73**:794–804.
- Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* **33**:31–35.
- Burgess, R. L., and D. M. Sharpe, editors. 1981. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Danielson, B. J. 1992. Habitat selection, interspecific interactions, and landscape composition. *Evolutionary Ecology* **6**:399–411.
- Dasmann, R. 1981. *Wildlife biology*. Second edition. John Wiley and Sons, New York, New York, USA.
- DeSante, D. F. 1981. Censusing technique in a California coastal scrub breeding bird community. *Studies in Avian Biology* **6**:177–186.
- Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of nature reserves. *Biological Conservation* **7**:129–146.
- Diamond, J. M., and R. M. May. 1977. Species turnover rates on islands and dependence on census interval. *Science* **197**:266–270.
- Fahrig, L. 1994. Conservation of fragmented populations. *Conservation Biology* **8**:50–59.
- Franklin, J. F., and R. T. T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecology* **1**:5–18.
- Franzreb, K. E. 1981. A comparative analysis of territorial mapping and variable-strip transect surveys methods. Pages 164–169 in C. J. Ralph and J. M. Scott, editors. *Estimating the numbers of terrestrial birds*. *Studies in Avian Biology* **6**.
- Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. *Conservation Biology* **8**:822–832.
- Galli, A. E., C. F. Leck, and R. T. T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. *Auk* **93**:356–364.
- Giles, R. H. 1978. *Wildlife management*. W. H. Freeman, San Francisco, California, USA.
- Harris, L. D. 1984. *The fragmented forest*. University of Chicago Press, Chicago, Illinois, USA.
- . 1988. Edge effects and conservation of biotic diversity. *Conservation Biology* **2**:330–339.
- Herkert, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. *Ecological Applications* **4**:461–471.
- Johnson, N. K. 1975. Controls on number of species on montane islands in the Great Basin. *Evolution* **29**:545–567.
- Johnston, V. R. 1947. Breeding birds of the forest edge in Illinois. *Condor* **49**:45–53.
- Kendeigh, S. C. 1944. Measurement of bird populations. *Ecological Monographs* **14**:67–106.
- Kroodsma, R. L. 1984. Ecological factors associated with the degree of edge effect in breeding birds. *Journal of Wildlife Management* **48**:418–425.
- Laurance, W. F., and E. Yensen. 1991. Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* **55**:77–92.
- Lay, D. 1938. How valuable are woodland clearings to bird-life? *Wilson Bulletin* **50**:254–256.
- Leopold, A. 1933. *Game management*. Charles Scribner and Sons, New York, New York, USA.
- Ludwig, J. A., and J. F. Reynolds. 1988. *Statistical ecology: a primer on methods and computing*. John Wiley and Sons, New York, New York, USA.
- Lynch, J. F., and D. F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation* **28**:287–324.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* **66**:185–194.
- McKelvey, K., B. R. Noon, and R. H. Lamberson. 1993. Conservation planning for species occupying fragmented landscapes: the case of the Northern Spotted Owl. Pages 424–450 in P. Kareiva, J. Kingsolver, and R. Huey, editors. *Biotic interaction and global change*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Mills, L. S. 1995. Edge effects and isolation: red-backed voles on forest remnants. *Conservation Biology* **9**:395–403.
- Munz, P. A. 1959. *California flora*. University of California Press, Berkeley, California, USA.
- Noss, R. F. 1991. Effects of edge and internal patchiness on avian habitat use in an old-growth hammock. *Natural Areas Journal* **11**:34–47.
- Pearson, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. *Landscape Ecology* **8**:3–18.
- Pulliam, H. R., J. B. Dunning, and J. Liu. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications* **2**:165–77.
- Ranney, J. W., M. C. Bruner, and J. B. Levinson. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67–96 in R. L. Burgess and D. M. Sharpe, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Reese, K. P., and J. T. Ratti. 1988. Edge effects: a concept under scrutiny. *Transactions of the North American Wildlife and Natural Resource Conference* **53**:127–136.

- Reichman, O. J., and H. R. Pulliam. 1996. The scientific basis for ecosystem management. *Ecological Applications* **6**:694–695.
- Reynolds, R. T., J. M. Scott, and R. A. Nussbaum. 1980. A variable circular plot method for estimating bird numbers. *Condor* **82**:309–313.
- Robinson, G. R., R. D. Holt, M. S. Gaines, S. P. Hamburg, M. C. Johnson, H. S. Fitch, and E. A. Martinko. 1992. Diverse and contrasting effects of habitat fragments. *Science* **257**:524–526.
- Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* **267**:1987–1990.
- Saunders, D. A., G. W. Arnold, A. A. Burbidge, and A. J. M. Hopkins, editors. 1987. *Nature conservation: the role of remnants of native vegetation*. Surrey Beatty and Sons, Sydney, New South Wales, Australia.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5**:18–32.
- Simberloff, D. S., and L. G. Abele. 1976. Island biogeography theory and conservation practice. *Science* **191**:285–286.
- Sisk, T. D. 1992. Distributions of birds and butterflies in heterogeneous landscapes. Dissertation. Stanford University, Stanford, California, USA.
- Sisk, T. D., and C. R. Margules. 1993. Habitat edges and restoration: methods for quantifying edge effects and predicting the results of restoration efforts. Pages 57–69 in D. Saunders, R. J. Hobbs, and P. R. Ehrlich, editors. *Nature conservation 3: reconstruction of fragmented ecosystems*. Surrey Beatty and Sons, Sydney, New South Wales, Australia.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Second edition. W. H. Freeman and Sons, New York, New York, USA.
- Szaro, R. C., and M. D. Jakle. 1985. Avian use of a desert riparian island and its adjacent scrub habitat. *Condor* **87**:511–519.
- Temple, S. A. 1986. Predicting impacts of habitat fragmentation of forest birds: a comparison of two models. Pages 301–304 in J. Verner, M. L. Morrison, and C. J. Ralph editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* **2**:340–347.
- Terborgh, J. 1976. Island biogeography and conservation: strategy and limitations. *Science* **193**:1029–1030.
- Thompson, F. R., III. 1993. Simulated responses of a forest-interior bird population to forest management options in central hardwood forests of the United States. *Conservation Biology* **7**:325–333.
- Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125–206 in R. L. Burgess and B. M. Sharpe, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Wiens, J. A. 1989. *The ecology of bird communities*. Volumes 1 and 2. Cambridge University Press, New York, New York, USA.
- . 1994. Habitat fragmentation: island vs. landscape perspective on bird conservation. *Ibis* **137**:S97–S104.
- Wilcove, D. S., C. J. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237–256 in M. E. Soulé, editor. *Conservation biology, the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* **125**:879–887.

APPENDIX

Common and scientific names and American Ornithologists' Union (AOU) abbreviations for species modeled and/or surveyed in six oak woodland patches.

Scientific name	Common name	AOU abbreviation
<i>Phasianus colchicus</i>	Ring-necked Pheasant	RNPH
<i>Callipepla californica</i>	California Quail	CAQU
<i>Zenaida macroura</i>	Mourning Dove	MODO
<i>Selasphorus sasin</i>	Allen's Hummingbird	ALHU
<i>Calypte anna</i>	Anna's Hummingbird	ANHU
<i>Melanerpes formicivorus</i>	Acorn Woodpecker	ACWO
<i>Picoides nuttallii</i>	Nuttall's Woodpecker	NUWO
<i>Colaptes auratus</i>	Northern Flicker	NOFL
<i>Myiarchus cinerascens</i>	Ash-throated Flycatcher	ATFL
<i>Empidonax difficilis</i>	Western Flycatcher	WEFL
<i>Sayornis nigricans</i>	Black Phoebe	BLPH
<i>Contopus sordidulus</i>	Western Wood-Pewee	WPPW
<i>Tyrannus verticalis</i>	Western Kingbird	WEKI
<i>Tachycineta thalassina</i>	Violet-green Swallow	VGSW
<i>Cyanocitta stelleri</i>	Steller's Jay	STJA
<i>Aphelocoma coerulescens</i>	Scrub Jay	SCJA
<i>Psaltriparus minimus</i>	Common Bushtit	COBU
<i>Thryomanes bewickii</i>	Bewick's Wren	BEWR
<i>Poliopitila caerulea</i>	Blue-gray Gnatcatcher	BGGN
<i>Sialia mexicana</i>	Western Bluebird	WEBL
<i>Turdus migratorius</i>	American Robin	AMRO
<i>Mimus polyglottos</i>	Northern Mockingbird	NOMO
<i>Toxostoma redivivium</i>	California Thrasher	CATH
<i>Bombycilla cedrorum</i>	Cedar Waxwing	CEDW
<i>Chamaea fasciata</i>	Wrentit	WREN
<i>Parus inornatus</i>	Plain Titmouse	PLTI
<i>Parus rufescens</i>	Chestnut-backed Chickadee	CBCH
<i>Sitta carolinensis</i>	White-breasted Nuthatch	WBNU
<i>Sturnus vulgaris</i>	European Starling	EUST
<i>Vireo huttoni</i>	Hutton's Vireo	HUVI
<i>Vermivora celata</i>	Orange-crowned Warbler	OCWA
<i>Dendroica coronata</i>	Yellow-rumped Warbler	YRWA
<i>Dendroica nigrescens</i>	Black-throated Gray Warbler	BTYW
<i>Dendroica townsendi</i>	Townsend's Warbler	TOWA
<i>Dendroica occidentalis</i>	Hermit Warbler	HEWA
<i>Geothlypis trichas</i>	Common Yellowthroat	COYE
<i>Wilsonia pusilla</i>	Wilson's Warbler	WIWA
<i>Piranga ludoviciana</i>	Western Tanager	WETA
<i>Pheucticus melanocephalus</i>	Black-headed Grosbeak	BHGR
<i>Pipilo erythrophthalmus</i>	Rufous-sided Towhee	RSTO
<i>Pipilo crissalis</i>	California Towhee	CATO
<i>Melospiza lincolnii</i>	Lincoln's Sparrow	LISP
<i>Zonotrichia atricapilla</i>	Golden-crowned Sparrow	GCSP
<i>Junco hyemalis</i>	Dark-eyed Junco	DEJU
<i>Agelaius phoeniceus</i>	Red-winged Blackbird	RWBL
<i>Sturnella neglecta</i>	Western Meadowlark	WEME
<i>Molothrus ater</i>	Brown-headed Cowbird	BHCO
<i>Icterus galbula</i>	Northern Oriole	NOOR
<i>Carpodacus purpureus</i>	Purple Finch	PUFI
<i>Carduelis psaltria</i>	Lesser Goldfinch	LEGO