

# Effects of Residential Development and Landscape Composition on the Breeding Birds of Placer County's Foothill Oak Woodlands<sup>1</sup>

Diana Stralberg<sup>2</sup> and Brian Williams<sup>3</sup>

## Abstract

This study examines the effect of rural residential development and landscape composition on breeding birds in Placer County's foothill oak woodlands. Point count survey data were used to construct generalized linear models for individual species' abundance or probability of occurrence, based on two sets of variables: GIS-derived landscape characteristics, including development density, oak woodland proportion, and habitat diversity; and field-collected local habitat parameters. We found that many species examined were sensitive to either development density or landscape composition at some distance between 250 and 4,000 m. Of the 48 breeding species common enough to analyze statistically, the occurrence of 24 species was significantly associated with landscape characteristics. Species shown to be associated with development density and/or urban edge proximity included the lark sparrow (-), Rufous-crowned sparrow (-), western meadowlark (-), black Phoebe (+), house finch (+) and western scrub-jay (+). Several other species were not development-sensitive but were positively associated with the proportion of oak woodland found in the surrounding landscape. For a subset of locations, some species also exhibited responses to local habitat variables, suggesting that further investigation of the importance of landscape vs. local factors is warranted. The diversity of responses observed across a range of species requires the recommendation of a multifaceted conservation strategy for oak woodland birds and their habitat.

## Introduction

Placer County's human population is the fastest growing in California, with a growth rate of 3.5 percent in 2000 (California Department of Finance 2001). Much of this population growth is occurring in the county's foothill oak woodlands, 93 percent of which are privately owned and over 50 percent of which (30,000+ acres) have rural residential or urban land-use designations (Placer Legacy 2000). Concern about this rapid growth and the loss of open space and rural character led to the development of the Placer Legacy Open Space and Agricultural Conservation Program, which seeks to balance growth with the conservation of open space and wildlife resources. Because foothill oak woodlands are rapidly urbanizing and poorly protected, though treasured for their scenic and wildlife values, much of the program's early emphasis has focused on acquiring one or more large parcels to preserve oak woodlands. In addition, the County is interested in understanding how

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<sup>2</sup> GIS Specialist, Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94970 (e-mail: dstralberg@prbo.org)

<sup>3</sup> Consulting Wildlife Ecologist, 8200 Turner Dr., Granite Bay, CA 95746 (e-mail: bwcal@sprynet.com)

the rural residential landscape can be better managed to preserve wildlife, sensitive resources and water quality. This project was initiated as a part of the Placer Legacy Program as an effort to assess the effects of rural residential development and habitat fragmentation on breeding birds as indicators for oak woodland habitat.

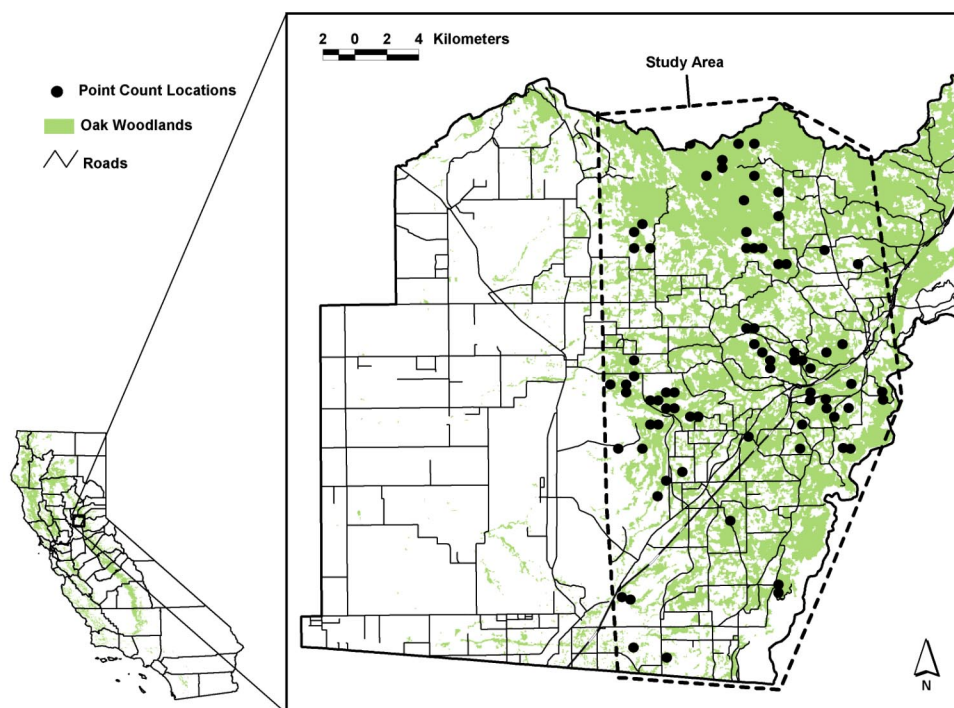
Habitat suitability for wildlife is an important consideration in reserve design, and local habitat relationships are relatively well studied in California's foothill oak woodlands (Avery and Van Riper 1990, Block 1989, Block and Morrison 1990, Block and others 1994, Tietje and others 1997, Verner and others 1997, Wilson and others 1991). Recently, much attention has also been focused on the potential effects of rural residential development, vineyard expansion and other human modifications to oak woodland landscapes. In Sonoma County, Merenlender and others (1998) found that the level of development of a parcel influences bird community composition and that neotropical migrants in particular demonstrate reduced abundances in suburban areas and, to a lesser extent, rural residential areas. Several recent studies of birds in other California habitats have suggested that characteristics of the surrounding landscape may influence habitat quality for many species and, in some cases, may even be better predictors of species occurrence than local habitat structure (e.g., Bolger and others 1997, Stralberg 1999). Currently, a need remains for a better understanding of landscape-scale processes that affect habitat suitability of oak woodlands beyond local habitat structure (Bell 1997, Garrison and Davis 1997, Thomas 1997). Such knowledge may be particularly valuable when candidates for reserves are structurally similar, as they are in foothill oak woodlands of Placer County.

We initiated this study to test the hypothesis that some birds will be affected by landscape-scale patterns of development irrespective of local habitat. One primary objective is to provide specific recommendations to the County of Placer regarding priorities for management, conservation and acquisition of foothill oak woodlands, as well as future zoning decisions and general plan revisions. We also hope to gain a better general understanding of the features of habitat and landscape patterns that determine species occupancy, in order to inform land-use planning and conservation, as well as wildlife management on private and public land. This may be accomplished in part through future revisions to the California Partners in Flight (CPIF) Oak Woodland Bird Conservation Plan (Zack and others 2000), an interagency effort to promote the conservation of migratory birds and their habitats throughout the Americas.

## Methods

### **Study Area**

Our study area in western Placer County ranged in elevation from 70 to 480 meters, and encompassed an area of approximately 550 km<sup>2</sup> (fig. 1). Dominant tree species included blue oak (*Quercus douglasii*), which occurs primarily on drier sites (especially ridges that were historically difficult to irrigate), and interior live oak (*Quercus wislizenii*), which tends to occur in more mesic areas such as drainage basins and north-facing slopes. A complex human history has altered the distribution and structure of many of these oak woodlands, including their understory structure and composition. Interspersed with oak woodlands is a combination of orchards, cropland, dry pasture rangeland, irrigated pasture, rural residential development ("ranchettes"), and urban and suburban development.



**Figure 1** Study area and point count locations.

In Placer County, large intact blocks of oak woodland are rare, and habitat patches are not easily defined or necessarily isolated from other habitat patches. We therefore chose a point-based approach for sampling habitat, rather than surveying entire habitat patches. Our intent was to sample bird species at random throughout a representative cross-section of the County's development spectrum: from urban park to rural residential to largely undeveloped rangeland.

### ***Study Design and Point Selection***

A total of 75 points was surveyed. We began by selecting a stratified random sample of 80 potential survey points by generating a 500-m sampling grid of points superimposed over the county's oak woodlands within the study area. Suitable points (>2,600) were defined as meeting one of the following CWHR habitat classifications (Mayer and Laudenslayer 1988) according to GIS vegetation data (Forest Service 2000): blue oak woodland or blue oak foothill pine, but also montane hardwood, urban, annual grassland, valley-foothill riparian or agricultural cropland if our familiarity with the area suggested that the amount of oak woodland at or adjacent to the point was underestimated. Selected points were stratified by general plan land-use categories (Placer County General Plan 1994): (1) Low Density Residential (LDR) and Rural Residential (RR) 1-2.5 acres; (2) RR 2.5-5 and RR 5-10; (3) RR 10, Agricultural (Ag) 10, and Ag 20; and (4) Ag 40, Ag 80, and Open Space (OS). Actual land use varied considerably from the General Plan designation because many parcels were not yet "built out," but this method allowed representation of a range of land uses and parcel sizes, as well as geographic area, among sample points.

To improve our sampling effectiveness, we developed a random clustering technique that began by randomly choosing one of nine 7.5 ft topographic map quadrangles followed by the random selection of a legal section (1 mi<sup>2</sup> or 2.59 km<sup>2</sup>) as a starting point. We then randomly chose points from the 500-m sampling grid within immediately adjoining sections, expanding the radius by 1 section as each layer of sections was exhausted. Constraints were that no more than 4 points could fall within one section and no more than 2 points of a given land-use category could occur in any one section. This process was repeated to produce two random sets of 40 semi-clustered points, each at least 500 m from the nearest sampling point.

Because the first 80 points included no parcels zoned for 80 acres and very few parcels smaller than 5 acres, we randomly selected an additional 22 points within these parcel size ranges (10 and 12 points, respectively). Each point was ground-truthed to meet the following minimum criteria: (1) oak woodland as the dominant habitat type, with at least two oaks within the 50-m radius and a canopy cover  $\geq$  10 percent; (2) no house or other large building within a 50-m radius; (3) not within 500 m of a major highway; (4) not excessively time-consuming to access; and (5) <5 percent paved two-lane public road within a 50-m radius (private single-lane dirt roads were fairly common and practically impossible to exclude). We did not exclude any points based on other habitat characteristics such as presence of water, understory composition, slope or aspect.

Of these original 122 locations, we were able to obtain access to 57 survey sites. The other 45 were either unsuitable (n = 16), or we were unable to contact the landowners (n = 15), or we were denied access (n = 8), or negotiating access was too time-consuming (n = 6). We repeated the selection process to find 6 stratified-random substitute points, identified 6 points semi-randomly (randomly chosen within a non-random area that was convenient to access), and added 6 points at widely separated urban parks for which we knew we could get immediate access. Within each park, the specific sample point was randomly determined in the field. The exact location of each site was later recorded with a Global Positioning System (to within approximately 5-15 m).

### ***Bird Counts***

Six-minute, unlimited-distance point counts (Ralph and others 1993) were done twice at each of the 75 sites, 7-28 days apart (mean = 16 days, SD = 4.4). Detections were recorded as within or beyond a 50-m radius. We assumed that 2 counts would be necessary to avoid problems with seasonal variation in vocalization frequency and hence detection probability. Point counts were done in the morning beginning at official sunrise to 4 hours after sunrise, during appropriate weather conditions (Verner 1985) between 17 May and 14 June 2001 by a single expert observer (B. Williams).

### ***Habitat Parameters***

We measured or estimated parameters describing the local habitat and physical conditions at 32 of the 75 point count locations (*appendix 1*). The intent was to statistically control for habitat-specific variation to focus on landscape-scale effects.

### ***Landscape Parameters Obtained from GIS Data***

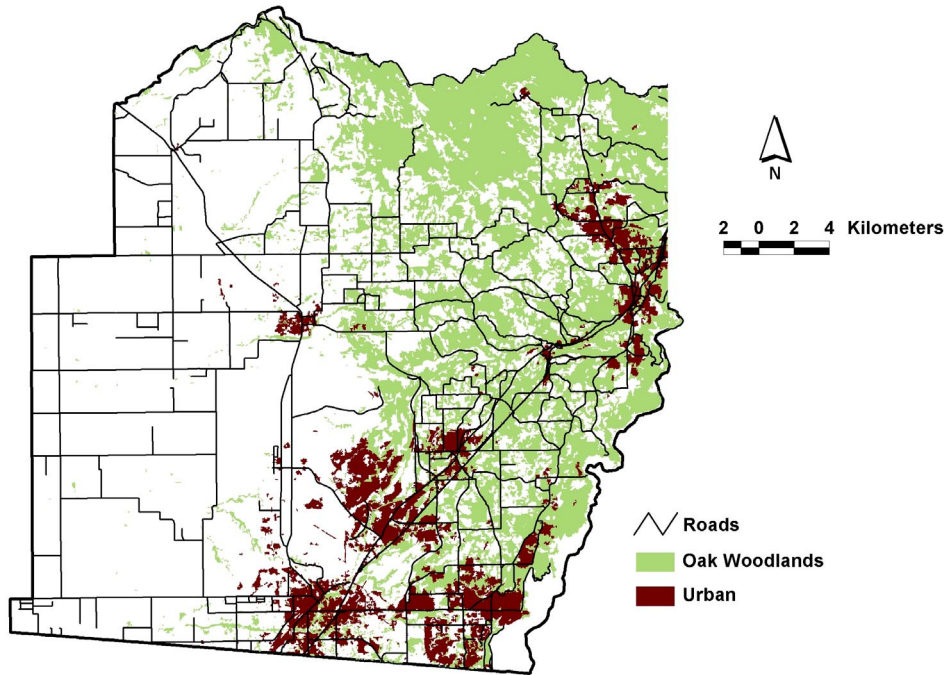
We calculated several urbanization and landscape composition metrics (*appendix 2*) for each point-count location using ArcView 3.2a and the Spatial Analyst Extension (ESRI 2000). The County's parcel base map and associated Assessor's database were used to determine the parcel size and overall property size of each site surveyed. In addition, the number of structures within various buffer distances (250 m, 500 m, 1000 m, 2000 m and 4000 m) of each point-count location was estimated based on the development status of each parcel centroid. Because structure locations were estimated based on parcel centroids, there is some uncertainty in the number of structures counted within point count radii. Furthermore, while the bird and vegetation data were collected in 2000, the parcel base map represents July 1998 parcels and the Assessor's database contains 1999 ownership information (matching years were not available at the time of analysis). Thus, parcels that were subdivided and developed after 1998 are not correctly represented in this database. The parcel data are nevertheless a major improvement over any other available urbanization measure (i.e., Forest Service vegetation data), particularly in the rural residential zone, where the built footprint is not easily discernable even from aerial photos. As an index of housing density, we feel this measure is the best available, short of ground-based inventories.

Geographic information system (GIS) vegetation data (Forest Service 2000, 2.5 acre minimum mapping unit) were then used to coarsely determine the landcover composition of each point count location within circles of increasing radius: 250 m, 500 m, 1,000 m, 1,500 m, 2,000 m and 4,000 m. A proportion was obtained for each cover category within each radius. For analysis, the following CWHR categories were combined to calculate oak woodland coverage: blue oak woodland, blue oak-foothill pine, valley oak woodland, montane hardwood, and montane hardwood-conifer. Finer distinctions between oak woodland categories were not made due to the presumed low accuracy of the vegetation layer beyond cover class. The other category used for analysis was annual grassland, some of which was actually open oak savanna. The urban classification was not used in analysis due to the coarseness of this vegetation layer with respect to rural residential development patterns, particularly in comparison with the more accurate parcel base map and Assessor's database (*fig. 2*). To evaluate the influence of landscape-level habitat diversity, we also calculated a Shannon-Wiener diversity index (Krebs 1989) for each of the above-listed radii ( $H = - \sum_i p_i \ln(p_i)$ , where  $p_i$  = area of  $i^{\text{th}}$  habitat type). For this metric, each CWHR category was treated separately to reflect diversity among oak woodland as well as other habitat types.

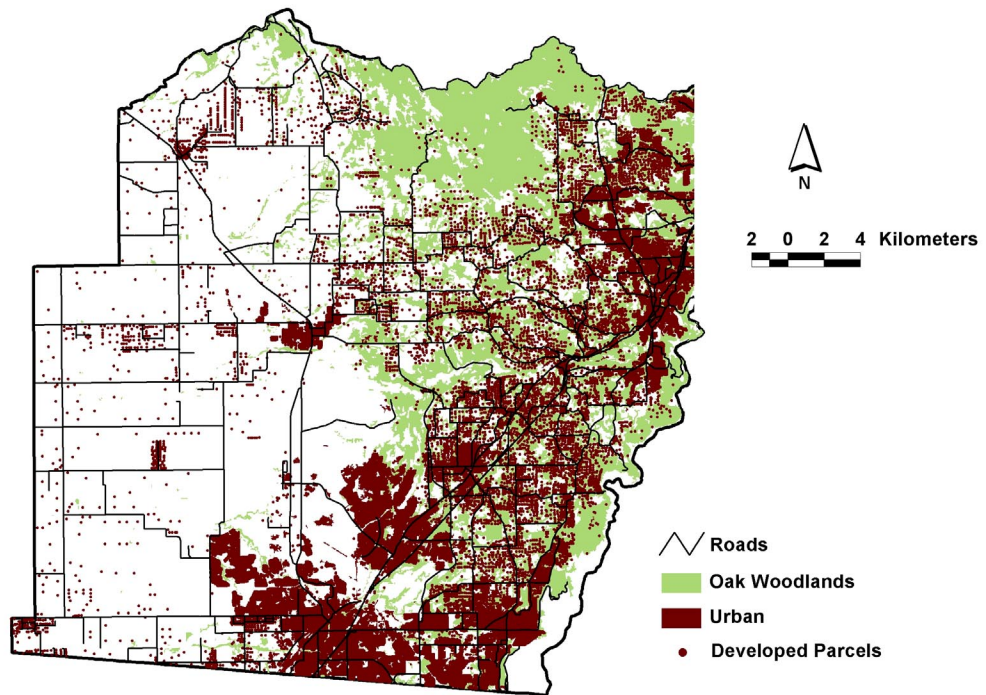
Finally, for each point we estimated the distance to the nearest structure or urban edge, using a combination of field notes, aerial photos and the GIS parcel basemap with associated Assessor's ownership database (in that order, depending on availability). We also used 1:100,000 scale road and hydrography GIS datasets (Teale Data Center 1997, 1999) to calculate the distance from a point count to the nearest stream and nearest paved road.

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A.



B.



**Figure 2** Differences in urban development identified by GIS vegetation data (Forest Service 2000) (a) and Placer County parcel base map and Assessor's database (Placer County 1999) (b).

## ***Statistical Analysis***

Species detected within 50 m at seven or more (10 percent) of the 75 sites throughout the sampling period were analyzed individually with respect to per point abundance or probability of occurrence. Because counts of most species had positively skewed distributions, we used generalized linear models with either a Poisson distribution and log link function or binomial distribution and logit link function (logistic regression). Poisson was the default model, but logistic regression was used for species that tended to exhibit low numbers or aggregated abundances (Hayek and Buzas 1997). Models were constructed and evaluated using Stata Version 7 (StataCorp 2000). Because many species had low detection rates within a 50-m radius (*appendix 3*) we also analyzed all detections with respect to probability of occurrence using logistic regression, statistically controlling for distance to the nearest urban edge, which at some point-count locations was within the range of bird detections (100 m or less for most species), potentially reducing the available habitat surveyed. We applied the same detection rate criterion (species occurring at 10 percent of sites or more) when analyzing all detections (unlimited distance).

To evaluate the influence of development density at various scales on bird abundance, we calculated Spearman rank correlation coefficients for each individual species and the number of structures within measurement radii of 250, 500, 1,000, 2,000 and 4,000 m. We selected landscape variables at the scales with the highest significant correlation ( $P < 0.05$ ) with bird abundance for inclusion in our initial model. Variables were included at more than one scale if graphing of correlation coefficients against measurement radius indicated more than one local maximum. We also included other landscape variables with significant Spearman correlations (distance to nearest road, distance to nearest creek or open water, elevation, parcel size and property size).

Using the subset of variables described above (pairwise correlations significant,  $P < 0.05$ ), we initially used a stepwise Poisson or logistic regression analysis (backward elimination,  $P < 0.15$ ) to select an appropriate model for each species. Variables with  $P$ -values greater than 0.05 were dropped or retained based on AIC (Akaike's Information Criterion) comparisons with simpler models. Final models were considered significant at  $P < 0.01$  based on the likelihood ratio  $\chi^2$  statistic. To determine the robustness of our models, we calculated bootstrap estimates of coefficients and standard errors (200 repetitions,  $n=75$ ) for each significant final model, scaling down models as necessary.

To translate results into terms meaningful to municipal planners and policymakers, we selected two development-sensitive species and calculated predicted bird abundances under existing general plan designations (as defined above).

To compare the effects of local and landscape-level variables, we constructed generalized linear models of habitat suitability for each species, using a subset of 32 sites for which local habitat variables were recorded. Again, Spearman rank correlations between species and habitat variables were used to determine significant ( $P < 0.05$ ) variables for inclusion in initial models. A stepwise regression analysis (backward elimination,  $P < 0.15$ ) using a subset of habitat variables (with models specifying the same distribution as in the analysis of landscape-level variables) was used to find the best-fitting (using AIC) significant model ( $P < 0.01$ ). Habitat models were constructed using only detections  $\leq 50$  m. For each significant final model, we also calculated bootstrap estimates of coefficients and standard errors (200 repetitions,  $n=75$ ).

## Results

Ninety-three species were detected in two visits to the 75 sites, approximately 76 of which are known or suspected to be local breeders. Limiting analysis to detections within 50 m resulted in 64 locally breeding native species. With respect to migratory status, 21 were neotropical migrants, 23 were short-distance migrants, and 22 were native residents. Nesting guilds were represented by 16 cavity nesters and 35 open cup nesters, 5 of which nest on the ground (*appendix 3*).

### ***Landscape-Level Associations***

Using generalized linear models for detections within 50 m, landscape characteristics combined explained up to 41 percent of the variation in species abundance or probability of occurrence as measured by pseudo- $R^2$  values (*table 1*). Species best predicted by landscape characteristics (significant bootstrap model with pseudo- $R^2$  greater than 0.15) were: black Phoebe, Hutton's vireo, western scrub-jay, spotted towhee, Rufous-crowned sparrow, lark sparrow, black-headed grosbeak and house finch. Development density at some scale was a significant explanatory factor for black Phoebe (+), tree swallow (-), western scrub-jay (+), Rufous-crowned sparrow (-), lark sparrow (-) and house finch (+). For tree swallow and Rufous-crowned sparrow, however, development density did not remain a significant factor in models based on bootstrap resampling trials. The violet-green swallow was positively associated with property size, while the black Phoebe and western scrub-jay were negatively associated with parcel size, but these parameters did not remain significant in bootstrap models for any species.



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**Table 1**—Significant ( $P < 0.01$ ) regression model results for landscape-level variables (detections limited to within 50 m).<sup>1, 2</sup>

| Species | Model type | Pseudo-R <sup>2</sup> | LR Chi <sup>2</sup>     | P                          | AIC                   | Landscape variables | Coeff.                      | Std.Err                     | P                           |
|---------|------------|-----------------------|-------------------------|----------------------------|-----------------------|---------------------|-----------------------------|-----------------------------|-----------------------------|
| BCHU    | Logistic   | <b>0.13</b>           | <b>9.28</b>             | <b>0.0023</b>              | <b>0.85</b>           | <b>GRS500</b>       | <b>-6.613</b>               | <b>2.690</b><br>(2.679)     | <b>0.014</b><br>(0.014)     |
| BLPH    | Logistic   | <b>0.25</b><br>(0.41) | <b>18.04</b><br>(28.01) | <b>&lt;0.0001</b>          | <b>0.78</b><br>(0.63) | <b>DEV250</b>       | <b>0.188</b><br>(0.159)     | <b>0.055</b><br>(0.055)     | <b>0.001</b><br>(0.004)     |
|         |            |                       |                         |                            |                       | Parcel size         | (-0.078)                    | (0.043)                     | (0.072)                     |
| WEKI    | Poisson    | (0.22)                | (17.53)                 | (<0.0001)                  | (0.89)                | GRS4000             | (9.614)                     | (2.396)                     | (<0.001)                    |
| HUVI    | Logistic   | <b>0.18</b>           | <b>11.99</b>            | <b>0.0025</b>              | <b>0.80</b>           | <b>OAK250</b>       | <b>4.306</b>                | <b>2.354</b><br>(2.104)     | <b>0.067</b><br>(0.041)     |
|         |            |                       |                         |                            |                       | <b>H2000</b>        | <b>4.457</b>                | <b>2.262</b><br>(1.905)     | <b>0.049</b><br>(0.019)     |
| TRES    | Poisson    | (0.28)                | (13.44)                 | (0.0012)                   | (0.55)                | DEV4000             | (-1.5E-03)                  | (6.9E-04)                   | (0.031)                     |
|         |            |                       |                         |                            |                       | GRS4000             | (7.252)                     | (3.413)                     | (0.034)                     |
| VGSW    | Poisson    | (0.18)                | (14.19)                 | (0.0008)                   | (1.18)                | OAK4000             | (4.600)                     | (1.555)                     | (0.003)                     |
|         |            |                       |                         |                            |                       | Property size       | (0.005)                     | (0.002)                     | (0.025)                     |
| CLSW    | Poisson    | <b>0.09</b><br>(0.25) | <b>5.30</b><br>(36.77)  | <b>0.0214</b><br>(<0.0001) | <b>1.62</b><br>(1.52) | <b>GRS250</b>       | <b>3.500</b><br>(2.589)     | <b>1.267</b><br>(0.736)     | <b>0.006</b><br>(<0.001)    |
|         |            |                       |                         |                            |                       | OAK4000             | (-3.9E-0)                   | (1.2E-0)                    | (0.002)                     |
| WESJ    | Poisson    | <b>0.19</b><br>(0.22) | <b>36.55</b><br>(41.90) | <b>&lt;0.0001</b>          | <b>2.08</b><br>(2.05) | <b>DEV250</b>       | <b>7.1E-02</b><br>(6.4E-02) | <b>1.5E-02</b><br>(1.1E-02) | <b>&lt;0.001</b><br>(0.050) |
|         |            |                       |                         |                            |                       | Parcel size         | (-0.005)                    | (0.003)                     | (0.050)                     |
| AMRO    | Logistic   | <b>0.13</b>           | <b>6.71</b>             | <b>0.0096</b>              | <b>0.64</b>           | <b>H250</b>         | <b>2.856</b>                | <b>1.241</b><br>(1.210)     | <b>0.021</b><br>(0.018)     |
| OCWA    | Logistic   | <b>0.10</b>           | <b>8.66</b>             | <b>0.0033</b>              | <b>1.04</b>           | <b>OAK4000</b>      | <b>4.999</b>                | <b>1.696</b><br>(2.670)     | <b>0.003</b><br>(0.008)     |
| SPTO    | Logistic   | <b>0.27</b>           | <b>21.59</b>            | <b>&lt;0.0001</b>          | <b>0.86</b>           | <b>OAK4000</b>      | <b>6.667</b>                | <b>2.461</b><br>(2.404)     | <b>0.007</b><br>(0.006)     |
|         |            |                       |                         |                            |                       | <b>H2000</b>        | <b>7.167</b>                | <b>2.459</b><br>(2.179)     | <b>0.004</b><br>(0.001)     |
| RCSP    | Logistic   | <b>0.20</b><br>(0.36) | <b>12.23</b><br>(22.81) | <b>0.0005</b><br>(<0.0001) | <b>0.72</b><br>(0.64) | <b>GRS1000</b>      | <b>-8.818</b><br>(-7.073)   | <b>4.169</b><br>(3.280)     | <b>0.034</b><br>(0.031)     |
|         |            |                       |                         |                            |                       | H4000               | (6.222)                     | (2.704)                     | (0.021)                     |
|         |            |                       |                         |                            |                       | DEV250              | (-0.277)                    | (0.161)                     | (0.086)                     |
| LASP    | Poisson    | <b>0.22</b>           | <b>29.57</b>            | <b>&lt;0.0001</b>          | <b>1.45</b>           | <b>DEV1000</b>      | <b>-0.018</b>               | <b>0.007</b><br>(0.006)     | <b>0.012</b><br>(0.003)     |
|         |            |                       |                         |                            |                       | Stream distance     | <b>9.2E-04</b>              | <b>4.7E-04</b><br>(3.4E-04) | <b>0.049</b><br>(0.006)     |
| BHGR    | Logistic   | <b>0.19</b>           | <b>11.14</b>            | <b>0.0008</b>              | <b>0.69</b>           | <b>Elevation</b>    | <b>0.004</b>                | <b>0.001</b><br>(0.004)     | <b>0.001</b><br>(0.004)     |
| LAZB    | Poisson    | <b>0.12</b>           | <b>14.79</b>            | <b>0.0001</b>              | <b>1.46</b>           | <b>OAK4000</b>      | <b>4.364</b>                | <b>1.245</b><br>(1.154)     | <b>&lt;0.001</b>            |
| RWBL    | Logistic   | (0.21)                | (8.87)                  | (0.0029)                   | (0.49)                | Stream distance     | (2.3E-03)                   | (8.4E-04)                   | (0.008)                     |
| HOFI    | Logistic   | <b>0.26</b>           | <b>26.66</b>            | <b>&lt;0.0001</b>          | <b>1.11</b>           | <b>DEV250</b>       | <b>0.162</b>                | <b>0.062</b><br>(0.070)     | <b>0.009</b><br>(0.021)     |
|         |            |                       |                         |                            |                       | <b>DEV4000</b>      | <b>4.4E-04</b>              | <b>1.6E-04</b><br>(1.9E-04) | <b>0.007</b><br>(0.023)     |

<sup>1</sup> Bold parameter estimates and model diagnostics are based on bootstrap resampling trials. Numbers in parentheses represent parameter estimates and diagnostics from non-bootstrap models.

<sup>2</sup> See appendix 2 for definitions of landscape variables and appendix 3 for species names.

When all detections were analyzed, several additional species exhibited significant responses to landscape characteristics, with logistic regression models explaining up to 54 percent of the variation in probability of occurrence (*table 2*). In addition to the above-listed species, the presence of black-chinned hummingbird, Pacific-slope flycatcher, ash-throated flycatcher, cliff swallow, yellow-billed magpie, northern mockingbird, orange-crowned warbler and western meadowlark were reasonably well-predicted by landscape factors (pseudo- $R^2$  greater than 0.15 for bootstrap models). The model for chipping sparrow was strong (pseudo- $R^2 = 0.39$ ), but due to low detection rates for this species (8 of 75 sites), parameter estimates did not withstand bootstrap resampling validation. Controlling for urban edge distance, the species for which development density at some scale was a significant predictor of occurrence were black Phoebe (+), ash-throated flycatcher (-), western kingbird (-), tree swallow (-), cliff swallow (+), western scrub-jay (+), Rufous-crowned sparrow (-), chipping sparrow (-), lark sparrow (-), Lazuli bunting (-), western meadowlark (-) and house finch (+). For the three sparrow species, development density did not remain significant in bootstrap models, although the Rufous-crowned and lark sparrows did demonstrate an urban edge aversion (positive association with edge distance). Species demonstrating an affinity for urban edges (negative association with edge distance) were black Phoebe, house wren, and American robin, while the northern mockingbird was negatively associated with property size, a more local index of development density.

Species that were positively associated with oak woodland proportion or negatively associated with grassland proportion at one or more scales (validated by bootstrap resampling) were black-chinned hummingbird, Pacific-slope flycatcher, ash-throated flycatcher, Hutton's vireo, orange-crowned warbler, Rufous-crowned sparrow, Lazuli bunting and spotted towhee (*tables 1 and 2*). Negatively associated with oak woodland proportion or positively associated with grassland proportion (after bootstrap resampling) were western kingbird, yellow-billed magpie, cliff swallow, western scrub-jay and American crow (*tables 1 and 2*). Several species—the mourning dove, Pacific-slope flycatcher, Hutton's vireo, American robin, orange-crowned warbler, spotted towhee and Rufous-crowned sparrow—were all positively associated with habitat diversity (Shannon-Wiener  $H'$ ) in the surrounding landscape (after bootstrap resampling) (*tables 1 and 2*).

Finally, some species were associated with other landscape elements. Elevation was a significant predictor of yellow-billed magpie (-), house wren (-) and black-headed grosbeak (+) presence (after bootstrap resampling). Lark sparrows occurred more frequently at sites farther away from streams, while black-chinned hummingbirds and orange-crowned warblers were more likely to occur at sites closer to streams (*tables 1 and 2*).

Predicted abundances for two development-sensitive species (lark sparrow and western scrub-jay) were calculated under a range of development density scenarios (assuming constant development density) using the best model developed for each species' detections within 50m (other variables held constant at mean values). For the lark sparrow, predicted abundance (over two counts) dropped from  $0.46 \pm 0.23$  at 40 acres per unit (Ag 40) to  $7.02 \times 10^{-7} \pm 4.52$  at 1 unit per acre (RR 1.0). For the western scrub-jay, predicted abundance rose from  $0.42 \pm 0.20$  at 40 acres per unit to  $8.27 \pm 0.43$  at 1 unit per acre (*fig. 3*).

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**Table 2**—Significant ( $P < 0.01$ ) logistic regression model results for landscape-level variables (unlimited detections).<sup>1, 2</sup>

| Species | Pseudo-R <sup>2</sup> | LR Chi <sup>2</sup> | P                  | AIC            | Landscape variables | Coeff.                 | Std.Err              | P                |
|---------|-----------------------|---------------------|--------------------|----------------|---------------------|------------------------|----------------------|------------------|
| MODO    | 0.13                  | 12.71               | 0.0017             | 1.23           | H250                | -2.468                 | 0.732<br>(0.793)     | 0.001<br>(0.002) |
| BCHU    | 0.23                  | 15.97               | 0.0011             | 0.82           | GRS500              | -7.640                 | 2.968<br>(3.688)     | 0.010<br>(0.009) |
|         |                       |                     |                    |                | Stream distance     | -1.6E-03               | 8.4E-04<br>(8.2E-04) | 0.066<br>(0.060) |
| PSFL    | 0.25                  | 12.69               | 0.0018             | 0.59           | H250                | 3.540                  | 1.656<br>(1.346)     | 0.033<br>(0.009) |
|         |                       |                     |                    |                | OAK4000             | 5.665                  | 3.13<br>(2.873)      | 0.070<br>(0.049) |
| BLPH    | 0.18                  | 17.86               | 0.0001             | 1.18           | DEV250              | 0.103                  | 0.045<br>(0.055)     | 0.022<br>(0.063) |
|         |                       |                     |                    |                | Edge distance       | -3.122                 | 1.586<br>(1.954)     | 0.049<br>(0.110) |
| ATFL    | 0.27                  | 24.73               | 0.0001             | 1.00           | DEV500              | -0.096                 | 0.039<br>(0.031)     | 0.013<br>(0.002) |
|         |                       |                     |                    |                | OAK500              | 4.410                  | 1.647<br>(1.603)     | 0.007<br>(0.006) |
|         |                       |                     |                    |                | DEV1000             | 0.012                  | 0.007<br>(0.005)     | 0.062<br>(0.013) |
| WEKI    | 0.14                  | 11.90               | 0.0026             | 0.99           | DEV250              | -0.118                 | 0.067<br>(0.078)     | 0.077<br>(0.128) |
|         |                       |                     |                    |                | GRS250              | 3.306                  | 1.590<br>(1.306)     | 0.037<br>(0.011) |
| HUVI    | 0.16                  | 13.53               | 0.0012             | 1.03           | OAK250              | 4.221                  | 1.349<br>(1.696)     | 0.002<br>(0.013) |
|         |                       |                     |                    |                | H4000               | 3.458                  | 2.297<br>(1.923)     | 0.132<br>(0.072) |
| TRES    | 0.14<br>(0.23)        | 9.47<br>(14.93)     | 0.0021<br>(0.0006) | 0.81<br>(0.76) | DEV4000             | -8.1E-04<br>(-1.3E-03) | 4.2E-04<br>(4.5E-04) | 0.043<br>(0.011) |
|         |                       |                     |                    |                | OAK4000             | (-4.981)               | (2.238)              | (0.026)          |
| CLSW    | 0.26                  | 18.61               | 0.0001             | 0.79           | DEV4000             | 3.7E-04                | 1.9E-04<br>(1.5E-04) | 0.053<br>(0.011) |
|         |                       |                     |                    |                | GRS250              | 3.520                  | 1.603<br>(1.400)     | 0.028<br>(0.012) |
| WESJ    | 0.21                  | 19.67               | 0.0001             | 1.09           | DEV500              | 0.059                  | 0.030<br>(0.020)     | 0.049<br>(0.003) |
|         |                       |                     |                    |                | OAK500              | -3.536                 | 1.981<br>(1.469)     | 0.074<br>(0.016) |
| YBMA    | 0.20                  | 15.38               | 0.0005             | 0.88           | GRS500              | 3.570                  | 1.907<br>(1.796)     | 0.061<br>(0.047) |
|         |                       |                     |                    |                | Elevation           | -2.3E-03               | 1.2E-03              | 0.068<br>(0.060) |
| AMCR    | 0.16                  | 14.71               | 0.0006             | 1.09           | GRS1000             | (4.209)                | (1.940)              | (0.030)          |
|         |                       |                     |                    |                | Edge distance       | (-6.572)               | (2.639)              | (0.013)          |

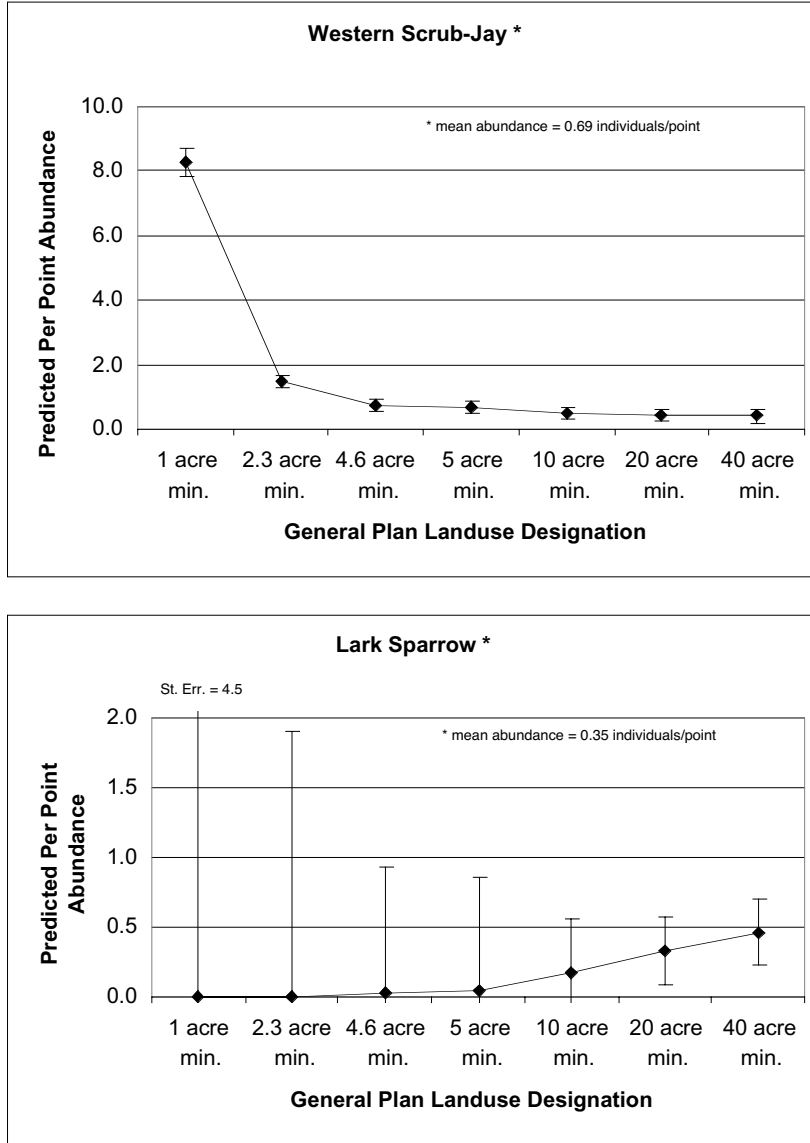
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Table 2 (cont.)

| Species | Pseudo-R <sup>2</sup> | LR Chi <sup>2</sup> | P                   | AIC            | Landscape variables | Coeff.                 | Std.Err              | P                  |
|---------|-----------------------|---------------------|---------------------|----------------|---------------------|------------------------|----------------------|--------------------|
| HOWR    | 0.13                  | 13.63               | 0.0011              | 1.25           | Elevation           | -2.1E-03               | 8.9E-04<br>(8.3E-04) | 0.018<br>(0.012)   |
|         |                       |                     |                     |                | Edge distance       | -3.363                 | 1.684<br>(1.588)     | 0.046<br>(0.034)   |
| AMRO    | 0.07                  | 7.11                | 0.0077              | 1.31           | Edge distance       | -3.012                 | 1.608<br>(1.388)     | 0.061<br>(0.030)   |
| NOMO    | 0.27                  | 24.20               | <0.0001             | 1.07           | Property size       | -0.031                 | 0.012<br>(0.011)     | 0.008<br>(0.006)   |
| OCWA    | 0.33<br>(0.39)        | 32.79<br>(38.60)    | <0.0001             | 0.98<br>(0.93) | OAK4000             | 8.939                  | 3.124<br>(3.702)     | 0.004<br>(<0.0001) |
|         |                       |                     |                     |                | H4000               | 7.049                  | 2.773<br>(2.979)     | 0.011<br>(0.019)   |
|         |                       |                     |                     |                | Stream distance     | -1.6E-03<br>(-1.4E-03) | 8.8E-04<br>(6.8E-04) | 0.078<br>(0.033)   |
|         |                       |                     |                     |                | Edge distance       | (-3.273)               | (1.462)              | (0.025)            |
| SPTO    | 0.26                  | 24.81               | <0.0001             | 1.04           | GRS500              | -5.949                 | 2.126<br>(2.149)     | 0.005<br>(0.006)   |
|         |                       |                     |                     |                | H2000               | 4.965                  | 1.980<br>(1.752)     | 0.012<br>(0.005)   |
| RCSP    | 0.23<br>(0.28)        | 17.88<br>(22.01)    | 0.0001<br>(<0.0001) | 0.88<br>(0.85) | H2000               | 4.499                  | 2.367<br>(1.709)     | 0.057<br>(0.007)   |
|         |                       |                     |                     |                | Edge distance       | 4.108<br>(4.499)       | 2.673<br>(1.707)     | 0.124<br>(0.040)   |
| CHSP    | (0.39)                | (20.01)             | (0.0002)            | (0.54)         | DEV250              | (-0.222)               | (0.149)              | (0.136)            |
|         |                       |                     |                     |                | DEV250              | (-0.926)               | (0.543)              | (0.088)            |
|         |                       |                     |                     |                | H500                | (-3.438)               | (1.730)              | (0.047)            |
| LASP    | 0.23<br>(0.28)        | 22.74<br>(27.39)    | <0.0001             | 1.07           | Stream distance     | 1.3E-03<br>(1.50E-03)  | 6.2E-04<br>(5.8E-04) | 0.036<br>(0.010)   |
|         |                       |                     |                     |                | Edge distance       | 4.521<br>(2.839)       | 2.280<br>(1.467)     | 0.0547<br>(0.053)  |
|         |                       |                     |                     |                | DEV250              | (-0.178)               | (0.099)              | (0.072)            |
| BHGR    | 0.08<br>(0.12)        | 7.63<br>(11.49)     | 0.0058<br>(0.0032)  | 1.24<br>(1.22) | GRS1000             | -4.185<br>(-5.790)     | 1.824<br>(2.079)     | 0.022<br>(0.005)   |
|         |                       |                     |                     |                | Edge distance       | (-2.002)               | (1.080)              | (0.064)            |
| RWBL    | (0.12)                | (10.10)             | (0.0064)            | (1.11)         | Stream distance     | (1.4E-03)              | (5.3E-03)            | (0.008)            |
|         |                       |                     |                     |                | Edge distance       | (-2.388)               | (1.413)              | (0.091)            |
| WEME    | 0.26<br>(0.52)        | 21.10<br>(42.01)    | <0.0001             | 0.84<br>(0.59) | DEV2000             | -0.007<br>(-0.015)     | 0.002<br>(0.006)     | 0.005<br>(0.017)   |
|         |                       |                     |                     |                | GRS250              | (9.017)                | (2.946)              | (0.002)            |
| HOFI    | 0.12                  | 11.93               | 0.0026              | 1.19           | DEV4000             | 5.5E-04                | 2.0E-04<br>(2.2E-04) | 0.007<br>(0.010)   |

<sup>1</sup> Bold parameter estimates and model diagnostics are based on bootstrap resampling trials. Numbers in parentheses represent parameter estimates and diagnostics from non-bootstrap models.

<sup>2</sup> See appendix 2 for definitions of landscape variables and appendix 3 for species names.



**Figure 3** Predicted effects of housing density (by general plan land-use designation) on development-sensitive species.

### Local Habitat Associations

Model results suggest that the occurrences of many species are significantly predicted by one or more habitat parameters (*table 3*). Due to low sample sizes, however, most of the final models were not sufficiently robust, as indicated by bootstrap resampling simulations. Species that were well-predicted by habitat variables (with bootstrap models significant at  $P < 0.01$ ) were, in order of model explanatory power (pseudo- $R^2$ ), western scrub-jay, orange-crowned warbler, Bewick's wren and brown-headed cowbird. Each of these species was predicted by different local habitat variables.

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**Table 3**—Significant ( $P < 0.01$ ) regression model results for local habitat variables (detections limited to within 50 m).<sup>1,2</sup>

| Species | Model type | Pseudo-R <sup>2</sup> | LR Chi <sup>2</sup>     | P                              | AIC                   | Habitat variables  | Coeff.                    | Std.Err                 | P                        |
|---------|------------|-----------------------|-------------------------|--------------------------------|-----------------------|--------------------|---------------------------|-------------------------|--------------------------|
| BCHU    | Logistic   | (0.34)                | (13.03)                 | (0.0003)                       | (0.91)                | # QW               | (0.022)                   | (0.008)                 | (0.004)                  |
| ACWO    | Poisson    | (0.52)                | (53.90)                 | (<0.0001)                      | (1.77)                | Granary Tree       | (3.581)                   | (0.578)                 | (<0.001)                 |
|         |            |                       |                         |                                |                       | # QL               | (0.202)                   | (0.057)                 | (<0.001)                 |
| NUWO    | Poisson    | (0.22)                | (11.68)                 | (0.0029)                       | (1.50)                | # QK               | (-0.911)                  | (0.415)                 | (0.028)                  |
|         |            |                       |                         |                                |                       | Grazing Level      | (0.991)                   | (0.326)                 | (0.002)                  |
| HUVI    | Logistic   | (0.44)                | (14.59)                 | (0.0007)                       | (0.79)                | Percent Slope      | (0.074)                   | (0.047)                 | (0.113)                  |
|         |            |                       |                         |                                |                       | # QK               | (1.113)                   | (0.498)                 | (0.025)                  |
| CLSW    | Poisson    | (0.49)                | (26.65)                 | (<0.0001)                      | (1.06)                | # QL               | (0.182)                   | (0.061)                 | (0.003)                  |
|         |            |                       |                         |                                |                       | Freq. Human Visits | (2.018)                   | (0.765)                 | (0.008)                  |
| WESJ    | Poisson    | <b>0.42</b><br>(0.52) | <b>41.03</b><br>(50.04) | <b>&lt;0.0001</b><br>(<0.0001) | <b>1.93</b><br>(1.71) | # QL               | <b>0.159</b><br>(0.139)   | <b>0.053</b><br>(0.032) | <b>0.003</b><br>(<0.001) |
|         |            |                       |                         |                                |                       | # Trees            | <b>-0.011</b><br>(-0.014) | <b>0.004</b><br>(0.005) | <b>0.013</b><br>(0.009)  |
|         |            |                       |                         |                                |                       | Habitat Edge       | (0.525)                   | (0.890)                 | (0.005)                  |
| BUSH    | Logistic   | (0.19)                | (7.25)                  | (0.0071)                       | (1.09)                | # QD               | (0.059)                   | (0.033)                 | (0.071)                  |
| BEWR    | Logistic   | <b>0.14</b><br>(0.42) | <b>10.64</b><br>(15.88) | <b>0.0011</b><br>(0.0012)      | <b>2.49</b><br>(1.09) | Avg. Height        | <b>-0.293</b><br>(-0.599) | <b>0.097</b><br>(0.329) | <b>0.002</b><br>(0.069)  |
|         |            |                       |                         |                                |                       | # Snags            | (1.020)                   | (0.576)                 | (0.069)                  |
|         |            |                       |                         |                                |                       | Grazing Level      | (-1.722)                  | (1.148)                 | (0.133)                  |
| HOWR    | Logistic   | (0.54)                | (10.71)                 | (0.0011)                       | (0.41)                | QW Canopy          | (0.147)                   | (0.082)                 | (0.074)                  |
| WEBL    | Poisson    | (0.73)                | (35.81)                 | (<0.0001)                      | (0.54)                | Avg. dbh           | (0.296)                   | (0.069)                 | (<0.001)                 |
| EUST    | Logistic   | (0.67)                | (23.68)                 | (<0.0001)                      | (0.57)                | # Trees            | (-0.044)                  | (0.021)                 | (0.039)                  |
|         |            |                       |                         |                                |                       | Max. dbh           | (0.120)                   | (0.053)                 | (0.024)                  |
| OCWA    | Logistic   | <b>0.25</b><br>(0.34) | <b>10.91</b><br>(14.55) | <b>0.0010</b><br>(0.0007)      | <b>1.14</b><br>(1.08) | QW Canopy          | <b>0.058</b><br>(0.051)   | <b>0.026</b><br>(0.022) | <b>0.024</b><br>(0.022)  |
|         |            |                       |                         |                                |                       | Avg. dbh           | (-0.172)                  | (0.105)                 | (0.103)                  |
| SPTO    | Logistic   | (0.37)                | (15.44)                 | (0.0004)                       | (0.99)                | Avg. dbh           | (-0.268)                  | (0.128)                 | (0.036)                  |
|         |            |                       |                         |                                |                       | # Snags            | (0.850)                   | (0.417)                 | (0.042)                  |
| CALT    | Poisson    | (0.48)                | (6.96)                  | (0.0083)                       | (0.42)                | Avg. Height        | (-1.075)                  | (0.510)                 | (0.035)                  |
| BRBL    | Poisson    | (0.44)                | (18.68)                 | (<0.0001)                      | (0.87)                | # Trees            | (-0.077)                  | (0.033)                 | (0.020)                  |
| BHCO    | Poisson    | <b>0.14</b><br>(0.32) | <b>8.12</b><br>(18.76)  | <b>0.0044</b><br>(<0.0001)     | <b>1.72</b><br>(1.45) | # QK               | <b>0.514</b><br>(0.500)   | <b>0.175</b><br>(0.177) | <b>0.003</b><br>(0.005)  |
|         |            |                       |                         |                                |                       | Rock Outcrop       | (-1.055)                  | (0.380)                 | (0.006)                  |
| BUOR    | Logistic   | (0.49)                | (9.74)                  | (0.0018)                       | (0.44)                | Avg. dbh           | (0.333)                   | (0.170)                 | (0.050)                  |

<sup>1</sup> Bold parameter estimates and model diagnostics are based on bootstrap resampling trials. Numbers in parentheses represent parameter estimates and diagnostics from non-bootstrap models.

<sup>2</sup> See *appendix 1* for definitions of local habitat variables and *appendix 3* for species names.

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Landscape and habitat associations are summarized in *table 4* for species with best-fitting landscape-level models (Pseudo-R<sup>2</sup> > 0.20) in addition to focal species included in the Oak Woodland Bird Conservation Plan (Zack and others 2000).

**Table 4**—Summary of landscape and habitat associations for species with best-fitting landscape models and CPIF focal species.<sup>1,2</sup>

| Species | CPIF focal species status | Frequency (50 m / all) | Landscape model R <sup>2</sup> (50 m / all) (pct) | Development response <sup>3</sup> | Landscape oak woodland response <sup>4</sup> | Habitat model R <sup>2</sup> (50 m) (pct) | Positive habitat correlates | Negative habitat correlates         |
|---------|---------------------------|------------------------|---|-----------------------------------|--|---|-----------------------------|-------------------------------------|
| CAQU    | 2°                        | 0.07 / 0.37            |   |                                   |  |   |                             |                                     |
| BCHU    |                           | 0.17 / 0.17            | 0 / 23  |                                   | <b>positive</b>                              | 34  | # QW                        |                                     |
| ACWO    | 1°                        | 0.29 / 0.73            |   |                                   |  | 52  | granary trees, # QL         |                                     |
| NUWO    | 2°                        | 0.27 / 0.63            |   |                                   |  | 22  | grazing level               | # QK                                |
| PSFL    |                           | 0.07 / 0.11            | - / 25  |                                   | <b>positive</b>                              |   |                             |                                     |
| BLPH    |                           | 0.19 / 0.39            | 41 / 18   | <b>positive</b>                   |  |   |                             |                                     |
| ATFL    | 2°                        | 0.36 / 0.71            | 0 / 27  | <b>negative</b>                   | <b>positive</b>                              |   |                             |                                     |
| WEKI    |                           | 0.08 / 0.23            | 22 / 14   | <b>negative</b>                   | <b>negative</b>                              |   |                             |                                     |
| HUVI    | 2°                        | 0.16 / 0.25            | 18 / 16   |                                   | <b>positive</b>                              | 44  | # QK, percent slope         |                                     |
| TRES    |                           | 0.08 / 0.16            | 28 / 23   | <b>negative</b>                   | positive                                     |   |                             |                                     |
| CLSW    |                           | 0.13 / 0.19            | 25 / 26   | <b>positive</b>                   | <b>negative</b>                              | 49  | freq. human visits, No. QL  |                                     |
| WESJ    | 1°                        | 0.39 / 0.67            | 22 / 21   | <b>positive</b>                   | <b>negative</b>                              | 52  | # QL*, habitat edge         | # trees*                            |
| YBMA    | 1°                        | 0.05 / 0.20            | - / 20  |                                   | <b>negative</b>                              |   |                             |                                     |
| OATI    | 1°                        | 0.93 / 0.99            |   |                                   |  |   |                             |                                     |
| WBNU    | 2°                        | 0.48 / 0.73            |   |                                   |  |   |                             |                                     |
| BEWR    | 2°                        | 0.47 / 0.67            |   |                                   |  | 42  | snags                       | <b>avg. height*</b> , grazing level |
| BGGN    | 1°                        | 0.01 / 0.05            |   |                                   |  | 0   |                             |                                     |
| WEBL    | 1°                        | 0.11 / 0.20            |   |                                   |  | 73  | avg. dbh                    |                                     |
| NOMO    |                           | 0.09 / 0.44            | - / 27  | <b>positive</b>                   |  |   |                             |                                     |
| EUST    | 2°                        | 0.41 / 0.53            |   |                                   |  | 67  | max. dbh                    | # trees                             |
| OCWA    |                           | 0.24 / 0.36            | 10 / 39   |                                   | <b>positive</b>                              | 34  | <b>QW canopy*</b>           | avg. dbh                            |
| SPTO    |                           | 0.23 / 0.35            | 27 / 26   |                                   | <b>positive</b>                              | 37  | snags                       | avg. dbh                            |
| CALT    | 2°                        | 0.12 / 0.40            |   |                                   |  | 48  | none                        | avg. height                         |
| RCSP    |                           | 0.15 / 0.21            | 36 / 28   | <b>negative</b>                   | <b>positive</b>                              |   |                             |                                     |
| LASP    | 1°                        | 0.17 / 0.35            | 22 / 28   | <b>negative</b>                   |  | 0   |                             |                                     |
| CHSP    |                           | 0.04 / 0.11            | - / 39  | negative                          | positive                                     |   |                             |                                     |
| WEME    |                           | 0.01 / 0.23            | - / 52  | <b>negative</b>                   | negative                                     |   |                             |                                     |

<sup>1</sup> Refer to *tables 1-3* for model details. R<sup>2</sup> values are Pseudo-R<sup>2</sup> values from Poisson or logistic regression analysis (non-bootstrap). Bold type indicates variables and species with robust bootstrap resampling results.

<sup>2</sup> See *appendix 1* for definitions of local habitat variables and *appendix 3* for species names.

<sup>3</sup> As measured by development density, parcel size, property size or edge distance.

<sup>4</sup> As measured by oak woodland proportion within any measurement radius.

## Discussion

Although the limited sampling of local habitat parameters reduced the robustness of our models, our data suggested fairly strong relationships between the occurrence and/or abundance of several bird species and local habitat variables. Clearly, local habitat characteristics directly influence a species' ability to feed, avoid predators and reproduce. Larger landscape characteristics may not be important for a songbird that meets all of its survival, feeding and reproduction goals within a small area, as long as the local habitat within its home range is suitable. This may especially be true in a landscape such as the Placer County foothills, where habitat fragmentation has generally not progressed to the stage of discrete, isolated oak woodland fragments (*sensu* Wiens 1994). Thus one would not predict that gradual extirpation of small populations from isolated habitat fragments (*sensu* MacArthur and Wilson 1967) would be an important process in this area.

Nevertheless, some of the species detected in our study did exhibit significant responses to characteristics of the surrounding landscape. Lark sparrow and Rufous-crowned sparrow abundances were negatively associated with development density, as was the occurrence of ash-throated flycatcher, western kingbird, tree swallow and western meadowlark. Conversely, the western scrub-jay, house finch and other species were positively associated with development density. This suggests that residential development in the oak woodland landscape may indirectly affect some bird species outside the area of immediate impact.

Urbanization-associated declines in bird abundance may be regulated by a variety of mechanisms, including increased urban-associated nest predators, anthropogenic habitat degradation, urban edge avoidance, increased dispersal mortality, and indirect responses to elimination of top-level predators (potentially resulting in the mesopredator release hypothesized by Soulé and others 1988). Ground-foraging birds such as lark, chipping and Rufous-crowned sparrows, may be particularly vulnerable to domestic cat (*Felis catus*) predation, as well as to ground-level disturbances such as mowing and grazing, which may limit seed availability.

With respect to nest predation, one might suspect that the higher presence of western scrub-jays, an important nest predator for many songbird species (Geupel and DeSante 1990), in more developed landscapes, could have detrimental effects on the reproductive success of other songbirds. Further demographic study would be needed to detect these effects.

Other species such as the Orange-crowned warbler, Hutton's vireo, Pacific-slope flycatcher and spotted towhee appear to respond to landscape composition and landscape-level habitat diversity but not necessarily to the presence of development *per se*. For these species, the amount, configuration and diversity of available oak woodland habitat in the surrounding landscape seems more important than the number of built structures. Although we were unable to control for local habitat conditions in our landscape models (due to small sample sizes), we did not find local habitat parameters to be strongly correlated with landscape composition. Thus we suspect that landscape-level fragmentation of oak woodland habitat, whether natural or human-induced, may affect populations of several bird species independent of local habitat conditions.

Variations in life history strategies probably make some species more susceptible than others to habitat fragmentation (Hansen and Urban 1992). Species with large foraging ranges, short dispersal distances, or widely-dispersed populations



may depend on landscapes with higher proportions of suitable habitat (oak woodland in this case). In addition, some neotropical migrants may respond to larger landscape patterns (Hansen and Urban 1992), although several researchers have argued that traditional fragmentation paradigms based on eastern U.S. studies may not apply in the western U.S., where wooded habitats tend to be naturally fragmented (Verner and Larson 1989, Tewksbury and others 1998). Our results, though preliminary, support the notion that migratory species may be more susceptible to changes in the amount and configuration of oak woodland habitat configuration. Of the eight species that were positively associated with the proportion of oak woodland habitat in the surrounding landscape (after bootstrap validation), all but the Rufous-crowned sparrow and possibly spotted towhee are short-distance or neotropical migrants.

### ***Comparisons with Other Studies***

For many of the species detected, our results are consistent with previous similar studies. The negative association between Rufous-crowned sparrow abundance and development density, as well as urban edge distance, is consistent with the results of two southern California scrub studies (Bolger and others 1997 and Stralberg 1999), which also found negative landscape-level associations with urbanization for this species. Rufous-crowned sparrows tend to be patchily-distributed in our study area, as they are generally restricted to grassy slopes with scattered boulders and/or shrubs. While this species is capable of colonizing successional habitats (Shuford 1993, Williams, personal observation), its dispersal ability through unsuitable habitats may be limited.

Results for other resident species generally correspond with those of similar studies, which also found positive urbanization associations for northern mockingbird (Bolger and others 1997, Stralberg 1999), house finch (Bolger and others 1997, Merenlender and others 1998) and western scrub-jay (Merenlender and others 1998). Other resident species for which we found no significant development associations, including Bewick's wren, California quail, California towhee and bushtit, are more scrub- than woodland-associated and often occupy shrubby habitats within residential areas (Blair 1996). In scrub habitat, neither Bolger and others (1997) nor Stralberg (1999) found significant urbanization associations for any of these species.

Among short-distance migrants, the lark sparrow and western meadowlark responded to both development density and landscape-level habitat composition (with lark sparrow preferring oak woodland and western meadowlark preferring grassland/oak savanna-dominated landscapes). These species were also found by Bolger and others (1997) to be edge/fragmentation sensitive. For the lark sparrow, Breeding Bird Atlases in Sonoma and Monterey Counties provide anecdotal evidence that the species is no longer found in apparently suitable habitat near urban areas where it was formerly present (Humble 1999).

### ***Caveats***

With respect to GIS data sources, the vegetation layer (Forest Service 2000) used to calculate landscape composition and habitat diversity was fairly coarse (2.5 acre minimum). It was thought to overestimate oak woodland types, misidentifying non-native ornamental trees as oaks or classifying open oak savanna as grassland. Furthermore, landscape metrics calculated at large scales, particularly at the 4000 m

radius, may reflect physical gradients unrelated to urbanization or landscape composition *per se*.

We are also cautious about interpreting local habitat relationships as they were based on a small subset of sites that was not randomly selected. Although they do represent the extreme ends of the development spectrum (urban parks and large undeveloped parcels), some portions of our study area are underrepresented, primarily those that contain smaller rural residential parcels. Habitat models for most of the species examined were not robust enough to withstand bootstrap resampling simulations. Thus some of the habitat relationships we found may have been spurious, and deserve further examination with a more complete dataset.

Furthermore, the results presented here are based on a single year of data. High levels of background variability in point count surveys found by other researchers in similar habitat (Verner and others 1996) suggest that additional years of data are needed to validate our models. Additional data would also increase detection rates, allowing more robust analyses of seemingly development-sensitive species with low detection rates (e.g., chipping sparrow).

Finally, as with any study that attempts to relate point count survey results with habitat or landscape characteristics, we must caution that adult abundance (or presence) is not necessarily an indication of habitat quality. Many areas may function as population sinks, drawing in birds from healthy populations elsewhere, yet failing to replace the population with new recruits (Brawn and Robinson 1996, Donovan and others 1995). To fully assess the relationship of rural residential development and habitat fragmentation on breeding birds, data on reproductive success and adult survival are needed.

### ***Implications for Conservation Planning***

Our results highlight the fact that the importance of local habitat and landscape characteristics may vary greatly by species. On one end of the response spectrum, several sparrow species appear to experience negative consequences of human development. Our models predict that lark sparrow densities would be reduced (below the mean detected in this study) at development densities greater than 5 acres per parcel, and would be virtually non-existent (albeit with large error bounds) at a one acre per parcel density (*fig. 5*). Although we lack information on sustainable densities for these species (but see Zack and others 2000), low densities predicted by our models are of concern. Further study over multiple years would be necessary to identify population trends.

For other woodland species, including orange-crowned warbler and Hutton's vireo, the quality, the amount and configuration of available habitat in the surrounding landscape seem more important than the number of built structures. This suggests that development that retains oak woodlands (including a significant interior live oak component within the blue oak matrix) may still provide adequate habitat for these species. Other species such as Bewick's Wren appear insensitive to development and landscape characteristics but are well-predicted by the presence of certain local habitat features.

Conserving habitat for birds across this development-sensitivity spectrum is no easy task, and may hinge upon several complementary strategies:

- Preserving the remaining large, undeveloped parcels of oak woodland (>40 acres) should help ensure the local persistence of landscape-sensitive species.
- Limiting the subdivision of rural residential parcels into small (1-5 acre) ranchettes may help sustain development-sensitive species in more marginal areas.
- Managing oak woodlands on small parcels to retain a variety of habitat components including large trees, snags and interior live oaks can provide habitat for a host of human-tolerant avian species.
- Oak woodland species have varying habitat needs, so maintaining a mosaic of habitat types is important for preserving a suite of oak woodland species.

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**Appendix 1**—Descriptions of local habitat variables measured (or estimated) at each survey location for the area within a 50 m radius.

| Variable      | Description                       | Variable           | Description   |
|---------------|-----------------------------------|--------------------|---|
| Percent slope | Percent slope of point            | Avg. height        | Average height of canopy (m)  |
| Aspect        | Slope aspect of point             | Max. height        | Height of tallest tree (m)  |
| # QD          | Number of blue oaks >2" dbh       | Shrub cover        | Shrub cover category (0-5)  |
| # QW          | Number of live oaks >2" dbh       | Bare soil          | Amount of exposed soil (0-3)  |
| # QL          | Number of valley oaks >2" dbh     | Grass height       | Herbaceous layer height category (1-4)  |
| # QK          | Number of black oaks >2" dbh      | Grass density      | Herbaceous layer density category (0-3)                                       |
| # PS          | Number of gray pines >2" dbh      | Grazing intensity  | Grazing intensity (0-3)   |
| # PP          | Number of ponderosa pines >2" dbh | Rock outcrops      | Rock outcrop amount (0-4)   |
| Trees         | Number of total trees >2" dbh     | Granary tree       | Number of Acorn Woodpecker granary trees                                      |
| Snags         | Number of snags >5" dbh           | Down wood          | Estimated number of pieces of downed wood >10cm in diameter and ≥1m in length |
| Canopy cover  | Percent tree canopy cover         | Freq. human visits | Estimated level of human visitation during breeding season (0-4)              |
| QW canopy     | Percent live oak canopy cover     | Habitat edge       | Presence of obvious ecotone   |
| Avg. dbh      | Average dbh of all trees          | Grazing level      | Estimated level of grazing intensity (0-3)                                    |
| Max. dbh      | Diameter of largest tree          |                    |   |

**Appendix 2**—Descriptions of landscape-level variables measured for each survey location.

| Variable                | Abbreviations                             | Description   |
|-------------------------|---|---|
| Development density     | DEV250, DEV500, DEV1000, DEV2000, DEV4000 | Number of human-built structures within 250 m-4000 m radius circle, as estimated by development status of parcel centroids  |
| Oak woodland proportion | OAK250, OAK500, OAK1000, OAK2000, OAK4000 | Percent of 250 m-4000 m radius circle containing oak woodland habitat, including blue oak woodland, blue oak-foothill pine, valley oak, montane hardwood and montane hardwood-conifer |
| Grassland proportion    | GRS250, GRS500, GRS1000, GRS2000, GRS4000 | Percent of 250 m-4000 m radius circle containing annual grassland, including some oak savanna   |
| Habitat diversity       | H250, H500, H1000, H2000, H4000           | Shannon-Wiener diversity index ( $H = - \sum_i p_i \ln(p_i)$ , where $p_i$ = area of $i^{\text{th}}$ habitat type) within 250 m-4000 m radius circle                                  |
| Elevation               |   | Elevation (m) of point count location based on 30 m digital elevation model (USGS)  |
| Stream distance         |   | Distance (m) to nearest stream based on 1:100K hydrography GIS layer (Teale Data Center)  |
| Road distance           |   | Distance (m) to nearest road based on 1:100K road GIS layer (Teale Data Center)   |
| Edge distance           |   | Distance (m) to nearest human structure based on a combination of field notes, parcel base map and digital aerial photos  |

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**Appendix 3**—Summary of bird species detected at 75 sites visited twice during the breeding season (excluding waterfowl, shorebirds and raptors).<sup>1</sup>

| Common name               | Latin name                                   | AOU Code | No. of sites detected (≤50 m) | No. of sites detected (unlimited) | Breeding status | Migratory status |
|---------------------------|--|----------|-------------------------------|-----------------------------------|-----------------|------------------|
| Ring-neck pheasant        | <i>Phasianus colchicus</i>                   | RPHE     | 4                             | 30                                | B               | R                |
| Wild turkey               | <i>Meleagris gallopavo</i>                   | WITU     | 4                             | 11                                | B               | R                |
| California quail          | <i>Callipepla californica</i>                | CAQU     | 5                             | 28                                | B               | R                |
| Mourning dove             | <i>Zenaida macroura</i>                      | MODO     | 20                            | 46                                | B               | R                |
| Black swift               | <i>Cypseloides niger</i>                     | BLSW     | 1                             | 2                                 | ?               | NTM              |
| Black-chinned hummingbird | <i>Archilochus alexandri</i>                 | BCHU     | 13                            | 13                                | B               | NTM              |
| Anna's hummingbird        | <i>Calypte anna</i>                          | ANHU     | 32                            | 34                                | B               | SDM              |
| Calliope hummingbird      | <i>Stellula calliope</i>                     | CAHU     | 1                             | 1                                 | ?               | NTM              |
| Acorn woodpecker          | <i>Melanerpes formicivorus</i>               | ACWO     | 22                            | 55                                | B               | R                |
| Nuttall's woodpecker      | <i>Picoides nuttallii</i><br><i>Picoides</i> | NUWO     | 20                            | 47                                | B               | R                |
| Downy woodpecker          | <i>pubescens</i>                             | DOWO     | 4                             | 4                                 | B               | R                |
| Hairy woodpecker          | <i>Picoides villosus</i>                     | HAWO     | 1                             | 2                                 | B               | R                |
| Western wood-pewee        | <i>Contopus sordidulus</i>                   | WEWP     | 3                             | 12                                | B               | NTM              |
| Willow flycatcher         | <i>Empidonax traillii</i>                    | WIFL     | 3                             | 3                                 | NB              | N/A              |
| Hammond's flycatcher      | <i>Empidonax hammondii</i>                   | HAFL     | 1                             | 1                                 | NB              | N/A              |
| Dusky flycatcher          | <i>Empidonax oberholseri</i>                 | DUFL     | 1                             | 1                                 | NB              | N/A              |
| Pacific slope flycatcher  | <i>Empidonax difficilis</i>                  | PSFL     | 5                             | 8                                 | B               | NTM              |
| Black Phoebe              | <i>Sayornis nigricans</i>                    | BLPH     | 14                            | 29                                | B               | R-SDM            |
| Ash-throated flycatcher   | <i>Myiarchus cinerascens</i>                 | ATFL     | 27                            | 53                                | B               | NTM              |
| Western kingbird          | <i>Tyrannus verticalis</i>                   | WEKI     | 6                             | 16                                | B               | NTM              |
| Hutton's vireo            | <i>Vireo huttoni</i>                         | HUVI     | 12                            | 19                                | B               | NTM              |
| Warbling vireo            | <i>Vireo gilvus</i>                          | WAVI     | 5                             | 8                                 | NB              | NTM              |
| Tree swallow              | <i>Tachycineta bicolor</i>                   | TRES     | 6                             | 12                                | B               | NTM              |
| Violet-green swallow      | <i>Tachycineta thalassina</i>                | VGSW     | 10                            | 13                                | B               | NTM              |

Appendix 3 (cont.)



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| Common name                 | Latin name                      | AOU code | No. of sites detected ( $\leq 50$ m) | No. of sites detected (unlimited) | Breeding status | Migratory status |
|-----------------------------|---------------------------------|----------|--------------------------------------|-----------------------------------|-----------------|------------------|
| Cliff swallow               | <i>Petrochelidon pyrrhonota</i> | CLSW     | 10                                   | 14                                | B               | NTM              |
| Barn swallow                | <i>Hirundo rustica</i>          | BASW     | 2                                    | 3                                 | B               | NTM              |
| Western scrub-jay           | <i>Aphelocoma californica</i>   | WESJ     | 29                                   | 50                                | B               | R                |
| Yellow-billed magpie        | <i>Pica nuttalli</i>            | YBMA     | 4                                    | 15                                | B               | R                |
| American crow               | <i>Corvus brachyrhynchos</i>    | AMCR     | 4                                    | 22                                | B               | R-SDM            |
| Oak titmouse                | <i>Baeolophus inornatus</i>     | OATI     | 70                                   | 74                                | B               | R                |
| Bushtit                     | <i>Psaltriparus minimus</i>     | BUSH     | 48                                   | 57                                | B               | R                |
| White-breasted nuthatch     | <i>Sitta carolinensis</i>       | WBNU     | 36                                   | 55                                | B               | R                |
| Bewick's wren               | <i>Thryomanes bewickii</i>      | BEWR     | 35                                   | 50                                | B               | R                |
| House wren                  | <i>Troglodytes aedon</i>        | HOWR     | 6                                    | 31                                | B               | SDM-NTM          |
| Blue-gray gnatcatcher       | <i>Polioptila caerulea</i>      | BGGN     | 1                                    | 4                                 | B               | SDM-NTM          |
| Western bluebird            | <i>Sialia mexicana</i>          | WEBL     | 8                                    | 14                                | B               | R-SDM            |
| Swainson's thrush           | <i>Catharus ustulatus</i>       | SWTH     | 1                                    | 2                                 | NB              | N/A              |
| American robin              | <i>Turdus migratorius</i>       | AMRO     | 8                                    | 31                                | B               | SDM              |
| Wrentit                     | <i>Chamaea fasciata</i>         | WREN     | 4                                    | 11                                | B               | R                |
| Northern mockingbird        | <i>Mimus polyglottos</i>        | NOMO     | 7                                    | 33                                | B               | R                |
| European starling           | <i>Sturnus vulgaris</i>         | EUST     | 31                                   | 40                                | B               | R                |
| Cedar waxwing               | <i>Bombycilla cedrorum</i>      | CEWA     | 1                                    | 3                                 | NB              | N/A              |
| Orange-crowned warbler      | <i>Vermivora celata</i>         | OCWA     | 18                                   | 27                                | B               | SDM-NTM          |
| Yellow warbler              | <i>Dendroica petechia</i>       | YWAR     | 5                                    | 7                                 | ?               | NTM              |
| Yellow-rumped warbler       | <i>Dendroica coronata</i>       | AUWA     | 1                                    | 2                                 | NB              | N/A              |
| Black-throated Gray warbler | <i>Dendroica nigrescens</i>     | BTYW     | 1                                    | 1                                 | NB              | N/A              |
| Townsend's warbler          | <i>Dendroica townsendi</i>      | TOWA     | 2                                    | 4                                 | NB              | N/A              |
| Wilson's warbler            | <i>Wilsonia pusilla</i>         | WIWA     | 7                                    | 9                                 | NB              | N/A              |
| Yellow-breasted chat        | <i>Icteria virens</i>           | YBCH     | 1                                    | 7                                 | B               | NTM              |
| Western tanager             | <i>Piranga ludoviciana</i>      | WETA     | 4                                    | 8                                 | NB              | N/A              |

**Appendix 3 (cont.)**

| Common name | Latin name | AOU code | No. of sites | No. of sites detected | Breeding status | Migratory status |
|-------------|------------|----------|--------------|-----------------------|-----------------|------------------|
|-------------|------------|----------|--------------|-----------------------|-----------------|------------------|

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|                        |                                  | detected (unlimited) |    |    |   |         |
|------------------------|----------------------------------|----------------------|----|----|---|---------|
|                        |                                  | (<=50 m)             |    |    |   |         |
| Spotted towhee         | <i>Pipilo maculatus</i>          | SPTO                 | 17 | 26 | B | R-SDM   |
| California towhee      | <i>Pipilo crissalis</i>          | CALT                 | 9  | 30 | B | R       |
| Rufous-crowned sparrow | <i>Aimophila ruficeps</i>        | RCSP                 | 11 | 15 | B | R       |
| Chipping sparrow       | <i>Spizella passerina</i>        | CHSP                 | 3  | 8  | B | SDM-NTM |
| Lark sparrow           | <i>Chondestes grammacus</i>      | LASP                 | 13 | 26 | B | SDM     |
| Song sparrow           | <i>Melospiza melodia</i>         | SOSP                 | 3  | 8  | B | SDM     |
| Black-headed grosbeak  | <i>Pheucticus melanocephalus</i> | BHGR                 | 10 | 25 | B | NTM     |
| Lazuli bunting         | <i>Passerina amoena</i>          | LAZB                 | 18 | 29 | B | NTM     |
| Western meadowlark     | <i>Sturnella neglecta</i>        | WEME                 | 1  | 17 | B | SDM     |
| Red-winged blackbird   | <i>Agelaius phoeniceus</i>       | RWBL                 | 6  | 20 | B | R-SDM   |
| Brewer's blackbird     | <i>Euphagus cyanocephalus</i>    | BRBL                 | 7  | 15 | B | SDM     |
| Brown-headed cowbird   | <i>Molothrus ater</i>            | BHCO                 | 25 | 36 | B | SDM-NTM |
| Bullock's oriole       | <i>Icterus bullockii</i>         | BUOR                 | 9  | 17 | B | NTM     |
| Hooded oriole          | <i>Icterus cucullatus</i>        | HOOR                 | 1  | 2  | B | NTM     |
| House finch            | <i>Carpodacus mexicanus</i>      | HOFI                 | 35 | 49 | B | SDM     |
| Lesser goldfinch       | <i>Carduelis psaltria</i>        | LEGO                 | 52 | 61 | B | SDM     |
| Lawrence's goldfinch   | <i>Carduelis lawrencei</i>       | LAGO                 | 3  | 2  | B | SDM     |
| American goldfinch     | <i>Carduelis tristis</i>         | AMGO                 | 15 | 21 | B | SDM     |
| House sparrow          | <i>Passer domesticus</i>         | HOSP                 | 3  | 10 | B | R       |

<sup>1</sup> B = Breeding, NB = Not Breeding, NTM = Neotropical Migrant, SDM = Short-distance Migrant, R=Resident