

REGIONAL ANALYSIS OF RIPARIAN BIRD SPECIES RESPONSE TO VEGETATION AND LOCAL HABITAT FEATURES

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ABSTRACT.—We investigated relationships between riparian bird abundance and local vegetation characteristics and habitat features across the Sacramento/San Joaquin Valley, California. Number of detections was analyzed for each of 21 species from point count surveys over a 4-year period at 22 sites from three regions (Sacramento River, Cosumnes River, and San Joaquin River) in relation to 16 measures of habitat and vegetation composition within 50 m of 184 survey points. Tree variables, including tree height and trunk diameter, were often important, as was specific composition of tree species, especially Fremont cottonwood (*Populus fremontii*) and valley oak (*Quercus lobata*). Effects of mugwort (*Artemisia douglasiana*) and blackberry (*Rubus* spp.) were generally positive. The median partial R^2 due to vegetation/habitat characteristics was 16% after controlling for regional differences in abundance per species. Comparisons of model results at the local versus regional scale revealed spatial variation in bird abundance was independent of spatial variation in habitat variables. The effect of a habitat variable differed among the three regions for 11 of 16 variables. Models that used one or more of the first three principal components (extracted from the 16 vegetation and habitat variables) had substantially lower predictive ability than models built using individual variables. The results emphasize the importance of both understory vegetation and tree characteristics at different spatial scales. Local vegetation and habitat characteristics are important in explaining variation in local abundance, but there is a need to develop models specific to each subregion. Received 28 July 2006. Accepted 1 March 2008.

Riparian habitat in the western United States is one of the most productive and valuable habitats for all wildlife, especially in California (Knopf 1985, Rich 2002, Faber 2003). It is also one of the most threatened habitats, with only 5% of California's original riparian habitat remaining (Katibah 1984, Abell 1989). Riparian restoration and management of riparian habitat have become management priorities for agencies and non-governmental organizations throughout California (RHJV 2004).

Successful management and conservation of birds using riparian habitat requires information on how birds respond to habitat characteristics, including changes resulting from habitat degradation or restoration. Specific information is needed regarding elements or attributes of habitats used by avian species. Earlier studies on bird-habitat associations emphasized general structural characteristics of vegetation (Lack 1933, Hildén 1965, Wiens 1969, Willson 1974, Cody 1985), but more recent studies have identified the importance of specific tree species for riparian-dependent birds (Strong and Bock 1990, Saab 1999). This is consistent with findings of Wiens and

Rotenberry (1981) that shrub-steppe birds respond more strongly to specific shrub species than to general vegetation and habitat structure. Riparian vegetation is composed of ground cover, herbs and forbs, shrubs, and trees; few studies have examined the importance of all components (Heath and Ballard 2003).

We also do not know the spatial scale at which birds respond. Previous riparian studies have either had broad spatial coverage (e.g., Tewksbury et al. 2002) or have examined factors influencing abundance at the local, territory-level scale (e.g., Strong and Bock 1990), but have rarely combined both components. Saab (1999) concluded that regional-scale factors were more important than local habitat factors in explaining variation in riparian bird abundance, but this conclusion has not been supported in other studies (Scott et al. 2003).

Little information is available as to whether bird-habitat correlations at a site or cluster of sites apply across larger spatial scales (e.g., across different watersheds or regions). This limits our ability to successfully generalize management recommendations based on one local study to that of other populations.

Riparian bird studies have often examined community-wide metrics (i.e., species diversity or richness), but relatively few have analyzed species-specific patterns of abundance

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for a wide variety of species. Bird species diversity is a useful metric (MacArthur and MacArthur 1961), but does not indicate how individual species respond to specific habitat features, which may vary by species (Howell et al. 2000). Studies focused on a few "focal" species can be informative, but raise the question of how representative findings or predictions are for the entire community (Chase et al. 2000).

We investigated relationships between the abundance of 21 landbird species (20 passerines and 1 near-passerine) and local habitat or vegetation characteristics at 22 sites spanning 400 km of the Central Valley of California, including the Sacramento, San Joaquin, and Cosumnes rivers. All sites were classified as "valley-foothills riparian habitat" (Mayer and Laudenslayer 1988). Specific objectives were to develop and evaluate statistical predictive models for each of the 21 species to: (1) identify which vegetation or habitat variables (hereafter habitat variables) explain variation in abundance in each species at the local scale, (2) characterize commonalities and differences among bird species in the variables of influence and direction of their influence, (3) examine the consistency of effects of these variables for each species across three different regions of the Central Valley, (4) quantify the magnitude of variation in abundance of individual species explained by variation in habitat characteristics at the local scale, and (5) compare predictive abilities of models based on principal components with models based on the individual habitat variables.

METHODS

Study Sites.—There were three study areas: along the Middle Sacramento River, Cosumnes River, and San Joaquin River, all within the Sacramento/San Joaquin River watershed (Fig. 1). Studies in the Sacramento River region were conducted at 10 sites, spanning 160 km between Colusa and Red Bluff ($n = 84$ point count stations). Data were collected at six sites in the Cosumnes River region spanning ~15 km ($n = 44$ point count stations). Data in the San Joaquin River region were collected at six sites within the San Luis National Wildlife Refuge spanning ~20 km ($n = 54$ point count stations).

Field Methods.—Point count surveys

(Ralph et al. 1993, 1995) were conducted three times per breeding season during May and early June. Surveys were conducted in 4 years, 1995–1998 for Cosumnes and Sacramento river sites, and 1995–1997 for San Joaquin sites. All species detected within 50 m of the observer were recorded over a 5-min period at each point count station. Surveys were conducted beginning 15 min after sunrise and concluding within 4 hrs of sunrise. Surveys were not conducted during rainy or excessively windy conditions. Stations were 200–250 m apart and in all habitats within a site; only those in riparian habitat (vs. those in crops, grasslands, orchards, etc.) were included in this study.

Fine-scale vegetation and habitat assessment were conducted at all point count stations at least once during 1995–1997. We used the most recent year of data if vegetation was surveyed in more than 1 year; there was no assessment of change in vegetation during the survey period. We used a modified version of the relevé (Estimation of Stand Characteristics) method of vegetation assessment following Ralph et al. (1993). Vegetation at each point count station was assessed using a 50-m radius (0.785 ha) plot centered on the point count survey station. General characteristics of the plot were recorded (including maximum tree dbh, tree height, presence of water, etc.), and cover, abundance, and height of each vegetation stratum (tree, shrub, herb) were estimated. These were defined following Ralph et al. (1993) with respect to height from ground, not botanically. The tree layer was >5 m, the shrub layer was 0.5 to 5 m, and the herb layer was <50 cm. Species composition and species richness of trees and shrubs were ascertained within each vegetation stratum. Percent absolute cover was recorded for each species. All willows (*Salix* spp.) were pooled for analysis. A given species could be recorded either as shrubs or trees depending on height. Presence of water was defined with respect to open water within the 50-m radius (1 if water present within 50 m, 0 otherwise).

Selection of Habitat Variables.—We considered 16 habitat variables, with region as an additional analytical variable (Table 1). We chose variables that we considered potentially biologically relevant and/or of management interest (Heath and Ballard 2003). A principal

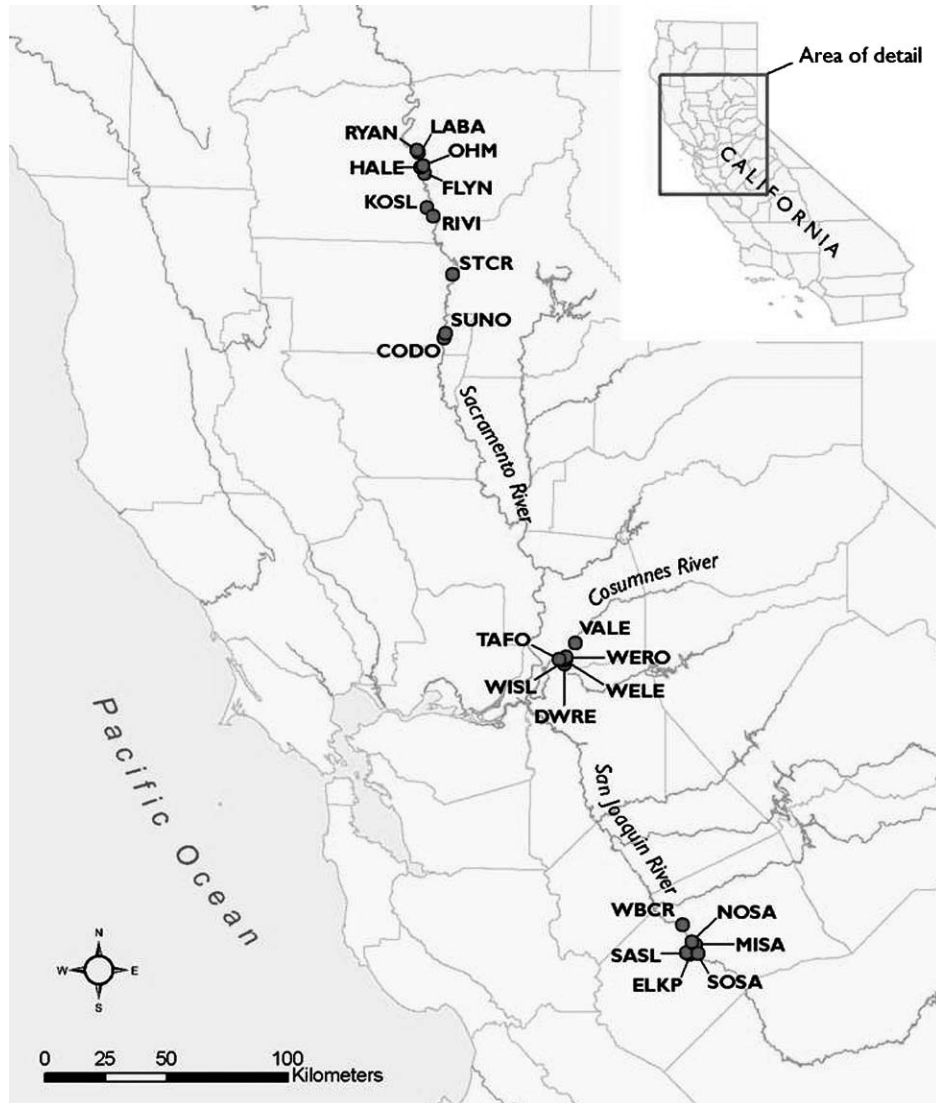


FIG. 1. Study area, showing 3 regions (Sacramento, Cosumnes, and San Joaquin rivers). Sites within region with four letter abbreviations, from north to south: RYAN = Ryan; LABA = Labaranca; OHM = Ohm; HALE = Haleakala; FLYN = Flynn; KOSL = Kopta Slough; RIVI = River Vista; STCR = Stony Creek; SUNO = Sul Norte; CODO = Codora; VALE = Valensin; TAFO = Tall Forest; WERO = Wendell's Road; WELE = Wendell's Levee; WISL = Wilson's Slough; DWRE = DWR East; WBCR = West Bear Creek; NOSA = North San Joaquin; MISA = Middle San Joaquin; SASL = Salt Slough; ELKP = Elk Pasture; and SOSA = South San Joaquin.

criterion for selection of vegetation variables was adequacy of representation in at least two of the three regions. Shrub, tree, or herb species prevalent in only one region were not included, nor were plant species that were uncommon. Preliminary analyses indicated that transformations of maximum tree height and

dbh provided better predictors of bird abundance than untransformed values for each variable. We used tree height index (Table 1) and the natural log of maximum tree dbh for analyses. The transformation allowed for non-linear, monotonic effects of tree height or maximum tree dbh on abundance.

TABLE 1. Principal component analysis ($n = 178$) for 16 vegetation and habitat variables. Loadings for the first five principal components. Variables with loadings of absolute value ≥ 0.35 indicated by*.

| Variable | Mean | Eigenvectors | | | | |
|--------------------------------|------|--------------|---------|--------|---------|---------|
| | | I | II | III | IV | V |
| Water (Yes = 1; No = 0) | 0.55 | 0.046 | 0.285 | 0.445* | -0.166 | 0.109 |
| Tree cover (%) | 35.1 | 0.318 | -0.317 | 0.075 | -0.217 | -0.264 |
| Shrub cover (%) | 24.5 | 0.289 | 0.288 | -0.127 | 0.395* | -0.108 |
| Herb cover (%) | 34.1 | -0.383* | 0.116 | 0.029 | -0.162 | 0.290 |
| Tree species richness | 3.42 | 0.357* | 0.177 | -0.109 | 0.097 | 0.079 |
| Shrub species richness | 4.31 | 0.305 | 0.266 | -0.172 | 0.044 | 0.168 |
| Tree dbh index ^a | 3.68 | 0.287 | -0.124 | 0.353* | -0.081 | 0.242 |
| Tree height index ^b | 3.20 | 0.340 | -0.269 | -0.056 | -0.029 | 0.243 |
| Willow shrub cover (%) | 7.88 | -0.012 | 0.165 | 0.362* | 0.478* | 0.007 |
| Willow tree cover (%) | 12.7 | -0.047 | 0.014 | 0.537* | -0.011 | -0.354* |
| Cottonwood tree cover (%) | 4.23 | 0.116 | -0.470* | -0.193 | -0.015 | -0.178 |
| Valley oak shrub cover (%) | 0.84 | -0.106 | 0.2556 | -0.329 | 0.175 | -0.381* |
| Valley oak tree cover (%) | 6.13 | 0.225 | 0.264 | -0.073 | -0.401* | 0.226 |
| Blackberry cover (%) | 3.12 | 0.269 | 0.302 | -0.053 | -0.221 | -0.089 |
| Mugwort cover (%) | 2.40 | 0.008 | -0.228 | 0.003 | 0.471* | 0.498* |
| Grass cover (%) | 15.0 | -0.315 | 0.074 | -0.192 | -0.181 | 0.246 |

^a Index = $\ln(\text{maximum tree dbh} + 1)$; maximum tree dbh measured in cm, 0 if no trees present.

^b Scored 0 if no trees; otherwise 1, 2, 3, 4, or 5, classifying height into groups corresponding to: <9, 9 to <13, 13 to <18, 18 to <25, and ≥ 25 m.

Distinguishing the potential effect of California blackberry (*Rubus ursinus*) from Himalayan blackberry (*R. discolor*) on bird species was of management interest (native vs. non-native invasive), but California blackberry was either uncommon or absent from most sites. Thus, we analyzed only the summed blackberry cover.

Selection of Avian Species for Analysis.—We focused on landbird species known to breed in the study region (presence throughout the breeding season, mist net captures, and nest-monitoring at nearby sites). We selected the 20 most abundant species based on detections at point count stations in the riparian sites. Four of the 20 species were identified as focal species by the Riparian Habitat Joint Venture (RHJV 2004). We also included as many additional RHJV-designated riparian focal species as possible with adequate sample size. Only Blue Grosbeaks (scientific names for bird species analyzed are in the Appendix), among species not in the top 20, met the requirement of at least 100 detections. Bank Swallows (*Riparia riparia*) were detected in similar numbers to Blue Grosbeaks but the species is colonial and not reliably surveyed using point counts (Ralph et al. 1993, 1995). Thus, this species was not included. Twenty-

one species were analyzed: 20 passerines species and Nuttall's Woodpecker (Appendix).

Treatment of Dependent Variables and Principal Components.—We calculated an abundance index for species by summing the number of detections per species over the three surveys in a year. We then analyzed $\ln(\text{mean detections} + \text{constant})$, where the mean was calculated over all years and the constant was the smallest non-zero abundance value (Nur et al. 1999). Log-transformation of mean total detections per species was used because it yielded better predictive relationships with independent variables than use of untransformed mean detections and served to better normalize residuals. Residuals of the resultant models in all cases but one were approximately normally distributed (*sktest* procedure and examination of quantile-quantile plots for a normal distribution) (Nur et al. 1999, StataCorp. 2003). The exception was Bullock's Oriole, but log transformation was still preferred to no transformation. Analysis of log-transformed data is preferred if birds respond in a multiplicative manner to habitat factors, which is reasonable (i.e., with every unit increase in the independent variable, abundance increases by a fixed proportion or decreases by the same proportion) (Nur et al. 1999).

Mean values analyzed were based on a different number of years per point count station. Analyses were weighted by the square-root of the number of years of data (mostly 4 yrs/point, but in some cases 2 or 3 yrs) because the standard error of the mean detection per point is inversely proportional to the square-root of the number of years of data (Neter et al. 1990). Abundance values derived from fewer years of data contributed less to model results than those with more years of data. We conducted a principal component analysis (PCA) of the habitat variables to examine how well the 16 variables were represented by a smaller number of principal components (Legendre and Legendre 1998, Lichstein et al. 2002).

Model Selection and Statistical Analysis.—We used backward variable selection, considering each species one at a time, following Catchpole et al. (2004:15) for identifying the best statistical model. We started with 16 independent, quantitative variables for each species, plus region, treated as a categorical variable in the model (Sacramento, Cosumnes, or San Joaquin rivers). We used a two-stage model selection process (Zuur et al. 2007); first using a backward stepwise-procedure to choose the model with lowest Akaike Information Criterion (AIC) value. We then used a stepwise procedure to drop, one at a time, any additional variables from the AIC-preferred model that were not significant at the $P \leq 0.10$ level, using an F -test. This second stage was necessary because AIC is often over inclusive, selecting models that include nonsignificant variables, even at the $P < 0.1$ level. Model selection using AIC, especially with large sample sizes, leads to inclusion of extraneous (ecologically unrelated) variables (Brooks et al. 2000, Hansen and Yu 2001, Davison 2003:404).

We considered an alternative approach, the Bayes Information Criterion (BIC; Schwarz 1978), which has been criticized for being too stringent (i.e., setting thresholds too high for including additional variables; Hansen and Yu 2001). The approach we used was intermediate between AIC alone and BIC.

We evaluated the consistency of the effect of each variable identified in the optimal statistical model for each species by testing for an interaction of that variable with region,

while including other identified variables in the statistical model. We did not evaluate interactions of variables not included in the final species-specific model. We evaluated the significance of the specified interaction while including the second (or third) interaction in the model where more than one interaction was identified for a species at $P < 0.1$. We compared total R^2 and partial R^2 (Neter et al. 1990) for models that explain variation in abundance in relation to: (1) habitat variables only, (2) regional differences only (region treated as a categorical variable), and (3) both sets of variables, considered simultaneously.

The first three principal components from the habitat variable PCA were used to statistically model the response of individual species' abundance. We compared models using the 16 habitat variables with models using the first three principal components with respect to R^2 and partial R^2 . We consider $P > 0.1$ to indicate lack of statistical significance and $P < 0.05$ to indicate statistical significance. We consider the results to be inconclusive where $0.05 < P < 0.10$, and report the P value.

RESULTS

Habitat Variables.—The overall 16-dimensional variation among independent variables was not well captured by a small number of easily interpretable principal components (Table 1). Sixty-one percent of the variance of the independent variables was accounted for by the first three principal components (proportion of the variance explained by each of the first 5 components was 0.301, 0.158, 0.151, 0.081, and 0.064, respectively).

The first component contrasted tree species richness with herb cover as those two variables loaded most strongly but in opposite directions. Thus, a survey station scored high on the first principal component if tree species richness was high and herb cover was low. The second component reflected Fremont cottonwood (*Populus fremontii*) tree cover more than any other variable. The third component loaded most strongly on willow tree cover, willow shrub cover, presence of water, and tree dbh index. The fourth component contrasted mugwort (*Artemisia douglasiana*) and willow shrub cover (both positive) with valley oak (*Quercus lobata*) tree cover (negative). The fifth component contrasted mugwort cov-

er (positive) with valley oak shrub cover and willow tree cover. Tree height index, tree cover, shrub species richness, and blackberry cover did not load strongly on any of the five components. The first three principal components were used in statistical analyses of predictors of species-specific abundance.

Species-specific Abundance Models in Relation to Vegetation and Region.—Number of detections for each species varied more than 10-fold with Spotted Towhee having the most detections and Blue Grosbeak the least (Appendix). Region was included in 17 of 21 species-specific preferred models, demonstrating variation in abundance due to region that could not be accounted for by differences due to habitat variables (Table 2). Regional differences were not apparent for House Finch, Tree Swallow, Nuttall's Woodpecker, or Bullock's Oriole. At least one habitat variable was retained for all species. Seventeen of the 21 species' models included at least three habitat variables and six species' models included at least six habitat variables (Brown-headed Cowbird, Red-winged Blackbird, House Wren, American Robin, Common Yellowthroat, and Western Wood-Pewee). Overall R^2 varied from 21 to 58% for most (17 of 21) species abundance models, but for two species overall R^2 was less than 20% (Bullock's Oriole and House Finch) and for two species overall R^2 was greater than 70% (Song Sparrow, Western Wood-Pewee).

Fifteen of the 16 habitat variables were included in at least one species model (Table 2). Grass cover was not included, either positively or negatively, for any species. Tree species richness was only included in models for two species (Spotted Towhee, negative; Bushtit, positive). Willow tree cover, was included only for House Wren. In contrast, willow shrub cover (i.e., which includes trees <5 m in height) was included in six species' models. Thirteen of the 16 variables were included in models for at least four species.

The three variables included in the most species models were herb cover (11 species), presence of water (9 species), and tree dbh index (8 species). Herb cover was often included, yet grass cover was not included. These two variables were the only two variables that tracked the herb stratum. Variables reflecting tree cover or tree size were often

included in the models. These included species-specific tree variables as well as tree dbh index (8 species) and tree height index (7 species). Tree dbh index and tree height index were not included in the same model. The effect of tree size could be captured by one of the two indices, although which index depended on the species.

Most habitat variables had both positive and negative effects, depending on bird species. The two exceptions were blackberry and mugwort, for which only positive effects were demonstrated (5 and 4 species, respectively).

Variability in the Effect of Habitat and Vegetation Across Regions.—The majority of variables, when examined species by species, did not demonstrate heterogeneity of slopes among regions (Table 3). However, most variables (11 of 15 examined) demonstrated a significant interaction ($P < 0.05$) with region for at least one species. Four variables (tree cover, shrub cover, herb cover, and tree dbh index) had significant interactions for two bird species and none had significant interactions for more than two species.

Slopes differed quantitatively, not qualitatively, in eight cases (Table 3). In these instances, slopes for the variable in question were in the same direction (all positive or all negative) when examined region by region, but because the region-specific coefficients were sufficiently dissimilar, an interaction was detected (coded "1" in Table 3). The evidence in six cases indicated the effect of a variable was confined to a single region (coded "2" in Table 3) with no effect apparent in the other two regions. There were four cases where the estimated slopes differed quantitatively and qualitatively among regions (coded "3" in Table 3). Marked contrasts were observed for the effect of tree dbh index for Common Yellowthroats (significantly positive for Sacramento sites, but significantly negative slope for Cosumnes sites), and for cottonwood tree cover for Western Kingbirds (significantly positive for Sacramento sites, but significantly negative slope for San Joaquin sites). House Wrens had a significant positive effect for mugwort cover at Sacramento sites but an apparently negative effect ($P = 0.085$) at San Joaquin sites; Blue Grosbeaks had a significant negative effect for valley oak tree cover at Co-

TABLE 2. Species-specific statistical models for abundance of 21 species in relation to 16 habitat/vegetation variables in the Central Valley of California, controlling for region (Sacramento, Cosumnes, or San Joaquin). Species names in Appendix.

| Variable | BHGR | BLGR | SPTO | ATFL | BHCO | RWBL | HOFI | HOWR | TRES | AMGO | SOSP | BUSH | WEKI | BEWR |
|---|-------|-------|-------|-------|------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Water presence | | | N** | | | N** | N**** | | P++++ | N**** | | | P+ | |
| Tree cover | | | P++ | | | | N** | | | | | | N**** | |
| Shrub cover | | | P++++ | | | | N* | | | N** | P+++ | | N**** | |
| Herb cover | N**** | | | | P+++ | P++++ | | N**** | | | | P++++ | | N**** |
| Tree species richness | | | N**** | | | | | | | | | | | |
| Shrub species richness | | | | P+++ | N* | | | | | | | | | |
| Tree dbh index | | N** | P++++ | | P++ | N**** | P++++ | P+++ | P+++ | P+++ | N**** | | | P++ |
| Tree height index | | | | P++++ | | | N**** | | | | | | | |
| Willow shrub cover | | P++ | | | | | | | | | | | | |
| Willow tree cover | | | | | | | | P+ | | | | | | |
| Cottonwood tree cover | | P++ | | | | | | P+++ | P+++ | N** | | | | P++ |
| Valley oak shrub cover | | | | | | | | | | | | | | |
| Valley oak tree cover | | N* | | | | P+++ | | | | | N* | | | |
| Blackberry cover | | N**** | | | N** | N**** | P++++ | P++++ | N** | N** | | P+++ | | P+++ |
| Mugwort cover | | | | | P+ | P+ | | | | | | | | |
| Grass cover | | | | | | | | | | | | | | |
| Region in final model? | Yes | Yes | Yes | Yes | Yes | Yes | No | Yes | No | Yes | Yes | Yes | Yes | Yes |
| R ² final model (%) | 57.4 | 25.7 | 44.8 | 29.6 | 26.4 | 57.6 | 18.4 | 48.7 | 29.1 | 20.9 | 71.2 | 37.7 | 45.7 | 44.0 |
| Vegetation/habitat variables in model (n) | 3 | 3 | 5 | 2 | 6 | 6 | 3 | 8 | 4 | 5 | 3 | 2 | 5 | 3 |

N and * are negative, P and + are positive. * or + indicates 0.05 < P < 0.10. ** or ++ indicates 0.05 < P < 0.01. *** or +++ indicates 0.001 < P < 0.01. **** or ++++ indicates P = 0.001 or less. Str (Strong) refers to P < 0.01; Mod (Moderate) refers to 0.01 ≤ P < 0.10.

TABLE 2. Continued.

| Variable | AMRO | NUWO | BUOR | WESJ | LAZB | COYE | WEWP | Response summary | | | | | |
|---|-------|-------|------|-------|-------|-------|-------|------------------|---------|---------|---------|---------|--|
| | | | | | | | | Totals | Str Neg | Mod Neg | Str Pos | Mod Pos | |
| Water presence | P+++ | | | | N** | N*** | P++ | 9 | 2 | 3 | 2 | 2 | |
| Tree cover | N** | | | P++++ | | P+++ | | 6 | 2 | 1 | 2 | 1 | |
| Shrub cover | N** | | | P+ | | N*** | | 7 | 2 | 3 | 2 | 0 | |
| Herb cover | N** | N*** | | P+ | P++++ | P++++ | N*** | 11 | 5 | 1 | 4 | 1 | |
| Tree species richness | | | | P+ | | | N*** | 2 | 1 | 0 | 1 | 0 | |
| Shrub species richness | P++ | | | | | P+++ | P++++ | 4 | 1 | 1 | 1 | 1 | |
| Tree dbh index | | | | | | | | 8 | 1 | 1 | 3 | 3 | |
| Tree height index | | P++++ | | | | | | 7 | 1 | 0 | 6 | 0 | |
| Willow shrub cover | | | | P++++ | | P+++ | | 6 | 2 | 0 | 3 | 1 | |
| Willow tree cover | | | | | | | | 1 | 0 | 0 | 0 | 1 | |
| Cottonwood tree cover | | | P+ | | | N*** | | 7 | 1 | 1 | 2 | 3 | |
| Valley oak shrub cover | P++++ | | | | | | | 4 | 0 | 2 | 2 | 0 | |
| Valley oak tree cover | | | | | | | | 7 | 2 | 3 | 2 | 0 | |
| Blackberry cover | P++ | | | | | | | 5 | 0 | 0 | 1 | 4 | |
| Mugwort cover | | | | | P++++ | P+++ | P++ | 4 | 0 | 0 | 2 | 2 | |
| Grass cover | | | | | | | | 0 | 0 | 0 | 0 | 0 | |
| Region in final model? | Yes | No | No | Yes | Yes | Yes | Yes | | | | | | |
| R ² final model (%) | 29.1 | 42.7 | 1.5 | 25.2 | 55.2 | 32.9 | 77.1 | | | | | | |
| Vegetation/habitat variables in model (n) | 6 | 2 | 1 | 4 | 4 | 7 | 6 | | | | | | |

N and * are negative, P and + are positive. * or + indicates 0.05 < P < 0.10, ** or ++ indicates 0.05 < P < 0.01, *** or +++ indicates 0.001 < P < 0.01, **** or ++++ indicates P = 0.001 or less, Str (Strong) refers to P < 0.01; Mod (Moderate) refers to 0.01 ≤ P < 0.10.

TABLE 3. Interactions of 16 habitat variables with region for 20 species (Western Wood-Pewee omitted). Species names in Appendix.

| Variable | BHGR | BLGR | SPTO | ATFL | BHCO | RWBL | HOFI | HOWR | TRES | AMGO | SOSP | BUSH | WEKI | BEWR | AMRO | NUWO | BUOR | WESI | LAZB | COYE | Species examined | Species detected | |
|------------------------|------|------|------|------|------|-------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------------------|------------------|---|
| Water presence | | | | | | | | | | 1* | | | | | | | | | | | 9 | 2 | |
| Tree cover | | | 2*** | | | 2*** | 1** | | | | | | | | | | | | | | | 6 | 2 |
| Shrub cover | | | | | | | | | | 2*** | 1** | | | | | | | | | | | 7 | 2 |
| Herb cover | | | | | | 1* | | | | | | | | | | | | 2** | 2*** | | 11 | 3 | |
| Tree species richness | | | | | | | | | | | | | | | | | | | | | | 2 | 0 |
| Shrub species richness | | | | 1** | | | | | | | | | | | | | | | | | | 4 | 1 |
| Tree dbh index | | | | | | 1**** | | | | | | | | | | | | | | | 3**** | 8 | 2 |
| Tree height index | | | | | | | | | | | 1** | | | | | | | | | | | 7 | 1 |
| Willow shrub cover | | | | | | | | | | | | | | | | | | | | | | 6 | 0 |
| Willow tree cover | | | | | | | | 2** | | | | | | | | | | | | | | 1 | 1 |
| Cottonwood t. cover | | | | | | | | | | | | | 3** | | | | | | | | | 7 | 1 |
| Valley oak shrub cover | | | | | | | | | | | | | | | | | | | | | | 4 | 0 |
| Valley oak tree cover | | | | | | | | | | | | | | | | | | | | | | 7 | 1 |
| Blackberry cover | | | | | | | | | | | | | | | | | | | | | | 5 | 1 |
| Mugwort cover | | | | | | | | | | | | | | | | | | | | 1* | | 4 | 2 |
| Grass cover | | | | | | | | | | | | | | | | | | | | | | 0 | 0 |
| Interactions (n) | 0 | 1 | 1 | 1 | 1 | 0 | 3 | 1 | 2 | 0 | 2 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 0 |

* 0.05 < P < 0.10; ** 0.01 < P < 0.05; *** 0.001 < P < 0.01; **** P < 0.001; 1 = all region-specific slopes in same direction; 2 = slopes differ in sign but only the slope(s) in one direction is (are) significant at P < 0.10; 3 = two region-specific slopes with opposite sign and both are significant at P < 0.10.

TABLE 4. Coefficients of determination and partial R^2 due to habitat variables only and to regional main effect only. No significant region main effects indicated by*.

| Species | R^2 Full model | R^2 Model with habitat variables; no region | R^2 Model with region only | Partial R^2 due to habitat variable, for full model |
|-------------------------|------------------|---|------------------------------|---|
| Black-headed Grosbeak | 0.574 | 0.400 | 0.413 | 0.161 |
| Blue Grosbeak | 0.257 | 0.009 | 0.15 | 0.107 |
| Spotted Towhee | 0.448 | 0.354 | 0.214 | 0.234 |
| Ash-throated Flycatcher | 0.296 | 0.038 | 0.143 | 0.153 |
| Brown-headed Cowbird | 0.264 | 0.194 | 0.168 | 0.096 |
| Red-winged Blackbird | 0.576 | 0.415 | 0.259 | 0.317 |
| House Finch* | 0.184 | 0.184 | 0 | 0.184 |
| House Wren | 0.494 | 0.366 | 0.179 | 0.315 |
| Tree Swallow* | 0.291 | 0.291 | 0 | 0.291 |
| American Goldfinch | 0.209 | 0.157 | 0.130 | 0.079 |
| Song Sparrow | 0.712 | 0.217 | 0.687 | 0.025 |
| Bushtit | 0.377 | 0.252 | 0.301 | 0.076 |
| Western Kingbird | 0.457 | 0.29 | 0.348 | 0.109 |
| Bewick's Wren | 0.44 | 0.423 | 0.036 | 0.404 |
| American Robin | 0.291 | 0.182 | 0.117 | 0.174 |
| Nuttall's Woodpecker* | 0.432 | 0.432 | 0 | 0.432 |
| Bullock's Oriole* | 0.015 | 0.015 | 0 | 0.015 |
| Western Scrub-jay | 0.252 | 0.205 | 0.128 | 0.124 |
| Lazuli Bunting | 0.552 | 0.354 | 0.454 | 0.098 |
| Common Yellowthroat | 0.329 | 0.086 | 0.108 | 0.221 |
| Western Wood-Pewee | 0.771 | 0.214 | 0.531 | 0.240 |

summes sites, but an apparently positive effect at San Joaquin sites ($P = 0.060$).

Variance in Bird Abundance Explained by Habitat Variables, Compared to Region.—We compared the magnitude of variance in abundance explained by habitat variables with that explained by region main effects for each of the 21 species, (Table 4). The R^2 in 13 cases was 20% or more and in 7 cases was 35% or more for habitat-only statistical models, excluding region main effects, (Table 4). The amount of variance explained by region differed even more among species than variance explained by habitat variables. There were four species for which region main effects, in the absence of habitat variables, accounted for 35% or more of the variance in species abundance: Song Sparrow, Western Wood-Pewee, Lazuli Bunting, and Black-headed Grosbeak. However, in two of the four cases (Lazuli Bunting and Black-headed Grosbeak), regional differences were reduced once habitat differences were controlled. Regional differences were paramount for Western Wood-Pewee and Song Sparrow, and consideration of habitat variables did not alter this finding. The effects of region were negligible for four species. The

most anomalous species was Bullock's Oriole for which a habitat model could only explain 1.5% of the variance and region was not included.

The median partial R^2 due to habitat variables was 16%; for four species the partial R^2 due to habitat variables was over 30% (Red-winged Blackbird, Bewick's Wren, House Wren, Nuttall's Woodpecker). The median partial R^2 due to region effects was 12.5%; the partial R^2 due to region was over 30% for Song Sparrow and Western Wood-Pewee.

Species-specific Models Using Principal Components of Vegetation and Habitat Features.—We compared the performance of models for the 21 species using the first three principal components (extracted from the 16 habitat variables; Table 1) with models using individual habitat variables (Table 2). At least one of the first three principal components was at least moderately associated ($P < 0.10$) with the abundance index in a model that included region main effects for each species with the exception of Brown-headed Cowbird, Song Sparrow, and Common Yellowthroat (Table 5). The P -values for those three species associated with the best-fitting principal com-

TABLE 5. Coefficients of determination for models with region and first three principal components of habitat variables. Results are shown for models with retained principal components^a. Partial R^2 , after controlling for region, is shown for principal component model and for individual habitat variables.

| Species | R^2 for model with region and principal component(s) ^a | Partial R^2 due to principal component(s) ^b | Partial R^2 due to individual habitat variables | Principal components retained ^c |
|-------------------------|---|--|---|--|
| Black-headed Grosbeak | 0.519 | 0.106 | 0.161 | I |
| Blue Grosbeak | 0.186 | 0.036 | 0.107 | I |
| Spotted Towhee | 0.382 | 0.168 | 0.234 | I |
| Ash-throated Flycatcher | 0.237 | 0.094 | 0.153 | I |
| Brown-headed Cowbird | 0.170 | 0.002 | 0.096 | (II) |
| Red-winged Blackbird | 0.531 | 0.272 | 0.317 | I, III |
| House Finch* | 0.056 | 0.056 | 0.184 | I |
| House Wren | 0.343 | 0.164 | 0.315 | I, II |
| Tree Swallow* | 0.126 | 0.126 | 0.291 | I, II, III |
| American Goldfinch | 0.145 | 0.015 | 0.079 | II |
| Song Sparrow | 0.700 | 0.013 | 0.025 | (II) |
| Bushtit | 0.359 | 0.058 | 0.076 | I |
| Western Kingbird | 0.376 | 0.028 | 0.109 | I |
| Bewick's Wren | 0.348 | 0.312 | 0.404 | I, III |
| American Robin | 0.171 | 0.054 | 0.174 | I |
| Nuttall's Woodpecker* | 0.378 | 0.378 | 0.432 | I, II |
| Bullock's Oriole* | 0.005 | 0.005 | 0.015 | III |
| Western Scrub-jay | 0.157 | 0.029 | 0.124 | I |
| Lazuli Bunting | 0.495 | 0.041 | 0.098 | I |
| Common Yellowthroat | 0.116 | 0.008 | 0.221 | (I) |
| Western Wood-Pewee | 0.752 | 0.221 | 0.240 | I, II, III |

^a Principal component retained if $P < 0.1$ in model with region; or if no component $P \leq 0.1$, then the one with lowest P value.

^b Model includes region main effects, except for asterisked species.

^c Principal component I, II, and/or III retained; shown in parentheses if $P > 0.1$.

ponent was $P > 0.2$ in each case. PC I (Table 1) was included in the final principal-component model for sixteen species, PC II was included for five species, and PC III was included for five species. The partial R^2 due to individual habitat variables, after controlling for region main effects, was greater, and usually much greater, compared to the partial R^2 due to the retained principal components (Table 5). Partial R^2 due to habitat variables for eight species was at least three times that of partial R^2 due to the principal components; partial R^2 due to habitat variables for seven species was between 50 and 150% greater than that due to principal components.

DISCUSSION

Importance of Habitat Differences at the Local Scale.—Variation in abundance of riparian-associated songbird species in the Central Valley of California was strongly associated with local-scale vegetation characteristics for each species examined, except one. Only for Bullock's Oriole was abundance not ex-

plained well by any habitat variable. Variables in the statistical models included both species-specific variables (e.g., cottonwood cover or mugwort cover) as well as more general variables (shrub cover or tree height index). Wiens and Rotenberry (1981) reported that vegetation composition was more predictive of bird abundance in shrub-steppe habitat than were measures of habitat structure (physiognomy).

Our findings emphasize the importance of including species-specific vegetation composition in analyses of habitat features influencing bird species presence or abundance. There is extensive literature reporting on habitat-associations for terrestrial bird species (Verner et al. 1986, McCullough and Barrett 1992, Scott et al. 2002), but most studies have analyzed general habitat characteristics and not species-specific vegetation composition, as exemplified by Block et al. (1986), Larson and Bock (1986), Sanders and Edge (1998), Salabanks et al. (2000), Vernier et al. (2002), and Miller et al. (2004).

The omission of potentially important vegetative characteristics has implications for studies that contrast the importance of local habitat features with that of landscape-scale features in predicting species-specific patterns of avian abundance or presence. Lichstein et al. (2002) and Miller et al. (2004) summarize recent studies, which have generally been mixed: some indicate that local scale is more important than landscape scale and others have come to the opposite conclusion. The problem of insufficient characterization of vegetation may explain the different conclusions reached by Saab (1999) and Scott et al. (2003), both of which focused on riparian songbirds in the Idaho/Montana region. The former concluded that landscape variables were more important than local variables, while the latter concluded that local variables were more important. However, only Scott et al. (2003) included understory vegetation in the analysis.

Specific Vegetation Features of Importance to Birds.—The two variables that were most often included with a positive effect on species-specific abundance were both measures of tree size: tree height index and tree dbh index. We also demonstrated that shrubs and, more specifically, understory vegetation, were predictive of the abundance of the 21 study species. This result is of interest as many studies of habitat associations for riparian songbirds have only examined plant species composition with regard to trees (e.g., Strong and Bock 1990, Saab 1999). Robertsen et al. (2002) also identified several songbird species in mixed forest habitat that responded to understory vegetation. Krueper et al. (2003) found that removal of cattle benefited riparian understory, which in turn influenced bird abundance.

Regional Variation and Spatial Scale.—We found marked variation in abundance among regions within a single, large watershed (Sacramento/San Joaquin Valley). All sites were within a single habitat classification (“valley-foothill riparian”), but a large amount of variation remained in bird species abundance attributable to region alone, after controlling for differences in vegetation composition.

Important differences in the effect of habitat variables were revealed across regions, similar to the findings of Heath and Ballard (2003).

In some cases, birds in one region do not appear to respond to the same habitat variable as conspecifics in another region, but in a few cases responses appeared to differ qualitatively from one region to another. The causal basis for this heterogeneity is not clear. Site to site variation may reflect the rarity of a plant species; for example, a bird species may be selecting habitat that contains that plant species if the species is rare, but avoiding the habitat if the plant species is common. Associations among plant species may also differ by region. For example, at the Cosumnes sites, presence of valley oak trees was associated with continuous valley oak forest cover; valley oak trees in other locations were often a component of a mixed forest type including cottonwoods, walnuts (*Juglans* spp.), or black willow (*Salix nigra*). Thus, the presence of a species (such as valley oak) implied a different set of associated plants, depending on region.

The influence of particular habitat variables also depends on spatial scale (Heath and Ballard 2003). This scale-dependence was well illustrated by studies in shrub-steppe birds; Rotenberry and Wiens (1980) demonstrated the importance of general habitat-structural variables at a large (continental) scale, but Wiens and Rotenberry (1981) demonstrated the greater importance of vegetational, species-specific composition at a more local (single-region) scale.

Response of Birds to Multivariate Factors.—Some studies have analyzed the effects of habitat variables using ordination to reduce a rich multivariate data set of independent variables to a few factors, for example, by using principal components or non-metric multidimensional scaling and analyzing bird response to multivariate factors (Lichstein et al. 2002). Our results raise concern about this practice. The factors or axes so obtained may concisely capture a large portion of variation with respect to vegetation and habitat among study sites (Legendre and Legendre 1998), but there is no assurance these axes reflect a coherent set of elements to which birds respond. An example of this problem was evident for Common Yellowthroat where the individual variable model performed well, but the principal component model did not (partial $R^2 = 0.221$ vs. 0.008). Two of the variables from the in-

dividual variable model (tree cover and herb cover) for this species loaded moderately strongly on principal component I, but with opposite signs. However, in the individual variable model, the coefficients for both variables were positive. Thus, Common Yellowthroats were more abundant where tree cover and herb cover were both high, but because the first principal component weighted these two variables with opposite signs, their effects tended to cancel out in the principal component statistical model. Other studies have also demonstrated stronger correlations between bird abundance and individual variables than with principal component or other multivariate factors (Wiens and Rotenberry 1981, Ambuell and Temple 1983).

Limitations of the Study.—We did not analyze differences in detection of birds due to habitat differences. We restricted detections to a distance of 50 m to reduce this problem (Ralph et al. 1993), but even within this distance there could be salient differences in detection which would be confounded with differences in abundance. All points surveyed were within a single, broad habitat type and this might be expected to reduce differences in detection rate within our sample.

One should be cautious in inferring causation from patterns of association among bird and habitat variables unless one analyzes bird response to a change in habitat characteristics (which we have not done). Each variable identified in a species-specific model (Table 2) has statistical support for its inclusion, but we recognize the ubiquity of model uncertainty (Burnham and Anderson 2002). Recently developed data-mining techniques, such as classification and regression trees (Hastie et al. 2001) are likely to be of great heuristic value, especially when one is analyzing 21 different dependent variables.

We restricted our analyses to species that were moderately abundant to improve statistical power. We may have failed as a result to capture characteristics of uncommon species. For example, some avian components of the ecosystem we investigated have been extirpated or drastically reduced within human history (e.g., Yellow-billed Cuckoo [*Coccyzus americanus*], Yellow Warbler [*Dendroica petechia*], and Bell's Vireo [*Vireo bellii*]), and we were unable to create habitat models for

them. It is possible the habitat features they require are drastically reduced or even absent within the region.

CONSERVATION IMPLICATIONS

Nearly all species studied were shown to respond predictably to local variation in vegetation and habitat, at the scale of a territory or home range. Obtaining information on vegetation composition is labor-intensive and requires in-the-field data collection; one cannot rely on remotely-sensed data. The second implication is that one cannot rely on a few focal species to capture the diverse response of the full set of species of interest (Chase et al. 2000, Chase and Geupel 2005). Conservation planners and managers must consider a large, diverse set of target species. The final implication is that recommendations and models need to be developed on a region-by-region basis, especially if one is drawing inferences based on patterns of correlation alone.

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APPENDIX. Common and scientific names of bird species analyzed and species code. Species identified by RHJV (2004) as riparian focal species and total detections by species at all point count stations ($n = 184$) shown.

| Common name | Scientific name | Code | Riparian focal species | Total detections |
|-------------------------|----------------------------------|------|------------------------|------------------|
| Nuttall's Woodpecker | <i>Picoides nuttallii</i> | NUWO | | 475 |
| Western Kingbird | <i>Tyrannus verticalis</i> | WEKI | | 581 |
| Ash-throated Flycatcher | <i>Myiarchus cinerascens</i> | ATFL | | 630 |
| Western Wood-Pewee | <i>Contopus sordidulus</i> | WEWP | | 335 |
| Western Scrub-jay | <i>Aphelocoma californica</i> | WESJ | | 435 |
| Brown-headed Cowbird | <i>Molothrus ater</i> | BHCO | | 1106 |
| Red-winged Blackbird | <i>Agelaius phoeniceus</i> | RWBL | | 726 |
| Bullock's Oriole | <i>Icterus bullockii</i> | BUOR | | 416 |
| House Finch | <i>Carpodacus cassinii</i> | HOFI | | 572 |
| American Goldfinch | <i>Carduelis tristis</i> | AMGO | | 415 |
| Song Sparrow | <i>Melodia melospiza</i> | SOSP | × | 757 |
| Spotted Towhee | <i>Pipilo maculatus</i> | SPTO | | 1425 |
| Black-headed Grosbeak | <i>Pheucticus melanocephalus</i> | BHGR | × | 638 |
| Blue Grosbeak | <i>Guiraca caerulea</i> | BLGR | × | 111 |
| Lazuli Bunting | <i>Passerina amoena</i> | LAZB | | 406 |
| Tree Swallow | <i>Tachycineta bicolor</i> | TRES | × | 680 |
| Common Yellowthroat | <i>Geothlypis trichas</i> | COYE | × | 403 |
| Bewick's Wren | <i>Thryomanes bewickii</i> | BEWR | | 767 |
| House Wren | <i>Troglodytes aedon</i> | HOWR | | 848 |
| Bushtit | <i>Psaltriparus minimus</i> | BUSH | | 605 |
| American Robin | <i>Turdus migratorius</i> | AMRO | | 208 |