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Effects of land use on riparian birds in a semiarid region



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ABSTRACT

We investigated the influence of landscape characteristics on avian species occupancy in riparian forests embedded in a matrix of urban and agricultural land use in a semiarid region of the Southwestern US. We conducted bird and vegetation (local-scale characteristics) surveys within 196 50-m radius sample points in 10 riparian forests in southern California. We quantified landscape composition within a 500 m-radius surrounding each point. For each species we developed 8 single-season occupancy models using principal components summarizing local- and landscape-scale characteristics and a spatial autocovariate as covariates. Of 21 species analyzed, occupancy by 11 was associated with landscape characteristics, by 6 with local vegetation characteristics, by 3 with both local and landscape characteristics, and by 1 with none. Five species positively responded to surrounding urban development (2 negative), whereas 4 negatively responded to agricultural land (1 positive). The amount of riparian forests had a strong positive effect on the occurrence of riparian obligates. Our results emphasize the importance of landscape characteristics on species occupancy patterns in riparian systems although relationships were also species-specific. Our results imply a positive effect of urbanization compared to agricultural land uses in this region, most likely due to enhanced vegetation development.

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1. Introduction

Riparian forests occupy less than 2% of the total land surface in the American Southwest but are often the most biologically productive and ecologically important lands in this semiarid and arid region (DeBano and Baker, 1999). In particular, avian and plant species diversity are greater in riparian forests, and habitat structure is more complex compared to vegetation types in adjacent uplands (Ohmart, 1994; Knopf and Samson, 1994). While the conservation values of riparian forests have been well recognized in less disturbed landscapes, less attention has been paid to the riparian forests in human-altered landscapes, especially urbanizing ones (Rottenborn, 1999; Hennings and Edge, 2003; Oneal and Rotenberry, 2009; Trammell et al., 2011).

Urban development is considered one of major threats to biodiversity (Czech et al., 2000) and the American Southwest has undergone extensive urbanization in recent decades. In the US

streamside development is restricted by the Clean Water Act. While riparian forests often appear intact, those riparian forests are susceptible to fluxes of energy, materials, and organisms from adjacent urban and agricultural lands that can increase surface runoff, erosion, and nutrient loading, lower water tables, facilitate spread of non-native vegetation, and attract avian brood parasites and predators (e.g., Saab, 1999; NRC, 2002; Allan, 2004; Smith and Wachob, 2006). However, it has also been reported that urban development in semiarid and arid regions may have positive effects on riparian systems. Urban development can increase water availability via enhanced runoff and, hence, the quantity of riparian vegetation in a system (White and Greer, 2006). Several studies have found greater bird species richness in riparian forests within a city (Trammell et al., 2011) and noted positive responses of some riparian bird species to surrounding urbanization (Oneal and Rotenberry, 2009).

Most avian studies conducted along an urban-rural gradient have focused primarily on urbanization itself. In some regions of the Southwest, urban development has replaced agricultural lands that were dominant in the past, and riparian forests may now be surrounded by both urban development and agricultural land. Although avian species in natural habitats embedded in an agricultural matrix may show positive or negative responses similar to those embedded in an urban matrix, it has been argued that a less

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intensive agricultural land use can be a more favorable matrix than urban development (Dunford and Freemark, 2004).

Understanding species-habitat relationships in human-altered landscapes requires a multi-scale approach because the extent to which the nature of the surrounding matrix influences avian species distributions largely depends on species' sensitivity to variations in habitat characteristics at different spatial scales (e.g., Bolger et al., 1997; Fahrig, 2003). Some birds in riparian forests may respond more to vegetation changes within a riparian forest (i.e., local characteristics) than development patterns in the surrounding landscape (Martin et al., 2006; Oneal and Rotenberry, 2009). Others may be strongly affected by the amount of riparian forest and other natural habitats within a landscape (i.e., landscape characteristics; Saab, 1999; Miller et al., 2003). Thus, to assess which habitat characteristics appear important to species distributions it is necessary to determine the relative influences of both local and landscape characteristics (Rodewald and Bakermans, 2006; Pennington et al., 2008).

Our principal objective was to examine the effects of surrounding land use on bird species' occupancy in riparian areas in semiarid southern California, in a region consisting of a mixture of agriculture, urban areas, and remnant native habitats. Our aims were two-fold: (1) to investigate the relationship between site occupancy by avian species in riparian forests at two spatial scales (local-scale structural features of the vegetation and landscape-scale composition); and (2) in particular, to assess the implications of agricultural development compared to urbanization for this avifauna. Although we expected responses to local and landscape characteristics would be species-specific, we also expected that more species would be influenced by landscape characteristics given the relatively strong explanatory power of landscape variables found in human-altered landscapes (e.g., Donovan et al., 1997; Saab, 1999; Miller et al., 2003). For those species that did show a response to landscape attributes, we expected positive relationships with the amount of riparian forest in the surrounding matrix (particular for riparian obligate species primarily restricted to nesting in riparian forest), and for more positive and fewer negative responses to agriculture compared to urbanization (e.g., Dunford and Freemark, 2004).

2. Methods

2.1. Study sites and survey points

The study was conducted in 10 riparian forest study sites in a landscape containing a gradient of natural vegetation covers as well as land uses in western Riverside County, California (Figs. 1 and 2). This region exhibits a Mediterranean-type climate characterized by a long, hot, dry summer and a short, cool, highly variably wet winter; mean annual precipitation is ~25 cm. Numerous agricultural lands have been converted to urban and suburban uses beginning in the 1970s (Hornor, 1972–1996).

Riparian vegetation is dominated by willows (*Salix* spp.), Fremont cottonwood (*Populus fremontii*), California sycamore (*Platanus racemosa*), and *Baccharis* spp., with non-native giant reed (*Arundo donax*) and salt-cedar (*Tamarisk* spp.) abundant in some areas. The natural vegetation of upland areas consists of coastal sage scrub dominated by California sagebrush (*Artemisia californica*), California buckwheat (*Eriogonum fasciculatum*), and California brittle-bush (*Encelia californica*). Exotic annual grasses (*Bromus* spp., *Avena barbata*) and wild mustards (*Hirschfeldia incana*) dominate the herbaceous understory of riparian forests as well as upland areas.

Historically, many of the streams were ephemeral or intermittent, but some, particularly those near high density urban or

irrigated agricultural areas, now have year-round water due to runoff. The width of riparian forests, except a small portion of Santa Ana River (SARI; Fig. 1), is narrow, ranging from 30 m to 70 m. Within each riparian forest, survey points were spaced at 200-m intervals alongside the stream, with the number varying from 4 to 32 depending on riparian forest length and accessibility. A total of 275 survey points was established across 10 study sites.

2.2. Bird sampling

Bird surveys were conducted at each sampling point twice between April and early July in 2004, using fixed-radius point counts (Ralph et al., 1993). At each point, an observer recorded species seen or heard within a 50-m radius of the sampling point for a 10-min duration. Three observers conducted surveys and they were rotated among sites to randomize any observer effects. We also alternated surveys to minimize the effect of time-of-day. Surveys were performed between dawn to 1030 PDT. We did not conduct surveys during periods of rain or high wind.

We classified each bird species within 3 guilds based on a review of the literature (Appendix A; Ohmart and Anderson, 1982; Ehrlich et al., 1988; Miller et al., 2003; Oneal and Rotenberry, 2009): riparian dependency (riparian dependent species including riparian obligates vs. riparian independent species including facultative users and other species), migratory behavior (migrant vs. resident), and nest placement (tree/shrub, cavity, or ground).

2.3. Local variables-vegetation sampling

We conducted vegetation sampling in June and July after bird surveys were completed using the Point Reyes Bird Observatory "Veggie" (relevé) protocol (PRBO, 2002). We focused on estimating structural attributes (i.e., percent vegetation cover at different layer) due to the importance of vegetation structure to avian distributions (e.g., Karr and Roth, 1971; Robinson and Holmes, 1982). Within a 50-m radius surrounding a sampling point, we visually estimated the percentage of riparian vegetation cover and percentage of any other vegetation types. Within riparian vegetation, we estimated the percent cover of each of three vegetation layers: tree (> 5 m), shrub (0.5–5 m), and herb (<0.5 m). Relevé methods such as this have been shown to efficiently capture relevant attributes of avian habitat (Wood et al., 2010). Vegetation sampling was done by a team of two biologists who were trained together to reduce bias in estimating percent cover of vegetation.

2.4. Landscape variables

We generated landscape variables using a land cover map prepared in 2005 for the Western Riverside County Multiple Species Habitat Conservation Plan. The map was created by both field surveys and the interpretation of aerial photography (a resolution of 1–2 m), considering unique vegetation characteristics in western Riverside County (Evens and Klein, 2006). Although the accuracy of the map was high, the scale of resolution (minimum mapping unit was 0.4 ha, about 60 m × 60 m) was not precise in depicting the spatial extent of several parts of the riparian forests we surveyed. However, this was limited to <5% of the total number of points surveyed, and these points also represented relatively low percent cover of riparian vegetation. Thus, we assume that this imprecision had no substantive effect on our analyses. We condensed 14 land cover types in the 2005 map into 4 types: urban development (developed/disturbed lands), agriculture, shrubland (mainly Riversidean coastal sage scrub), and riparian areas. We calculated percent cover of each of the 4 land cover types within a 500-m radius area surrounding a sampling point. We also calculated 2

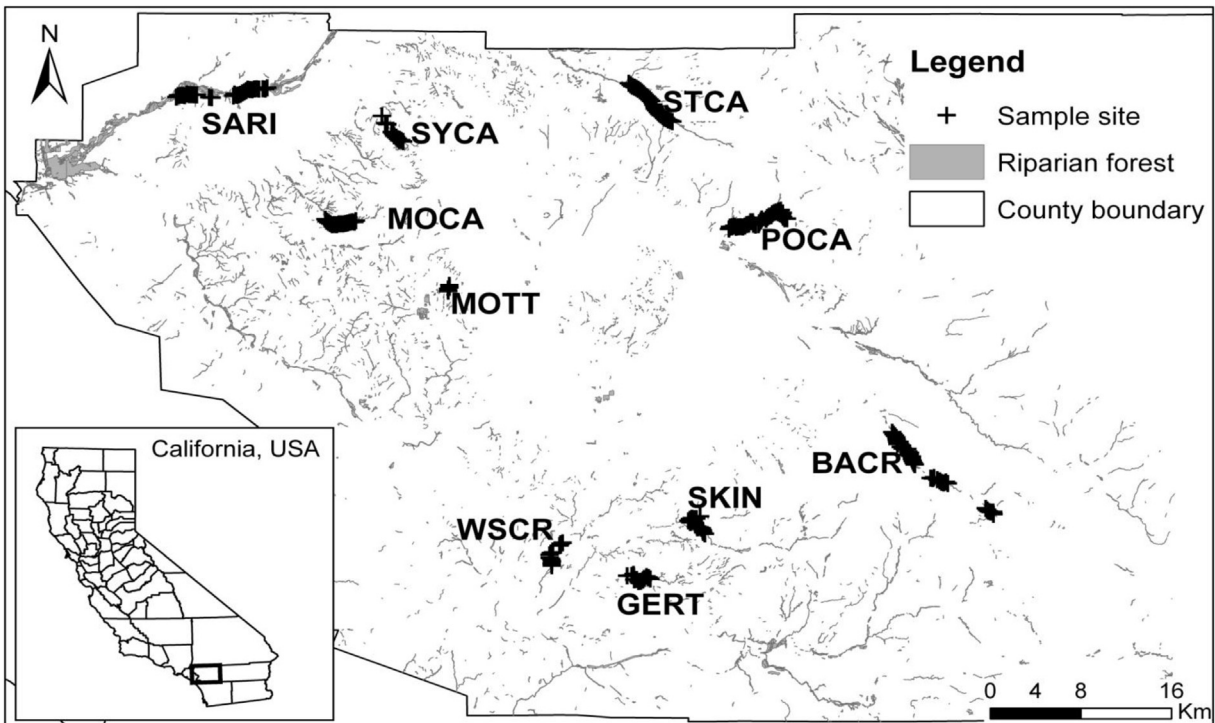


Fig. 1. Study sites (riparian forests) surveyed in 2004. Name of sites: BACR, Bautista Creek; GERT, Santa Gertrudis Creek; MOCA, Mockingbird Canyon; MOTT, Motte Reserve; POCA, Potrero Canyon; SARI, Santa Ana River; SKIN, Shipley-Skinner Reserve; STCA, San Timeteo Canyon; SYCA, Sycamore Canyon; WSCR, Warm Springs Creek.

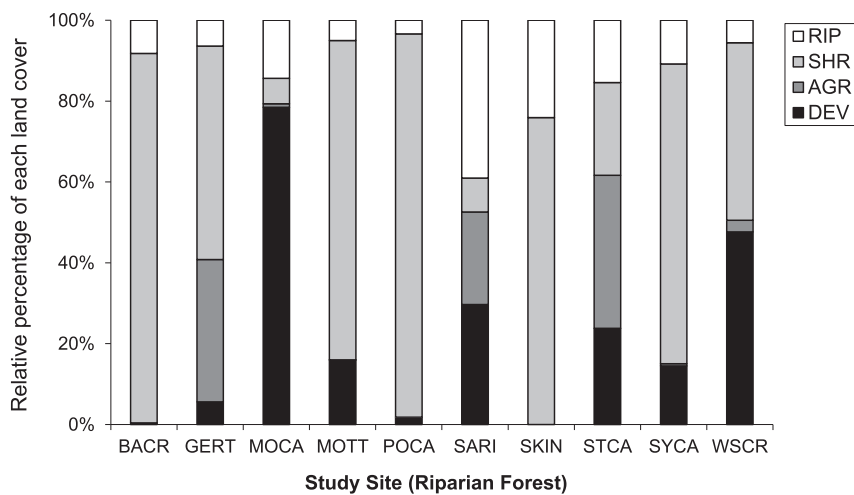


Fig. 2. Relative proportion of four land cover types at each study site used for analysis. Name of sites: BACR, Bautista Creek; GERT, Santa Gertrudis Creek; MOCA, Mockingbird Canyon; MOTT, Motte Reserve; POCA, Potrero Canyon; SARI, Santa Ana River; SKIN, Shipley-Skinner Reserve; STCA, San Timeteo Canyon; SYCA, Sycamore Canyon; WSCR, Warm Springs Creek. Legend abbreviations: RIP, riparian forest; SHR, native shrubland vegetation; AGR, agricultural land; DEV, urban development.

other landscape characteristics: distance from a sampling point to the edge of the nearest urban development and to the edge of the nearest agriculture.

2.5. Data analysis

2.5.1. Covariates and bird species

To minimize the potential effects of major compositional difference in vegetation, we excluded sampling points that had sycamore, salt-cedar, or giant reed as the dominant vegetation in the tree and shrub layer. A total of 196 sample points composed primarily of willow-cottonwood vegetation was used for analysis.

We performed separate principal component analyses with varimax rotation on local and landscape variables to identify independent patterns of environmental variation within each data set. We retained all principal components whose eigenvalues were ≥ 1 : two principal components (PCs) at the local scale and three PCs at the landscape scale (Table 1). The PC scores were used in occupancy analysis as scale-specific habitat covariates.

For analysis, we excluded flyovers, waterfowl, and species that were detected at <10% of the points. A total of 44 species, including four federally endangered species or species of conservation concern to state and local governments (least Bell's vireo, Wilson's warbler, yellow-breasted chat, and yellow warbler; see Appendix A

Table 1
Principal component (PC) factor loadings for environmental variables at each spatial scale. Two PCs at the local scale and three PCs at the landscape scale captured 81% and 90% of the total variation in explanatory variables, respectively.

Variable	PC 1	PC 2	PC 3
Local^a			
Percent cover of tree layer (>5 m tall)	-0.80	-0.30	-
Percent cover of shrub layer (0.5 m-5 m tall)	0.86	-0.18	-
Percent cover of herb layer (<0.5 m tall)	0.03	0.97	-
Variance (%)	46.94	34.22	-
Cumulative variance (%)	46.94	81.16	-
Landscape^b			
Percent cover of urban development	-0.93	-0.15	0.04
Percent cover of agriculture lands	0.08	0.96	0.07
Percent cover of native shrubland	0.69	-0.48	-0.44
Percent cover of riparian forest	-0.08	0.07	0.99
Distance to the nearest urban area from a point	0.48	-0.8	-0.08
Distance to the nearest agricultural land from a point	0.79	-0.41	-0.07
Variance (%)	52.80	21.00	16.00
Cumulative variance (%)	52.80	73.80	89.80

^a PCs at local scale: PC 1 (Local 1), tree vs. shrub (i.e., a gradient in vegetation cover from tree-dominated native to shrub-dominated); PC 2 (Local 2), a gradient of increasing herbaceous vegetation.

^b PCs at landscape scale: PC 1 (Landscape 1), urban development vs. native shrub cover (i.e., a gradient in land cover from urban development to native shrubland); PC 2 (Landscape 2), a gradient of increasing agricultural land; PC 3 (Landscape 3), a gradient of increasing riparian forest.

for scientific names of all species mentioned in text or tables), was analyzed. However, some occupancy models (see below) of 23 species showed problems in parameter estimation, convergence, or model fit. To avoid biased results, we eliminated these species and used 21 species for final analysis (See Appendix A for species list).

2.5.2. Modeling species site occupancy

In wildlife surveys, the probability of detecting a species is almost always <1.0 (i.e., a species may not be detected even if present at a site). Ignoring this imperfect detection can result in biased estimations of population attributes such as species occurrence and abundance, which can lead to misleading inferences about the species-habitat relationship (e.g., MacKenzie et al., 2006). We accounted for the imperfect detection using occupancy models as developed by MacKenzie et al. (2006) in our analysis.

We developed 8 single-season occupancy models in Program MARK (Table 2). We modeled detection probability (*p*) as constant [*p*(.)] and time-dependent [*p*(*t*)]. Occupancy (*ψ*) was modeled as a function of no covariate (*ψ*(.)), local characteristics (*ψ*(Local)), landscape characteristics (*ψ*(Landscape)), and a combination of

Table 2
Occupancy models used in analysis. *ψ* is the probability that a site is occupied by a species; *p* is the detection probability of the species if it is present. Detection was modeled as either constant (.) or variable among sampling occasions (*t*). Occupancy was modeled as either constant (.) or as a function of habitat variables (PC scores) at the local scale (Local), landscape scale (500 m; Landscape), and a combination of both scales (Local + Landscape). ACOV (autocovariate) was added to the models for species with spatial dependency (Model with ACOV). *K* is the number of parameters.

Model	K	Model with ACOV	K
<i>p</i> (.) <i>ψ</i> (.)	2	<i>p</i> (.) <i>ψ</i> (Local + ACOV)	5
<i>p</i> (<i>t</i>) <i>ψ</i> (.)	3	<i>p</i> (<i>t</i>) <i>ψ</i> (Local + ACOV)	6
<i>p</i> (.) <i>ψ</i> (Local)	4	<i>p</i> (.) <i>ψ</i> (Landscape + ACOV)	8
<i>p</i> (<i>t</i>) <i>ψ</i> (Local)	5	<i>p</i> (<i>t</i>) <i>ψ</i> (Landscape + ACOV)	9
<i>p</i> (.) <i>ψ</i> (Landscape)	7	<i>p</i> (.) <i>ψ</i> (Local + Landscape + ACOV)	11
<i>p</i> (<i>t</i>) <i>ψ</i> (Landscape)	8	<i>p</i> (<i>t</i>) <i>ψ</i> (Local + Landscape + ACOV)	12
<i>p</i> (.) <i>ψ</i> (Local + Landscape)	10		
<i>p</i> (<i>t</i>) <i>ψ</i> (Local + Landscape)	11		

local and landscape characteristics (*ψ*(Local + Landscape)). Single season occupancy models assumed no change in occupancy status at a site over the survey periods, no false detection, and independence of detection among sampling points. We conducted our surveys during the breeding season, observers were experienced, and 200 m intervals between sampling points should be sufficient to avoid double counting individuals in our study. Thus, we concluded that our data met model assumptions.

2.5.3. Modeling spatial autocorrelation

Ecological data collected over some area are often spatially autocorrelated (Fortin and Dale, 2005), a condition where observations located closer together are more likely to have similar values than observations located further apart due to some unmeasured process. Spatial autocorrelation is known to bias ordinary hypothesis test results and generate biased parameter estimates (e.g., Legendre, 1993; Fortin and Dale, 2005; Beale et al., 2010).

We examined spatial structure in the residuals of the occupancy models to assess the degree of spatial autocorrelation in the response variable that was not accounted for by explanatory variables (Moore and Swihart, 2005). We calculated residuals following Moore and Swihart (2005): the observed values at a site minus the predicted probabilities (calculated from model-averaged estimates) of detecting the species at least once. Then, we constructed a Moran's I correlogram of the residuals in SAM 4.0 (Spatial Analysis in Macroecology: Rangel et al., 2010). We used a 500-m maximum lag distance because that distance was greater than the interval between sampling points, and was the same as the spatial extent of landscape scale used in our study. For a species whose model residuals were positively correlated (Moran's I ≥ 0.1 and P ≤ 0.05) we calculated an autocovariate (ACOV) to account for spatial autocorrelation, following Moore and Swihart (2005):

$$autocov_i = \frac{\sum_{j=1}^{J_i} \omega_{ij} y_j}{\sum_{j=1}^{J_i} \omega_{ij}}$$

where *y_j* = 1 for all sample points where a species was detected in a set *J_i* (neighbors of point *i*, namely, other points within a certain distance class of point *i*); otherwise, *y_j* = 0; *ω_{ij}*, the weight given to point *j* (the inverse of the Euclidean distance between points *i* and *j*). The neighborhood of *J_i* was determined by the distance at which the residual was autocorrelated. ACOV can also be interpreted as the probability of observing a species at a site conditional on the presence of the same species at a site(s) within a neighborhood of the site (Augustin et al., 1996; Klute et al., 2002). ACOV was calculated using R and added to occupancy models as an additional covariate for those species where spatial dependency was found (Table 2).

2.5.4. Model selection and model averaging

We used an information-theoretical model-selection approach based on Akaike's Information Criterion (AIC, Burnham and Anderson, 2002) to determine the relative importance of local variables and landscape variables on species' occupancy. Due to small sample size relative to the number of parameters, we used the AICc. We constructed a confidence set of candidate models whose ΔAICc were <4, as recommended by Burnham and Anderson (2002), and calculated Akaike weights of the models. Each of the models in a confidence set can be considered a plausible explanation for occupancy of the species, given the data. However, if the AICc difference between the best model and the null models (no covariates for occupancy model, *p*(.)*ψ*(.) and *p*(*t*)*ψ*(.)) was <2, we considered that the occupancy of the species was not associated

with variables in the model. Lastly, we calculated variable weights within a confidence set of models and used them to determine the relative importance of local vs. landscape variables in relation to species occupancy.

We also calculated the model-averaged parameter estimates, unconditional standard errors, and 90% confidence interval (CI) for the parameters (covariates) included in the confidence set of models as described in Burnham and Anderson (2002). Inferences about the influence of each variable (covariates) on species occupancy were made considering the magnitude of parameter estimates and their precision. We determined the precision of model-averaged parameter estimates based on 90% CI. We did not back-transform any estimate or its 90% CI. When the 90% CI included zero, the effect of the parameter was considered insignificant.

We performed the Hosmer and Lemeshow goodness-of-fit (GOF) test for a global model ($p(t)\psi(\text{Local} + \text{Landscape})$) in SAS to evaluate model fit. If the models of the species showed lack-of-fit (p -value < 0.05), we eliminated the species from further analysis. We also conducted a GOF test after ACOV was added to the global model.

3. Results

3.1. Local versus landscape variables

The relationship between local and landscape variables and species occupancy varied among species. Of 21 species, occupancy of 11 species was associated with landscape variables, of 6 species with local variables, and of 3 species with both local and landscape variables (Table 3; see Appendix B for model selection details). Occupancy of only one species, brown-headed cowbird, was not related to variables at either of the scales used in this study. Spatial autocorrelation was detected in the residuals of occupancy models

Table 3

Spatial scale(s) selected based on variable weights. If the difference in variable weight between local scale and landscape scale was <0.3, it was concluded that both scales influenced the occupancy of the species. Variable weight is a re-scaled AIC weight of a confidence set of models. See Appendix B for a summary of model selection procedures.

Species	Variable weight		Scale
	Local	Landscape	
American Crow	0.32	0.88	Landscape
American Goldfinch	0.43	0.73	Landscape
Anna's Hummingbird ^a	0.10	1.00	Landscape
Ash-throated Flycatcher	0.36	0.73	Landscape
Blue Grosbeak	0.30	0.83	Landscape
Brown-headed Cowbird ^a	–	–	None ^b
California Quail ^c	0.87	1.00	Local + Landscape
California Thrasher ^a	0.18	1.00	Landscape
Costa's Hummingbird ^a	0.44	1.00	Landscape
House Finch	0.56	0.59	Local + Landscape
Least Bell's Vireo	0.70	0.30	Local
Mourning Dove ^a	1.00	0.32	Local
Northern Flicker ^c	0.27	0.73	Landscape
Northern Rough-winged Swallow	0.34	0.87	Landscape
Oak Titmouse ^a	0.70	1.00	Landscape
Song Sparrow ^{a,c}	0.81	0.39	Local
Spotted Towhee	0.82	–	Local
Western Scrub-Jay	0.72	0.28	Local
Wrentit	0.72	0.28	Local
Yellow-breasted Chat	0.30	1.00	Landscape
Yellow Warbler	0.45	0.68	Local + Landscape

^a Species whose model residuals were not spatially correlated; ACOV was not included in the occupancy models.

^b No relationship between species occupancy and variables at any of the scales used in the analysis.

^c Species showed poor fit of a global model with ACOV.

of the majority (14) of the 21 species analyzed (Table 3 and Appendix B).

Similar patterns were also found at guild levels. Occupancy of migrants was associated with landscape variables (Fig. 3a), whereas resident species were more related to local variables. Although the number of cavity-nesting species was low, all were associated with landscape variables (Fig. 3b). Riparian independent species responded more to landscape variables than to local or a combination of local and landscape variables, whereas riparian obligates showed diverse associations with local and landscape variables (Fig. 3c).

3.2. Responses to habitat variables

Although specific local vegetation characteristics were important to occupancy by some species, most parameter estimates were insignificant (Table 4). Only mourning dove showed a significant positive response to Local 1; probability of occupancy by doves increased with percent cover of shrub vegetation and decreased with percent cover of tree vegetation. Occupancy by oak titmouse was negatively related to Local 1, but the estimate was only marginally significant. California quail responded negatively to percent cover of herbaceous vegetation (Local 2); however, the occupancy model of the species was poorly fit.

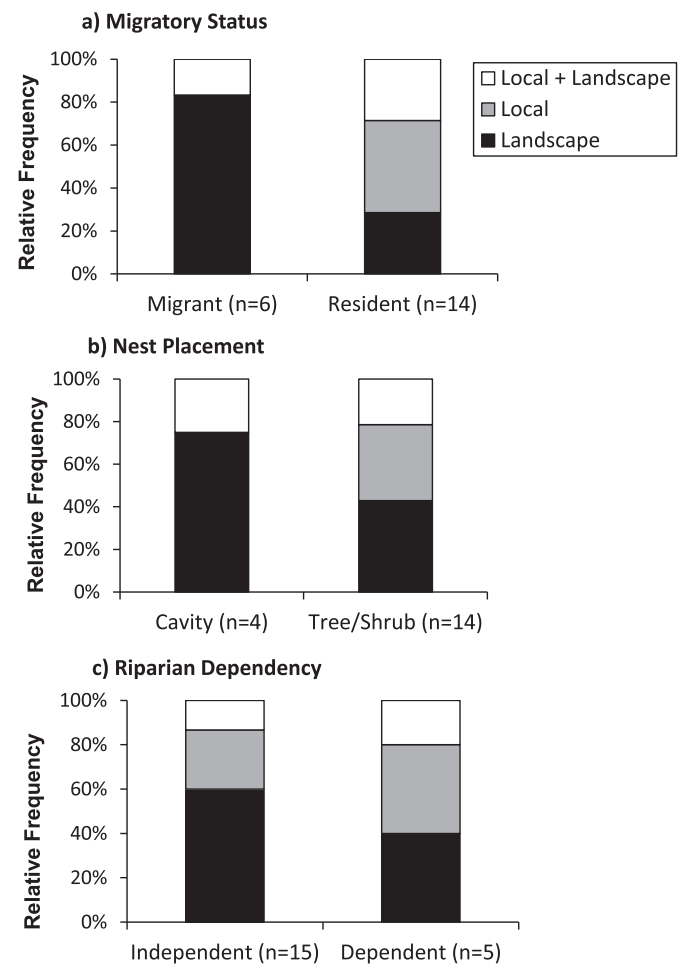


Fig. 3. Relative frequency (%) of spatial scales for each guild type based on (a) migratory status, (b) nest placement, and (c) riparian dependency. n indicates the number of species classified into the guild. In (b), ground nesting guild was excluded due to too small sample size ($n = 2$). Brown-headed cowbird was not included because no scale-dependency was found.

Table 4
Untransformed model-averaged parameter estimates and standard errors (SE) for covariates of occupancy models in a confidence set of models. Brown-headed cowbird was excluded because it was not associated with any of the scales used in the study. Local 1 and Local 2 represent 2 PCs at local scale, and Landscape 1, Landscape 2, and Landscape 3 are 3 PCs at landscape scale (Table 1). Significant estimates based on 90% CI are in bold.

Species	Parameter estimate (SE)				
	Local 1 (tree to shrub)	Local 2 (increasing herbaceous)	Landscape 1 (urban to shrubland)	Landscape 2 (increasing agriculture)	Landscape 3 (increasing riparian)
American Crow	−0.090 (0.121)	−0.131 (0.132)	−0.687 (0.391)	0.285 (0.277)	0.859 (0.464)
American Goldfinch	−0.110 (0.136)	−0.162 (0.150)	−0.060 (0.285)	0.147 (0.287)	0.906 (0.732)
Anna's Hummingbird	−0.025 (0.042)	0.017 (0.036)	−3.38 (1.278)	−0.573 (0.356) ^a	0.338 (0.319)
Ash-throated Flycatcher	0.042 (0.081)	0.051 (0.113)	0.375 (0.237) ^a	−0.214 (0.190)	0.106 (0.187)
Blue Grosbeak	−0.007 (0.082)	−0.084 (0.108)	−0.111 (0.238)	0.584 (0.301)	0.082 (0.216)
California Quail ^b	0.291 (0.298)	−0.881 (0.491)	0.551 (0.343)	−0.901 (0.414)	−0.845 (0.503)
California Thrasher	0.091 (0.121)	−0.029 (0.086)	−1.577 (0.868)	−2.195 (0.884)	−1.24 (0.634)
Costa's Hummingbird	0.026 (0.057)	−0.034 (0.084)	0.663 (0.61)	−0.747 (0.65)	−1.259 (0.573)
House Finch	0.171 (0.160)	0.048 (0.152)	−0.309 (0.221)	0.081 (0.166)	−0.066 (0.139)
Least Bell's Vireo	−0.200 (0.298)	0.056 (0.338)	−0.016 (0.105)	0.102 (0.159)	0.129 (0.182)
Mourning Dove	1.144 (0.666)	1.835 (1.685)	0.630 (0.583)	−0.434 (0.420)	−0.319 (0.378)
Northern Flicker ^b	0.080 (0.110)	−0.008 (0.089)	0.234 (0.275)	−0.145 (0.258)	0.469 (0.316)
Northern Rough-winged Swallow	−0.131 (0.152)	−0.108 (0.135)	−0.632 (0.312)	0.280 (0.252)	0.508 (0.325)
Oak Titmouse	−0.512 (0.330) ^a	0.158 (0.218)	0.679 (0.349)	−1.509 (0.513)	−0.449 (0.380)
Song Sparrow ^b	−0.156 (0.261)	−0.575 (0.293)	−0.175 (0.180)	0.165 (0.178)	0.212 (0.202)
Spotted Towhee	0.264 (0.868)	−1.286 (1.065)			
Western Scrub-Jay	0.128 (0.223)	0.023 (0.188)	−0.012 (0.082)	−0.057 (0.095)	−0.058 (0.121)
Wrentit	0.021 (0.157)	0.129 (0.174)	0.067 (0.093)	−0.014 (0.063)	0.008 (0.054)
Yellow-breasted Chat	0.315 (0.310)	0.055 (0.249)	−1.310 (0.651)	0.656 (0.933)	2.119 (0.766)
Yellow Warbler	−0.091 (0.143)	−0.142 (0.155)	−0.182 (0.200)	0.049 (0.216)	0.554 (0.345) ^a

^a Marginally significant estimates (i.e., significant at 85% CI).

^b Species shown poor fit of a global model with ACOV.

Occupancy by 7 species was significantly influenced by urban development (Table 4, Landscape 1). Occupancy increased with percent cover of urban development (i.e., species had a significantly negative coefficient) for 5 species (American crow, Anna's hummingbird, California thrasher, northern rough-winged swallow, yellow-breasted chat), with only 2 species (oak titmouse, ash-throated flycatcher) having a negative association (i.e., a positive coefficient). Likewise, agricultural land use influenced species occupancy in both negative and positive fashions (Table 4, Landscape 2). Occupancy by blue grosbeak increased with percent cover of agricultural land use, whereas probability of occupancy by Anna's hummingbird (marginally significant), California quail (but poor model fit), California thrasher, and oak titmouse decreased with increasing percent cover of agricultural land surrounding survey points. Response to the amount of riparian forest also varied among species (Table 4, Landscape 3). Yellow-breasted chat and yellow warbler, which are riparian obligates and species of special concern in California, responded positively to Landscape 3 significantly or marginally significantly. American crow also showed a positive relationship, whereas occupancies by California quail, California thrasher, and Costa's hummingbird were negatively associated with Landscape 3.

4. Discussion

4.1. Local characteristics versus landscape characteristics

In our study, landscape characteristics had a significant influence on twice as many species as did local characteristics. This pattern is consistent with the findings of several other riparian studies that observed a stronger effect of landscape-level variables on avian species compared to that of local (or patch)-level variables in human-altered landscapes (e.g., Saab, 1999; Rottenborn, 1999; Miller et al., 2003; Smith and Wachob, 2006; Rodewald and Bakermans, 2006; Pennington et al., 2008). This pattern confirms that the landscape matrix surrounding a riparian forest can be an

important factor influencing species occupancy in this region. However, the relationship between local and landscape characteristics and species occupancy also varied among species and guilds, which was not surprising because the relative importance of local and landscape variables on species distribution can change based on the species considered (e.g., Graham and Blake, 2001; Hennings and Edge, 2003; O Neal and Rotenberry, 2009).

Among avian species, riparian obligates that critically depend on the riparian forest itself are of particular interest because the guild includes species of conservation concern and target species for riparian habitat management in this region. Of 5 riparian dependent species, 3 had occupancy patterns influenced by landscape or a combination of landscape and local variables. Our results contradict the findings of two recent studies in California that showed strong association of the riparian obligates' abundance and/or occurrence with local characteristics (Luther et al., 2008; O Neal and Rotenberry, 2009). This inconsistency between our study and theirs may likely be associated with differences in the landscape elements dominant in the surrounding matrix and the variables used for analysis. While mixed oak woodlands was a primary land cover in the study by Luther et al. (2008), coastal sage scrub was the dominant natural land cover in our region. Unlike our study, landscape variables in O Neal and Rotenberry's (2009) study did not include agricultural lands simply because that land use was mostly not present in their study region, a mixture of urban and natural land covers.

4.2. Species responses to land use and other landscape characteristics

In the current study where urban areas are mixed with agriculture, species responses to urbanization and agricultural land uses varied. However, most species whose occupancy was significantly influenced by urban development showed positive responses. This positive effect of development may be related to the moderate level of urbanization common throughout our study sites. In naturally sparsely vegetated habitats in semiarid and arid

areas, moderate urban development, particularly residential suburbanization, can enhance vegetation cover and diversity and hence contribute to overall higher richness and abundance of birds (Blair, 1999). Our study sites included a wide range of urban development levels. However, the average percentage of urban development within a 500-m radius of a sample point was below 30% at most sites. Most residential areas include ornamental vegetation, especially shrubs and trees, and frequently have some native vegetation set aside in parks or reserves. This vegetation can increase heterogeneity in the landscape and may provide diverse habitats for unique sets of birds (Marzluff, 2005; McKinney, 2008). Moreover, land uses in some semiarid and arid regions can increase cover of riparian vegetation, especially of willow species, by augmenting stream flows via urban runoff (White and Greer, 2006). Although there is no information about how this change specifically influences riparian birds, increased native riparian vegetation such as willows can increase available resources for nesting and foraging. It has been observed that the amount of vegetation associated with small and low-order streams in some regions in the Southwest, including our study area, has spatially expanded with urbanization and agriculture, and riparian vegetation has even newly formed at some sites during the past decade (T. Scott, personal communication, February 14, 2007). We did not examine the relationship between urbanization and cover of riparian vegetation, and we lack sufficient historical information to analyze change in riparian vegetation through time. However, even a small increase in the amount of riparian vegetation may positively affect some species, especially riparian obligates such as yellow-breasted chats.

Unlike urban development, species influenced by agricultural land use showed positive and mostly negative responses. While the positive effect of agricultural land use could be related to potential water input as noted previously, the negative effect may be caused by the citrus orchard dominant agriculture in our study region. We did not make a distinction between types of agricultural lands (orchard, crop field, or pasture/hay field) in our study. The citrus industry had its genesis in Riverside County in the 1870s (Webber, 1967), and citrus orchards have been a dominant form of agricultural activity, particularly in upland areas, since. It is possible that some birds may be less attracted to orchards, despite the superficial physiognomic similarity to riparian vegetation, than to other agricultural lands such as crop fields and pasture/hay fields. However, this remains speculative, and additional studies are needed to clarify whether avian species respond differently to specific types of agriculture uses in a surrounding landscape.

In our study, facultative species as well as riparian obligates appeared related positively to percent cover of riparian forest, although only 2 species (yellow-breasted chat and yellow warbler) showed significant or marginally significant responses. The parameter estimates for these species were also higher compared to those of other landscape variables, suggesting the importance of the amount of riparian forest to these species. The amount of available habitat in a landscape is known to be an important variable affecting avian habitat specialists (e.g., Ambuel and Temple, 1983; Freemark and Merriam, 1986). Considering that riparian obligates are by definition habitat specialists in this region, our results concur with this general pattern. On the other hand, some riparian-independent species were negatively influenced by riparian forest cover within a landscape. Although this result contradicts that of Rottenborn (1999), it was not completely unexpected because our riparian independent birds are primarily shrubland species more commonly found in relatively open habitats rather than forest-associated.

We detected positive spatial autocorrelation in model residuals of most species. There are likely to be three principal sources for this. Certainly some arises through the natural pattern of spatial

autocorrelation in environmental variables that appears in some form in virtually all ecological studies (Legendre, 1993; Fortin and Dale, 2005). Secondly, although a 200-m interval between sample points is commonly used in avian studies to ensure independent observations of birds, the actual between-point distance may be shorter to the extent that the riparian corridor wanders. In the extreme, in our case there was an instance where 5 survey points were included within a 500 m-radius spatial extent. Although it remained unlikely that we double-counted individual birds on these points, it does introduce correlation into environmental attributes measured at that scale. Finally, some spatial correlation arises simply because of the aggregation of survey points into well-separated study sites, a common sampling design associated with riparian-based surveys. When positive spatial autocorrelation exists, the estimated confidence interval (CI) is narrower than actually it is and one might often conclude that the effect of a covariate is statistically significant (e.g., Legendre, 1993; Fortin and Dale, 2005; Beale et al., 2010). We observed this effect in our study; although we did not describe it in our results, 90% CI of estimates of a model without ACOV were narrower than those of a model with ACOV, and more variables had apparently significant effects. We conclude that incorporating ACOV into occupancy models provides more robust estimates of the effects of environmental variables, and that the lack of explicit consideration of spatial covariation in other, similar analyses may have led to an overestimation of significant relationships.

4.3. Implications for conservation and management

Recently, riparian bird conservation planning in semiarid and arid regions has emphasized incorporating landscape-level considerations such as protection of adjacent upland habitats or restriction on adjacent land use. Our results provide empirical support to this recent change. Our results also highlight the importance of preserving riparian forests and increasing riparian vegetation for riparian bird conservation, which are consistent with major management recommendations of the Riparian Habitat Joint Venture (RHJV, 2004) in California. However, we note that the scale-dependency of avian species and their responses to landscape characteristics were species-specific. This suggests that only managing vegetation structure within a riparian forest (i.e., local-scale management) or only protecting riparian forests or restricting land use nearby riparian forests (i.e., landscape-scale management) may be not enough to conserve riparian bird species in this region. For successful management, one must consider habitat characteristics at both local and landscape scales (Rodewald and Bakermans, 2006; Pennington et al., 2008).

While our results support several current management recommendations, there are several differences between our study and much conservation planning. For one, many plans are focused on riparian forests along higher order streams (e.g., rivers or large streams). Riparian vegetation along first or second order streams can be more common (but narrower and patchier) than those along rivers in a region. However, little attention has been paid to these riparian forests, which comprise the majority of those used in our study, and are indeed common throughout the arid Southwest. Thus, riparian forests in low order streams, particularly embedded in an urban or agricultural landscape matrix, need to be incorporated into regional avian conservation planning. Second, most conservation plans view urban or agriculture lands as inappropriate anthropogenic habitats and as a source of avian predators or invasive species. Significantly, we found a positive effect of moderate level of urban development on occupancy of several riparian obligates. In the Southwest, riparian forests harbor numerous endemic species and Neotropical migrants, many of which are

riparian dependent species (e.g., RHJV, 2004). These species have been targets for conservation, and they are often used as indicators to assess the quality of riparian forests. However, it remains possible that riparian forests in a landscape dominated by anthropogenic land uses may function as ecological traps, providing habitat cues that attract species to settle, but containing predators, parasites, or resources inadequate to support successful reproduction (Kristan, 2003), which could jeopardize long term persistence of a species (e.g., Robertson and Hutto, 2006). Studies estimating demographic parameters such as annual productivity rate and survival rate of individual species can clarify this possibility, and sharpen our understanding of the value of riparian forests in urbanized and/or agricultural landscapes.

5. Conclusion

Protection and restoration of riparian ecosystems have been one of the top environmental management priorities in the USA during the past several years due to their important role in ecosystem services and conservation (Jones et al., 2010). Our results suggest that the landscape matrix surrounding a riparian forest, such as amount of available riparian forest, type of land use, and degree of land use, is a crucial feature influencing avian species distribution in semiarid and arid regions. More importantly, our results indicate that the patchy and relatively small riparian forests in the urbanizing landscape may have a positive role to maintain or promote avian diversity in these regions, particularly if large and intact riparian forests become degraded. Thus despite the challenges of implementing landscape-scale management practices in existing urban areas (e.g., lands tend to be highly parcelized and frequently under many different ownerships), there remains room for conservation in urbanized landscapes (Marzluff and Rodewald, 2008; Trammell et al., 2011).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2015.04.001>.

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