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EFFECTS OF ANTHROPOGENIC FRAGMENTATION AND LIVESTOCK GRAZING ON WESTERN RIPARIAN BIRD COMMUNITIES

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Abstract. Deciduous vegetation along streams and rivers provides breeding habitat to more bird species than any other plant community in the West, yet many riparian areas are heavily grazed by cattle and surrounded by increasingly developed landscapes. The combination of cattle grazing and landscape alteration (habitat loss and fragmentation) are thought to be critical factors affecting the richness and composition of breeding bird communities. Here, we examine the influence of land use and cattle grazing on deciduous riparian bird communities across seven riparian systems in five western states: Montana, Idaho, Nevada, Oregon and California. These riparian systems are embedded in landscapes ranging from nearly pristine to almost completely agricultural. We conducted landscape analysis at two spatial scales: local landscapes (all land within 500 m of each survey location) and regional landscapes (all land within 5 km of each survey location). Despite the large differences among riparian systems, we found a number of consistent effects of landscape change and grazing. Of the 87 species with at least 15 detections on two or more rivers, 44 species were less common in grazed sites, in heavily settled or agricultural landscapes, or in areas with little deciduous riparian habitat. The Veery (*Catharus fuscescens*), Song Sparrow (*Melospiza melodia*), Red-naped Sapsucker (*Sphyrapicus nuchalis*), Fox Sparrow (*Passerella iliaca*), and American Redstart (*Setophaga ruticilla*) were all less common under at least three of these conditions. In contrast, 33 species were significantly more common in one or more of these conditions. Sites surrounded by greater deciduous habitat had higher overall avian abundance and 22 species had significantly higher individual abundances in areas with more deciduous habitat. Yet, areas with more agriculture at the regional scale also had higher total avian abundance, due in large part to greater abundance of European Starling (*Sturnus vulgaris*), American Robin (*Turdus migratorius*), Brown-headed Cowbird (*Molothrus ater*), and Black-billed Magpie (*Pica pica*), all species that use both agricultural and riparian areas. Grazing effects varied considerably among riparian systems, but avian abundance and richness were significantly lower at grazed survey locations. Fifteen species were significantly less abundant in grazed sites while only five species were more abundant therein. Management should focus on (1) preserving and enlarging deciduous habitats, (2) reducing cattle grazing in deciduous habitats, and (3) protecting the few relatively pristine landscapes surrounding large deciduous riparian areas in the West.

Key Words: agriculture; avian abundance and richness; cattle grazing; landscape fragmentation; multi-scale; riparian habitat.

Deciduous riparian areas bordering rivers and streams in the western United States support a higher density of breeding birds than any other habitat type (Carothers and Johnson 1975, Rice et al. 1983, Ohmart and Anderson 1986), and studies explicitly comparing deciduous riparian areas with surrounding upland communities repeatedly have found diversity and density of breeding birds to be greater in riparian communities (Carothers et al. 1974, Johnson et al. 1977, Stamp 1978, Conine et al. 1979, Hehnke and Stone 1979, Knopf 1985; Anderson et al. 1985a,b; Strong and Bock 1990, Cubbedge 1994). The importance of these habitats to the maintenance of avian communities cannot be overemphasized. Deciduous riparian habitat makes up less than 1% of the western land area (Knopf et al. 1988), yet over 50% of western bird species breed primarily or exclusively in deciduous riparian communities (Johnson et al. 1977, Mosconi and Hutto 1982, Johnson 1989, Saab and Groves 1992, Dobkin 1994). Due to the proliferation of dams, intensive water management practices, and the effects of domestic livestock, riparian areas are considered the most heavily degraded ecosystems in the West (Rosenberg et al. 1991, Dobkin 1994, Ohmart 1994, Saab et al. 1995); some western states have already lost as much as 95% of their historic riparian habitat (Rosenberg et al. 1991, Ohmart 1994). The importance of remaining riparian areas for avian and other wildlife populations is thus greatly magnified.

Two of the primary threats to the quality of remaining deciduous riparian habitats are the conversion of land near riparian areas into agricultural and urban land (Tewksbury et al. 1998, Saab 1999), and cattle grazing within riparian areas (Carothers 1977, Crumpacker 1984, Chaney et al. 1990, Saab et al. 1995, Saab 1998). The effects of these activities on individual rivers have often been studied using different metrics, focusing on different groups of birds, and there have been few attempts to combine data across riparian systems to look for common patterns (Hochachka et al. 1999).

Although it is widely recognized that the richness and composition of breeding bird assemblages are at least partially dependent on the landscape within which they are embedded (Robinson et al. 1995a; Donovan et al. 1995b, 1997; Freemark et al. 1995, Faaborg et al. 1995, Saab 1999), it is not clear what scale or scales are appropriate to use when considering the effects of landscapes on bird populations (Freemark et al. 1995, Donovan et al. 2000). Indeed, given the many factors that can affect the structure of bird communities (nest predation, brood parasitism, competition for food and nesting sites, habitat area limitations), landscapes likely affect bird communities at multiple scales (Wiens 1989, 1995; Urban et al. 1987, Turner 1989, Kareiva 1990, Kotliar and Wiens 1990, Barrett 1992, Andrén 1995, Freemark et al. 1995, Hansson et al. 1995). To date, however, few empirical studies have considered the relative importance of multiple landscape scales (but see Tewksbury et al. 1998, Hochochka et al. 1999, Saab 1999, Donovan et al. 2000), and there has been no attempt to examine the relative effects of multiple land-uses across scales when studying the composition of riparian bird communities.

A focal concern in the western United States is cattle grazing. Domestic cattle graze 70% of the land area in the 11 western states (Crumpacker 1984) causing extensive modifications to vegetation (Holechek et al. 1989). These effects are particularly apparent in deciduous riparian areas (Carothers 1977, Crumpacker 1984, Platts and Nelson 1985, Fleischner 1994, Saab et al. 1995). However, it is not clear which grazing effects are dependent on local factors and levels of grazing intensity, and to what extent grazing effects can be generalized across a broad array of riparian systems and grazing regimes.

Here we examine the influence of regional (within 5 km of each study site) and local (within 500 m of each study site) landscapes and the influence of cattle grazing on the richness and relative abundance of bird communities in seven riparian systems dominated by deciduous trees and shrubs. This work is the result of collaboration by five independent research teams working in five western states over the past decade. By combining efforts, we provide the first meta-analysis of human-induced landscape change and cattle grazing on the avian communities breeding in these critical western habitats in the hope of detecting consistent patterns across the West.

METHODS

Riparian Systems, Survey Locations, and Landscape Characterization

The seven riparian systems included in this work vary considerably in size, physical character, local and regional vegetation patterns, and land use (Fig. 1; Appendix 1), but all possess streamside vegetation dominated by woody deciduous species (see Appendix 1 for detailed descriptions of each riparian system).

We analyzed bird species-abundance data from a total of 437 survey locations (Fig. 1; Table 1). Survey locations were separated by at least 150 m and located in vegetation dominated by cottonwood (*Populus* spp.), aspen (*Populus tremuloides*), or a mixture of species including willow (*Salix* spp.), valley oak (*Quercus lobata*), dogwood (*Cornus* spp.), hawthorn (*Crataegus* spp.), cherry (*Prunus* spp.), alder (*Alnus* spp.), and birch (*Betula* spp.). At each survey location, relative abundance was calculated as the total number of each species detected per visit. Surveys were either fixed-radius point counts (five of the seven systems) or 150-m fixed-width line transects (Table 1). We defined a survey as a single visit to a point or transect location. All studies conducted three surveys per year. The radius of point counts was either 40 m or 50 m, and point duration was either five or 10 min (Table 1).

We defined two spatial scales at each study location: regional landscapes (all land within 5 km of each survey location = 7,854 ha) and local landscapes (all land <500 m of each survey location = 78 ha). Regional landscape character was quantified using state GAP databases (Scott et al. 1993) derived from satellite images (Table 1). Local landscape data were gathered from low elevation aerial photography, ortho-photo quadrangle maps, and high resolution digital data, depending on the riparian system. Using a different data set for local analyses allowed us to include smaller features in analyses, such as linear riparian components and individual buildings that could not be detected at the regional scale. Metrics such as average patch size and edge-to-interior ratios depend on mapping resolution, and our data resolution varied considerably among sources (Table 1). Thus we confined our analyses to the percent cover of four landscape components: forest cover, agriculture, human habitation, and deciduous riparian cover. The first three have been used previously to index landscape fragmentation and habitat conversion (Donovan et al. 1995b, 1997; Robinson et al. 1995a, Young and Hutto 1999). Deciduous riparian cover also has been used in landscape studies. Percent cover blends aspects of patch size and isolation, both of which have been found to affect riparian bird communities (Brown and Dinsmore 1986, Gibbs et al. 1991, Craig and Beal 1992, Saab 1999).

Our decision to compare high-resolution local data with low-resolution regional data also reflects the choice available to land managers, where detailed land-use data are available only at local scales. This approach, however, confounds differences in resolution with differences in scale. Therefore, on three riparian systems (Sacramento, San Joaquin, and Bitterroot rivers), we compared GAP data (used for the regional scale) with aerial photography data (used at the local scale) on the same 500 m local landscapes to examine correlations between estimates derived from different

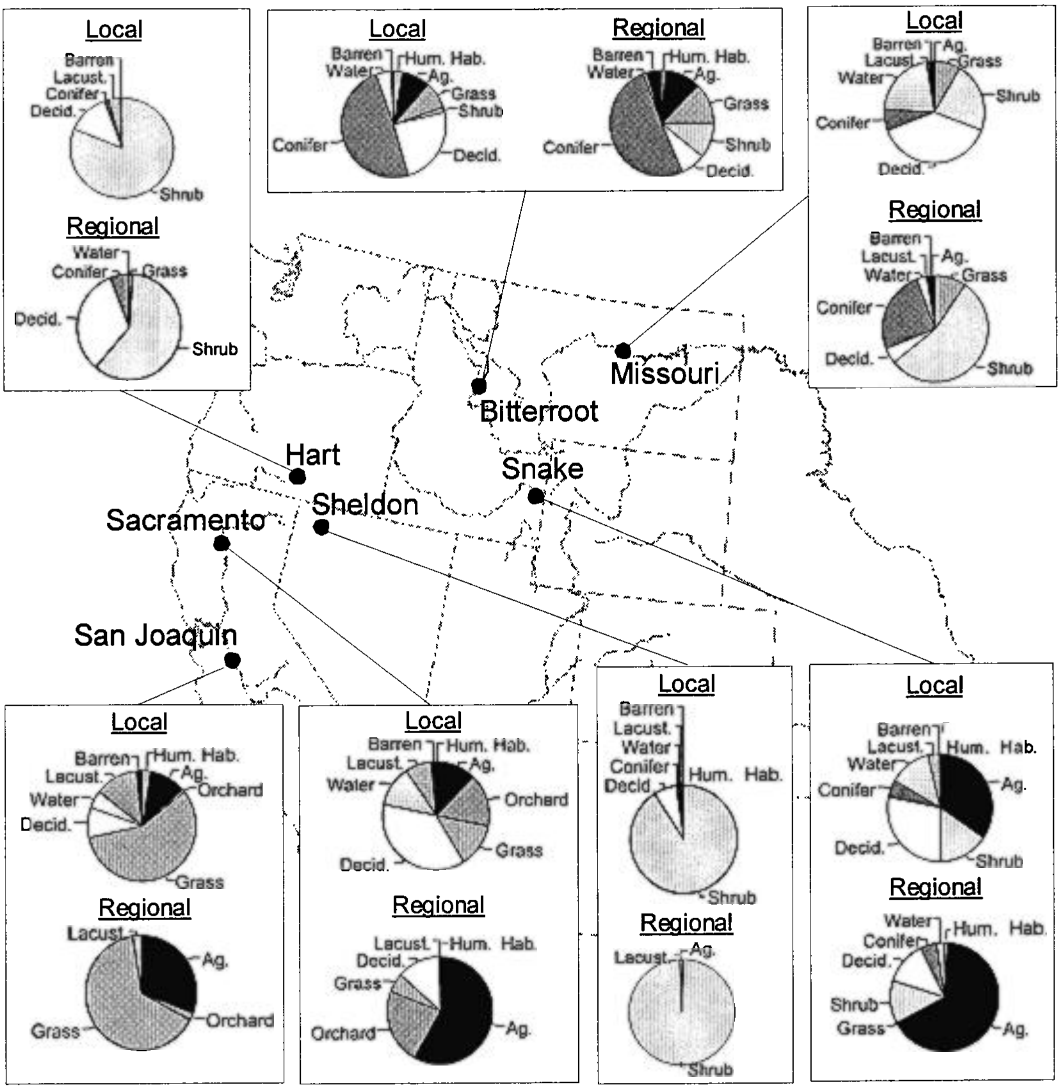

FIGURE 1. River system locations and general landscape character of each river system. Pie charts are mean percent cover for each landscape component averaged across all survey locations, at both local and regional scales. Hum. Hab. = all human habitations, including houses, farms, commercial developments, and industrial areas. Ag. = all agriculture, including row crops and land used for pasture and row crop, but excluding vineyards and orchards. Orchard = all orchards, primarily fruit and nut trees, and vineyards. Grass = all grasslands. Shrub = all shrublands and juniper woodlands, as bird communities were similar. Decid. = all deciduous habitats. Conifer = Conifer forests. Water = all large bodies of water, including river channels. Lacust. = Lacustrine, partially submerged and wet meadow habitat. Barren = permanent snow, ice, rock, or talus.

data types. For the Bitterroot River, the resolution of GAP data is quite high (Table 1), so we expected some concordance between the two techniques. For the Sacramento and San Joaquin Rivers, the GAP resolution is low, and this shift in resolution could affect results considerably. Because the regional scale contains 100 times the area of the local scale, however, lower resolution at the regional landscape scale should have less effect than lower resolution at the local scale.

Livestock Grazing

In five of the seven riparian systems studied, grazing occurred on some but not all of the study sites. Within these five systems, the intensity and timing of grazing differed considerably, from the Missouri River with long term high-intensity grazing on grazed sites and no cattle on rested ("ungrazed") sites for the past 30 years, to the Snake River where grazing intensity dif-

TABLE 1. RIVER SYSTEMS, DATA TYPES, AND SAMPLE SIZES

River system	State	Bird survey type	Duration/ length	Years	Sites	Survey locations	Local landscape: Landscape data source	Local landscape: Minimum mapping unit	Regional landscape: Landscape data source	Regional landscape: Minimum mapping unit
Sacramento	CA	Point count	5 min	1993–1997[a]	10	55	CWIS[g]	900 m^2	California GAP	100 ha
San Joaquin	CA	Point count	5 min	1995–1997[b]	6	54	CWIS[g]	900 m^2	California GAP	100 ha
Snake	ID	Point count	10 min	1991–1994[c]	46	148[e]	Aerial photos, Ortho-photo Quads.	~650 m^2	Idaho GAP	2 ha, 0.81 ha in riparian
Bitterroot	MT	Point count	10 min	1995–1997[d]	38	120	Aerial photos, Ortho-photo quads.	~650 m^2	MT GAP	2 ha, 0.81 ha in riparian
Missouri	MT	Point count	10 min	1998	9	29	MT GAP	2 ha, 0.81 ha in riparian	MT GAP	2 ha, 0.81 ha in riparian
Sheldon	NV	Transect	150 m long	1991 & 1993	5	10[f]	Aerial photography	~650 m^2	Nevada GAP	100 ha
Hart Mountain	OR	Transect	150 m long	1991 & 1993	7	21[f]	Aerial photography	~650 m^2	Western U.S. GAP[h]	100 ha

[a] Surveys conducted on seven sites (58 points) from 1993–1997, surveys conducted on one site (11 points) from 1994–1997, surveys conducted on one site (three points) from 1995 to 1997, and surveys conducted on one site (nine points) from 1996–1997.
[b] Surveys conducted on one site (15 points) from 1995–1997, surveys conducted on four sites (39 points) from 1996–1997, and surveys conducted on one site (nine points) in 1997 only.
[c] Two surveys at each location in 1991, three at each location in all other years.
[d] Surveys conducted on 16 sites (78 points) from 1995–1997, survey conducted on 22 sites (29 points) in 1996 only.
[e] Bird data were provided for each site (averaged across all points on a site).
[f] Surveys are strip transects (see text) run both in 1991 (grazed) and 1993 (ungrazed) and analyzed separately.
[g] California Wetlands Inventory System map of the Central Valley. Map was classified by the California Department of Fish and Game (1997) from spring and fall 1992/1993 30m satellite images. Available on-line at: http://ceres.ca.gov/wetlands/geo_info/cal_wetland_riparian.html.
[h] The Western GAP is an unreleased GAP cover combining all GAP maps in the western United States; Source: Idaho GAP Lab.

fered considerably among sites and was often moderate or light (Appendix 1). The methods of comparison differ as well; in the Hart Mountain and Sheldon systems, the same sites were surveyed in 1991 and 1993, the first and third growing seasons following cessation of long term livestock grazing. We considered the 1991 surveys "grazed" and the 1993 surveys rested. In all other riparian systems, bird abundance was compared in the same years among different locations, rather than in the same locations among different years. Given all these differences, we expected to find great variation among riparian systems in the effects of grazing, and any consistent effects should represent general effects applicable to a wide variety of riparian ecosystems in the West.

ANALYSIS

Relative abundance data were available for each point count or transect survey except on the Snake River, where data were averaged to the study site level. To accommodate this, we performed analyses at the site level for all riparian systems, and at the survey location level for all areas except the Snake. Both methods gave similar results. However, combining data to the site level resulted in a considerable loss of statistical power, so we present analysis of the survey location data for all rivers except the Snake, which is analyzed at the study site level. Our analysis of species richness includes all areas except the Snake because average richness per survey location could not be calculated from the data available.

All variables were initially screened for deviations from normality using one-sample Kolmogorov-Smirnov tests (Sokal and Rohlf 1995), and transformed where necessary. We used square-root transformations for count data (bird variables), and arcsine square-root transformations for percent data (landscape components). We examined four landscape components—human habitation, agriculture, deciduous forest, and coniferous forest—each at local and regional landscape scales.

Within each riparian system, we examined the effects of landscape differences on the relative abundance of all individual species detected an average of 15 or more times per year on that riparian system. Because we were primarily interested in effects that can be generalized throughout western riparian areas, we limited our analysis to species meeting this criterion on at least two riparian systems (102 species in total). In addition, we examined community level effects by grouping species into different guilds: primary hosts of Brown-headed Cowbirds (see Appendix 2 for scientific names of all species) vs. non-hosts; and long-distance migrants vs. short-distance migrants vs. permanent residents. In examining the effects of grazing, we also divided species into open nesting species vs. primary and secondary cavity nesting species, and low vs. high nesting species. Relative abundance of each species is defined as the average number of individuals detected per survey calculated by averaging values for separate visits within a year and then averaging across years. We also examined overall richness, calculated as the cumulative number of species detected at each location over the three surveys within a single year, averaged across years.

Migratory status followed Sauer et al. (2000). Primary hosts included all species listed as common or frequent cowbird hosts in *The Birder's Handbook* (Ehrlich et al. 1988); species listed as uncommon or rare cowbird hosts were termed secondary hosts (not analyzed in this manuscript). For nest height, we used the mean nest height from nesting studies on the riparian systems in this study, and examined the effect of grazing on the abundance of birds nesting below 2.5 m and above 5 m (Appendix 2).

To control for the large differences in methods among riparian systems, we first tested the effects of each landscape component within each riparian system to maintain consistency in sampling. To assess landscape effects on the avian community, we regressed total relative abundance, richness, and the relative abundance of each avian guild against each of the landscape components at both local and regional scales, using all survey locations within each riparian system for each river-specific analysis. To test for grazing effects we used t-tests within each riparian system, comparing community metrics and individual species between grazed and ungrazed sites. We assumed equal variance among population means unless $P < 0.1$ in Levene tests for equality of variance. Because these analyses are based on overall relative abundance of all species in a guild, the results are heavily influenced by the most common species. To examine landscape and grazing effects on community metrics with all species receiving equal weight, as well as to determine the response of individual species to differences in landscapes, we designated each survey location as low (lower 25%), middle (25 to 75%) or high (upper 25%) with respect to each landscape component within each riparian system. For tests of landscape effects on overall abundance, and the effects of landscapes and grazing on each guild, we coded each species as either more or less abundant in the low sites when compared to the high sites, then used binomial tests to determine if a significant majority of species within each guild were significantly more abundant in the high or low sites. For analysis of individual species, we used Mann-Whitney U-tests to compare the abundance of species in low and high sites for each landscape component within each riparian system and to compare abundance in grazed vs. ungrazed sites. We tested all species on a given riparian system with an average of 15 or greater detections per year. As our purpose was to evaluate the consistency of landscapes and grazing effects across rivers, we limit our results to species tested in at least two riparian systems. This analysis controls for landscape differences among different riparian systems because it compares abundances of birds across the landscape extremes within each riparian system.

To examine landscape and grazing effects across riparian systems, we used Fisher's combined probabilities test (Fisher 1954, Sokal and Rohlf 1995). This test evaluates the P-values from each riparian system against the null hypothesis that there is no general trend of significance across tests (in this case, riparian systems). The value -2 times the sum of the natural logs of all the P values from a group of independent tests of a single hypothesis falls along a cumulative Chi-square distribution with $2k$ degrees of freedom,

TABLE 2. CORRELATIONS AND MEAN DIFFERENCE (1 SE) BETWEEN LANDSCAPE COMPONENTS IDENTIFIED USING HIGH RESOLUTION LOCAL LANDSCAPE DATA AND LOWER RESOLUTION GAP DATA (USED FOR THE REGIONAL SCALE ANALYSIS) BOTH AT THE LOCAL SCALE

	Human habitation		Agriculture		Deciduous riparian		Coniferous forest	
	r	Diff (%)[b]	r	Diff (%)[b]	r	Diff (%)[b]	r	Diff (%)[b]
Bitterroot	0.20*	−5.4 (0.7)	0.78***	−9.0 (1.3)	0.76***	−6.3 (1.2)	0.97***	11.6 (1.0)
Sacramento	—[a]	−1.2 (0.2)	−0.23	5.9 (5.4)	0.11	0.2 (5.7)	—	—
San Joaquin	—[a]	−2.9 (0.3)	0.17	0.8 (3.9)	−0.07	7.6 (3.6)	—	—

Note: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.
[a] Lower resolution data-source picked up no human habitation.
[b] % difference = % component at regional scales (low resolution) − % component at local scales (high resolution).

where k = the number of separate tests (riparian areas) being compared. The combined probabilities test evaluates where the summed value lies along the cumulative Chi-square distribution. Because we are comparing the significance of tests for a general trend in one direction, but trends may be either positive or negative, we had to account for the sign associated with each P value. To do this, we used $-ln$ P for all results whose significance referred to a test opposite in sign from that being evaluated. We evaluated trends in both directions. This procedure produced a more conservative test for an overall pattern across riparian systems, as it is more difficult to reject the null hypothesis of no general effect. Using Fisher's combined probabilities tests also circumvents the problems of combining data with inherent differences in detection probabilities resulting from differences in survey techniques and observers. To determine the most abundant species across river systems, we ranked the abundance of all species within each river system in descending order, and computed mean abundance ranks for all species across rivers (a mean abundance rank of one would mean a species had the highest detection frequency in all rivers it occurred in).

To correct for inflation of significance due to multiple testing, we used sequential Bonferroni adjustment of significance (Rice 1989) for all correlation, regression, and t-tests. Thus for tests of landscape effects, we corrected for a total of 64 tests within each riparian system (four landscape components, two scales, and eight bird community components). We also corrected for 64 tests when examining the significance of the combined probabilities tests across riparian systems. For grazing effects, we corrected for 12 tests (one for each aspect of the bird community examined).

RESULTS

For all studies combined, 180 species were detected across 437 survey locations. Eleven species were detected on all seven river systems. These species, in order of mean abundance rank (lower ranks being more abundant) were the Brown-headed Cowbird, with a mean abundance rank of 7.2; American Robin, 13.7; House Wren, 14.6; Yellow Warbler, 16.1; European Starling, 17.9; Black-headed Grosbeak, 18.9; Bullock's Oriole, 21.3; Mourning Dove, 22.1; Warbling Vireo, 24.1; Brewer's Blackbird, 29.4; and Lazuli Bunting, 30.1. Of the 87 species tested individually for effects of landscape components and grazing, 44 species were significantly less common either in grazed areas, areas with high human habitation or extensive agriculture, or areas with less deciduous riparian habitat; 33 species were more common under these conditions.

CORRELATIONS AMONG LANDSCAPE COMPONENTS AND BETWEEN DATA RESOLUTIONS

Correlations among landscape components varied considerably among riparian systems, depending on the landscape context within which each stream or river was embedded (Fig. 1). Not surprisingly, both within and between scales, the strongest correlations were found where the four components we examined—human habitation, agriculture, deciduous area, and coniferous forest—dominated the landscape (e.g., Snake and Bitterroot rivers), as opposed to landscapes dominated by shrub or grass (Appendix 3). Landscape components varied considerably in their correlations across scales. Relatively homogeneous and broad land uses, such as agriculture, were always correlated positively across scales, whereas clumped and small land-uses, such as human habitation, were correlated weakly across scales in most riparian systems (Appendix 3). Differences in data resolution also affected correlations across scales. When we controlled for scale and compared both local (high resolution) and regional (low resolution) data at the local scale, we found strong positive correlations on the Bitterroot River (Table 2), where regional analysis was relatively fine grained (Table 1). Even with this higher resolution regional data (minimum mapping unit = 2 ha), however, smaller landscape components were underemphasized compared with dominant landscape components (Table 2). Where regional data were coarse-grained, as on the Sacramento and San Luis rivers, correlations were not significant, and differences had high variance because components identified with the high-resolution local data were either missed entirely, or overemphasized by the low resolution landscape data.

Human Habitation

At local scales, the majority of all species (62% ± 5% SE, five rivers) had lower relative abundances in areas with high human habitation compared to areas with low human habitation. This trend was particularly apparent in long-distance migrants (66% ± 6% less abundant in areas with high human habitation, five rivers). These relationships were significant for both groups in binomial tests, but because the Brown-headed Cowbird, Yellow Warbler, and the Black-headed Grosbeak (all very common species) were more abundant in areas with high human habitation, there was no relationship between the total number of detections of all species, or detections of long-distance migrants, vs. local human habitation (Table 3). Human habitation was strongly and positively correlated with the number of Brown-headed Cowbirds detected at both scales (Table 3), and the number of non-host species detections was higher in areas with higher regional human habitation, due primarily to the greater abundance of European Starlings, House Wrens, and American Robins in more densely settled areas (Table 4). The five species showing the greatest reduction in frequency in regional landscapes with high proportions of human settlement were Yellow-rumped Warbler, MacGillivray's Warbler, Warbling Vireo, Swainson's Thrush, and Dusky Flycatcher (Table 4). Populations of each of these species are highly vulnerable to cowbird parasitism (Tewksbury et al. 1998).

Agriculture

High abundances of abundant species such as American Robins, Yellow Warblers, and Brown-headed Cowbirds in areas with agriculture (Table 4) led to highly significant positive relationships between total and guild detection frequency and the amount of agriculture at both scales. However, binomial tests for direction of change of all species in each guild were not significant (Table 3; 53% ± 6% of species had higher abundance in areas with more agriculture), and the only river system to show a significant majority of species increasing with regional agriculture was the Bitterroot (Appendix 4). In addition, regional agriculture was significantly, positively correlated with the abundance of Brown-headed Cowbirds, which were twice as abundant in areas with high proportions of agriculture compared with areas with low proportions of agriculture. Primary hosts, although not related to agriculture at the local scale, showed a strong positive relationship with the amount of agriculture regionally. This positive trend was driven almost entirely by Yellow Warblers, the most abundant host. Yellow Warblers were detected far more often in areas with greater amounts of agriculture and human habitation. In contrast, many less abundant cowbird host species, such as Swainson's Thrush, Warbling Vireo, MacGillivray's Warbler, and Yellow-rumped Warbler, were rarely detected at survey locations with high regional agriculture (Table 4). Overall, there was no indication that the majority of hosts were more or less abundant in landscapes dominated by agriculture (Table 3; Appendix 4).

Non-hosts showed a strong positive relationship with agriculture at both scales (Table 3), primarily due to higher abundances of American Robins, House Wrens, European Starlings, Tree Swallows, and Bullock's Orioles in areas with greater proportions of agriculture (Table 4). The effects of human habitation and agriculture appear similar; in total, 24 species were significantly more abundant in areas with high local or regional agriculture, and 17 of these species were also significantly more abundant in areas with high human habitation.

Deciduous Riparian

Across riparian systems, areas with more deciduous riparian habitat tended to have greater avian abundance and diversity. Fifteen species were significantly more abundant in areas with a high proportion of deciduous habitat at the local scale; six of these species were present in at least four riparian systems: Yellow Warbler, Black-headed Grosbeak, Song Sparrow, Western Wood Pewee, Cedar Waxwing, and Orange-crowned Warbler. Only two species were significantly less abundant in areas with greater local deciduous riparian habitat, MacGillivray's Warbler and Townsend's Warbler. Effects at the regional scale were similar (Tables 3 and 4), though almost half of the individual species increasing were different from those increasing at the local scale.

The amount of local deciduous riparian habitat was positively correlated with virtually all avian guilds at both scales. Binomial tests were less convincing of a significant overall effect, where the only significant relationship was between all species and regional deciduous riparian habitat (Table 3; 57% of species ± 4.3%, five rivers). The lack of significant effects in binomial tests at the local scale was caused primarily by effects on the Sacramento River, where greater local deciduous riparian habitat was associated with lower detection frequencies in 67% of all species (Appendix 4).

Coniferous Forest

At the local scale, the proportion of coniferous forest was not significantly related to total relative abundance, richness, or any guild examined, after correcting for multiple tests. However, at the regional scale, conifer cover had a strong negative effect on cowbird abundance (combined $P < 0.001$). Cowbirds were detected only half as often at survey locations with high conifer forest when compared to locations with low conifer forest (Table 4). Coniferous cover was also related negatively to the abundance of non-hosts, driven primarily by the low abundance of European Starlings, American Robins, and House Wrens in sites with high coniferous cover. In addition, long-distance migrant abundance was associated positively with percent conifer forest (Table 3), due primarily to many more detections of Warbling Vireo, MacGillivray's Warbler, Townsend's Warbler, Violet-green Swallow, and Fox Sparrow in areas with more conifers (Table 4). Binomial tests agreed in direction with regressions on total guild abundance, but were non-significant across rivers, showing considerable variation in results among individual rivers (Appendix 4).

GRAZING

The majority of all species (63% ± 5%) were less abundant in grazed locations (Fig. 2A; combined probabilities test $\chi^2 = 42.8$, $P < 0.001$). After correcting for multiple tests, six species were significantly less abundant at grazed survey locations when all riparian systems were considered, while no species were significantly more abundant at grazed locations (Table 5). In addition, total relative abundance was significantly lower in grazed areas (Fig. 2B; combined probabilities test $\chi^2 = 48.9$, $P < 0.001$), and species richness showed a non-significant trend to be lower in grazed areas (Fig. 2C; combined probabilities test $\chi^2 = 19.8$, $P = 0.01$, not significant after correction for multiple tests). The intensity of grazing effects varied greatly among the seven riparian systems. On the Missouri, Sacramento, and Hart systems, 68–73% of species were less abundant in grazed areas (Fig. 2A; binomial tests, P's < 0.007). The Missouri showed the most dramatic effects, with 13 species significantly less abundant in grazed areas and only one more abundant (Appendix 5), and the average detections per count shifted from 36 on ungrazed survey locations to 21 on grazed survey locations. In contrast, on the Snake and Sheldon riparian systems, species were no more likely to be less or more abundant in these areas (Fig. 2A). On the Sheldon, only two species differed significantly between recently grazed and ungrazed sites, with one species more abundant in each condition (Appendix 5).

Cowbird abundances were not significantly different between grazed and ungrazed locations for any of the five large riparian systems (Fig. 3A). Total primary cowbird hosts, however, were less abundant in grazed areas (Fig. 3B; combined $\chi^2 = 25.3$, $P = 0.005$), with strong effects on the Missouri River ($t = 3.3$, $P = 0.003$) and the Snake River ($t = 3.2$, $P = 0.002$; Appendix 5). While the majority of host species were less abundant on grazed sites in all river systems except the Sheldon, the low number of species in the guild precluded significant effects (Fig. 3C). On the Missouri River, the effects of grazing on hosts was driven primarily by lower abundance of Red-eyed Vireo, American Redstart, Lazuli Bunting, Least Flycatcher, and Yellow Warbler in grazed areas (Appendix 5). Lazuli Buntings and Yellow Warblers were also significantly less abundant in grazed sites along the Snake River, as were Veerys and Song Sparrows (Appendix 5). Total non-host abundance showed no consistent response to grazing pressure (Fig. 3D; combined probabilities test $\chi^2 = 11.3$, $P = 0.33$), but the proportion of species that were more abundant in ungrazed systems was typically higher than expected by chance (Fig. 3E; combined probabilities test $\chi^2 = 20.0$, $P = 0.023$).

Of the migratory guilds, long-distance migrants were the only group significantly less abundant in grazed areas (Total abundance Fig. 4A: combined probabilities test $\chi^2 = 47.7$, $P < 0.001$; binomial mean response Fig. 4B: combined probabilities test $\chi^2 = 26.4$, $P = 0.003$). Across all riparian systems, five of the ten species with significantly lower relative abundances in grazed areas were long-distance migrants (Table 5). The lower relative abundance of long-distance migrants in grazed areas was particularly apparent on the Missouri River, where the average number of long-distance migrants was 21 individuals per survey in ungrazed areas and only 12 per survey in grazed areas (Fig. 4A), and 84% of the species were less abundant in grazed sites (Fig. 4B). In addition to large effects on the Missouri, long-distance migrants were significantly less abundant in grazed sites on the Sacramento ($t = 2.1$, $P = 0.037$), and exhibited similar non-significant trends in both Hart Mountain and Snake River systems ($P = 0.07$ and 0.18, respectively). Residents showed no significant differences between grazed and ungrazed sites for any of the riparian systems (Fig. 4C and 4D). The total abundance of short-distance migrants tended to be lower in grazed areas (Fig. 4E; combined probabilities test $\chi^2 = 19.3$, $P = 0.03$, not significant after correction for multiple tests) with large differences in detection frequency only on the Missouri River ($t = 3.2$, $P = 0.003$). Individual species in this guild were no more likely to be less or more

TABLE 3. EFFECTS OF LANDSCAPE VARIABLES ON TOTAL DETECTIONS, RICHNESS, AND DETECTIONS BY GUILD

Landscape variable		Statistic	All birds[c]	Richness[d]	Cowbirds[e]	Prime hosts[f]	Non-hosts[g]	Long-distance migrant[h]	Residents[i]	Short-distance migrant[j]
Local Human Habitation	Σ[a]	Dir	Neg	Pos	Pos	Pos	Neg	Neg	Neg	Pos
		χ^2	5.25	1.8	28.61	9.21	1.73	11.67	1.79	0.23
		P	0.874	0.985	0.001*	0.512	0.998	0.308	0.998	>0.99
	#[b]	Dir	Neg			Neg	Neg	Neg	Neg	Neg
		χ^2	39.8	N/A	N/A	18.4	18.4	25.6	7.12	12.9
		P	<0.001*	N/A	N/A	0.047	0.047	0.004*	0.525	0.231
Regional Human Habitation	Σ	Dir	Pos	Pos	Pos	Neg	Pos	Pos	Pos	Pos
		χ^2	6.36		25.71	10.73	16.18	5.44	9.30	14.26
		P	0.174	0.080[k]	0.001*	0.030	0.002*	0.245	0.054	0.026
	#	Dir	Neg			Neg	Neg	Neg	Neg	Neg
		χ^2	9.6	N/A	N/A	2.2	4.5	4.7	1.7	5.1
		P	0.144	N/A	N/A	0.903	0.605	0.585	0.944	0.531
Local Agriculture	Σ	Dir	Pos	Pos	Pos	Pos	Pos	Pos	Pos	Pos
		χ^2	22.94	15.12	34.98	7.67	31.59	7.52	10.90	38.08
		P	0.011*	0.019	<0.001*	0.661	0.001*	0.676	0.366	<0.001*
	#	Dir	Neg			Neg	Neg	Neg	Pos	Pos
		χ^2	0.5	N/A	N/A	0.79	0.4	9.8	3.1	0.3
		P	>0.99	N/A	N/A	0.999	>0.99	0.279	0.926	>0.99
Regional Agriculture	Σ	Dir	Pos	Pos	Pos	Pos	Pos	Pos	Pos	Pos
		χ^2	50.66	17.14	56.91	26.72	34.47	14.46	26.96	55.29
		P	<0.001*	0.029	<0.001*	0.003*	<0.001*	0.153	0.003*	<0.001*
	#	Dir	Pos			Pos	Pos	Neg	Pos	Pos
		χ^2	14.3	N/A	N/A	7.4	1.9	1.9	1.7	6.2
		P	0.159	N/A	N/A	0.690	0.997	0.997	0.998	0.794
Local Deciduous	Σ	Dir	Pos	Pos	Pos	Pos	Pos	Pos	Pos	Pos
		χ^2	38.01	15.70	31.33	56.87	14.07	16.71	29.28	34.42
		P	<0.001*	0.204	0.005*	<0.001*	0.445	0.272	0.010	0.002*
	#	Dir	Pos			Pos	Pos	Neg	Pos	Pos
		χ^2	15.7	N/A	N/A	4.51	10.47	2.3	15.08	0.29
		P	0.334	N/A	N/A	0.991	0.727	>0.99	0.237	>0.99
Regional Deciduous	Σ	Dir	Pos	Pos	Pos	Pos	Pos	Pos	Pos	Neg
		χ^2	12.89	15.12	20.89	20.34	24.25	17.17	28.30	0.62
		P	0.230	0.056	0.022	0.026	0.007*	0.071	0.002*	>0.99
	#	Dir	Pos			Pos	Pos	Pos	Pos	Pos
		χ^2	20.4	N/A	N/A	1.1	8.5	7.9	6.9	2.7
		P	0.026*	N/A	N/A	>0.99	0.576	0.635	0.735	0.987
Local Conifer	Σ	Dir	Neg	Neg	Neg	Neg	Neg	Neg	Neg	Neg
		χ^2	18.66	13.73	26.49	7.67	18.64	0.57	23.77	22.38

TABLE 3. CONTINUED

Landscape variable		Statistic	All birds[c]	Richness[d]	Cowbirds[e]	Prime hosts[f]	Non-hosts[g]	Long-distance migrant[h]	Residents[i]	Short-distance migrant[j]
		P	0.017	0.033	0.001*	0.466	0.045	>0.99	0.002*	0.004*
	#	Dir	Neg			Pos	Neg	Pos	Neg	Neg
		χ^2	5.1	N/A	N/A	3.0	5.9	12.1	6.2	4.0
		P	0.748	N/A	N/A	0.936	0.655	0.146	0.629	0.857
Regional Conifer	Σ	Dir	Neg	Pos	Neg	Neg	Neg	Pos	Neg	Neg
		χ^2	6.45	7.03	43.87	3.42	23.72	23.30	11.90	21.27
		P	0.597	0.318	<0.001*	0.905	0.003*	0.003*	0.156	0.006*
	#	Dir	Neg			Neg	Neg	Pos	Neg	Neg
		χ^2	8.5	N/A	N/A	1.4	8.4	14.2	3.0	10.4
		P	0.383	N/A	N/A	0.994	0.392	0.076	0.932	0.241

Note: Results from combined probabilities tests of linear regression of summed detections of all species in each guild (Σ) and from binomial tests on direction of change of each species in the guild (#).
* Significant ($P < 0.05$) after Bonferroni correction for multiple tests.
[a] Chi-square value and significance from multiple comparison tests based on regression of landscape value on total abundance within each guild.
[b] Chi-square value and significance from multiple comparison tests based on binomial tests examining the proportion of species more or less abundant in sites with high values for each landscape component.
[c] Average number of all detections per survey.
[d] Average number of species detected per year at a given survey location (3 surveys).
[e] Number of Brown-headed Cowbirds detected.
[f] Number of primary cowbird hosts detected (Appendix 2).
[g] Average number of non-hosts detected (Appendix 2).
[h] Average number of long-distance migrants detected per survey (Appendix 2).
[i] Average number of residents detected per survey (Appendix 2).
[j] Average number of short-distance migrants detected per survey (Appendix 2).
[k] Regression run only on the Bitterroot River; P-value is for regression (Appendix 4).

TABLE 4. INDIVIDUAL SPECIES RESPONSES TO LANDSCAPE COMPONENTS

Landscape component	N	P	Ratio	River system						
				Bitterroot	Sacramento	San Joaquin	Missouri	Snake	Sheldon	Hart Mountain
High Local Human Habitation										
More Abundant Species										
Bullock's Oriole	4	<0.001*	2.33	0.01/0.11	0.14/0.29	0.30/0.38			0.18/0	
Yellow Warbler	4	<0.001*	3.23	0.18/1.05	0.01/0.01	0.02/0.00			0.73/0.50	
Brown-headed Cowbird	4	<0.001*	1.83	0.40/0.84	0.38/0.59	1.01/1.27			0.82/1.50	
Red-winged Blackbird	4	<0.001*	1.54	0.01/0.20	0.00/0.00	1.22/1.17			1.45/1.25	
Black-headed Grosbeak	4	0.001*	1.62	0.10/0.11	0.42/0.76	0.00/0.11			0.18/0.50	
American Robin	4	0.009	1.79	0.26/0.48	0.10/0.17	0.03/0.05			0.18/0.75	
Western Wood-pewee	3	<0.001*	2.21	0.04/0.27	0.43/0.87				0.45/0.25	
Spotted Towhee	3	0.005*	1.67		0.79/1.30	0.50/0.69			0.09/0.00	
Song Sparrow	3	0.009*	1.99	0.04/0.20		0.60/0.84			0.64/0.50	
Willow Flycatcher	3	0.014	3.13	0.02/0.14	0.01/0.00				0.09/0.00	
Downy Woodpecker	3	0.030	1.90	0.03/0.05	0.06/0.14	0.01/0.00				
Red-shafted Flicker	3	0.034	1.68	0.07/0.23		0.05/0.03			0.27/0.00	
Cedar Waxwing	2	<0.001*	2.51	0.08/0.42	0.16/0.0					
Marsh Wren	2	0.042*	13.21			0.0/0.75			0.09/0.0	
Less Abundant Species										
MacGillivray's Warbler	3	<0.001*	4.92	0.52/0.08	0.00/0.00				0.27/0.25	
Townsend's Warbler	3	0.024	107.20	0.25/0.00	0.00/0.01				0.18/0.00	
Ash-throated Flycatcher	2	0.009	1.28		0.51/0.23	0.75/0.70				
Western Scrub-Jay	2	0.011*	2.03		0.26/0.17	0.59/0.17				
High Regional Human Habitation										
More Abundant Species										
European Starling	2	<0.001*	23.12	0.01/0.22				0.11/1.43		
Western Wood-pewee	2	<0.001*	4.70	0.08/0.36				0.02/0.31		
Bullock's Oriole	2	<0.001*	6.46	0.02/0.09				0.18/0.70		
House Wren	2	<0.001*	18.19	0.01/0.04				0.10/1.42		
Red-winged Blackbird	2	<0.001*	6.13	0.03/0.16				0.02/0.15		
Brown-headed Cowbird	2	<0.001*	1.57	0.50/0.77				0.17/0.58		
American Robin	2	0.002*	2.00	0.35/0.49				0.87/1.62		
Yellow Warbler	2	0.003*	2.14	0.39/0.96				2.32/2.39		
Willow Flycatcher	2	0.004*	1.77	0.05/0.11				0.01/0.01		
Downy Woodpecker	2	0.010*	2.30	0.04/0.08				0.03/0.12		
Tree Swallow	2	0.010*	2.99	0.02/0.06				0.12/0.18		
American Goldfinch	2	0.019	3.49	0.01/0.05				0.61/0.96		

TABLE 4. CONTINUED

Landscape component	N	P	Ratio	River system: Bitterroot	Sacramento	San Joaquin	Missouri	Snake	Sheldon	Hart Mountain
Less Abundant Species										
Yellow-rumped Warbler	2	<0.001*	4.92	0.10/0.02				0.21/0.02		
MacGillivray's Warbler	2	<0.001*	2.56	0.39/0.19				0.14/0.01		
Warbling Vireo	2	<0.001*	2.00	0.53/0.36				1.07/0.17		
Swainson's Thrush	2	<0.001*	2.39	0.21/0.11				0.04/0.00		
Dusky Flycatcher	2	<0.001*	5.64	0.44/0.08				0.09/0.04		
Ruffed Grouse	2	<0.001*	6.90	0.07/0.01				0.06/0.00		
Red-naped Sapsucker	2	0.006*	2.09	0.14/0.08				0.26/0.06		
Veery	2	0.006*	2.47	0.11/0.03				0.45/0.15		
Song Sparrow	2	0.012	1.34	0.09/0.14				1.01/0.21		
American Crow	2	0.021*	1.43	0.00/0.00				0.26/0.07		
Western Tanager	2	0.023*	3.06	0.07/0.02				0.08/0.03		
High Local Agriculture										
More Abundant Species										
American Robin	4	<0.001*	2.19	0.23/0.65	0.09/0.18	0.07/0.03		1.12/1.90		
Bullock's Oriole	4	<0.001*	2.76	0.00/0.10	0.21/0.37	0.31/0.24		0.29/0.88		
House Wren	4	<0.001*	3.52	0.00/0.05	0.17/0.23	0.79/1.18		0.17/1.53		
European Starling	4	<0.001*	8.28	0.00/0.22	0.11/0.04	0.20/0.08		0.09/1.99		
Brown-headed Cowbird	4	<0.001*	1.75	0.39/0.81	0.35/0.51	0.96/1.38		0.34/0.52		
Yellow Warbler	4	<0.001*	1.97	0.19/1.21	0.03/0.00	0.03/0.03		2.68/2.29		
Great Horned Owl	4	0.004*	N/A	0.00/0.01	0.00/0.02	0.00/0.08		0.00/0.03		
Tree Swallow	4	0.006*	1.33	0.00/0.08	0.68/0.43	0.48/0.55		0.11/0.21		
Black-headed Grosbeak	4	0.006*	1.72	0.10/0.16	0.36/0.80	0.02/0.08		0.25/0.14		
Spotted Sandpiper	4	0.010*	6.94	0.00/0.13	0.01/0.01	0.02/0.00		0.03/0.01		
Downy Woodpecker	4	0.014	2.24	0.04/0.08	0.03/0.12	0.01/0.00		0.04/0.13		
American Goldfinch	4	0.030	1.57	0.00/0.02	0.32/0.28	0.09/0.25		0.79/0.90		
Western Wood-pewee	3	<0.001*	5.26	0.03/0.40	0.29/0.69			0.09/0.42		
Red-winged Blackbird	3	<0.001*	1.26	0.00/0.20		1.18/0.66		0.07/0.05		
Red-shafted Flicker	3	<0.001*	2.02	0.05/0.26		0.04/0.02		0.28/0.15		
Song Sparrow	3	<0.001*	1.73	0.02/0.23		0.72/1.51		0.95/0.12		
Cedar Waxwing	3	0.004*	1.51	0.12/0.36	0.07/0.00			0.36/0.15		
Willow Flycatcher	3	0.014	3.48	0.03/0.13	0.01/0.02			0.00/0.01		
Spotted Towhee	3	0.033	1.98	0.00/0.00	0.02/1.22	0.63/0.96				
Black-billed Magpie	2	0.001*	1.77	0.26/0.40				0.22/0.54		
Eastern Kingbird	2	0.001*	76.67	0.00/0.02				0.00/0.04		
White-breasted Nuthatch	2	0.032*	3.29	0.01/0.03	0.04/0.09					
Less Abundant Species										
Warbling Vireo	3	<0.001*	2.16	0.61/0.41	0.07/0.03			0.74/0.16		
Dusky Flycatcher	3	<0.001*	7.05	0.39/0.06	0.01/0.00			0.06/0.03		

TABLE 4. CONTINUED

Landscape component	N	P	Ratio	River system: Bitterroot	Sacramento	San Joaquin	Missouri	Snake	Sheldon	Hart Mountain
Yellow-rumped Warbler	3	0.005*	2.26	0.09/0.06	0.01/0.00			0.16/0.02		
N. Rough-winged Swallow	3	0.017*	N/A		0.02/0.00	0.13/0.00		0.03/0.00		
Townsend's Warbler	3	0.019	46.12	0.29/0.00	0.00/0.01	0.00/0.01				
MacGillivray's Warbler	2	<0.001*	11.87	0.60/0.06				0.12/0.01		
Veery	2	0.001*	3.60	0.11/0.04				0.40/0.07		
Ruffed Grouse	2	0.001*	5.29	0.07/0.02				0.06/0.00		
Nuttall's Woodpecker	2	0.003*	1.87		0.60/0.41	0.31/0.08				
Chipping Sparrow	2	0.005*	9.25	0.10/0.01				0.04/0.01		
Violet-green Swallow	2	0.007*	9.30		0.01/0.00			0.32/0.03		
Ruby-crowned Kinglet	2	0.010*	25.32	0.16/0.01	0.01/0.00					
Red-naped Sapsucker	2	0.012*	1.77	0.12/0.09				0.22/0.05		
Western Scrub-Jay	2	0.017*	1.82		0.28/0.11	0.57/0.35				
Orange-crowned Warbler	2	0.017	7.42	0.13/0.02	0.02/0.00					
High Regional Agriculture										
More Abundant Species										
Brown-headed Cowbird	5	<0.001*	1.97	0.26/0.79	0.32/0.61	0.94/1.44	0.44/0.50	0.25/0.63		
Bullock's Oriole	5	<0.001*	1.59	0.00/0.08	0.19/0.31	0.44/0.27	0.39/0.59	0.20/0.74		
House Wren	5	<0.001*	1.12	0.00/0.07	0.24/0.58	0.99/0.95	2.44/2.45	0.18/1.16		
Yellow Warbler	5	<0.001*	1.35	0.07/0.97	0.02/0.00	0.05/0.03	3.03/3.73	2.10/2.67		
American Robin	5	<0.001*	1.13	0.33/0.65	0.08/0.23	0.03/0.07	2.14/1.36	0.81/1.86		
American Goldfinch	5	<0.001*	1.37	0.00/0.06	0.33/0.37	0.05/0.43	1.78/2.41	0.56/1.32		
European Starling	5	0.002*	2.45	0.00/0.25	0.13/0.01	0.17/0.26	0.44/0.45	0.18/1.26		
Tree Swallow	5	0.015*	1.26	0.00/0.06	0.87/0.48	0.42/0.73	0.03/0.09	0.13/0.30		
Western Wood-pewee	4	<0.001*	1.21	0.04/0.34	0.32/0.99		1.78/1.18	0.04/0.39		
Spotted Towhee	4	0.002*	1.55	0.01/0.00	0.62/1.40	0.51/0.85	0.97/1.41			
Common Yellowthroat	4	0.004*	1.04	0.00/0.03	0.05/0.08	0.03/0.24	1.14/1.36			
Red-winged Blackbird	4	0.004*	1.38	0.00/0.13	0.01/0.00	0.91/0.84		0.02/0.16		
Downy Woodpecker	4	0.037	0.92	0.05/0.09	0.04/0.16		0.33/0.09	0.04/0.10		
Black-billed Magpie	3	<0.001*	3.09	0.13/0.66			0.03/0.09	0.36/0.29		
Eastern Kingbird	3	<0.001*	2.81	0.00/0.02			0.11/0.36	0.00/0.03		
Black-capped Chickadee	3	0.003*	1.33	0.13/0.66			0.72/0.05	0.29/0.30		
Willow Flycatcher	3	0.012	7.40	0.01/0.11	0.01/0.00			0.00/0.01		
Less Abundant Species										
Swainson's Thrush	5	<0.001*	6.17	0.34/0.02	0.00/0.01	0.10/0.04	0.11/0.09	0.07/0.00		
Warbling Vireo	4	<0.001*	4.73	0.59/0.16	0.05/0.01		0.31/0.00	0.96/0.16		
MacGillivray's Warbler	3	<0.001*	8.68	0.52/0.06	0.01/0.00			0.09/0.00		
Violet-green Swallow	3	0.003*	17.63		0.01/0.00		0.14/0.00	0.84/0.05		
American Crow	3	0.004*	8.57	0.01/0.01		0.10/0.02		0.26/0.02		
Yellow-rumped Warbler	3	0.007*	2.98	0.16/0.07	0.01/0.00			0.17/0.03		

TABLE 4. CONTINUED

Landscape component	N	P	Ratio	River system						
				Bitterroot	Sacramento	San Joaquin	Missouri	Snake	Sheldon	Hart Mountain
Townsend's Warbler	2	<0.001*	166.26	0.47/0.00	0.00/0.01					
Western Kingbird	2	0.015*	2.22		0.38/0.24	1.69/0.69				
Western Scrub-Jay	2	0.030	1.77		0.27/0.18	0.63/0.33				
High Local Deciduous Riparian										
More Abundant Species										
Yellow Warbler	7	<0.001*	1.25	0.03/0.77	0.00/0.01	0.00/0.03	2.71/3.21	1.90/2.81	1.00/0.50	2.00/0.30
Black-headed Grosbeak	7	0.014*	1.80	0.05/0.11	0.72/0.44	0.02/0.17	0.21/0.57	0.08/0.23	0.00/0.33	0.09/0.70
Song Sparrow	6	<0.001*	1.85	0.01/0.21		0.53/1.33	0.50/0.79	0.35/0.48	1.00/0.50	0.18/0.00
Western Wood-pewee	6	0.015	1.60	0.03/0.21	0.62/0.54		0.71/2.29	0.27/0.24	0.67/0.17	0.27/0.40
Cedar Waxwing	4	<0.001*	1.58	0.06/0.25	0.27/0.02		0.36/0.79	0.24/0.34		
Orange-crowned Warbler	4	0.034	2.81	0.12/0.04	0.00/0.02				0.33/0.17	0.00/1.10
Black-capped Chickadee	3	<0.001*	3.48	0.10/0.51			0.00/0.43	0.27/0.36		
Red-eyed Vireo	3	<0.001*	19.60	0.00/0.04			0.07/1.29	0.00/0.01		
Red-naped Sapsucker	3	<0.001*	4.23	0.06/0.21				0.07/0.22		0.09/0.60
Gray Catbird	3	0.007*	3.72	0.00/0.04			0.21/0.57	0.05/0.19		
Veery	2	<0.001*	16.23	0.00/0.08				0.03/0.38		
Fox Sparrow	2	<0.001*	N/A					0.00/0.12		0.00/0.90
Least Flycatcher	2	0.006*	3.68	0.00/0.03			0.71/2.50			
American Redstart	2	0.011*	14.27	0.02/0.19			0.00/0.43			
Bewick's Wren	2	0.031*	1.57		0.49/0.72	0.45/0.75				
Less Abundant Species										
MacGillivray's Warbler	4	0.001*	3.90	0.58/0.13	0.00/0.00			0.04/0.04	0.33/0.17	0.18/0.00
Townsend's Warbler	4	0.004*	12.66	0.40/0.00		0.00/0.01			0.00/0.17	0.18/0.00
Western Kingbird	3	0.026	1.87		0.39/0.14	0.92/0.56			0.00/0.17	
High Regional Deciduous Riparian										
More Abundant Species										
Western Wood-pewee	5	<0.001*	2.23	0.01/0.33	0.51/0.92		1.07/2.00	0.23/0.05		0.20/0.70
American Robin	5	0.020	1.19	0.31/0.65	0.05/0.25		1.36/1.93	1.66/0.94		1.60/1.90
Song Sparrow	4	<0.001*	2.30	0.01/0.20			0.00/0.21	0.45/1.03		0.30/0.00
Yellow Warbler	4	<0.001*	1.27	0.07/0.90			2.43/3.43	2.53/2.13		1.40/0.50
Red-shafted Flicker	4	0.011*	1.47	0.08/0.23			0.79/1.36	0.20/0.32		0.90/0.80
Cedar Waxwing	4	0.012	2.25	0.04/0.23	0.01/0.00		0.29/0.64	0.27/0.32		
Black-capped Chickadee	3	<0.001*	3.14	0.17/0.69			0.29/1.29	0.26/0.26		
Red-eyed Vireo	3	0.004*	67.64	0.00/0.03			0.00/0.71	0.01/0.02		
Willow Flycatcher	3	0.009*	9.86	0.00/0.10	0.02/0.00			0.01/0.00		
Red-naped Sapsucker	3	0.012*	1.87	0.03/0.09				0.12/0.20		0.40/0.70
Red-winged Blackbird	3	0.046	0.45	0.00/0.13				0.15/0.05		0.80/0.00
White-breasted Nuthatch	3	0.046	3.32	0.00/0.03	0.07/0.10		0.00/0.14			

TABLE 4. CONTINUED

Landscape component	N	P	Ratio	River system: Bitterroot	Sacramento	San Joaquin	Missouri	Snake	Sheldon	Hart Mountain
Black-billed Magpie	2	<0.001*	2.45	0.17/0.69				0.39/0.34		
Less Abundant Species										
Townsend's Warbler	2	<0.001*	159.60	0.45/0.00	0.00/0.01					
Orange-crowned Warbler	2	0.006*	2.33	0.11/0.04						1.10/0.50
MacGillivray's Warbler	2	0.019	4.52	0.54/0.09				0.05/0.08		
Ruby-crowned Kinglet	2	0.024	4.50	0.18/0.01						0.00/0.10
High Local Conifer Forest										
More Abundant Species										
Swainson's Thrush	4	<0.001*	4.92	0.01/0.31			0.00/0.14	0.00/0.07		0.19/0.20
Warbling Vireo	4	<0.001*	1.96	0.21/0.57			0.00/0.14	0.17/0.71		1.25/1.90
MacGillivray's Warbler	3	<0.001*	13.61	0.05/0.50				0.01/0.11		0.00/0.10
Yellow-rumped Warbler	3	0.007*	2.86	0.03/0.09				0.02/0.12		0.06/0.10
Dusky Flycatcher	3	0.023	0.97	0.02/0.29				0.02/0.03		1.81/1.30
Western Tanager	3	0.034	3.97	0.01/0.08				0.02/0.04		0.06/0.20
Ruffed Grouse	2	<0.001*	11.67	0.01/0.09				0.00/0.06		
Ruby-crowned Kinglet	2	0.007*	6.22	0.01/0.19						0.06/0.10
Veery	2	0.028	2.14	0.02/0.00				0.17/0.59		
Violet-green Swallow	2	0.029	5.30				0.07/0.00	0.05/0.43		
Less Abundant Species										
Western Wood-pewee	4	<0.001*	1.64	0.40/0.03			1.79/1.07	0.33/0.06		0.50/1.00
American Robin	4	<0.001*	1.88	0.72/0.25			2.07/0.93	1.57/0.95		1.94/1.70
House Wren	4	<0.001*	1.60	0.07/0.00			2.50/1.93	1.24/0.05		4.50/4.50
Bullock's Oriole	4	<0.001*	1.90	0.14/0.00			0.64/0.36	0.69/0.25		0.50/0.80
European Starling	4	<0.001*	2.44	0.25/0.00			0.71/0.14	1.27/0.11		0.50/1.40
Yellow Warbler	4	<0.001*	1.41	1.30/0.07			3.21/3.29	2.49/2.80		0.75/1.20
Red-shafted Flicker	4	<0.001*	1.53	0.30/0.06			1.43/0.64	0.17/0.25		1.06/1.10
Downy Woodpecker	4	0.003*	2.11	0.11/0.04			0.00/0.14	0.13/0.03		0.38/0.20
Mourning Dove	4	0.003*	2.01	0.02/0.00			2.21/1.29	0.55/0.14		0.06/0.10
Brown-headed Cowbird	4	0.004*	1.61	0.84/0.36			0.43/0.64	0.54/0.42		1.00/0.70
Cedar Waxwing	3	<0.001*	1.32	0.33/0.08			0.86/0.79	0.19/0.38		
Black-billed Magpie	3	0.009*	1.76	0.44/0.23			0.00/0.14	0.47/0.22		
Black-capped Chickadee	3	0.013	1.74	0.44/0.23			0.64/0.07	0.29/0.32		
American Goldfinch	3	0.024	1.43	0.05/0.00			2.07/1.93	1.08/0.81		
Red-winged Blackbird	2	<0.001*	5.64	0.24/0.00				0.09/0.09		
Willow Flycatcher	2	0.001*	5.14	0.16/0.02				0.01/0.01		
Least Flycatcher	2	0.001*	2.30	0.03/0.00				2.50/1.14		
Spotted Sandpiper	2	0.007*	6.49	0.12/0.00				0.02/0.04		
Great Blue Heron	2	0.017*	8.67	0.04/0.00				0.02/0.01		

TABLE 4. CONTINUED

Landscape component	N	P	Ratio	River system: Bitterroot	Sacramento	San Joaquin	Missouri	Snake	Sheldon	Hart Mountain
High Regional Conifer Forest										
More Abundant Species										
Swainson's Thrush	4	<0.001*	1.89	0.01/0.34			0.00/0.14	0.00/0.08		0.42/0.10
Warbling Vireo	4	<0.001*	1.81	0.25/0.65			0.14/0.64	0.14/0.85		1.11/1.30
MacGillivray's Warbler	3	<0.001*	7.25	0.04/0.60				0.00/0.15		0.11/0.00
Dusky Flycatcher	3	<0.001*	1.41	0.02/0.31				0.02/0.06		1.37/2.10
Western Tanager	3	0.002*	1.28	0.01/0.10				0.00/0.04		0.16/0.00
Chipping Sparrow	3	0.003*	6.77	0.01/0.12			0.07/0.00	0.00/0.03		
Pine Siskin	3	0.003*	4.31	0.06/0.35				0.02/0.04		0.05/0.00
Yellow-rumped Warbler	3	0.009*	2.72	0.03/0.17				0.02/0.17		0.11/0.00
Townsend's Warbler	2	<0.001*	7.96	0.00/0.43						0.11/0.00
Orange-crowned Warbler	2	<0.001*	1.73	0.00/0.10						0.53/1.10
Ruffed Grouse	2	0.002*	9.95	0.01/0.09				0.00/0.03		
Violet-green Swallow	2	0.003*	12.60				0.00/0.07	0.04/0.51		
Mountain Chickadee	2	0.008*	N/A	0.00/0.05						0.00/0.30
Ruby-crowned Kinglet	2	0.025	3.03	0.01/0.18						0.11/0.00
Fox Sparrow	2	0.032	2.25					0.05/0.15		0.32/0.80
Less Abundant Species										
Western Wood-pewee	4	<0.001*	1.92	0.47/0.04			1.07/1.57	0.39/0.05		0.58/0.40
Yellow Warbler	4	<0.001*	1.97	1.34/0.05			2.43/3.21	2.75/2.26		1.68/0.30
Bullock's Oriole	4	<0.001*	3.16	0.14/0.00			0.21/0.43	0.75/0.20		0.79/0.30
European Starling	4	<0.001*	11.34	0.25/0.00			1.14/0.00	1.33/0.20		0.63/0.10
Brown-headed Cowbird	4	<0.001*	2.01	0.84/0.23			0.36/0.71	0.63/0.23		1.05/0.90
American Robin	4	<0.001*	1.39	0.73/0.26			1.36/2.79	1.81/1.00		1.95/1.80
House Wren	4	<0.001*	1.37	0.07/0.00			2.21/3.00	1.18/0.11		3.32/3.80
Downy Woodpecker	4	0.012*	2.55	0.10/0.06			0.36/0.00	0.10/0.04		0.32/0.20
Cedar Waxwing	3	<0.001*	1.26	0.31/0.01			0.29/1.00	0.25/0.32		
Red-winged Blackbird	3	<0.001*	38.45	0.24/0.00				0.13/0.03		0.42/0.00
American Goldfinch	3	<0.001*	1.67	0.05/0.00			1.29/1.71	1.25/0.40		
Eastern Kingbird	3	0.003*	3.57	0.02/0.00			0.36/0.14	0.05/0.00		
Willow Flycatcher	2	<0.001*	11.96	0.16/0.01				0.01/0.00		
Spotted Sandpiper	2	0.001*	27.55	0.12/0.00				0.03/0.01		

Notes: Includes all species with study-wide differences in average abundance between the lower 25% of plots (*Low*) and the upper 25% of plots (*High*) when all plots within each river system are ranked from lowest to highest for each landscape variable. The N is the number of rivers in which the species and landscape component were present. P-values are from Fisher's combined probability tests across rivers. We report the ratio of detection frequency (detections per survey) in all of the less abundant class (*Low* or *High*) to detection frequency in all of the more abundant class as 1:x, where x = Ratio. In addition, detection frequency in each river system for *Low* and *High* plots (*Low*/*High*) is indicated.

* Significant after Bonferroni correction for multiple tests.

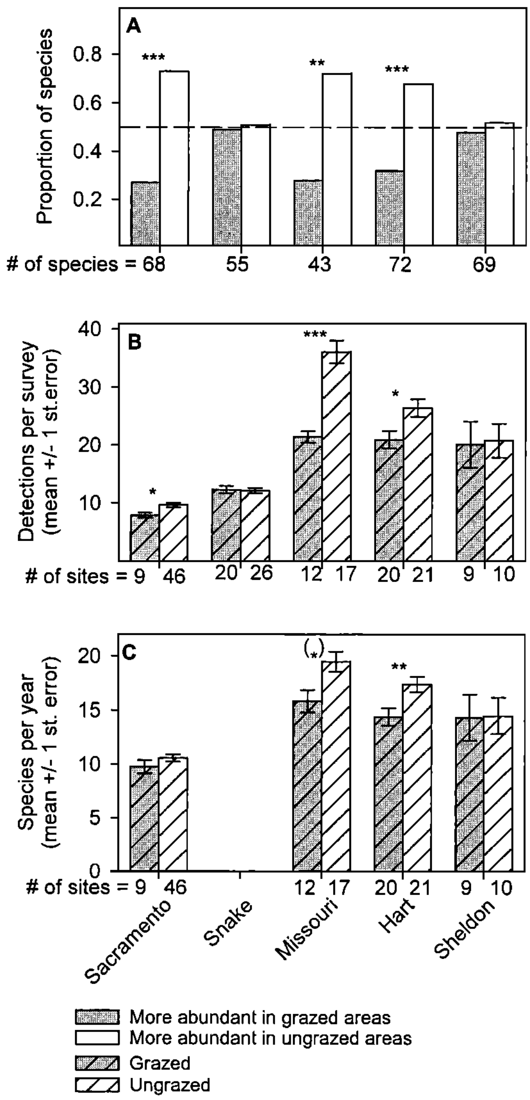

FIGURE 2. Total response of all species to grazing in each riparian system. Proportion of all species more abundant in grazed or ungrazed plots (A), average number of birds detected per survey (B), and the average number of species detected over the course of a single year at a given location (C) for grazed and ungrazed plots in each river system. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$. (*) = P-value not significant after correction for multiple tests.

abundant in grazed sites (Fig. 4F; combined probabilities test $\chi^2 = 7.5$, $P = 0.679$).

Total abundance of open cup nesters was significantly higher in ungrazed survey locations (Fig. 5A; combined probabilities test $\chi^2 = 46.4$, $P < 0.0005$) and an average of 65% (± 8%) of open-cup nesting species were less abundant in grazed areas (Fig. 5B; combined probabilities test $\chi^2 = 35.3$ $P < 0.001$). Primary cavity nesting species trended in the same direction (Fig. 5C; combined probabilities test $\chi^2 = 20.4$, $P = 0.026$, not significant after correction for multiple tests), and secondary cavity nesters showed conflicting patterns on different riparian systems with no overall effect (Fig. 5E; combined probabilities test $\chi^2 = 4.4$, $P = 0.92$). Binomial tests suggested no overall trend for cavity nesters (Fig. 5D and 5F), though the number of species in each guild was too small for rigorous analysis. On the Missouri, total abundances of open cup and primary cavity nesters were significantly greater on ungrazed sites (t's > 4.2, P's < 0.001) and 22 of 25 open-cup nesting species were more abundant in ungrazed sites. Open-cup nesting abundance was also lower on the Hart Mountain (total abundance; $t = 2.6$, $P = 0.013$) and Sacramento River ($t = 2.1$, $P = 0.04$) systems, with 30 of 40 species less abundant in grazed areas on Hart Mountain (binomial test $P = 0.003$) and 27 of 40 species less abundant in grazed locations on the Sacramento (binomial test $P = 0.04$).

The overall abundance of all species nesting below 2.5 m was significantly lower in grazed sites compared to ungrazed sites (Fig. 6A; combined probabilities test $\chi^2 = 26.4$, $P = 0.003$) and 67% of species in this category (± 5%) were less abundant in grazed sites (combined probabilities test $\chi^2 = 17$, $P = 0.07$), with all rivers showing the same trend (Fig. 6B). In contrast, the combined abundance of all species with average nesting heights higher than 5 m showed only a non-significant trend to be lower in grazed areas (Fig. 6C; combined probabilities test $\chi^2 = 18.6$, $P = 0.045$, not significant after correction for multiple tests), and only 58% (± 9%) of species in this guild were less abundant in grazed sites, with the Snake and Sheldon systems showing either opposite trends or no effect (Fig. 6D; combined probabilities test $\chi^2 = 5.8$, $P = 0.23$).

DISCUSSION

This synthesis includes seven different western riparian systems, each embedded in a different landscape. In each system, data were gathered by different investigators using similar but not identical methodologies. Despite these differences, our results demonstrate that both landscape character and livestock grazing have some consistent, potentially West-wide effects on bird communities. Although some of these effects are similar to those found in the Midwest (landscape effects on Brown-headed Cowbirds, for example), others will require further study to determine the mechanisms responsible for the patterns (the effects of grazing and agriculture

TABLE 5. SPECIES SHOWING OVERALL TREND IN RESPONSE TO GRAZING

Less common in grazed areas			More common in grazed areas		
Species	Rivers	P	Species	Rivers	P
American Robin	5	0.005*	Dusky Flycatcher	4	0.040
Western Wood-pewee	5	0.031	Western Meadowlark	3	0.056
Black-headed Grosbeak	5	0.080	Brewer's Sparrow	2	0.110
Song Sparrow	4	0.020			
Hairy Woodpecker	4	0.031*			
Mallard	4	0.055			
Red-shafted Flicker	4	0.115			
MacGillivray's Warbler	4	0.129			
Cedar Waxwing	3	0.073			
Cordilleran Flycatcher	2	0.003*			
Red-eyed Vireo	2	0.008*			
Fox Sparrow	2	0.014*			
Green-tailed Towhee	2	0.015*			
Black-capped Chickadee	2	0.017			
Gray Catbird	2	0.032			
Ovenbird	2	0.177			
Turkey Vulture	2	0.197			

Note: Species are ranked by the number of riparian systems included in the analysis (minimum of two) and significance ($P < 0.2$). * Denotes significant after Bonferroni correction for multiple tests.

on Yellow Warblers, for example). Below, we summarize effects of different landscape components and provide a brief synthesis of our findings.

SCALE AND RESOLUTION

Until recently, there has been a significant gap between theoretical work stressing the scale-dependent nature of landscape effects (Wiens 1989, 1995; Dunning et al. 1992) and empirical studies that confine analysis to a single landscape scale (Donovan et al. 1995b, Robinson et al. 1995a, Thompson et al. 2000, Hejl and Young 1999; but see Tewksbury et al. 1998, Young and Hutto 1999, Donovan et al. 2000). The abundance and composition of bird communities are affected by multiple processes across different landscape scales (Dunning et al. 1992, Freemark et al. 1995); even a single process, such as nest predation, acts across multiple scales dependent on the range size and habitat affinities of the primary predators (Andrén 1995, Tewksbury et al. 1998). This variation in the scaling of processes suggests that conservation planning will be best served by examination of multiple scales. Multiple-scale landscape analyses allows the discovery of relationships that are relatively scale-insensitive, and thus more easily applied in management contexts, and it allows determination of appropriate scales when processes such as brood parasitism or nest predation are considered.

Our results show that different landscape components influence bird abundance and diversity at different scales. Overall, 40% of species significantly affected by landscape factors at one scale were not affected by these factors at the other scale (Table 4), suggesting that examination of landscapes at only a single spatial scale may result in loss of considerable information. Importantly, our examination of two landscape scales does not allow us to determine the point when considering more land area decreases rather than increases the explanatory power of a certain landscape variable, as we can only say that a larger landscape is better than a smaller one, or the other way around. Analyses comparing the effect sizes of landscape components at multiple scales would allow estimation of the relative importance of landscape features at different distances from an area of interest.

The appropriate scale is also a function of mapping resolution. Linear landscape components and components that typically have small patch sizes are usually underestimated when mapping resolution is coarse. It is not particularly surprising that we found no significant correlations between data gathered using the low resolution California GAP data and the detailed CWIS data (Table 2), as the resolution of the California GAP data (100 ha minimum patch size) is greater than the entire area of our local landscapes (78 ha). This coarse resolution is inappropriate for local scale habitat mapping, but it may still be appropriate for larger landscape scales as long as the biases are recognized. At our regional scale, where we used these data, we mapped 8000 ha around each survey location, which allowed for a mosaic of patches even

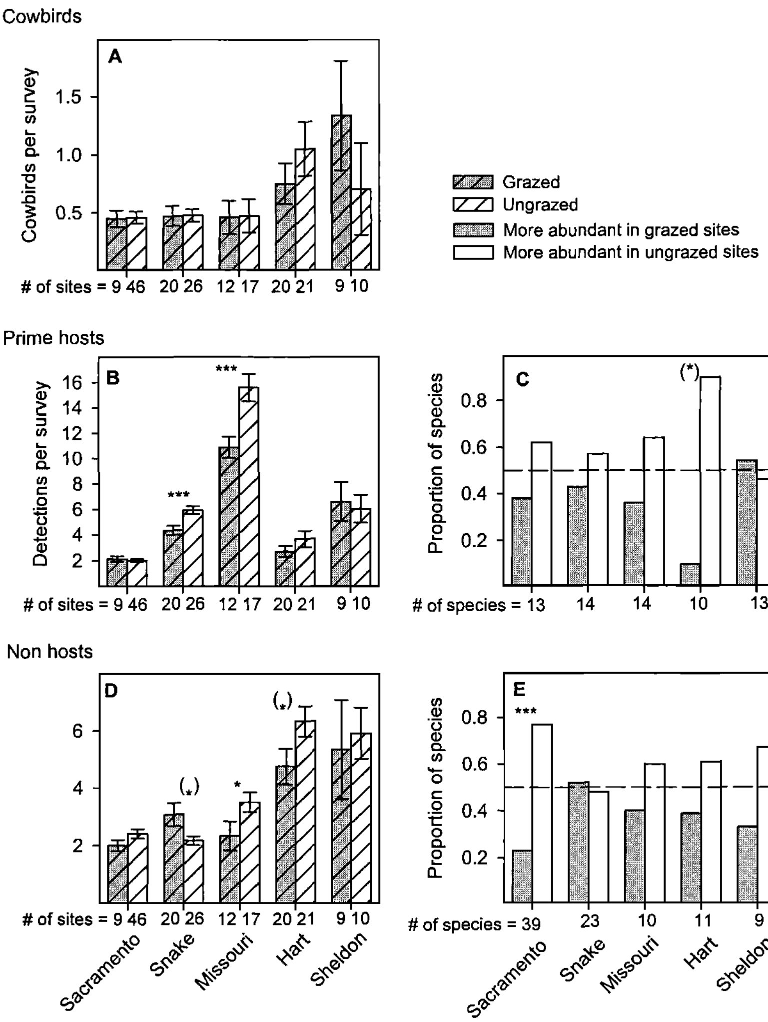

FIGURE 3. Grazing effects on cowbirds, prime hosts, and non-hosts. Total detections per survey on grazed and ungrazed sites (A, B, and D), and proportion of species in each guild more abundant in grazed or ungrazed sites (C and E), for cowbirds (A), prime hosts (B and C), and non-hosts (D and E) in each river system. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$. (*) = P-value not significant after correction for multiple tests.

when these patches were 100 ha and larger. At this level, large differences in the regional landscape are fully apparent, but features such as dispersed housing or small riparian areas are not detected. Thus the effect of changing regional agriculture or coniferous forest cover is well represented in the coarse-grained data, while changes in linear deciduous riparian areas may go undetected. As landscape data of higher resolution become more broadly available, comparisons across regions should be possible using the same data sources for all landscape sizes, eliminating the confounding issues of shifting mapping resolution and allowing explicit comparison of scale.

Human Habitation and Agriculture

Our finding that overall avian abundance was positively related to regional agricultural abundance runs counter to findings from the East (Croonquist and Brooks 1991, 1993), but is not without precedent in the western United States (Carothers et al. 1974). These results may be better understood by examining the individual species with large differences in abundance, rather than by focusing on guilds (Mannan and Meslow 1984). The high congruence in the species increasing due to agriculture and human habitation is partly a function of the positive correlation that typically exists between agriculture

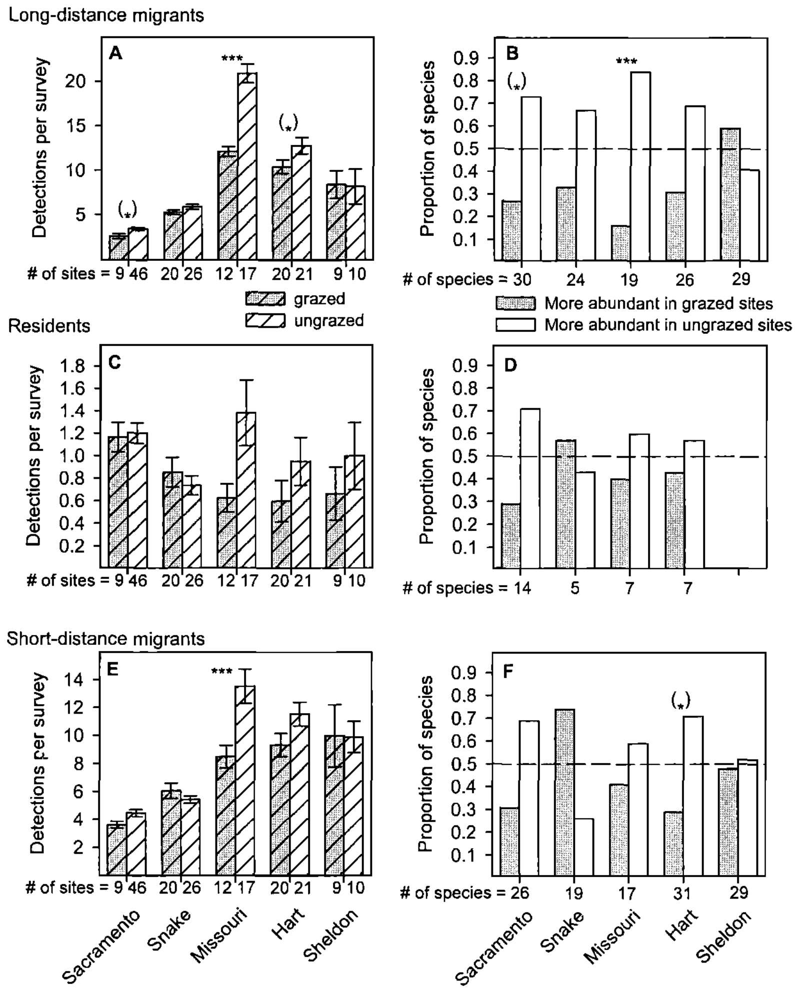

FIGURE 4. Grazing effects on long-distance migrants, residents, and short-distance migrants. Total detections per survey on grazed and ungrazed sites (A, C, and E), and proportion of species within each guild more abundant in grazed or ungrazed sites (B, D, and F), for long-distance migrants (A and B), year-round residents (C and D), and short-distance migrants (E and F) in each river system. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$. (*) = P-value not significant after correction for multiple tests.

and houses (Appendix 3). It is likely, however, that many species with higher relative abundance in areas with more agriculture also show similar numerical responses to high human habitation. Brown-headed Cowbirds use both agricultural and farm areas for foraging (Thompson 1994), and European Starlings often forage in suburban and agricultural areas (Fischl and Caccamise 1985). Indeed, most of the species that are more abundant in areas with high agriculture or human habitation often utilize multiple habitats; American Robins, Black-billed Magpies, starlings, and cowbirds are all examples. Increases in starlings may have consequences for other secondary cavity nesters, as starlings can exclude less aggressive species from cavities (Ingold 1989, 1994, 1998; Nilsson 1984, Kerpez and Smith 1990, Rich et al. 1994, Dobkin et al. 1995). Indeed, densities of Violet-green Swallows were significantly lower in sites with high agriculture at either scale—the same sites in which starlings were significantly more abundant (Table 4).

Higher Brown-headed Cowbird detection frequency in areas with more agriculture has been found previously across both local and regional scales (Conine et al. 1979, Donovan 1997, Tewksbury et al. 1999, Hejl and Young 1999, Hochachka et al. 1999, Young and Hutto 1999). Our finding that the detection frequency of pri-

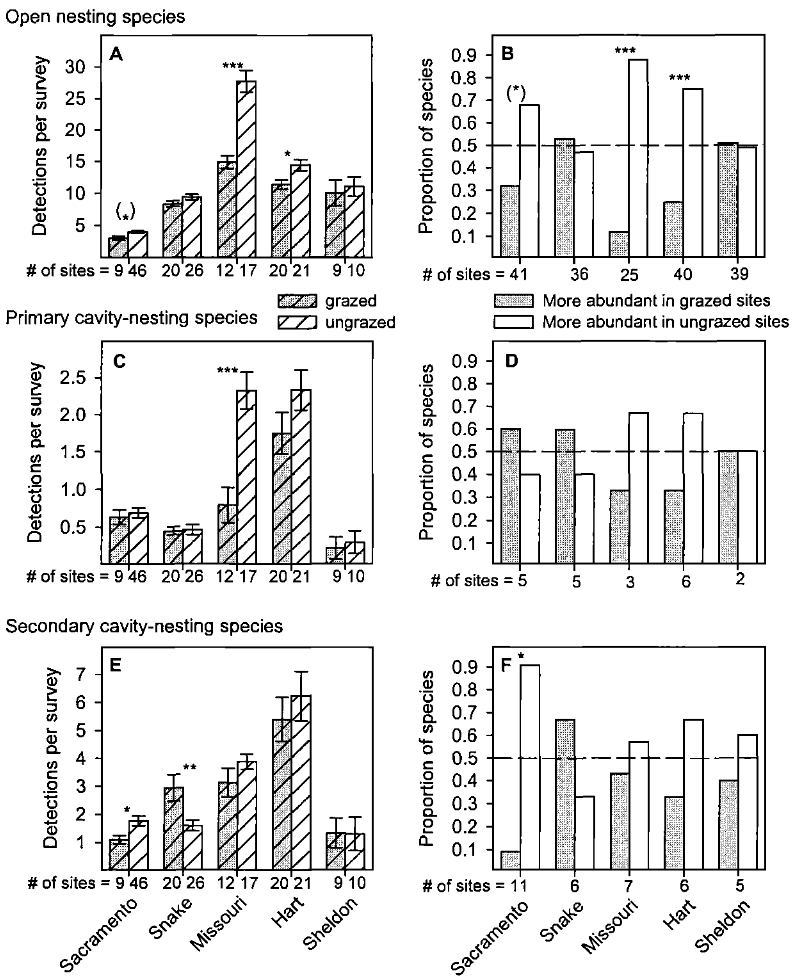

FIGURE 5. Grazing effects on open nesting species, primary cavity nesters, and secondary cavity nesting species. Total detections per survey on grazed and ungrazed sites (A, C, and E), and proportion of species in each guild more abundant in grazed or ungrazed sites (B, D, and F), for open-cup nesting species (A and B), primary cavity nesting species (C and D), and secondary cavity nesting species (E and F) in each river system. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$. (*) = P-value not significant after correction for multiple tests.

mary hosts was not lower in areas where cowbirds were common is consistent with other comparisons of cowbird density and host density (Donovan et al. 1997, Tewksbury et al. 1999, Young and Hutto 1999), and does not indicate that cowbirds have no effect on host communities (De Groot et al. 1999). The demographic effect of brood parasitism varies greatly among different host species (Lorenzana and Sealy 1999), and we first expect lower abundances of species that are particularly susceptible to parasitism. Indeed, the Dusky Flycatcher, Swainson's Thrush, Veery, Warbling Vireo, Orange-crowned Warbler, MacGillivray's Warbler, and American Redstart all suffer complete or nearly complete brood loss when parasitized (J. J. Tewksbury, unpubl. data) and are all less abundant in areas with high human habitation or high agriculture (Table 4), areas where cowbirds are abundant. In contrast, Yellow Warblers are more resistant to the demographic effect of brood parasitism (Clark and Robertson 1981, Sealy 1995), and they were more abundant in areas with high human habitation and agriculture. Importantly, human habitation and agriculture are often concentrated near productive riparian habitat with large flood-plains, areas where many long-distance migrants susceptible to parasitism are more abundant. Thus the trend for Yellow Warblers (more abundant in these areas) may characterize the natural response of other species, as they respond to larger riparian areas, but the ef-

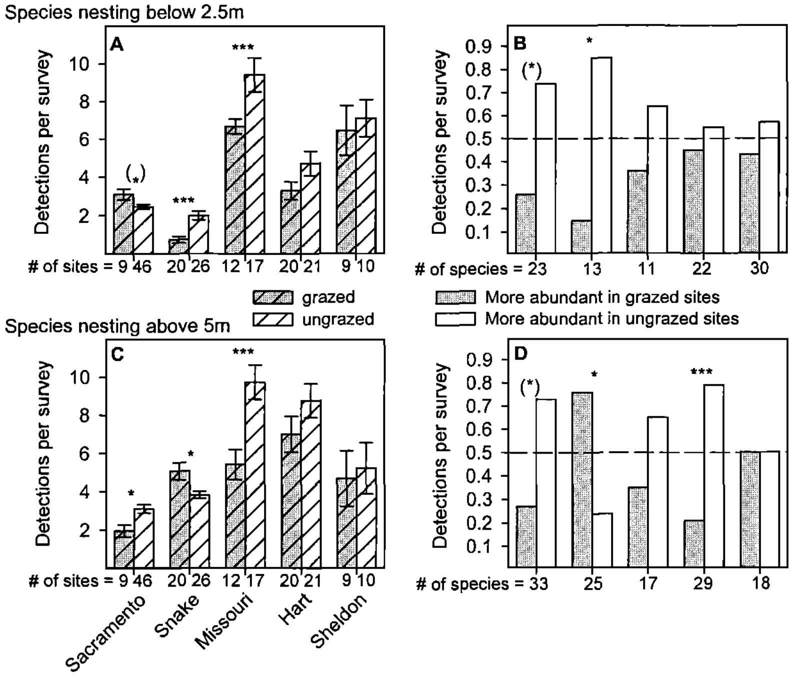

FIGURE 6. Effects of grazing on low and high nesting species. Total detections per survey on grazed and ungrazed sites (A and C), and proportion of species in each guild more abundant in grazed or ungrazed sites (B and D), for species nesting below 2.5m (A and B), and species nesting above 5 m (C and D) in each river system. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$. (*) = P-value not significant after correction for multiple tests.

fect of cowbirds may counter this trend. In addition, negative correlations between cowbird and host detection frequencies suggest that rates of brood parasitism are positively related to cowbird detection frequencies. While this assumption is reasonable across most levels of cowbird detection, where cowbird numbers are high, further increases may not change parasitism rates. This may be the case along the Sacramento River, where high-levels of parasitism at all sites may have already caused large regional declines in many species (Gaines 1974), so that current variation in cowbird detection frequency is uncorrelated with parasitism rates.

The largest limitations in understanding the effects of changing landscapes on riparian bird communities are the correlations among components of the landscape. In our study, we cannot separate unambiguously the effects of agriculture and human habitation because of the high correlation between these components (Appendix 3). In some cases, however, correlations between landscape components differ significantly among riparian systems, allowing insights into which relationships are causative, and which are simply due to covariation in landscape components. For example, local deciduous habitat is correlated strongly with higher host abundance (Table 3). In the Bitterroot Valley, agriculture is correlated positively with the amount of local deciduous habitat (Appendix 3; $r = 0.47$, $P < 0.001$), and, as a result, we see positive associations between host abundance and regional agriculture. Conversely, along the Snake River, local agriculture and deciduous habitats are negatively correlated (Appendix 3; $r = -0.55$, $P < 0.001$), and we see a strong negative relationship between host abundance and agriculture at the local scale (Appendix 4). Thus, changes in host abundance are likely caused by differences in the amount of deciduous habitat, not the amount of agriculture, but the effects are difficult to separate where these components are positively correlated.

Deciduous Riparian Area

Deciduous riparian area at the local scale is a function of the width of the riparian corridor; thus the positive correlations between avian abundance and deciduous habitat likely are consequences of greater habitat availability and heterogeneity associated with larger riparian corridors (Tyser 1983, Brown and Dinsmore 1986, Dobkin and Wilcox 1986, Craig and Beal 1992, Keller et al. 1993). All of the species that were significantly more abundant at survey locations with high local deciduous habitat are species traditionally considered riparian associates. The guild-level examination of the effects of increasing local deciduous area and increasing regional agriculture suggested similar effects (Table 3), but the individual species responding to these landscape components were quite different (Table 4). Fifteen species had significantly higher abundance in larger deciduous areas, and 17 species were higher in abundance in areas with more regional agriculture. However, only three species were more abundant under both these conditions (Table 4). Thus the bird communities in areas with high agricultural abundance share little in common with the communities in areas with large amounts of deciduous habitat, and guild-based analysis may lead to erroneous conclusions unless the responses of individual species are examined.

Within riparian systems, the breeding bird community found in smaller deciduous tracts was most often a subset of the birds found in larger tracts. Only three species were less abundant in sites with more local deciduous forest, and one of these, the Townsend's Warbler, is typically associated with coniferous habitats. Thus, preserving and restoring large tracts of deciduous habitat likely will do more to preserve riparian-associated species than will any other action. In addition, large deciduous patches also may reduce parasitism in parts of the patch as distance from the nearest cowbird feeding area increases.

Coniferous Forest

Studies in the Midwest have found that areas with higher conifer abundance, at scales similar to our regional scale, have lower cowbird abundance and parasitism (Donovan et al. 1995b, 1997; Robinson et al. 1995a). Recent work in the western United States, however, has suggested that the abundance of human habitation (Tewksbury et al. 1998), agriculture (Hejl and Young 1999, Young and Hutto 1999, Donovan et al. 2000), and the abundance of suitable hosts (Barber and Martin 1997; Tewksbury et al. 1998, 1999) are better predictors of parasitism pressure than is conifer abundance. Our study supports both bodies of work—cowbirds were not significantly less abundant in areas with more local coniferous forest, but they were related positively to both human habitation and agriculture, and they were also higher in larger riparian areas, where host abundance is also higher. At a regional scale, cowbirds did show a strong negative correlation with the amount of coniferous forest on the landscape, similar to results from the Midwest and East. This relationship at the regional scale is most likely due to the strong negative correlation between regional coniferous forest cover and agriculture on the Snake and the Bitterroot rivers (Appendix 3), the two rivers where cowbirds and coniferous forest are negatively related (Appendix 4). In the Bitterroot River system, rates of brood parasitism have been directly related to the amount of human habitation on the landscape, not the amount of coniferous forest (Tewksbury et al. 1998). The effects of coniferous forest on individual species were very similar across scales, with over 70% of species affected showing significant effects at both scales.

Grazing

Variation in the intensity, duration, and timing of grazing has been shown to influence bird communities (Saab et al. 1995), and its effects are particularly apparent in deciduous systems (Fleischner 1994). Our study includes a diversity of grazing regimes, and the effects on bird communities generally match the intensity and duration of the grazing. In the Missouri River, grazed sites have had cattle on them for over 50 years, and ungrazed sites have been free of grazing for over 25 years. This is reflected in the severe effects of grazing on the bird communities. In contrast, grazing-related differences were few in the Sheldon system, where long-term livestock grazing has left a highly degraded set of riparian habitats. Ungrazed survey locations were only in their third year of rest, and the general lack of differences in avian community composition reflected the very limited recovery made by the riparian plant community (D. Dobkin et al., unpubl. data).

Our finding that grazing had no effect on detection frequencies of Brown-headed Cowbirds in any riparian system runs counter to most previous studies (Page et al. 1978, Mosconi and Hutto 1982, Knopf et al. 1988, Schulz and Leninger 1991; but see Taylor 1986). However, we measured grazing pressure on individual study sites, not on the landscape as a whole; thus cowbirds may be foraging in grazed sites but searching for nests in ungrazed sites, where hosts are generally more abundant. Thus grazed and ungrazed sites may offer different resources for cowbirds; previous research in the Bitterroot River system has shown that cowbird abundance is strongly related to host abundance, as well as distance from agriculture (Tewksbury et al. 1999), supporting this possibility.

As cowbirds are not consistently more abundant in grazed areas, the much lower primary host abundance in grazed areas may not be simply the result of higher parasitism pressure, but instead may be due to interactions between vegetation differences and predation rates (Knopf

1985), lack of appropriate settling cues in grazed sites, or indirect interactions between food availability, foraging behavior, and nest predation (Martin 1992). Many primary hosts are also long-distance migrants, and we found that this group was lower in abundance in grazed areas as well. Saab et al. (1995) found the same result after reviewing the literature, and suggested that this could be due to the high proportion of open-cup nesters among long-distance migrants and greater sensitivity of open-cup nesters to grazing. Our data are consistent with this interpretation: open-cup nesters were more heavily affected by grazing than were primary or secondary cavity nesters. Open-cup nesters accounted for 96% of species and 81% of detections for long distance migrants, 82% of species and 28% of detections for short-distance migrants, and only 58% of species and 37% of all detections for residents.

Along the Missouri River, differences in primary cavity nesters between grazed and ungrazed areas were as great as differences in open-cup nesters, a finding that contrasts sharply with previous work (Good and Dambush 1943, Mosconi and Hutto 1982, Medin and Clary 1991). The strong community-wide effects seen on the Missouri may be related to changes in vegetation that take place with continued grazing over long time scales (Ohmart 1994). High-nesting birds and primary cavity nesters may escape the immediate effects of grazing, but as cottonwood and aspen forests age, lack of recruitment of new trees causes a reduction in small and eventually large tree classes, which will affect the density of cavity nesters (Sedgwick and Knopf 1990, Dobkin et al. 1995) and the density of high-nesting species in general. This process may be well advanced in grazed locations along the Missouri, but is unlikely where grazing has been less continuous. Our results comparing low-nesting species to high-nesting species further support this possibility. Low open-cup nesting species have been shown to be particularly sensitive to grazing due to the large effects cattle have on the lower strata of vegetation (Sedgwick and Knopf 1987, Saab et al. 1995, Saab 1998). We also found that while both low and high nesting species had lower detection frequencies in grazed areas, these differences were greater for low nesting species. Along the Missouri, however, equally strong differences were found for both low- and high-nesting species, suggesting that long-term grazing may have affected canopy structure, snag retention, and recruitment of trees into the canopy (Ohmart 1994).

COWBIRDS AND LANDSCAPES

Cowbirds could pose regional threats to riparian avifaunas due to their ubiquitous nature, their tendency to reach high densities in riparian areas (Tewksbury et al. 1999, Ward and Smith 2000), and the effects of parasitism both on individual hosts (Pease and Grzybowski 1995, Woodworth 1999) and on community composition (De Groot et al. 1999). Because of this, much work has examined landscape-scale effects on cowbird abundance and parasitism pressure locally (Gustafson and Crow 1994, Coker and Capen 1995, Gates and Evans 1998, Hejl and Young 1999; Tewksbury et al. 1998, 1999; Young and Hutto 1999), regionally (Donovan et al. 1995b, 1997, 2000; Robinson et al. 1995a, Thompson et al. 2000) and nationally (Hochachka et al. 1999). The majority of this work investigated only one or two factors that could limit cowbird abundance, in contrast to our results, which suggest that multiple landscape components may be important in the western United States.

To date, the species that are most often affected by parasitism appear to be extremely habitat limited (Robinson et al. 1995b), suggesting that the primary cause of population decline is not parasitism but habitat loss. With the steady increase in human encroachment upon riparian systems, and the highly mobile nature and generalist feeding strategy of the cowbird (Thompson 1994, Robinson et al. 1995b), we already have lost most of our opportunity to set aside large riparian areas in landscapes that are remote enough to preclude cowbirds altogether. Thus most communities will be affected by cowbirds, and attention should shift to strategies for minimizing the effect of cowbirds at local and regional scales. We suggest that preserving and enhancing the size of deciduous areas that are surrounded by few human habitations and little agriculture will have the greatest benefit for host populations, as cowbirds in these landscapes are likely limited by feeding habitat. In largely agricultural landscapes, cowbirds are more likely limited by availability of host nests, not feeding areas; thus moderate reductions in feeding areas in these areas (feedlots, bird-feeders, corrals, livestock pastures) may have little effect on rates of brood parasitism.

MANAGEMENT IMPLICATIONS AND SPECIES OF PARTICULAR CONCERN

Our data suggest that the greatest threats to western deciduous riparian systems are (1) continued deciduous habitat loss and reduction in riparian area, (2) continued cattle grazing in remaining deciduous systems, and (3) increasing concentration of homes and farms along major riparian systems in the western United States. All of these factors are likely to have negative effects on bird communities in deciduous riparian areas, but rarely is it possible to extrapolate

TABLE 6. SUMMARY OF ALL SPECIES SIGNIFICANTLY LESS ABUNDANT IN AREAS WITH MORE HUMAN HABITATION, MORE AGRICULTURE, OR LESS DECIDUOUS HABITAT AT EITHER SCALE, OR IN GRAZED HABITATS, TESTED IN AT LEAST TWO RIPARIAN SYSTEMS

Species	More human habitation	More agriculture	Less deciduous	Grazing	Negative responses	Net negative–positive responses	West BBS[a]
Red-naped Sapsucker	0/−	−/0	−/−		4	4	
MacGillivray's Warbler	−/−	−/−	+/+		4	2	
Song Sparrow	+/−	+/0	−/−	−	4	2	**
Western Scrub-jay	−/0	−/−			3	3	
Veery	0/−	−/0	−/0		3	3	
Warbling Vireo	0/−	−/−			3	3	
Red-eyed Vireo			−/−	−	3	3	**
Yellow-rumped Warbler	0/−	−/−			3	3	
Black-capped Chickadee		−0/+	−/−	−	3	2	**
Townsend's Warbler	−/0	−/−	+/+		3	1	
Ruffed Grouse	0/−	−/0			2	2	*
American Crow	0/−	0/−			2	2	
Violet-green Swallow		−/−			2	2	
Swainson's Thrush	0/−	0/−			2	2	
Gray Catbird			−/0	−	2	2	
Fox Sparrow			−/0	−	2	2	
Dusky Flycatcher	0/−	−/0		+	2	1	*
Orange-crowned Warbler		−/0	−/+		2	1	*
Western Wood-pewee	+/+	+/+	−/0	−	2	−2	**
American Robin	+/+	+/+	0/−	−	2	−2	
Cedar Waxwing	+/0	+/0	−/−		2	−2	
Yellow Warbler	+/+	+/+	−/−		2	−2	
Nuttall's Woodpecker		−/0			1	1	
Hairy Woodpecker				−	1	1	
Least Flycatcher			−/0		1	1	
Ash-throated Flycatcher	−/0				1	1	
Cordilleran Flycatcher				−	1	1	
Western Kingbird		0/−			1	1	
Northern Rough-winged Swallow		−/0			1	1	
Bewick's Wren			−/0		1	1	
American Redstart			−/0		1	1	
Western Tanager	0/−				1	1	
Green-tailed towhee				−	1	1	
Chipping Sparrow		−/0			1	1	**
White-breasted Nuthatch		+/0	0/−		1	0	
Ruby-crowned Kinglet		−/0	0/+		1	0	
Black-billed Magpie		+/+	0/−		1	−1	
Black-headed Grosbeak	+/0	+/0	−/0		1	−1	
Red-shafted Flicker	+/0	+/0	0/−		1	−2	*
Red-winged Blackbird	+/+	+/+	0/−		1	−3	**
Willow Flycatcher	+/+	+/+	0/−		1	−3	**

Notes: Significantly ($P = 0.05$) lower detection frequency (−), significantly higher detection frequency (+), and no significant difference in detection frequency (0) are listed for each species in which at least 2 river systems were used in the analysis. Significant effects at local and regional scales are listed (local/regional). Species are ranked by the number of negative responses and the net (negative − positive) responses.

[a] Trend estimates from the Western Breeding Bird Survey region (Sauer et al. 2000). Species with a declining trend ($P < 0.25$) in the past 20 years, or over the course of the entire survey period, are single-starred (*) and species showing significant declines ($P < 0.05$) are marked with double stars (**).

from local studies to regional population trends. The data provided here allow us to highlight consistent trends, and by summarizing the responses to individual land uses we can also identify those species that appear to be at particular risk due to human landscape modification and livestock grazing (Table 6). We ranked each species based on the number of negative responses (lower abundance due to grazing, higher amounts of human habitation or agriculture, or lower amounts of deciduous habitat) making the assumption that species vulnerable to multiple human land-uses should receive greater attention than species vulnerable to only one type of land-use. Ten species had at least three negative responses. Of these, the Veery, MacGillivray's

Warbler, Song Sparrow, Warbling Vireo, and Red-eyed Vireo may be the most at risk, as all but the Warbling Vireo nest lower in dense vegetation (Ehrlich et al. 1988; J. J. Tewksbury unpubl. data) and all frequently suffer brood parasitism (Friedmann et al. 1977; J. J. Tewksbury unpubl. data). These species were all less abundant in landscapes with high human habitation and agriculture or low amounts of riparian habitat, and three respond negatively to livestock grazing. In addition, all of these, as well as the Red-naped Sapsucker, are found almost exclusively in deciduous vegetation. We suggest that these species should be monitored closely in western riparian habitats, and research should be initiated to examine mechanisms behind these patterns.

CONCLUSIONS

Management that focuses on enhancing the size of remaining deciduous riparian areas and reducing cattle grazing on these areas is likely to produce the greatest benefits for bird species dependent on western deciduous riparian habitats. In addition, strict limitations on building in floodplains will reduce the need for absolute flood control on riparian systems, which results in reduced riparian area. Protecting the few areas where riparian systems run through landscapes that are relatively free of human disturbance should be a high conservation priority both to protect the last unaltered pieces of one of the most endangered and important breeding habitats for western birds, and to preserve these few natural landscapes as benchmarks to use in examining the effects of land conversion. Without natural landscapes, we may lose sight of the conditions we are attempting to preserve.

ACKNOWLEDGMENTS

The results summarized here were produced by five independent field teams working over the past decade, and our work would not have been possible without the sharp eyes and strong ears of the many people who conducted surveys in these riparian systems. We thank R. Hutto, B. Kus, and L. George for their comments on earlier drafts of this manuscript.

APPENDIX 1

DESCRIPTIONS OF INDIVIDUAL RIPARIAN SYSTEMS

Sacramento

Location: all study sites are between Red Bluff and Colusa, California. Most sites are in remnant forest patches in the Sacramento National Wildlife Refuge.

Vegetation: the floodplain is a complex of early- to late-successional deciduous forests dominated successively by willows (*Salix* spp.) and cottonwood (*Populus* spp.), sycamore (*Platanus* spp.), ash (*Fraxinus* spp.), and valley oak (*Quercus lobata*). Adjacent upper terraces are dominated by valley oak. See Gaines (1974) for a detailed description of study sites.

Grazing: moderate to heavy cattle grazing for the past 15+ years on grazed sites. Ungrazed sites had been without cattle for at least 3 years before data collection.

San Joaquin

Location: all survey locations are in the northern portion of California's San Joaquin Valley, on levee roads adjacent to riparian stringers, grasslands, and recently (last decade) re-flooded grasslands in the San Luis National Wildlife Refuge.

Vegetation: similar to Sacramento River, dominated by willows and cottonwood, sycamore, ash, and valley oak. Willows and marsh vegetation are more common than valley oak.

Grazing: moderate to heavy cattle grazing for the past 15+ years on grazed sites. Ungrazed sites have been without cattle for at least 3 years before data collection.

Snake

Location: Sites are in an 80-km stretch just downstream of the Idaho/Wyoming border in eastern Idaho. For a detailed description of sites see Saab (1999).

Vegetation: Cottonwood (*Populus angustifolia*) forests. Understory species include dogwood (*Cornus stolonifera*), thin-leafed alder (*Alnus incana*), water birch (*Betula occidentalis*), and willows.

Grazing: moderate to heavy grazing for the past 30+ years on grazed sites. Ungrazed sites have been without cattle for at least three years before data collection.

Bitterroot

Location: survey locations were located along a 40-km stretch of the Bitterroot River and smaller tributaries throughout the Bitterroot Valley between Corvallis to the north and continuing past Darby to the south. See Tewksbury et al. (1998, 1999) for details of study sites.

Vegetation: cottonwood and willow dominate sites along the Bitterroot River, with dogwood, thin-leafed alder, and water birch in smaller quantities. Along tributaries, cottonwood, aspen, and willow are dominant.

Grazing: all study sites were ungrazed or rested for at least five years; thus the Bitterroot River is not included in our analysis of grazing effects.

Missouri

Location: ungrazed survey locations were located on the Charles M. Russell National Wildlife Refuge, and grazed survey locations were in a 40-km stretch of river bordering the refuge to the west.

Vegetation: riparian stands consist of mid- to late-seral riparian vegetation (Hansson et al. 1995) dominated by Great Plains cottonwood (*Populus deltoides*), green ash (*Fraxinus pennsylvanica*), and willow. Floodplains are bounded by the steep, highly eroded "Missouri Breaks," which rise to 300m from the floodplain and support upland vegetation dominated by shrubs.

Grazing: moderate to heavy grazing for the past 30–120 years on grazed sites, ungrazed sites have had no cattle for the past 30 years.

Hart Mountain

Location: all Hart Mountain sites were located in the northwestern Great Basin on the 115,000 ha Hart Mountain National Antelope Refuge (42°25′ N, 119°40′ W) in southeastern Oregon. Data were used from surveys conducted along small streams in five separate drainages.

Vegetation: riparian woodlands occurred as narrow ribbons of riparian habitat, primarily aspen and willows, surrounded by sagebrush (*Artemisia* spp.) steppe, or as dense stands of smaller-stature trees on sideslopes and snowpocket areas in the higher reaches of riparian drainages. For additional details see Dobkin et al. (1995, 1998).

Grazing: in the autumn of 1990, livestock were removed completely from the Hart Mountain refuge, ending continuous livestock use dating back to the 1870s. For this study, we classified data from 1991 (the first growing season following livestock removal) as "grazed," and data from 1993 (the third growing season following livestock removal) as "rested" or "ungrazed." We did not use data for 1992.

Sheldon

Location: all Sheldon sites were on the Sheldon National Wildlife Refuge located in the northwestern corner of Nevada, approximately 55 km southeast of Hart Mountain. Riparian areas occur mostly as narrow valleys and canyons bordered by the steep rimrock of tablelands.

Vegetation: riparian habitat is severely limited at Sheldon, and nearly all riparian habitat in this study consisted of degraded willow-dominated areas.

Grazing: as at Hart Mountain, livestock were removed from the Sheldon Refuge in the autumn of 1990 following continuous livestock use dating back to the 1870s. For this study, we classified data from 1991 (the first growing season following livestock removal) as "grazed," and data from 1993 (the third growing season following livestock removal) as "rested" or "ungrazed." We did not use data for 1992.

APPENDIX 2. COMMON AND SCIENTIFIC NAMES AND ECOLOGICAL ATTRIBUTES OF ALL SPECIES ANALYZED

Common Name	Scientific Name	Rivers	Mean abundance rank	Migration guild	Host guild	Nest Type	Nest Height
Pied-billed Grebe	*Podilymbus podiceps*	1	61.5		non host		
Western Grebe	*Aechmophorus occidentalis*	1	84		non host		
American White Pelican	*Pelecanus erythrorhynchos*	1	72		non host	open	<2.5m
Double-crested Cormorant	*Phalacrocorax auritus*	1	53		non host	open	
American Bittern	*Botaurus lentiginosus*	1	54		non host	open	<2.5m
Great Blue Heron	*Ardea herodias*	4	44.5		non host	open	>5m
Great Egret	*Ardea alba*	1	34		non host	open	>5m
Black-crowned Night-Heron	*Nycticorax nycticorax*	1	47		non host	open	>5m
Turkey Vulture	*Cathartes aura*	3	46	Short-distance	non host		
Canada Goose	*Branta canadensis*	1	54		non host	open	<2.5m
Wood Duck	*Aix sponsa*	3	58.5		non host	secondary cavity	>5m
Gadwall	*Anas strepera*	2	56		non host	open	<2.5m
Mallard	*Anas platyrhynchos*	6	35.6		non host	open	<2.5m
Green-winged Teal	*Anas crecca*	1	63		non host	open	<2.5m
Cinnamon Teal	*Anas cyanoptera*	1	23		non host	open	<2.5m
Hooded Merganser	*Lophodytes cucullatus*	1	86		non host	secondary cavity	
Common Merganser	*Mergus merganser*	2	59.3		non host	secondary cavity	>5m
Red-breasted Merganser	*Mergus serrator*	1	69		non host		
Osprey	*Pandion haliaetus*	2	61.5	Short-distance	non host	open	>5m
Bald Eagle	*Haliaeetus leucocephalus*	1	81.5	Short-distance	non host	open	>5m
Northern Harrier	*Circus cyaneus*	2	48.3	Short-distance	non host		<2.5m
Sharp-shinned Hawk	*Accipiter striatus*	1	48.5	Short-distance	non host	open	>5m
Cooper's Hawk	*Accipiter cooperii*	2	83.3	Short-distance	non host	open	>5m
Northern Goshawk	*Accipiter gentilis*	2	37	Resident	non host	open	>5m
Red-shouldered Hawk	*Buteo lineatus*	1	50	Short-distance	non host		
Swainson's Hawk	*Buteo swainsoni*	1	45	Long-distance	non host	open	>5m
Red-tailed Hawk	*Buteo jamaicensis*	6	43.1	Short-distance	non host	open	>5m
Golden Eagle	*Aquila chrysaetos*	1	53	Short-distance	non host	open	>5m
American Kestrel	*Falco sparverius*	5	47.8	Short-distance	non host	secondary cavity	>5m
Ring-necked Pheasant	*Phasianus colchicus*	1	23	Resident	non host	open	<2.5m
Ruffed Grouse	*Bonasa umbellus*	2	39	Resident	non host	open	<2.5m
Wild Turkey	*Meleagris gallopavo*	1	69	Resident	non host	open	<2.5m
California Quail	*Callipepla californica*	2	23.5	Resident	non host	open	<2.5m
Virginia Rail	*Rallus limicola*	1	39		non host	open	<2.5m
American Coot	*Fulica americana*	1	51		non host		
Killdeer	*Charadrius vociferus*	4	53.1	Short-distance	non host	open	<2.5m
Solitary Sandpiper	*Tringa solitaria*	1	41		non host		
Spotted Sandpiper	*Actitis macularia*	4	48.1		non host	open	<2.5m
Common Snipe	*Gallinago gallinago*	2	55.8		non host	open	<2.5m

APPENDIX 2. CONTINUED

Common Name	Scientific Name	Rivers	Mean abundance rank	Migration guild	Host guild	Nest Type	Nest Height
Wilson's Phalarope	*Phalaropus tricolor*	1	64		non host	open	<2.5m
Red-necked Phalarope	*Phalaropus lobatus*	2	46.5		non host		
Caspian Tern	*Sterna caspia*	1	58		non host	open	<2.5m
Plain Pigeon	*Columba inornata*	1	86	Resident	non host		
Mourning Dove	*Zenaida macroura*	7	22.1	Short-distance		open	
Yellow-billed Cuckoo	*Coccyzus americanus*	2	61.5	Long-distance	non host	open	>5m
Great Horned Owl	*Bubo virginianus*	5	49.9	Resident	non host	open	>5m
Barred Owl	*Strix varia*	1	61	Resident	non host	secondary cavity	>5m
Long-eared Owl	*Asio otus*	2	63.5		non host	open	
Short-eared Owl	*Asio flammeus*	1	79	Short-distance	non host	open	<2.5m
Lesser Nighthawk	*Chordeiles acutipennis*	1	61.5	Long-distance	non host	open	<2.5m
Common Nighthawk	*Chordeiles minor*	1	68	Long-distance	non host	open	<2.5m
White-throated Swift	*Aeronautes saxatalis*	2	46	Long-distance	non host		
Black-chinned Hummingbird	*Archilochus alexandri*	1	31	Long-distance	non host	open	>5m
Anna's Hummingbird	*Calypte anna*	1	66	Resident	non host	open	
Calliope Hummingbird	*Stellula calliope*	3	53.5	Long-distance	non host	open	<2.5m
Broad-tailed Hummingbird	*Selasphorus platycercus*	3	60	Long-distance	non host	open	
Rufous Hummingbird	*Selasphorus rufus*	2	40	Long-distance	non host	open	>5m
Belted Kingfisher	*Ceryle alcyon*	3	53		non host		
Lewis's Woodpecker	*Melanerpes lewis*	1	80	Short-distance	non host	primary cavity	>5m
Acorn Woodpecker	*Melanerpes formicivorus*	1	45.5	Resident	non host	primary cavity	>5m
Red-naped Sapsucker	*Sphyrapicus nuchalis*	3	17.5	Short-distance	non host	primary cavity	>5m
Red-breasted Sapsucker	*Sphyrapicus ruber*	1	64	Short-distance	non host	primary cavity	>5m
Nuttall's Woodpecker	*Picoides nuttallii*	2	10.5	Resident	non host	primary cavity	
Downy Woodpecker	*Picoides pubescens*	6	35	Resident	non host	primary cavity	>5m
Hairy Woodpecker	*Picoides villosus*	5	36.9	Resident	non host	primary cavity	>5m
Northern Flicker	*Colapetes auratus*	6	20.5	Short-distance	non host	primary cavity	>5m
Pileated Woodpecker	*Dryocopus pileatus*	1	77	Resident	non host	primary cavity	>5m
Olive-sided Flycatcher	*Contopus cooperi*	1	53.5	Long-distance		open	
Western Wood-Pewee	*Contopus sordidulus*	6	13	Long-distance		open	>5m
Willow Flycatcher	*Empidonax traillii*	4	48.6	Long-distance	primary host	open	<2.5m
Least Flycatcher	*Empidonax minimus*	2	34.3	Long-distance		open	
Hammond's Flycatcher	*Empidonax hammondii*	2	51	Long-distance	non host	open	>5m
Gray Flycatcher	*Empidonax wrightii*	1	20.5	Long-distance	non host	open	
Dusky Flycatcher	*Empidonax oberholseri*	5	27.7	Long-distance		open	
Cordilleran Flycatcher	*Empidonax occidentalis*	3	46	Long-distance		open	<2.5m
Pacific-slope Flycatcher	*Empidonax difficulis*	1	45.5	Long-distance		open	<2.5m
Ash-throated Flycatcher	*Myiarchus cinerascens*	2	7	Long-distance	non host	open	
Say's Pheobe	*Sayornis saya*	1	63	Short-distance			

APPENDIX 2. CONTINUED

Common Name	Scientific Name	Rivers	Mean abundance rank	Migration guild	Host guild	Nest Type	Nest Height
Black Phoebe	*Sayornis nigricans*	2	40.5	Resident			
Western Kingbird	*Tyrannus verticalis*	3	26.7	Long-distance		open	>5m
Eastern Kingbird	*Tyrannus tyrannus*	3	47.3	Long-distance	primary host	open	>5m
Loggerhead Shrike	*Lanius ludovicianus*	2	34.5	Short-distance	non host	open	
Warbling Vireo	*Vireo gilvus*	7	24.1	Long-distance	primary host	open	>5m
Red-eyed Vireo	*Vireo olivaceus*	4	45	Long-distance	primary host	open	>5m
Gray Jay	*Perisoreus canadensis*	1	90.5	Resident	non host	open	
Steller's Jay	*Cyanocitta stelleri*	1	70	Resident	non host	open	>5m
Western Scrub-Jay	*Aphelocoma californica*	2	12.5	Resident	non host		
Clark's Nutcracker	*Nucifraga columbiana*	1	62.5	Resident	non host	open	>5m
Black-billed Magpie	*Pica hudsonia*	5	22	Resident	non host	open	>5m
Yellow-billed Magpie	*Pica nuttalli*	1	21	Resident	non host	open	
American Crow	*Corvus brachyrhynchos*	4	50.8	Short-distance	non host	open	>5m
Common Raven	*Corvus corax*	3	54.3	Resident	non host	open	>5m
Horned Lark	*Eremophila alpestris*	1	53	Short-distance		open	<2.5m
Tree Swallow	*Tachycineta bicolor*	6	20.7	Short-distance		secondary cavity	>5m
Violet-green Swallow	*Tachycineta thalassina*	4	30.8	Long-distance	non host	secondary cavity	>5m
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	4	44.3	Long-distance	non host		
Bank Swallow	*Riparia riparia*	1	29	Long-distance			
Cliff Swallow	*Petrochelidon pyrrhonota*	6	44.8	Long-distance			
Barn Swallow	*Hirundo rustica*	3	47.5	Long-distance			
Black-capped Chickadee	*Poecile atricapilla*	3	12.8	Resident		secondary cavity	
Mountain Chickadee	*Poecile gambeli*	3	53.2	Resident	non host	secondary cavity	<2.5m
Chestnut-backed Chickadee	*Poecile rufescens*	1	44.5	Resident	non host	secondary cavity	<2.5m
Oak Titmouse	*Baeolophus inornatus*	2	32	Resident			
Bushtit	*Psaltriparus minimus*	1	21	Resident		open	
Red-breasted Nuthatch	*Sitta canadensis*	4	48.3	Short-distance	non host	primary cavity	>5m
White-breasted Nuthatch	*Sitta carolinensis*	3	42	Resident		secondary cavity	>5m
Pygmy Nuthatch	*Sitta pygmaea*	1	60	Resident	non host	primary cavity	>5m
Brown Creeper	*Certhia americana*	1	75.5	Short-distance		open	>5m
Rock Wren	*Salpinctes obsoletus*	1	29	Short-distance			
Bewick's Wren	*Thryomanes bewickii*	2	5	Short-distance		secondary cavity	<2.5m
House Wren	*Troglodytes aedon*	7	14.6	Long-distance		secondary cavity	
Winter Wren	*Troglodytes troglodytes*	1	48	Short-distance		open	<2.5m
Marsh Wren	*Cistothorus palustris*	2	33	Short-distance	non host	open	<2.5m
Golden-crowned Kinglet	*Regulus satrapa*	1	23	Short-distance		open	>5m
Ruby-crowned Kinglet	*Regulus calendula*	4	37.9	Short-distance		open	>5m

APPENDIX 2. CONTINUED

Common Name	Scientific Name	Rivers	Mean abundance rank	Migration guild	Host guild	Nest Type	Nest Height
Blue-gray Gnatcatcher	*Polioptila caerulea*	1	63	Long-distance	primary host	open	
Western Bluebird	*Sialia mexicana*	1	39	Short-distance		secondary cavity	<2.5m
Mountain Bluebird	*Sialia currucoides*	2	34.3	Short-distance		secondary cavity	
Townsend's Solitaire	*Myadestes townsendi*	2	73	Short-distance	non host	open	<2.5m
Veery	*Catharus fuscescens*	2	20	Long-distance	primary host	open	<2.5m
Swainson's Thrush	*Catharus ustulatus*	6	32.3	Long-distance		open	
American Robin	*Turdus migratorius*	7	13.7	Short-distance		open	
Gray Catbird	*Dumetella carolinensis*	3	34.3	Long-distance		open	<2.5m
Northern Mockingbird	*Mimus polyglottos*	1	26	Resident		open	
Sage Thrasher	*Oreoscoptes montanus*	1	45	Short-distance		open	<2.5m
Brown Thrasher	*Toxostoma rufum*	1	18	Short-distance		open	<2.5m
California Thrasher	*Toxostoma redivivum*	1	46	Resident	non host	open	<2.5m
European Starling	*Sturnus vulgaris*	7	17.9	Short-distance	non host	secondary cavity	>5m
Cedar Waxwing	*Bombycilla cedrorum*	4	16	Short-distance		open	
Orange-crowned Warbler	*Vermivora celata*	4	32.1	Long-distance		open	<2.5m
Nashville Warbler	*Vermivora ruficapilla*	2	64.5	Long-distance		open	<2.5m
Yellow Warbler	*Dendroica petechia*	7	16.1	Long-distance	primary host	open	
Yellow-rumped Warbler	*Dendroica coronata*	5	33.6	Short-distance	primary host	open	>5m
Townsend's Warbler	*Dendroica townsendi*	5	51.5	Long-distance		open	>5m
Hermit Warbler	*Dendroica occidentalis*	1	58.5	Long-distance		open	>5m
American Redstart	*Setophaga ruticilla*	2	19	Long-distance	primary host	open	
Ovenbird	*Seiurus aurocapillus*	2	45	Long-distance	primary host	open	<2.5m
Northern Waterthrush	*Seiurus noveboracensis*	1	51	Long-distance		open	<2.5m
MacGillivray's Warbler	*Oporornis tolmiei*	5	37.4	Long-distance		open	<2.5m
Common Yellowthroat	*Geothlypis trichas*	5	22	Long-distance	primary host	open	<2.5m
Wilson's Warbler	*Wilsonia pusilla*	5	26.6	Long-distance		open	<2.5m
Yellow-breasted Chat	*Icteria virens*	5	38.7	Long-distance	primary host	open	<2.5m
Western Tanager	*Piranga ludoviciana*	6	39.8	Long-distance		open	>5m
Green-tailed Towhee	*Pipilo chlorurus*	2	36	Long-distance		open	<2.5m
Spotted Towhee	*Pipilo maculatus*	5	32.7	Short-distance	primary host	open	<2.5m
California Towhee	*Pipilo crissalis*	2	34	Long-distance		open	<2.5m
Chipping Sparrow	*Spizella passerina*	4	46	Long-distance	primary host	open	
Brewer's Sparrow	*Spizella breweri*	2	20.5	Long-distance		open	<2.5m
Vesper Sparrow	*Pooecetes gramineus*	3	45.3	Short-distance	primary host	open	<2.5m
Black-throated Sparrow	*Amphispiza bilineata*	1	35	Short-distance		open	<2.5m
Sage Sparrow	*Amphispiza belli*	1	39	Short-distance		open	<2.5m
Lark Sparrow	*Chondestes grammacus*	3	48	Long-distance		open	<2.5m
Savannah Sparrow	*Passerculus sandwichensis*	2	33.8	Short-distance		open	<2.5m
Fox Sparrow	*Passerella iliaca*	2	20.5	Short-distance		open	<2.5m

APPENDIX 2. CONTINUED

Common Name	Scientific Name	Rivers	Mean abundance rank	Migration guild	Host guild	Nest Type	Nest Height
Song Sparrow	*Melospiza melodia*	6	15.4	Short-distance	primary host	open	<2.5m
White-crowned Sparrow	*Zonotrichia leucophrys*	1	10	Short-distance		open	<2.5m
Golden-crowned Sparrow	*Zonotrichia atricapilla*	2	66	Short-distance		open	
Black-headed Grosbeak	*Pheucticus melanocephalus*	7	18.9	Long-distance		open	
Blue Grosbeak	*Guiraca caerulea*	2	38.5	Long-distance	primary host	open	
Lazuli Bunting	*Passerina amoena*	7	30.1	Long-distance	primary host	open	<2.5m
Red-winged Blackbird	*Agelaius phoeniceus*	6	29.1	Short-distance	primary host	open	<2.5m
Tricolored Blackbird	*Agelaius tricolor*	1	52	Resident		open	<2.5m
Western Meadowlark	*Sturnella neglecta*	5	37.2	Short-distance		open	<2.5m
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	1	63	Long-distance		open	<2.5m
Brewer's Blackbird	*Euphagus cyanocephalus*	7	29.4	Short-distance	primary host	open	
Common Grackle	*Quiscalus quiscula*	1	15	Short-distance		open	>5m
Brown-headed Cowbird	*Molothrus ater*	7	7.21	Short-distance	non host		
Bullock's Oriole	*Icterus bullockii*	7	21.3	Long-distance		open	>5m
Purple Finch	*Carpodacus purpureus*	1	78	Short-distance		open	>5m
Cassin's Finch	*Carpodacus cassinii*	3	35.7	Short-distance	non host	open	>5m
House Finch	*Carpodacus mexicanus*	5	40.4	Short-distance		open	>5m
Red Crossbill	*Loxia curvirostra*	1	9	Short-distance	non host	open	>5m
Pine Siskin	*Carduelis pinus*	4	31.6	Short-distance		open	>5m
Lesser Goldfinch	*Carduelis psaltria*	1	17	Short-distance		open	>5m
American Goldfinch	*Carduelis tristis*	5	17.8	Short-distance	primary host	open	>5m
Evening Grosbeak	*Coccothraustes vespertinus*	1	11	Short-distance		open	>5m
House Sparrow	*Passer domesticus*	1	41	Resident	non host		

Notes: the number of river systems in which the species was detected (Rivers) and the mean rank of each species (Mean abundance rank; 1 = most often detected species on a river). All species were ranked in descending order of detection frequency within each river system. Mean rank abundance is the average rank across all rivers where the species were detected. Species membership in migration, cowbird host, nest type, and nest height guilds is also included.

APPENDIX 3. PEARSON CORRELATIONS (AND P-VALUES) FOR ALL LANDSCAPE VARIABLES WITHIN EACH RIVER SYSTEM (SEE TABLE 1 FOR SAMPLE SIZES)

River system	Landscape variable	Local human habitation	Local agriculture	Local deciduous forest	Local coniferous forest	Regional human habitation	Regional agriculture	Regional deciduous forest
Sacramento	Local agriculture	0.383 (0.004)						
	Local deciduous forest	−0.139 (0.311)	−0.322 (0.016)					
	Local coniferous forest	. .	. .	. .				
	Regional human habitation	−0.220 (0.106)	−0.001 (0.993)	−0.251 (0.064)	. .			
	Regional agriculture	0.714 (<0.001)	0.688 (<0.001)	−0.125 (0.364)	. .	−0.166 (0.227)		
	Regional deciduous forest	0.774 (<0.001)	0.179 (0.190)	−0.239 (0.079)	. .	−0.166 (0.225)	0.630 (<0.001)	
	Regional coniferous forest	. .	. .	. .	. .	. .	. .	. .
San Joaquin	Local agriculture	0.612 (<0.001)						
	Local deciduous forest	0.275 (0.044)	0.369 (0.006)					
	Local coniferous forest	. .	. .	. .				
	Regional human habitation	. .	. .	. .	. .			
	Regional agriculture	0.215 (0.119)	0.577 (<0.001)	0.213 (0.1216)	. .	. .		
	Regional deciduous forest	. .	. .	. .	. .	. .	. .	
	Regional coniferous forest	. .	. .	. .	. .	. .	. .	. .
Snake	Local agriculture	0.074 (0.604)						
	Local deciduous forest	−0.304 (0.029)	−0.555 (<0.001)					
	Local coniferous forest	−0.022 (0.876)	−0.706 (<0.001)	0.035 (0.805)				
	Regional human habitation	0.286 (0.040)	0.665 (<0.001)	−0.099 (0.485)	−0.648 (<0.001)			
	Regional agriculture	−0.377 (0.006)	0.589 (<0.001)	0.075 (0.598)	−0.562 (<0.001)	0.596 (<0.001)		
	Regional deciduous forest	0.417 (0.002)	−0.409 (0.003)	−0.114 (0.421)	0.343 (0.013)	−0.410 (0.003)	−0.884 (<0.001)	

APPENDIX 3. Continued

River system	Landscape variable	Local human habitation	Local agriculture	Local deciduous forest	Local coniferous forest	Regional human habitation	Regional agriculture	Regional deciduous forest
	Regional coniferous forest	0.398 (0.003)	−0.546 (<0.001)	−0.094 (0.509)	0.561 (<0.001)	−0.556 (<0.001)	−0.927 (<0.001)	0.798 (<0.001)
Bitterroot	Local agriculture	0.675 (<0.001)						
	Local deciduous forest	0.437 (<0.001)	0.473 (<0.001)					
	Local coniferous forest	−0.623 (<0.001)	−0.851 (<0.001)	−0.688 (<0.001)				
	Regional human habitation	0.242 (0.008)	0.439 (<0.001)	0.335 (<0.001)	−0.581 (<0.001)			
	Regional agriculture	0.470 (<0.001)	0.603 (<0.001)	0.700 (<0.001)	−0.717 (<0.001)	0.561 (<0.001)		
	Regional deciduous forest	0.418 (<0.001)	0.537 (<0.001)	0.690 (<0.001)	−0.651 (<0.001)	0.544 (<0.001)	0.951 (<0.001)	
	Regional coniferous forest	−0.574 (<0.001)	−0.759 (<0.001)	−0.637 (<0.001)	0.869 (<0.001)	−0.623 (<0.001)	−0.909 (<0.001)	−0.833 (<0.001)
Missouri	Local agriculture	.						
	Local deciduous forest	.	0.049 (0.801)					
	Local coniferous forest	.	0.150 (0.438)	−0.575 (0.001)				
	Regional human habitation	.	.	.	.			
	Regional agriculture	.	0.594 (<0.001)	−0.061 (0.754)	0.186 (0.333)	.		
	Regional deciduous forest	.	0.104 (0.593)	0.824 (<0.001)	−0.407 (0.028)	.	−0.003 (0.988)	
	Regional coniferous forest	.	0.201 (0.295)	0.777 (<0.001)	−0.158 (0.413)	.	0.233 0.2245	0.809 (<0.001)
Hart	Local coniferous forest	.	.	−0.628 (<0.001)				
	Regional human habitation	.	.	.	.			
	Regional agriculture	.	.	.	.	.		

APPENDIX 3. CONTINUED

River system	Landscape variable	Local human habitation	Local agriculture	Local deciduous forest	Local coniferous forest	Regional human habitation	Regional agriculture	Regional deciduous forest
	Regional deciduous forest	.	.	0.226	0.373	.	.	
		.	.	(0.155)	(0.016)	.	.	
	Regional coniferous forest	.	.	0.599	−0.123	.	.	0.433
		.	.	(<0.001)	(0.445)	.	.	(0.005)
Sheldon	Local deciduous forest	−0.248	.					
		(0.305)	.					
	Local coniferous forest	0.344	.	−0.195				
		(0.150)	.	(0.424)				
	Regional human habitation	.	.	.	.			
		.	.	.	.			
	Regional agriculture	−0.380	.	0.924	−0.199	.		
		(0.109)	.	(<0.001)	(0.413)	.		
	Regional deciduous forest	.	.	.	.	.	.	
		.	.	.	.	.	.	
	Regional coniferous forest	.	.	.	.	.	.	.
		.	.	.	.	.	.	.

APPENDIX 4. EFFECTS OF LANDSCAPE VARIABLES WITHIN INDIVIDUAL RIVER SYSTEMS ON TOTAL DETECTIONS (TOTAL BIRDS), TOTAL RICHNESS (RICHNESS), BROWN-HEADED COWBIRDS, COWBIRD HOST GUILDS, AND MIGRATION GUILDS (SEE APPENDIX 2)

Landscape variable and river system	Statistic	Total birds	Richness	Cowbirds	Prime hosts	Non-hosts	Long-distance migrant	Residents	Short-distance migrant
Local Human Habitation									
Sacramento									
Σ	Dir	Pos		Pos	Pos	Neg	Pos		
	B	0.13		0.19	0.19	−0.27	0.20		
	R^2	0.016		0.036	0.035	0.072	0.039		
	P	0.361		0.166	0.173	0.048	0.150		
#	Dir	Neg			Neg	Neg	Neg	Neg	Neg
	Inc	38%			31%	34%	33%	29%	36%
	P	0.038			0.267	0.074	0.100	0.180	0.230
San Joaquin									
Σ	Dir			Pos	Pos	Neg		Neg	Pos
	B			0.25	0.26	−0.12		−0.29	0.12
	R^2			0.063	0.031	0.015		0.086	0.015
	P			0.062	0.049	0.375		0.028	0.371
#	Dir	Neg				Neg	Neg		
	Inc	43%				41%	35%		
	P	0.313				0.377	0.263		
Snake									
Σ	Dir	Neg		Neg	Neg	Pos	Neg	Pos	Neg
	B	−0.38		−0.17	−0.52	0.11	−0.44	0.17	−0.23
	R^2	0.143		0.029	0.265	0.013	0.187	0.030	0.051
	P	0.005*		0.224	<0.001*	0.415	0.001*	0.211	0.104
#	Dir	Neg			Neg	Neg	Neg	Neg	Neg
	Inc	33%			21%	35%	29%	14%	37%
	P	0.015			0.057	0.210	0.064	0.125	0.359
Bitterroot									
Σ	Dir	Pos	Pos	Pos	Pos	Pos	Pos	Pos	Pos
	B	0.26	0.15	0.38	0.40	0.25	0.11	0.16	0.19
	R^2	0.070	0.021	0.141	0.158	0.060	0.012	0.024	0.035
	P	0.004	0.143	<0.001*	<0.001*	0.007	0.238	0.091	0.040
#	Dir	Pos			Pos	Pos			
	Inc	57%			75%	61%			
	P	0.213			0.077	0.243			
Sheldon									
Σ	Dir	Neg	Neg		Neg	Neg	Neg	Neg	Neg
	B	−0.51	−0.42		−0.42	−0.43	−0.31	−0.33	−0.39
	R^2	0.259	0.176		0.175	0.183	0.099	0.110	0.150
	P	0.026	0.074		0.075	0.068	0.190	0.166	0.101

APPENDIX 4. CONTINUED

Landscape variable and river system	Statistic	Total birds	Richness	Cowbirds	Prime hosts	Non-hosts	Long-distance migrant	Residents	Short-distance migrant
#	Dir	Neg			Neg	Neg	Neg		Neg
	Inc	19%			0%	18%	18%		23%
	P	<0.001			<0.001	0.004	0.001		0.011
Regional Human Habitation									
Snake									
Σ	Dir			Pos	Neg	Pos	Neg	Pos	Pos
	B			0.36	−0.48	0.20	−0.17	0.23	0.23
	R^2			0.126	0.230	0.040	0.034	0.051	0.054
	P			0.009	<0.001*	0.153	0.228	0.105	0.095
#	Dir	Neg				Neg	Neg		
	Inc	40%				35%	38%		
	P	0.178				0.210	0.307		
Bitterroot									
Σ	Dir	Pos	Pos	Pos	Pos	Pos	Neg	Pos	Pos
	B	0.16	0.17	0.33	0.17	0.28	−0.10	0.16	0.24
	R^2	0.026	0.030	0.106	0.030	0.079	0.009	0.024	0.058
	P	0.078	0.080	<0.001*	0.060	0.002	0.289	0.091	0.008
#	Dir								
	Inc								
	P								
Local Agriculture									
Sacramento									
Σ	Dir	Pos	Pos	Pos			Pos		
	B	0.21	0.16	0.24			0.28		
	R^2	0.044	0.025	0.057			0.079		
	P	0.126	0.245	0.080			0.037		
#	Dir					Neg			
	Inc					38%			
	P					0.230			
San Joaquin									
Σ	Dir			Pos	Pos				Pos
	B			0.27	0.24				0.19
	R^2			0.074	0.070				0.035
	P			0.042	0.070				0.167
#	Dir						Neg		
	Inc						38%		
	P						0.381		
Snake									

APPENDIX 4. CONTINUED

Landscape variable and river system	Statistic	Total birds	Richness	Cowbirds	Prime hosts	Non-hosts	Long-distance migrant	Residents	Short-distance migrant
Σ	Dir	Pos		Pos	Neg	Pos	Neg	Pos	Pos
	B	0.23		0.25	−0.54	0.48	−0.13	0.39	0.37
	R^2	0.053		0.063	0.294	0.225	0.013	0.132	0.134
	P	0.097		0.069	<0.001*	<0.001*	0.364	0.004	0.007
#	Dir	Neg				Neg	Neg		
	Inc	40%				36%	26%		
	P	0.310				0.286	0.035		
Bitterroot									
Σ	Dir	Pos	Pos	Pos	Pos	Pos		Pos	Pos
	B	0.26	0.29	0.38	0.33	0.31		0.22	0.33
	R^2	0.068	0.082	0.142	0.106	0.095		0.049	0.109
	P	0.004	0.003	<0.001*	<0.001*	0.001*		0.015	<0.001*
#	Dir	Pos			Pos	Pos		Pos	Pos
	Inc	69%			71%	71%		69%	61%
	P	<0.001*			0.143	0.018		0.210	0.281
Regional Agriculture									
Sacramento									
Σ	Dir	Pos	Pos	Pos			Pos	Pos	Pos
	B	0.34	0.25	0.24			0.27	0.30	0.22
	R^2	0.113	0.063	0.057			0.075	0.091	0.049
	P	0.012*	0.065	0.078			0.044	0.026	0.105
#	Dir			Neg					Neg
	Inc			38%					33%
	P			0.265					0.189
San Joaquin									
Σ	Dir		Neg	Pos		Pos	Neg		Pos
	B		−0.2	0.26		0.15	−0.16		0.33
	R^2		0.041	0.068		0.023	0.037		0.111
	P		0.141	0.052		0.260	0.246		0.012*
#	Dir								
	Inc								
	P								
Snake									
Σ	Dir	Pos		Pos			Pos		Pos
	B	0.51		0.55			0.27		0.51
	R^2	0.256		0.298			0.068		0.260
	P	<0.001*		<0.001*			0.049		<0.001*
#	Dir	Neg				Neg	Neg		

APPENDIX 4. CONTINUED

Landscape variable and river system	Statistic	Total birds	Richness	Cowbirds	Prime hosts	Non-hosts	Long-distance migrant	Residents	Short-distance migrant
	Inc	0.4				35%	33%		
	P	0.178				0.210	0.152		
Bitterroot									
Σ	Dir	Pos	Pos	Pos	Pos	Pos		Pos	Pos
	B	0.23	0.28	0.43	0.33	0.44		0.38	0.30
	R^2	0.083	0.081	0.202	0.109	0.191		0.148	0.089
	P	0.001*	0.004	<0.001*	<0.001*	v*		<0.001*	0.001*
#	Dir	Pos			Pos	Pos	Pos	Pos	Pos
	Inc	69%			71%	71%	64%	69%	65%
	P	<0.001*			0.143	0.018*	0.164	0.210	0.170
Missouri									
Σ	Dir	Pos	Pos		Pos	Pos	Pos	Neg	Pos
	B	0.45	0.28		0.45	0.26	0.39	−0.33	0.49
	R^2	0.202	0.078		0.203	0.065	0.158	0.111	0.235
	P	0.015	0.142		0.014*	0.180	0.038	0.078	0.008*
#	Dir	Pos			Pos			Neg	Pos
	Inc	60%			71%			20%	76%
	P	0.222			0.180			0.375	0.049
Local deciduous riparian									
Sacramento									
Σ	Dir	Neg	Neg	Neg		Neg	Neg		Pos
	B	−0.33	−0.31	−0.17		−0.13	−0.41		0.19
	R^2	0.107	0.093	0.028		0.017	0.167		0.036
	P	0.015*	0.024	0.218		0.345	0.002*		0.163
#	Dir	Neg			Neg	Neg	Neg		Neg
	Inc	33%			33%	29%	25%		38%
	P	0.007*			0.388	0.038*	0.023*		0.383
San Joaquin									
Σ	Dir	Pos	Pos	Pos	Pos	Pos		Pos	Pos
	B	0.27	0.12	0.13	0.244	0.27		0.28	0.24
	R^2	0.073	0.014	0.017	0.059	0.073		0.078	0.056
	P	0.044	0.396	0.343	0.070	0.045		0.038	0.080
#	Dir	Pos			Pos	Pos		Pos	
	Inc	67%			80%	69%		82%	
	P	0.009*			0.109	0.052		0.065	
Snake									
Σ	Dir				Pos	Neg	Pos	Neg	Neg
	B				0.40	−0.42	0.25	−0.25	−0.17
	R^2				0.160	0.175	0.053	0.062	0.029

APPENDIX 4. CONTINUED

Landscape variable and river system	Statistic	Total birds	Richness	Cowbirds	Prime hosts	Non-hosts	Long-distance migrant	Residents	Short-distance migrant
	P				0.003*	0.002*	0.072	0.072	0.224
#	Dir	Pos			Pos		Pos		
	Inc	58%			71%		63%		
	P	0.281			0.180		0.307		
Bitterroot									
Σ	Dir	Pos	Pos	Pos	Pos	Pos	Pos	Pos	Pos
	B	0.37	0.34	0.40	0.51	0.34	0.13	0.32	0.30
	R^2	0.140	0.113	0.161	0.259	0.113	0.017	0.100	0.090
	P	<0.001*	0.001*	<0.001*	<0.001*	<0.001*	0.164	<0.001*	0.001*
#	Dir	Pos			Pos	Pos	Pos	Pos	Pos
	Inc	68%			75%	71%	61%	75%	68%
	P	0.001*			0.070	0.015	0.296	0.077	0.089
Missouri									
Σ	Dir	Pos	Pos		Pos	Pos	Pos	Pos	Pos
	B	0.59	0.27		0.34	0.25	0.65	0.37	0.33
	R^2	0.344	0.073		0.117	0.064	0.416	0.139	0.110
	P	0.001*	0.115		0.070	0.187	<0.001*	0.047	0.079
#	Dir	Pos					Pos		
	Inc	63%					72%		
	P	0.144					0.096		
Hart									
Σ	Dir				Neg	Neg		Pos	
	B				−0.43	−0.14		0.27	
	R^2				0.182	0.019		0.071	
	P				0.005*	0.390		0.093	
#	Dir	Neg			Neg			Pos	Neg
	Inc	40%			11%			80%	31%
	P	0.131			0.039*			0.375	0.063
Sheldon									
Σ	Dir	Pos		Pos	Pos	Pos	Pos		Pos
	B	0.42		0.54	0.50	0.33	0.21		0.62
	R^2	0.180		0.290	0.252	0.110	0.044		0.381
	P	0.071		0.017*	0.028	0.166	0.383		0.005*
#	Dir					Pos	Neg		
	Inc					62%	37%		
	P					0.383	0.248		
Regional deciduous riparian									
Sacramento									
Σ	Dir	Pos		Pos		Neg	Pos	Pos	

APPENDIX 4. CONTINUED

Landscape variable and river system	Statistic	Total birds	Richness	Cowbirds	Prime hosts	Non-hosts	Long-distance migrant	Residents	Short-distance migrant
	B	0.16		0.17		−0.21	0.26	0.17	
	R^2	0.025		0.029		0.045	0.067	0.027	
	P	0.253		0.217		0.122	0.056	0.228	
#	Dir				Neg	Neg			
	Inc				30%	39%			
	P				0.343	0.281			
Snake									
Σ	Dir	Neg		Neg			Neg	Neg	Neg
	B	−0.47		−0.46			−0.31	−0.12	−0.41
	R^2	0.221		0.213			0.088	0.014	0.170
	P	<0.001*		0.001*			0.026	0.399	0.002*
#	Dir								
	Inc								
	P								
Bitterroot									
Σ	Dir	Pos	Pos	Pos	Pos	Pos		Pos	Pos
	B	0.26	0.27	0.48	0.32	0.41		0.39	0.25
	R^2	0.066	0.073	0.234	0.103	0.167		0.149	0.062
	P	0.005	0.006	<0.001*	<0.001*	<0.001*		<0.001*	0.006
#	Dir	Pos			Pos	Pos	Pos	Pos	Pos
	Inc	68%			71%	71%	63%	69%	65%
	P	0.001*			0.143	0.018	0.216	0.210	0.170
Missouri									
Σ	Dir	Pos	Pos		Pos	Pos	Pos	Pos	Pos
	B	0.61	0.38		0.39	0.34	0.65	0.38	0.33
	R^2	0.368	0.146		0.151	0.118	0.413	0.144	0.110
	P	<0.001*	0.041		0.037	0.068	<0.001*	0.043*	0.079
#	Dir	Pos				Pos	Pos	Pos	
	Inc	69%				78%	73%	100%	
	P	0.030				0.180	0.118	0.125	
Hart									
Σ	Dir			Neg	Neg		Pos		Neg
	B			−0.20	−0.15		0.17		−0.24
	R^2			0.039	0.023		0.040		0.057
	P			0.213	0.342		0.279		0.134
#	Dir						Pos		
	Inc						63%		
	P						0.359		

APPENDIX 4. CONTINUED

Landscape variable and river system	Statistic	Total birds	Richness	Cowbirds	Prime hosts	Non-hosts	Long-distance migrant	Residents	Short-distance migrant
Local Coniferous Forest									
Snake									
Σ	Dir			Neg	Pos	Neg		Neg	Neg
	B			−0.21	0.45	−0.20		−0.23	−0.17
	R^2			0.044	0.202	0.042		0.051	0.030
	P			0.132	0.001*	0.143		0.104	0.217
#	Dir	Pos			Pos		Pos		
	Inc	64%			71%		71%		
	P	0.059			0.180		0.064		
Bitterroot									
Σ	Dir	Neg	Neg	Neg	Neg	Neg		Neg	Neg
	B	−0.29	−0.34	−0.38	−0.40	−0.29		−0.26	−0.29
	R^2	0.081	0.116	0.144	0.162	0.084		0.069	0.086
	P	0.002	<0.001*	<0.001*	<0.001*	0.001*		0.004	0.001*
#	Dir	Neg			Neg	Neg		Neg	Neg
	Inc	36%			31%	33%		31%	38%
	P	0.007*			0.210	0.055		0.210	0.265
Missouri									
Σ	Dir	Neg				Neg	Neg	Neg	Neg
	B	−0.31				−0.26	−0.32	−0.37	−0.18
	R^2	0.095				0.066	0.090	0.136	0.034
	P	0.103				0.180	0.094	0.049	0.341
#	Dir								
	Inc								
	P								
Hart									
Σ	Dir				Pos		Pos	Neg	Neg
	B				0.18		0.18	−0.15	−0.21
	R^2				0.032		0.032	0.024	0.044
	P				0.266		0.250	0.337	0.186
#	Dir						Pos	Neg	
	Inc						76%	17%	
	P						0.027*	0.219	
Regional Coniferous Forest									
Snake									
Σ	Dir	Neg		Neg			Neg		Neg
	B	−0.50		−0.57			−0.35		−0.44
	R^2	0.251		0.327			0.118		0.178
	P	<0.001*		<0.001*			0.010		0.002*

APPENDIX 4. CONTINUED

Landscape variable and river system	Statistic	Total birds	Richness	Cowbirds	Prime hosts	Non-hosts	Long-distance migrant	Residents	Short-distance migrant
#	Dir								
	Inc								
	P								
Bitterroot									
Σ	Dir	Neg	Neg	Neg	Neg	Neg	Pos	Neg	Neg
	B	−0.23	−0.27	−0.38	−0.29	−0.35	0.14	−0.28	−0.29
	R^2	0.055	0.072	0.146	0.086	0.124	0.019	0.078	0.084
	P	0.010	0.006	<0.001*	0.001*	<0.001*	0.137	0.002	0.001*
#	Dir	Neg				Neg		Neg	Neg
	Inc	35%				32%		33%	32%
	P	0.004*				0.035		0.302	0.089
Missouri									
Σ	Dir	Pos	Pos	Pos	Pos	Pos	Pos		Pos
	B	0.77	0.69	0.18	0.69	0.19	0.81		0.521
	R^2	0.554		0.034	0.480	0.036	0.664		0.271
	P	<0.001*	<0.001*	0.339	<0.001*	0.325	<0.001*		0.004*
#	Dir	Pos			Pos		Pos		
	Inc	71%			69%		89%		
	P	0.015*			0.267		0.001*		
Hart									
Σ	Dir	Neg	Neg		Neg	Neg	Neg		Neg
	B	−0.25	−0.21		−0.40	−0.32	−0.21		−0.31
	R^2	0.064	0.043		0.160	0.100	0.032		0.097
	P	0.109	0.194		0.010*	0.044*	0.199		0.048*
#	Dir	Neg			Neg	Neg			Neg
	Inc	36%			25%	35%			31%
	P	0.036*			0.289	0.170			0.063

Notes: Results are from linear regression (Σ), with directionality of change (Dir: Pos = higher relative abundance in areas with more of the landscape variable; Neg = lower relative abundance in areas with more of the landscape variable), standardized regression coefficient (B), R^2, and P-value shown; and from Binomial tests across all species in the guild (#) for directionality (more or less abundant) with high amounts of each landscape variable, with directionality of the majority of species (Dir), the percent of species more abundant in areas with high amounts of the landscape variable (Inc), and the P-value for the binomial test shown. All results with a trend ($P < 0.4$) are shown. * = significant after Bonferroni adjustment for multiple tests.

APPENDIX 5. GRAZING EFFECTS ON INDIVIDUAL SPECIES, BY RIVER

River system	Detection/survey		Mann-Whitney U-test		P
	Ungrazed	Grazed	U	W	
Sacramento					
Less Abundant in Grazed Areas					
Tree Swallow	0.5873	0.0597	66.5	111.5	0.001
Black-headed Grosbeak	0.6412	0.2735	95.5	140.5	0.011
Downy Woodpecker	0.0960	0.0094	105.5	150.5	0.013
American Robin	0.1555	0.0409	123.0	168.0	0.044
California Towhee	0.0406	0.0000	144.0	189.0	0.060
Mourning Dove	0.1550	0.0472	127.5	172.5	0.062
Bank Swallow	0.0821	0.0000	153.0	198.0	0.089
White-breasted Nuthatch	0.0761	0.0189	146.5	191.5	0.122
Turkey Vulture	0.1250	0.0189	155.5	200.5	0.152
European Starling	0.1061	0.0094	157.0	202.0	0.156
Western Wood-pewee	0.5840	0.3741	148.0	193.0	0.179
More Abundant in Grazed Areas					
California Quail	0.0457	0.2169	78.5	1159.5	0.001
Warbling Vireo	0.0341	0.0880	105.5	1186.5	0.004
Wilson's Warbler	0.1370	0.2578	91.0	1172.0	0.007
Bewick's Wren	0.6334	0.8708	116.5	1197.5	0.039
Lazuli Bunting	0.3520	0.4999	123.5	1204.5	0.057
Lesser Goldfinch	0.1702	0.3804	142.5	1223.5	0.130
Snake					
Less Abundant in Grazed Areas					
Veery	0.4791	0.1161	118.0	328.0	0.001
Song Sparrow	0.8020	0.3124	117.0	327.0	0.001
Fox Sparrow	0.1606	0.0131	134.5	344.5	0.002
Black-capped Chickadee	0.3667	0.2178	150.5	360.5	0.015
Lazuli Bunting	0.1176	0.0678	154.0	364.0	0.016
Yellow Warbler	2.7632	2.2466	152.0	362.0	0.017
Mallard	0.0474	0.0118	174.5	384.5	0.029
Black-headed Grosbeak	0.2386	0.1465	162.5	372.5	0.030
Belted Kingfisher	0.0293	0.0091	189.0	399.0	0.041
Gray Catbird	0.1490	0.0763	172.5	382.5	0.047
Cedar Waxwing	0.3268	0.1940	172.0	382.0	0.050
Ruffed Grouse	0.0321	0.0056	203.5	413.5	0.058
Violet-green Swallow	0.2309	0.0971	179.0	389.0	0.059
Broad-tailed Hummingbird	0.0118	0.0022	213.0	423.0	0.096
MacGillivray's Warbler	0.0532	0.0149	196.0	406.0	0.107
Spotted Sandpiper	0.0302	0.0158	198.0	408.0	0.118
Swainson's Thrush	0.0403	0.0068	211.0	421.0	0.147
More Abundant in Grazed Areas					
House Wren	0.4621	1.1689	107.0	458.0	0.001
Mourning Dove	0.2488	0.5509	149.5	500.5	0.014
Pine Siskin	0.0044	0.0529	180.5	531.5	0.019
Black-billed Magpie	0.2475	0.4988	160.0	511.0	0.026
European Starling	0.3474	1.2135	163.5	514.5	0.032
Cassin's Finch	0.0201	0.0326	208.0	559.0	0.167
Missouri					
Less Abundant in Grazed Areas					
Mourning Dove	2.2941	0.7917	19.5	97.5	<0.001
American Robin	2.3824	1.0833	27.0	105.0	0.001
Red-eyed Vireo	0.7059	0.0417	45.5	123.5	0.004
Red-shafted Flicker	1.6765	0.4583	39.0	117.0	0.004
Least Flycatcher	2.1176	1.2083	43.5	121.5	0.008
Brown Thrasher	0.7059	0.1250	48.0	126.0	0.009
Western Wood-pewee	1.8824	1.0833	48.0	126.0	0.011
Lazuli Bunting	1.6765	0.9167	46.0	124.0	0.011
Ovenbird	0.4706	0.0000	60.0	138.0	0.013
House Wren	2.7647	2.0000	54.0	132.0	0.028
Black-headed Grosbeak	0.7353	0.1667	57.5	135.5	0.029
Bullock's Oriole	0.6471	0.2083	57.0	135.0	0.031

APPENDIX 5. CONTINUED

River system	Detection/survey		Mann-Whitney U-test		P
	Ungrazed	Grazed	U	W	
American Redstart	0.4706	0.0833	63.0	141.0	0.034
Yellow Warbler	3.7941	2.5833	58.0	136.0	0.047
Yellow-breasted Chat	2.8529	2.0417	59.0	137.0	0.051
Hairy Woodpecker	0.4118	0.0833	65.0	143.0	0.052
Gray Catbird	0.6176	0.1250	70.5	148.5	0.108
Common Grackle	0.6471	0.3333	76.5	154.5	0.132
Black-capped Chickadee	0.6471	0.2083	74.5	152.5	0.161
American Goldfinch	2.3529	1.5417	72.0	150.0	0.177
More Abundant in Grazed Areas					
Eastern Kingbird	0.1176	0.3333	67.0	220.0	0.048
Spotted Towhee	0.9706	1.3750	67.5	220.5	0.115
Hart					
Less Abundant in Grazed Areas					
Cordilleran Flycatcher	0.3333	0.0000	140.0	350.0	0.005
Hairy Woodpecker	0.4286	0.0500	130.5	340.5	0.005
Green-tailed Towhee	0.5714	0.1500	121.5	331.5	0.006
Rock Wren	0.2619	0.0000	170.0	380.0	0.043
Wilson's Warbler	0.2381	0.0500	170.5	380.5	0.092
Red-tailed Hawk	0.2857	0.1000	171.0	381.0	0.138
More Abundant in Grazed Areas					
Swainson's Thrush	0.1905	0.4000	160.0	391.0	0.091
Black-headed Grosbeak	0.3333	0.6500	154.0	385.0	0.094
Sheldon					
Less Abundant in Grazed Areas					
Western Wood-pewee	0.6000	0.0000	22.5	67.5	0.017
More Abundant in Grazed Areas					
Brewer's Sparrow	0.2000	0.7778	23.0	78.0	0.039
Yellow Warbler	0.3000	0.7778	27.0	82.0	0.096

Notes: Values are mean detections per survey, and results of Mann-Whitney U-test for differences between grazed and ungrazed. All species detected at least 15 times on a given river system with a $P < 0.2$ from a Mann-Whitney U-test are included.