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IMPORTANCE OF SPATIAL SCALE TO HABITAT USE BY BREEDING BIRDS IN RIPARIAN FORESTS: A HIERARCHICAL ANALYSIS

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Abstract. Patterns of habitat use by breeding birds were studied in cottonwood riparian forests along 100 km of the South Fork of the Snake River in southeastern Idaho, United States, from 1991 to 1994. A hierarchical approach was used to examine habitat use at three spatial scales: microhabitat (local vegetation characteristics), macrohabitat (cottonwood forest patch characteristics), and landscape (composition and patterning of surrounding [matrix] vegetation types and land uses). This paper addresses a series of predictions about species' distributions that incorporate the different spatial scales. Bird distribution and abundance and vegetation data were collected on 57 cottonwood forest patches ranging in size from 0.40 ha to 205 ha. The surrounding landscape changed from a valley surrounded by mountains, on the upstream end of the study area, to a narrow canyon adjacent to natural upland vegetation in the middle section, and to a wide, open floodplain dominated by agriculture on the downstream end. The best predictors of high species richness ($r^2 = 0.71$) were natural and heterogeneous landscapes, large cottonwood patches, close proximity to other cottonwood patches, and microhabitats with relatively open canopies. Distribution and frequency of occurrence were evaluated for 32 species of small land birds. The most frequent significant predictor of species occurrence was the landscape component: increases in upland natural vegetation with decreases in agriculture. Both interior and edge specialists were found in arid land, cottonwood riparian forests that are linear in nature, with large amounts of edge. Nest predators, brood parasites, and exotic species responded positively to human-altered landscapes. Landscape patterns were the primary influence on distribution and occurrence of most bird species, whereas macrohabitat and microhabitat were of secondary importance. Thus, surrounding landscape (matrix) features should be a primary consideration for selecting riparian reserve areas.

Key words: arid-land riparian fragments; bird abundance; bird–habitat relationships; breeding bird assemblages; cottonwood riparian birds; edge specialists; interior specialists; landscape patterns; spatial scale; species richness.

INTRODUCTION

Traditionally, ecologists frequently assumed that the most important ecological processes affecting populations and communities operated at local spatial scales (e.g., Bond 1957, Carothers et al. 1974, Urban and Smith 1989). Animal species richness and abundance often have been considered functions of variation in local resource availability, vegetation structure, and the size of the habitat patch (MacArthur and MacArthur 1961, Willson 1974, Cody 1985).

Recently, scientists have begun to realize that knowledge of structural features and local habitat may not be adequate to understand bird population dynamics, and that surrounding habitats also should be considered (e.g., Wiens 1989, Forman 1995, Freemark et al. 1995). Habitat variation exists at a variety of scales, and ecologists have become increasingly aware of the importance of examining ecological processes at spatial and temporal scales relevant to both the organisms and the processes under study (Wiens 1989, Allen and Hoekstra 1992, Forman 1995).

Biological components are sorted by processes nested within a spatial hierarchy of habitat units, or ''patches'' (Kolasa 1989, Kotliar and Wiens 1990). Hierarchical approaches are recommended for developing, evaluating, and implementing conservation or management plans (Freemark et al. 1995). Allen and Hoekstra (1992) argue that it is necessary to consider three scales at once: the one in question; the one below, which gives mechanisms; and the one above, which gives context. Landscapes surrounding habitat patches provide context. Habitats are distributed within landscapes and their spatial patterns may have a strong influence on the distribution, abundance, and dynamics of vertebrate populations inhabiting those landscapes (Wiens 1989).

Human activities that alter landscape patterning often have substantial effects on plant and animal communities. To the extent that some habitats, especially riparian forests, are lost in human-altered landscapes, so are the species that depend on them (Wilson 1988,

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Best et al. 1995). At the same time, organisms that adapt to human habitats are likely to expand and may become pests (Mooney and Drake 1986). Agricultural and residential development, interspersed with natural habitats, can attract nest predators, e.g., magpies and crows (Andren 1992), brood parasites, i.e., Brown-headed Cowbird [scientific names in Appendix A] (Robinson et al. 1995*a*), and exotic species that potentially compete with native species (Temple 1990).

Habitat fragmentation as a result of agricultural and urban development generally causes loss of bird species (e.g., Whitcomb et al. 1981, Lynch 1987, Robbins et al. 1989, Faaborg et al. 1995). Much attention has been given to evaluating the effects of fragmentation on breeding birds in eastern deciduous forests of North America (e.g., Galli et al. 1976, Whitcomb et al. 1981, Ambuel and Temple 1983, Robbins et al. 1989, Faaborg et al. 1995). Fragmentation effects on avian assemblages associated with streamside woodlands are relatively unknown (Stauffer and Best 1980, Gutzwiller and Anderson 1987*a*, *b*).

Island biogeography theory (MacArthur and Wilson 1967) has frequently been used to explain variation in species richness in habitat fragments that differ in area and isolation (e.g., Diamond 1975, Forman et al. 1976). Positive relationships between the species richness of habitat-interior birds and habitat patch area have been consistent with this model (e.g., Whitcomb et al. 1981, Ambel and Temple 1983, Robbins et al. 1989, Herkert 1994). Because small habitat patches have proportionately more edge than large habitat patches, biotic interactions (e.g., nest predation, brood parasitism, and competition) are expected to be more pronounced in small habitats, thus contributing to the ‘‘area effect’’ observed for many species in habitat mosaics (Urban and Shugart 1986).

Edge effects may be of less concern in riparian habitats of semiarid regions because of the very nature of these systems, which are long and narrow with large amounts of edge. The nature of adjacent habitat (e.g., riparian woodlands adjacent to aspen forests vs. riparian woodlands adjacent to agriculture) might be more important than the existence of forest edge per se (cf. Szaro and Jakel 1985, Martin 1988).

Riparian forests cover <1% of the landscape in arid portions of western North America (Knopf et al. 1988), yet more species of breeding birds are found in this limited habitat than in the extensive surrounding uplands (e.g., Ohmart and Anderson 1986, Knopf et al. 1988). Several studies have evaluated bird–habitat relationships in riparian forests of western North America (e.g., Finch 1989, Sedgwick and Knopf 1990, Strong and Bock 1990), but no prior study has investigated the relative importance of several spatial scales to habitat use by breeding birds (but see Gutzwiller and Anderson 1987*a*, *b*). Because riparian habitats in arid lands have unique features among forests (i.e., long, narrow shapes with large amounts of edge), adjacent landscape patterns might be particularly important to avian community structure.

In this study, I designed a hierarchical approach to examining the patterns of habitat use by breeding birds in cottonwood riparian forests in southeastern Idaho. Habitat use was evaluated at three spatial scales: microhabitat (local vegetation characteristics), macrohabitat (cottonwood forest patch characteristics such as size, length, and width), and landscape (composition and structure of vegetation and land uses surrounding forest patches [matrix habitats]). I addressed a series of predictions that incorporated these different spatial scales:

1) Riparian forests in arid lands are linear elements fragmented and surrounded by a matrix of other habitats; therefore, landscape features surrounding these habitats, rather than microhabitat or macrohabitat, will be the most important and frequent predictors of bird distribution and abundance.

2) Nest predators (i.e., corvids), brood parasites (i.e., cowbirds), and exotic species (i.e., starlings) will respond positively to human-altered landscapes.

3) Species–area relationships (i.e., species richness in large patches is greater than in small patches) will exist in naturally fragmented and human-altered riparian forests. Some species will be large patch/interior specialists, whereas others will be small patch/edge specialists.

4) Cottonwood patches surrounded by natural landscapes will have higher species richness of native birds than cottonwood patches surrounded by agricultural landscapes.

5) Cottonwood patches in close proximity to other cottonwood patches will have higher avian species richness than isolated patches that are distant to other cottonwood patches.

STUDY AREA AND METHODS

The study area encompassed the cottonwood (*Populus angustifolia*) riparian forests along 100 km of the South Fork of the Snake River (South Fork) in southeastern Idaho, United States (Fig. 1). The South Fork supports the most extensive cottonwood gallery forest remaining in Idaho and probably the largest such ecosystem in the Intermountain West (Palmer 1991). Elevation ranges from 1700 m on the upstream end to 1460 m on the downstream end.

The surrounding landscape changes from a valley surrounded by mountains on the upstream end of the study area, to a narrow canyon adjacent to natural upland vegetation in the middle section, to a wide, flat floodplain dominated by agriculture on the downstream end (see Fig. 1). Cottonwood fragments vary in size (<1 ha to >200 ha), width (<40 m to >1 km), and shape (long and linear to short and round). Inspection of 1:12 000 and 1:24 000 aerial photographs from the 1940s revealed that, prior to extensive agricultural development and water impoundments (including a large

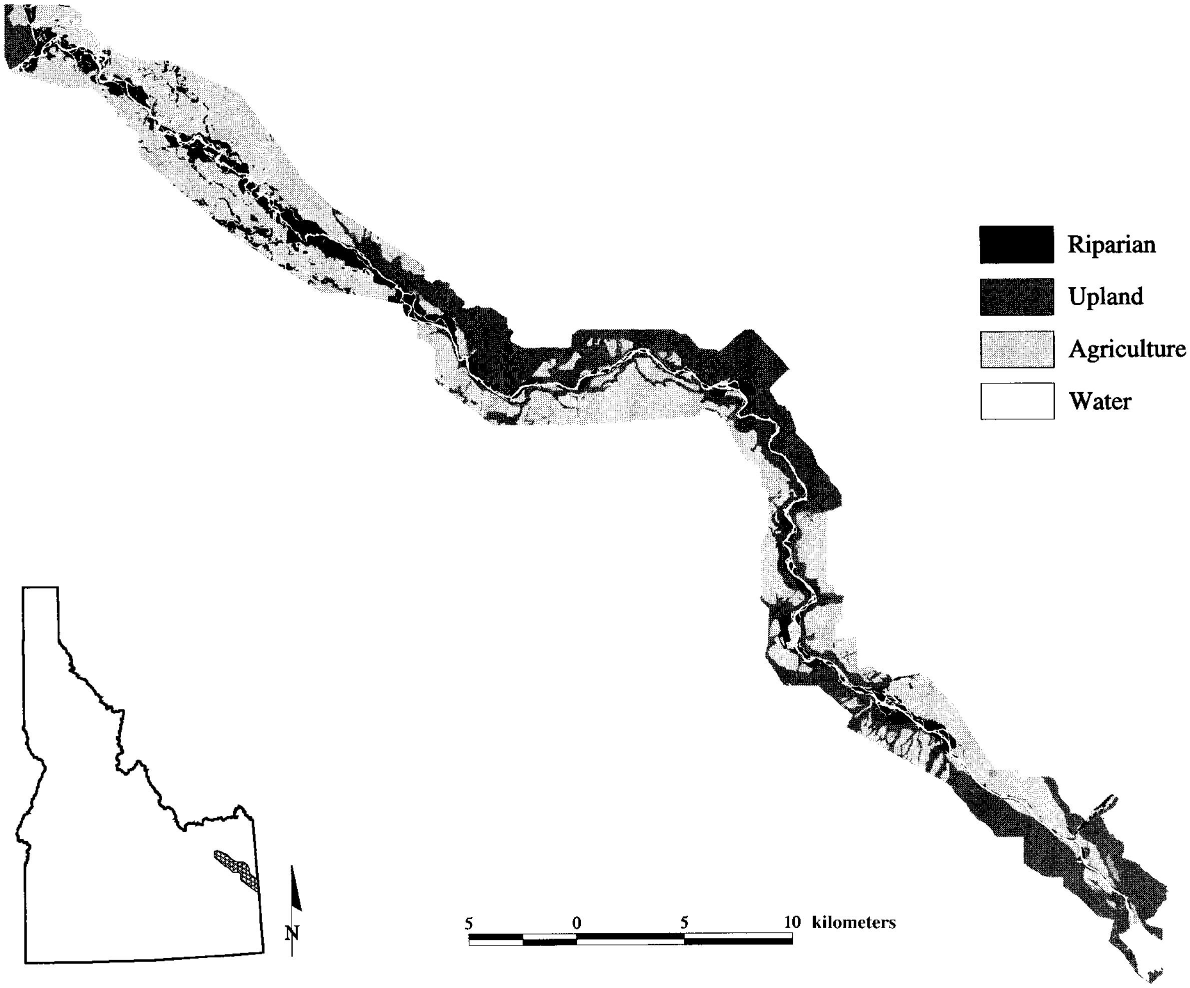

FIG. 1. Location and general landscape classes of the cottonwood riparian study area, South Fork of the Snake River, Idaho, United States. The upstream end of the study area is in the bottom right, and the downstream end is in the upper left of the figure.

dam that controls the flow regime of the river), cottonwood forests were >2 km wide in the broad floodplain along the downstream section. Flood control since dam closure has reduced new stream deposits suitable for cottonwood regeneration, and cottonwood forest area has declined and become proportionately older (Merigliano 1996). Currently, the largest remaining cottonwood forests are found in the downstream area, where flat terrain provides the best conditions for both agricultural development and extensive cottonwood forests.

The streamside vegetation is dominated by narrowleaf cottonwoods in the canopy, with the woody understory vegetation composed primarily of red-stemmed dogwood (*Cornus stolonifera*), thin-leaved alder (*Alnus incana*), water birch (*Betula occidentalis*), and willows (*Salix* spp.). Adjacent uplands include habitats of Douglas-fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), juniper (*Juniperus osteosperma*)/sagebrush (*Artemisia* spp.) along the upstream end, and agriculture (croplands of potatoes, wheat, and alfalfa) dominating the downstream/wide floodplain section. The stream corridor is managed for irrigation, power generation, flood control, recreation, and livestock grazing (Saab 1996).

Study sites

Study sites were 57 cottonwood forest patches, located along a 100-km section of the South Fork. Cottonwood patch sizes ranged from 0.4 ha to 206 ha. More than half (54%) of the cottonwood patches were created as a result of agricultural development; the remaining patches were created by river channels. To determine patch size, age of cottonwood stand (young, mature, old), and spatial patterns of cottonwood forests and surrounding patch types, 1987 aerial photographs (1:12 000 and 1:24 000) were interpreted and land class coverages were digitized using ARC-INFO, a Geographic Information System (GIS). All study sites were located in mature cottonwood stands and were isolated from other mature cottonwood stands by ≥100 m.

Bird surveys

Relative bird abundance was quantified using point-count surveys (Ralph et al. 1993) in 40-m fixed-radius circular sampling stations (cf. Szaro and Jakle 1985) that were placed ≥20 m from a forest edge or in the center of cottonwood patches. Circles of 40 m radius were selected because the smallest cottonwood patches approximated this width. The number of circular sampling stations varied depending on the area of the cottonwood patch, from one on sites <4 ha to as many as six on a site >200 ha. On sites with more than one sampling station, station centers were separated by ≥150 m. In total, 153 stations were sampled in this study. For 2 wk prior to data collection, observers were trained to estimate distances to the sight and sound of birds. Observers surveyed birds for 10 min per visit at each station. Each station was visited twice during the 1991 breeding season (from 6 June to 15 July) and three times during 1992–1994 (from 15 May to 15 July). Bird counts were conducted by two people during 1991 and by three people during other years (1992–1994). Each observer visited every station in each season in an attempt to minimize observer effects (Ralph et al. 1993). Bird surveys were conducted between 0600 and 1100 and were confined to days with good weather (wind <32 km/h and light or no precipitation). To reduce the bias of surveying at different periods of the breeding season, the first survey was conducted 15 May–4 June, the second survey June 5–24, and the third survey 25 June–15 July of each year. The total number of species, the number of individuals of each species, and the total number of individuals were recorded for each circular sampling station.

The survey detected 97 species (Appendix A), 65 of which were found on fewer than 12 cottonwood patches during all years and were included only in estimates of total species. Data collected for 32 species of small land birds were used for all analyses (Appendix A), and these species were recorded at a minimum of 12 cottonwood patches.

Habitat measurements

Microhabitat measurements (local vegetation characteristics) were collected during 1991 and 1992 at the 153 40 m radius (0.5 ha) circular sampling stations used for bird surveys (Tables 1 and 2). Within each 0.5-ha sampling station, estimates of vegetation structure and composition were made in four 5 m radius subcircles (0.008 ha). The initial subcircle was located at the center of the sampling station. The center of the next subcircle was located at a random compass direction and a fixed distance of 29 m from the station center. Each of the two remaining subcircles was positioned 120° from the first subcircle (cf. Ralph et al. 1993).

Stem densities of trees and shrubs were recorded by species and diameter size class at breast height. Woody vegetation was grouped into stem dbh classes as follows: ≤2 cm, >2–5 cm, and >5–8 cm within the 5 m radius subcircle; and >8–23 cm, >23–38 cm, and >38 cm within a 11.3 m radius circle extended from the 5 m radius plot. Tree canopy was measured by using a densiometer at the center of each subcircle.

Ground cover was estimated within 0.5 m above ground on the 5 m radius subcircles by using an ocular tube. Ten readings were taken along transects using tape measures oriented parallel to the stream channel and the other perpendicular, such that they crossed at the center of the subcircle. At 2-m intervals along each tape, the ground cover was estimated as percentages of shrub, herbaceous, bare ground, or litter cover.

Macrohabitat and landscape measurements (Table 1) were determined from ARC-INFO files by using the landscape metrics software FRAGSTATS (McGarigal and Marks 1995). Macrohabitat variables were measured to describe cottonwood patch characteristics of size, shape, and edge. I used a conservative 100-m buffer to determine core area for each patch, because changes in microclimate conditions can extend >240 m into forested habitats adjacent to unforested habitats (cf. Chen et al. 1995), although nest predation and parasitism rates are generally highest within 50 m of habitat edge (Paton 1994).

Landscape variables were measured within 1.0 km of the edge of the 57 cottonwood patches. Measurements from the edge, rather than the center of the patch, were used to exclude the area of the patch of interest, because that measurement was included as a macrohabitat feature. Thus, landscape coverages varied in size (3.1–14.4 km^2), depending on cottonwood patch area. The areas covered in the landscapes encompassed the home range/territory sizes of most songbirds in the Northwest (see Hansen and Urban 1992), although cowbirds (Rothstein et al. 1984) and corvids (Andren 1992) might range farther.

The percentage occupied by each of 10 patch types was determined for landscape composition surrounding each sampled cottonwood site. The 10 patch types were residential, agriculture, upland shrubs (primarily *Artemisia* spp., *Prunus* spp., *Amelanchier* spp.), aspen, Douglas-fir, juniper, river, herbaceous wetlands (primarily *Carex* spp., *Scirpus* spp., *Typha* spp.), shrub wetlands (*Salix* spp.), and cottonwood. For a measure of landscape heterogeneity surrounding each sampled cottonwood patch, I calculated Simpson's diversity index, relative patch richness, Simpson's eveness index, and an interspersion index shown in Tables 1 and 2 (see McGarigal and Marks 1995). Landscape structural metrics included distance to contiguous cottonwood forest (adjacent to the river), mean distance to the nearest cottonwood patch neighbor, and landscape edge contrast.

TABLE 1. Habitat variables that were recorded for each circular plot (microhabitat), each cottonwood patch (macrohabitat), and landscapes surrounding each cottonwood patch.

Variables	Description
Microhabitat	
Stem density of trees and shrubs (no./ha)	Recorded by structure (dbh size class: ≤2, >2–5, >5–8, >8–23, >23–38, >38 cm) and species composition.
Tree canopy cover (%)	Recorded for all plant species (structure) and individually by plant species (composition).
Ground cover (%)	Recorded as herbaceous, shrub, down log, or bare ground (structure).
Macrohabitat	
Patch size of cottonwood stand (ha)	
Perimeter to area ratio (m/ha)	Index of amount of edge.
Length of cottonwood patch (m)	
Width of cottonwood patch (m)	Averaged over three measurements.
Patch edge contrast index (%)	Percent of edge involving the sampled cottonwood patch weighted by degree of structural and floristic contrast between adjacent patches; equals 100% when all edge is maximum contrast (e.g., cottonwood vs. agriculture) and approaches 0 when all edge is minimum contrast (e.g., cottonwood vs. aspen).
Core area (ha)	Amount of core area of each sampled cottonwood patch defined by eliminating a 100 m wide buffer along the perimeter of each patch.
Landscape	
Composition	
Percentage of landscape	Percentage of landscape (within 1.0 km of edge of sampled cottonwood patches) composed of corresponding patch types.
Simpson's diversity index (0–1)	Represents probability that any patch types selected at random (within 1 km of each sampled cottonwood patch) would be different patch types; the higher the value the greater the likelihood that any two randomly drawn patches would be different patch types (i.e., greater diversity).
Relative patch richness (%)	Patch richness as a percentage of the maximum potential richness, which includes 10 patch types within 1 km of each sampled cottonwood patch.
Simpson's evenness index (0–1)	Represents distribution of area among patch types within 1 km of each sampled cottonwood patch; larger values imply greater landscape diversity; maximum diversity for any level of richness is based on an equal distribution among patch types.
Interspersion index (%)	Measures extent to which patch types are interspersed; higher values result from landscapes in which patch types are well interspersed (i.e., equally adjacent to each other and greater landscape heterogeneity), whereas lower values characterize landscapes in which patch types are poorly interspersed with a disproportionate distribution of patch type adjacencies.
Structure	
Distance to contiguous cottonwood forest (m)	Mean distance from edge of sampled cottonwood patches to edge of contiguous cottonwood forests adjacent to river.
Distance to nearest cottonwood neighbor (m)	Mean distance from edge of sampled cottonwood patches (mature stands only) to edges of nearest cottonwood patches (including young, mature, and old stands of cottonwoods).
Landscape edge contrast index (m/ha)	Density of edge involving all corresponding patch types (within 1 km of sampled cottonwood patches) weighted by degree of contrast between adjacent patches; approaches 0 when all edge is minimum contrast.

Analyses

For each bird species, I calculated an index of occurrence for each cottonwood patch to serve as the dependent variable in the analyses of bird–habitat relationships. In this calculation, the dependent variable assumed a value of ''0'' if the species was not detected on a visit to the sampling station, and ''1'' every time it was detected on a single visit (cf. Robbins et al. 1989). Most sampling stations were visited 11 times over four breeding seasons, and data for all years were combined because the coefficient of variation for individual species' abundances and species turnover rates did not differ statistically among years (Saab 1996). To account for potential biases created by having different numbers of sample stations per patch, the mean number of occurrences observed among all stations surveyed within each cottonwood patch was used to calculate a species' frequency of occurrence for a single patch. For example, if an individual was recorded once across all visits on each of six sampling stations within a large cottonwood patch, the index of occurrence would be calculated by taking six observations divided

TABLE 2. Summary statistics on microhabitat, macrohabitat, and landscape characteristics for 57 cottonwood patches along a 100-km section of the South Fork of the Snake River in Jefferson and Madison Counties, Idaho, 1991–1992.

Scale	Units	Minimum	Maximum	Mean	1 SE
Microhabitat					
Stems <2 cm	no./ha	0	53 721.25	17 295.00	1 301.61
Stems 2–5 cm	no./ha	0	2 253.75	762.50	80.72
Stems >5–8 cm	no./ha	0	665.00	132.50	21.23
Stems >8–23 cm	no./ha	1.00	37.20	9.14	0.94
Stems >23–38 cm	no./ha	0.38	21.40	8.24	0.56
Stems >38 cm	no./ha	0	13.80	5.20	0.36
Canopy	%	26.14	95.05	65.31	2.07
Bare ground	%	0	58.75	9.80	1.63
Herbaceous cover	%	0.70	75.83	23.20	1.98
Shrub cover	%	0	28.03	10.12	0.88
Down logs	%	0	10.00	1.90	0.25
Litter	%	30.00	87.05	59.30	1.85
Alder stem densities	no./ha	0	61.66	4.60	1.41
Birch stem densities	no./ha	0	213.06	28.09	6.46
Dogwood stem densities	no./ha	0	26 196.25	10 060.00	1 033.19
Hawthorn stem densities	no./ha	0	4 875.00	251.14	95.16
Silverberry stem densities	no./ha	0	11 208.75	1 472.21	307.17
Juniper stem densities	no./ha	0	66.00	4.44	1.27
Cottonwood stem densities	no./ha	8.16	155.20	30.38	2.96
Willow stem densities	no./ha	0	8 487.50	1 903.75	250.95
Clematis stem densities	no./ha	0	31 500.00	6 618.75	1 107.09
Dogwood subcanopy	%	0	80.68	12.33	2.55
Cottonwood canopy	%	26.14	93.75	56.68	2.08
Willow canopy	%	0	97.66	6.99	2.09
Macrohabitat					
Patch size	ha	0.40	204.83	14.61	4.45
Perimeter: area	m/ha	140.01	813.65	408.87	23.39
Length	m	62.00	3 461.00	767.02	115.35
Width	m	39.00	667.00	138.02	19.92
Patch edge contrast	%	49.30	100.00	81.38	1.70
Core area	ha	0	10.20	1.32	0.24
Landscape					
Residential	%	0	8.02	0.59	0.22
Agriculture	%	4.43	94.52	44.13	2.72
Upland shrubs	%	0	54.85	16.03	2.23
Aspen	%	0	23.08	3.71	0.75
Douglas-fir	%	0	19.21	3.72	0.70
Juniper	%	0	29.73	2.87	0.81
River	%	0.50	15.53	8.44	0.47
Herbaceous wetlands	%	0	10.38	2.78	0.32
Shrub wetlands	%	0	13.87	4.47	0.41
Cottonwood	%	0.07	37.63	12.89	1.26
Simpson's diversity index	0–1	0.11	0.84	0.66	0.02
Relative patch richness	%	45.46	100.00	74.01	2.27
Simpson's evenness index	0–1	0.13	0.94	0.76	0.02
Interspersion index	%	31.28	82.32	70.15	1.10
Distance to contiguous cottonwoods	m	0	886.00	93.89	23.56
Distance to nearest neighbor	m	17.05	937.23	100.72	18.56
Landscape edge contrast	m/ha	25.23	126.38	79.14	2.64

by a possible 66 visits at that particular patch, for a mean of 0.09. This frequency of occurrence would be equal to that on a small patch with one sampling station where an individual is recorded once across all 11 visits, for a mean of 0.09.

More individuals were usually encountered in large patches than in small patches, because large patches had more sampling stations. To control for differences in the number of individuals surveyed among patch sizes, rarefaction (James and Rathbun 1981) was used to examine differences in the total number of species among patch sizes. Rarefaction standardizes samples to the number of species expected based on equal numbers of individuals surveyed in equal-sized patches (James and Rathbun 1981).

I used principal components analyses, PCA (PROC FACTOR METHOD=PRIN; SAS Institute 1990), to reduce 46 habitat variables and because several variables within each habitat scale were correlated. PCA was performed twice to derive habitat principal components from the original variables: once for 23 microhabitat variables and once for 23 macrohabitat/landscape variables. Components were rotated using PROMAX (SAS Institute 1990). The habitat components derived from the PCAs were used as the predictor (independent) variables; frequency of occurrence of individual bird species and bird species richness within a patch were the response (dependent) variables.

Multiple linear regression (SAS Institute 1990) was used to identify habitat characteristics that best predicted avian species richness. Logistic regression was used to examine the strength and nature of the relationship between habitat components (derived from the PCA) and bird frequency of occurrence. Within one habitat component, slope parameters (derived from logistic regression) allowed comparison of the relative strength of the habitat relationship among species, where the set of available habitats was the same for all species. Using logistic regression, I also determined standardized estimates of the slope parameters for each habitat component. Standarized estimates are used to determine the probability that a randomly selected resource unit will be in component i if all components are equally abundant in the original population of available resource units (Manly et al. 1993). For an individual species, standarized estimates allowed comparison of relative selection among habitat components and spatial scales.

RESULTS

Bird occurrence

Over a 4-yr period, observers recorded 18 675 bird detections (individuals) representing 97 species (Appendix A) during 1565 visits distributed over 153 sampling stations placed among 57 cottonwood patches. Of these detections, 87% ($n = 16\,247$) were of 32 species occurring on at least 12 patches and known to nest in the study area (Appendix B). Bird species richness per patch averaged 29 species for all 57 cottonwood patches, with a range of 6–51 species. After using rarefaction, species richness ranged from 16 to 29 species for the 51 patches with large enough sample sizes to predict an expected number of species, given an equal number (100) of individuals sampled.

Distribution and abundance varied greatly among species. Yellow Warblers and American Robins were the most abundant and widespread species in the study area, recorded in all 57 patches and at every sampling station (Appendix B). Other widely distributed species, recorded on at least 44 patches, included Brown-headed Cowbirds, Black-billed Magpies, and European Starlings. Eastern Kingbird, Yellow-breasted Chat, Swainson’s Thrush, Cassin’s Finch, and Fox Sparrow were breeding birds with narrow or patchy distributions within the study area.

Habitat

Local vegetation was characterized by a cottonwood canopy, dogwood subcanopy, and plant litter at ground level (Table 2). Cottonwood patch size averaged ~15 ha (Table 2), with size distributions of 43 patches ≤10 ha, 7 patches >10 to ≤50 ha, and 7 patches >50–205 ha. Long, narrow shapes with relatively large amounts of edge characterized cottonwood patches, indicated by the mean values of perimeter to area ratio, length, width, and core area (Table 2). On average, surrounding landscapes were relatively heterogeneous, based on patch diversity, richness, evenness, and interspersion indices (Table 2). Some percentage of agriculture was adjacent to every cottonwood patch (Table 2), and it was the dominant feature in the surrounding landscape.

Six principal components for microhabitat variables and six components for macrohabitat/landscape variables were judged meaningful by the scree criterion (SAS Institute 1990) and with eigenvalues above one (Tables 3 and 4). Each of the components loaded mainly on a set of conceptually interrelated original variables that were descriptive of microhabitat, macrohabitat, or landscapes. Thus, these components were easily interpretable in biologically meaningful terms, and I named them accordingly (Tables 3 and 4).

Of the total variance in the microhabitat variables, 64% was explained by six selected components (Table 3). The first microhabitat principal component (M-PC1) described a gradient in *cottonwood densities and canopy.* Microhabitats positively associated with M-PC1 contained high densities of cottonwood trees and relatively closed canopies compared to average microhabitat features. The second principal component (M-PC2) represented a gradient in ground cover from herbaceous vegetation to litter (*herb cover vs. litter*). Microhabitats positively associated with M-PC2 were characterized by relatively large amounts of herbaceous cover, little plant litter, and a greater than average willow canopy. The third principal component (M-PC3) represented a gradient in *shrub densities and cover,* including stem densities of the vine *Clematis* spp. Microhabitats positively associated with M-PC3 contained a dense shrub layer in the understory. The fourth principal component (M-PC4) described a gradient of *willow densities and canopy.* Local habitats positively related with M-PC4 had high densities and canopies of willow, with little bare ground. *Birch and small-tree densities* represented the fifth principal component (M-PC5); microhabitats positively associated with this component were characterized by a subcanopy of birch and other relatively small trees. The sixth principal component (M-PC6) described a gradient in *juniper and silverberry densities.* Microhabitats positively related to M-PC6 contained high stem densities of silverberry and juniper in the subcanopy/canopy and low coverage of dogwood in the subcanopy. Interfactor correlations were low (0.04–0.25) among microhabitat components, except for a negative correlation (−0.35) between M-PC2 (*herb vs. litter cover*) and M-PC4 (*willow densities and canopy*).

Of the total variance in the landscape/macrohabitat variables, 80% was explained by six components (Table 4). The first principal component (L-PC1) represented

TABLE 3. Principal component loadings for microhabitat variables measured at 57 cottonwood forest patches. The principal components were rotated with the promax method (SAS Institute 1990).

Variables	M-PC1 Cottonwood densities and canopy	M-PC2 Herb vs. litter cover	M-PC3 Shrub densities and cover	M-PC4 Willow densities and canopy	M-PC5 Birch and small tree densities	M-PC6 Juniper and silverberry densities
Percentage explained†	20.0	13.3	9.5	7.4	7.1	6.4
Microhabitat structure						
Stems <2 cm	0.06	0.16	0.80	0.04	0.12	0.26
Stems 2–5 cm	−0.11	−0.49	0.19	0.21	0.48	−0.23
Stems >5–8 cm	0.31	0.06	0.08	−0.01	0.91	−0.12
Stems >8–23 cm	0.90	−0.08	0.06	0.18	0.37	0.24
Stems >23–38 cm	0.82	−0.08	−0.01	0.24	−0.28	−0.04
Stems >38 cm	0.27	0.34	−0.18	−0.31	−0.00	−0.36
Canopy	0.59	−0.15	−0.08	−0.28	−0.02	−0.46
Bare ground	−0.02	0.03	−0.42	−0.59	0.30	−0.09
Herbaceous cover	−0.05	0.88	−0.05	0.17	0.06	−0.09
Shrub cover	0.06	−0.10	0.74	0.05	0.06	−0.17
Down logs	−0.50	0.00	−0.17	0.20	−0.11	−0.05
Litter	0.17	−0.77	−0.17	0.22	−0.22	0.13
Microhabitat composition						
Alder stem densities	−0.13	0.02	−0.04	0.37	0.08	−0.17
Birch stem densities	−0.14	0.18	−0.02	−0.13	0.76	0.07
Dogwood stem densities	−0.35	−0.33	0.15	0.34	0.12	−0.05
Hawthorn stem densities	−0.12	0.06	0.45	−0.40	−0.29	−0.09
Silverberry stem densities	−0.05	−0.29	0.07	−0.04	−0.21	0.67
Juniper stem densities	0.22	−0.09	0.03	−0.30	0.03	0.67
Cottonwood stem densities	0.87	−0.07	−0.09	0.06	0.13	0.16
Willow stem densities	0.06	−0.17	0.01	0.65	−0.05	−0.14
Clematis stem densities	0.18	0.31	0.70	−0.16	−0.16	0.27
Dogwood subcanopy	−0.09	−0.22	0.11	0.38	−0.12	−0.51
Cottonwood canopy	0.52	−0.11	−0.05	−0.42	−0.23	−0.23
Willow canopy	0.20	0.52	−0.04	0.83	−0.06	−0.26

Note: Variables with high positive or high negative loadings are underlined to indicate the ''named'' principal component.
† Percentage of total variance explained by the rotated principal components.

a gradient of upland natural landscapes to agricultural landscapes (*upland natural vs. agricultural landscapes*). Landscapes positively associated with L-PC1 contained a high percentage of upland shrubs, aspen, and Douglas-fir communities; a low percentage of cottonwood communities, agriculture, and herbaceous wetlands compared to the average landscape; and cottonwood patches with low edge contrasts and little core area compared to the average macrohabitat. Cottonwood forest communities and agriculture (at the landscape level) and core area of cottonwood patches (at the macrohabitat level) had high negative loadings on this component (L-PC1), indicating that these variables were highly correlated. Suitable terrain of a wide, flat floodplain in the downstream portion of the study area allowed for extensive development of cottonwood forests and was also the most suitable topography for agricultural development. The second principal component (L-PC2) described a gradient in *landscape heterogeneity with wetlands.* Landscapes postively related to L-PC2 were characterized by adjacent patch types with high edge contrast, high patch diversity, evenness, and interspersion; high percentages of river, herbaceous and shrub wetlands; low percentages of agriculture; and study site cottonwood patches in close proximity to contiguous cottonwood forest. The third principal component (L-PC3) represented a gradient in patch size and edge (*patch size vs. edge*). Cottonwood patches (i.e., macrohabitats) positively associated with L-PC3 were relatively large, with small amounts of edge habitat.

The fourth principal component (L-PC4) describing landscapes represented an independent gradient in *juniper* communities. Landscapes positively associated with L-PC4 contained high percentages of juniper patches, and patch types were not well interspersed. The fifth component (L-PC5) described an independent gradient in *residential* areas with patch edge contrast. Landscapes positively associated with L-PC5 included a relatively high percentage of residential areas, and sampled cottonwood patches were in high edge contrast with adjacent patch types. The sixth principal component (L-PC6) represented a gradient in distance to the nearest cottonwood neighbor (*nearest neighbor*) and aspen communities. Cottonwood patches positively associated with L-PC6 were in close proximity to other cottonwood patches, and landscapes surrounding those patches contained high percentages of aspen communities. Among all landscape components, the only interfactor correlation was low (0.29) and was exhibited between L-PC2 (*landscape heterogeneity with wetlands*) and L-PC4 (*juniper*).

TABLE 4. Principal component loadings for macrohabitat and landscape variables measured at 57 cottonwood forest patches. The principal components were rotated with the promax method (SAS Institute 1990).

Variables	L-PC1 Upland natural vs. agricultural landscape	L-PC2 Landscape heterogeneity with wetlands	L-PC3 Patch size vs. edge	L-PC4 Juniper	L-PC5 Residential with edge contrast	L-PC6 Nearest cottonwood patch neighbor
Percentage explained	29.4	18.7	13.0	7.2	6.3	5.0
Macrohabitat						
Patch size	−0.09	−0.06	0.91	0.06	−0.08	0.05
Perimeter: area	0.10	−0.26	−0.64	0.11	−0.16	0.25
Length	0.24	−0.05	0.85	0.04	−0.02	−0.12
Width	−0.16	0.05	0.88	−0.08	−0.15	0.02
Patch edge contrast	−0.64	0.04	−0.02	−0.16	0.66	0.20
Core area	−0.71	0.02	0.36	0.19	0.13	0.19
Landscape composition						
Residential	0.15	0.13	0.03	−0.10	0.78	−0.11
Agriculture	−0.57	−0.52	0.09	−0.32	−0.02	−0.09
Upland shrubs	0.86	0.09	0.01	0.09	0.06	−0.02
Aspen	0.58	0.21	−0.18	−0.03	−0.04	0.53
Douglas-fir	0.73	0.11	−0.06	−0.16	0.21	0.18
Juniper	−0.19	−0.01	−0.05	0.94	−0.10	−0.12
River	−0.13	0.87	0.10	−0.40	−0.14	0.04
Herbaceous wetlands	−0.58	0.45	−0.24	0.29	−0.09	−0.27
Shrub wetlands	−0.12	0.39	0.19	−0.08	−0.67	0.19
Cottonwood	−0.95	0.20	−0.08	0.15	0.03	−0.11
Simpson's diversity index	0.30	0.72	0.07	0.29	0.02	0.02
Patch richness	0.59	0.06	0.13	0.51	0.05	0.01
Simpson's evenness index	0.23	0.81	0.04	0.21	0.02	0.01
Interspersion index	0.14	0.79	−0.07	−0.52	−0.01	−0.28
Landscape structure						
Distance to contiguous cottonwoods	−0.12	−0.77	−0.24	−0.07	−0.13	−0.02
Nearest neighbor	0.14	0.04	−0.09	−0.10	−0.11	0.89
Landscape edge contrast	−0.30	0.89	−0.14	0.10	−0.03	0.13

Bird–habitat relationships

Species richness.—Based on multiple linear regression, five components were significantly related to predicted bird species richness within cottonwood patches ($r^2 = 0.71$, $F_{12,38} = 7.73$, $P = 0.0001$). The best predictors, listed in decreasing order of the significance of their regression coefficient (t statistic) in the model, were patches with the following characteristics: (1) adjacent to natural landscapes, L-PC1 ($t = 4.2$, $P = 0.0001$); (2) surrounded by heterogeneous landscapes with river and wetlands, L-PC2 ($t = 2.9$, $P = 0.006$); (3) large cottonwood patch size, L-PC3 ($t = 2.7$, $P = 0.01$); (4) in close proximity to other cottonwood patches, L-PC6 ($t = -2.22$, $P = 0.03$); and (5) microhabitats with open canopies, M-PC1 ($t = -2.2$, $P = 0.04$).

Macrohabitat and landscapes.—Logistic regression was used to examine the relationship between patch/landscape components and frequency of occurrence for each of 32 bird species. Figure 2 indicates that the most frequent significant predictor of species' occurrence (22 species) was L-PC1, increases in upland natural vegetation with decreases in agriculture. The fewest species (seven) responded to the juniper component (L-PC4). Three species (Eastern Kingbird, Cedar Waxwing, and Black-headed Grosbeak) did not respond to any landscape feature.

Among 11 species exhibiting significant positive associations to L-PC1, Swainson's Thrush had the strongest relationship with natural landscapes (Fig. 2A). In contrast, Western Wood-Pewee had the strongest negative relationship with this component, suggesting that this species is strongly associated with agricultural landscapes that include extensive cottonwood forests. Western Wood-Pewees also had a negative relationship with L-PC2, providing further evidence for their positive association with agriculture.

Heterogeneous landscapes with large amounts of river and wetland vegetation (L-PC2) were good predictors of three species, whereas seven species had significant negative associations with this component (Fig. 2B). Cassin's Finch, an uplands associate, had the strongest negative relationship with L-PC2, whereas Yellow Warbler, a wetlands associate, had the strongest positive relationship.

In this riparian system, six species were large-patch associates and were considered to be interior specialists, whereas seven species showed significant relationships with edge habitats (Fig. 2C). At one extreme were Yellow Warblers and Song Sparrows, which were small-patch, edge specialists, and at the other extreme were Yellow-rumped Warblers and Dusky Flycatchers, which appeared to be area-sensitive, interior specialists.

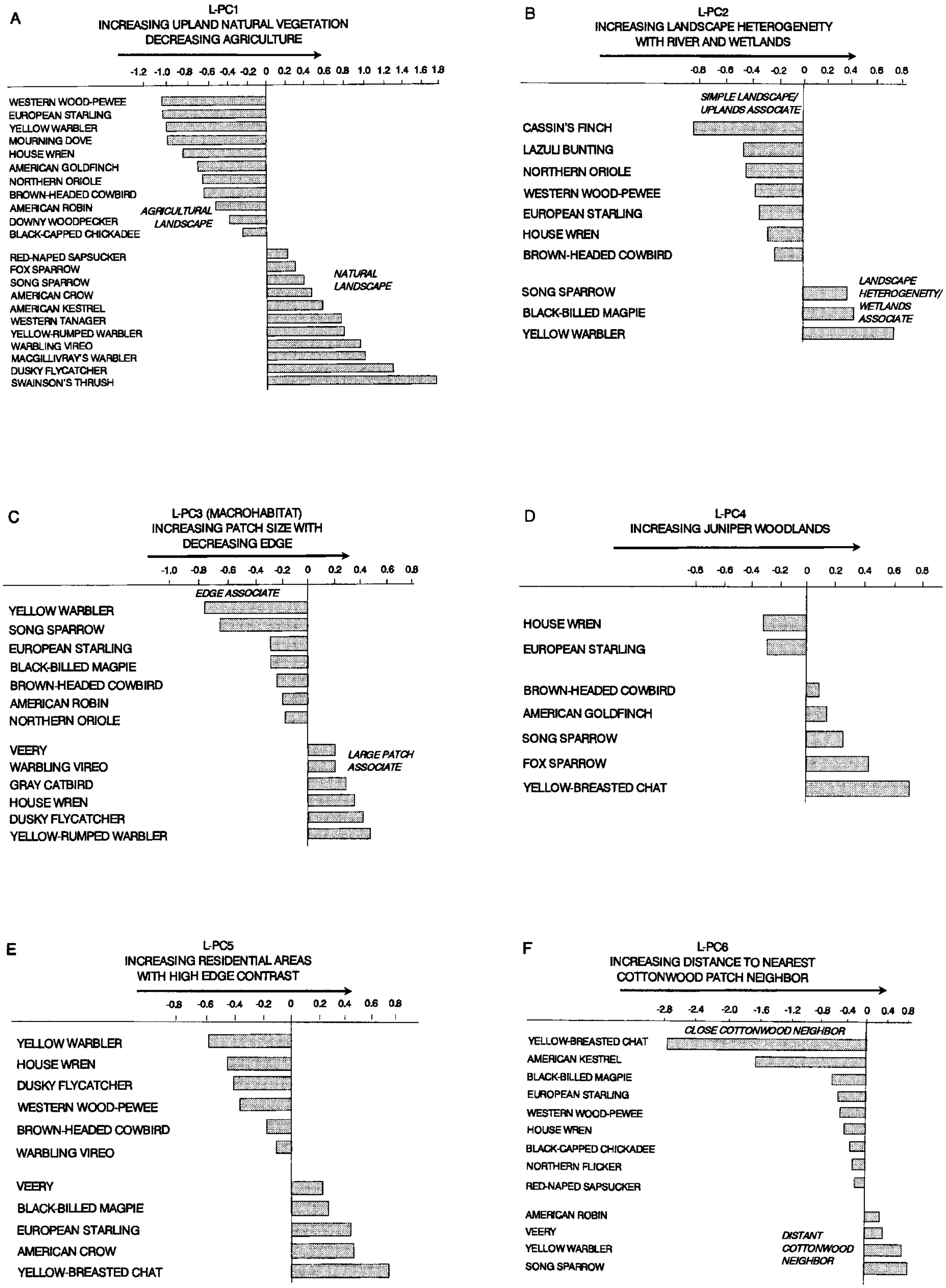

FIG. 2. Strength and nature of significant bird–habitat relationships, based on slope parameters derived from logistic regression for landscape and macrohabitat components. Bars represent parameter estimates for each species, showing the relative distance from zero, where there would be no significant relationship with habitat components.

Probability of occurrence adjacent to residential areas (L-PC5) was significant for five species including American Crows, European Starlings, and Black-billed Magpies (Fig. 2E). Six species apparently avoided cottonwood patches near residences. The component describing residential areas also loaded high on patch edge contrast, which might explain why Veeries and Yellow-breasted Chats were positively associated with this component (Fig. 2E). Both of these species were strongly associated with shrubby subcanopies of willows and birch, respectively (Fig. 3D, E). Adjacent macrohabitats of willow and birch provided high edge contrast to cottonwood patches and were probably attractive to Veery and Yellow-breasted Chat.

Thirteen species showed significant relationships with nearest cottonwood patch neighbor. Yellow-breasted Chat had the strongest positive relationship with this component (Fig. 2F). Six of nine species positively related to nearest neighbor were cavity-nesting birds. Perhaps the distribution of suitable cavity trees may be clustered and limited in availability within cottonwood patches. Song Sparrow had the strongest negative relationship with nearest neighbor.

Microhabitat.—Among microhabitat components, M-PC4, increasing willow densities with decreasing bare ground, was the most frequent significant predictor of species occurrence (20 species), whereas the fewest species (eight) responded to M-PC5, increasing birch densities (Fig. 3).

Among 11 species with positive relationships to M-PC4, Swainson's Thrush had the strongest association with increasing willow densities and decreasing bare ground (Fig. 3D). In contrast, American Kestrel had the strongest negative relationship with M-PC4, suggesting that this species used microhabitats with bare ground and open understories.

Only two species (House Wren and American Goldfinch) responded positively to M-PC1, microhabitats characterized by a closed canopy with high densities of cottonwoods (Fig. 3A). Eleven species, however, responded negatively to M-PC1, suggesting that they used microhabitats with open canopies. Eastern Kingbird showed the strongest negative relationship with this component.

Eleven species showed significant relationships with M-PC2, increasing herbaceous ground cover with decreasing litter (Fig. 3B). Yellow-breasted Chat had the strongest positive association with M-PC2, whereas Veery had the strongest negative relationship with this component, suggesting that Veeries used microhabitats characterized by heavy ground litter.

A dense shrub layer (M-PC3) was a significant component of the microhabitat for seven species (Fig. 3C), with Yellow-breasted Chats showing the strongest positive association with M-PC3. Four species, three of which were cavity nesters, had a significant negative relationship with M-PC3, suggesting that they used open subcanopies.

Eight species responded to microhabitats with a birch understory (M-PC5), and Yellow-breasted Chats had the strongest positive association with this component (Fig. 3E). Among five species responding negatively, American Kestrels had the strongest relationship to increasing birch densities in the understory.

Microhabitats characterized by increasing densities of silverberry and juniper, with decreasing dogwood in the subcanopy (M-PC6), were a significant component for 13 species (Fig. 3F). Among 10 species with a positive relationship, Yellow Warblers had the strongest association with M-PC6. Three species (Gray Catbird, Veery, and House Wren) responded negatively to M-PC6, suggesting that they selected microhabitats with a dogwood subcanopy.

Relative importance of spatial scale. —Standardized estimates, derived from the logistic regression, allowed comparison of relative selection among all habitat components and spatial scales for an individual species (cf. Manly et al. 1993, Knick and Rotenberry 1995). Landscape features were more important than either macrohabitat or microhabitat for most species (Appendix B). Landscape patterns were the most important predictor of occurrence for 21 species, whereas microhabitat components were the best determinant of occurrence for 10 species, and macrohabitat for one species. For nearly half (47%) of 32 species analyzed, the standardized estimates indicated that the most important factor influencing habitat use was an increase in upland natural landscapes with a decrease in agricultural landscapes (L-PC1; Appendix B). The microhabitat component describing cottonwood tree density and canopy closure (M-PC1) was the most important determinant of occurrence for four species (13%), all of which responded negatively to this habitat feature. The frequency of occurrence of four other species (Black-billed Magpie, Gray Catbird, Cedar Waxwing, and Black-headed Grosbeak) was best determined by willow density and canopy (M-PC4), and nearest cottonwood patch neighbor (L-PC6) was most important for habitat use by three species (American Kestrel, Black-capped Chickadee, and Yellow-breasted Chat). The occurrence of a few species was most influenced by shrub cover (M-PC3, for Lazuli Bunting), landscape heterogeneity (L-PC2, for Cassin's Finch), patch size (L-PC3, for Song Sparrow), juniper woodlands (L-PC4, for Fox Sparrow), and residential areas (L-PC3, for American Crow).

DISCUSSION

Distributions of breeding birds in cottonwood forest patches were correlated to habitat factors at a variety of spatial scales. Surrounding landscape features, rather than macrohabitat or microhabitat, were the most important and frequent predictors of bird occurrence (prediction 1). This indicates that matrix habitats strongly influence the organization of bird assemblages within riparian forest patches, and suggests the need to con-

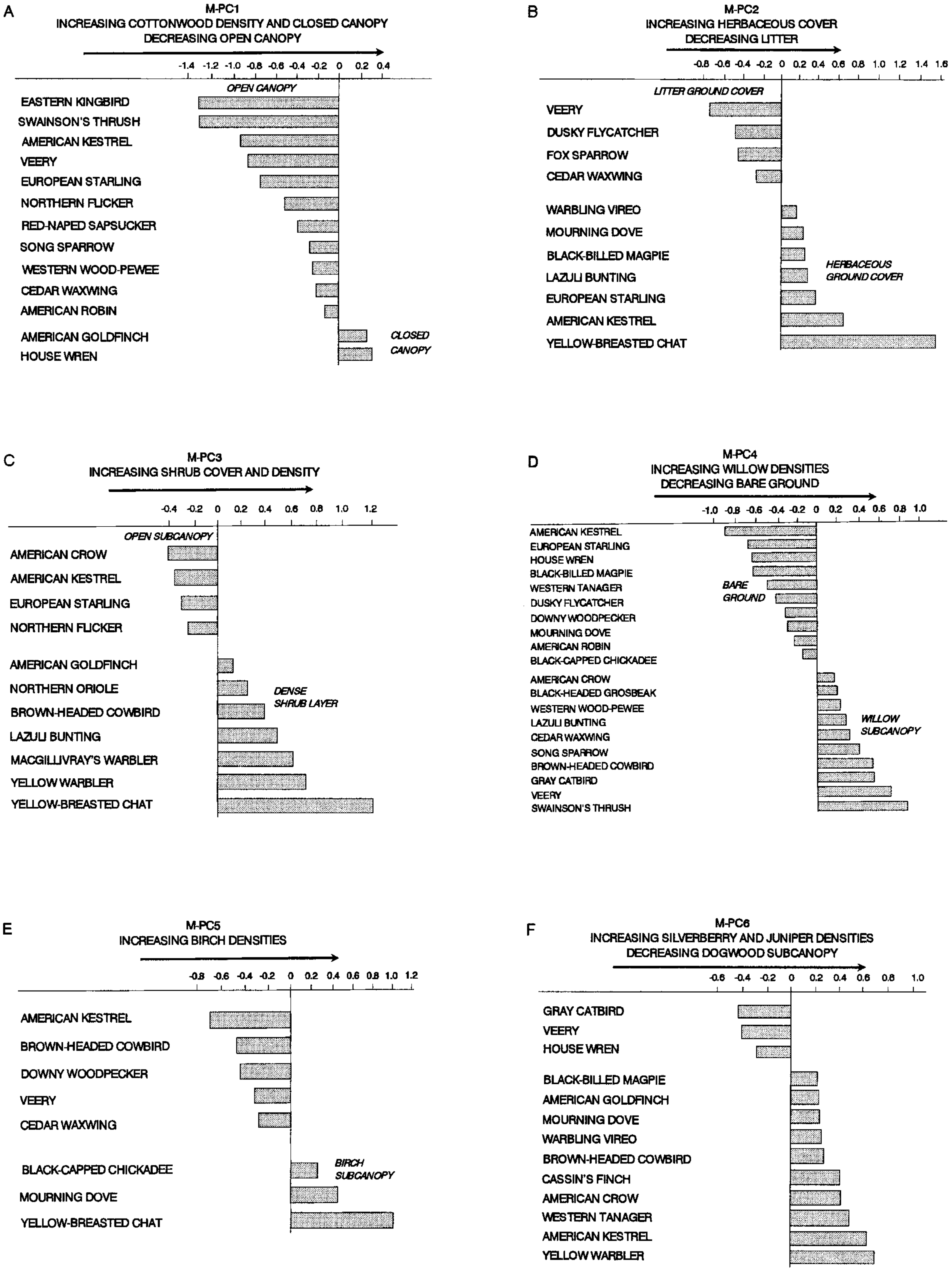

FIG. 3. Strength and nature of significant bird–habitat relationships, based on slope parameters derived from logistic regression for microhabitat components. Bars represent parameter estimates for each species, showing the relative distance from zero, where there would be no significant relationship with habitat components.

sider surrounding landscapes for riparian reserve design. My results support the increasing number of studies documenting the important effects of matrix habitats on animal distributions in fragmented landscapes (e.g., Szaro and Jakle 1985, Hansen and Urban 1992, Pearson 1993, McGarigal and McComb 1995, Mills 1995).

Patches surrounded by an agricultural matrix supported a different bird assemblage than did patches surrounded by a natural habitat matrix. For example, Brown-headed Cowbirds and European Starlings nested in cottonwood patches and were positively related to agricultural landscapes in my study (prediction 2). Elsewhere in North America, these species are commonly known to use agriculture for foraging and to use adjacent natural habitats for nesting (cf. Rodenhouse et al. 1995). Presumably, characteristics of the surrounding matrix habitat influence habitat quality within patches (e.g., proximity to other foraging habitats and risks of brood parasitism or competition).

Agricultural development has caused changes in species composition and a loss of bird species within small remnants of natural habitat (e.g., Whitcomb et al. 1981, Robbins et al. 1989, Best et al. 1995, Rodenhouse et al. 1995). Many of the negative effects associated with agriculture are manifested as edge effects. Edges created by agriculture can serve as travel lanes for predators (e.g., Glueck et al. 1988) and as new cowbird feeding areas (Best 1978, Johnson and Temple 1990), resulting in increased nest predation and brood parasitism, respectively. In my study area, Brown-headed Cowbirds were strongly associated not only with agricultural landscapes, but also with small cottonwood patches with relatively large amounts of edge (predictions 2 and 3).

Species–area relationships were exhibited in this cottonwood riparian forest (prediction 3). Bird species showing positive relationships with cottonwood patch size were considered large-patch associates or interior specialists, and those associated with small patches were edge specialists. I found consistent patterns of habitat use by some species of both interior and edge specialists in other studies. For example, Yellow-rumped Warbler and Warbling Vireo were interior specialists in my study, they also selected the widest riparian forests available in a Quebec study area (Darveau et al. 1995) and in Iowa (Stauffer and Best 1980). My results on Veeries were consistent with studies in eastern deciduous forests, where this species is considered an area-sensitive, interior specialist (Freemark and Merriam 1986, Robbins et al. 1989, Herkert 1995). All species (Yellow Warbler, Song Sparrow, European Starling, Black-billed Magpie, Brown-headed Cowbird, American Robin, and Northern Oriole) associated with small patches have been widely reported as edge specialists in other habitats (e.g., Galli et al. 1976, Freemark and Merriam 1986, Robbins et al. 1989, Herkert 1994, Vickery et al. 1995). Both the amount of edge and the type of adjacent habitat were important to the occurrence of bird species in my study area, suggesting that edge effects should be of management concern in arid-land riparian habitats.

Residential development was another human alteration of the landscape that influenced frequency of bird occurrence (prediction 2). Generalist predators (i.e., American Crow and Black-billed Magpie) and European Starling, an introduced species that potentially competes with native cavity nesters, were positively associated with residential areas. Thus, nest predators (i.e., corvids), brood parasites (i.e., cowbirds), and exotic species (i.e., starlings) all responded positively to human-altered landscapes as a result of agricultural development (cowbirds, and starlings), fragmentation (magpies, cowbirds, and starlings), residential areas (crows, magpies, and starlings), or all three factors (starlings). Much of the residential development in natural landscapes was vacation homes in the mountainous section of the study area. Forests cannot be expected to retain their ecological functions as adjacent land is developed for housing. In Ontario, Canada, neotropical migrants were lost from avian communities in forests surrounded by human settlement, not because of habitat loss, but because of negative influences associated with nearby residential development (Friesen et al. 1995).

Species richness of the native avifauna was also most strongly and frequently associated with the principal component describing a natural habitat matrix vs. an agricultural matrix (prediction 4). Additionally, species richness was correlated with large cottonwood forests, which were located in the downstream section of my study area where agriculture dominated the landscape. Therefore, I was unable to separate the influences of agriculture and presence of large cottonwood forests in this component (L-PC1). Flat terrain characterized the section dominated by agriculture, suggesting that fewer vegetative communities (and, thus, lower species richness) naturally occurred in this section than in the upstream portion, which is characterized by relatively high topographic relief. However, the component describing landscape heterogeneity with wetlands (L-PC2) also had high negative loadings on agriculture, yet a positive loading on cottonwood forest communities. Landscape heterogeneity with wetlands was the second best predictor of high species richness, suggesting that, indeed, there was a negative correlation between species richness and agriculture.

The best predictors of high species richness were measures of the habitat matrix, which was not considered an important function of island biogeography (MacArthur and Wilson 1967), because the intervening matrix was homogeneously water (i.e., ocean). Island biogeography is frequently used to explain variation in species richness in habitat fragments that differ in area and isolation (e.g., Diamond 1975, Forman et al. 1976), two variables that were of secondary importance in explaining high species richness along the South Fork.

My results support the arguments as to why this theory is an insufficient explanation of patterns in avian use of terrestrial habitat islands (cf. Merriam 1988). Other factors such as unfavorable environmental conditions or biotic interactions (e.g., competition, predation, parasitism), influenced by the landscape context, may explain why some habitat interior species were absent from small habitat patches (Ambuel and Temple 1983, Herkert 1994).

Close proximity to the nearest cottonwood patch and to continuous cottonwood forest (prediction 5) were also associated with species richness and frequency of occurrence for many individual bird species along the South Fork. In woodland habitats that were once continuous, these habitat patterns are potentially very important for animal dispersal routes, movement corridors, and gene exchange (e.g., Best et al. 1995, Haas 1995, Hagan et al. 1996), particularly for resident bird species. Should a migratory bird find its traditional nest site unsuitable due to habitat degradation, searching for suitable nesting habitat could be more efficient if continuous cottonwood forests and nearest cottonwood patches are in close proximity to traditional nesting sites (cf. Hagan et al. 1996).

Macrohabitat and microhabitat were of secondary importance, compared to landscape features, in explaining the distribution and frequency of occurrence of most bird species. In this regard, my results differed from studies of bird communities in other forest types of the northwestern United States (Rosenberg and Raphael 1986, Lehmkuhl et al. 1991, McGarigal and McComb 1995), although they were more consistent with bird community studies in eastern/midwestern North America (e.g., Whitcomb et al. 1981, Robbins et al. 1989, Robinson et al. 1995*b*). These differences and similarities are probably related to the timing and nature of disturbance.

Studies from eastern deciduous forests of North America have evaluated bird responses to forest fragmentation caused by agricultural development and urbanization that had taken place many decades earlier (e.g., Whitcomb et al. 1981, Robbins et al. 1989, Faaborg et al. 1995, Rodenhouse et al. 1995), whereas studies in the Pacific Northwest have assessed responses to fragmentation caused by recent timber management (Rosenberg and Raphael 1986, Lehmkuhl et al. 1991, McGarigal and McComb 1995). In my study, the primary cause of forest fragmentation was agricultural development that was initiated >100 years ago. In this form of fragmentation (caused by either agriculture or urbanization), forest tracts are progressively reduced to smaller and more isolated patches embedded within a relatively permanent matrix of largely unsuitable habitat (see Merriam 1988). In contrast, vertebrate population responses in forests being fragmented by timber management activities are likely to differ, because sharp forest–nonforest edges are transient in managed coniferous forests as a result of forest regrowth (McGarigal and McComb 1995, Hagan et al. 1996). In addition, coniferous forest in the Pacific Northwest still represents the matrix habitat (McGarigal and McComb 1995), unlike riparian forests in arid lands, where the landscape matrix is either another vegetation type or agriculture.

CONSERVATION IMPLICATIONS

This study demonstrates the importance of using hierarchical approaches in developing conservation plans for birds in western riparian habitats. In an evaluation of three spatial scales (landscape, macrohabitat, and microhabitat), landscape features were the most important and frequent predictors of bird distribution and frequency of occurrence. Therefore, surrounding landscape features should be a primary consideration in selecting riparian reserve areas. Land acquisition and maintenance of large cottonwood patches surrounded by natural landscapes should take precedence over conserving large patches surrounded by agriculture, if maintaining high species richness of native birds is a management objective. Conservation of contiguous patches of cottonwood forest adjacent to palustrine wetlands is also desirable for many individual species and for maintenance of species richness. Both large and naturally small fragments of riparian habitat are needed for conservation of interior and edge specialists. Small patches, generally are not limiting in aridland riparian habitats, but those that exist should be conserved for bird species associated with edge habitats. Management objectives for natural landscapes should consider controlling residential growth to reduce the likelihood of avian nest predators (i.e., crows and magpies) and exotic species (i.e., starlings). Among microhabitat characteristics, a relatively open cottonwood forest canopy was the most important predictor of high species richness and of occurrence for several species. This microhabitat feature may reflect pre-dam conditions, when natural flooding disturbances created more patchiness in the mature forest canopy interspersed with younger cottonwood stands (cf. Merigliano 1996). Flood control can greatly alter riparian plant communities by increasing cover of plant species that would otherwise be removed by flood scour, causing plant desiccation, reduced growth, competitive exclusion, ineffective seed dispersal, or failure of seedling establishment (see Poff et al. 1997). The magnitude and timing of peak flows should approximate pre-dam conditions for the long-term maintenance of cottonwood forests (Rood and Heinze-Milne 1989, Johnson 1992, Merigliano 1996) and the associated bird community.

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APPENDIX A

Bird species recorded within point count circles during the 1991–1994 breeding seasons along the South Fork Snake River in southeastern Idaho, United States. Species shown in boldface were used in all analyses and were recorded on ≥12 patches.

Common name	Scientific name	Common name	Scientific name
Double-crested Cormorant	*Phalacrocorax auritus*	**Black-capped Chickadee**	***Parus atricapillus***
Great Blue Heron	*Ardea herodias*	Red-breasted Nuthatch	*Sitta canadensis*
Sandhill Crane	*Grus canadensis*	Rufous Hummingbird	*Selasphorus rufus*
Canada Goose	*Branta canadensis*	Broad-tailed Hummingbird	*Selasphorus platycercus*
Mallard	*Anas platyrhynchos*	**House Wren**	***Troglodytes aedon***
Common Merganser	*Mergus merganser*	Ruby-crowned Kinglet	*Regulus calendula*
Sora	*Porzana carolina*	**Gray Catbird**	***Dumetella carolinensis***
Spotted Sandpiper	*Actitis macularia*	Townsend's Solitaire	*Myadestes townsendi*
Killdeer	*Charadrius vociferus*	**American Robin**	***Turdus migratorius***
Red-necked Phalarope	*Phalaropus lobatus*	**Swainson's Thrush**	***Catharus ustulatus***
Common Snipe	*Gallinago gallinago*	**Veery**	***Catharus fuscescens***
Turkey Vulture	*Cathartes aura*	Hermit Thrush	*Catharus guttatus*
Osprey	*Pandion haliaetus*	American Dipper	*Cinclus mexicanus*
Golden Eagle	*Aquila chrysaetos*	**Cedar Waxwing**	***Bombycilla cedrorum***
Bald Eagle	*Haliaeetus leucocephalus*	**European Starling**	***Sturnus vulgaris***
Red-tailed Hawk	*Buteo jamaicensis*	Plumbeus Vireo	*Vireo plumbeus*
American Kestrel	***Falco sparverius***	**Warbling Vireo**	***Vireo gilvus***
Northern Goshawk	*Accipiter gentilis*	Red-eyed Vireo	*Vireo olivaceus*
Cooper's Hawk	*Accipiter cooperii*	**Yellow Warbler**	***Dendroica petechia***
Sharp-shinned Hawk	*Accipiter striatus*	**Yellow-rumped Warbler**	***Dendroica coronata***
Ruffed Grouse	*Bonasa umbellus*	Black-throated Gray Warbler	*Dendroica nigrescens*
Rock Dove	*Columba livia*	**MacGillivray's Warbler**	***Oporornis tolmiei***
Mourning Dove	***Zenaida macroura***	Orange-crowned Warbler	*Vermivora celata*
White-throated Swift	*Aeronautes saxatilis*	**Yellow-breasted Chat**	***Icteria virens***
Yellow-billed Cuckoo	*Coccyzus americanus*	Common Yellowthroat	*Geothlypis trichas*
Black-chinned Hummingbird	*Archilochus alexandri*	**Western Tanager**	***Piranga ludoviciana***
Calliope Hummingbird	*Stellula calliope*	**Black-headed Grosbeak**	***Pheucticus melanocephalus***
Belted Kingfisher	*Ceryle alcyon*	**Lazuli Bunting**	***Passerina amoena***
Great Horned Owl	*Bubo virginianus*	Green-tailed Towhee	*Pipilo chlorurus*
Common Nighthawk	*Chordeiles minor*	Chipping Sparrow	*Spizella passerina*
Red-naped Sapsucker	***Sphyrapicus nuchalis***	Dark-eyed Junco	*Junco hyemalis*
Hairy Woodpecker	*Picoides villosus*	Western Meadowlark	*Sturnella neglecta*
Downy Woodpecker	***Picoides pubescens***	Red-winged Blackbird	*Agelaius phoeniceus*
Northern Flicker	***Colaptes auratus***	Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*
Eastern Kingbird	***Tyrannus tyrannus***	Brewer's Blackbird	*Euphagus cyanocephalus*
Olive-sided Flycatcher	*Contopus cooperi*	Common Grackle	*Quiscalus quiscula*
Western Wood-Pewee	***Contopus sordidulus***	**Bullock's Oriole**	***Icterus bullockii***
Willow Flycatcher	*Empidonax traillii*	**Brown-headed Cowbird**	***Molothrus ater***
Dusky Flycatcher	*Empidonax oberholseri*	House Sparrow	*Passer domesticus*
Empidonax sp.	*Empidonax* sp.	**Cassin's Finch**	***Carpodacus cassinii***
Tree Swallow	*Tachycineta bicolor*	Pine Siskin	*Carduelis pinus*
Violet-green Swallow	*Tachycineta thalassina*	**American Goldfinch**	***Carduelis tristis***
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	Red Crossbill	*Loxia curvirostra*
Bank Swallow	*Riparia riparia*	White-crowned Sparrow	*Zonotrichia leucophrys*
Cliff Swallow	*Hirundo pyrrhonota*	**Fox Sparrow**	***Passerella iliaca***
Barn Swallow	*Hirundo rustica*	**Song Sparrow**	***Melospiza melodia***
Black-billed Magpie	***Pica pica***	Evening Grosbeak	*Coccothraustes vespertinus*
Common Raven	*Corvus corax*		
American Crow	***Corvus brachyrhynchos***		
Mountain Chickadee	*Parus gambeli*		

APPENDIX B

A table presenting standard estimates with significant coefficients ($P < 0.05$) derived from logistic regression among 12 predictors of occurrence for 32 bird species is available at ESA's Electronic Data Archive: *Ecological Archives* A009-001.