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EFFECTS OF HUMAN SETTLEMENT ON BIRD COMMUNITIES IN LOWLAND RIPARIAN AREAS OF COLORADO (USA)

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Abstract. Riparian areas in western North America have been characterized as centers of avian diversity, yet little is known about the ways that native species in streamside habitats are affected by development nearby. To address this issue, we examined patterns of habitat use by birds during the 1995–1997 breeding seasons at 16 lowland riparian sites representing an urban-to-rural gradient. As development increased, riparian woodlands tended to have fewer native trees and shrubs, less ground and shrub cover, higher tree densities, and greater canopy closure. Bird species richness also declined as urbanization increased in the surrounding landscape. Canonical correspondence analysis (CCA) revealed that measures of settlement intensity best explained variation in habitat use by riparian birds, although some residual variation was accounted for by differences in woodland understory features. Migrant and low-nesting species were associated with lower-than-average levels of development, whereas resident and cavity-nesting species tended to increase with urbanization. In partial CCA analyses, however, local habitat variables explained twice the variation that measures of settlement did; nearly half of all explained variation could be attributed to local and landscape variables simultaneously. For avian guilds based on migratory, nesting, and foraging behavior, regression analyses showed that the best variables for explaining patterns of habitat use were usually those that reflected levels of urbanization, particularly at broad scales. When the effects of local habitat variation were removed, however, the best variables for explaining residual variation in habitat use tended to describe development at relatively fine scales, especially for species that nested or foraged low for insects or seeds. These species were also the most sensitive to human trail use. Our analyses indicated that bird communities and local habitat conditions in riparian areas were both affected by development in the surrounding landscape. It may be possible to mitigate the negative impacts of human settlement on native birds in streamside woodlands by maintaining or restoring vegetation structure and composition, and by imposing limits on human recreational activity in these habitats.

Key words: avian guilds; bird community; Colorado Front Range (USA); gradient design; habitat structure; recreation trails; riparian habitat; urbanization.

INTRODUCTION

The conservation value of riparian areas is disproportionate to their spatial extent, particularly in arid and semi-arid environments. In the western United States, these habitats account for <1% of the total land surface (Knopf et al. 1988), yet up to 80% of vertebrate species depend on them during all or part of their life cycles (Chaney et al. 1990). Riparian areas in this region provide critical resources for migrating and breeding birds (Knopf and Samson 1994, Skagen et al. 1998) and harbor some of the most diverse avian assemblages in North America (Johnson et al. 1977, Ohmart 1994).

People also tend to settle near streams and rivers. Throughout history, rivers have provided a means of transportation, water for drinking and irrigation, food, barriers for defense, power generation, scenic beauty, and recreational opportunities. Examine a typical roadmap of the United States and it is difficult to find a watercourse that is not bordered by human population centers; as aridity increases, it is rare to find towns and cities elsewhere. The association is even stronger if one considers forms of settlement that are usually not depicted on maps, such as exurban and rural development. How do birds in riparian habitats respond to these patterns?

We know that birds are affected by urbanization, but the magnitude of these effects and whether they are positive or negative varies among species (Marzluff et al. 2001). Most studies of the effects of development

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on birds focus on areas directly affected, where native habitats are altered or replaced by buildings and paved surfaces. A few species thrive under these conditions by exploiting the unique nesting and foraging opportunities that such environments provide (Lancaster and Rees 1979, Beissinger and Osborne 1982, DeGraaf and Wentworth 1986), but many species decline or disappear as settlement intensity increases (Blair 1996, Clergeau et al. 1998). Factors that have been implicated in these declines, such as interactions with human commensal species (including domestic pets) or changes in the availability of food resources, may also affect birds in streamside habitats that are proximate to urban and suburban areas. On the other hand, the effects of settlement may be less direct in the riparian zone itself because, in many cases, floodplain designations relegate construction to the uplands.

Numerous studies have shown that, for a variety of taxa (including birds in riparian woodlands; Saab 1999), it is important to consider features of the surrounding landscape when examining patterns of habitat use (Mazerolle and Villard 1999). Moreover, there is evidence that birds in habitat remnants respond to human settlement in adjacent areas (Engels and Sexton 1994, Friesen et al. 1995). Few studies have examined the effects of development on riparian bird communities, however, despite recognition of the conservation value of these habitats. In a recent review of published studies (n = 101) on the effects of urbanization on birds (Marzluff 2001), only five considered riparian areas. Of these, two focused on a single species and one examined the suitability of suburban habitats for riparian birds in terms of vegetation structure and composition (Rosenberg et al. 1987). Dowd (1992) compared the bird communities in two forested wetlands in New York City, one surrounded by development and one embedded in a large greenway, and found that the latter supported more forest-interior species. Only Rottenborn (1999) studied the relationship between development and the composition of bird communities at multiple sites, and included measures of local habitat and the surrounding landscape in his analyses. He found that bird species richness and overall density were lower at more urbanized sites, as was the density of most individual species, and he concluded that habitat characteristics at both scales influenced these results.

Clearly, variation in riparian-habitat features is not independent of human land use in the surrounding landscape. In populated areas, both the structure and composition of riparian vegetation may be altered by the planting or removal of trees and shrubs. Creeks and streams in urban and suburban settings are frequently subjected to diversion, straightening, or stabilization, and such modifications may adversely affect native vegetation that is adapted to a more natural hydrologic regime (Miller et al. 1995, Auble et al. 1997). Birds are likely to be affected not only by structural changes to riverine habitats, but also by an increased human presence there. Riparian corridors often serve as the backbone for greenway networks, partly because people like to be near water and also because other forms of development may be restricted by zoning regulations. Paved trails that parallel the watercourse are typically the centerpiece of such greenways, and trail use tends to reflect the degree of urbanization nearby. Several studies have documented effects of pedestrian traffic on birds (Nowakowski 1994, Fernández-Juricic 2000, Miller and Hobbs 2000), but, as with development generally, species vary in their sensitivity to this type of disturbance.

In regions with an expanding human population, it is not likely that settlement will be completely excluded from lands near rivers and streams. It may be possible, however, to mitigate the adverse effects of development on birds that use riparian habitats, but it is first necessary to achieve a clearer understanding of potential mechanisms underlying such effects. Here, we ask how human settlement has affected riparian birds by documenting patterns of habitat use in streamside woodlands near the Colorado Front Range (USA). We emphasize community-level impacts throughout to gain a broader perspective than that provided by studies focused on single species (Wiens 1989). To assess the effects of human settlement, we compare lowland riparian bird communities at sites associated with different levels of development on adjacent lands, and examine the degree to which variation in community structure and composition can be explained by local habitat features and by patterns of settlement in the surrounding landscape.

METHODS

Study sites

In the spring of 1995 we selected 16 study sites on four drainages, just east of the Front Range of Colorado, USA. Sites on three of these drainages (Coal Creek, South Boulder Creek, and Boulder Creek) were located in and around the City of Boulder, and sites on the remaining drainage (the Cache la Poudre River) were located ~48 km to the north in and around the City of Fort Collins (Fig. 1). Colorado's population has grown at a rate three times the national average since 1990 (U.S. Bureau of the Census 2000), with much of this growth manifested by urban and suburban sprawl. The overall study area is located on the western edge of the Plains Grassland zone as described by Marr (1961, 1964), where ~80% of the state's population lives in a corridor that is roughly 30 km wide and bisects the state from Fort Collins in the north to Pueblo in the south. Elevations range from ~1550 m in eastern Boulder and Larimer counties to 1640 m near the foothills of the Rocky Mountains.

Sites were chosen to represent a gradient of human settlement intensity from urban to exurban areas (Aus-

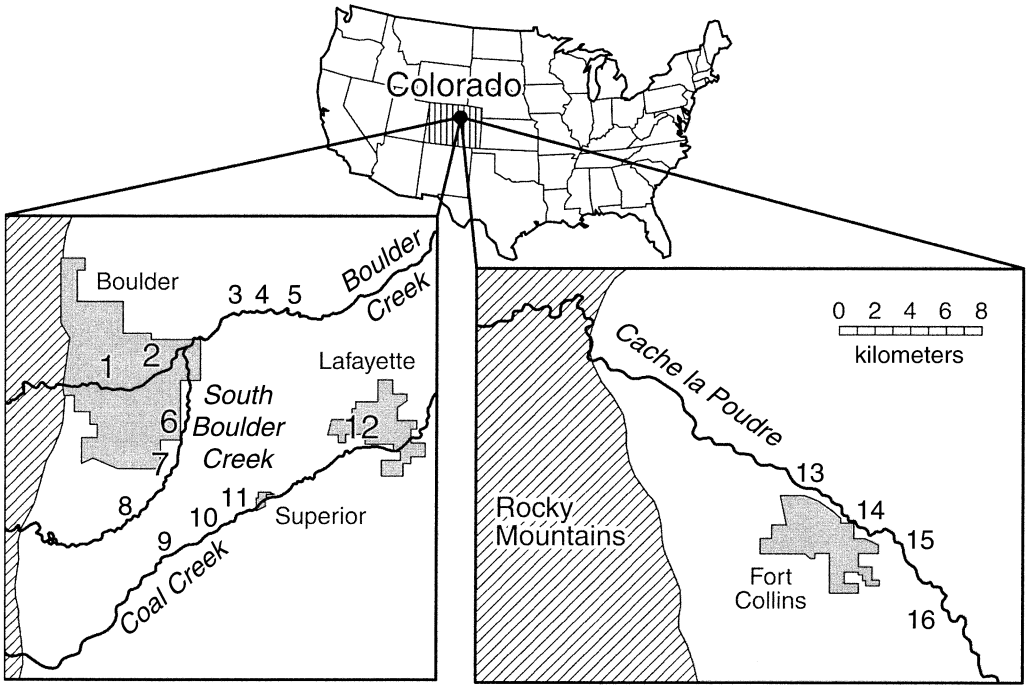

FIG. 1. Location of the 16 study sites used to examine the relationship between avian communities in lowland riparian areas and human settlement in Larimer and Boulder counties, Colorado, USA: (1) University of Colorado, (2) 30th Street, (3) Walden, (4) Kaufman, (5) Ertl, (6) Bobolink, (7) Eldorado, (8) South Vale, (9) Vista View, (10) Mine, (11) Superior, (12) Lafayette, (13) Shields, (14) Lemay, (15) 7 Ponds, and (16) Gateway. (Lower left panel [Boulder] is ∼48 km south of lower right panel [Fort Collins].)

tin and Heyligers 1991, Wiens and Parker 1995). Study sites in Boulder County were all under the jurisdiction of either the Boulder County Parks and Open Space Department or the City of Boulder Open Space Department, and those in Larimer County were managed by the Fort Collins Department of Natural Resources. All of the sites were wooded and relatively narrow, averaging 60–110 m in the width of the woody riparian zone. Dominant tree species included plains cottonwood (*Populus deltoides*), green ash (*Fraxinus pennsylvanicus*), box elder (*Acer negundo*), hybrids (*Populus* × *acuminata*) of plains cottonwood and narrowleaf cottonwood (*Populus angustifolia*), and an exotic, crack willow (*Salix fragilis*). The understorys were dominated by snowberry (*Symphoricarpus occidentalis*), chokecherry (*Prunus virginiana*), wild rose (*Rosa woodsii*), lead plant (*Amorpha fruticosa*), and sandbar willow (*Salix exigua*). Most of the sites have a history of grazing by livestock since European settlement, but only Eldorado Springs, Vista View, the Mine, and Superior (see Fig. 1) were grazed during the course of the study and these only in fall and winter. The uplands surrounding the sites were comprised of shortgrass and mixed-grass prairie prior to settlement, and have since been used for livestock grazing, haying, and irrigated row crops, or have been subjected to commercial or residential development.

Local habitat and landscape variables

We established a transect that paralleled the watercourse at each site. Each transect had a random start and was comprised of 12 avian census points spaced at 110-m intervals (Bibby et al. 1992). At each point we quantified vegetation structure and composition using a modified point-centered-quarter method (Friedman et al. 1996*a*). We first identified the 10 closest trees, with the distance to the farthest tree serving as the radius of a circle used in quantifying other vegetation features (Table 1). This method provided an efficient means for gathering data over a large number of points and, for our purposes, offered two additional advantages over the traditional point-centered quarter method (Cottam and Curtis 1956). First, sample size was fixed for estimating tree density, which was especially important where trees were sparse; and second, time was saved in densely wooded areas.

At each point, we noted the species and measured the height and the dbh (diameter at breast-height [∼1.5 m]) of each of the 10 trees. Total basal area per point was later derived from the dbh measurements. Indices of total vegetation cover for the canopy, subcanopy, shrub, and ground layers were derived by multiplying estimates of a particular layer's coverage by its density within the area covered. These data were visually estimated using discrete categories: 5 = >75%, 4 = 50–

TABLE 1. Landscape and site variables for 16 lowland riparian areas near the Front Range of Colorado, USA.

Variable code	Description
Local habitat variables	
TREEDENS	Average tree density (number/hectare) for points on a transect
TREEHT	Average tree height (in meters) for points on a transect
BASAL	Average basal area (in square centimeters) for points on a transect
NTREE	Average percentage of trees for points on a transect that are native to study area
NSHRUB	Average percentage of shrubs for points on a transect that are native to study area
TRICH	Average number of tree species for points on a transect
SRICH	Average number of shrub species for points on a transect
CAN	Total coverage of tree canopy on a transect (for trees >8 m tall)
SUBCAN	Total coverage of tree subcanopy on a transect (for trees 3–8 m tall)
SHRUB	Total coverage of shrubs on a transect (for shrubs 0.5–3 m tall)
SAPL	Average sapling (dbh <15 cm) density (number/hectare) for points on a transect
GRND	Total coverage of herbaceous vegetation (0.5–3 m tall) on a transect
HERB	Average height (in centimeters) of herbaceous vegetation for points on a transect
SNAG	Average number of standing dead trees for points on a transect
Landscape variables	
D1500	Buildings per hectare within 1500 m of a transect
D500	Buildings per hectare within 500 m of a transect
D100	Buildings per hectare within 100 m of a transect
D10	Average distance (in meters) to the 10 buildings closest to the transect
AGE_D10	Average age (in years) of buildings in D10
WIDTH	Width (in meters) of the woody riparian zone

75%, 3 = 25 to <50%, 2 = 5 to <25%, and 1 = <5%. At each point, we also noted the species composition of the shrub layer and recorded the abundance of saplings, standing dead trees, and the height of herbaceous vegetation.

In addition to local habitat variables, we measured characteristics of the surrounding landscape (Table 1). The UTM (Universal Transverse Mercator) coordinates of all census points were determined to within ±3 m using a global positioning system; these coordinates were subsequently used to position transects in digital data layers. We used ArcView software (ESRI 1995) and digital parcel maps to quantify building density within 100 m, 500 m, and 1500 m of each transect (hereafter, D100, D500, and D1500, respectively) and to measure the distance from each transect to the 10 nearest buildings (hereafter, D10). Building density is a good surrogate for settlement intensity (Marzluff et al. 1998, Theobald 2000) and the parcel maps, made available to us by the Boulder and Larimer County planning offices, delineated property boundaries and provide standardized information on the status of a property (developed vs. undeveloped), as well as the number of buildings located there. Building age was not available for all parcels at all study sites, but was available for the 10 nearest buildings at each site and so we used the average age of these structures to represent the length of time since development.

The buffer distances were chosen a priori to describe the general patterns of settlement surrounding the sites based on our initial visual estimates. At some sites, building density was more or less constant with increasing distance from the riparian zone, but other riverine woodlands were separated from development by small undeveloped areas, such as hay meadows or tracts of prairie. The buffer distances also had an ecological basis, in that the shorter distances encompassed the territory sizes for most of the species we studied (Schoener 1968), whereas the longer distances allowed us to describe settlement at broader scales that might be important to migrating species when selecting habitats (e.g., Hutto 1985).

For smaller watercourses, the width of streamside woodlands has been shown to exert a strong influence on the composition and abundance of riparian bird communities, similar to the effect of patch area for upland birds (Stauffer and Best 1980, Keller et al. 1993, Darveau et al. 1995, Hodges and Krementz 1996, Groom and Grubb 2002). Using 1:24 000 digital aerial photos, we measured the width of woody riparian vegetation at each census point along an axis that was perpendicular to watercourse.

Avian surveys

We surveyed the avifauna at each site 3 times annually from mid-May to mid-July, 1995–1997, using fixed-radius point counts (Ralph et al. 1993, 1995). At each point a motionless observer recorded the species and number of all birds seen and heard within 50 m during an 8-min sampling period. Bird surveys were conducted between sunrise and approximately 0830 hours on days with no rain and wind speeds <32 km/h. Observers rotated visits to each site throughout the breeding season in order to minimize observer bias. On each day that censuses were conducted, sampling effort was distributed as evenly as possible among sites that had different levels of development (Verner 1985). Recreational trails were located in the riparian areas at eight of our study areas; in 1997, we counted people at each site using these trails during each of our avian

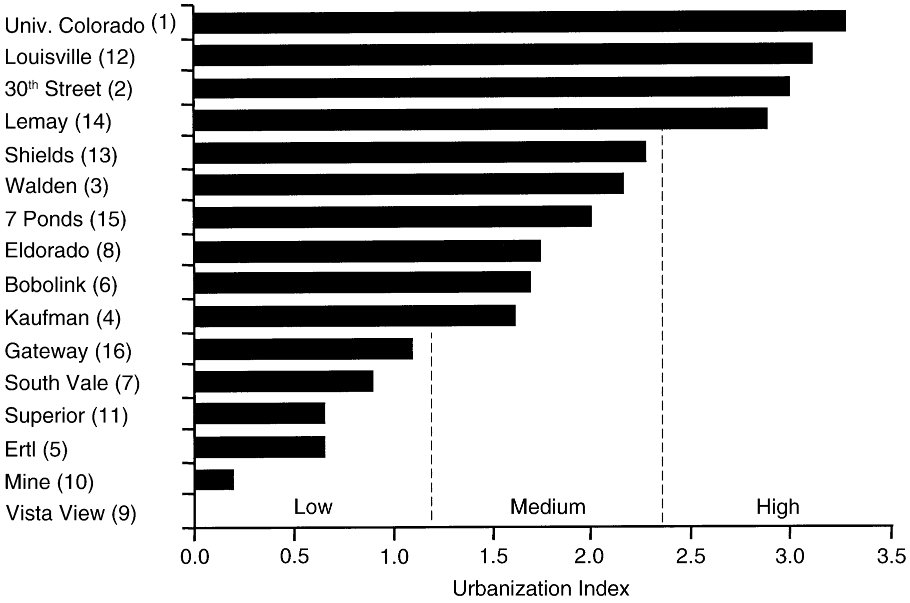

FIG. 2. Values of the urbanization index (URBAN, see *Methods: Data analyses*) for the study sites shown in Fig. 1, as indicated by numbers in parentheses.

surveys and for a 2-h period in the early evening (1700–2000 hours).

Surveys were conducted each year by 3–4 observers, all of whom had experience conducting point counts and were familiar with the avifauna of this region; two individuals participated in the study during each of the three years. Prior to each field season, all observers underwent a two-week training period to sharpen identification skills, with periodic recalibration throughout the season. Before the first field season, distances to obvious landmarks were measured at each census point to delineate the plot.

Data analyses

Transects were treated as the units of analysis in this study. We therefore averaged riparian width and all local habitat measures across the 12 points on each transect to produce an overall estimate for each site. In addition, we averaged the counts of people using trails in 1997 to estimate human activity at each site; this variable was treated separately in data analyses because only half of the study areas had trails. To obtain an overall measure of human settlement for each site, we created a synthetic variable (hereafter, URBAN; Fig. 2) from the Axis 1 scores of a rotated principal components analysis (PCA; ter Braak and Smilauer 1998) on D1500, D500, D100, and D10. Axis 1 of the PCA accounted for 90.6% of the variance in the data, and the correlations between Axis 1 and the four measures of building density were -0.893, -0.934, -0.907, and 0.890, respectively. We then used Spearman rank correlations to examine the relationship between the intensity of human settlement and local habitat variables.

We considered a bird species to be present at a site if it occurred on two or more surveys over the course of the study. Birds detected outside of the riparian corridor and species flying through or over the census plots were not included because we could not be sure that they were using riparian habitat. We also excluded nocturnal and crepuscular species, aerial insectivores, raptors, shorebirds, and waterfowl because point counts are not an effective method for censusing such species (Bibby et al. 1992). The maximum number of individuals recorded on a single survey during each year was used as an estimate of the annual abundance of each species at each site. Maximum rather than average counts were used because some species were either not present or were not singing during some visits, depending on migratory patterns or breeding cycles. Using the mean of all visits would therefore tend to underestimate the relative abundance of these species. We used a repeated-measures analysis of variance to test for annual differences in bird abundance, using drainage as the main effect and year as the repeated measure. There was no evidence of strong interannual effects on avian abundance (time, $P = 0.798$), or year × drainage interactions ($P = 0.523$), and because we were primarily interested in the overall impact of human settlement on bird communities and not annual variation, we averaged species relative abundance across years.

Because our study sites were spatially clustered (Fig. 1), there was a possibility that response variables lacked independence due to spatial autocorrelation. To test whether sites that were closer together were more likely to have similar bird communities, we computed a Mantel test statistic (Mantel 1967, McCune and Mefford 1999) between a geographical distance matrix and an ecological distance matrix (Villard et al. 1999). The ecological distance values were based on the dissimilarity in species composition between sites and were calculated by subtracting the Jaccard index of similarity (Magurran 1988) from 1. Probability values were calculated based on 5000 random permutations of one of the two matrices. Because the study areas in Boulder County were closer to each other than to any of the sites in Larimer County, we conducted the Mantel test twice, once with all sites included and the second time including only the Boulder County sites.

An indirect ordination technique, correspondence analysis (CA), was used to obtain a general overview of variation in avian community composition among sites. Environmental gradients are not studied directly in indirect ordination analyses, but rather are inferred from the species data. In CA, a reciprocal averaging algorithm orders species and sites along synthetic gradients or axes (ter Braak and Smilauer 1998). This method results in the maximum possible correlation between site and species scores along each axis, subject to the constraint that the axes are orthogonal (Gauch 1982). Thus, CA constructs a theoretical variable, represented by the *x*-axis, that best explains the species data and then, by the same process, constructs a second variable, represented by the *y*-axis, to explain residual variation (ter Braak 1995). Species abundances were log-transformed to counteract skewness (ter Braak 1986); because rare species can exert a strong influence on ordination results, we excluded species whose average relative abundance was <10.

We used canonical correspondence analysis (CCA), an extension of CA, to examine the relationship between bird community structure and measured environmental variables. CCA is a direct ordination technique because the axes are constrained to be linear combinations of designated environmental variables; the resulting diagram depicts the relationship between the abundance of individual species, study sites, and measured environmental gradients (ter Braak 1986, ter Braak and Prentice 1988). By comparing the results of CCA with those of CA, it is possible to evaluate the extent to which patterns in the species data can be explained by the environmental variables that have been measured. Congruent configurations indicate that the appropriate environmental variables have been measured (Økland 1996). Environmental variables were selected by stepwise forward-selection procedures (ter Braak and Smilauer 1998). Variables explaining a significant amount of variation, as determined by Monte Carlo permutation tests (199 random permutations of the samples in the species data), were included in the CCA analyses and the means of these variables are represented by the origin in the resulting diagram. Bird species abundances were transformed as in CA. Because our limited sample size could lead to low power in statistical tests, we used an α level of 0.10 to screen for significant effects in these and all subsequent analyses unless otherwise noted.

In addition to examining the overall relationship between patterns of habitat use by birds and environmental variables, we wished to assess the relative influence of landscape and local habitat measures on these patterns. Partial constrained ordinations allow one to determine the effect of one set of variables after removing the effect of a second set, the latter being treated as covariables (ter Braak 1998). We used partial CCA to partition the variation in the species abundance data into the fraction explained by local habitat measures alone, by landscape measures alone, the variation that can be related simultaneously to both sets of variables, and variation that cannot be explained by either set (Borcard et al. 1992, Økland and Eilertsen 1994, Økland 1999). This was accomplished by conducting four ordinations. The first CCA was constrained by significant local habitat variables as determined by the stepwise forward-selection procedures described above. In the second ordination, the process was repeated using only landscape variables. We then conducted a third CCA constrained by the significant local habitat variables with landscape measures identified in the second step treated as covariables. The roles of these two variable sets were reversed for the fourth ordination.

To identify potential mechanisms underlying patterns of riparian habitat use at our study sites, we classified bird species into functional groups based on a review of the literature (DeGraaf et al. 1985, Ehrlich et al. 1988, Andrews and Righter 1992, Kaufman 1996, Poole and Gill 1996, Kingery 1998). Functional groups were selected to reflect different aspects of each species' life history and ecological traits; hence, species simultaneously belonged to several groups. We first examined single-variable regressions to identify the environmental measure with the greatest explanatory power for each response. We then developed multiple-regression models using only local habitat variables to explain variation in total bird species richness and abundance, and the richness of each functional group. The variable list was customized for each group, depending on which habitat variables were relevant. Because the number of study sites was relatively small, we included no more than three variables per model to avoid overfitting. We examined all possible regression models and identified the ''best'' model on the basis of biological relevance, adjusted R^2, and a second-order variant of Akaike's Information Criterion (AIC; Akaike 1973) that corrects for small-sample bias (AIC_c; Hurvich and Tsai 1991, Burnham and Anderson 1998). AIC is an extension of likelihood theory and provides a robust and objective means for model selection. Although models with the minimum AIC_c value were considered ''best,'' we also examined all models with $\Delta\mathrm{AIC}_c \leq 2$ of the minimum because these are also viable alternatives (Burnham and Anderson 1998).

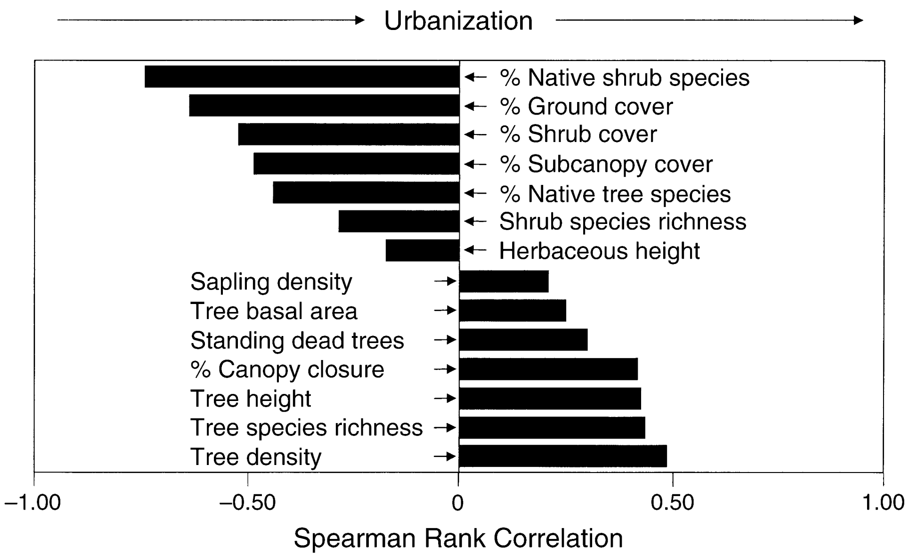

FIG. 3. Spearman rank correlations between the urbanization index and local habitat variables.

Once a local-habitat model was selected, we then regressed landscape measures against the residuals of the model to determine whether or not these terms explained a significant amount of the remaining variation. The variables URBAN, D1500 (buildings per hectare within 1500 m of a transect), D500, D100, D10, and WIDTH (width of the woody riparian zone) were regressed one-at-a-time; AGE_D10 (average age of buildings in D10) was also added to these models to see if additional variation could be explained. Again, the model with the minimum AIC_c was considered ''best,'' with the provision that its AIC_c was at least 2 less than that of an intercept-only model. Failure to meet this last condition would essentially mean that the ''best'' model had no more explanatory power than a model that contained only the intercept.

RESULTS

Habitat measures

Our 16 study sites (east of Colorado Front Range, USA) represented a gradient of overall levels of human settlement (Fig. 2). Building densities at the broadest scale (within 1500 m of a transect, D1500) ranged from 374 buildings/ha at the C.U. (University of Colorado) site to <0.1 building/ha at the Vista View site. There were no buildings within 100 m of the transect at five study areas (Bobolink, Kaufman, South Vale, the Mine, and Vista View), although one of these (Bobolink) was essentially a suburban site. The average distance to 10 buildings ranged from 39 m (Louisville) to >2 km (Vista View).

Compared to undeveloped sites, urban and suburban areas have often been characterized by reduced vegetation structure and the predominance of nonnative trees and shrubs (Beissinger and Osborne 1982, Sharpe et al. 1986, Mills et al. 1989, Germaine et al. 1998). Similarly, we found a strong negative correlation between overall settlement intensity and native shrubs in riparian woodlands, as well as moderate inverse relationships with native trees, ground cover, overall shrub cover, and subcanopy cover (Fig. 3). Tree density, tree height, the number of tree species, and canopy closure in the riparian zone all tended to increase with development levels, reflecting an increase in nonnative species. There was also a positive correlation (albeit weak) between the density of standing dead trees and settlement intensity.

Bird community

Riparian habitats on the plains along Colorado's Front Range support a diverse assemblage of bird species. Over the three-year period we recorded 15 473 detections representing 95 species. We limit subsequent discussion to the 43 species that met our criteria for inclusion in analyses and are known to breed in lowland riparian areas in this region (Table 2; Appendix A; Andrews and Righter 1992, Kingery 1998). Many species were fairly widespread; 22 species occurred in over half the sites and 16 species were found in more than 75% of the areas (Fig. 4). It has been suggested that widespread species also tend to be more abundant than restricted species (Brown 1984, Wiens 1989, Gaston 1994). We observed this same general pattern, but there was considerable variation in mean abundance for species occupying the same number of sites. Three of the species that occurred at all sites were also the most abundant: the Common Grackle, the American Robin, and an exotic, the European Starling. The next two most abundant species, the House Wren and the Red-winged Blackbird, occurred at only 14 of the sites, whereas the Northern Flicker and Downy Woodpecker had noticeably lower abundances but were observed at 15 sites.

TABLE 2. Scientific names and species code of the 43 bird species included in analyses (following American Ornithologists' Union [1983] and Pyle [1997]); see Appendix A for the ecological and life-history traits of these species.

Scientific name	Common name	Species code
Columbia livia	Rock Dove	RODO
Zenaida macroura	Mourning Dove	MODO
Selasphorus platycercus	Broad-tailed Hummingbird	BTLH
Ceryle alcyon	Belted Kingfisher	BEKI
Colaptes auratus	Northern Flicker	NOFL
Picoides pubescens	Downy Woodpecker	DOWO
Contopus sordidulus	Western Wood Pewee	WEWP
Tryannus tyrannus	Eastern Kingbird	EAKI
T. verticalus	Western Kingbird	WEKI
Corvus brachyrhynchos	American Crow	AMCR
Cyanocitta cristata	Blue Jay	BLJA
Pica pica	Black-billed Magpie	BBMA
Poecile atricapilla	Black-capped Chickadee	BCCH
Troglodytes troglodytes	House Wren	HOWR
Turdus migratorius	American Robin	AMRO
Dumetella carolinensis	Gray Catbird	GRCA
Mimus polyglottus	Northern Mockingbird	NOMO
Toxostoma rufum	Brown Thrasher	BRTH
Bombycilla cedrorum	Cedar Waxwing	CEDW
Sturnus vulgaris	European Starling	EUST
Vireo gilvus	Warbling Vireo	WAVI
V. olivaceus	Red-eyed Vireo	REVI
Dendroica petechia	Yellow Warbler	YWAR
Geothlypis trichas	Common Yellowthroat	COYE
Icteria virens	Yellow-breasted Chat	YBCH
Guiraca caerulea	Blue Grosbeak	BLGR
Pheucticus melanocephalus	Black-headed Grosbeak	BHGR
Passerina amoena	Lazuli Bunting	LAZB
P. cyanea	Indigo Bunting	INBU
Chondestes grammacus	Lark Sparrow	LASP
Melospiza melodia	Song Sparrow	SOSP
Pipilo maculatus	Spotted Towhee	SPTO
Agelaius phoeniceus	Red-winged Blackbird	RWBL
Sturnella neglecta	Western Meadowlark	WEME
Euphagus cyanocephalus	Brewer's Blackbird	BRBL
Quiscalus quiscula	Common Grackle	COGR
Icterus spurius	Orchard Oriole	OROR
I. bullockii	Bullock's Oriole	BUOR
Molothrus ater	Brown-headed Cowbird	BHCO
Carduelis psaltria	Lesser Goldfinch	LEGO
C. tristis	American Goldfinch	AMGO
Carpodacus mexicanus	House Finch	HOFI
Passer domesticus	House Sparrow	HOSP

Note: All these bird species are known to breed in lowland riparian areas in the Colorado Front Range region (USA).

Mantel tests indicated that our study areas could be considered statistically independent. There was no significant spatial autocorrelation in bird community composition, whether all sites in both counties were considered ($P = 0.923$, $r = -0.173$) or when the Larimer County sites were excluded from the analysis ($P = 0.152$, $r = 0.138$). There was a negative relationship between overall levels of urbanization and bird species richness ($R^2 = 0.478$, $P = 0.008$) but the effect of urbanization on total avian abundance was not significant ($R^2 = 0.038$, $P = 0.469$).

The primary axis of variation in the correspondence analysis (CA), which accounted for 43.8% of the variation in species composition, segregated sites based on their level of urbanization (Fig. 5). Study areas with moderate or high levels of development (see Fig. 2) were clustered more tightly around this axis than were low-urbanization sites, although our most urban site, C.U., was an exception to this general pattern. Sites associated with low levels of settlement intensity were positioned along a narrow range of values on the primary axis, yet exhibited a substantial amount of variation along the secondary axis, which accounted for 15.7% of the variation in species composition.

The canonical correspondence analysis (CCA) (Fig. 6) revealed similar patterns to those described in the CA, suggesting that the important sources of variation had been captured by the selected environmental variables. Sites were arranged along the primary axis by urbanization levels, similar to the pattern in CA, and the percentage of variation in species composition explained by the first two axes (Table 3) was close to that

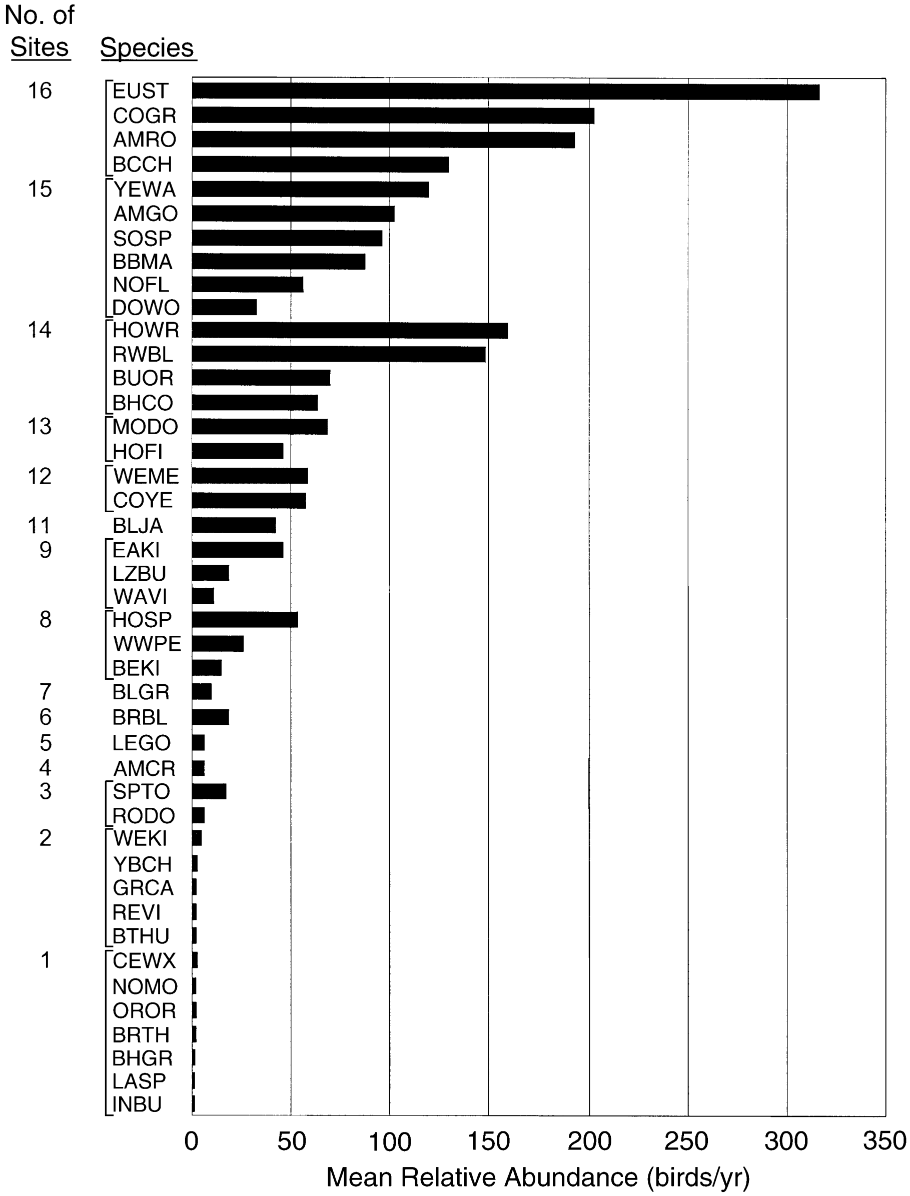

FIG. 4. Mean relative abundance (1995–1997) of bird species for all sites combined, and the number of sites at which they were observed. For each species, mean relative abundance was derived by summing the maximum abundance across all sites in each year and averaging over the three years. For species codes, see Table 2.

explained by the first two axes in CA. There were significant relationships between species composition and four environmental variables, two describing patterns of settlement and two describing vegetation structure. Both the first canonical axis and the overall relationship between species and environmental variables (all canonical axes) were significantly different from those derived from randomized data ($F = 6.775$ and $F = 4.133$, respectively; $P = 0.005$), based on Monte Carlo permutation tests. The primary axis had a strong, positive correlation with settlement intensity at the broadest scale that we considered, a strong negative correlation with the average distance to 10 buildings, and a moderate negative correlation with shrub cover. The secondary axis exhibited a somewhat stronger, positive relationship with shrub cover and a strong, negative correlation with the height of herbaceous vegetation (Table 3). Migrant and low-nesting species were generally associated with lower-than-average levels of development, whereas the abundance of residents and cavity-nesters increased with increasing urbanization (Fig. 7). High-nesting species were more evenly distributed along the primary axis.

Local habitat variables alone explained 23.3% of the variation in bird species composition, whereas landscape measures alone explained 12.3%. The amount of

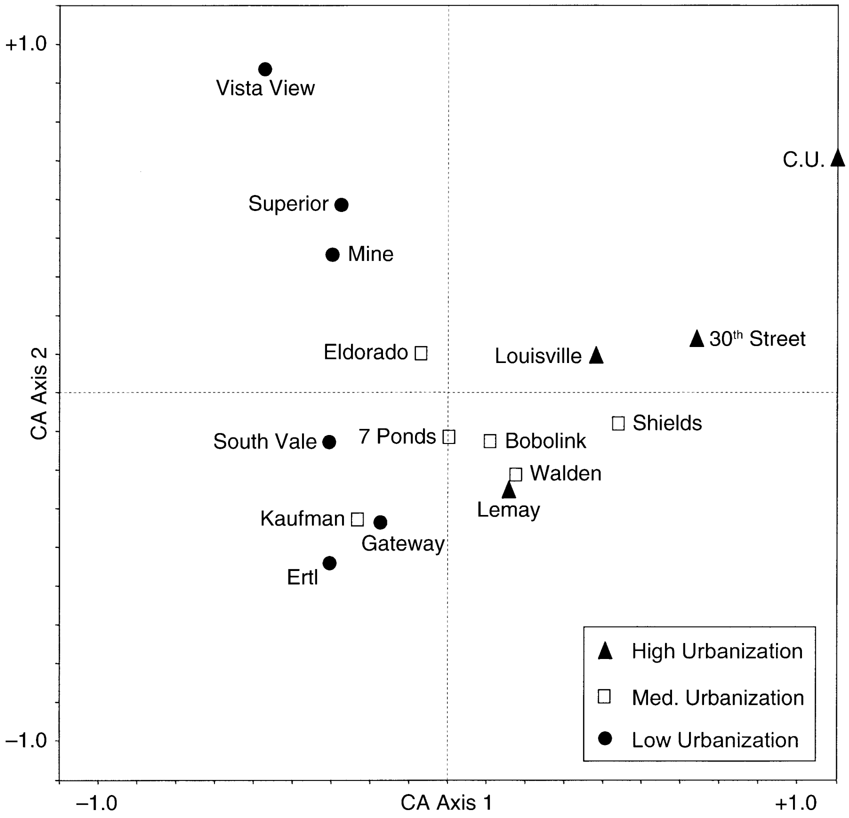

FIG. 5. Locations of site scores of high-, medium-, and low-urbanization sites in the space defined by a correspondence analysis (CA) of bird community composition during the avian breeding season, 1995–1997.

variation that could not be partitioned, but was shared between the two sets of variables was 29.2%. These findings suggest that the avian community and local habitat conditions were both influenced by the intensity of settlement in the surrounding landscape. The amount of unexplained variation (35.2%) was not unusually high, considering the nature of community data (ter Braak 1986), and was attributable either to unmeasured variables or to lack of fit of the data to the model (Økland 1999).

Single-variable regression models explained a fairly high percentage of the variation in habitat use for a number of the guilds that we examined (Table 4). Rare species generally occurred only at sites with moderate or low levels of settlement intensity. Indeed, there was a negative response to settlement intensity for most groups, but there was a strong positive relationship between the number of resident and cavity-nesting species and proximity to the nearest buildings. These relationships were also unique, in that the variable with the greatest explanatory power for these guilds reflected patterns of settlement at the finest scale that we examined, in contrast to the majority of models, which emphasized building densities at the broadest scale. Whereas the index of urbanization (URBAN) tended to weight development patterns at different scales equally, D1500 captured patterns at broad scales and this variable had the greatest explanatory power in over half of the single-variable models. We found a strong negative relationship between D1500 and the richness of neotropical-migratory and low-nesting species, as well as the richness of short-distance migrants, insectivores, generalist or high-foraging species, and species that foraged either high or low on insects and seeds (Table 4).

There were no a priori reasons for assuming that resident and migrant species would respond differently to variation in local habitat features, so we did not include these groups in our two-stage regression analyses. For nesting and foraging guilds, the amount of variation explained by models that included only local habitat variables ranged from 14.8%, for the number of omnivorous species, to 60.5%, for insectivorous species (Table 5). Landscape terms were no better than intercept-only models in explaining residual variation from regressions of local habitat variables in half of the cases that we examined (Table 6). When such variables did improve the models, the emphasis was on measures of settlement intensity at the finest scales that we examined and, in these cases, increasing levels of development near riparian habitats had adverse effects on low-nesting and low-foraging species. Building age

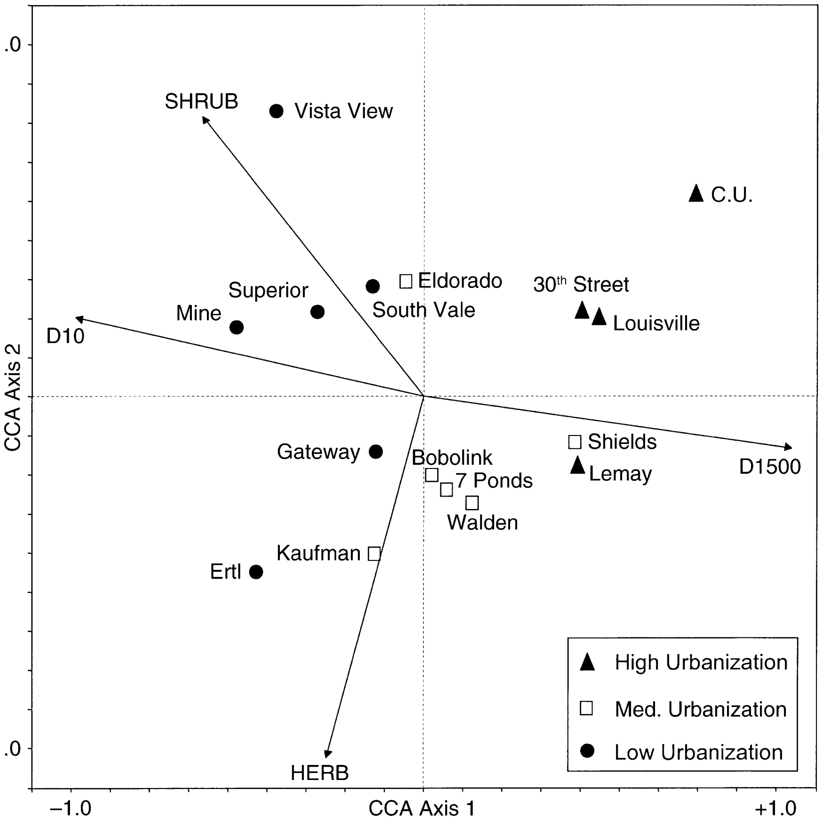

FIG. 6. Locations of site scores of high-, medium-, and low-urbanization sites in the space defined by a canonical correspondence analysis (CCA) of bird community composition during the avian breeding season, 1995–1997. Environmental variables are depicted as vectors, and the rank of a site with respect to a given variable is approximated by projecting the site point in the diagram perpendicularly onto the environmental vector (see Table 1 for explanations of environmental-variable codes). The lengths of the arrows indicate the relative importance of each environmental variable in the model, and the direction of each arrow indicates how well the environmental variable is correlated with each axis. The origin (0,0) is the mean of each environmental variable, so that transects projecting onto the axis of but on the side opposite the arrow are inferred to exhibit a lower-than-average value of the variable.

was also prominent in these models and had a negative coefficient in all cases (Appendix B).

Because only half of our study sites were associated with paved trails, we analyzed the effect of trail use separately. Human activity at these eight sites primarily included walking, jogging, and bicycling. Trail use reached its maximum in the heart of the city of Boulder near the University of Colorado, where trail use averaged 141 people/h, and was least at Walden, where average trail use was less than 1 person/h. The correlation between levels of human activity and overall settlement intensity was not as strong as might be expected ($R^2 = 0.605$). Trail use at Bobolink, for example, averaged 33 people/h, although this site was associated with lower levels of urbanization (Fig. 2) than was Walden, Louisville (mean trail use = 17 people/h), or 7 Ponds (mean trail use = 14 people/h). We reasoned that birds most likely to be affected by human activity

TABLE 3. Summary statistics for the first two axes in canonical correspondence analysis (CCA) and correlations of these axes with environmental variables that were used to constrain the ordination.

Statistic	CCA axis 1	CCA axis 2
Eigenvalues	0.152	0.052
Cumulative variance of species data	0.381	0.511
Intraset correlations		
D1500	0.939	−0.132
D10	−0.885	0.202
SHRUB	−0.549	0.698
HERB	−0.248	−0.924

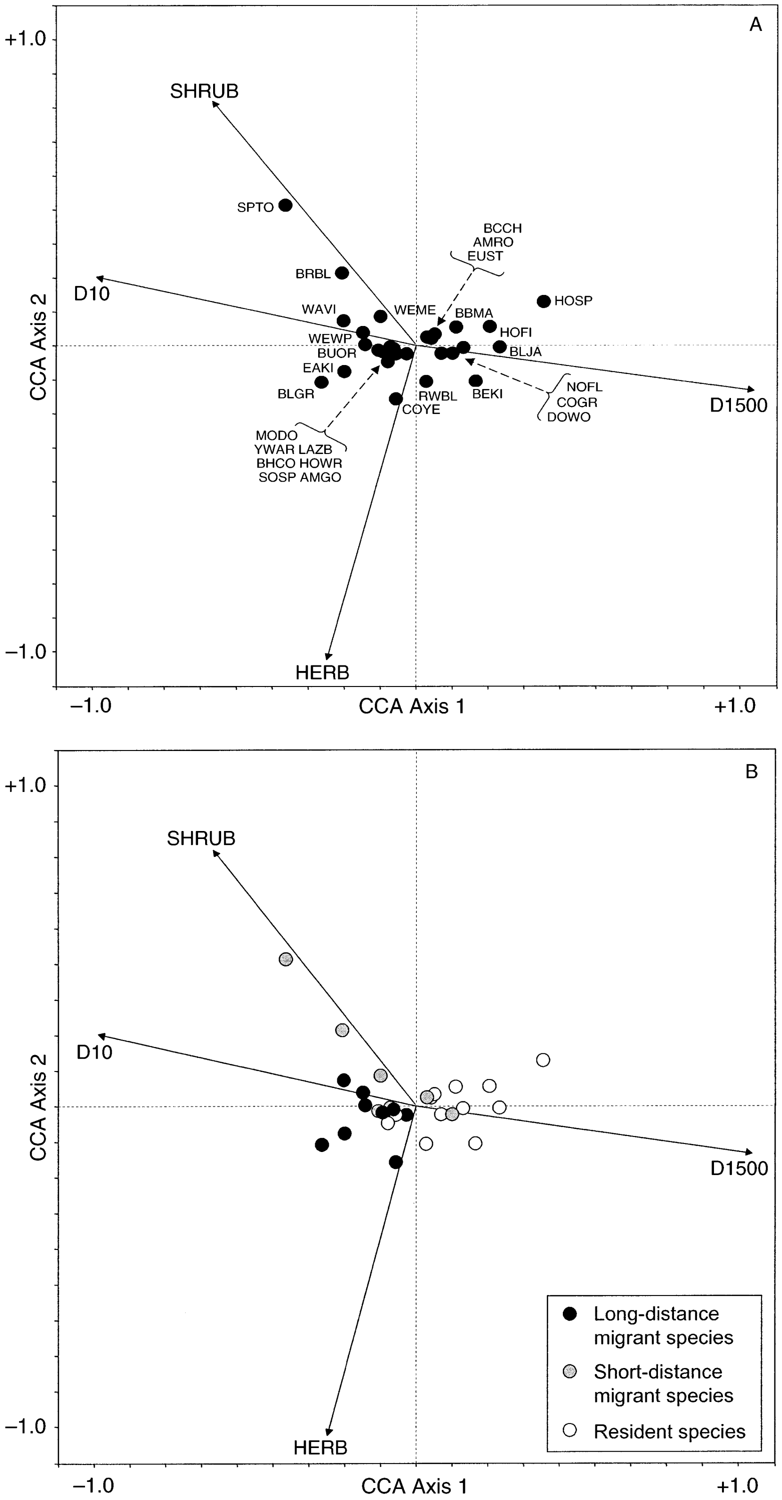

FIG. 7. Locations of species scores in the space defined by a canonical correspondence analysis (CCA) of bird community composition during the avian breeding season, 1995–1997. Species are depicted (A) by common name (see Table 2 for codes), (B) by migration strategy, (C) by nesting position, and (D) by foraging location.

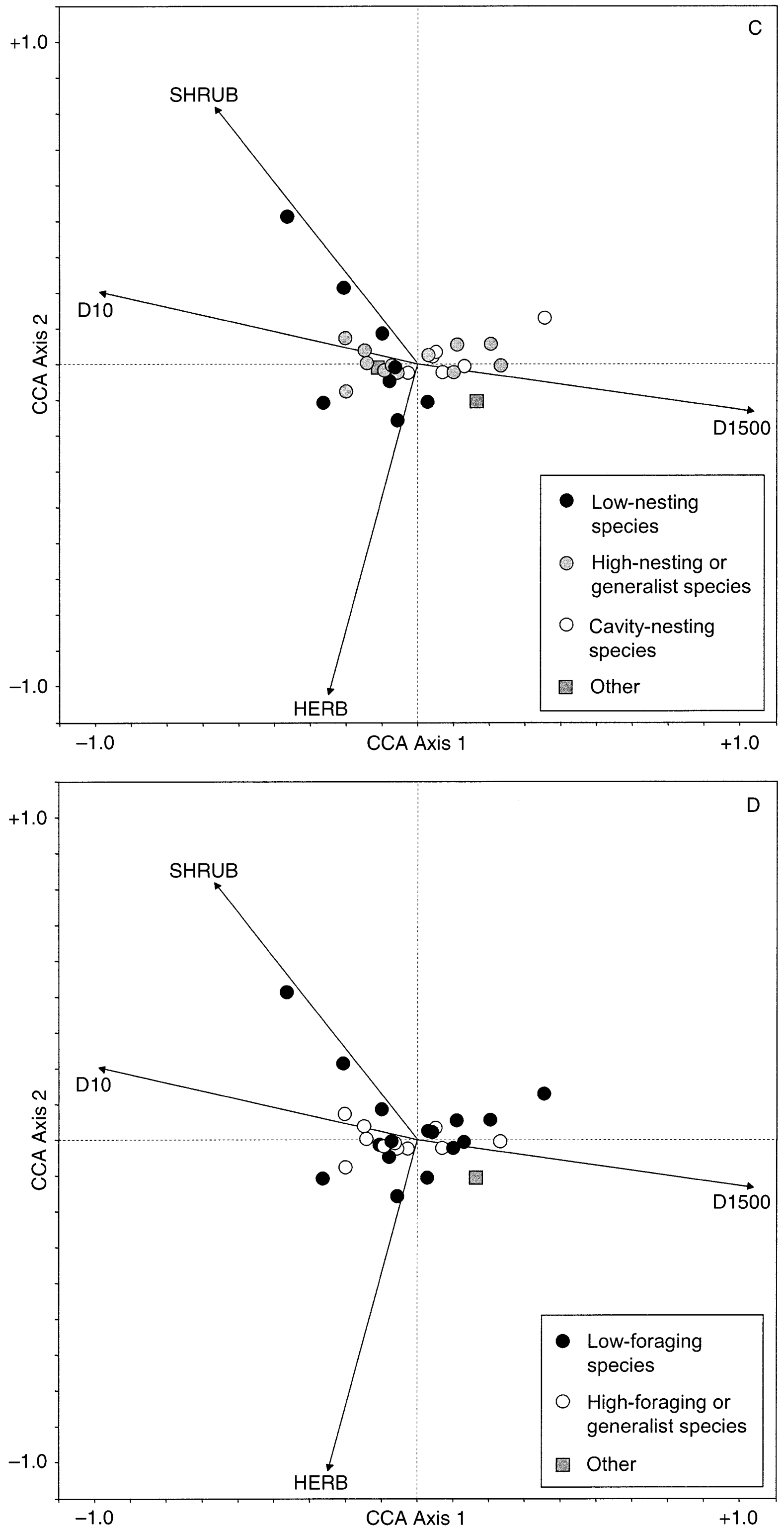

FIG. 7. Continued.

TABLE 4. Results of single-variable regression models for species richness of migration groups and guilds (low = shrubs or ground; high = subcanopy, canopy, or generalist) indicating ''best'' models, based on biological relevance and AIC_c (see *Methods: Data analyses* for details).

Functional group	Variable†	Coefficient	Adjusted R^2
Migration			
Neotropical migrants	D1500	−0.026	0.744
Short-distance migrants	D1500	−0.014	0.633
Residents	D10	−0.001	0.730
Nesting			
Low-nesting spp.	D1500	−0.016	0.635
High-nesting spp.	D1500	−0.013	0.459
Cavity-nesting spp.	D10	−0.002	0.735
Foraging diet			
Omnivores	URB	0.594	0.395
Insectivores	D1500	−0.027	0.720
Granivores	D1500	−0.004	0.230
Foraging position			
Low-foraging spp.	D1500	−0.009	0.356
High-foraging spp.	D1500	−0.022	0.666
Foraging position and diet			
Low-foraging spp., insect–seed	D1500	−0.016	0.767
High-foraging spp., insect–seed	D1500	−0.016	0.723

† See Table 1 for variable codes.

on trails would nest or forage on the ground, and focused our analyses on these guilds. There was a negative effect of trail use on all guilds that we examined (Table 7). Although the relationship between trail use and the number of low-nesting species was not particularly strong, the intensity of trail use explained >60% of the variation in the occurrence of low-foraging species and nearly 90% of the variation in habitat use by species that forage on the ground for insects or seeds (Table 7).

DISCUSSION

Clearly, human settlement had a profound impact on riparian bird communities at the sites that we studied. Species richness declined as the level of development on surrounding lands increased, similar to the findings reported in most investigations of urbanization and its effects on birds. Most of the variation in community composition was accounted for by measures of settlement intensity, and the best single variable, in terms

TABLE 5. Results of multiple-linear-regression analyses for species richness of guilds based on foraging and nesting (low = shrubs or ground; high = subcanopy, canopy, or generalist) indicating ''best'' models, based on biological relevance and AIC_c (see *Methods: Data analyses* for details).

Functional group	First variable		Second variable		Third variable		Adjusted R^2
	Code	Coefficient	Code	Coefficient	Code	Coefficient	
Nesting							
Low-nesting spp.	SHRUB	0.521	HERB	0.165	SAPL	−0.364	0.499
High-nesting spp.	TREEDENS	−0.007	CAN	−0.384	⋯	⋯	0.241
Cavity-nesting spp.	CAN	0.180	SNAG	1.365	⋯	⋯	0.335
Foraging diet							
Omnivores	CAN	0.163	TREEDENS	0.002	⋯	⋯	0.148
Insectivores	HERB	0.341	SHRUB	0.591	NTREE	3.919	0.605
Granivores	SHRUB	0.293	HERB	0.062	TREEDENS	0.004	0.286
Foraging position							
Low-foraging spp.	GRND	−1.317	HERB	0.194	SHRUB	0.619	0.417
High-foraging spp.	TREEDENS	−0.009	SUBCAN	0.569	SAPL	−0.597	0.383
Foraging position and diet							
Low-foraging spp., insect–seed	HERB	0.089	NSHRUB	7.062	SAPL	−0.347	0.487
High-foraging spp., insect–seed	SUBCAN	0.496	SAPL	−0.403	TREEDENS	−0.007	0.475

Notes: Variables are entered in order to importance; see Table 1 for variable codes. See Appendix B for other candidate models, based on ΔAIC_c.

TABLE 6. Results from regressing landscape measures on residuals from multiple linear regression (low = shrubs or ground; high = subcanopy, canopy, or generalist).

Functional group	First variable		Second variable		Adjusted
	Code	Coefficient	Code	Coefficient	R^2
Nesting					
Low-nesting spp.	D10	0.001	AGE_D10	−0.054	0.478
High-nesting spp.	D1500	−0.007	WIDTH	0.026	0.243
Cavity-nesting spp.	D10	−0.001	···	···	0.268
Foraging diet					
Omnivores	···	···	···	···	···
Insectivores	···	···	···	···	···
Granivores	···	···	···	···	···
Foraging position					
Low-nesting spp.	···	···	···	···	···
High-nesting spp.	D100	−0.023	AGE_D10	−0.075	0.280
Foraging position and diet					
Low-foraging spp., insect-seed	D10	0.001	AGE_D10	−0.059	0.589
High-foraging, insect-seed	···	···	···	···	···

Notes: Variables were entered in order of importance; see Table 1 for variable codes. See Appendix B for other candidate models, based on $\Delta\mathrm{AIC}_c$.

of accounting for variation in habitat use by birds, was the density of buildings within 1500 m of transects.

Although the width of streamside woodlands strongly influenced bird community structure and composition in other studies, we did not find this to be the case. Many of those investigations focused on riparian forests that had been reduced by agricultural or silvicultural activities (e.g., Keller et al. 1993, Darveau et al. 1995, Hodges and Krementz 1996). On the western Great Plains, groves of trees bordering smaller streams tend to be relatively narrow, even in the absence of timber harvest or crop production. It has been suggested that edge effects, of the sort often associated with small or narrow woodlands, may not be as pronounced in the western United States compared to the eastern part of the country because many western habitats, including riparian areas, are naturally patchy due to a combination of aridity, topography, and frequent disturbance (Finch 1991, Tewksbury et al. 1998, Saab 1999). The influence of width in this study may also have been muted by the profound and varied development nearby.

In these riparian habitats much of the impact of human settlement on bird communities was indirectly expressed through changes in local habitat features. Modification of vegetation structure and composition in urbanizing environments has frequently been identified as a primary reason that such habitats are less suitable for many avian species (Beissinger and Osborne 1982, Mills et al. 1989, Jokimaki and Suhonen 1993, Rolando et al. 1997, Germaine et al. 1998). Even though our study sites were relatively free of buildings and paved surfaces (except trails), we observed declines in native trees and shrubs, a more open understory, reduced ground cover, higher tree density, and greater canopy closure as development intensified in the surrounding landscape. These differences explained a substantial portion of the variation in patterns of avian habitat use; indeed, when such variation was partitioned in the partial CCA, local habitat measures explained a slightly greater percentage than did landscape variables.

Of all the changes to riparian-habitat features associated with increased development, reductions in understory vegetation and herbaceous ground cover were particularly strong determinants of bird community structure. The declines in low-nesting and low-foraging species that we observed were not surprising under such circumstances. For insectivorous species and species that forage low for insects or seeds, the best local habitat models also included a term for native vegetation, lending support to the notion that native trees and shrubs may be superior to exotic vegetation in terms of providing food resources for these birds (Southwood 1961, Beissinger and Osborne 1982). Nonnative plants, on the other hand, appear more likely to benefit omnivorous species, at least regarding dietary needs (Reichard et al. 2001).

The age of development emerged as an important consideration in accounting for variation in habitat use by birds, once the effects of local habitat features were removed statistically. Others have noted compositional changes in avian assemblages over time in developed areas (Guthrie 1974, Walcott 1974, Aldrich and Coffin 1980, Munyenyembe et al. 1989), and have generally attributed this phenomenon to temporal changes in habitat structure. There was an inverse relationship between building age and habitat use for several of the guilds that we examined, which may have resulted from temporal changes in features that we did not measure or from lagged responses to habitat alteration for these species.

Residual variation in habitat occupancy was better explained by fine-scale patterns of settlement, as measured by D10, than by development over broad scales

TABLE 7. Results from regressing trail use (number of people per hour) on avian nesting and foraging guilds (low = shrubs or ground; high = subcanopy, canopy, or generalist).

Functional group	Trail-use coefficient	Adjusted R^2	P
Nesting			
Low richness	−0.029	0.370	0.064
High richness	−0.018	0.137	0.196
Foraging position			
Low richness	−0.029	0.612	0.013
High richness	−0.040	0.440	0.044
Foraging position and diet			
Low, insect-seed richness	−0.044	0.883	<0.001
High, insect-seed richness	−0.027	0.461	0.038

(D1500). Both variables were shown to be significant in the multivariate analyses. Together, these results imply that although alterations to riparian vegetation were more likely to be found near urban and suburban areas, the proximity of riparian habitats to houses adversely affected some bird species even where settlement occurred at lower densities. This was particularly true for species that nested in shrubs or on the ground and for species that foraged low for insects or seeds. These were the same functional groups that were most affected by high levels of trail use, suggesting that riparian woodlands near houses may experience more human activity. Birds that nest or forage near or on the ground are also more likely to be disturbed by free-ranging domestic pets, and the incidence of such disturbance is likely to be greater near places where people live (Weber 1975, Rubin and Beck 1982, Warner 1985).

One way to mitigate the adverse effects of human settlement close to riverine habitats, especially in the early stages of development, may be to set aside parcels of adjacent land as buffers. Although we cannot recommend an exact buffer distance on the basis of this study, one alternative would be to designate buffers to include the area historically comprising the floodplain. Aside from reducing the pressures of nearby settlement on riparian birds, this arrangement would give land managers more latitude in restoring the flow variability and channel movement that is characteristic of meandering rivers (Auble et al. 1997, Richter and Richter 2000) but may be undesirable in close proximity to development. Such movement is essential to the formation of the seed beds necessary for regeneration of cottonwood and other riparian species native to the streams of the Colorado Piedmont (Miller et al. 1995, Friedman et al. 1996*b*).

Periodic flooding may also result in the more-open canopies typical of cottonwood stands, thus providing an additional benefit to some riparian birds. The closed-canopy riparian woodlands that increasingly dominate river terraces in this region likely contribute to conditions that are unsuitable for birds dependent on understory vegetation. Furthermore, our analyses have shown that even species that nest or forage in the canopy tend to decline with increases in tree density and more continuous cover. This apparent relationship may stem, in part, from negative effects of development on some avian species (given the positive correlation between settlement intensity and both tree density and canopy cover), but it also reflects the preference of some species for more-open stands. This latter group includes birds with broad distributions, such as the Warbling Vireo (Gardali and Ballard 2000), as well as species such as the Bullock's Oriole (Rising and Williams 1999) or Western Kingbird (Gamble and Bergin 1996) whose nesting or foraging habits may be adapted to the open canopies that typified riverine habitats in the western United States prior to settlement. Where the restoration of open-canopied cottonwood stands by flooding is undesirable or impracticable (e.g., where development already borders the riparian zone), it may be possible to employ methods used to mimic the effects of floods by removing exotic trees and shrubs and inducing the establishment of native species (Friedman et al. 1995).

Even if vegetation structure and composition are restored, however, the findings of this study suggest that some species may avoid riparian areas that are associated with high levels of human activity. Several birds that forage on or near the ground, such as American Crows, Black-billed Magpies, European Starlings, and Common Grackles, are quite tolerant of human activity and were present even at sites with heavily used trails; these species are omnivorous and the dietary rewards of foraging in close proximity to people may outweigh any disadvantages. Our data suggest that this is not the case for many other low-foraging species, particularly those whose diet is restricted to insects or seeds. Still, it is unreasonable to expect that people can be excluded from all of these areas, nor is this necessarily desirable. The benefits to conservation of excluding human visitors from such places must be weighed against the value derived from people being able to experience nature close to home (Miller and Hobbs 2002). Nonetheless, it is advisable to keep at least some riparian habitats free of recreational trails so that they may serve as baselines against which the effects of human activity can be measured and mitigated.

Overall, there is a lack of reliable information on the ways that human activities and patterns of development affect birds and other components of biodiversity. Although there is abundant advice on ways to manage greenways and remnants of native habitats that are proximate to human settlement (Smith and Hellmund 1993, Arendt 1996, Duerkson et al. 1997), much of this information has been derived from island biogeography theory and would be better viewed as testable hypotheses than as established truth (Marzluff 2001, Miller and Hobbs 2002). To go beyond such prescriptions, it will be necessary for conservation scientists to allocate greater research effort to areas where people live. Community, guild, and single-species investigation should be viewed as complementary approaches to studying the effects of settlement on native species with the ultimate goal of providing empirically based guidelines to policy makers and land-use planners.

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APPENDIX A

Life-history and ecological traits of the 43 bird species included in the analyses are available in ESA's Electronic Data Archive: *Ecological Archives* A013-018-A1.

APPENDIX B

A listing of additional candidate multiple-regression models, based on $\Delta \mathrm{AIC}_c < 2$ of the minimum AIC_c, for explaining variation in bird species richness, is available in ESA's Electronic Data Archive: *Ecological Archives* A013-018-A2.