



Scale-dependent habitat relations of birds in riparian corridors in an urbanizing landscape

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ABSTRACT

As the amount of urbanization in the landscape surrounding a riparian zone increases, local riparian vegetation structure and composition change in complex ways. The impact of increasing urbanization on birds in and around riparian zones will depend on their differential sensitivity to local- versus landscape-scale habitat variation. Thus, our principal objective was to determine which spatial scale has a greater association with the distribution of each bird species using riparian corridors in a landscape mosaic comprised of anthropogenic land uses and undeveloped native shrublands in coastal southern California. We surveyed 137 points in riparian vegetation along an urbanization gradient, and used logistic regression and information theory to select best supported models describing the distribution of each of 52 bird species. Models based only on local-scale vegetation variables were best supported for 19 species, whereas landscape-scale (amount of urbanization within a 1000-m radius) models were best supported for 13. Ten species were best described by models combining local- and landscape-scale variables, and 10 had no well-supported models. Within guilds, woodland and riparian-dependent species appeared to respond to local vegetation variables whereas shrubland species appeared more sensitive to landscape context. Likewise, insectivores were more likely to be associated with variation in local-scale variables. In contrast to other studies, Neotropical migrants were not sensitive to increasing urbanization. Provided that local vegetation remains in good condition, our results suggest that riparian bird species may persist even in areas with extensive urbanization.

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1. Introduction

A major threat to native habitats in areas experiencing rapid human population growth is urbanization, which can produce profound changes in the structure and function of natural ecosystems that remain within an urbanizing landscape (Grimm et al., 2000). Marzluff and Ewing (2001) assert that habitat conversion due to urbanization has a greater impact on natural environments than either forestry or agriculture because urban environments are more dissimilar to natural areas than is agriculture or forestry, and because urban areas do not revert back to a natural state once the conversion has taken place. However, when some landscapes undergo urbanization, riparian systems may be left intact while development occurs in the upland areas and intervening watersheds. Nevertheless, the riparian vegetation that remains is subject to many novel indirect effects (Paul and Meyer, 2001; Groffman et al., 2003). These effects may include changes in hydrology, such as

an altered flood regime or creation of a year-round water supply in an area that was previously ephemeral, or changes in water quality from increases in pollutants or nutrients due to run-off. These changes may further facilitate invasion by exotic plant species, which may be enhanced by the availability of propagules from urban landscaping (Loewenstein and Loewenstein, 2005). Indeed, numerous studies have documented changes in riparian vegetation structure and composition that occur in association with increasing urbanization (e.g., Airola and Buchholz, 1984; Kuss and Hall, 1991; King and Buckney, 2000; Moffatt et al., 2004; Loewenstein and Loewenstein, 2005; Burton et al., 2005; Oneal and Rotenberry, 2008).

Riparian zones are protected under the Clean Water Act (Title 33, United States Code, 1977), but are often also preserved for their aesthetic and recreational value within an urbanizing landscape, where they also serve the ecological function of providing habitat to a variety of wildlife species that might otherwise not persist in the surrounding landscape matrix. This ecological significance of riparian areas is enhanced in arid and semiarid regions, where highly productive riparian corridors are clearly discernible from the surrounding matrix even in natural landscapes, and where riparian areas frequently serve as corridors for species constrained by the adjacent terrestrial systems (Malanson and Cramer, 1999). In the

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western United States, riparian habitat supports more species of breeding birds than any other plant community (Faber et al., 1989; Ohmart, 1994; Knopf and Samson, 1994). Although less than 1% of the western landscape of the United States supports riparian vegetation, it has been estimated that as much as 51% of all bird species are dependent on riparian habitats for breeding (Johnson et al., 1977; Knopf et al., 1988), while another ~20% use riparian habitat during the breeding season (Faber et al., 1989; Ohmart, 1994; Knopf and Samson, 1994). In addition, riparian habitats are preferred by insectivorous landbirds migrating in the spring (Johnson et al., 1977; Stevens et al., 1977; Emmerich and Vohs, 1982), probably because food and cover are more abundant than in other vegetation types (Skagen et al., 1998). Many species of upland birds also move between upland and riparian habitats to forage or to obtain water or nesting substrate (Knopf and Samson, 1994), and it is estimated that riparian community effects, at least in an arid matrix, extend up to 1.0 km into the surrounding uplands (Szaro and Jakle, 1985). In such landscapes, the bird species richness of riparian habitats is often attributed to the structural complexity of the vegetation in comparison to the surrounding shrublands or grasslands (Anderson and Ohmart, 1977; Bull and Skovlin, 1982; Knopf and Samson, 1994).

As vegetation communities change along a hydrological gradient, it is reasonable to expect that bird distributions might change as well. However, there are a variety of other potential effects independent of vegetation that may also influence avian distributions in an urbanizing landscape. Urban-associated changes that may affect avian habitat quality include increases in noise or light from adjacent land uses; alteration in predation regime (either increased or decreased; Vander Haegen and Degraaf, 1996; Sinclair et al., 2005; Tewksbury et al., 2006); and increased nest parasitism by the Brown-Headed Cowbird (Tewksbury et al., 2002; Chace et al., 2006; see Appendix A for scientific names of all species of birds mentioned in text or tables). Ultimately, the impact of increasing urbanization on birds in and around riparian zones will depend on their differential sensitivity to local- versus landscape-scale habitat variation. Therefore, we asked, which spatial scale has a greater association with the distribution of birds using riparian corridors in a landscape mosaic dominated by urbanization?

To answer this question, we examined the composition of riparian bird communities within a rapidly urbanizing portion of southern California. Our principal objective was to determine which spatial scale has a greater association with the distribution of each bird species using the riparian corridor, the local-scale riparian plant community composition and structure, or the landscape-scale extent of surrounding urbanization. Because local vegetation attributes influence riparian bird distributions (e.g., Stevens et al., 1977; Rice et al., 1983; Skagen et al., 1998; Saab, 1999; Johnson et al., 2007; Pennington et al., 2008), we also addressed changes in plant community composition at the local scale to provide a context within which to analyze any changes in the bird community. Secondarily, we also examined whether certain ecological groups of species were more sensitive to landscape-scale urbanization than to local-scale vegetation (e.g., cavity nesters may be adversely affected by increased competition from European Starlings as urbanization increases, but indifferent to riparian plant species composition; Rottenborn, 1999). Emergent patterns associated with ecological groups may provide insights into mechanisms that may produce sensitivity to different scales, and permit generalizations that extend beyond the sample at hand. Determining whether riparian birds, either collectively or by ecological guild, are affected by urbanization at a landscape scale or by vegetation at the local spatial scale will allow us to better predict species' responses to future urbanization, and perhaps minimize its effects on bird communities.

2. Materials and methods

2.1. Study area

We conducted this study within a rapidly urbanizing area of Orange County, located in coastal southern California. It has been estimated that as much as 90% of the historic riparian habitat in the southern part of California has been completely lost to agriculture, urban development, flood control, and other human-caused impacts (Katibah, 1984; Jones and Stokes Associates, 1987), thus greatly magnifying the importance of remaining riparian areas for avian and other wildlife populations (Tewksbury et al., 2002).

Most of the development within the study area has occurred within the last 10–25 years. Development consists primarily of high-density single-family housing, supporting infrastructure, and commercial development. However, within the study area, most riparian systems have been retained in a system of regional parks and nature preserves, often with the entire corridor or canyon remaining as open space as development occurs on the ridgelines and intervening areas.

We surveyed 137 points located along approximately 110 km of riparian corridors within 20 different canyons (Fig. 1). Points within a corridor were located 0.8 km apart, although due to topography we placed a few at a distance of 0.5 km. Some riparian systems were long enough to support up to 15 survey points, whereas others were limited in size and contained only two or three. The majority of points were located along streams that are ephemeral or intermittent, and are dry most of the year. In the study area, the topography is such that riparian vegetation typically occurs in the bottom of a canyon, with upland vegetation immediately adjacent, and development on the ridgeline above (e.g., Fig. 2). For each accessible drainage in the study area, we placed points from the most upstream point accessible to the furthest accessible area downstream, or to where the drainage became channelized. Thus, we did not place any points in areas lacking some form of riparian vegetation. Width of riparian vegetation was highly variable, from a few meters to >50 m.

Development in the study area consists primarily of high-density suburban housing (20–30 houses/hectare for single-family detached housing; condominiums and attached housing are at lower densities but higher coverages), commercial development (strip malls, shopping centers), and supporting infrastructure (mainly roads; e.g., Fig. 2). Developed areas include some ornamental vegetation (e.g., landscaped medians, yards, and planters); however, sports fields and large recreational parks containing substantial ornamental vegetation were considered open space, and were not included in developed areas in the analyses presented below. Agricultural land uses are uncommon in the study area and were classified as a separate land cover; they were not included with developed areas in the analyses presented below. Although points were not specifically selected based on the amount of development within the surrounding landscape, there was a range from <10% to >95% developed within a 1000-m radius of each point.

2.2. Bird surveys

A survey consisted of a 10-min, unlimited radius point count, during which we recorded all bird species that were observed. Species observed flying overhead were recorded, but most were not used in statistical analyses because these species were detected at <10% of the points. The great majority of detections were within 50 m of the survey point.

We conducted a total of four survey visits in 2003 and 2004, two visits per year with one in early spring (March–May) and one in late spring to early summer (May–July). We conducted the second visit each year in reverse chronological order from

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