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Avian assemblages along a gradient of urbanization in a highly fragmented landscape

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Abstract

Our goal was to evaluate how avian assemblages varied along a gradient of urbanization in the highly fragmented landscape of coastal southern California. We measured species richness and abundance of birds within continuous blocks of habitat, within urban habitat fragments that varied in landscape and local habitat variables, and within the urban matrix at different distances from the wildland interface. These comparisons allowed us to characterize patterns of avifaunal response to a gradient of urban fragmentation. At the fragment scale, we found that fragment area was a strong, positive predictor of the total number of breeding species detected per fragment; total bird abundance per point count also increased with fragment size. Tree cover was higher in small fragments, as was the abundance of birds that typically occupy wooded habitats. Comparisons between core, fragment, and urban transects revealed differing patterns of response of individual bird species to urbanization. In unfragmented habitat, we recorded a relatively high diversity of urbanization-sensitive birds. In urban transects, these species were rare, and a relatively few species of non-native and anthropophilic birds were common. These urbanization-enhanced birds were also recorded in previous urban gradient studies in northern California and Ohio. Bird communities along the urban gradient reached their highest richness and abundance in fragments. The marked difference in vegetation structure between urban and natural landscapes in this arid shrubland system likely contributed to this pattern; the presence of native shrubs and exotic trees in fragments enabled both shrub and arboreal nesters to co-occur. As is characteristic of biotic homogenization, urban fragmentation in coastal southern California may increase local diversity but decrease overall regional avifaunal diversity.
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1. Introduction

Although urbanization can provide a large-scale mensurative experiment to test the effects of habitat fragmentation on ecological communities, urbanizing landscapes have received relatively little attention because ecologists have traditionally focused on more natural systems (Gilbert, 1989; McDonnell and Pickett, 1990; McDonnell et al., 1993; Adams, 1994; Pickett et al., 2001). An especially promising avenue of research is the use of urban gradients in ecological studies (Matson, 1990; McDonnell and Pickett, 1990; McDonnell et al., 1993; Blair, 1996, 2002). Urbanization can create a complex environmental gradient, from undisturbed natural areas to highly-modified urban landscapes, that can be useful in exploring relationships between environmental heterogeneity and the diversity and abundance of species (Matson, 1990; McDonnell and Pickett, 1990; McDonnell et al., 1993).

Most studies of urban bird communities have reported that species richness generally decreases with urbanization and that total avian density or biomass generally increases with urbanization (e.g. Emlen, 1974; Lancaster and Rees, 1979; Aldrich and Coffin, 1980; Beissenger and Osborne, 1982; Mills et al., 1989; Clergeau et al., 1998; Cam et al., 2000). However, most previous studies (reviewed in Blair, 1996 and Cam et al., 2000) have not investigated bird communities across a complete gradient of urbanization, from undisturbed to

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highly urbanized landscapes, but rather often have been limited to comparisons between a site before and after urban development or between two sites of differing levels of development. Recent studies that did compare bird communities across a complete urban gradient found that both species richness and total avian abundance peaked at moderate levels of development (Blair, 1996, 2001; McKinney and Lockwood, 2001); several other studies also have demonstrated increased avian diversity at intermediate levels of development (Nuorteva, 1971; Lancaster and Rees, 1979; Jokimaki and Suhonen, 1993). Because the study of urban–rural gradients is relatively new, however, little is known about the actual patterns of species richness and abundance along urban gradients, or the nature of presumptive mechanisms that may create these patterns (McDonnell et al., 1993).

Most research on the effects of habitat fragmentation on birds has focused on forest habitat, yet other habitats in North America are rapidly disappearing and the bird populations they support may be particularly sensitive to fragmentation effects (Soulé et al., 1988; Herkert, 1994; Bolger, 2001, 2002). Urban fragmentation particularly threatens Mediterranean scrub habitats in coastal southern California, creating a ''hot-spot'' of endangerment and extinction for the highly endemic biota in the region (Myers, 1990; Wilson, 1992; Dobson et al., 1997). Unlike forested systems, the predominant natural habitat in the area primarily consists of arid, low-growing, scrub vegetation, with native tree cover generally limited to riparian areas. Urbanization therefore adds novel structural elements, such as non-native trees, lush ornamental vegetation, and human edifices. Further, urban run-off considerably increases water and nutrient inputs into the arid natural habitat, potentially creating steep productivity gradients along the urban edge. Urban fragmentation in southern California therefore may generate a unique set of ecological changes along the urban–wildland interface that should be expected to impact arid region avifauna (Morrison and Bolger, 2002; Bolger, 2002).

Our goal was to evaluate how avian assemblages varied along a gradient of urbanization in this highly fragmented landscape. Urban development in San Diego and neighboring cities has left discrete patches of natural habitat immersed within a vast urban matrix, thereby creating an excellent opportunity to investigate the effects of urban fragmentation on bird communities (Soulé et al., 1988). Previous studies have documented the presence/absence of eight scrub-breeding bird species within these urban habitat islands (Soulé et al., 1988; Bolger et al., 1991; Crooks et al., 2001). We expanded on these prior studies by estimating both richness and abundance of the entire bird community within these fragments. These patches were distributed across a gradient of urban exposure, from small and old

habitat remnants within the urban core to larger and more recently isolated fragments near the urban fringe. We expected that avian assemblages would differ along this gradient of urban fragmentation, varying with landscape biogeographic variables such as fragment area and age (Soulé et al., 1988; Bolger et al., 1991; Crooks et al., 2001) and with local characteristics such as habitat structural complexity (Guthrie, 1974; Cody, 1975; Vale and Vale, 1976; Lancaster and Rees, 1979; Beissenger and Osborne, 1982; Mills et al., 1989; Blair, 1996; Clergeau et al., 1998; Cam et al., 2000).

We further extended previous studies by assessing avian richness and abundance along a full gradient of urbanization, including: (1) core habitat expanses—minimally disturbed habitat representing low urbanization exposure at the rural end of the urbanization gradient, (2) large and small habitat fragments—a range of urban habitat patches representing moderate urbanization exposure, and (3) the urban matrix—transects at different distances from the wildland interface representing high urbanization exposure within the developed end of the urbanization gradient. This represents a new variation of urban gradient sampling, in that most other studies typically have not included habitat fragments within urban areas as part of the gradient scheme (e.g. Blair, 1996, 2001). We then classified species based upon their patterns of response along the urban gradient, and compared these patterns to those of avifaunal assemblages along urban gradients in other systems.

2. Methods

2.1. Surveys

At the fragment level, we surveyed 34 remnant patches of chaparral and coastal sage scrub habitat in San Diego County, California, isolated at different times over the past century of urban development (for a map of the study area and exact location of the fragments, see Soulé et al., 1988 and Suarez et al., 1998). Thirty of these fragments were the same as those used in prior work on birds (Soulé et al., 1988). Most of the sites are fragments of dendritic canyons dissecting coastal mesas, although a few also contain mesa-top habitat. These canyons, typically ranging from 15 to 60 m in depth, are completely surrounded by human-modified landscapes. The fragments support a mosaic of shrub habitat, including coastal sage scrub, mixed chaparral, chamise chaparral, and maritime succulent shrub (Alberts et al., 1993). Disturbed areas within fragments were often dominated by ruderal species, ornamental plants invading from surrounding residences, fire-retardant ground cover such as South African iceplant (*Carpobrotus edulis*), and non-native trees (e.g. palms and species of *Eucalyptus* and *Acacia* spp.) (Alberts et al., 1993).

Species occurrences in each fragment were assessed through transect and point-count surveys. Surveys were conducted in each fragment at least three times by at least two different teams of observers from 4 April to 9 June 1997 between sunrise and 1030 h. For transect surveys, we slowly walked the long axis of the entire fragment a minimum of three times and recorded all species detected (mean time spent per transect survey in each fragment = 107 min, S.D. = 82.34). In addition, a minimum of three 8-min point counts (following Bolger et al., 1997a) were conducted at stations established in native habitat at ca. 250 m intervals along the long axis of each fragment; a total of 97 point count stations were established among the 34 fragments. The species detections from the point counts were combined with those from transect surveys to generate species richness estimates for each habitat fragment. In all subsequent analyses, we only included species known to breed in the coastal habitat mosaic in southern California. Species excluded from the analyses included non-breeding migrants, waterfowl, seabirds and shorebirds. In addition, all raptors were excluded because they were mainly detected as fly-overs (see later) and actual use of the sites was difficult to determine.

During point counts within habitat fragments, we recorded all individuals detected, method of detection (e.g. call, song, visual, fly-over), distance to the observer, and whether the bird was in the fragment or the adjacent urban matrix. We excluded all fly-overs, detections > 100 m from the observer, and detections within the adjacent urban matrix for analyses of point count data within fragments. To generate fragment-level abundance indices for each species, we first calculated the mean number of detections per 8-min point count at each station (averaging among multiple samples at each station), and then the mean number of detections per fragment (averaging among multiple stations within each fragment). We also calculated the mean number of species detected per 8-min point count per fragment. Where possible, point count stations were located ⩾ 100 m from fragment edges. However, because many fragments were narrow or small, a number of stations were located within 100 m of the fragment edge. Because we excluded detections within the urban matrix, the sampling radius was partially restricted for these stations, resulting in a smaller total area sampled and possibly lower abundance indices and species richness estimates. To correct for this potential bias, we estimated the area sampled at each station by measuring the distance from the station to the nearest urban edge and calculating the proportion of the 100 m radius point count circle that fell within the fragment. Abundance indices and species richness estimates were then corrected to an equal-area basis using this proportion. If detectability of birds decreases at farther distances from the observer (up to 100 m), then this correction may slightly inflate counts in smaller fragments.

To compare avifaunal assemblages across a full gradient of urbanization, we also conducted point counts within core habitat expanses and within the urban matrix in coastal San Diego County. For counts in core habitat, we established a total of 21 point count stations, separated by a minimum of 250 m, in three large core areas (> 1000 ha) of a regional habitat reserve network in San Diego: Mission Trails Regional Park, Los Penasquitos Canyon Preserve, and San Diego National Wildlife Refuge, Sweetwater Unit (for map of control sites see Morrison and Bolger, 2002). For urban counts, we established four parallel transects at 250, 500, 750, and 1000 m distances into the urban matrix from the boundary of Mission Trails Regional Park. Each distance transect consisted of 10 point count stations at ca. 250 m intervals along streets and/or sidewalks through the residential neighborhood parallel to the southwest and southeast boundary of the park. These urban transects allowed us to document birds occurring within urban areas and to investigate the extent that scrub birds within large habitat expanses penetrate the urban matrix. All control sites, habitat fragments, and urban transects were within a ca. 25 km radius semi-circle. Point count methodology and calculation of abundance indices and species richness estimates for unfragmented and urban sites were the same as for fragments.

2.2. Data analyses

2.2.1. Fragment-level analyses

We used fragment area, age, isolation, and% native cover as descriptors of the patch characteristics associated with each habitat fragment. We selected these measures because they have been identified as important predictors of occurrence of scrub-breeding birds (Soulé et al., 1988, 1992; Bolger et al., 1991; Crooks et al., 2001) and other animals (Bolger et al., 1997b, 2000; Suarez et al., 1998; Crooks and Soulé, 1999; Crooks, 2002) in this system. Total area of each habitat fragment was measured from digitized images of scaled aerial photographs taken in 1995; mean area for the 34 fragments was 17.7 ha (S.D. = 23.4; range = 1.6–101.6 ha). Fragment age, defined as the number of years since isolation of the habitat fragment by urban development, was obtained from San Diego County records (Soulé et al., 1988); mean age of fragments was 40.2 years (S.D. = 23.9; range = 8–95 years). Fragment isolation was measured as the distance to the nearest fragment that was equal to or larger in size than the given fragment (Soulé et al., 1988); mean fragment isolation was 643 m (S.D. = 657.2, range = 40–2865 m). Fragment area, age, and isolation were log-transformed to achieve normality. Percentage native shrub cover remaining in fragments was estimated from aerial photographs and from ground surveys in each habitat fragment (Suarez et al., 1998). Among the landscape variables, fragment

age is positively correlated to fragment isolation ($r = 0.342$, $P = 0.048$) and negatively correlated to % native cover ($r = -0.719$, $P < 0.001$).

We used standard multiple regression to assess which landscape variables (fragment size, age, isolation, % native cover) were significant predictors of (1) total species richness per fragment, (2) mean species richness per point count per fragment, and (3) total abundance, the mean abundance indices (per point count per fragment) summed over all breeding species. Throughout, all species richness and total abundance indices were log-transformed to meet normality assumptions for these analyses.

For each species, we used Spearman rank correlations to evaluate the relationship between fragment area and the mean abundance index (per point count per fragment); non-parametric rank correlations were used because the abundance of individual bird species could not be normalized to meet assumptions of parametric tests. $P < 0.05$ was considered statistically significant and $0.05 < P < 0.10$ was considered marginally significant throughout.

To characterize heterogeneity in local habitat structure within fragments, we used a Braun–Blanquet categorical scale (Kent and Coker, 1992) to estimate percent cover of bare ground, grasses, shrubs, and trees within a 20 m radius around each point count station. The cover scale was 0 ($<1\%$), 1 ($1–5\%$), 2 ($6–25\%$), 3 ($26–50\%$), 4 ($51–75\%$), and 5 ($76–100\%$). We then used linear regression to evaluate the relationship between fragment area and the mean score for each cover variable per station in each fragment. Our results (see later) indicated that tree cover was the only cover variable significantly related to fragment area. To investigate how variation in tree cover among fragments influenced avian communities, we summed for each fragment the mean abundance indices for those species classified as woodland, arboreal, or riparian in descriptions of the regional avifauna (Unitt, 1984, 2000). We then used linear regression to examine the relationship between fragment area and the total abundance of the arboreal (and non-arboreal) species.

2.2.2. Core/fragment/urban analyses

We compared species richness and abundance among the three core sites, 34 habitat fragments, and four urban distance transects. Because we surveyed four transects within one section of the urban matrix of San Diego, our statistical inferences regarding avifaunal assemblages within urban areas are necessarily limited to the portion of the matrix that these urban transects sampled. This section was typical of mature residential communities through much of coastal San Diego County. The neighborhood sampled was a ca. 20–40 years old, high-density, single-family residential community that supported a mature landscaped vegetative

component; each residence typically was fronted and backed by lawns and bordered by mature ornamental shrubs and trees.

Comparisons were conducted at the species and at the community level. First, for each species, we calculated and compared ratios of mean abundance indices between core, fragment, and urban transects. Second, we used Kruskal–Wallis nonparametric analysis of variance to compare community-level richness and abundance patterns among the core sites, urban transects, and two size classes of fragments, large (>30 ha: median = 56.4 ha; range = 31.0–101.6 ha; $n = 7$) and small (<30 ha: median = 7.14 ha; range = 1.6–18.4 ha; $n = 27$). The fragments were divided into two size classes to further dichotomize the degree to which natural habitat fragments and the birds within them may be influenced by urbanization impacts (Suarez et al., 1998; Bolger et al., 2000). Non-parametric tests were used because, due to relatively low sample sizes, the community-level variables often could not be transformed to meet assumptions of parametric tests. Community-level variables included: (1) abundance indices of non-native birds (European Starling, House Sparrow, Rock Dove), (2) abundance indices and species richness per point count, summed among all bird species, and (3) abundance indices and species richness per point count, summed among the eight native scrub-specialist birds that were focal species in previous fragmentation studies in this system (Soulé et al., 1988; Bolger et al., 1991; Crooks et al., 2001): California Quail, Wrentit, Spotted (formerly Rufous-sided) Towhee, Bewick's Wren, California Thrasher, Greater Roadrunner, Cactus Wren, and California Gnatcatcher (see Table 1 for scientific names).

3. Results

3.1. Fragment-level analyses

We detected a total of 88 species of birds during our transect and point count surveys within the 34 urban habitat fragments. Of these, 51 species breed in this region and were included in subsequent fragment analyses.

In multiple regression models, fragment area was a positive, significant predictor of the total number of species detected per fragment; the positive effect of % native cover was marginally significant (Table 2). Abundance indices, summed across all breeding species, was marginally related to fragment area (positive effect) and fragment isolation (negative effect). No landscape variables were significant predictors of the mean species richness per point count.

Fragment-level abundance indices increased with fragment area for California Gnatcatcher (Spearman

Table 1
Ratios[a] of mean abundance indices of breeding bird species between three unfragmented core sites, 34 urban habitat fragments, and four urban transects bordering Mission Trails Regional Park. Species are categorized by those that are urbanization enhanced (most abundant in urban transects), urbanization intermediate (most abundant in fragments), and urbanization sensitive (most abundant in core sites)[b]

		Ratios				Abundance index
Urbanization-enhanced		urban:fragment	urban:core	fragment:core	Average urban:fragment and urban:core	
Mourning Dove	Zenaida macroura	2.37	82.13	34.61	42.25	
Rock Dove	Columba livia	36.16			36.16	
European Starling	Sturnus vulgaris	3.39	43.65	12.89	23.52	
House Sparrow	Passer domesticus	12.28			12.28	
House Finch	Carpodacus mexicanus	1.06	23.06	21.75	12.06	
Northern Mockingbird	Mimus polyglottos	1.98	9.28	4.70	5.63	
Brown-headed Cowbird	Molothrus ater	2.07			2.07	
Cassin's Kingbird	Tyrannus vociferans	1.60			1.60	
American Crow	Corvus brachyrhynchos	1.59			1.59	
Common Raven	Corvus corax	1.58			1.58	
Hooded Oriole	Icterus cucullatus	1.15			1.15	
Only in Urban						
Brewer's Blackbird	Euphagus cyanocephalus					0.017
Urbanization-intermediate		fragment:urban	urban:core	fragment:core	Average fragment:urban and fragment:core	
Song Sparrow	Passerella melodia	18.55	1.80	33.38	25.96	
Pacific-slope Flycatcher	Empidonax difficilis	8.63	1.80	15.53	12.08	
Orange-crowned Warbler	Vermivora celata	12.46	0.90	11.22	11.84	
Bewick's Wren	Thryomanes bewickii	13.78	0.15	2.02	7.90	
House Wren	Troglodytes aedon	4.85	1.80	8.72	6.79	
Common Yellowthroat	Geothylpis trichas	8.19	0.23	1.84	5.02	
Bushtit	Psaltriparus minimus	4.54	0.74	3.38	3.96	
Western Tanager	Piranga ludoviciana	3.04			3.04	
Black-headed Grosbeak	Pheucticus melanocephalus			2.92	2.92	
Western Scrub Jay	Aphelocoma californica	1.62	1.61	2.61	2.12	
Anna's Hummingbird	Calypte anna	1.92	1.20	2.30	2.11	
Black Phoebe	Sayornis nigricans	1.09	2.59	2.81	1.95	
Bullock's Oriole	Icterus bullockii	1.54			1.54	
Western Kingbird	Tyrannus verticalis	1.19	1.35	1.60	1.40	
Only in Fragment						
Nuttall's Woodpecker	Picoides nuttallli					0.079
Ash-throated Flycatcher	Myiarchus cinerascens					0.067
Northern Flicker	Colaptes auratus					0.045
Horned Lark	Eremophila alpestris					0.025
Chipping Sparrow	Spizella passerina					0.024
Cactus Wren	Campylorhynchus brunneicapillus					0.004
Black-chinned Hummingbird	Archilochus alexandri					0.001
Western Wood-Pewee	Contopus sordidulus					0.001
Urbanization sensitive		fragment:urban	core:urban	core:fragment	Average core:urban and core:fragment	
Rufous-crowned Sparrow	Aimophila ruficeps			50.86	50.86	
Spotted Towhee	Pipilo maculatus	34.07	81.53	2.39	41.96	
Greater Roadrunner	Geococcyx californianus			36.26	36.26	
Phainopepla	Phainopepla nitens			31.86	31.86	
California Towhee	Pipilo crissalis	5.71	6.17	1.08	3.62	
California Gnatcatcher	Polioptila californica			4.22	4.22	
Wrentit	Chamaea fasciata			3.09	3.09	
California Quail	Callipepla californica			2.81	2.81	
Lesser Goldfinch	Carduelis psaltria	2.85	3.58	1.26	2.42	

Table 1 (*continued*)

		Ratios				Abundance index
		fragment:urban	*core:urban*	*core:fragment*	*Average core:urban and core:fragment*	
Lazuli Bunting	*Passerina amoena*			2.22	2.22	
California Thrasher	*Toxostoma redivivum*			1.73	1.73	
Costa's Hummingbird	*Calypte costae*	0.80	1.18	1.47	1.33	
Only in Core						
Grasshopper Sparrow	*Ammodramus savannarum*					0.266
Black-chinned Sparrow	*Spizella atrogularis*					0.137
Lark Sparrow	*Chondestes grammacus*					0.058
Warbling Vireo	*Vireo gilvus*					0.039
Canyon Wren	*Catherpes mexicanus*					0.014

[a] For each pairwise comparison, ratios are only presented for species detected in both site classifications (urban, fragment, or core).

[b] Within each category, species are listed in descending order of the degree to which they are urbanization enhanced, urbanization intermediate, or urbanization sensitive, based on average ratios calculated from urban, fragment, and core abundances, respectively. The numerator of the ratio is typically the largest value within each category. Species detected In only one site classification are ranked by their abundance indices at that site.

Table 2
Standard multiple regression models of the effects of landscape variables (fragment area, age, isolation,% cover) on mean abundance indices per fragment (summed over all breeding species), the mean number of breeding species detected per point count per fragment, and the total number of breeding species detected per fragment

	β	Standard Error	*P*-level
Log mean abundance index per fragment[a]			
Intercept			0.000
Log Area	0.295	0.166	0.086
Log Age	−0.210	0.246	0.400
Log Isolation	−0.356	0.175	0.051
% Native Cover	−0.360	0.233	0.134
Log mean species richness per point count[b]			
Intercept			0.000
Log Area	−0.027	0.182	0.883
Log Age	−0.153	0.269	0.573
Log Isolation	−0.253	0.191	0.196
% Native Cover	−0.096	0.256	0.709
Log species richness per fragment[c]			
Intercept			0.000
Log Area	0.840	0.103	0.000
Log Age	−0.151	0.152	0.329
Log Isolation	−0.179	0.108	0.108
% Native Cover	−0.275	0.145	0.067

[a] $R^2 = 0.248$; Adjusted $R^2 = 0.144$; df = 4, 29; $P = 0.074$.
[b] $R^2 = 0.095$; Adjusted $R^2 = -0.029$; df = 4, 29; $P = 0.557$.
[c] $R^2 = 0.711$, Adjusted $R^2 = 0.671$; df = 4, 29; $P < 0.001$.

$R = 0.578$, $P < 0.001$), California Quail ($R = 0.500$, $P = 0.003$), California Thrasher ($R = 0.684$, $P < 0.001$), Wrentit ($R = 0.599$, $P < 0.001$), Cassin's Kingbird ($R = 0.516$, $P = 0.002$), California Towhee ($R = 0.423$, $P = 0.013$), House Wren ($R = 0.348$, $P = 0.043$), Lesser Goldfinch ($R = 0.435$, $P = 0.010$), Phainopepla

($R = 0.343$, $P = 0.047$), and Song Sparrow ($R = 0.435$, $P = 0.010$). Abundance indices of the other species were not significantly related to fragment area ($P > 0.05$).

The mean percent tree cover within a fragment was negatively related to fragment area (Fig. 1a: $r = -0.468$, $P = 0.006$). Fragment area, however, was not significantly associated with shrub ($r = 0.137$, $P = 0.448$), grass ($r = 0.038$, $P = 0.835$) or bare ($r = 0.262$, $P = 0.141$) cover classes at each station. The total abundance of species defined as arboreal, woodland or riparian increased with declining fragment area (Fig. 1b: $r = -0.341$, $P = 0.049$). In contrast, the combined abundance indices of species not defined as arboreal, woodland, or riparian increased with fragment area (Fig. 1b: $r = 0.349$, $P = 0.043$). The inverse responses by arboreal and non-arboreal birds likely contributed to the weak relationships we recorded between total bird abundance and fragment area.

3.2. Core/fragment/urban analyses

Within the urban matrix adjacent to Mission Trails Regional Park, analyses revealed no difference among the 250, 500, 750, and 1000 m distance transects in species richness (Kruskal–Wallis $H_{3,40} = 1.100$, $P = 0.777$) or total avian abundance (Kruskal–Wallis $H_{3,40} = 2.328$, $P = 0.507$); abundance estimates of individual species also did not differ among distance transects (Kruskal–Wallis: $P > 0.05$).

Comparisons of mean abundance indices among core, fragment, and urban transects revealed three general patterns of response to urbanization: urbanization-enhanced, urbanization-intermediate, and urbanization-sensitive (Table 1). Urbanization-enhanced species were most abundant in urban transects and, if detected in both fragment and core transects, were more abundant
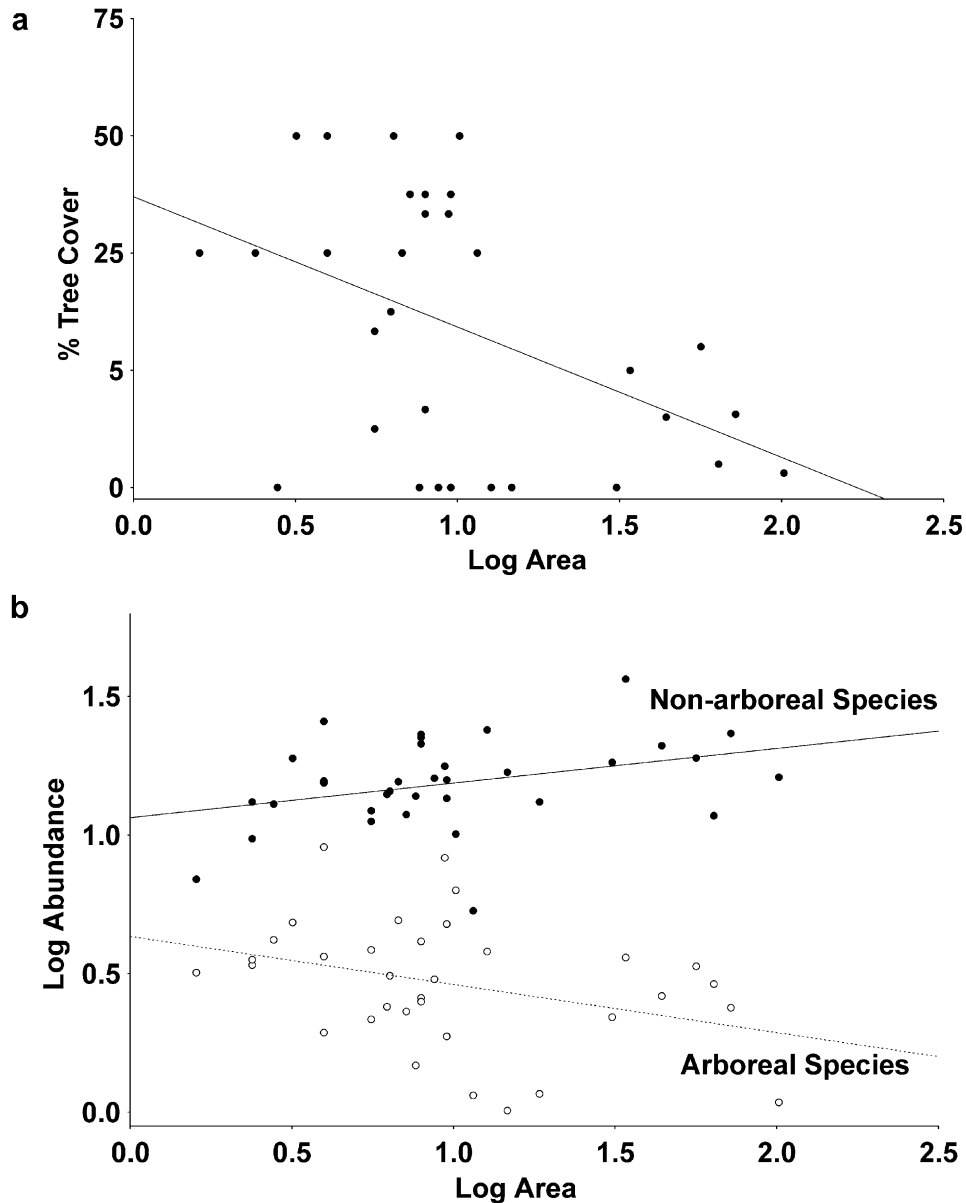
Fig. 1. The relationship between log fragment area and (a) mean% tree cover per point count station per fragment and (b) log total abundance indices of non-arboreal (solid line, filled circles) and arboreal (dashed line, open circles) species (as defined by Unitt, 1984, 2000).

in fragments than in unfragmented habitat. Mourning Dove, Rock Dove, European Starling, House Sparrow, and House Finch were particularly urbanization-enhanced and were, on average, over 10 times more abundant in urban transects than in fragments or unfragmented habitat.

Urbanization-intermediate species were most abundant in the fragments. Song Sparrow, Pacific-slope Flycatcher, and Orange-crowned warbler were particularly urbanization-intermediate and were, on average, over 10 times more abundant in fragments than in the urban matrix or core habitat. In addition, a suite of urbanization-intermediate species were only detected in the fragments and not in the urban or core transects (Table 1).

Finally, urbanization-sensitive species were most abundant in unfragmented habitat and, if detected in both fragments and urban transects, were more abundant in fragments than in the urban matrix (except for Costa's Hummingbird). Rufous-crowned Sparrow, Spotted Towhee, Greater Roadrunner, and Phainopepla were particularly urbanization-sensitive and were, on average, over 30 times more abundant in unfragmented habitat than in fragments or the urban matrix. In addition, a suite of species was only detected in core habitat and was never detected in fragments or the urban matrix (Table 1).

The abundance indices of non-native bird species (European Starling, House Sparrow, Rock Dove) significantly

differed among core, large fragment, small fragment, and urban classifications (Kruskal–Wallis $H_{3,41} = 12.820$, $P = 0.005$); abundance of exotic species was much higher in the urban matrix (mean = 4.58, S.E. = 0.417, $n = 4$) than in small fragments (mean = 0.61, S.E. = 0.160, $n = 27$), large fragments (mean = 0.21, S.E. = 0.315, $n = 7$), or core habitat (mean = 0.02, S.E. = 0.481, $n = 3$). Thus, exotic bird species in this system exhibited an urbanization-enhanced pattern of abundance.

Overall, the number of breeding bird species detected per point count differed among site classifications (Kruskal–Wallis $H_{3,41} = 13.607$, $P = 0.004$) and was higher in the large and small fragments, lower in core sites, and lowest in the urban transects (Fig. 2 a). Abundance indices, summed among all species, also differed among site classifications (Kruskal–Wallis $H_{3,41} = 8.038$, $P = 0.045$); total abundance was highest in the largest fragments, followed by small fragments and the urban matrix, and was lowest in core sites (Fig. 2a). Thus, both mean species richness per point count and mean abundance indices, summed across all species, exhibited an urbanization-intermediate pattern.

For the eight species of scrub-breeding birds used as focal species in previous studies (Soulé et al., 1988; Bolger et al., 1991; Crooks et al., 2001), species richness per point count differed among site classifications (Kruskal–Wallis $H_{3,41} = 16.659$, $P < 0.001$) and was highest in core habitat and large fragments, lower in smaller fragments, and minimal in the urban transects (Fig. 2b). A similar pattern was evident for total abundance, which differed among site classifications (Kruskal–Wallis $H_{3,41} = 19.311$, $P < 0.001$) and also was highest in core habitat and large fragments and lowest in the urban matrix (Fig. 2b). Thus, both mean species richness per point count and mean abundance indices for scrub-breeding birds exhibited an urbanization-sensitive pattern.

4. Discussion

Clear patterns emerged in the responses of individual bird species to urbanization, and this variation in sensitivity resulted in assemblages specific to the degree of disturbance along a gradient of urbanization. At one extreme, core habitat blocks, we recorded a relatively high richness of birds that occurred at relatively low abundances. At the opposite extreme of the urban–rural gradient, the urban matrix, many of these species were rare or absent. Instead, the assemblage we recorded consisted of a high abundance of a relatively few species of birds, including both non-native (Rock Dove, European Starling, House Sparrow) and anthropophilic (e.g. Mourning Dove, House Finch, Northern Mockingbird) species. Although our inferences are limited to

the neighborhood we sampled, the avifaunal assemblages we detected along our urban transects are typical of other urban systems (e.g. Guthrie, 1974; Emlen, 1974; Vale and Vale, 1976; Lancaster and Rees, 1979; Mills et al., 1989; Blair, 1996, 2001; Clergeau et al., 1998) and likely of much of the residential urban matrix surrounding natural areas in San Diego.

Thus, it appears that progressive urbanization has resulted in the replacement of many species by a smaller number of widespread and successful species that thrive in urbanized habitats. This process of a few "winners" replacing many "losers" in disturbed systems has been termed "biotic homogenization" and has become increasingly recognized as a serious threat to global diversity, resulting in ecological communities that become both more depauperate and more similar (Kareiva et al., 1993; Baskin, 1998; McKinney and Lockwood, 1999; Lockwood and McKinney, 2001). Homogenization of avifauna also has been documented along urban gradients in oak-woodlands in Palo Alto in northern California and eastern broadleaf forests in Oxford, Ohio (Blair, 2001). As might be expected, the assemblage of bird species we recorded in coastal southern California was more similar to the avifauna in northern California than in Ohio. Twenty-four (60%) of the 40 species of birds detected along the urban gradient in northern California were also detected in our study. In comparison, 11 (25%) of 44 species detected in the urban gradient in Ohio were also detected in southern California, an overlap in species composition similar to that recorded between northern California and Ohio (Blair, 2001). More importantly, avian assemblages in southern California became progressively more similar to those in northern California and Ohio as sites became more urban. Six (35%) of the 17 species classified as urbanization-sensitive, 10 (45%) of the 22 species classified as urbanization-intermediate, and 8 (66%) of the 12 species classified as urbanization-enhanced in our study were also found in the northern California urban gradient. Likewise, 1 (6%) of the 17 urbanization-sensitive species, 3 (14%) of the 22 urbanization-intermediate species, and 7 (58%) of 12 urbanization-enhanced species in our study were also found in the Ohio urban gradient. A similar pattern of homogenization in highly urbanized areas also occurred between northern California and Ohio (Blair, 2001). Clearly, urbanization is homogenizing avifaunal communities, even across distinct habitat types and geographic regions.

Our results also suggest that bird communities in this system may reach both their highest richness and abundance at moderate exposure to urbanization, in the fragments of natural habitat embedded within the urban matrix. Increased avian diversity and abundance at moderate levels of development of scrub habitat in coastal southern California are similar to the patterns described for birds in northern California and Ohio
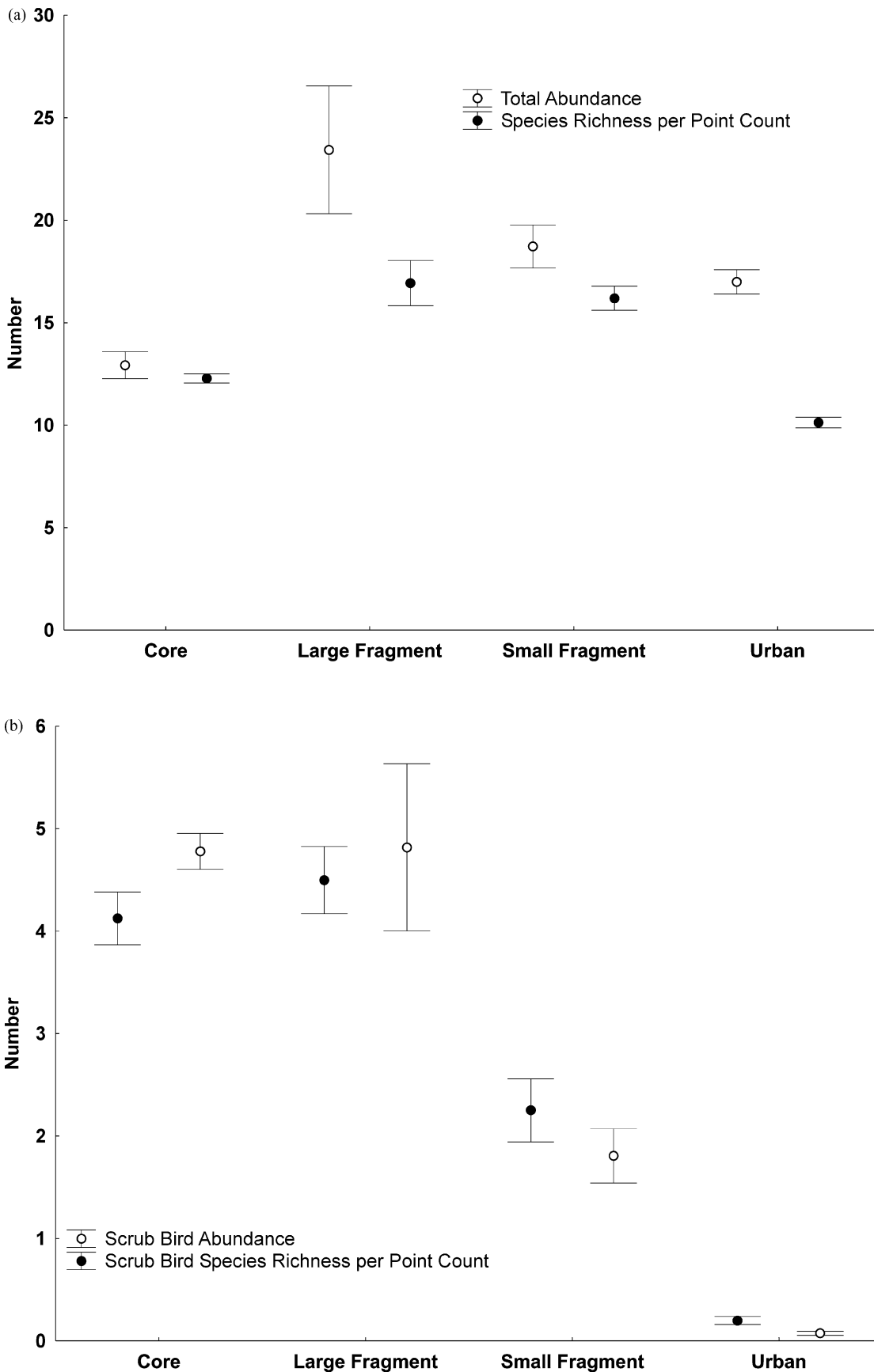
Fig. 2. Mean number of species detected per point count and mean abundance indices, summed across (a) all species (b) scrub-breeding species among three core sites, seven large fragments (> 30 ha), 27 small fragments (< 30 ha), and four urban transects. Error bars represented standard errors.

(Blair, 1996, 2001; McKinney and Lockwood, 2001). Our results are also consistent with predictions from a conceptual model developed for urban gradients that predicted highest diversity at intermediate levels of development (McDonnell et al., 1993). Following from previous work on environmental gradients and disturbance impacts (Whittaker, 1967; Connell, 1978), McDonnell et al. (1993) hypothesized that biotic constraints (e.g. competition and predation) in less developed habitats and physical constraints (e.g. habitat, resources, dispersal limitation) in urbanized habitats may be causal mechanisms underlying patterns of higher diversity at intermediate points in an urban gradient. In our study system, however, the juxtaposition of developed and natural landscapes along urban edges was likely a key factor contributing to the relatively high avian diversity we recorded within fragments (see also Case, 1996; McKinney and Lockwood, 2001).

Urbanization in arid shrublands results in increased structural elements, high water and nutrient inputs, and steep productivity gradients along the urban-wildland interface (Morrison and Bolger, 2002; Bolger, 2002). The habitat fragments we studied thus offered a mosaic of landscape elements, retaining enough native scrub habitat to support some species of urbanization-sensitive scrub breeding species, but also supporting enough modified habitat to attract arboreal and anthropophilic birds. Tree cover increased in smaller habitat fragments, as did the combined abundance indices of birds that typically live in oak woodlands and riparian areas in coastal southern California (e.g. Black Phoebe, Orange-crowned Warbler, Pacific-slope Flycatcher). Such species nest off the ground, are accustomed to the non-native tree cover present in disturbed fragments and the urban matrix, and therefore seem to adapt well to developed environments (Guthrie 1974). In general, habitat edges or ecotones often support relatively high diversity of species by providing greater vegetative complexity and access to multiple habitat types (Leopold, 1933; Yahner, 1988; Harris, 1988; Andren, 1994), and ecotones between urban and natural habitat can be especially ecologically active (McDonnell et al., 1993).

It is essential to emphasize, however, that although overall richness and abundance peaked in fragments, this clearly does not imply that parcelization of continuous habitat into remnant pieces should be a goal of conservation and management plans or would ultimately maximize diversity at a regional scale. Although the fragments may attract a wide diversity of birds, these habitat remnants also may function as "ecological traps" (Gates and Gysel, 1978) by providing suitable nesting conditions yet exposing birds to a variety of negative impacts, including increased predation and competition along fragment edges (Yahner, 1988; Paton, 1994). Further, the conservation status of birds along the urban gradient must be considered. We did

detect some rare bird species, including neo-tropical migrants, within the urban habitat fragments, and these patches also support a diversity of other native species, including plants (Alberts et al., 1993), rodents (Bolger et al., 1997b), invertebrates (Suarez et al., 1998; Bolger et al., 2000), and mammalian carnivores (Crooks, 2002). As such, the fragments, particularly the largest patches, should serve as important components of regional conservation strategies. However, many urbanization-enhanced and urbanization-intermediate species detected within smaller fragments and the urban matrix are widespread, common birds of low conservation priority. Moreover, such disturbed sites often failed to support populations of urbanization-sensitive birds that are of considerable conservation concern in the region, including the California Gnatcatcher, a federally listed species that has been the focus of habitat conservation plans and reserve designs throughout coastal southern California (Atwood and Noss, 1994). Of the eight scrub-specialist birds that were focal species in previous studies (Soulé et al., 1988; Bolger et al., 1991; Crooks et al., 2001), we recorded only seven Bewick's Wren and two Spotted Towhee detections, and no other scrub birds, along our urban transects (Crooks et al., 2001). Thus, as is characteristic of biotic homogenization, urban fragmentation may increase local diversity but can also decrease overall regional avifaunal diversity (Case, 1996; McKinney and Lockwood, 2001).

Overall, our results suggest that avian assemblages in this urbanizing landscape are shaped by the differential responses of individual species to development and habitat fragmentation. Identification of species-specific traits associated with sensitivity to urbanization is essential to understand the processes involved in community assembly. Selective extirpation of "losers" and selective success of "winners" will act to enhance large-scale biotic homogenization and to accelerate biodiversity loss (McKinney and Lockwood, 1999, 2001). A variety of ecological characteristics may help determine winners and losers in a developing landscape. Populations of the most successful species, such as House Sparrow, European Starling, House Finch, Mourning Dove, and Rock Dove, may be able to flourish in urban areas because they are gregarious and not limited by the costs associated with the development and maintenance of territories (Emlen, 1974; Mills et al., 1989), a trait that may facilitate the invasion of exotic species into natural systems (Holway et al., 1998; Holway and Suarez, 1999). Subsidized food resources, urban runoff, and nest and roost sites associated with human structures also help facilitate the invasion of urbanization-enhanced birds, such as woodland and non-native species, in developed areas (Lancaster and Rees, 1979; Tweit and Tweit, 1986; Mills et al., 1989). Successful urban-adapted species also tend to be omnivorous, whereas other feeding guilds, such as granivores, frugivores, and insectivores, may be

more limited by resource availability (Emlen, 1974; Lancaster and Rees, 1979; Beissenger and Osborne, 1982; Clergeau et al., 1998). Continued ecological and behavioral studies investigating diet, resource specializations, and inter- and intra-specific interactions are necessary to determine the mechanisms behind persistence and success in urban landscapes.

Acknowledgements

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