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EFFECTS OF URBANIZATION ON BREEDING BIRD COMMUNITY STRUCTURE IN SOUTHWESTERN DESERT HABITATS[1]

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Abstract. Breeding bird communities in Sonoran Desert habitats show strong correlations between total bird density and an index of vegetation volume. We have suggested that this empirical relationship is due to responses of breeding birds to critical resources, for which vegetation volume is an accurate estimator. In 1987, we conducted a study in Tucson, Arizona, to determine how this empirical relationship is affected by the presence of exotic species of plants and birds, and other factors associated with urbanization. We supported five predictions of our resource-based hypothesis by examining patterns of bird density and diversity in 34 neighborhoods. Densities of territorial native bird species, as well as native species richness and overall species diversity, were strongly correlated with the vegetation volume of native plant species, and uncorrelated with volume of exotic plant species. Densities of exotic and nonterritorial native birds correlated with exotic vegetation volume, the factor which best estimated the distribution of roosting and nesting sites preferred by these species. Vegetation factors explained more of the variance in breeding bird density than did measures of housing density. We interpret these results as confirming our hypothesis that densities of breeding birds correlate strongest with factors associated with critical resources. In addition, these patterns suggest that native bird populations may be better retained in areas of urban development by landscaping with native plants in such a way as to retain predevelopment distributions of vegetation volume.

Key words: Arizona; breeding bird density; avian community structure; vegetation volume; urbanization.

INTRODUCTION

The ability of urban habitats to support diverse assemblages of breeding birds has received widespread study (Graber and Graber 1963, Woolfenden and Rohwer 1969, Emlen 1974, Lancaster and Rees 1979, Aldrich and Coffin 1980, Williamson and DeGraaf 1981). In general, total breeding bird density is often higher in urban areas, while species richness and diversity are usually lower than in nearby natural habitats (Emlen 1974, Lancaster and Rees 1979, Aldrich and Coffin 1980, Beissinger and Osborne 1982, DeGraaf and Wentworth 1986, Geis 1986, Rosenberg et al. 1987). Although the number of native bird species may be reduced in urban habitats, certain neighborhood types may provide refuges for bird species whose native habitats have been severely reduced (Rosenberg et al. 1987). To evaluate the potential of urbanized land to provide such refuges, the population characteristics of native birds in urban settings must be better understood. In particular, we must determine the critical resources required by native birds, and whether urban bird populations respond to resources in a manner similar to populations in natural habitats.

Recently, we determined that breeding bird densities in native southwestern habitats correlated strongly with volume of native vegetation (Mills, Dunning, and Bates, unpubl.). We hypothesized that the strong empirical relationship between vegetation volume and breeding bird density resulted from a correlation between vegetation volume and the resources upon which breeding birds depend. If this resource-based hypothesis is correct, and if birds respond to resources in urban areas in a manner similar to their response in natural areas, then urban bird communities should also show strong correlations between breeding bird density and vegetation volume. However, urban habitats are complicated by the presence of both exotic species of plants and birds, and disturbance factors as-

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sociated with houses and human occupation. In this paper, we present the results of a study designed to measure the effect of these complicating factors in urban areas on the previously established relationship between resource-related variables and breeding densities of southwestern birds.

We censused birds and measured vegetation in 34 neighborhoods of Tucson, Arizona. Three previous studies have examined characteristics of Arizona urban bird communities. Emlen (1974) compared birds of a Tucson residential area with a relatively natural desert area near town. Tweit and Tweit (1986) described urban avifaunas of several Tucson sites, while Rosenberg et al. (1987) compared avifaunas of two Tempe, Arizona sites with local riparian bird communities. Each of these studies focused on describing components of the urban bird communities; relatively little quantitative data were collected on vegetative or other resource-related variables. Emlen (1974) measured vegetative and other structural characteristics of his sites sufficiently to compare foliage height diversity and other overall vegetation descriptors, but he did not examine other factors such as vegetation volume or the relative dominance of particular plant species or groups of species.

We conducted our study primarily to determine if birds in urban habitats in the desert southwest showed the same relationship between vegetation volume and breeding bird density that had been demonstrated by our previous work in natural habitats. Based on this previous work and the published descriptions of southwestern urban bird communities cited above, we predicted the following patterns between Tucson breeding bird densities and resource-related environmental variables:

(1) Native territorial bird density in urban areas should correlate best with the volume of native plant species, just as in natural habitats. Mills, Dunning, and Bates (unpubl.) suggest that native vegetation volume may be an accurate estimator of available food, among other resources, to breeding birds. Many exotic plants, such as eucalyptus, support low insect populations. Indeed, nonnative plants are often selected for landscaping because they are not damaged by insect "pests." Thus, the vegetation volume of exotic plants should not provide an accurate index to available food resources, and should not correlate with native territorial bird density.

(2) Density of nonterritorial native birds such as doves should correlate better with total or exotic vegetation volume than with native vegetation volume. These species are known to roost and nest in areas of dense vegetation regardless of plant species (Anderson et al. 1977) and often forage at some distance from roost and nest areas. Tall, dense trees in southwestern urban areas are usually exotic species; and these plants attract large numbers of nonterritorial birds (pers. observ.). Since roosting sites appear to be important resources for these birds, the resource-based hypothesis predicts that the density of nonterritorial native birds will correlate best with exotic vegetation volume.

(3) Densities of exotic birds are not expected to correlate positively with native vegetation volume, but may correlate with exotic vegetation volume or housing density. The lack of exotic birds in most natural habitats suggests that these species do not obtain their critical resources from native plants. Previous studies suggest that artificial sources of food and roost sites associated with man-made structures are the resources most responsible for maintaining populations of exotic birds (Geis 1986, Tweit and Tweit 1986). Thus, exotic birds should correlate with measures that estimate availability of artificial food supplies (housing factors) or roost sites (exotic vegetation volume, housing factors).

(4) Total densities of urban birds should correlate with vegetation factors better than with housing density. Housing density should be the predominate factor correlated with urban bird densities only if resources associated with houses are more important than vegetation-associated resources. This might be true, for instance, if factors associated with houses, such as pets or noise, decrease bird abundances. Negative correlations between bird densities and housing factors would be expected in this case.

(5) Species richness and diversity of native birds should correlate best with native vegetation volume. Individual native bird species are often strongly associated with particular native plant species (Rotenberry 1985). As the total volume of native vegetation increases in an area, sufficient amounts of each plant providing the critical resource needed by particular birds are more likely to be found. Since few native species of birds depend on resources associated with exotic plant species, increases in exotic vegetation volume should not increase the number of native

TABLE 1. Housing densities and vegetation volumes of Tucson, Arizona study sites. Housing densities are expressed as units per hectare including houses only partially in or immediately adjacent to study sites. Total vegetation volume = sum of native, exotic, and near-native (not shown) vegetation volumes.

Site number	Housing density	TVV[a]	VVNAT[b]	VVEXOT[c]
Native Urban sites				
1	1.1	0.70	0.61	0.01
2	1.1	0.33	0.32	0.00
3	0.8	0.83	0.35	0.36
6	0.8	0.10	0.08	0.00
7	1.2	0.25	0.23	0.01
11	1.1	0.45	0.24	0.04
18	2.6	0.33	0.13	0.01
23	2.2	0.08	0.03	0.03
38	2.7	0.30	0.05	0.03
Mean	1.5	0.37	0.23	0.05
Exotic Urban sites				
4	1.1	0.63	0.12	0.45
5	1.6	0.59	0.04	0.47
10	1.5	0.58	0.15	0.35
12	2.3	0.61	0.00	0.50
13	0.8	0.34	0.00	0.31
14	3.2	0.08	0.02	0.03
16	2.6	0.19	0.02	0.11
17	2.9	0.16	0.00	0.11
20	3.4	0.31	0.05	0.17
21	3.6	0.67	0.00	0.63
22	2.9	0.08	0.01	0.02
24	3.1	0.04	0.01	0.02
25	2.8	0.03	0.00	0.01
Mean	2.4	0.33	0.03	0.24
Native Control sites				
26	0	0.43	0.43	0.00
27	0	0.46	0.46	0.00
30	0	0.40	0.40	0.00
31	0	1.02	1.02	0.00
36	0	0.30	0.30	0.00
37	0	0.15	0.07	0.05
Mean	0	0.46	0.44	0.01
Exotic Control sites				
28	0	0.93	0.01	0.87
29	0	0.52	0.00	0.45
32	0	0.09	0.00	0.05
33	0.7[d]	0.01	0.00	0.01
Mean	0.2	0.39	0.00	0.34

[a] Total vegetation volume (all volumes in m^3/m^2).
[b] Vegetation volume of native plant species.
[c] Vegetation volume of exotic plant species.
[d] Commercial buildings, not residential units.

species supported in an area. Thus, native bird species richness and diversity should not be correlated with vegetation volume of exotic plants.

METHODS

We selected as study sites Tucson neighborhoods that had particular combinations of housing density (low, medium, or high), vegetation type (native or exotic), and vegetation volumes (low or high). Certain combinations of these characteristics were too rare to allow us to select two sites in each cell of the idealized matrix of our original study design. For instance, few Tucson neighborhoods with low housing density also have a low density of mostly exotic vegetation. Nevertheless, we sampled 34 urban and native-habitat sites covering a wide range of vegetation volumes and housing densities (Table 1). These areas fell into four basic categories: urban areas with high percentages of native vegetation (hereafter, Native Urban sites), urban areas with high percentages of exotic vegetation (Exotic Urban sites), natural desert areas with native vegetation and no houses (Native Control sites), and urban parks and cemeteries with exotic vegetation and no houses (Exotic Control sites). Native Control sites spanned a variety of native plant communities, including creosote flats, upland desert scrub, and mesquite washes, selected to duplicate the range of vegetation volumes found in Tucson urban neighborhoods.

In each neighborhood we censused strips which were 812 m (0.5 miles) long, 49 m (160 feet) wide, and which included the front yards of houses in each site. Each study area encompassed 3.9 ha (9.7 acres). The width of each strip was limited by the distance that an observer could be reasonably sure of counting all birds along the route. Thus, total width was imposed by the size of the yards in neighborhoods with homes closest to the road. The length of the transects was the longest distance for which we could find neighborhoods in the Tucson area with reasonably uniform vegetation and housing characteristics. To compare our methods with previous studies, we included one of Emlen's (1974) original study sites as an Exotic Urban site.

At each study site we measured the volume of vegetation, area of lawn, housing area, housing density, and censused breeding birds. We used a 6-m pole marked in decimeter and meter sections to count the amount of vegetation in each meter layer above the ground at up to 200 points per study site. These vegetation counts were summed into an index of Total Vegetation Volume (TVV). Our technique is similar to that of Wiens and Rotenberry (1981) and allows calculation of vegetation volumes for individual plant species, and for each meter layer. A more complete description of the pole technique and applications in native habitats is in preparation;

a summary of the technique is available from the senior author. We calculated TVV on each plot using measurements of the vegetated portion of each neighborhood only. Nonvegetated areas, such as houses, streets, and driveways, were measured from aerial photographs, and TVV indices were adjusted proportionally.

Housing and lawn areas were calculated from aerial photographs by measuring the portions of each study area that were occupied by buildings and lawns. To measure housing density, we counted the number of houses along the street(s) on which the study plot was centered. We included these variables in the analysis since some researchers feel housing factors such as these are effective measures of human-related disturbance and artificial food supplies in urban areas (e.g., Lancaster and Rees 1979).

To calculate native and exotic vegetation volumes, we classified plant species into one of three categories. Native plants were species which occur naturally in the Tucson Basin. Near-native species included those plants native to the southwestern United States or northwestern Mexico, but not the Tucson Basin. Examples of near-native plants include higher-elevation species such as sotol (*Dasylirion wheeleri*), as well as species from adjacent Texas or Mexico such as Texas ranger (*Leucophyllum texanum*) and sweet acacia (*Acacia farensiana*). We also included in the near-native category plants from South America which are very similar to native species, such as Chilean mesquite (*Prosopis chilensis*). In most study sites, near-native plants made up a small fraction of the total vegetation volume. The third category of plants, exotics, were species from other parts of the United States or the world.

Most species of birds were readily classified as native (those which occur naturally in the Tucson Basin) or exotic (those which have been introduced by man). However, like the plants, some bird species did not fit either category. A few species, such as Inca Dove and Great-tailed Grackle (see Appendix for scientific names and classifications of bird species encountered on censuses), did not occur originally in the Tucson Basin, but have expanded their range to include the cities of southern Arizona. These species are generally dependent on urban or agricultural environments (Phillips et al. 1964). We placed these species in a separate category of near-native birds.

We censused birds in each study area eight to 12 times between 29 April and 13 June 1987, the early breeding period for most species. We conducted the censuses over as short a period as possible to minimize seasonal variation in breeding behavior and numbers. Censuses at each site were spread over the census period to minimize further these effects. All censuses were conducted between 05:00 and 09:00, when birds were usually most active, on days with no rain or high winds. Censuses were conducted by two trained observers (JBD and JMB). Preliminary trials determined that differences between the observers' censusing abilities were not significant. However, to minimize any bias from this variable, half of the censuses at each study site were done by each observer.

Since the transect areas were narrow and vegetation relatively open, we assumed that all individuals could be counted directly and made no adjustments for detectability. Birds flying over the study areas, fledglings, and migrants were excluded from data analysis. We calculated from the census data the following variables for each site: mean number of individuals summed over all species (hereafter, total density); mean number of individuals recorded for each species; total number of species recorded at each site summed over all censuses (species number); and species diversity as measured by the H′ information index.

To determine how far the effects of urbanization extended away from housing, we established three parallel transects in native desert vegetation adjacent to an Exotic Urban transect in a mobile home park. This site had a high density of housing and a relatively high volume of exotic vegetation. The desert transect closest to the neighborhood bordered the backyards of the development. Since each transect was 49 m wide, the center line of the outermost transect was approximately 122 m (400 feet) from the edge of the development. The outermost desert transect was included in the overall data analysis as a Native Control site, while the middle two transects were used only in determining how far the effect of urbanization extended into the surrounding desert scrub. Thus, we used 32 of the 34 study sites in most of the analyses reported below.

We searched for significant relationships between bird density and potential causal factors with simple linear and stepwise multiple regression procedures using SAS modified for use on a personal computer (SAS 1986). Because study

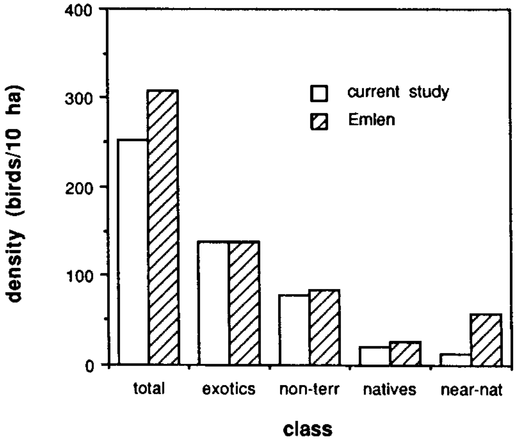

FIGURE 1. Bird densities at an Exotic Urban site censused by Emlen (1974) and in the current study.

areas were not randomly selected, r^2 calculated from these data reflect the amount of variance explained in the sample, not the overall population. Since our goal was to compare the relative effect of particular factors on bird densities in our sample, nonrandom selection of sites did not pose a problem for analysis.

To determine how vegetation volume and housing density affected the different components of the bird community, we ran regressions using the total density of breeding birds (TOTAL), and the densities of native (NAT), exotic (EXOT), and near-native (NEAR) bird species as dependent variables. To separate the effects of territorial and nonterritorial native species, we also used the density of territorial native birds (TERR = NAT minus densities of Mourning Dove, White-winged Dove, and House Finch) as a dependent variable in the regression analyses. Independent variables included total vegetation volume (TVV), the vegetation volume of native plant species (VVNAT), vegetation volume of exotic plant species (VVEXOT), area of lawn (LAWN), housing area (HAREA), and housing density (NUMHOUS).

We tested goodness of fit to the linear regression models by examining regression residuals. Residuals not normally distributed about the regression line, as determined by Kolmogorov-Smirnov goodness-of-fit tests, may indicate nonlinear relationships exist between variables (Sokal and Rohlf 1981). Correlations were accepted as significant if $P < 0.05$, and all reported correlations were positive unless otherwise stated.

RESULTS

COMPARISON WITH EMLEN (1974)

To determine if our technique of censusing birds only in the front yards of each site accurately estimated local bird density, we compared the bird densities we recorded at one Exotic Urban site with those reported by Emlen (1974) who censused the same site, but used a different methodology which also covered backyards. We could not compare densities statistically because Emlen (1974) did not include variance estimates with his densities; however, no differences in total bird densities, or the densities of native, territorial native, or exotic species were apparent (Fig. 1). Our study recorded fewer near-native birds (only 23% of the total reported by Emlen; in all other bird classes we recorded 80–100% of Emlen's totals). Inca Doves, the most common near-native species, roosted on power lines in the backyards in this neighborhood (Emlen 1974); these individuals were not recorded by our technique. Since dove roosts in other neighborhoods were within our censusing areas, and since no other significant differences were noted, we feel our technique recorded bird densities as accurately as previous studies.

COMPARISONS OF DENSITIES IN URBAN AND NATURAL HABITATS

We compared mean densities at the Exotic Urban, Native Urban, and Exotic Control sites to mean densities at the Native Control sites and those reported from 15 native vegetation areas in the Tucson Basin analyzed in Mills, Dunning, and Bates (unpubl.). Because bird densities may vary with increasing vegetation volume, this comparison is valid only if distributions of vegetation volumes in each category of sites were similar. Mean TVVs for the five classes of study areas were not significantly different (Table 2, Kruskal-Wallis H-test, $P > 0.05$).

Total bird densities were much higher in the urban sites, including the Exotic Control sites, than in natural habitats (Table 2). Much of this difference was due to exotic and near-native birds, which are essentially absent from natural habitats. However, densities of native birds were also higher in urban areas than in natural habitats. The higher density of native birds in the urban sites was due to increased numbers of doves and House Finches, since densities of territorial natives were lower in urban areas than in nearby

TABLE 2. Comparisons of mean densities and species number in each bird category at each site class. Densities are birds per 10 ha, vegetation volumes are m^3/m^2. Mean number of species is not included for the Native Sites because study plots in this sample were not of equal size to the urban plots, and therefore species numbers are not directly comparable. Abbreviations for bird density categories as in Methods.

	Site class				
	Exotic Urban	Exotic Control	Native Urban	Native Control	Native sites[a]
Number of sites	13	4	9	6	15
Mean TVV	0.33	0.39	0.37	0.46	0.43
Mean bird density					
TOTAL	154	198	92	48	50
EXOT	68	59	30	0.37[b]	0.03
NEAR	17	31	2.5	0.11[b]	0.0
NAT	68	109	60	48	50
TERR	14	13	28	39	43
Mean native species number	9.6	9.0	14.5	17.4	—

[a] From Mills, Dunning, and Bates, unpubl.
[b] All exotics and near-natives at native control sites were from one site close to urban development.

natural habitats. Territorial native densities in urban areas were slightly higher than expected from native vegetation volumes alone (Fig. 2). Nonterritorial natives were much more common in urban areas dominated by exotic plants than in areas dominated by native vegetation (Table 2).

VEGETATION AND HOUSING FACTORS AS CORRELATES OF BIRD DENSITY

When all sites were analyzed together, TVV correlated significantly with all categories of bird density except that of exotic birds (Table 3). When sites were separated into categories, TVV correlated with all density measures except exotics and near-natives at the nine Native Urban sites and the six Native Control sites. TVV correlated with all density measures at the 17 sites dominated by exotic vegetation (Exotic Urban and Exotic Control combined; there were too few Exotic Control sites to analyze separately). Examination of residuals showed few departures from normality. No significant model in Table 3 had residuals which suggested better fit by a nonlinear model.

We tested Predictions 1–3 by separating TVV into components of native vegetation volume and exotic vegetation volume. Over all sites, total and native bird densities correlated strongly with exotic vegetation volume, and did not correlate significantly with native vegetation volume (Table 3). In our previous studies in natural habitats, both of these density measures correlated strongly with native vegetation volume (Mills, Dunning, and Bates, unpubl.). The correlations between exotic vegetation volume and both total and native bird densities found in the present study were largely due to the preference of native White-winged Doves and House Finches to roost and nest in large, dense, exotic trees, especially aleppo pines (*Pinus halopensis*). When these nonterritorial native birds were removed from the data set, the density of territorial native

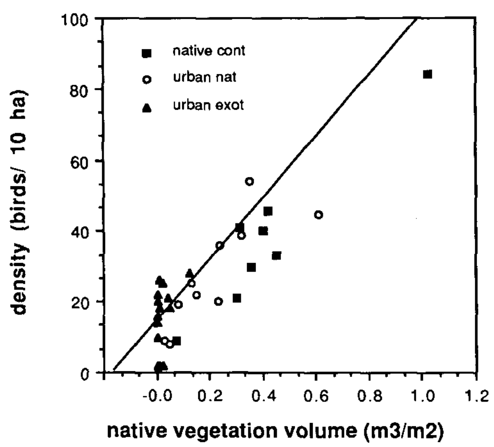

FIGURE 2. Density of territorial native bird species in urban areas as a function of the volume of native vegetation. Line represents the significant regression between avian density and vegetation volume found in a previous study of natural habitats (Mills, Dunning, and Bates, unpubl.). Open circles = Native Control sites, closed squares = Native Urban sites, open triangles = Exotic Urban and Exotic Control sites. Notice most points fall above the line, indicating that most sites had higher densities than expected.

TABLE 3. Correlation coefficients (*r*) from simple linear regression analyses of various density factors vs. environmental parameters. Abbreviations defined in Methods. Coefficients for density vs. TVV presented for all sites and for different classes of neighborhood types. No exotic or near-native birds were recorded at five of the six Native Control sites.

Environmental parameter	Bird densities				
	TOTAL	EXOT	NAT	TERR	NEAR
TVV all sites	0.60***	0.26	0.78***	0.67***	0.34*
Native Urban	0.83***	0.25	0.85**	0.87**	0.17
Exotic Urban	0.86***	0.57*	0.91***	0.57*	0.91***
Native Control	0.89*	–	0.89*	0.97***	–
VVEXOT	0.85***	0.62***	0.82***	−0.07	0.66***
VVNAT	−0.20	−0.40**	0.07	0.88***	−0.30
HAREA	−0.19	0.00	−0.33	−0.47**	−0.09
NUMHOUS	−0.06	0.16	−0.24	−0.46**	−0.03
LAWN	0.62***	0.49**	0.54***	−0.24	0.56***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
[a] Mean number of native bird species.
[b] Species diversity calculated with all species.
[c] Species diversity calculated with territorial native species only.

birds (TERR) was strongly correlated with native vegetation volume, as predicted (Table 3). A similarly high correlation between territorial native bird density and native vegetation volume was obtained even when the Native Control sites were removed ($r = 0.78$, $P < 0.001$). Densities of exotic and near-native birds correlated strongly with both exotic vegetation volume and area of lawn (Table 3); however, these two vegetation measures positively covaried (Table 4). Exotic bird density also correlated negatively with native vegetation volume. The strong correlations between exotic and near-native densities with lawn area were expected since both categories of bird density were dominated by ground-foragers attracted to grassy areas (EXOT: House Sparrow, European Starling; NEAR: Inca Dove, Great-tailed Grackle).

Housing factors did not correlate significantly with any measure of bird density except the density of territorial native birds (Table 3). In the stepwise multiple regression models for each measure of bird density, TVV explained more of the variance in bird density than either housing area or number of houses, and was the only variable loaded into each stepwise model. The significant negative correlations between territorial native density and the two housing factors were expected since significant negative covariance existed between native vegetation volume and both housing area and number of houses (Table 4). Again, in a stepwise model, native vegetation volume loaded before either housing variable in explaining the variance in density of territorial natives.

AVIAN SPECIES RICHNESS AND DIVERSITY

Most bird species recorded on our sites were native birds (46 of 54 species, 84%). The mean number of native bird species in our urban study sites was lower than in the Native Control sites, but the mean number of native species was higher in Native Urban sites than in either class of sites dominated by exotic vegetation (Table 2). As with native territorial bird densities, native species richness and diversity correlated more strongly with native vegetation volume than with any other variable (Table 3). Examination of residuals showed no significant departures from normality; however, the residuals suggested some nonlinearity may exist in the relationships between native vegetation volume and the diver-

TABLE 4. Correlation coefficients between environmental variables. Significance levels as in Table 3.

	VVEXOT	VVNAT	HAREA	NUMHOUS	LAWN
TVV	0.61***	0.54***	−0.39*	−0.33	0.23
VVEXOT	–	−0.32	−0.09	0.00	0.65***
VVNAT	–	–	−0.46*	−0.48**	−0.39*
HAREA	–	–	–	0.93***	−0.25
NUMHOUS	–	–	–	–	−0.21

TABLE 3. Extended.

Species number[a]	H' ALL[b]	H' TERR[c]
0.54**	0.43*	0.36*
−0.13	−0.17	−0.24
0.74***s	0.71***	0.63***
−0.43*	−0.62***	−0.33
−0.45*	−0.63***	−0.41*
−0.31	−0.17	−0.35

sity measures. Housing area and number of houses were negatively correlated with both the number of native bird species, and overall species diversity. The negative correlations between the housing factors and species diversity were due to the tendency for dense housing developments to have large numbers of a few exotic and non-territorial native species. When these species were removed and territorial native birds alone were analyzed, diversity was less correlated with housing factors (H' TERR, Table 2).

We examined the distribution patterns of species occurrence in various habitats by plotting the percentage of study sites within each habitat type in which each species occurred. For this analysis we considered the Native Control, Native Urban, and Exotic Urban sites, since sample sizes of Exotic Control sites were too small for meaningful analysis. Of the 46 native species which were observed in the study, 26 were recorded at more than three sites. Eighteen of these 26 had their highest frequency of occurrence in the Native Control sites (see Fig. 3 for examples). These species typically had similar or lower frequencies in Native Urban sites, and much lower frequencies in Exotic Urban sites. Five of these 18 native species were not found at any Exotic Urban site.

Two native species, Anna's Hummingbird and Northern Mockingbird, occurred most frequently in Exotic Urban sites and least frequently in Native Control areas. White-winged Dove, Western Kingbird, and Hooded Oriole were most frequent in Native Urban sites, decreasing in frequency in both Exotic Urban and Native Control

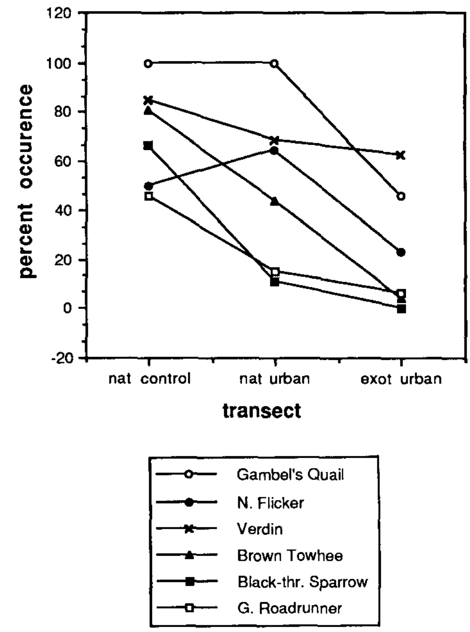

FIGURE 3. Percent occurrence of selected species in three habitat types showing the pattern most common for native species. Data shown is percentage of all sites at which the species occurred.

sites. As noted before, White-winged Doves attained their greatest densities in those Exotic Urban sites with aleppo pines; however, not all Exotic Urban sites contained this plant. White-winged Doves are less common in urban sites dominated by native vegetation, but they are generally found in moderate numbers throughout the city of Tucson. Finally, House Finch, Northern Cardinal, and Lesser Goldfinch occurred with equal frequency in all housing classes. House Finches were recorded at all sites. Densities and frequencies of occurrence of all species in each of the four major habitat types are presented in the Appendix.

INFLUENCE OF URBANIZATION ON BIRDS IN ADJACENT NATIVE HABITAT

We established a set of four adjacent parallel transects (one in an Exotic Urban site, three in nearby desert, see Methods) to determine how far birds associated with urbanized areas range into adjacent natural habitats. Vegetation volumes of all four transects were similar, but increased slightly with increasing distance from the urban area (Table 5). Total bird density, and densities of exotic, near-native, and native birds were higher in the urban area than in the adjacent

TABLE 5. Vegetation volumes, number of territorial native species, and diversity indices (H′) in an Exotic Urban site and three parallel transects in adjacent desert scrub. Vegetation volumes expressed in m^3/m^2. H′ calculated for all species (ALL) and for territorial native species (TERR).

Transect	TVV	VVNAT	VVEXOT	Territorial native species	H′ ALL	H′ TERR
Urban site	0.31	0.05	0.17	9	1.52	1.81
Inner transect	0.32	0.32	0.00	13	2.31	1.94
Middle transect	0.36	0.36	0.00	14	2.62	2.26
Outer transect	0.40	0.40	0.00	15	2.73	2.46

desert (Fig. 4). On the three parallel transects in the adjacent desert, total bird density was highest on the transect immediately bordering the urban site. This higher density was due to large numbers of nonterritorial doves and House Finches which roosted and nested immediately adjacent to the houses (pers. observ.). Territorial native densities were lowest on the urban transect, and similar in the three desert transects.

Densities of exotic and near-native species dropped very rapidly with distance away from the urban site. Most of the decrease in densities of these two groups occurred in the transect immediately adjacent to the urban site. The centerline of this transect was only 25 m from the buildings. Inca Doves and House Sparrows were the only near-native or exotic species recorded in the parallel desert transects.

As expected, the number of territorial native species was higher in the three desert transects than in the urban area (Table 5). Species number and diversity increased slightly with distance from the urban site. The outermost transect had the highest H′ value of all 34 sites in this study; this transect covered an area between 98 m and 146 m from houses.

DISCUSSION

Results of this study indicate that bird populations in urban areas are as complex and variable as those in natural habitats. Different species and groups of species appear to respond to different environmental parameters, though various aspects of vegetation appear to be the most important determinants of urban bird community parameters. As in natural communities (Mills, Dunning, and Bates, unpubl.), volume of native vegetation was the primary factor correlated with territorial native bird density and species richness, supporting Predictions 1 and 5 of our resource-based hypothesis. Although volume of native vegetation was the primary factor correlated with density of territorial native birds in our Tucson study sites, we found that urban areas with native vegetation supported slightly higher densities of native territorial birds than expected from similar analyses from natural habitats in the Tucson area (Fig. 2). There are at least two explanations for this. First, some territorial native birds use exotic or near-native plants to some degree (e.g., Northern Mockingbird). Our measure of native vegetation volume (VVNAT) underestimates vegetation-correlated resources somewhat for these birds. Secondly, some resources in urban areas, such as bird feeders or roost sites on buildings, are not associated with vegetation at all. Many people in our study sites supplied birds with both seed and sugar water during our study period. Densities of nonterritorial native birds correlated strongly with volume of exotic vegetation, supporting Prediction 2. The increased densities of doves, House Finches, and several native territorial species (Northern Mockingbird, Anna's Hummingbird) in our urban sites confirm Emlen's (1974) observation that certain native desert birds respond positively to urbanization.

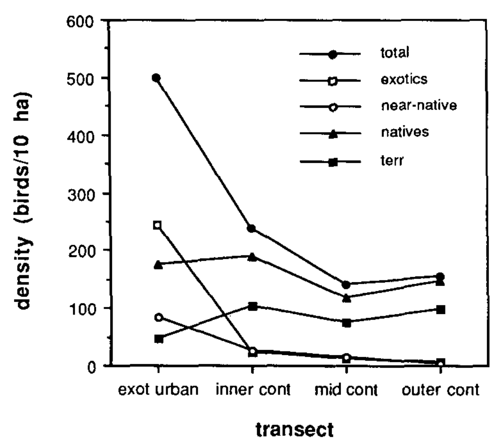

FIGURE 4. Bird densities in a series of parallel transects in and adjacent to an Exotic Urban site. Vegetation volumes for all transects are presented in Table 7.

Densities of exotic and near-native birds correlated best with volume of exotic vegetation, area of lawn, and total vegetation volume in the Exotic Control sites (which were heavily dominated by exotic plants). These results strongly support Prediction 3.

Housing density explained little of the variance in bird density (Prediction 4). Housing density, per se, and parameters directly associated with housing such as predation by dogs and cats, did not appear to have major direct impacts on bird densities or species numbers in the Tucson area, though they may have significant effects on individual bird species. In a stepwise regression model, volume of native vegetation loaded before any housing factor and explained 50% of the variance in species diversity of territorial native birds. Housing density explained an additional 11% of the variance in diversity. Housing density may have an important indirect effect on native birds through its effect on vegetation volume. Increasing housing in an area reduces the total area which can support vegetation. As the area covered by houses, driveways, roads, etc., is increased, less area is available on which to plant vegetation, and total vegetation volume will therefore decrease. In any urban area with high housing density, ground vegetation is especially reduced, eliminating habitat for species that nest or forage in low vegetation. In the Tucson area, the species that appear to be most affected by reduction of ground vegetation are Black-tailed Gnatcatcher, Black-throated Sparrow, and Brown Towhee (Tweit and Tweit 1986).

Previous studies have demonstrated that species richness and diversity are typically lower in urban areas compared to nearly natural habitats (Emlen 1974, Walcott 1974, Gavareski 1976, Lancaster and Rees 1979, Aldrich and Coffin 1980, Beissinger and Osborne 1982). Presence of native plants in our urban sites had a strong effect on the number and diversity of native bird species. Volume of native vegetation explained more of the variation in native bird species richness and diversity than did either total vegetation volume or housing factors (Table 2), supporting Prediction 5. Native vegetation was extremely rare in some of our study sites (Table 1); in general, these sites had few native bird species.

Previous studies have also established a strong correlation between vegetation volume and avian species richness (Geis 1986, Goldstein et al. 1986). Woody vegetation volume explained 50% of the variance in breeding bird species number in a Massachusetts study (Goldstein et al. 1986), very similar to the 55% of variance in species number explained by native vegetation volume in our study. Another factor found to be important in some studies of urban birds is the area of unfragmented native habitat (Aldrich and Coffin 1980, Beissinger and Osborne 1982). Since all of our study sites were of equal size, we cannot evaluate the relative importance of area and vegetation volume for particular birds in our study.

Our one series of parallel transects set at increasing distances from an Exotic Urban site indicated that the influence of exotic bird species on adjacent natural habitats diminished very rapidly with distance from the urban area. Exotic and near-native bird species were virtually absent at a distance of only 100 m from the housing development despite being very common in the urban area itself. Outside of the housing area, densities and species numbers of territorial native birds appeared to be little affected by distance from the urban site. Nonterritorial native birds were more abundant immediately adjacent to the housing area, where they roosted in large numbers. These patterns are only suggestive, however, since we examined only one set of parallel transects. It is possible that some native birds (e.g., hawks) were eliminated from the general area of this particular urban site, and thus did not appear on any transect. The diversity of the outermost transect was the highest recorded on any site in our study, however; so the bird assemblage in this area did not appear to be less diverse than elsewhere.

We did not look at seasonal variation in our study. Patterns of variation in winter bird populations at urban sites would be especially interesting because of the lack of seed-producing annual plants in urban areas (pers. observ.). Winter bird populations in southern Arizona are dominated by granivorous species (sparrows, doves, quail) which feed on these seeds (Tweit and Tweit 1986, Rosenberg et al. 1987).

IMPLICATIONS FOR RESIDENTIAL DEVELOPMENT

Our study indicated that impacts of urban development on bird communities depend on the amount and kinds of vegetation planted. We agree with Rosenberg et al. (1987) that by increasing the proportion of native vegetation used in landscaping, urban habitats can provide refuges for species whose native habitats have been greatly diminished. It may be possible with proper landscaping to maintain or increase the volume of native vegetation at a developed site compared to that available prior to development. Our study suggests that such practice would maintain densities of native birds similar to those existing before development. Some bird species, such as Black-throated Sparrows or Brown Towhees, may be lost regardless, since they appear to be particularly susceptible to negative effects of development.

Although it may be possible to maintain natural densities of territorial native birds in urban areas by using native plants in landscaping, one cannot merely duplicate the original volume without considering the predevelopment distribution of volume among layers and plant species. Both the amount (volume) and types of plants used are important in maintaining bird diversity. It may be possible, for instance, to restore predevelopment levels of native vegetation volume in areas of high housing density by planting a few large trees; however, the resulting changes in floristics and vegetation structure are likely to reduce or eliminate populations of some bird species.

Our study has shown that the types and amount of landscaping can have a strong effect on the composition of breeding bird assemblages in southwestern urban neighborhoods. Densities and species richness of urban neighborhoods dominated by native vegetation were most similar to those of natural habitats. As predicted by the resource-based hypothesis, exotic vegetation and housing density factors contributed little to models explaining the density of territorial native birds. Our study suggests that the effect of urbanization on breeding bird populations can be at least partially mitigated by the use of native vegetation in urban environments.

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APPENDIX. Densities and frequency of occurrence for bird species encountered during censuses. Densities in birds per 4 ha; % column shows percentage of sites within each neighborhood category in which the species was recorded.

	Exotic Urban		Exotic Control		Native Urban		Native Control	
	Density	%	Density	%	Density	%	Density	%
Exotic birds								
Rock Dove (*Columba livia*)	0.76	46	0.10	25	0.00	0	0.00	0
European Starling (*Sturnus vulgaris*)	1.27	62	3.85	100	0.70	33	0.00	0
House Sparrow (*Passer domesticus*)	25.56	100	19.71	100	11.20	100	0.15	17
Near-native								
Mallard (*Anas platyrhynchos*)	0.00	0	0.58	25	0.00	0	0.00	0
Inca Dove (*Columbina inca*)	6.81	69	5.48	100	0.87	67	0.04	17
American Robin (*Turdus migratorius*)	0.01	8	0.10	25	0.00	0	0.00	0
Great-tailed Grackle (*Quiscalus mexicanus*)	0.01	8	6.06	100	0.07	22	0.00	0
Bronzed Cowbird (*Molothrus aeneus*)	0.06	31	0.13	50	0.06	44	0.00	0
Native								
Turkey Vulture (*Cathartes aura*)	0.01	8	0.00	0	0.00	0	0.00	0
Cooper's Hawk (*Accipiter cooperi*)	0.00	0	0.00	0	0.00	0	0.02	17
Prairie Falcon (*Falco mexicanus*)	0.00	0	0.03	25	0.00	0	0.00	0
Gambel's Quail (*Callipepla gambelii*)	0.90	46	0.74	50	2.09	100	2.48	100
Killdeer (*Charadrius vociferus*)	0.00	0	0.48	25	0.02	11	0.00	0
White-winged Dove (*Zenaida asiatica*)	10.06	77	24.74	100	3.89	100	1.54	67
Mourning Dove (*Zenaida macroura*)	2.45	85	4.26	100	2.71	100	1.18	100
Greater Roadrunner (*Geococcyx californianus*)	0.00	0	0.00	0	0.01	11	0.11	50
Common Barn-Owl (*Tyto alba*)	0.00	0	0.00	0	0.00	0	0.28	33
Black-chinned Hummingbird (*Archilochus alexandri*)	0.28	46	0.06	25	0.31	56	0.19	67
Anna's Hummingbird (*Calypte anna*)	0.18	62	0.48	50	0.03	11	0.00	0
Gila Woodpecker (*Melanerpes uropygialis*)	0.65	62	0.19	25	1.16	78	0.36	67
Ladder-backed Woodpecker (*Picoides scalaris*)	0.00	0	0.06	50	0.06	22	0.13	50
Northern Flicker (*Picoides auratus*)	0.03	23	0.00	0	0.14	67	0.26	50
Northern Beardless-Tyrannulet (*Camptostoma imberbe*)	0.00	0	0.00	0	0.00	0	0.02	17
Say's Phoebe (*Sayornis saya*)	0.01	8	0.10	25	0.09	22	0.00	0
Ash-throated Flycatcher (*Myiarchus cinerascens*)	0.01	8	0.00	0	0.07	33	0.11	50
Brown-crested Flycatcher (*Myiarchus tyrannulus*)	0.06	23	0.00	0	0.40	44	0.62	67
Cassin's Kingbird (*Tyrannus vociferans*)	0.00	0	0.10	50	0.01	11	0.00	0
Western Kingbird (*Tyrannus verticalis*)	0.07	15	0.00	0	0.07	33	0.02	17
Horned Lark (*Eremophila alpestris*)	0.01	8	0.00	0	0.00	0	0.04	17
Verdin (*Auriparus flaviceps*)	0.23	62	0.06	25	0.80	67	2.24	83
Cactus Wren (*Campylorhynchus brunneicapillus*)	0.42	77	1.51	75	3.40	100	1.75	83
Canyon Wren (*Catherpes mexicanus*)	0.00	0	0.00	0	0.01	11	0.00	0
Bewick's Wren (*Thryomanes bewickii*)	0.00	0	0.00	0	0.00	0	0.56	17
Black-tailed Gnatcatcher (*Polioptila melanura*)	0.00	0	0.00	0	0.03	22	0.49	67
Northern Mockingbird (*Mimus polyglottos*)	2.03	54	1.38	75	0.30	44	0.06	17
Bendire's Thrasher (*Toxostoma bendirei*)	0.02	15	0.00	0	0.00	0	0.00	0
Curve-billed Thrasher (*Toxostoma curvirostre*)	0.47	54	0.03	25	0.79	89	0.43	83
Phainopepla (*Phainopepla nitens*)	0.00	0	0.00	0	0.00	0	0.04	17
Loggerhead Shrike (*Lanius ludovicianus*)	0.00	0	0.00	0	0.00	0	0.02	17
Bell's Vireo (*Vireo bellii*)	0.00	0	0.00	0	0.14	22	0.58	17
Lucy's Warbler (*Vermivora luciae*)	0.01	8	0.00	0	0.18	22	1.86	67
Yellow Warbler (*Dendroica petechia*)	0.02	15	0.00	0	0.00	0	0.02	17
Northern Cardinal (*Cardinalis cardinalis*)	0.23	54	0.00	0	0.63	56	0.41	50
Pyrrhuloxia (*Cardinalis sinuatus*)	0.01	8	0.00	0	0.14	44	0.60	50
Blue Grosbeak (*Guiraca caerulea*)	0.00	0	0.00	0	0.00	0	0.17	33
Brown Towhee (*Pipilo fuscus*)	0.00	0	0.00	0	0.17	44	0.51	83
Abert's Towhee (*Pipilo aberti*)	0.00	0	0.00	0	0.00	0	0.34	17
Rufous-winged Sparrow (*Aimophila carpalis*)	0.00	0	0.00	0	0.01	11	0.11	17

APPENDIX. Continued.

	Exotic Urban		Exotic Control		Native Urban		Native Control	
	Density	%	Density	%	Density	%	Density	%
Lark Sparrow (*Chondestes grammacus*)	0.00	0	0.03	25	0.00	0	0.00	0
Black-throated Sparrow (*Amphispiza bilineata*)	0.00	0	0.00	0	0.01	11	0.49	67
Brown-headed Cowbird (*Molothrus ater*)	0.07	38	0.00	0	0.04	33	0.26	67
Hooded Oriole (*Icterus cucullatus*)	0.07	23	0.03	25	0.07	44	0.00	0
House Finch (*Carpodacus mexicanus*)	9.24	100	9.71	100	6.33	100	1.07	100
Lesser Goldfinch (*Carduelis psaltria*)	0.07	15	0.00	0	0.14	11	0.04	17