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SEASONAL CHANGES IN AVIAN DENSITIES AND DIVERSITIES

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ABSTRACT.—We examined changes in avian species richness and densities over each season for four and one-half years. Data are from a variety of riparian areas along the lower Colorado River. We found that species richness and density estimates tended to vary through time and space in a nonrandom fashion, resulting in skewed or abnormally peaked distributions. Investigating this further with an analysis of variance, we found that significant variation is introduced through differences in the kinds of dominant vegetation present, vertical structure being nearly the same, and by seasonal variation. Both of these factors were further affected by annual changes; that is, the extent of variation in species richness and densities differed, not only from one type of vegetation to another and from season to season, but also from year to year. We concluded that one must be cautious in making inferences from comparative data collected in: (1) the same year but in different seasons; (2) vegetation differing in plant species composition even though structurally similar; and (3) the same season and vegetation but in different years. Before meaningful habitat evaluations can be made, data should be collected over several seasons and years.

It is important to biologists and crucial for natural resource managers to determine the factor(s) that account for variation in avian densities and diversities. It is also useful to know if a given habitat is of equal value to birds during all seasons, if density and species richness vary, and whether similarly structured vegetational communities, differing in species composition of the dominant vegetation, also differ with respect to avian numbers and species richness. While addressing these issues, we consider whether conclusions about avian use of the vegetation would differ if drawn from a single season or a number of seasons over a period of years. In this report we examine variation in avian numbers and species richness at specific sites over several seasons and years. We investigated these factors from 55 months of avian censusing (4950 censuses) in riparian ecosystems.

STUDY AREA

Our studies were conducted along the lower reach of the Colorado River from Davis Dam, Arizona-Nevada border, to the Mexican boundary south of Yuma, Arizona. Water flow in this area of the Colorado River is controlled for production of electrical power and irrigation. Natural flooding has been eliminated since the 1930s; consequently litter accumulates in the vegetation along the river, and fires are common. For this reason most of the vegetation consists of pure stands of the exotic fire-adapted salt cedar (*Tamarix chinensis*), or salt cedar mixed with arrowweed (*Tessaria sericea*), honey mesquite (*Prosopis glandulosa*), screwbean mesquite (*Prosopis pubescens*), cottonwood (*Populus fremontii*), or willow (*Salix gooddingii*). All of these stands of vegetation have been burned at some time during the last 10 to 20 years. Because burning has not been uniform, the vegetation has a patchy horizontal profile of dense to moderately open vegetation, with the bulk of the foliage being from 3 to 6 m high, except in recently burned areas.

Most riparian plant species are deciduous, with leaf drop occurring in November and December. Climate in the winter months of December through February varies annually, from years that are frost-free to years that have 45 or more nights of frost, with temperatures dropping to as low as −9°C.

Spring (March and April) temperatures along the lower Colorado River are also variable, with some years having numerous cold days with frost, whereas other years are mild and frost-free. These variable spring temperatures, combined with precipitation, play a major role in the timing of phenological events.

The summer months of May, June, and July are least variable since they are consistently hot and dry with varying amounts of wind. If rainfall occurs, it is generally during August and September, when humidity is also higher. Both day and night temperatures are relatively hot. The fall months of October and November are usually mild and dry with low temperatures occasionally dropping below 0°C by the end of November.

For the purpose of this report we recognized five types of vegetation. The species composition varied from pure salt cedar and pure honey mesquite to stands of approximately half salt cedar-half screwbean mesquite, half salt cedar-half honey mesquite, or salt cedar with scattered cottonwood and/or willow. In all vegetation types considered in this report, the vertical configuration was similar; about 25% of the volume was between 0 and 0.6 m, 50% was between 0.6 and 4.5 m, and about 25% was between 4.5 and 7.5 m. This configuration is typical of about 63% of the riparian vegetation in the lower Colorado River valley.

METHODS

In each of five types of vegetation, we established six avian census lines which totaled 4 to 8 km in length. On each of the 30 transects, three avian censuses were conducted each month, either in mid-month or during each third of the month from December 1974 through July 1979, using the variable distance transect technique developed by J. T. Emlen (1971). The data presented are based on these 4950 censuses. Censusers were rotated to balance possible observer differences across vegetation types.

The year was divided into five seasons: winter (December–February), spring (March–April), summer

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TABLE 1
RESULTS OF THREE-WAY ANALYSIS OF VARIANCE FOR AVIAN DENSITIES

	DF	*F*	*P*	R^2
Main effects	11	45.7	<0.001	75.5
Years	4	32.0	<0.001	14.4
Vegetation	4	53.6	<0.001	32.2
Season	4	48.0	<0.001	28.8
Two-way interaction	40	2.9	<0.001	17.2
Year-vegetation	12	0.3	NS	0.5
Year-season	12	2.2	<0.030	3.9
Vegetation-season	16	5.3	<0.001	12.8
Total R^2				92.7

	N	Deviation
Years		
1975	25	−0.14
1976	25	−0.03
1977	25	0.04
1978	25	0.13
Vegetation		
Cottonwood-willow-salt cedar	20	0.11
Honey mesquite	20	0.17
Salt cedar	20	−0.25
Salt cedar-honey mesquite	20	−0.07
Screwbean mesquite-salt cedar	20	0.04
Seasons		
Winter	20	−0.21
Spring	20	−0.09
Summer	20	0.19
Late summer	20	0.10
Fall	20	0.00

TABLE 2
RESULTS OF A THREE-WAY ANALYSIS OF VARIANCE FOR SPECIES RICHNESS

	DF	*F*	*P*	R^2
Main effects	11	48.2	<0.001	76.1
Years	3	47.5	<0.001	20.3
Vegetation	3	78.5	<0.001	44.9
Season	4	18.5	<0.001	10.9
Two-way interactions	40	3.1	<0.001	17.5
Year-vegetation	12	4.4	<0.001	7.6
Year-season	12	2.6	<0.010	4.4
Vegetation-season	16	2.4	<0.010	5.5
Total R^2				93.6

	N	Deviation
Years		
1975	35	−4.65
1976	25	−1.01
1977	25	2.23
1978	25	3.43
Vegetation		
Cottonwood-willow-salt cedar	20	7.73
Honey mesquite	20	1.18
Salt cedar	20	−6.12
Salt cedar-honey mesquite	20	−3.12
Screwbean mesquite-salt cedar	20	0.33
Seasons		
Winter	20	−3.77
Spring	20	2.38
Summer	20	−1.37
Late summer	20	1.28
Fall	20	1.48

(May–July), late summer (August–September), and fall (October–November). The population estimates from the three censuses were averaged for each census line each month. Monthly avian densities in each type of vegetation were calculated as the mean of the monthly estimates of all transects within that type. Seasonal avian densities were derived by taking the monthly means and computing a mean of means to represent the seasonal value for each vegetation-structural type.

Distributions were analyzed by a three-way analysis of variance and were normalized with $\log_{10}$ transformations.

RESULTS

DENSITIES

Main effects.—Initially we determined if seasons, years, and types of vegetation had a significant and systematic effect on the observed variation in avian densities. The combined effect of seasons, years, and types of vegetation was significant ($P < 0.001$) and explained 76% of the variance (Table 1). All three effects were also independently significant ($P < 0.001$). The greatest proportion of the variance was due more to differences between types of vegetation than to variation between years. The deviation from the "overall" or "grand" mean density indicated that 1975 densities were lowest among the years; among the types of vegetation, in salt cedar; among the seasons, in winter (Table 1). Densities were highest among the years, in 1978; among the types of vegetation, in honey mesquite; among the seasons, in summer.

Two-way interactions.—Combined, the two-way interactions explained an additional 17% of the variance (Table 1). Avian densities differed between years, but the amount of difference depended on which season (but not which type of vegetation) was considered. A year of high density in one type of vegetation was a year of high density in others as well. Not surprisingly, from the main effects we determined that the avian densities were different between seasons, but the amount of difference depended on both the year (year-season) and the type of vegetation (vegetation-season). The avian densities in the types of vegetation differed overall, and the amount of difference depended on season, but not on year; i.e., a favored type of vegetation in a good year was still favored in a poor year.

Species Richness

Main effects.—The effects of years, vegetation type, and season collectively explained 76% of the variance in the species richness data (Table 2). All three of these effects independently explained a significant ($P < 0.001$) amount of the variance. Habitat was the overwhelmingly most important factor, followed by annual variation, with seasonal variation of less (but still significant) importance. Species richness was lowest in 1975 among the years; in salt cedar, among the types of vegetation; and in winter, among the seasons (Table 2). Species richness was highest in 1978 among the years; in cottonwood-willow, among the vegetation types; and in spring among the seasons.

Two-way interactions.—Two-way interactions were all significant ($P < 0.001$) and accounted for an additional 18 percent of the variance (Table 2). Species richness varied annually, but the amount of difference depended on the type of vegetation and on the season. Similarly, richness varied seasonally, but the extent of difference depended on the year and type of vegetation. Finally, species richness varied with the type of vegetation, but the extent of the difference depended on the year and season.

DISCUSSION

Data presented demonstrate that, at least in the lower Colorado River area, significant differences in densities and diversities between vegetation types occur and should be looked for even though these communities differ very little in height and foliage volume. Differences can also be expected in the same vegetation type from season to season. Finally, given the same vegetation type and season, differences can be expected to occur between years. This suggests that considerable caution must be exercised when comparing census data. We need to be cautious in making inferences from comparative data with the following characteristics: (1) same year but different seasons; (2) vegetation differing in plant species composition even though structurally similar; and (3) same season and type of vegetation but different years.

It may be reasoned that limited data provide a poor basis for making fundamental comparisons and management decisions. Some examples of misleading comparisons include:

(1) Average avian density in mixed cottonwood-willow-salt cedar communities in spring 1975 was 128 birds per 40 ha. In salt cedar in spring 1979, the density was also 128 birds per 40 ha. One might conclude, erroneously, that salt cedar supported as many birds as the mixed communities, whereas in most years, salt cedar consistently contained fewer birds, and 1975 was simply a year of low avian densities.

(2) In summer 1979 there were 429 birds per 40 ha in salt cedar and 361 birds per 40 ha in cottonwood-willow-salt cedar mixes. One might conclude that pure salt cedar supported a higher density of birds than the mixed communities. However, over five summers the mean density was 276 birds per 40 ha in salt cedar and 339 birds per 40 ha in the mixed communities. For the entire study, salt cedar averaged 135 birds per 40 ha, and the mixed communities averaged 247 birds per 40 ha. In general, salt cedar did not support as large a population as the mixed communities. These data stress the biological importance of the significant interactions we report.

Numerous additional examples involving species richness in addition to densities could be cited. It seems clear that before habitat evaluations can be made, data should be collected over a considerable time frame. Attention should also be given to censusing during more than one season. Comparisons of avian population density estimates, like all other types of comparisons in science, should be based on sufficient replications of seasons and years to give credence to conclusions.

Legitimately one can ask: What kinds of comparisons can be made which will lead to worthwhile conclusions? We have not fully and finally answered this question. It is apparent that careful consideration must be given to avian density or species richness variations which might result from even slight variations in vegetation (species composition, foliage volume, diversity), differences in seasonality, and annual variation.

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