VEGETATION CHARACTERISTICS ASSOCIATED WITH ABERT'S TOWHEE NUMBERS IN RIPARIAN HABITATS

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ABSTRACT.—Abert's Towhee (*Pipilo aberti*) numbers and their associations with various characteristics of riparian vegetation along the lower Colorado River were examined for 4 yr. Towhee numbers were positively correlated with horizontal patchiness, foliage density, and foliage height diversity. Correlations of towhee numbers with vegetation parameters were generally significant from January to September and nonsignificant the remainder of the year. Preferred habitats were the same throughout the year. Vegetation relationships of the resident population were obscured in the fall and early winter months because some birds dispersed into marginal habitats. Climatic and/or resource influences probably modify this pattern of dispersal. *Received 8 October 1980, accepted 10 April 1981.*

THE importance of habitat structure to birds is generally accepted by ecologists and has been thoroughly reviewed by Hildén (1965), Orians (1969), Balda (1975), Verner (1975), and Karr (in press). Bird-species relationships with vegetation may be important in winter as well as during the breeding season (Fretwell 1972).

The Abert's Towhee (*Pipilo aberti*), a permanent resident in desert riparian vegetation of the southwestern United States, is frequently associated with honey mesquite (*Prosopis glandulosa*), cottonwood (*Populus fremontii*), and willow (*Salix gooddingii*). It is found in a variety of dense habitats, including those dominated by the exotic salt cedar (*Tamarix chinensis,* Marshall 1960). The Abert's Towhee population of the lower Colorado River valley is probably relatively isolated from other populations of the species, because the riparian habitat is geographically removed from areas with similar vegetation and the towhees are nonmigratory. This situation allowed us to examine a fairly well-delineated population occupying a range of vegetation types.

This study examines annual population cycles of the Abert's Towhee and its seasonal relationships with riparian vegetation of the lower Colorado River valley. Specifically, we classified the riparian vegetation into a variety of habitat types and censused towhees in the habitats in order to determine the associations between towhee numbers and vegetation characteristics of the habitats.

METHODS

The study included riparian vegetation along the lower Colorado River from the Mexico border north to Davis Dam (600 km), on the Arizona-Nevada border. The various plant associations in the riparian habitat were classified into six vegetation types based on the dominant tree species. These vegetation types included cottonwood-willow, honey mesquite, screwbean mesquite (*Prosopis pubescens*), salt cedar, salt cedar-honey mesquite, and arrowweed (*Tessaria sericea*). The six vegetation types were further divided into as many as six structural types based on foliage density at various levels. Structural Type 1 was most dense overall. The remaining types were progressively less dense at the upper levels (above 9 m). Further details of the vegetation and structural types are presented in Anderson et al. (1977). Vegetation-structural types are referred to here as habitats. Two to 11 transects (800–1,600 m long) were established in relatively homogeneous stands of each habitat. Beginning in December 1975, each transect was divided into 150-m-long subplots in order to examine towhee distribution more specifically. Over the course of the study, the number of transects censused each month sometimes varied because some

TABLE 1. Variables used in analysis of the vegetation.

Variables	Number of variables
Foliage density and patchiness	
0.0–0.6 m	2
1.5–3.0 m	2
4.5–6.0 m	2
≥7.5 m	2
Total density and patchiness	2
Tree density (*n*/40 ha)	
Cottonwood-willow	1
Mesquite species	1
Salt cedar	1
Proportion of trees that are salt cedar	1
Shrub density (*n*/ha)[a]	1
Foliage height diversity	1

[a] Includes quail bush (*Atriplex lentiformis*), four-wing salt bush (*A. canescens*), inkweed (*Suaeda torreyana*), wolfberry (*Lycium* spp.), and smotherweed (*Bassia hyssopifolia*).

areas were lost due to burning or clearing; lost transects were replaced with transects in similar habitats whenever possible.

A modification of the Emlen (1971) variable-transect census method was used to estimate avian densities (Anderson et al. 1977). Monthly densities of Abert's Towhees per transect and subplot were determined by taking the average of 2–4 censuses from a particular transect each month. Densities for each habitat type were the average number of birds per 40 ha for all transects representative of each type. Monthly and seasonal densities were considered. Seasons include winter (December–February), spring (March–April), summer (May–July), late summer (August–September), and fall (October–November). Censusing for this study extended from January 1975 to December 1978.

Habitat breadth was calculated from information theory (Shannon and Weaver 1949) by considering the proportion of the total towhee population contributed by the number found in each habitat.

Foliage density (DEN) was measured using the board technique (MacArthur and MacArthur 1961). Foliage height diversity (FHD) was computed from relative foliage density estimates using information theory (Shannon and Weaver 1949). Patchiness (PI) was determined from the sum of the variance of foliage density measures taken at various heights in 150-m plots along the transect (Anderson et al. 1978). All trees and shrubs within 15 m of both sides of each transect line were counted to obtain densities of each species. Further details of vegetation measurement techniques are in Anderson et al. (1977, 1978). The measurements, usually made in May or June, were used to characterize each habitat for all months of that year under the rationale that measurements involving green foliage in summer also represent density of leaf-bearing parts in winter. Thus, a habitat with dense leaves in summer should have more foliage-bearing parts in winter than a habitat that possessed few leaves in summer. This assumption was validated by field measurements from selected study sites (unpubl. data).

A Principal Components Analysis was used to evaluate vegetation data (Nie et al. 1975). Sixteen vegetation variables (Table 1) were analyzed to determine the number of independent vegetational trends (principal components). Each principal component (PC) includes highly intercorrelated variables from the original set. A variable was included on a particular PC if it had a loading of 0.5 or more on that PC. A stepwise multiple linear regression of the vegetation PC's that had eigenvalues >1.0 was then run with the monthly towhee densities as dependent variables to evaluate towhee-vegetation relationships. A regression series including the vegetation principal components (VPC) raised to the second, third, and fourth powers was also run in order to discern certain nonlinear relationships. The level of statistical significance was determined by an F-test ($P < 0.05$ accepted in this study).

RESULTS

Towhee numbers.—The towhee population gradually increased over the 4-yr study, and population density exhibited a seasonal pattern (Fig. 1). Densities were highest in June, July, and August, decreased sharply in fall, and were at lowest

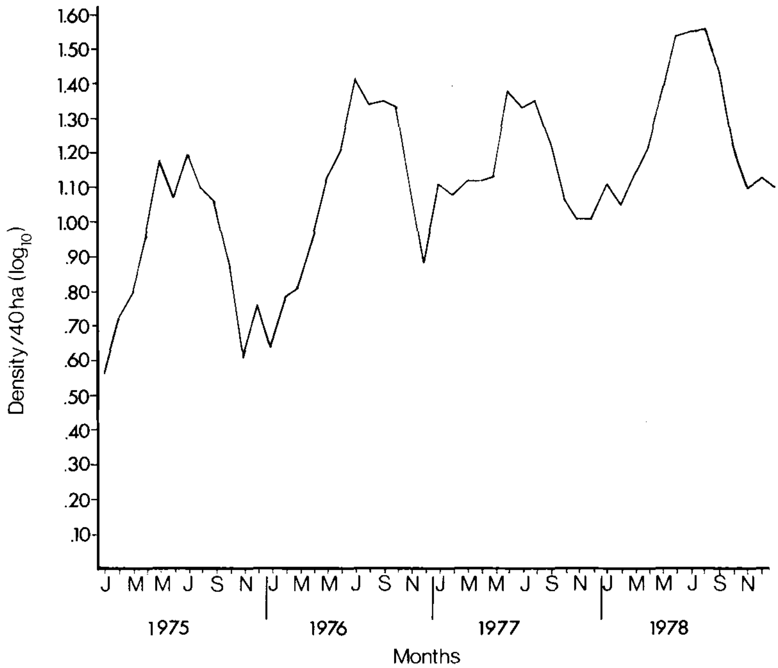

Fig. 1. Average densities of Abert's Towhees in riparian vegetation of the lower Colorado River valley, January 1975–December 1978.

levels during November, December, and January. Densities gradually increased between February and May.

The number of birds per subplot and the proportion of subplots on which towhees were detected also showed seasonal changes (Table 2). The number of birds per subplot had a pattern similar to that shown by the total population—highest densities occurred in summer and lowest densities in winter. The proportion of subplots on which towhees were found increased sharply during summer and then declined in early winter. Dispersal in late summer was indicated by a decrease in the number of birds per subplot and an increase in the proportion of subplots used.

TABLE 2. Average number of Abert's Towhees per 1.8-ha subplot and average proportion of subplots in which towhees were detected, December 1975–December 1978. Number of subplots varied from 900 to 1,000. Standard error shown in parentheses.

Month	Number of birds/subplot	Proportion of subplots occupied
January	1.32 (0.05)	0.26 (0.09)
February	1.39 (0.09)	0.25 (0.06)
March	1.36 (0.05)	0.31 (0.08)
April	1.47 (0.09)	0.32 (0.08)
May	1.56 (0.14)	0.40 (0.04)
June	1.60 (0.15)	0.44 (0.06)
July	1.61 (0.08)	0.53 (0.03)
August	1.59 (0.13)	0.56 (0.09)
September	1.55 (0.12)	0.55 (0.08)
October	1.39 (0.01)	0.44 (0.05)
November	1.30 (0.02)	0.39 (0.03)
December	1.38 (0.11)	0.31 (0.02)

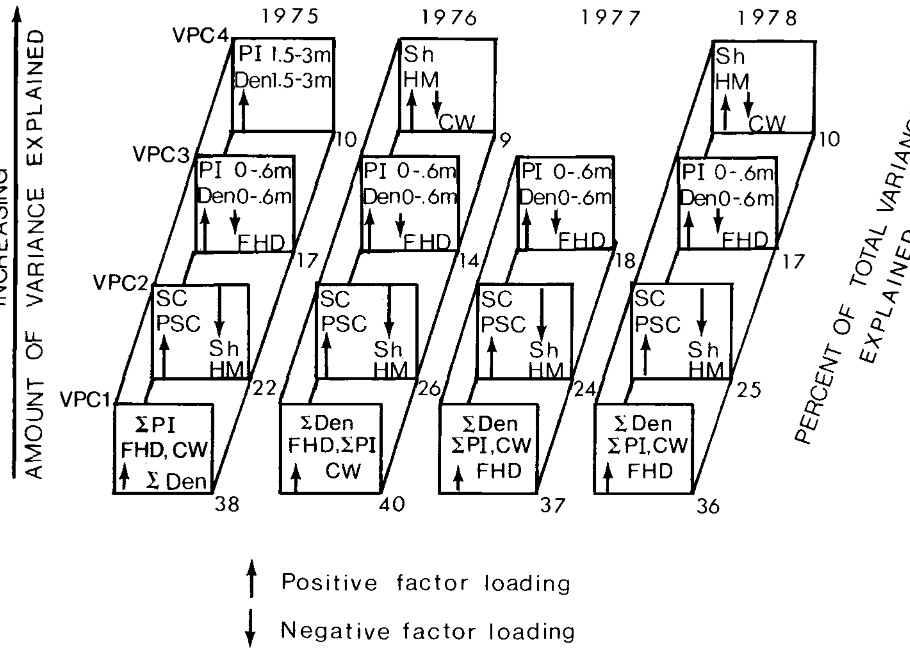

Fig. 2. Vegetation principal components resulting from analysis of riparian vegetation in the lower Colorado River valley, 1975–1978. Variables are listed in the order of their relative contribution to the factor.

Vegetation analysis.—The first vegetation principal component (VPC1) was a complex factor including total foliage density, FHD, total PI, and the number of cottonwood and willow trees (Fig. 2). This single factor accounted for 36–40% of the variance in the vegetation data. The number and proportion of salt cedar had high positive loadings and honey mesquite and shrubs had moderate negative loadings on VPC2; this component accounted for 22–26% of the variance. The third VPC had high loadings for PI 0–0.6 m and foliage density 0–0.6 m and an intermediate negative loading for FHD. The third VPC accounted for an additional 14–18% of the variance. The first three PC's each consistently included the same vegetation variables throughout the 4 yr, although the relative loadings of the variables and the amount of variance accounted for by each factor were slightly different

TABLE 3. Relationships between Abert's Towhee numbers and vegetation in the lower Colorado River valley. VPC indicates the vegetation principal components of most importance in linear and nonlinear relationships.

	Average proportion of variance accounted for		
Season	Linear relationships	Nonlinear relationships	Total
March–July (1975–1978)	0.416 VPC1	0.171 $VPC3^4$, $VPC4^2$	0.587
August–November (1975–1978)	0.297 VPC1	0.226 $VPC1^2$	0.523
Mildest winters (1975–1976, 1977–1978)	0.404 VPC1	0.222 $VPC3^2$	0.625
Coldest winters (1976–1977, 1978–1979)	0.202 VPC1	0.321 − $VPC3^3$, $VPC1^2$	0.523

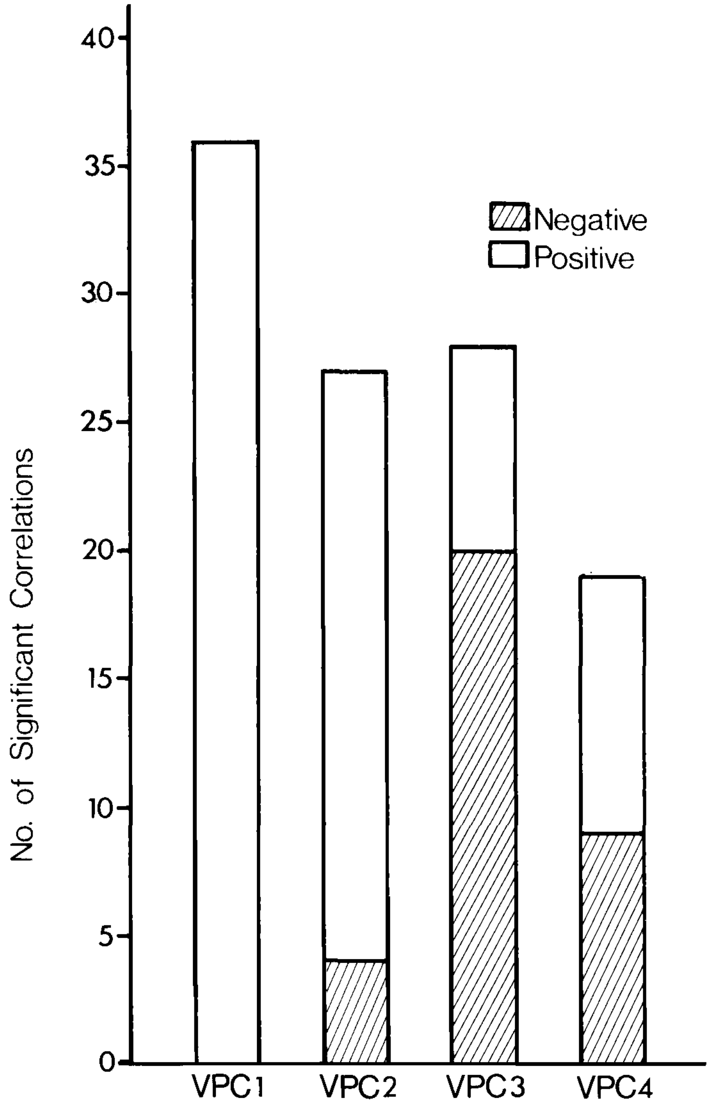

Fig. 3. Significant correlations between monthly towhee densities and four vegetation principal components.

between some years (Fig. 2). Changes between years reflect the loss or addition of transects as well as real changes in the sampled vegetation. In 3 yr there was a fourth VPC. In 1975, foliage density and PI 1.5–3.0 m had high loadings on this axis. In 1976 and 1978, shrubs and honey mesquite had positive loadings, and cottonwood and willow trees had a moderate negative contribution.

Towhee-vegetation relationships.—A multiple linear regression of the four vegetation principal components on the monthly towhee density data evaluated towhee-vegetation relationships (Fig. 3). Towhee numbers had significant relationships with the measured vegetation parameters in 37 of 48 months. The first VPC (foliage density, diversity and patchiness, and the number of cottonwood and willow trees)

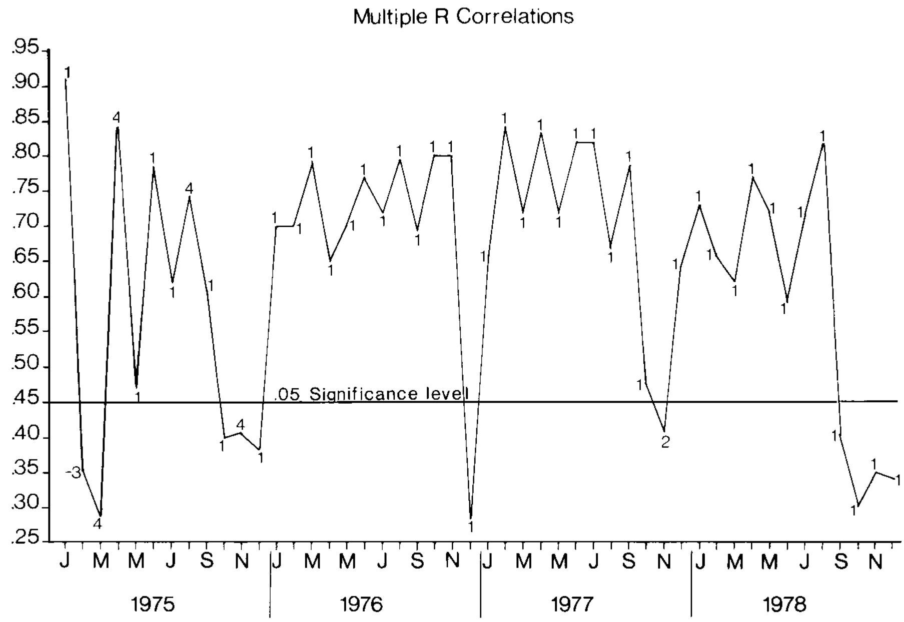

Fig. 4. Multiple *R* correlations of towhee numbers with vegetation characteristics, January 1975–December 1978. Numbers shown on the graph represent the first vegetation principal component that entered the stepwise multiple linear regression each month. Inclusion of nonlinear correlations would tend to increase the multiple *R* values.

was the most significant factor in 35 months and accounted for an average of 42% of the variance in towhee populations. It always showed a positive relationship. In the other 2 months when towhee-vegetation relationships were significant, VPC4 (foliage density and patchiness at 1.5–3.0 m) was most important and also showed a positive relationship. The second significant principal component chosen in the stepwise procedure was variable between months and years but generally accounted for about the same amount of additional variance ($\bar{x}$ = 0.10, SD = 0.08). Mixed positive and negative associations were shown by VPC's 2, 3, and 4 when they were selected in the second or subsequent steps of the regressions.

These results indicated that when vegetation structure was related to Abert's Towhee numbers, foliage density, vertical and horizontal diversity, and the presence of cottonwood and willow trees were the most important characteristics. In those months when vegetation was important, all significant VPC's accounted for an average of 55% of the total variation in towhee densities. The unexplained 45% suggests that environmental features not examined may also be important at these times, as well as in those months when towhee numbers showed no significant relationship to the vegetation principal components. Alternatively, the lack of linear correlations in some months, as well as the low amount of variance accounted for, might mean that towhee-vegetation relationships were not linear. To test this, the multiple regressions were redone with the vegetation factor scores raised to the second, third, and fourth powers to detect nonlinear associations of towhee numbers with vegetation. For all months but August through November, the relationship between the vegetation principal components and towhee densities that accounted

TABLE 4. Habitat breadth of Abert's Towhees based on distribution among the various vegetation-structural types, January 1975–December 1978.

Month	Year				
	1975	1976	1977	1978	$\bar{x}$
January	0.81	0.72	0.92	0.90	0.86
February	0.83	0.88	0.94	0.92	0.91
March	0.78	0.84	0.94	0.92	0.87
April	0.87	0.81	0.95	0.94	0.89
May	0.90	0.90	0.91	0.94	0.91
June	0.93	0.94	0.93	0.95	0.94
July	0.93	0.90	0.94	0.97	0.94
August	0.89	0.94	0.92	0.95	0.93
September	0.89	0.95	0.96	0.96	0.94
October	0.93	0.93	0.94	0.92	0.93
November	0.91	0.94	0.95	0.93	0.93
December	0.71	0.91	0.92	0.96	0.88
$\bar{x}$	0.87	0.89	0.94	0.94	0.91

for the greatest amount of variance was linear and was always VPC1, confirming the original analysis. In the months August to November, nonlinear relationships were important in explaining variance in towhee numbers. Inclusion of nonlinear factors sometimes led to towhee-vegetation correlations that were significant, whereas they had been nonsignificant when only a linear relationship was assumed. For example, in the combined months of August–November 1976, $VPC3^3$ accounted for 45% of the variance; VPC1 was next to enter the series and accounted for an additional 11% of the variance. Overall, the principal components raised to the second, third, and fourth powers explained 17–32% of the variance. In general, nonlinear relationships were important in late summer and fall and during the two coldest winters of our study (Table 3).

Average correlations of towhee densities with vegetation characteristics were highest in the months of January through September (Fig. 4). Habitat breadths in the months of December to May (Table 4) were at or below the annual mean 83% of the time; the rest of the year habitat breadths were broader than the mean 75% of the time. An ANOVA showed that habitat breadth was significantly narrower from December to May than the rest of the year (df = 11/33, $F = 3.41$, $P < 0.025$). This pattern was consistent even though there were also significant differences in habitat breadth between years (ANOVA, df = 3/33, $F = 9.28$, $P < 0.05$). These two factors indicate that towhees were more specialized in habitat use (responding to specific vegetation features) during mid- to late winter, spring, and early summer. Use of a broader variety of habitats occurred after the breeding season when the densities of towhees were generally not related to any measured vegetation characteristic. It is important to note, however, that the most preferred habitats, as determined by relative density, were the same in nearly all seasons (Table 5).

DISCUSSION

The Abert's Towhee population increase over the 4 yr was part of a general trend noted for many species in the lower Colorado River valley. No changes in censusing intensity or expertise occurred during this time. The increase in total density apparently represents recovery of the towhee population after a particularly severe winter in 1974–1975 (Anderson pers. obs.). The seasonal increase before the begin-

TABLE 5. Relative density of Abert's Towhees in each of the vegetation-structural types, 1975–1978. Boldface numbers indicate the five habitats with the highest proportion of towhees in each season.

Vegetation-structural type[b]	Season[a]				
	Winter	Spring	Summer	Late summer	Fall
SM3	0.036	0.068	0.059	0.055	0.036
SM4	0.044	0.045	0.052	0.050	0.053
SM5	0.032	0.041	0.034	0.040	0.052
SM6	0.024	0.009	0.006	0.012	0.022
CW1	**0.177**	**0.218**	**0.116**	**0.089**	**0.139**
CW3	**0.074**	**0.081**	**0.119**	**0.089**	0.062
CW4	0.046	**0.081**	**0.069**	**0.092**	**0.080**
CW5	0.059	0.053	**0.069**	**0.090**	**0.093**
CW6	**0.088**	0.068	0.072	0.072	0.058
SC3	**0.090**	**0.076**	**0.092**	**0.079**	**0.105**
SC4	0.036	0.049	0.041	0.055	0.044
SC5	0.039	0.026	0.045	0.030	0.035
SC6	0.035	0.043	0.043	0.047	0.033
HM3	**0.099**	**0.075**	**0.076**	**0.090**	**0.077**
HM4	0.061	0.057	0.040	0.055	0.052
HM5	0.018	0.018	0.020	0.022	0.024
HM6	0.026	0.023	0.027	0.014	0.020
AR6	0.034	0.035	0.031	0.039	0.030
SH4	0.047	0.071	0.049	0.063	0.070

[a] Winter = December–February; spring = March–April; summer = May–July; late summer = August–September; fall = October–November.

[b] SM = screwbean mesquite; CW = cottonwood-willow; SC = salt cedar; HM = honey mesquite; AR = arrowweed; SH = salt cedar-honey mesquite; number refers to structural type (see text and Anderson et al. 1977).

ning of the breeding season in March was probably the result of greater detectability of the birds rather than an actual increase in the population.

Because towhees were observed to prefer the same habitats throughout the year, we would expect densities that correlate with the vegetation parameters characterizing these habitats. The lack of linear correlations in the late summer and fall months is apparently due to population dispersal, which occurred at this time. Although the population showed an average increase of 15% between June and July, the proportion of subplots occupied increased an average of 20% (Table 2). Towhees became habitat generalists after the breeding season. This pattern was contrary to that observed for most other avian species inhabiting the lower Colorado River valley (Rice et al. 1980). Habitat selectivity of most species was highest in the late summer and fall and least precise in spring and summer.

The observed distribution changes in late summer occurred because some birds dispersed out of areas occupied in summer. Abert's Towhees are territorial year round (Marshall 1960), and dispersing birds may have been subdominants that were forced out of the preferred habitats of the resident population (Anderson et al. MS). The presence of birds in marginal habitats obscured the selectivity of the resident population and caused towhee-vegetation relationships to be reduced or become more complex (nonlinear). By mid-winter many birds had disappeared from the population (probably due to mortality), and habitat selectivity was again apparent. Evidence for this phenomenon comes from the population decline in fall and subsequent habitat specialization beginning in January.

Environmental and/or resource conditions probably modify the pattern of population dispersal. If environmental conditions are particularly harsh during or shortly after the breeding season, mortality should increase, and habitat selectivity will be more apparent year round. Years of particularly abundant resources may delay or

TABLE 6. Winter climatic characteristics in the lower Colorado River valley, 1975–1979 (data from Poston, Arizona). Standard error shown in parentheses.

	Winter			
Characteristic	1975–1976	1976–1977	1977–1978	1978–1979
Mean temperature (°C)				
High	21.4 (0.7)	21.0 (0.8)	20.1 (0.8)	17.2 (0.9)
Low	1.3 (0.8)	−0.3 (0.7)	3.9 (0.6)	0.1 (0.6)
Lowest temperature (°C)	−7.8	−5.6	−1.7	−8.9
Days frost	32	52	10	50
Mean wind (km/day)	122.7 (5.2)	104.9 (2.9)	102.2 (3.0)	137.8 (17.9)
Mean solar radiation (langleys)	307	286	252	271
Total precipitation (cm)	4.2	2.0	16.1	6.9

diminish mortality of birds in marginal habitats, and habitat selection may appear more generalized. Alternatively, particularly abundant resources may lead to less dispersal from preferred habitats, with the result that habitat selectivity remains high.

The winters of 1975–1976 and 1977–1978 may serve as examples of this last possibility. These two winter seasons were relatively mild, with fewer days of frost than 1976–1977 and 1978–1979 (Table 6). The winter of 1977–1978 was also wetter than other years. Mild winters in the lower Colorado River valley increase the availability of food resources for insectivores such as the Abert's Towhee (Anderson and Ohmart unpubl. data). Vegetation correlations with towhee numbers remained relatively high in these two mild winters compared to the more harsh alternate years (Table 3), although differences in habitat breadth between harsh and mild winters were not statistically significant.

An important point arising from this study is that habitat requirements are not always most apparent during the breeding season, as many studies assume. Towhees exhibit their most restricted habitat use from December to May. Field studies limited to the summer breeding season, when some birds were already dispersing into less preferred habitats, could have resulted in misleading conclusions about habitat breadth and vegetation relationships of the Abert's Towhee. Similar caution in interpreting breeding-season habitat relationships should be applied to migratory species. Many migrant species winter in habitats that are quite different from those on their breeding grounds (Fretwell 1972, Keast and Morton 1980). More important, conditions on these wintering grounds may limit species' populations (Fretwell 1972), so emphasis on breeding-season habitat relationships may be especially misleading.

A second assumption that is often made when examining environmental relationships is that these relationships are only linear (Green 1979). In the towhee-vegetation relationships, nonlinear correlations were important in the fall and early winter and indicated that more complex reactions to the vegetation were taking place.

Abert's Towhees interact significantly with the measured vegetation variables (or variables correlated with those measured), and areas of high foliage density and diversity (horizontal as well as vertical), in general, support the greatest numbers of towhees. The presence of cottonwood and willow trees seems further to enhance an area. This observation is further substantiated by the generally low populations found in areas with low vertical diversity (Structural Types 5 and 6) and no cottonwood or willow trees. Thus, we can successfully predict which riparian vegetation types will support the largest and smallest numbers of towhees. An average of 45% of the variation in towhee density data, however, was unexplained by our analysis. Other variables must also be important. Investigations currently under way may explain towhee interactions with the vegetation in even greater detail.

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