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MULTIVARIATE ANALYSIS OF EARLY AND LATE NEST SITES OF ABERT'S TOWHEES

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ABSTRACT.—Seasonal variation in nest site selection by the Abert's towhee (*Pipilo aberti*) was studied in honey mesquite (*Prosopis glandulosa*) habitat along the lower Colorado River from March to July, 1981. Stepwise discriminant function analysis identified nest vegetation type, nest direction, and nest height as the three most important variables that characterized the difference between early and late nest sites. Early nests were typically placed low on the southeastern sides of small shrubs or mistletoe, while later nests were built higher in mesquite and mistletoe. Although mesquite was a preferred nest shrub species after it leafed out in April, flexibility in nest site choice allowed towhees to initiate reproduction in early March. By breeding earlier than migratory songbirds, multi-brooded Abert's towhees lengthen their breeding season, and thus increase their chances of nesting successfully.

Abert's towhee (*Pipilo aberti*) is a sedentary species endemic to the Southwest and is restricted to desert riparian habitats. Along the lower Colorado River, mesquite woodlands are its preferred breeding habitat (Anderson and Ohmart, 1976a), yet only anecdotal information is available on its nest site preferences (Bendire, 1890; Dawson, 1968). Because the Abert's towhee is nonmigratory, it is able to breed as soon as conditions are favorable (Marshall, 1963). Consequently, its breeding period is longer than that of migratory songbirds in the Southwest, and encompasses seasonal variation in climate, vegetation growth, and resources (Meents et al., 1981; Anderson et al., 1982; Rosenberg et al., 1982). In response to temporal changes in the environment, towhees may alter their choice of nest sites and may improve the probability of nesting successfully. In this study, I asked the following questions: 1) Does towhee nest site selection vary with time in mesquite habitat along the lower Colorado River, and 2) if so, is it merely correlated with seasonal changes in habitat, or does it reflect active preference for particular sites. Selection is active if nest sites vary in suitability, and suitability varies seasonally.

The combination of factors that characterize the habitat niche of a species has been described by the term "niche-gestalt" (James, 1971). I used the niche-gestalt approach to describe the nesting habitat of the Abert's towhee. Multivariate analyses were applied to the nest site variables in order to organize them into a meaningful combination (e.g., MacKenzie and Sealy, 1981; Clark et al, 1983).

METHODS.—During the summer of 1979, I established a grid that covered 20 ha in a honey mesquite shrub community 10 km north of Ehrenberg, Arizona, on the Colorado River Indian Reservation. Plants associated with honey mesquite in the study area were exotic salt cedar (*Tamarix chinensis*), willow (*Salix gooddingii*), saltbush (*Atriplex lentiformis*), inkweed (*Suaeda torreyana*), and mistletoe (*Phoradendron californicum*), a parasite of honey mesquite. A detailed description of tree and shrub densities and composition is given by Anderson and Ohmart (1976b). Habitat selection by the Abert's towhee has been described by Meents et al. (1981). The avifauna of the lower Colorado River valley has been described by Grinnell (1914) and Rice et al. (1980, 1983).

TABLE 1.—*Means ($\bar{X}$), standard errors (SE), and results of step-down multivariate analysis of variance testing the significance of differences between early and late nests.*

Variables	Early $\bar{X} \pm SE$	Late $\bar{X} \pm SE$	F-ratio	Significance Level
Nest Direction (deg)	145.5 ± 16.35	216.0 ± 17.10	7.4	.009*
Nest Height (cm)	155.8 ± 29.58	224.0 ± 17.10	13.5	.001*
Relative Nest Height	4.8 ± 0.37	6.4 ± 1.54	0.9	.771
Nest Shrub Height (cm)	289.9 ± 26.44	433.2 ± 21.24	0.3	.600
Veg. Height above Nest (cm)	182.4 ± 29.27	230.5 ± 20.72	1.3	.262
Nest Distance from Center	60.0 ± 18.00	80.0 ± 18.00	0.1	.725

*Significant.

From January to July 1980, 15 hours each week (a total of 84 5-hour searches) were spent looking for nests on or near the study grid. Abert's towhee had a nesting season of 118 days from first to last nest initiated. Nesting began in mid-March before honey mesquite leafed out. Field work terminated in July when no new nests were initiated.

After the young had fledged from the nests, the vegetation at each nest site was sampled. Eight shrub characteristics were recorded: nest shrub height, nest height, distance of the nest from the shrub center, height of vegetation above the nest, compass direction of the nest with respect to the shrub center, nest shrub position (isolated, open, marginal, interior), nest substrate (shrub stems < 2 mm, branch 2 mm-10 mm, trunk > 10 mm, mistletoe-branch association and pure mistletoe), and nest vegetation type. To facilitate statistical analyses, plant species were categorized on the basis of their crown width into three vegetation types: 1) > 1.5 m (mesquite, salt cedar, willow) = Type 1, 2) 0.5-1.5 m (saltbush, arrowweed, inkweed) = Type 2, and 3) $<$ 0.5 m (mistletoe) = Type 3. Two additional variables were calculated (MacKenzie and Sealy, 1981): relative shrub height (relative to the average nest shrub height) and relative nest height (relative to the height of the nest shrub).

To determine if changes in plant phenology affected nest site selection by towhees, I allocated nests to early (mid-March through April) and late (May through July) seasons. I then used multivariate analysis of variance with Roy-Bargmann step-down analysis to determine if nest site characteristics differed significantly between early and late nests, and if so, what variables accounted for the observed difference. If a variable proved to be highly correlated ($r \geq 0.8$) with another variable, it was considered redundant and removed from the analysis. A significant F statistic for any variable in the step-down analysis indicated that this variable was important for testing the difference between early and late nest sites, and could not be accounted for by a linear combination of the preceding variables. Nominal, discrete variables were excluded. The SPSS program MANOVA (Hull and Nie, 1981) was used for the analysis.

I used discriminant function analysis (DFA) to maximize the difference between early and late nest site data for the set of 10 variables. To discriminate between nest groups, I used a stepwise procedure tha maximized the Mahalonobis distance between the two groups. Prior probabilities were set equal to 0.40 (N = 25) for early nests and 0.60 (N = 38) for late nests. Variables that did not have significant discriminating power when tested with the F-ratio were not used in predicting group membership.

Statistical analyses were performed at the University of Wyoming using programs from the SPSS (Nie et al., 1975) and BMDP (Dixon and Brown, 1979) packages.

RESULTS.—Nest site data were collected on 63 Abert's towhee nests. Relative nest height was highly correlated (r = 0.99) with nest shrub height and was consequently removed from all further analyses to reduce possible effects of multicolinearity. Multivariate analysis of variance indicated that only two continuous variables, nest height and nest direction, were significant for testing the difference between early and late nests (Table 1). (Note that the nominal variables, vegetation type, nest position, and nest substrate, were excluded from MANOVA.)

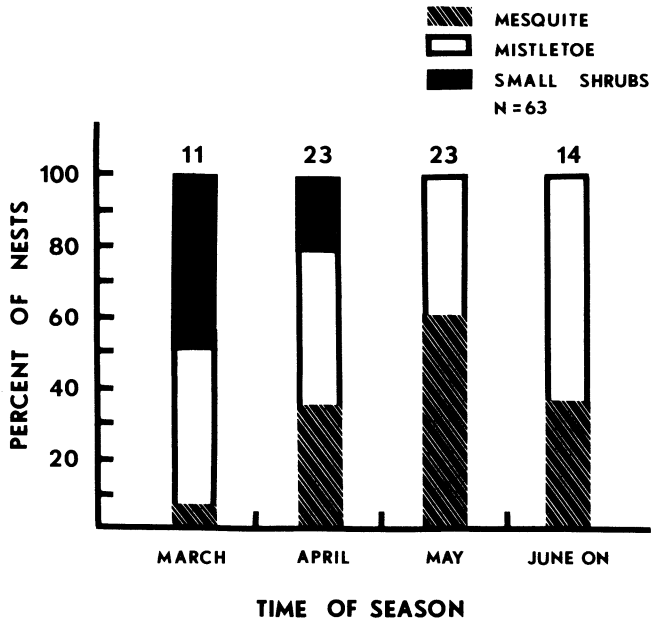

FIG. 1.—Percent of Abert's towhee nests placed in three vegetation types in relation to time of season.

DFA performed on the variables to maximize the difference between early and late nests identified vegetation type as the best discriminating variable, followed by nest direction and nest height. The other variables were excluded from the analysis because F levels were insufficient, and thus, they did not function as discriminators.

Separation based on these variables was interpreted as follows. Early in the season, significantly more nests were built in mistletoe or small shrubs such as saltbush, arrowweed, and inkweed (G-test, $p < 0.005$) (Figure 1). Mesquite and mistletoe became the dominant nest vegetation types after mesquite leafed out in late April. Early nesting towhees built nests predominantly on the southeastern sides of shrubs, while later nests were placed randomly (Finch, 1983a). In addition, early nests were placed significantly lower in shrubs (G-test, $p < 0.05$) (Figure 2) than later nests.

Nests were correctly classified 81.0% of the time, of which 76.0% were accurately grouped as early nests and 84.2% were correctly classed as late nests. Jackknifed classification produced 79.4% accuracy (76.0% early; 81.6% late). One discriminant function explained 100% of the variance and had an eigenvalue of 0.62. The mean discriminant scores (i.e., centroids) were -0.954 for the early nest group and 0.628 for the late nest group. Based on Wilk's lambda and Mahalanobis distance tests, the difference between the centroids of early and late nests was significant (F-ratio, $p < 0.0001$). An ordination in the form of a frequency distribution of discriminant scores indicated that earlier nests had a narrower range of variation than late nests (Figure 3).

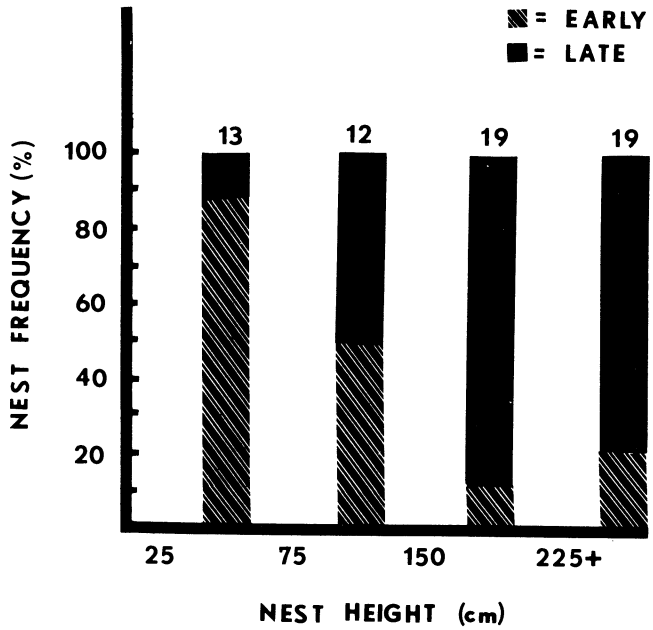

FIG. 2.—Frequency distribution of nest height classes selected as early and late nest sites by Abert's towhees.

DISCUSSION.—DFA identified vegetation type, nest direction, and nest height as the three most important discriminating variables. Early in the season, Abert's towhees selected nest sites that were predominantly in small shrubs or mistletoe. Mistletoe was a preferred nest site throughout the breeding season, and therefore was probably not important in discriminating between early and late nests. Small shrubs such as saltbush, arrowweed, and inkweed were ignored by towhees after honey mesquite leafed out.

The composition of nesting material also changed over time (Finch, 1983a). Early nests were constructed of salt cedar, saltbush, and arrowweed leaves, mesquite bark, and grasses, whereas later nests were made principally of mesquite leaves. Thus, mesquite leaves were a preferred resource.

The seasonal shift in nest site selection by towhees represents active preference for particular nest sites rather than merely correlational changes with the environment. By choosing mesquite over smaller shrubs later in the season, the Abert's towhee demonstrates a decided preference for a shrub species that was unsuitable (i.e., unleafed) earlier in the season. With its greater canopy, mesquite offers more protective cover from climatic elements in addition to concealment from nest predators and parasitic cowbirds. Mistletoe, which was possibly the most desirable nest site (approximately 50% of all nests) provided even greater cover due to its dense, cluster-like nature.

Nesting success of Abert's towhee declined after an influx of the brood parasite, the brown-headed cowbird (*Molothrus ater obscurus*) (Finch,

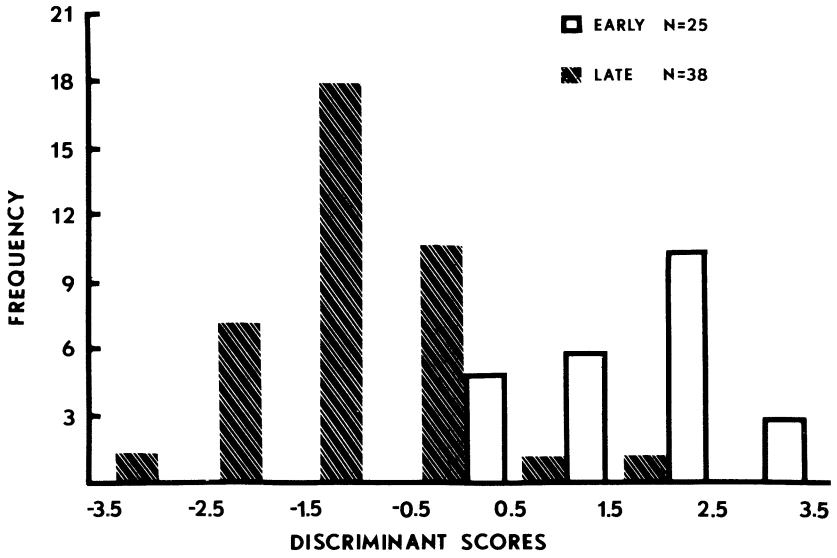

FIG. 3.—Frequency distribution of discriminant scores derived from discriminant function analysis of early and late nest sites of the Abert's towhee.

1983b). The increased cover provided by mesquite leaves and mistletoe stems may be necessary to cope with a high rate of cowbird parasitism in May, June, and July.

Nest direction, the second variable included in discriminant analysis, changed as maximum daily air temperature rose from 23.8°C in March to 42.9°C in July (Finch, 1983a, 1984) and as prevailing winds altered from a west-northwest direction to south-southeast (Finch, 1983a). Early nests were placed predominantly on the southeastern sides of shrubs, while later nests were placed randomly (Finch, 1983a). A southeasterly direction allowed rapid nestling heat gain in the early morning and protected the nest from cooling, destructive winds.

Nest height, the last variable included in DFA, increased later in the season. As the season progresses, predators may increase foraging pressure in response to reproductive demands on time and energy. By increasing nest height, towhees may reduce the probability of nest detection by predators that typically forage on the ground (Finch, 1981).

The availability of suitable nest sites may limit the population of a species in a particular habitat (MacKenzie and Sealy, 1981). Along the lower Colorado River, densities of Abert's towhees are higher in habitats dominated by mesquite than in habitats dominated by saltbush, arrowweed, or inkweed (Anderson et al., 1976a). Meents et al. (1981) and Anderson et al. (1982) refer to these latter habitat types as marginal or suboptimal, occupied by dispersing Abert's towhees. Nest sites in small shrubs apparently are less desirable than those in mesquite or mistletoe, but are nevertheless chosen in March and April. Presumably, food and nest-building material are abundant enough for towhees to initiate reproduction early in March despite the lack of preferred nest sites.

In conclusion, mesquite stands interspersed with smaller shrubs may be more suitable to breeding towhees than pure stands of either mesquite or small shrubs. That habitat selection by Abert's towhees is broader in late summer and fall (Meents et al., 1981) supports the hypothesis that availability of preferred nest sites restricts habitat choice during the breeding season.

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