

REGIONAL ANALYSIS OF BLACK-CAPPED VIREO BREEDING HABITATS¹

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Abstract. Structural vegetation components of Black-capped Vireo (*Vireo atricapillus*) breeding habitats and unoccupied scrubland areas were analyzed at 13 sites from three regions: the Lampasas Cut Plains in central Texas; the Wichita Mountains and adjacent areas in western Oklahoma; and the Edwards Plateau (Kerr County) in central Texas. We evaluated 61 vegetation variables from individual vireo territories and equivalent scrubland plots unoccupied by vireos. Principal components indicated strong vegetation trends for all plots involving the abundance of junipers (from high to low) and openness (from low to high) extending from the Lampasas Cut Plains to the Wichita Mountains and then to the Edwards Plateau. In all regions, vireo territories had relatively high densities of deciduous vegetation (primarily oaks) close to the ground (i.e., up to 1–2 m, and in one region 3 m). In addition, vireo territories occurred where variation in relative density measures of woody vegetation was highest. However, even with the vireo's limited geographic range, differences were found among regions in the vegetational characteristics of areas defended by territorial males. Vireos avoided higher juniper densities on the Lampasas Cut Plains and more open areas on the Edwards Plateau. On the Edwards Plateau, with generally less dense vegetation and the lowest density of junipers, the older (ASY; after-second-year) males selected territories with higher juniper densities at lower height intervals than found on nonvireo plots. Territories of second-year males (SY) and older males (ASY) differed in vegetation characteristics. On the Edwards Plateau, SY males occupied territories with vegetation structurally more like nonvireo plots than like territories of ASY males. In the Wichita Mountains, where a remnant vireo population occurs, territories of SY males were similar to those of ASY males. In both regions, however, SY males were found in more open habitats. Competition with other foliage-gleaning species may have played a role in restricting the Black-capped Vireo to early successional stages of scrubland habitats, where they also may effectively avoid several species of nest predators. Periodic habitat disturbance has beneficial effects for vireos and can be used in management of this endangered species. Attempts should be made to maintain 35 to 55% dispersed scrub cover (primarily deciduous) in spatially heterogeneous configurations. Sometimes inherent site characteristics (e.g., poor soils) may naturally promote the degree of vegetational heterogeneity requisite for Black-capped Vireos. Managers should employ techniques that encourage thick regrowth of deciduous woody vegetation. Typically, juniper cover should be kept well below 10%, which may be possible only through habitat manipulation. However, in areas where amounts of deciduous vegetation are marginal (e.g., Edwards Plateau region and to the southwest), junipers may contribute important cover. Thus, site and regional characteristics need consideration when making decisions about juniper control.

Key words: Black-capped Vireo; *Vireo atricapillus*; Oklahoma; Texas; habitat; habitat selection; endangered species.

INTRODUCTION

Since Grinnell's (1917) study of the "niche" of the California Thrasher (*Toxostoma redivivum*),

many ornithologists have worked under the premise that predictable relationships exist between the occurrence of a species and certain characteristics of the habitat (Rotenberry 1981). Habitat provides the basic requirements for many breeding birds, and habitat selection has adap-

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tive significance to individual bird species (Hilden 1965). Thus, it is not surprising that naturalists and field biologists have studied habitats in numerous ways reflecting their proximate and ultimate importance (e.g., Hilden 1965, Klopfer 1969, Cody 1985).

For many species, habitats are often described in terms of the vegetation structure or floristic components comprising what James (1971) has termed "niche-gestalt." A number of investigators have demonstrated strong correlations between bird-species distributions and certain structural features of the vegetation (MacArthur and MacArthur 1961, James 1971, James and Wamer 1982). Associations of bird species with particular points along habitat gradients (e.g., Bond 1957, Able and Noon 1976, Smith 1977) or with specific seral stages (e.g., Johnston and Odum 1956, Martin 1960, Shugart and James 1973, Kendeigh and Fawver 1981, Smith 1982, May 1982, Mehlhop and Lynch 1986) also have been recognized. In addition to evaluating the presence/absence of avian species, several investigators have been able to predict successfully the relative densities of bird species from habitat variables (e.g., Anderson and Shugart 1974, Robbins 1978).

A number of these studies evaluated habitat in broad terms, using a comparative approach to contrast habitat uses of different avian species. Relatively few have focused on habitat preferences of species across geographically diverse sites to evaluate consistencies or dissimilarities in habitat associations of bird species, or to quantify the extent of a species' habitat niche (Cody 1978; Collins 1983a,b; Knopf et al. 1990). Studies of geographic variation or consistency in habitat use can evaluate sources of variation not represented at a single locality and may provide information on variables important in a species' survival that go beyond relatively simplistic representations of niche-gestalt. Such studies may help investigators elucidate potential behavioral, physiological and structural adaptations of birds. They also may help researchers predict species' responses to habitat changes, as well as gauge the relative importance of selective pressures (e.g., competition or predation) that may affect individual survival and reproductive success.

For endangered species, detailed knowledge of habitat use is important, particularly when habitats are subject to relatively rapid changes over time that could affect their suitability. Identifi-

cation of potentially critical or consistently present habitat conditions can be an essential part of effective management for these species. Here we evaluate structural habitat characteristics of the Black-capped Vireo (*Vireo atricapillus*), which has been designated as endangered (Ratzlaff 1987) and occupies a successional stage of scrubland that can mature in a short time period. Identifying and understanding critical features of their habitat clearly can be important for effective management of Black-capped Vireos.

METHODS

SAMPLING TECHNIQUES

Our goal was to characterize features of the physical habitat potentially available to Black-capped Vireos. We employed the general plot method developed by James and Shugart (1970) and added to these, measures that characterize the vertical and horizontal structure of the vegetation. Within 405-m² (0.1-acre) circles, we recorded: (1) the numbers of woody plants with diameters at waist height (dbh) of 7.5 cm or greater; (2) the numbers of stems (<7.5 cm in diameter) intercepted by a rod 1.52 m long that was passed horizontally through the vegetation at a height of 1 m along two orthogonal diameters; and (3) ground cover types at 20 points spaced 2 m apart (taken along the two orthogonal diameters). From these data, relative densities, basal areas, and relative dominances were computed for life forms of woody plants (i.e., oaks, deciduous nonoaks, junipers and vines); we also calculated stem counts per unit area and the percentages of the various life forms. Life forms were evaluated, rather than individual plant species, so that analyses among regions would not simply reflect floristic differences (e.g., the presence of different species of oaks).

Other habitat data were collected, including the heights of all tree species with diameters of 7.5 cm or greater. In addition, a rod was passed vertically through the vegetation and evaluated at a total of 20 points 2 m apart along two 20-m orthogonal diameters; we recorded the number of decimeter intervals within larger height-class intervals that contained the various life forms of woody plants, as well as forbs and grasses. Cover types over two linear orthogonal diameters 1 m high also were recorded within each circle. The 61 vegetation variables used, along with their abbreviations, are listed in Table 1.

TABLE 1. Habitat variables evaluated for five or six 405-m² circles in vireo and nonvireo plots. Variable number, code, description, and units of measure given.^a

No.	Code	Vegetation variable
1-3	OAKA-OAKC	No. oaks with dbh 7.5-15 cm, >15-38 cm, and >38 cm, respectively (/ha)
4-5	NONA-NONB	No. nonoaks with dbh 7.5-15 cm, and >15 cm, respectively (/ha)
6-8	JUNA-JUNC	No. junipers with dbh 7.5-15 cm, >15-38 cm, and >38 cm, respectively (/ha)
9-11	DENSO, DENSN, DENSJ	Relative densities of oaks, nonoaks, and junipers, respectively (percent = 100[no. oaks/total no. trees])
12-14	BAOAK, BANON, BAJUN	Basal areas of oaks, nonoaks, and junipers, respectively (cm ² /ha)
15-17	VAROAK, VARNON, VARJUN	Variances in basal area of oaks, nonoaks, and junipers, respectively ([cm ² /ha] ²)
18-20	RDOAK, RDNON, RDJUN	Relative dominance of oaks, nonoaks, and junipers, respectively (percent = 100[basal area oaks/total basal area trees])
21	MHEIGHT	Mean height of all trees (meters)
22-25	NSTEMSO, NSTEMSN, NSTEMSJ, NSTEMSV	No. oak, nonoak, juniper, and vine stems, respectively at 1-m height (/ha)
26-30	WOODYCOV, FORBCOV, GRASSCOV, ROCKCOV, CACTCOV	Ground cover of woody plants, forbs, grasses, rocks, and cactuses, respectively (percent)
31-35	DASUM-DESUM	No. decimeters with deciduous-vegetation hits in 0.0-0.5 m, >0.5-1.0 m, >1.0-2.0 m, >2.0-3.0 m, >3.0-8.0 m height intervals, respectively (/circle)
36-40	JASUM-JESUM	No. decimeters with juniper hits in 0.0-0.5 m, >0.5-1.0 m, >1.0-2.0 m, >2.0-3.0 m, >3.0-8.0 m height intervals, respectively (/circle)
41-43	FASUM-FCSUM	No. decimeters with forb hits in 0.0-0.5 m, >0.5-1.0 m, and >1.0-2.0 m height intervals, respectively (/circle)
44-46	GASUM-GCSUM	No. decimeters with grass hits in 0.0-0.5 m, >0.5-1.0 m, and >1.0-2.0 m height intervals, respectively (/circle)
47	TOTSUM	Sum decimeter hits (variables 31-46) (/circle)
48-50	D1SD-D3SD	SD of circle values for deciduous-vegetation hits in 0.0-2.0 m, >2.0-3.0 m, and >3.0-8.0 m height intervals, respectively
51-53	J1SD-J3SD	SD of circle values for juniper hits in 0.0-2.0 m, >2.0-3.0 m, and >3.0-8.0 m height intervals, respectively
54	TOTSD	SD of circle sums for total hits
55	PERCDECI	Deciduous cover at 1-m height (percent)
56	PERCJUNI	Juniper cover at 1-m height (percent)
57	PERCOPEN	Open at 1-m height (percent)
58-60	PERC1-PERC3	Cover with only one plant, two overlapping plants, or with three or more overlapping plants at 1-m height (percent)
61	NCHANGES	No. changes from open to cover at 1-m height (/circle)

^a For multivariate and univariate statistical analyses: (1) arcsine transformation (Sokal and Rohlf 1981) employed on relative dominance and percentage values (variables 9-11, 18-20, 26-30, 55-60); (2) square root of basal-area measures taken after means or variances calculated (variables 12-17). Values for variables 26-47 based on total of 20 points placed 2 m apart along two 20-m orthogonal diameters. Those for variables 55-61 based on two orthogonal lines 10 m long.

Vegetation was sampled for a series of randomly selected vireo territories (vireo plots) from all territories known in each of 13 study areas, as well as for equivalent areas of scrubland habitat unoccupied by vireos (nonvireo plots). Boundaries of vireo territories were established by following birds during several time periods and by noting locations where interactions occurred between adjacent territorial males. Po-

tential nonvireo plots located in habitats clearly unacceptable for vireos (e.g., grasslands or cedar brakes) were not sampled. This species seldom establishes territories in nonscrubland areas.

For each vireo or nonvireo plot, six circles were established in a grid oriented by the cardinal directions. Circles were separated by a distance equal to the diameter of a circle. To randomize the starting point in any territory, the center of

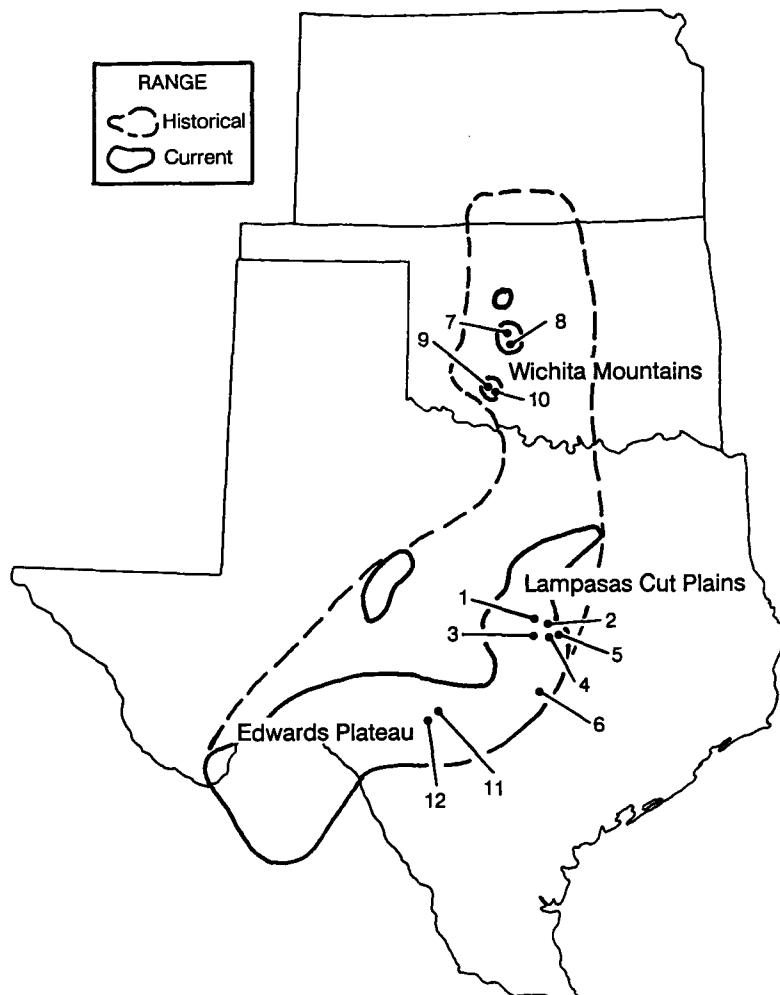


FIGURE 1. Map showing approximate current and historical ranges of Black-capped Vireo, as well as localities studied: (1) Texas, Coryell Co., Ft. Hood Military Reservation (MR), Manning and Williamson mountains; (2) Texas, Coryell Co., Ft. Hood MR, Areas 2 and 75; (3) Texas, Coryell Co. and Bell Co., Ft. Hood MR, West Ft. Hood; (4) Texas, Bell Co., Ft. Hood MR, Area 12; (5) Texas, Bell Co., Ft. Hood MR, Area 6 (east Ft. Hood); (6) Texas, Travis Co., Austin, Davenport Ranch and Wild Basin Wilderness Preserve; (7) Oklahoma, Canadian Co., Methodist Canyon Camp; (8) Oklahoma, Caddo Co., near Scott; (9) Oklahoma, Comanche Co., Wichita Mountains Wildlife Refuge, Greenleaf Canyon Area; (10) Oklahoma, Comanche Co., Ft. Sill MR, Area J; (11) Texas, Kerr Co., Kerr Wildlife Management Area; (12) Texas, Kerr Co., South Fork Ranch. Localities grouped into three regions for most analyses: (1–6) Lampasas Cut Plains; (7–10) Wichita Mountains; and (11–12) Edwards Plateau.

the initial circle was determined by pacing 50 steps in a cardinal direction from the initial entry point into a territory. In a few cases, only five circles would fit in a vireo territory; James and Shugart (1970) indicated that four or five circles can adequately characterize an area to be sampled. The center of the initial circle in nonvireo plots was determined by pacing 100 steps (500

steps in some cases) in a cardinal direction from the edge of a vireo territory or from some point in a scrubby area unoccupied by vireos. None of the nonvireo plots overlapped vireo territories. Additional nonvireo plots in an area were positioned in a similar fashion by starting from the center of the last circle of the most recently selected nonvireo plot.

STUDY REGIONS

Data were grouped for three regions designated as: the Lampasas Cut Plains; the Wichita Mountains; and the Edwards Plateau (Fig. 1). Analyses were conducted on the entire data set, and then for each regional data set separately. In addition, distinctions were made between territories occupied by second-year males (SY) and older males (ASY; after-second-year males). The year-class designations follow a convention employed by the Bird Banding Laboratory, U.S. Fish and Wildlife Service (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1984); SY birds are in their second calendar year of life, which is their first potential breeding season.

For the Lampasas Cut Plains, 38 territories and 31 nonvireo plots were sampled from six widely spaced sites located on Fort Hood Military Reservation in Bell and Coryell counties, Texas, and on the properties of the Davenport Ranch in Travis County. The Davenport Ranch, though technically not located on the Lampasas Cut Plains, was included in this designated region because of its close proximity and its location along the eastern edge of the Balcones Escarpment; the climate regime of the Davenport Ranch is more similar to that of Fort Hood than to that of other sites sampled.

In the Wichita Mountains region of Oklahoma, we selected 16 territories for analysis, including: nine on the Wichita Mountains Wildlife Refuge, Comanche County; five on the adjacent Fort Sill Military Reservation, Comanche County; and one each from the Methodist Canyon Camp in Canadian County, and from a site near Scott in Caddo County. The sites on the wildlife refuge and the military reservation are technically in the Wichita Mountains, while the others are not. In addition, 13 equivalent nonvireo plots with scrubland vegetation were sampled for comparison, 11 in the Wichita Mountains and one each near the other two sites. For convenience, the entire sample is designated as being from the Wichita Mountains.

The sample for the region designated as the Edwards Plateau for our study was obtained from Kerr County, Texas. Twenty territories were selected, including 15 from the Kerr Wildlife Management Area and five from the South Fork Ranch. Thirteen nonvireo plots were sampled, nine on the Kerr area and four on the South Fork Ranch.

STATISTICAL PROCEDURES

Four statistical techniques were employed to compare and contrast sample plots: principal-components analysis; stepwise discriminant-function analysis (which we refer to as canonical-variates analysis when more than two groups are evaluated); row-by-column tests of independence in contingency tables; and single-classification analysis of variance (ANOVA). Principal components were used to summarize covariation among vegetation variables and to determine general trends: (1) among regions; (2) for different age groups; and (3) between vireo and nonvireo plots. We used programs from NT-SYS (Rohlf et al. 1982), BIOM (Rohlf 1992), and BMDP (Dixon 1990) computer packages.

Similarities of sample plots were graphically represented with respect to the first three principal components extracted from a matrix of correlations among vegetation variables (Sneath and Sokal 1973, Duntzman 1989, Afifi and Clark 1990). Because many of the variables are correlated, it is possible to describe major trends of variation in the 61 original variables with a smaller number of new composite axes. A table of loadings (i.e., correlations) of original variables with principal components was produced, and sample plots were projected (based on standardized variables) onto these components.

Stepwise discriminant-function analysis (Klecka 1980, Afifi and Clark 1990, Dixon 1990, McLachlan 1992) was used to determine which of the 61 variables in combination provide the maximum discrimination between selected groups of sample plots (e.g., vireo vs. nonvireo plots). Variables are favored that exhibit low variation within and high variation among the groups of interest. A basic assumption is that covariance matrices for the groups are equal; groups represented in our data did not exhibit any marked deviations from this premise. After identifying linear combinations of variables that best separate the groups, sample plots were projected on the resulting discriminant axes. Classification functions were calculated and a jackknife procedure was used to determine the degree to which we were able to differentiate between the test groups. The classification functions were used to assign plots to one of the groups, depending on the relative probability of group membership based on the characteristics of the groups and of the given plot. A plot had an equal

probability of being assigned to any particular group (e.g., vireo vs. nonvireo). This is not to say that an equal number of plots would be assigned to each group; rather, by selecting this option we did not bias the possibility of a particular plot being categorized in one group or another. Often more plots were assigned to one group or another (which is what would be expected, for example, with a discerning discriminant function if one started with more vireo than nonvireo plots) simply because individual plots had the particular characteristics of that group.

The jackknife procedure is a special case of a general cross-validation method (Dixon 1990); it classifies each plot into the group with the highest *a posteriori* probability according to classification functions computed from all of the data except for the plot being evaluated. Thus, one avoids the overly optimistic estimate of the probability of correct classification that comes with *a posteriori* use of classification functions based on data that include the plot being evaluated. The program employed (BMDP-7M) computed the Mahalanobis distance as the distance from the plot being considered to the groups formed by the remaining plots. We used row-by-column *G*-tests of independence in contingency tables (Sokal and Rohlf 1981, Rohlf 1992) to assess whether discrimination between groups using these classification functions was better than expected simply by chance. Such an approach is justified given that the jackknife procedure removes the influence on the classification functions of the plot being evaluated.

In two cases, we assessed the degree of differentiation that could be achieved among three groups using stepwise canonical-variates analysis (Klecka 1980, Dixon 1990). In addition, the differences between groups for selected single variables were tested using a single-classification ANOVA (Sokal and Rohlf 1981).

RESULTS

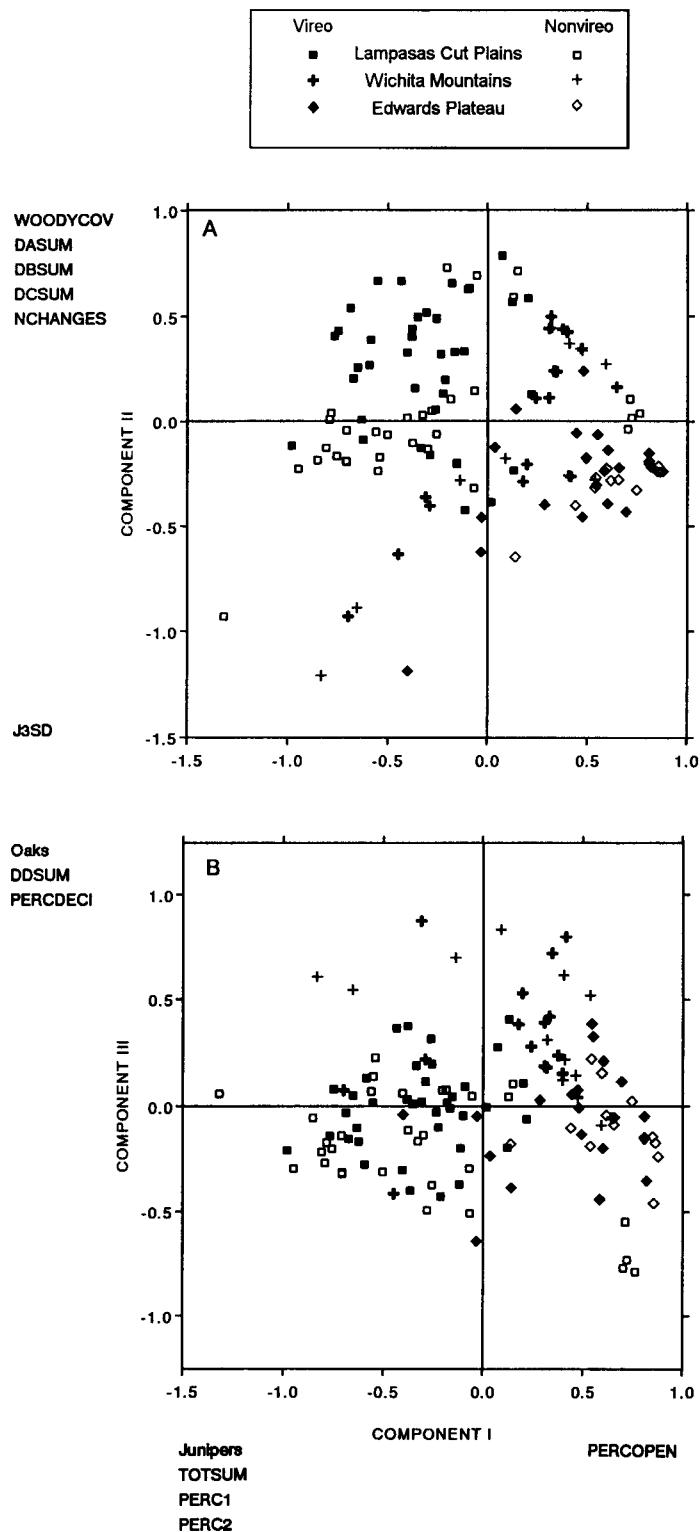
PRINCIPAL-COMPONENTS ANALYSIS

Interregional assessment. Summarizing vegetation data using principal components can assist in characterizing primary gradients, and provides an overview of relationships among sample plots. Projections onto the first three principal-component axes for all plots from all three regions are depicted in Figure 2, with character loadings on the components provided in Table 2. We con-

ducted a similar analysis using only vireo plots from the three regions. The resulting projections and loadings were very similar to those based on all plots; therefore, we present here only the results of the assessment based on the vireo and nonvireo plots combined.

The first three principal components explain 52.9% of the total variance in the 61 vegetation variables (see bottom of Table 2). On component I (Fig. 2; Table 2), the sample plots to the right are characterized as being in more open habitats (PERCOPEN) relative to other plots, while those to the left have higher values for juniper variables and total vegetation density (TOTSUM), as well as for two variables (PERC1 and PERC2) indicating a higher degree of plant overlap. The second component contrasts plots near the top of Figure 2A (that have higher values for woody cover [WOODYCOV], low-level deciduous vegetation density [DASUM, DBSUM, DCSUM], and a relatively high number of transitions between openings and woody cover [NCHANGES]) and those near the bottom (with more variation in juniper hits in the 3.0–8.0 m height interval [J3SD]). The third component positions plots along a gradient (starting at top of Fig. 2B) from those with a higher proportion of deciduous vegetation [PERCDECI, DDSUM], particularly oaks, to those with relatively fewer oaks. General regional differences are evident, with plots from the Edwards Plateau having relatively large values for projections on component I (Fig. 2), and those from the Lampasas Cut Plains exhibiting mostly negative component I projections; the plots from the Wichita Mountains tend to be intermediate. Considerable overlap exists among regions on component II (Fig. 2A). Component III, with Wichita Mountains plots projected near the top of Figure 2B, corroborates a point that is evident if one visits the Wichita Mountains—species diversity is relatively low and oaks (blackjack and post oaks, *Quercus marilandica* and *Q. stellata*, respectively) predominate on most plots. The diversity of deciduous species is much greater in the Texas regions.

This principal-components analysis indicates regional differences in occupied habitats, as well as in the habitats available in different regions (see Fig. 2). Although the Edwards Plateau and Lampasas Cut Plains are adjacent regions and more closely related floristically, the Wichita Mountains plots have physiognomic characteristics intermediate between those for the other



two regions. Furthermore, vireos use areas that span most of the range of scrubland habitats sampled in each region. Regional differences are evident in the characteristics of sites used by nesting Black-capped Vireos, indicating the important reason for taking a regional approach when evaluating habitat use by these birds.

Intraregional assessments. For the three separate intraregional analyses that include all plots from within a given region, principal-component projections and loadings of variables are summarized in Figure 3 and Table 2. The total percent variances explained by the first three components in the three analyses were: Lampasas Cut Plains, 48.7%; Wichita Mountains, 63.3%; and Edwards Plateau, 54.1% (for summary statistics on individual components, see bottom of Table 2).

Numerous variables summarizing data for junipers are negatively associated with principal component I within all regions (Table 2), indicating that junipers are a predominant source of environmental variation, not only among regions (as indicated earlier), but also within regions. For the Wichita Mountains and Edwards Plateau, component I also describes a gradient of increasing oaks (DENSO, RDOAK); in the Wichita Mountains, substantial negative loadings also were found for the total number of hits (TOT-SUM) and variability in high-level deciduous-tree hits (D3SD), while a positive association was found with the mean tree height (MHEIGHT). Much of the variation for the Wichita Mountains component I reflects differences of territories or nonvireo plots measured at the Methodist Canyon Camp and at Scott (those to left in Figs. 3C, D) that had more junipers than plots in the Wichita Mountains proper. The data for territories at Methodist Canyon Camp and Scott indicate that vireos are capable of tolerating the presence of relatively large numbers of junipers. However, the information concerning territories and nonvireo plots for the Lampasas Cut Plains suggests that vireos are more likely to use areas containing relatively few junipers.

Component II for the Lampasas Cut Plains

(Fig. 3A) is a contrast between plots that are more open (PERCOPEN) and those with more woody cover (WOODYCOV, PERCDECI, also PERC1) including greater deciduous-vegetation density, increased numbers of deciduous stems (NSTEM-SO, NSTEMSN), and more transitions from open to cover (NCHANGES). For the Edwards Plateau (Fig. 3E), component II represents a gradient of increasing foliage density involving deciduous trees (DBSUM, DCSUM, PERCDECI) and increasing heterogeneity of deciduous vegetation at the lower levels (D1SD). For the Wichita Mountains, component II positions sites that are relatively more open (near bottom of Fig. 3C) from those with more deciduous cover including oaks (near top). For at least two of the regions (Lampasas Cut Plains and Edwards Plateau), vireo territories tend to be nearer the top end of the component II axis with higher values for deciduous-vegetation hits and PERCDECI, although there is considerable overlap with nonvireo plots.

Component III is different for each of the three intraregional analyses. The variables with high positive and negative loadings on this component are summarized in Table 2 and Figures 3B, 3D, and 3F. In none of the three regional analyses does component III separate vireo and nonvireo plots.

DISCRIMINANT ANALYSES

While principal-components analyses illustrate general vegetation trends for plots, discriminant analyses highlight combinations of variables that best differentiate between specified groups of plots. Below we report on contrasts between: (A) vireo and nonvireo plots for all regions; (B) territories of ASY males and nonvireo plots for all regions; (C) territories of ASY and SY males for the Wichita Mountains and Edwards Plateau; and (D) SY male territories, ASY male territories, and nonvireo plots for the Wichita Mountains and Edwards Plateau. The sets of variables included in the discriminant functions may provide insight into the important habitat parameters involved in territorial occupancy by Black-capped Vireos. However, as noted by James et

FIGURE 2. Projection of 131 sample plots (vireo territories and nonvireo plots) from all regions onto first three principal components based on 61 vegetation variables. Variables with relatively high positive or negative loadings on component indicated next to appropriate scale by specific variable code in capital letters (e.g., WOODYCOV; see Table 1) or general category that subsumes several variables (e.g., junipers).

TABLE 2. Principal-component loadings for four separate analyses: all 131 plots (vireo and nonvireo); Lampasas Cut Plains; Wichita Mountains; and Edwards Plateau. Each analysis based on 61 vegetation variables.^a

Variable	All plots			Lampasas Cut Plains			Wichita Mountains			Edwards Plateau		
	I			II			I			II		
	I	II	III	I	II	III	I	II	III	I	II	III
1 OAKA	0.092	-0.406	0.737	-0.356	-0.200	0.726	-0.560	0.696	0.162	0.223	0.163	0.016
2 OAKB	0.103	-0.488	0.611	-0.318	-0.268	0.497	-0.650	0.615	0.026	0.253	0.134	-0.611
3 OAKC	0.177	-0.254	0.414	-0.162	-0.117	0.020	-0.110	0.381	0.160	-0.267	-0.314	-0.172
4 NONA	-0.393	-0.167	-0.268	-0.427	0.001	-0.012	-0.525	-0.662	-0.380	-0.448	0.294	-0.207
5 NONB	0.011	-0.204	-0.194	-0.062	0.053	0.156	-0.283	-0.185	-0.796	-0.100	0.448	-0.505
6 JUNA	-0.751	-0.279	-0.075	-0.683	0.084	-0.410	-0.885	-0.044	0.158	-0.720	0.045	-0.087
7 JUNB	-0.643	-0.434	0.065	-0.698	-0.003	-0.233	-0.771	0.024	0.152	-0.767	-0.332	0.091
8 JUNC	-0.242	-0.501	0.029	-0.265	-0.003	-0.322	-0.806	-0.356	-0.078	-0.695	-0.381	-0.113
9 DENSO	0.628	0.040	0.560	0.156	0.077	0.786	0.903	0.311	0.067	0.807	-0.171	0.130
10 DENSN	-0.336	-0.071	-0.423	-0.292	0.062	-0.089	-0.520	-0.564	-0.539	-0.331	0.455	-0.230
11 DENSJ	0.816	-0.097	-0.238	-0.615	0.253	-0.491	-0.932	-0.191	0.068	-0.875	-0.120	0.061
12 BAOAK	0.193	-0.547	0.731	-0.512	-0.228	0.701	-0.576	0.689	0.040	0.269	0.057	-0.571
13 BANON	-0.337	-0.261	-0.250	-0.521	-0.021	0.021	-0.490	-0.379	-0.691	-0.317	0.529	-0.477
14 BAJUN	-0.755	-0.501	0.009	-0.825	0.047	-0.292	-0.965	-0.084	0.012	-0.909	-0.247	-0.032
15 VAROAK	0.261	-0.552	0.582	-0.370	-0.272	0.541	-0.528	0.592	-0.004	0.114	0.032	-0.580
16 VARNON	-0.122	-0.218	-0.077	-0.426	-0.019	0.119	-0.300	-0.195	-0.797	-0.175	0.522	-0.500
17 VARJUN	-0.517	-0.568	0.047	-0.652	0.065	-0.340	-0.902	-0.902	-0.121	-0.882	-0.223	-0.113
18 RDOAK	0.661	0.066	0.524	0.185	0.012	0.788	0.928	0.287	0.074	0.865	-0.102	0.046
19 RDNON	-0.282	-0.014	-0.373	-0.207	0.089	-0.028	-0.441	-0.398	-0.675	-0.271	0.503	-0.234
20 RDJUN	-0.812	-0.136	-0.231	-0.619	0.281	-0.488	-0.942	-0.245	0.031	-0.871	-0.149	0.121
21 MHEIGHT	-0.586	0.550	-0.179	-0.294	0.489	-0.130	0.733	-0.276	-0.081	0.037	-0.093	-0.574
22 NSTEMSO	-0.142	0.547	0.518	0.075	0.730	0.108	0.470	0.596	0.007	0.212	0.585	0.085
23 NSTEMSN	-0.464	-0.030	0.495	0.197	0.630	0.156	-0.390	-0.623	-0.460	-0.569	0.237	-0.277
24 NSTEMSI	-0.808	-0.380	-0.170	-0.849	-0.207	-0.183	-0.852	-0.233	0.151	-0.928	-0.242	0.051
25 NSTEMSV	-0.361	0.281	0.091	-0.065	0.305	0.408	-0.340	0.157	-0.781	-0.095	0.580	0.439
26 WOODYCOV	-0.664	0.608	0.073	-0.210	0.718	-0.082	0.441	-0.224	-0.370	0.556	0.602	
27 FORBCOV	0.496	-0.156	-0.464	0.593	-0.232	-0.397	0.175	-0.418	0.634	-0.070	-0.315	-0.666
28 GRASSCOV	0.693	-0.438	0.076	0.154	-0.525	0.446	0.141	-0.216	0.532	0.511	-0.203	-0.293
29 ROCKCOV	0.301	0.152	0.141	0.090	-0.041	-0.307	0.644	0.110	-0.513	-0.044	-0.031	-0.086
30 CACTCOV	-0.168	-0.171	-0.273	-0.210	-0.070	-0.096	-0.499	-0.684	0.144	0.274	-0.135	0.347
31 DASUM	-0.397	0.737	-0.128	0.436	0.693	-0.154	0.400	-0.255	-0.448	-0.111	0.579	0.637
32 DBSUM	-0.352	0.828	0.098	0.373	0.844	-0.046	0.631	-0.268	-0.274	-0.187	0.664	0.581
33 DCSUM	-0.347	0.623	0.429	0.199	0.803	0.233	0.164	0.164	-0.086	-0.134	0.766	0.102

TABLE 2. Continued.

Variable	All plots			Lampasas Cut Plains			Wichita Mountains			Edwards Plateau		
	I	II	III	I	II	III	I	II	III	I	II	III
34 DDSUM	-0.418	0.429	0.518	0.030	0.741	0.287	-0.192	0.568	-0.052	-0.065	0.465	-0.460
35 DESUM	-0.593	0.102	0.292	-0.492	0.319	0.320	-0.334	0.602	-0.341	-0.007	-0.370	-0.815
36 JASUM	-0.666	-0.329	-0.140	-0.672	-0.332	-0.034	-0.726	-0.107	0.270	-0.867	-0.176	0.036
37 JBSUM	-0.715	-0.387	-0.062	-0.800	-0.364	0.014	-0.765	-0.129	0.281	-0.709	-0.007	0.220
38 JCSUM	-0.685	-0.506	0.020	-0.783	-0.323	0.008	-0.853	-0.092	0.170	-0.915	-0.218	0.107
39 JDSUM	-0.711	-0.514	-0.025	-0.793	-0.224	-0.193	-0.915	-0.060	0.100	-0.813	-0.358	0.089
40 JESUM	-0.763	-0.306	-0.111	-0.807	-0.075	-0.315	-0.759	0.137	0.075	-0.820	-0.402	-0.018
41 FASUM	0.488	-0.260	-0.392	0.591	-0.292	-0.346	-0.170	-0.223	0.592	-0.137	-0.236	-0.595
42 FBSUM	-0.018	-0.234	-0.052	0.052	-0.025	0.024	-0.364	-0.659	0.303	-0.659	0.145	-0.347
43 FCSUM	-0.045	-0.150	-0.014	-0.020	-0.041	0.066	-0.261	-0.325	-0.184	-0.304	0.045	-0.170
44 GASUM	0.639	-0.565	0.128	0.008	-0.541	0.545	-0.432	-0.031	0.540	0.354	-0.052	-0.234
45 GBSUM	0.345	-0.456	0.140	-0.076	-0.374	0.444	-0.614	-0.263	0.259	0.012	0.369	0.213
46 GCSUM	-0.059	-0.099	-0.025	-0.061	-0.060	0.282	-0.389	-0.691	0.080	-0.447	0.013	0.126
47 TOTSUM	-0.805	-0.039	0.315	-0.670	0.566	0.234	-0.864	0.158	0.162	-0.482	0.460	-0.320
48 DISD	-0.185	0.154	0.094	-0.016	0.449	-0.102	-0.233	0.031	0.195	-0.250	0.664	0.436
49 D2SD	-0.221	-0.002	0.416	-0.117	0.390	0.276	-0.420	0.243	0.225	-0.226	0.412	-0.363
50 D3SD	0.172	-0.543	0.422	-0.207	-0.282	0.451	-0.717	0.579	-0.112	0.003	-0.758	0.165
51 J1SD	-0.644	-0.356	0.013	-0.657	-0.241	0.014	-0.770	0.182	0.035	-0.675	0.005	0.274
52 J2SD	-0.623	-0.533	0.105	-0.742	-0.225	-0.012	-0.879	0.131	-0.089	-0.811	-0.309	0.138
53 J3SD	-0.194	-0.639	0.232	-0.336	-0.260	0.023	-0.837	0.173	-0.071	-0.812	-0.380	-0.011
54 TOTSD	-0.239	-0.237	0.095	-0.393	0.379	0.036	-0.356	0.002	0.152	-0.523	0.163	-0.645
55 PERCDEC1	-0.485	0.499	0.591	-0.194	0.807	0.375	0.093	0.674	-0.444	-0.103	0.803	0.065
56 PERCJUN1	-0.849	-0.413	-0.119	-0.932	-0.198	-0.138	-0.966	0.000	-0.001	-0.920	-0.211	0.113
57 PERCOPEN	0.822	-0.204	-0.436	0.665	-0.630	-0.198	-0.530	-0.619	0.416	0.654	-0.516	-0.058
58 PERC1	-0.739	0.246	0.476	-0.548	0.702	0.141	-0.442	0.616	-0.401	-0.609	0.562	0.114
59 PERC2	-0.801	0.084	0.283	-0.752	0.403	0.306	-0.498	0.393	-0.335	-0.407	0.124	-0.149
60 PERC3	-0.627	-0.003	0.062	-0.609	0.212	0.260	-0.522	0.078	-0.038	-0.114	-0.160	-0.135
61 NCHANGES	-0.565	0.615	0.111	0.064	0.779	-0.106	0.341	-0.033	-0.127	-0.452	0.313	-0.057
Eigenvalue	16.71	9.56	6.00	14.04	9.47	6.41	23.07	8.53	7.00	17.44	7.99	7.56
Percentage explained	27.4	15.7	9.8	23.0	15.2	10.5	37.8	14.0	11.5	28.6	13.1	12.4

* Relatively high loadings highlighted in bold as follows: (component I) > |0.7|; (component II) > |0.6|; (component III) > |0.5|.

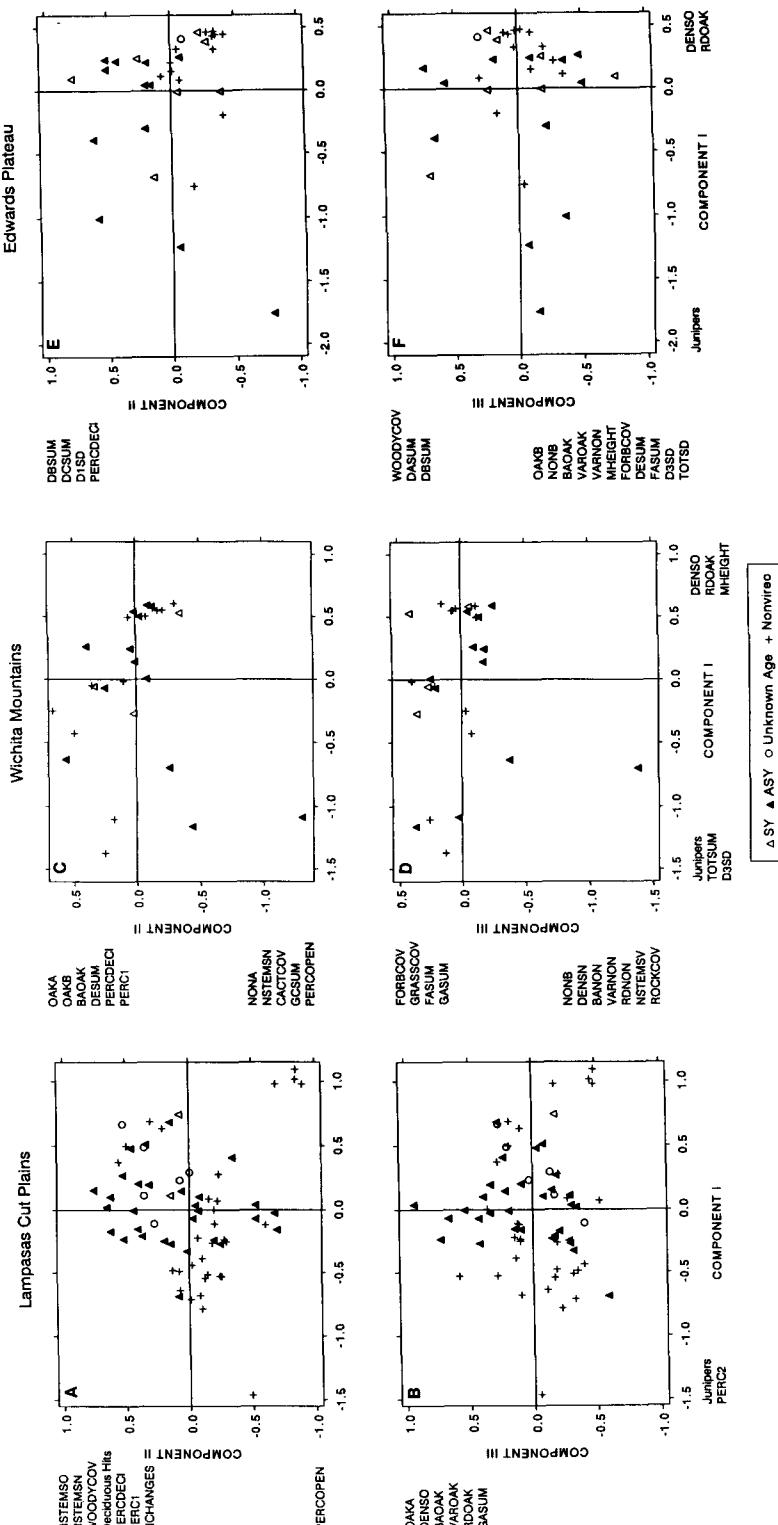


FIGURE 3. Separate principal-components analyses based on 61 variables for plots in each of three regions: (A, B) Lampasas Cut Plains; (C, D) Wichita Mountains; and (E, F) Edwards Plateau. Projections of plots within each region identified as: territories of second-year vireos (SY); territories of after-second-year vireos (ASY); territories of unknown-age vireos; and nonvireo plots. Variables with relatively high positive or negative loadings on components indicated next to appropriate scale by specific variable code in capital letters (e.g., DENS); see Table 1) or general category that subsumes several variables.

TABLE 3. Statistics for stepwise discriminant-function analysis of vireo versus nonvireo plots.

Variable	<i>F</i> -value to enter	Order of entry	Coefficient	Classification function ^a	
				Vireo	Nonvireo
All regions					
33 DCSUM	22.48	1	0.1350	0.3231	0.1260
21 MHEIGHT	11.79	2	-0.1348	0.0774	0.2742
25 NSTEMSV	10.90	3	0.0003	0.0003	-0.0002
1 OAKA	7.38	4	-0.0040	0.0099	0.0158
54 TOTSD	4.96	5	0.0288	0.2088	0.1668
Constant			-1.3720	-7.0767	-5.2113
Lampasas Cut Plains					
34 DDSUM	38.49	1	0.1934	0.6930	0.0199
7 JUNB	6.96	2	-0.0392	-0.0557	0.0009
17 VARJUN	7.67	3	0.0016	0.0039	0.3203
Constant			-1.9611	-6.0763	-2.4866
Wichita Mountains					
31 DASUM	9.36	1	0.5560	6.7992	4.9352
21 MHEIGHT	11.00	2	-0.1925	-1.9318	-1.2864
28 GRASSCOV	10.85	3	0.1248	1.9649	1.5467
54 TOTSD	5.57	4	0.0652	0.9002	0.6818
16 VARNON	4.09	5	0.0018	0.0251	0.0192
Constant			-11.0816	-90.4817	-53.9090
Edwards Plateau					
58 PERC1	9.86	1	0.0932	0.9457	0.7402
43 FCSUM	7.78	2	-5.5382	-15.3055	-3.0897
30 CACTCOV	6.09	3	-0.2422	-0.0007	0.5335
48 D1SD	4.03	4	0.0684	0.0822	-0.0686
Constant			-2.8509	-15.3492	-9.5769

^a Used with original measurements. Add products of measurements and corresponding function values to constant; classify as vireo or nonvireo plot depending on which classification function results in the higher numerical value.

al. (1984), caution should be practiced when interpreting the results of discriminant analyses.

Vireo and nonvireo plots. When assessing plots from all regions simultaneously, the resulting stepwise discriminant function separating vireo and nonvireo plots (Fig. 4A) included five variables (Table 3). Statistically, the most important variable is DCSUM, a measure of deciduous-vegetation density in the >1.0–2.0 m height interval. Vireo nests often were found in deciduous vegetation at this height (Grzybowski, unpubl. data). Other variables included the mean tree height (MHEIGHT), number of vine stems (NSTEMSV), number of small oaks (OAKA), and a measure of overall heterogeneity in vegetation density (TOTSD). Vireo territories typically were located in areas with shorter trees, more vines, fewer small oaks, and greater heterogeneity (see Table 4 for mean values). Using a jackknife procedure, vireo territories and nonvireo plots together from all regions were classified correctly 74.8% of the time (Table 5), with

80.7% and 70.3% of nonvireo and vireo plots, respectively, being correctly assigned. Table 3 includes the classification functions used to predict on the basis of the selected set of habitat variables whether a given site represented a vireo or nonvireo plot. In this and all subsequent applications of classification functions and the jackknifed procedure, the functions performed substantially better than expected by chance alone (see *G*-values and associated probabilities in Table 5).

Not unexpectedly, discrimination was better when within-region assessments were made (Figs. 4B–D), thus removing the interregional variability from consideration in a given analysis. Separation of vireo and nonvireo plots was successful 93.1% of the time for the Wichita Mountains, while the percentages of plots correctly allocated for the Lampasas Cut Plains and Edwards Plateau were 81.2% and 81.8%, respectively (Table 5).

In the Lampasas Cut Plains, the statistically

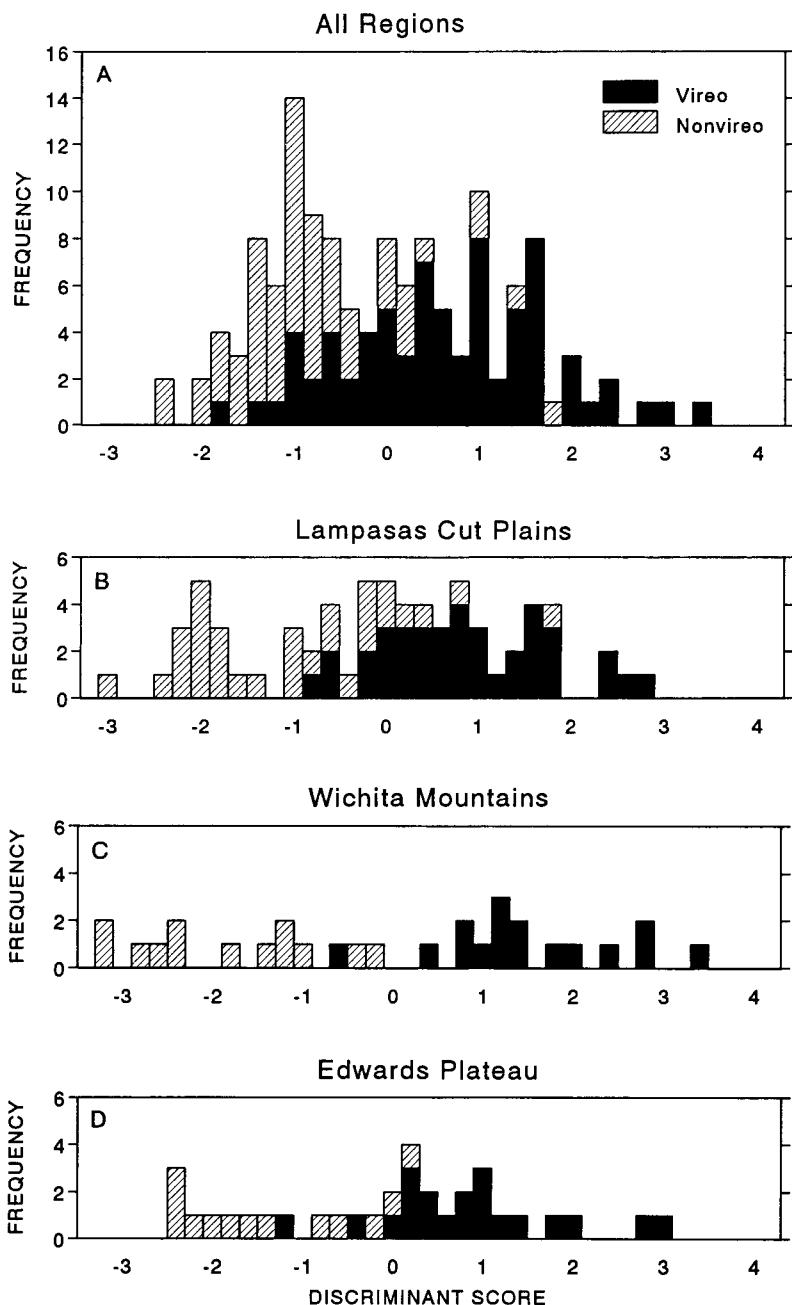


FIGURE 4. Discriminant-function analyses based on vegetation characteristics contrasting vireo and nonvireo plots. Projections of plots onto discriminant-function axes for analyses of data from: (A) all regions; (B) Lampasas Cut Plains; (C) Wichita Mountains; and (D) Edwards Plateau.

most important variable was DDSUM, which represents density of deciduous vegetation in the >2.0–3.0 m height interval (Table 3). Vireos were found at locations with relatively higher decid-

uous-vegetation density in this height interval (Table 4). Vireos also tended to occupy territories with relatively fewer intermediate-sized junipers (JUNB). On average, vireo plots had less vari-

ability than nonvireo plots in juniper basal area (VARJUN; Table 4). However, when taken in combination with other variables, discrimination was enhanced by emphasizing more variability in vireo than nonvireo plots (i.e., positive coefficient for VARJUN in Lampasas Cut Plains discriminant function; Table 3). This somewhat counterintuitive finding, with the overall mean difference being in one direction but the contribution to the discriminant function being in the opposite direction, results from the fact that the discriminant function involves values for a series of variables taken in combination. This indicates why it sometimes can be misleading to look only at individual variables in isolation from other habitat characteristics when attempting to differentiate between two groups of plots. Of course, this could be a statistical effect that may not have biological significance. Figure 4B shows the distribution of vireo and nonvireo plots on this discriminant function.

Five variables were selected for the discriminant function in the analysis of plots in the Wichita Mountains (Table 3). The measure of deciduous-vegetation density in the lowest height interval (i.e., 0.0–0.5 m; DASUM) was the first variable entered, with vireos more often being found on plots with relatively high values for this variable. Also, vireos were found more often where the mean tree height (MHEIGHT) was relatively low and where grass cover was more extensive (GRASSCOV) than in nonvireo plots (Table 4). Birds used sites with relatively higher heterogeneity in overall vegetation density (TOTSD) and in basal area of nonoak deciduous trees (VARNON; Table 4). As indicated in Figure 4C, almost complete separation was achieved for vireo and nonvireo plots using these five variables; only one vireo and one nonvireo plot were misclassified (Table 5) using the classification functions (Table 3).

The list of variables selected in the discriminant-function analysis for the Edwards Plateau was notably different than those incorporated in similar analyses for the other two regions. The first variable entered (Table 3), PERC1, reflects percent cover by one plant at the height of 1 m. As indicated by the coefficient in Table 3, vireos occupied plots with higher values for this variable (for mean values, see Table 4). Their territories had relatively few forbs in the >1.0–2.0 m height interval (FCSUM) and less cactus cover (CACTCOV) than nonvireo plots (Table 4). In

addition, the vireo territories exhibited relatively higher variability for deciduous-vegetation hits in the 0.0–2.0 m height interval (D1SD; Table 4). Three vireo and three nonvireo plots were miscategorized (Table 5) by the classification functions (Table 3).

ASY and SY plots. For the Wichita Mountains and the Edwards Plateau, data were available for both younger (SY) or older (ASY) males. Habitat characteristics were assessed to determine whether they could be used effectively to differentiate between territories of birds in the two age groups. When birds from the two regions were analyzed simultaneously, the distribution of territories of SY and ASY males on the resulting discriminant function (Table 6) exhibited substantial overlap (Fig. 5A). Based on habitat characteristics, the analysis was able to determine with 80.0% accuracy whether or not a territory was that of an SY or ASY male (Table 5). Predictions were more frequently correct for ASY males (87.5%) than for SY males (63.6%). The discriminant function included two variables, one indicating the percent openness at a height of 1 m (PERCOPEN) and the other reflecting the presence of large oaks (i.e., dbh > 38 cm; Table 6). The older males tended to select sites that were less open but with fewer large oaks (Table 6, Fig. 5A) than those occupied by the younger males.

For the 16 SY and ASY males from the Wichita Mountains, the analysis correctly classified 93.8% of the plots (Table 5, Fig. 5B). The first variable of three incorporated was PERC1, which indicates the percent of the ground covered by only one plant at 1-m height. The older ASY birds used sites with relatively more of this type of cover than did the younger SY males (Table 4). The second variable entered indicates the within-plot variability in basal area of oaks (VAROAK); territories of ASY males typically were in areas with less variability (Table 6; for mean values, see Table 4). The third variable reflects within-plot variability in the number of juniper hits for the 0.0–2.0 m height interval (J1SD). Territories of older males were more variable relative to those of younger males (Table 4). All 12 territories of older males were correctly classified, while one territory of a younger male was misclassified.

A much larger number of variables (i.e., eight) was incorporated into the discriminant function for the 19 SY and ASY territories from the Ed-

TABLE 4. Means (and standard deviations) of characteristic variables for all samples and for each region. Values provided for nonvireo, vireo, after-second-year (ASY), and second-year (SY) plots. Vireo plots include those for ASY and SY birds, as well as for birds not aged.

Variable (units)	Nonvireo	Vireo	ASY	SY
All regions				
1 OAKA (/ha)	111.7 (126.6)	98.9 (96.4)	100.2 (101.5)	120.1 (83.3)
21 MHEIGHT (m)	9.33 (7.19)	7.53 (6.73)	7.96 (6.81)	2.72 (4.03)
25 NSTEMSV (/ha)	890 (1.457)	1,723 (1.884)	1,943 (1.991)	574 (1.117)
33 DCSUM (/circle)	9.98 (5.93)	15.43 (6.95)	16.12 (6.85)	10.94 (5.84)
54 TOTSD (SD of circle sums)	21.57 (9.71)	27.21 (12.74)	28.47 (12.58)	23.50 (14.70)
55 PERCDEC1 (%)	31.98 (13.95)	39.74 (13.81)	42.23 (13.06)	27.68 (12.64)
Lampasas Cut Plains				
7 JUNB (/ha)	37.33 (35.81)	18.25 (25.56)	20.78 (27.22)	0.00 (—)
17 VARJUN ([cm ² /ha] ²)	225,690 (322,966)	112,974 (177,691)	125,076 (185,565)	0 (—)
25 NSTEMSV (/ha)	1,439 (1.767)	2,525 (2.098)	2,665 (2.207)	0 (—)
26 WOODYCOV (%)	32.93 (12.40)	31.82 (12.86)	30.47 (13.49)	38.10 (—)
31 DASUM (/circle)	13.06 (3.58)	16.30 (6.04)	15.33 (6.16)	21.5 (—)
34 DBSUM (/circle)	7.12 (4.36)	13.99 (4.74)	14.08 (5.18)	13.17 (—)
51 JISD (SD of circle hits)	6.90 (4.95)	6.59 (4.67)	7.03 (4.84)	1.97 (—)
Wichita Mountains				
15 VAROAK ([cm ² /ha] ²)	126,098 (231,393)	79,764 (113,119)	79,751 (124,071)	79,805 (86,815)
16 VARNON ([cm ² /ha] ²)	1,042 (3.755)	13,407 (36,458)	17,876 (41,537)	0 (0)
19 RDNON (%)	0.038 (0.139)	2.512 (5.818)	3,350 (6,564)	0.000 (0.000)
21 MHEIGHT (m)	6.55 (5.30)	4.50 (5.03)	3.91 (4.86)	6.26 (5.85)
28 GRASSCOV (%)	26.00 (6.69)	27.66 (15.75)	24.35 (9.57)	37.60 (26.99)
31 DASUM (/circle)	6.81 (3.35)	10.05 (2.36)	10.39 (2.31)	9.04 (2.53)
32 DBSUM (/circle)	12.76 (6.83)	17.66 (5.59)	18.28 (5.56)	15.79 (6.06)
51 JISD (SD of circle hits)	3.58 (5.16)	4.68 (6.67)	5.60 (7.43)	1.92 (2.61)
54 TOTSD (SD of sums circle hits)	14.84 (5.86)	27.62 (15.34)	27.78 (13.59)	27.14 (22.37)
58 PERC1 (%)	37.59 (9.51)	40.80 (8.89)	43.58 (7.53)	32.45 (7.96)

TABLE 4. Continued.

	Variable (units)	Nonvireo	Vireo	ASY	SY
10 DENSN (%)	3.05 (4.81)	11.94 (16.31)	15.19 (19.57)	8.06 (8.84)	
16 VARNON (cm^2/ha^2)	4,390 (9,583)	70,044 (141,750)	112,674 (172,344)	6,970 (8,963)	
17 VARJUN (cm^2/ha^2)	123,907 (273,528)	36,276 (107,031)	40,345 (128,871)	34,233 (74,780)	
18 RDOAK (%)	85.86 (23.65)	70.32 (31.35)	66.48 (35.04)	72.90 (26.29)	
19 RDNON (%)	1.69 (2.80)	11.24 (16.47)	13.42 (19.23)	9.11 (12.05)	
23 NSTEMSN (/ha)	1,306 (1,660)	2,048 (2,249)	2,994 (2,476)	719 (477)	
25 NSTEMSV (/ha)	257 (51.5)	1,083 (1,160)	1,258 (1,069)	887 (1,404)	
27 FORBCOV (%)	15.68 (6.82)	14.90 (8.59)	15.61 (9.72)	14.63 (7.24)	
30 CACTCOV (%)	0.362 (0.457)	0.085 (0.221)	0.117 (0.272)	0.043 (0.113)	
43 FCSSUM (/circle)	0.103 (0.259)	0.017 (0.074)	0.028 (0.096)	0.000 (0.000)	
45 GBSSUM (/circle)	1.76 (1.52)	2.42 (1.75)	2.24 (1.46)	2.21 (1.87)	
47 TOTSUM (/circle)	90.27 (15.05)	101.88 (19.32)	107.04 (18.72)	94.19 (20.14)	
48 DISD (SD of circle hits)	12.91 (5.70)	18.95 (10.15)	21.54 (11.68)	15.43 (6.41)	
57 PERCOPEN (%)	81.00 (6.59)	70.32 (10.92)	64.82 (7.77)	77.89 (10.55)	
58 PERCI (%)	15.48 (6.23)	25.12 (9.70)	29.36 (7.84)	19.09 (9.71)	

TABLE 5. Numbers of plots classified correctly or incorrectly using classification functions and jackknifed procedure.^a

Group	Percent correctly classified	Classified in group		Total		
		1	2			
Vireo vs. Nonvireo						
All regions ($G = 35.43^{***}$)						
1 Vireo	70.3	52	22	74		
2 Nonvireo	80.7	11	46	57		
Total	74.8	63	68	131		
Lampasas Cut Plains ($G = 28.52^{***}$)						
1 Vireo	81.6	31	7	38		
2 Nonvireo	80.6	6	25	31		
Total	81.2	37	32	69		
Wichita Mountains ($G = 25.36^{***}$)						
1 Vireo	93.8	15	1	16		
2 Nonvireo	92.3	1	12	13		
Total	93.1	16	13	29		
Edwards Plateau ($G = 13.30^{***}$)						
1 Vireo	85.0	17	3	20		
2 Nonvireo	76.9	3	10	13		
Total	81.8	20	13	33		
ASY vs. SY						
Wichita Mountains and Edwards Plateau combined ($G = 9.37^{**}$)						
1 ASY	87.5	21	3	24		
2 SY	63.6	4	7	11		
Total	80.0	25	10	35		
Wichita Mountains ($G = 10.94^{***}$)						
1 ASY	100.0	12	0	12		
2 SY	75.0	1	3	4		
Total	93.8	13	3	16		
Edwards Plateau ($G = 25.01^{***}$)						
1 ASY	100.0	12	0	12		
2 SY	100.0	0	7	7		
Total	100.0	12	7	19		
ASY vs. Nonvireo						
All regions ($G = 50.18^{***}$)						
1 ASY	80.0	44	11	55		
2 Nonvireo	84.2	9	48	57		
Total	82.1	53	59	112		
Lampasas Cut Plains ($G = 29.22^{***}$)						
1 ASY	74.2	23	8	31		
2 Nonvireo	90.3	3	28	31		
Total	82.3	26	36	62		
Wichita Mountains ($G = 27.57^{***}$)						
1 ASY	100.0	12	0	12		
2 Nonvireo	92.3	1	12	13		
Total	96.0	13	12	25		

TABLE 5. Continued.

Group	Percent correctly classified	Classified in group		Total
		1	2	
Edwards Plateau ($G = 34.62^{***}$)				
1 ASY	100.0	12	0	12
2 Nonvireo	100.0	0	13	13
Total	100.0	12	13	25

^a *G*-values from row-by-column contingency test of independence of original groups versus those assigned using classification functions and jackknifed procedure. **, $P < 0.01$; ***, $P < 0.001$.

wards Plateau (Table 6). The first variable entered indicates the percent of the habitat that is open at 1-m height (PERCOPEN), while the highest *F*-values to enter were achieved for a variable registering the relative dominance of oaks (RDOAK) and one reflecting the total vegetation density (TOTSUM; Table 6). The signs of discriminant-function coefficients (Table 6) indicate that, when considering characters in combination, the territories of the older ASY males were located in less open areas with greater dominance of oaks and greater overall vegetation density. Territories of SY males occurred in locations that on average were about 78% open, compared to 65% for territories of ASY males (PERCOPEN; Table 4). ASY male territories in general had higher values for four other variables (three reflecting density and within-plot variability of nonoak deciduous trees [NSTEMSN, VARNON, and DENSN] and one mirroring within-plot variability in juniper basal area [VARJUN]; see Table 4). When the characters were taken in combination, discrimination was enhanced by considering higher GBSUM (grass hits in the >0.5–1.0 m height interval) values for ASY versus SY males (i.e., negative coefficient for Edwards Plateau discriminant function in Table 6), although on average the ASY territories had lower values than SY territories for GBSUM (see Table 4). All 19 territories were classified correctly relative to whether they were those of younger or older males (Table 5, Fig. 5C).

One of us (Grzybowski, unpubl. data) has noted differences between the two age classes on the Edwards Plateau in terms of the percent of males mated; 37% of SY males compared to 88% of ASY males. Indirectly, this may reflect on the ability of SY males to select, occupy, and defend territories in the most suitable habitats, and to attract a female to such a territory.

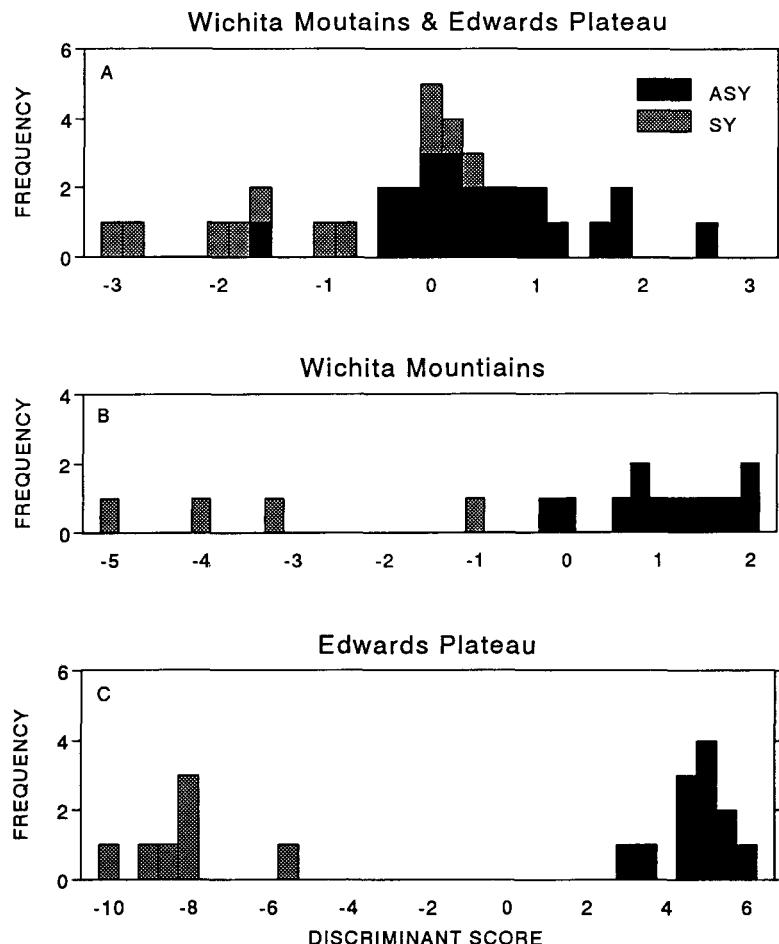


FIGURE 5. Discriminant-function analyses based on vegetation characteristics contrasting territories of second-year (SY) and after-second-year (ASY) vireos. Projections of plots onto discriminant-function axes for analyses of data from: (A) Wichita Mountains and Edwards Plateau combined; (B) Wichita Mountains; and (C) Edwards Plateau.

ASY and nonvireo plots. When contrasting all territories of ASY males with all nonvireo plots, six variables were selected for the discriminant function (Table 7). While there was considerable overlap in discriminant-function scores for the two groups (Fig. 6A), the analysis placed 82.1% of the plots in the correct group (Table 5). The first variable in the discriminant function indicates the number of decimeters with deciduous-vegetation hits in the >1.0–2.0 m height interval (DCSUM); ASY territories were found in places with a relatively higher number of hits (Table 4). For three other variables (within-site variability in hit numbers [TOTSD], number of vine stems

[NSTEMSV], and deciduous cover [PERCDECI]), ASY territories tended to have higher values (Table 4). However, plots with ASY males also tended to have shorter trees (MHEIGHT) and relatively fewer small oaks (OAKA) than nonvireo plots (Table 7; see Table 4 for means).

For the Lampasas Cut Plains, overlap still occurred when comparing ASY and nonvireo plots (Fig. 6B). The discriminant function successfully identified 82.3% of the ASY and nonvireo plots (Table 5). Five variables were selected (Table 7), with DDSUM (number of decimeters with deciduous-vegetation hits in >2.0–3.0 m height interval) being the first and the most important

TABLE 6. Statistics for stepwise discriminant-function analysis of plots for after-second-year (ASY) and second-year (SY) vireos.

Variable	<i>F</i> -value to enter	Order of entry	Coefficient	Classification function	
				ASY	SY
Wichita Mountains and Edwards Plateau combined					
57 PERCOPEN	12.79	1	-0.1439	1.1003	1.3364
3 OAKC	5.25	2	-0.1120	0.6218	0.8056
Constant			7.8388	-28.4307	-41.7930
Wichita Mountains					
58 PERC1	6.54	1	0.4475	7.8585	5.8558
15 VAROAK	14.34	2	-0.0020	-0.0314	-0.0224
51 J1SD	8.59	3	0.1435	2.0865	1.4444
Constant			-15.6681	-149.3270	-84.2072
Edwards Plateau					
57 PERCOPEN	9.83	1	-0.6702	1.1717	9.8055
23 NSTEMSN	5.31	2	0.0007	-0.0011	-0.0100
18 RDOAK	13.21	3	0.3117	0.8614	-3.1537
16 VARNON	4.13	4	0.0075	-0.0133	0.0833
10 DENSN	4.61	5	0.4507	1.2459	-4.5599
17 VARJUN	6.46	6	0.0016	0.0089	-0.0113
45 GBSUM	8.13	7	-2.1023	-6.4838	20.5980
47 TOTSUM	13.82	8	0.1239	0.8651	-0.7306
Constant			3.8982	-108.7542	-180.8048

statistically; ASY males tended to have higher values for this variable (Table 4). However, overall ground cover by woody plants (WOODY-COV) was lower in ASY plots when compared with nonvireo plots (Table 4). For the other three variables (deciduous-vegetation hits near the ground [DASUM], intraplot variability in juniper hits near the ground [J1SD], and number of vine stems [NSTEMSV]), ASY plots typically had higher values than nonvireo plots (Table 4).

In the Wichita Mountains, differences between ASY and nonvireo plots were more prominent (Fig. 6C), and the classification functions (Table 7) correctly categorized all but one of the plots based on habitat characteristics (Table 5). The first variable, TOTSD, reflects within-plot variability in total hits, while the variable with the highest *F*-value to enter was DBSUM (deciduous-vegetation hits in >0.5–1.0 m height interval). The other three variables included were RDNON (relative dominance of nonoak deciduous trees), PERC1 (cover by one plant at 1-m height), and GRASSCOV (ground cover by grasses). Taking into account all five variables simultaneously, ASY territories were in areas with higher values for these variables than those for nonvireo plots (see coefficients, Table 7), although when taken individually, GRASSCOV

was actually less in ASY territories than in nonvireo plots (Table 4).

The discriminant function for the Edwards Plateau (Fig. 6D) also included five variables (Table 7). The most influential was PERCOPEN (percent open at 1-m height). For this and FCSUM (hits of forbs in >1.0–2.0 m height interval), the coefficients indicate that ASY males are found on plots with lower values than characteristic of nonvireo plots (Table 4). The other variables are NSTEMSV (number of vine stems), FORBCOV (percent forb ground cover), and RDNON (relative dominance of nonoak deciduous trees); when the characters are taken in combination, plots for ASY males typically had higher values for each of these three variables when compared to nonvireo plots (coefficients in Table 7), although when taken separately (Table 4), FORBCOV is, on average, less in ASY than nonvireo plots. The classification functions correctly identified all plots (Table 5, Fig. 6D).

SY, ASY, and nonvireo plots. Two canonical variables were produced when SY, ASY, and nonvireo plots of the Wichita Mountains were assessed simultaneously (Fig. 7, Table 8). The first variable contrasts nonvireo plots (to left in Fig. 7) from SY and ASY territories. Canonical variable 2 primarily contrasts one SY plot with

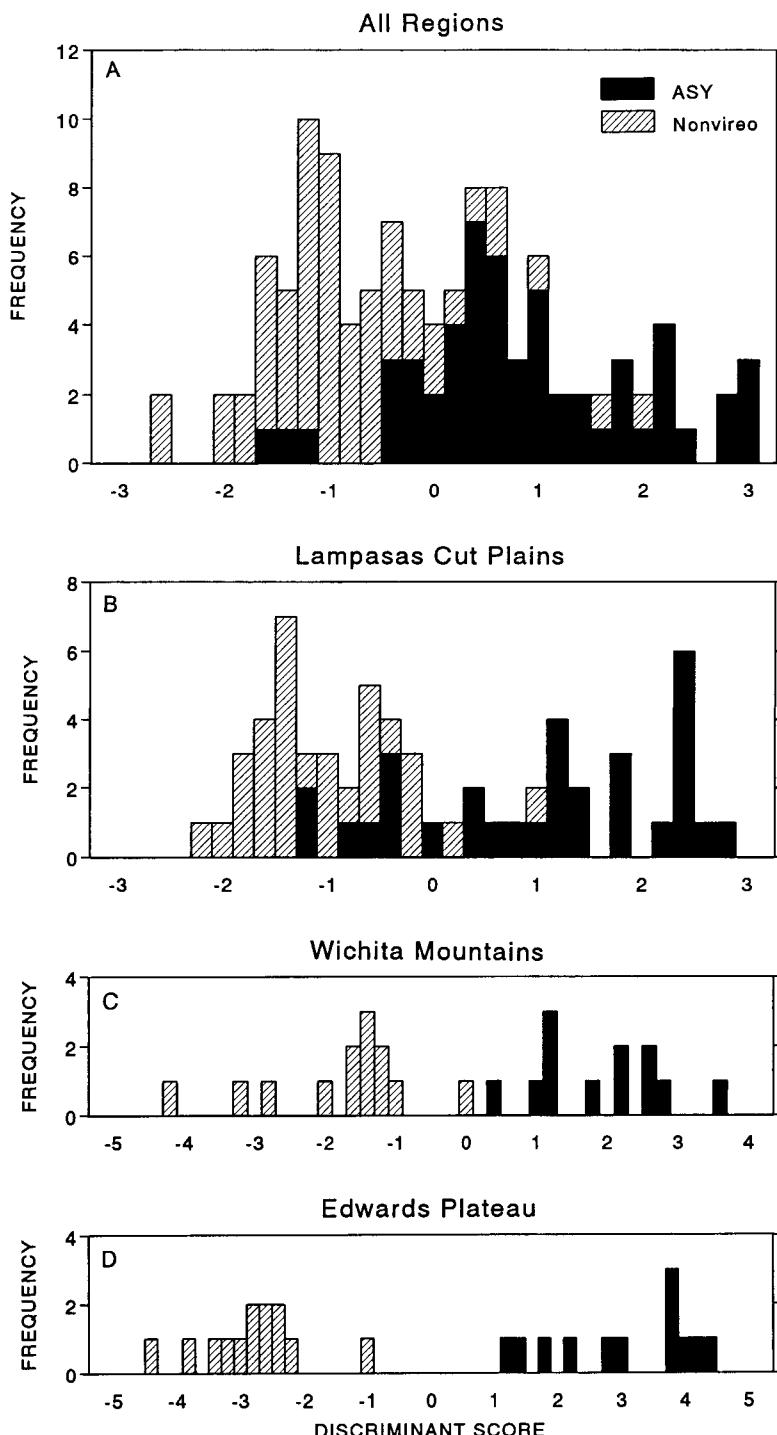


FIGURE 6. Discriminant-function analyses based on vegetation characteristics contrasting nonvireo plots with those for territories of after-second-year vireos (ASY). Projections of plots onto discriminant-function axes for analyses of data from: (A) all regions; (B) Lampasas Cut Plains; (C) Wichita Mountains; and (D) Edwards Plateau.

TABLE 7. Statistics for stepwise discriminant-function analysis of plots for after-second-year vireos (ASY) and for nonvireo plots.

Variable	<i>F</i> -value to enter	Order of entry	Coefficient	Classification function	
				ASY	Nonvireo
All regions					
33 DCSUM	25.83	1	0.0818	-0.2581	-0.3987
54 TOTSD	10.55	2	0.0368	0.2581	0.1947
21 MHEIGHT	6.56	3	-0.1293	-0.2073	0.0150
25 NSTEMSV	12.47	4	0.0003	0.0001	-0.0004
1 OAKA	5.31	5	-0.0047	-0.0110	-0.0030
55 PERCDECI	4.22	6	0.0576	0.8046	0.7056
Constant			-2.9077	-17.2369	-12.2116
Lampasas Cut Plains					
34 DDSUM	32.81	1	0.1941	0.4619	0.0449
26 WOODYCOV	6.28	2	-0.0850	0.0988	0.2813
31 DASUM	5.14	3	0.1483	0.5654	0.2468
51 J1SD	5.33	4	0.0986	0.5474	0.3356
25 NSTEMSV	4.26	5	0.0002	0.0001	-0.0003
Constant			-1.0018	-12.7569	-10.6049
Wichita Mountains					
54 TOTSD	9.83	1	0.1099	1.7519	1.3516
19 RDNON	7.71	2	0.1440	2.0091	1.4847
32 DBSUM	10.77	3	0.1807	3.2489	2.5909
58 PERC1	4.33	4	0.1413	3.7834	3.2689
28 GRASSCOV	5.62	5	0.0866	2.4423	2.1270
Constant			-15.0240	-192.8410	-137.8594
Edwards Plateau					
57 PERCOPEN	30.63	1	-0.3489	5.0965	7.1476
25 NSTEMSV	11.45	2	0.0012	-0.0047	-0.0119
43 FCSUM	4.48	3	-4.5567	65.7657	92.5487
27 FORBCOV	6.84	4	0.1328	-1.0234	-1.8038
19 RDNON	4.16	5	0.0621	-0.5591	-0.9243
Constant			14.9043	113.7353	-200.6484

all others (Fig. 7). Three variables were incorporated into the canonical variables (Table 8): DASUM, deciduous-vegetation hits near ground; MHEIGHT, mean tree height; and GRASSCOV, grass cover. Canonical variable 1 (Table 8) suggests that ASY males select sites with relatively more deciduous-vegetation hits near the ground, shorter trees, and more grass cover when these characters are considered in combination; note that when considered individually, the overall mean for GRASSCOV is actually higher for SY than ASY territories (see Table 4). The second canonical variable (Table 8) contrasts habitat differences of the one outlier territory, which was found on a site with relatively more deciduous-vegetation hits near the ground, taller trees, and more grass cover. Classification functions (Table 8) correctly assigned 65.5% of all plots (Table 9) with the most frequent mistake being classifi-

cation of ASY territories with those of SY males. Only one of the four SY territories was identified correctly, while 58.3% of ASY territories were placed in the correct category. Nonvireo plots were assigned correctly 84.6% of the time.

When the plots from the Edwards Plateau for the three groups were analyzed, a single discriminant axis was obtained (Fig. 8). The function incorporated only one habitat variable, PERCOPEN (Table 8), which indicates the degree of openness at the height of 1 m. ASY males occupied sites with lower values for this variable than typical for nonvireo plots (Table 4). The SY territories were widely distributed on the discriminant axis (Fig. 8). The classification function correctly allocated 62.5% of the plots (Table 9). While 11 of 12 ASY plots (91.7%) were assigned appropriately, only 1 of 7 SY plots (14.3%) were placed in the correct group (Table 9). Two

Wichita Mountains

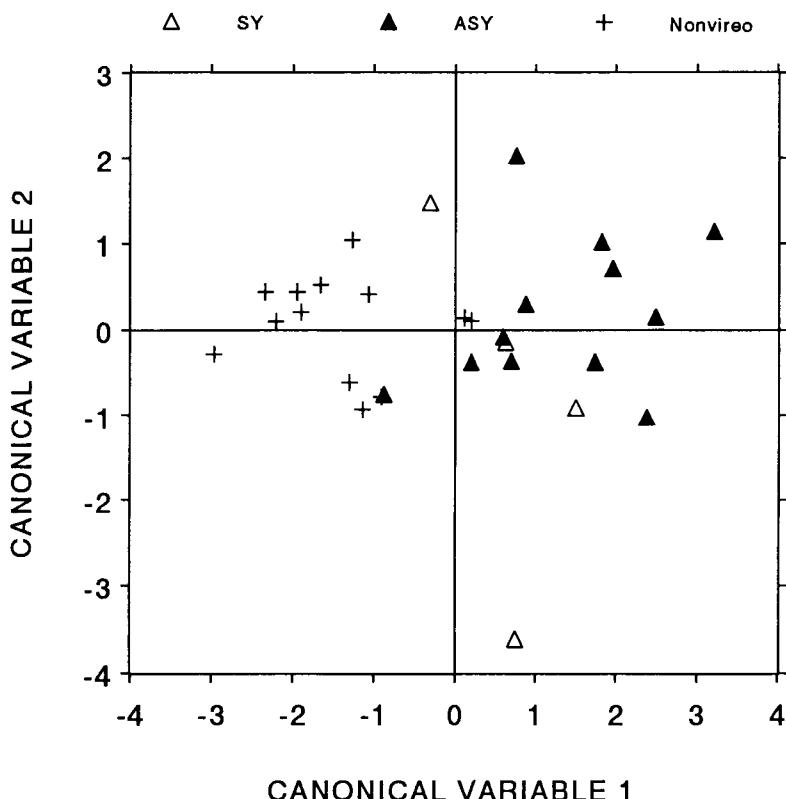


FIGURE 7. For Wichita Mountains region, projections of nonvireo plots and those for territories of second-year (SY) and after-second-year (ASY) vireos onto two canonical variables based on analysis of 61 vegetation measures.

of the SY plots were appraised to be ASY plots, while four were miscategorized as being nonvireo plots. Of the five misclassified nonvireo plots, four were assessed as being SY territories. Non-

vireo plots were more frequently misassigned to the SY group. Thus, in general, territories of SY males were more similar to nonvireo plots than they were to the territories of the older ASY males.

TABLE 8. Statistics for stepwise discriminant-function analysis involving the Wichita Mountains and Edwards Plateau for plots of after-second-year vireos (ASY), those of second-year vireos (SY), and nonvireo plots.

Variable	F-value to enter	Order of entry	Coefficients ^a	Classification function		
				ASY	SY	Nonvireo
Wichita Mountains						
31 DASUM	4.95	1	0.6048	-0.0383	-2.1434	-1.9260
21 MHEIGHT	7.51	2	-0.2769	-0.0290	1.0966	1.1391
28 GRASSCOV	5.41	3	0.0770	-0.0956	5.4284	5.0547
Constant			-7.2551	4.9001	-49.1272	-48.6814
Edwards Plateau						
57 PERCOPEN	13.05	1	-0.1845		1.8293	2.1258
Constant			11.0695		-50.2718	-67.5020
						-71.7678

^a Used with unstandardized values. For Wichita Mountains, coefficients for canonical variables 1 and 2; for Edwards Plateau, coefficients for discriminant function.

TABLE 9. Numbers of plots from Wichita Mountains and Edwards Plateau classified as second-year vireo (SY), after-second-year vireo (ASY), and nonvireo using classification functions and a jackknifed procedure.

Group	Percent correctly classified	Classified as			Total
		ASY	SY	Nonvireo	
Wichita Mountains ($G = 21.04^{***}$)					
ASY	58.3	7	4	1	12
SY	25.0	2	1	1	4
Nonvireo	84.6	0	2	11	13
Total	65.5	9	7	13	29
Edwards Plateau ($G = 22.54^{***}$)					
ASY	91.7	11	0	1	12
SY	14.3	2	1	4	7
Nonvireo	61.5	1	4	8	13
Total	62.5	14	5	13	32

^a G -values from row-by-column contingency test of independence of original groups versus those assigned using classification functions and jackknifed procedure. ***, $P < 0.001$.

These analyses, along with those reported above contrasting ASY and SY plots, as well as ASY and nonvireo plots, suggest that SY and ASY males have territories with similar characteristics in the Wichita Mountains, but that many of the territories of SY males on the Edwards Plateau have habitat characteristics similar to those of nonvireo plots. SY males generally were found in more open habitats than ASY males in both regions; however, the difference was more pronounced on the Edwards Plateau.

EVALUATION OF SELECTED HABITAT VARIABLES

The results suggest four generalizations about habitats that can be useful in describing the por-

tions of scrublands that are occupied by Black-capped Vireos: (1) greater deciduous foliage density in the 0–3 m height classes; (2) fewer junipers; (3) less-open habitats; and (4) greater heterogeneity in density of woody vegetation (particularly deciduous). The second and third items are closely related, as indicated on the habitat gradient identified in principal component I for all plots (see Fig. 2). Vireos did not occupy sites at either extreme of this spectrum, indicating that the range of acceptable vireo habitats on this gradient was sampled.

The clearest and recurring suggestion from our data and analyses is that deciduous-vegetation densities from 0–2 m height (0–3 m height in the Lampasas Cut Plains) are the most important elements of habitats selected by vireos. One or more variables associated with this general characteristic of the habitats was statistically important in many analyses. Figures 9 and 10 are profiles of an index of average vegetation density at various heights for deciduous trees and junipers. Data are summarized for nonvireo and ASY plots in all regions taken together (Figs. 9A, B) and the Lampasas Cut Plains (Figs. 9C, D), as well as for nonvireo, SY, and ASY plots in the Wichita Mountains (Figs. 10A–C) and Edwards Plateau (Figs. 10D–F). In general vireos were found where the deciduous-vegetation density was greater in the lower height classes than was typical of unoccupied areas.

Other suites of variables do not appear to be important throughout the range; they were not identified consistently in all analyses. Their inclusion in particular analyses may simply reflect

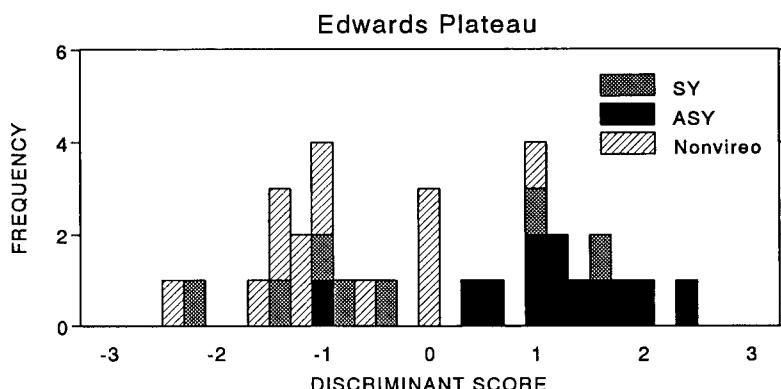
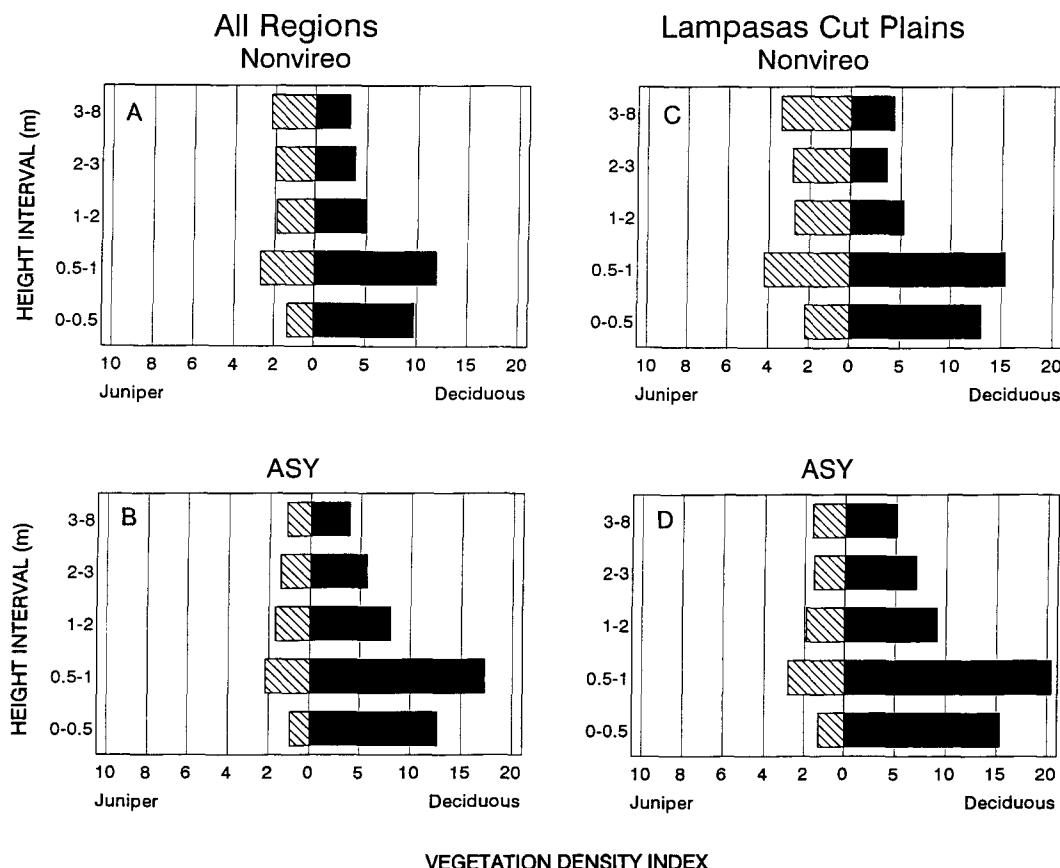


FIGURE 8. For Edwards Plateau region, single discriminant function resulting from canonical analysis of nonvireo plots and those for territories of second-year (SY) and after-second-year (ASY) vireos based on 61 vegetation measures.



VEGETATION DENSITY INDEX

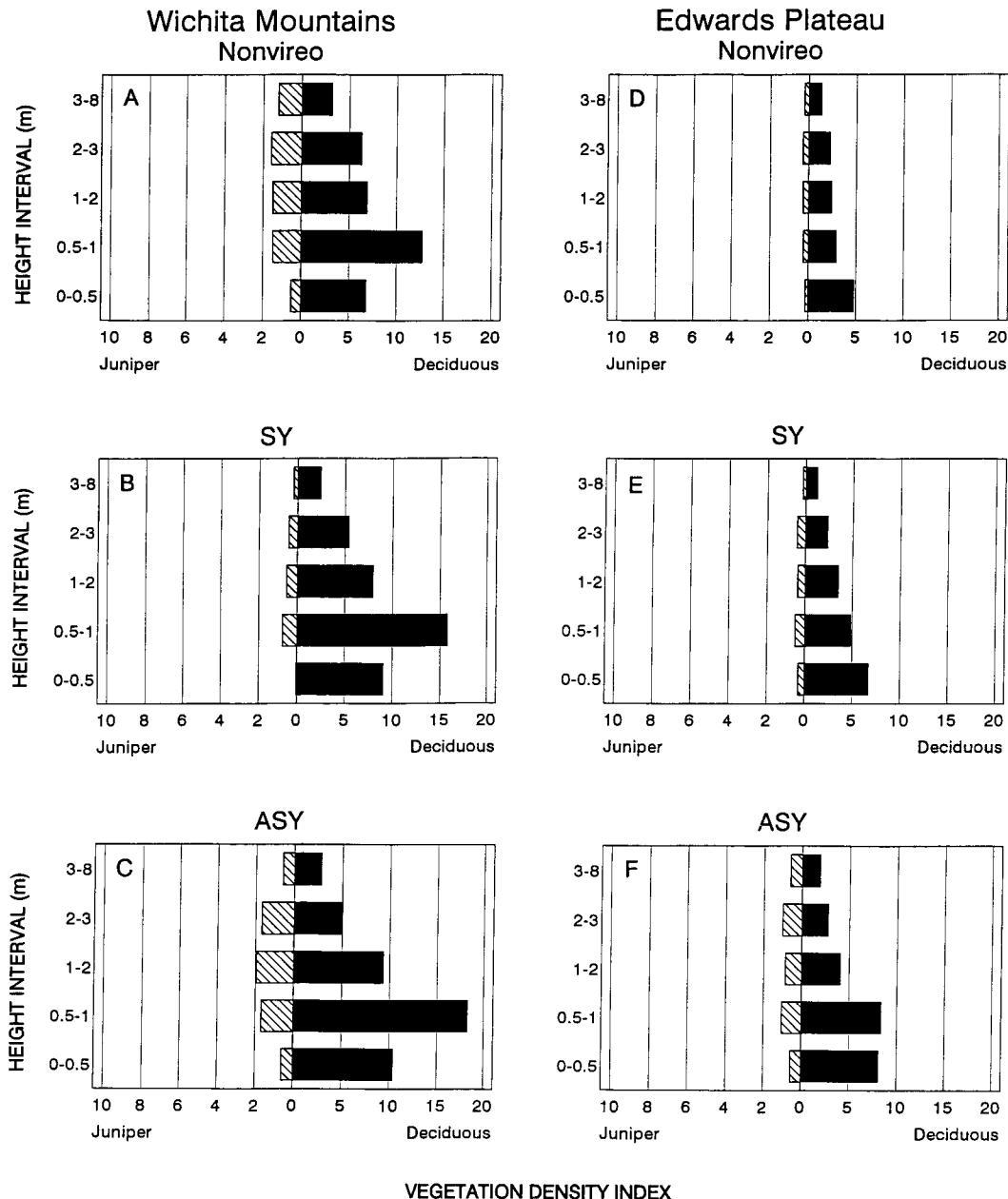
FIGURE 9. Vegetation profiles for mean relative densities of junipers and deciduous trees for nonvireo plots and territories of male ASY (after-second-year) vireos: (A, B) all regions; and (C, D) Lampasas Cut Plains. Note that scale for junipers (left half of each panel) is expanded two times relative to that for deciduous trees (right). Values, derived from variables 31–40 (Table 1), indicate average number of possible “decimeter hits” per height interval.

other considerations related to the requirements of vireos for a relatively high density of deciduous vegetation in lower height classes. Relatively open areas will not have a sufficient number of deciduous bushes to produce the requisite density of low-level deciduous vegetation. However, as areas mature, junipers invade and become more prevalent. Two things may happen. First, the junipers may replace too many of the deciduous plants to maintain a sufficient density of deciduous vegetation in lower height classes. Second, as areas mature, junipers fill in, and deciduous bushes coalesce and form a canopy, thus reducing light penetration to the lower levels of vegetation, reducing the extent of edge, and decreasing lower-level foliage density. Spacing between bushes appears to be important. This fac-

tor is measured by the heterogeneity variable (TOTSD), which increases with moderate to close spacing, but is lower in more open areas and in areas where plants coalesce into a more homogeneous format.

On the Lampasas Cut Plains, where junipers were more prevalent (Figs. 2 and 9), values for many juniper variables on sites occupied by ASY males were significantly lower ($P < 0.05$) than on nonvireo sites, including three of the five height classes (JASUM, JDSUM and JESUM) in the juniper vegetation-density profile (Figs. 9C, D). No statistically significant differences for juniper variables were found when comparing the nonvireo, SY, and ASY plots in the Wichita Mountains.

For the Edwards Plateau, density of juniper



VEGETATION DENSITY INDEX

FIGURE 10. Vegetation profiles for mean relative densities of junipers and deciduous trees for nonvireo plots and territories of male ASY (after-second-year) and SY (second-year) vireos: (A-C) Wichita Mountains; and (D-F) Edwards Plateau. Note that scale for junipers (left half of each panel) is expanded two times relative to that for deciduous trees (right). Values, derived from variables 31-40 (Table 1), indicate average number of possible "decimeter hits" per height interval.

vegetation in the >0.5-1 m height class (JBSUM) was significantly higher ($F = 4.30$, $P < 0.05$) in ASY than nonvireo plots (Fig. 10F and 10D, respectively). In addition, juniper densities gen-

erally were higher in vireo than nonvireo plots (compare Figs. 10E and 10F with 10D), although differences for individual variables were not significant ($P > 0.05$). The general finding for ju-

TABLE 10. Mean percentages (and standard deviations) for variables indicating extent of tree cover and openness for all samples and for each region. Values provided for nonvireo, vireo, after-second-year (ASY), and second-year (SY) plots. Vireo plots include those for ASY and SY birds, as well as for birds not aged.

Variable	Nonvireo	Vireo	ASY	SY
All regions				
55 PERCDECI	30.98 (13.95)	39.74 (13.81)	42.23 (13.06)	27.68 (12.64)
56 PERCJUNI	12.57 (14.40)	7.59 (8.66)	9.16 (9.28)	2.39 (3.59)
57 PERCOPEN	59.50 (19.62)	54.38 (14.57)	50.73 (12.60)	70.66 (13.02)
Lampasas Cut Plains				
55 PERCDECI	33.21 (14.07)	45.63 (10.44)	45.73 (11.34)	47.20 (-)
56 PERCJUNI	19.35 (14.55)	10.03 (8.05)	11.34 (8.10)	0.20 (-)
57 PERCOPEN	52.21 (19.46)	46.74 (10.42)	45.84 (11.05)	52.60 (-)
Wichita Mountains				
55 PERCDECI	39.30 (9.83)	43.76 (12.42)	46.22 (12.91)	36.38 (7.93)
56 PERCJUNI	6.80 (12.41)	4.91 (7.75)	5.83 (8.72)	2.12 (2.84)
57 PERCOPEN	55.40 (12.27)	52.59 (11.14)	49.28 (9.98)	62.52 (8.94)
Edwards Plateau				
55 PERCDECI	17.35 (5.29)	25.34 (9.86)	29.22 (9.15)	19.93 (8.79)
56 PERCJUNI	2.15 (3.45)	5.11 (9.50)	6.85 (11.70)	2.86 (4.31)
57 PERCOPEN	81.00 (6.59)	70.32 (10.92)	64.82 (7.77)	77.89 (10.55)

niper-density variables on the Edwards Plateau may appear incongruent with the findings for the Lampasas Cut Plains. However, nonvireo plots on the Edwards Plateau were in the most open habitats evaluated and had relatively little deciduous or juniper vegetation. The mean juniper-vegetation densities for vireo territories on the Edwards Plateau (Figs. 10E, F) were, in fact, much lower than those for the other two regions (Figs. 9D, 10B, and 10C). The scatter of points on principal component I (Figs. 3E, F) for the Edwards Plateau shows that the juniper gradient in these data is created primarily by differences (i.e., more junipers, lower density of oaks) of six vireo territories and two nonvireo plots from the other vireo and nonvireo plots. Thus, the presence of higher mean densities of junipers in occupied versus unoccupied plots on the Edwards Plateau simply may reflect vireos making choices to compensate for the generally sparse woody cover available. In fact, WOODYCOV, a combination of the percent deciduous and juniper vegetation, was significantly higher in ASY territories than in nonvireo plots ($F = 9.51, P < 0.01$). On the Edwards Plateau, it appears that vireos occupied territories in areas with the most woody vegetation, irrespective of whether deciduous shrubs or junipers were responsible.

The percentages of openness (PERCOPEN) and cover (PERCDECI and PERCJUNI; see Table

10) are relatively easily measured and manipulated. When appropriate, they can be incorporated as targets in management plans. Data are presented for nonvireo, vireo, ASY, and SY classes in Table 10. Previous analyses have suggested that plots for ASY males are the best representation of suitable habitat for Black-capped Vireos. PERCDECI was very highly significantly different ($P < 0.001$) between ASY and nonvireo plots in the Lampasas Cut Plains ($F = 14.65$) and the Edwards Plateau ($F = 15.43$), with values being higher in ASY than nonvireo plots (Table 10); PERCDECI was not significantly different in the Wichita Mountains ($F = 2.21, P < 0.15$) for ASY and nonvireo plots. Means of PERCDECI in ASY plots ranged from 29% in the Edwards Plateau to 46% in the Lampasas Cut Plains and Wichita Mountains. Means of PERCDECI in SY plots were lower (20–36%).

When the variable PERCJUNI was taken individually, no significant differences were found for nonvireo-ASY comparisons. PERCOPEN, however, was significantly different between nonvireo and ASY plots for all regions combined ($F = 8.66, P < 0.004$), with nonvireo plots being more open (Table 10). The comparison of nonvireo and ASY plots for PERCOPEN was not significant for the Lampasas Cut Plains ($F = 2.82, P < 0.10$) or for the Wichita Mountains ($F = 1.91, P < 0.18$). However, in the Edwards Pla-

teau, the difference was striking ($F = 30.63, P < 0.001$), with nonvireo plots being 81% open, while ASY territories were only about 65% open (Table 10).

DISCUSSION

Through these analyses, we have attempted to identify and characterize habitat attributes that are important to the Black-capped Vireo across its breeding range. Below, we consider some factors that may relate to habitat limitations. We put forth several possibilities, but undoubtedly address only a subset of the factors that promote dependence of a species on a particular array of habitat resources. James et al. (1984) pointed out the strengths of this autecological approach compared to those that consider species in competition models (Hutchinson 1968), as well as the value of using multiple comparisons embracing a significant portion of the range of a species

GEOGRAPHIC VARIATION

While many investigators would support the notion that, in general, habitat selection will vary little within a species, there are compelling reasons to expect geographic variation in habitat use (Hilden 1965, Collins 1983b, Karr and Freemark 1983). For example, competition between species may mold differential responses to habitat (Morse 1974, Cody 1978), resulting in substantial geographic variation. At the same time, when noting geographic differences one may be elucidating habitat differences between regions that are not particularly relevant in terms of the bird's survival, its reproduction, or its perceptions of habitat. Thus, caution is required when attempting to draw conclusions concerning the possible significance of geographic differences.

In spite of the relatively restricted range of the Black-capped Vireo compared to those of most North American passernines, we found differences among regions in habitat characteristics of territories. For example, interregional differences in juniper densities of nonvireo plots and ASY territories became evident when comparing on a region-by-region basis, even though no major differences were found when conducting the same analysis for plots from all three regions simultaneously. For the Lampasas Cut Plains, where juniper densities were relatively high, ASY males had territories with lower-density juniper cover overall when contrasted with nonvireo plots (Fig. 9). There was no evidence of such a difference in juniper densities between ASY male territories

and nonvireo plots in the Wichita Mountains (Fig. 10). However, in the Edwards Plateau, with generally less dense vegetation and the lowest density of junipers of the three regions, the ASY male territories actually had higher juniper densities at lower height levels than nonvireo plots, with the SY male territories being somewhat intermediate, but much like the nonvireo plots (Fig. 10). In all regions, however, juniper densities were relatively low in vireo territories.

While these geographic differences in juniper densities of territories and nonvireo plots were found, a common theme across regions emerged relative to deciduous vegetation. Black-capped Vireo males select territories in areas with dense, low deciduous vegetation in all regions, which suggests that this type of deciduous vegetation is an important component of the habitats selected for use by Black-capped Vireo males. These observations are consistent with those of Gruber (1961) and Barlow (1978).

AGE AND POPULATION-DENSITY FACTORS

A number of factors other than intrinsic habitat characteristics may influence the degree to which a given habitat is occupied by a particular bird species. For instance, the age structure of the bird population and the overall population density relative to available habitat could interact to affect habitat use by breeding birds. However, for only a few passerine species is it possible in the field to distinguish morphologically males that are in their first breeding season from those that are older (Rohwer et al. 1980). Thus, Black-capped Vireos, for which we can differentiate between SY and ASY males, afford a special opportunity to determine whether there are differences in territorial characteristics of inexperienced first-time breeding males from older birds.

In our initial analysis that considered all breeding males in one group, we found little difference in habitat characteristics between vireo territories and nonvireo plots on the Edwards Plateau. Separating age classes (SY and ASY males) clarified this situation, and showed that SY males in general occupied areas very much like the nonvireo plots we sampled, and notably different from ASY males. The population of Black-capped Vireos in Kerr County (Edwards Plateau) appears to be relatively large (Grzybowski, unpubl. data). While not totally conclusive, available data suggest that habitat may be limiting in the area, with the inexperienced SY males being

relegated to areas with less favorable habitat characteristics.

The remnant population in the Wichita Mountains appears to have low densities relative to available habitat (Grzybowski et al. 1986, unpubl. data). The habitats occupied by SY males were more like those of ASY males than like nonvireo plots. The interrelationships of population size relative to available, suitable habitat and age of breeding males can be complex and represent topics worthy of further attention from investigators. SY males often are assumed to occupy inferior territories relative to ASY males. However, Morris and Lemon (1988), studying American Redstarts (*Setophaga ruticilla*), were not able to demonstrate that differences in territory characteristics of the two age groups resulted in different reproductive success.

In a removal experiment on ASY male American Redstarts, Sherry and Holmes (1988) found that removed ASY males were replaced disproportionately by SY males. The presence of both SY and ASY "floaters" suggested that suitable habitat is limiting for redstarts in Sherry and Holmes' (1988) study area. Intraspecific competitive interactions may be important where habitat is limiting. This may be similar to the situation we have found for Black-capped Vireos in the Edwards Plateau, where suitable habitat may be limiting and SY males occupy distinguishably different habitat from ASY males. Where population densities are low, however, such as in the Wichita Mountains, SY males have the opportunity to occupy the same type of habitat as ASY males.

CONSTRAINTS ON HABITAT SELECTION

Vegetation provides the foliage-gleaning Black-capped Vireo with foraging and nesting sites, as well as potential protection from the elements and predators. Our analyses and those of Gruber (1957, 1961) show that Black-capped Vireos establish territories only in the relatively low vegetation of early seral stages. Barlow (1978) also noted that "Localities inhabited by [Black-capped] vireos were characterized by deciduous scrub having leafy growth to ground level." Black-capped Vireos are the first foliage-gleaning bird species to appear in the maturing successional series of scrubland habitats in central Texas and western Oklahoma (Grzybowski, pers. observ.). Since these early seral stages with less leafy substrate do not afford the greatest opportunities for glean-

ing, factors other than availability of feeding substrate undoubtedly are responsible for the relatively restricted range of habitats used by this species.

Potential competitive interactions. Given the number of foliage gleaners found within the Black-capped Vireo's geographic range (including several vireo and warbler species, as well as Blue-gray Gnatcatchers [*Polioptila caerulea*]), competition may have played a role in limiting the habitats used by Black-capped Vireos. Competition theory has been employed to explain negative correlations in occurrences between bird species (e.g., Svardson 1949, Cody 1974) and the segregation of species along habitat gradients (e.g., Sabo 1980, Noon 1981, but see James et al. 1984). Although Strong et al. (1984) and Connor and Simberloff (1986) in evaluating such correlations downplayed the relative importance of interspecific competition in structuring communities, removal experiments (e.g., Garcia 1983, Alatalo et al. 1985, Sherry and Holmes 1988) have suggested that interspecific competition for habitat occurs regularly.

The Black-capped Vireo is one of the smallest vireo species, and indirect evidence suggests it probably is subordinate to other vireos. For example, Robinson (1981) noted interactions where Red-eyed Vireos (*V. olivaceus*) displaced the smaller and socially subordinate Philadelphia Vireos (*V. philadelphica*) to serally less mature habitats. Potential competitive interactions helped explain differences in habitats used by three species of vireos in southern Ontario (James 1976).

While Black-capped Vireos co-occur commonly with Blue-gray Gnatcatchers, the gnatcatchers do not occupy habitats with the shortest vegetation acceptable to the vireo (Grzybowski, pers. observ.). Substantial structure must be added for White-eyed Vireos (*V. griseus*), and much more for the next most common guild member in the region, the Black-and-white Warbler (*Mniotilla varia*; James 1971; Grzybowski, pers. observ.). Golden-cheeked Warblers (*Dendroica chrysoparia*) and, formerly, Prairie Warblers (*D. discolor*) also were associated with Black-capped Vireo territories in a few localities (Gruber 1961; Tazik and Cornelius, unpubl. data; Grzybowski, unpubl. data). However, Golden-cheeked Warblers are dependent on mature oak-juniper woodlands (Pulich 1976), and overlaps were at interfaces and interdigitations of respective habitats. Prairie Warblers also require more vertical

structure than found in habitats occupied by Black-capped Vireos (Nolan 1978). Territories of Bell's Vireos (*V. bellii*) and, locally, Gray Vireos (*V. vicinior*) overlapped with those of Black-capped Vireos in the Edwards Plateau, although both more typically used habitats not preferred by the latter (Grzybowski, pers. observ.; see also Gruber 1961, Barlow 1967). Thus, by inhabiting early seral stages, Black-capped Vireos likely are not in direct competition with other foliage gleaners.

Potential predator avoidance. Nest predation contributes substantially to nesting mortality (Ricklefs 1969). Martin (1988), examining Arizona bird assemblages, found correlations of species occurrences with vegetation densities of nest substrates and indicated that minimizing risk to predation was important in habitat selection. Vegetation density at nest level is known to influence predation rates in several species (Nolan 1978, Murphy 1983, Martin and Roper 1988). For Black-capped Vireos, nests average about 1 m above the ground (Gruber 1961), and it is at this level and below that territories have relatively lush deciduous vegetation. As scrub areas develop, light penetration becomes less intense at the lower height intervals, thus decreasing foliage density and rendering an area less suitable for Black-capped Vireos.

By using early successional habitats, Black-capped Vireos also may effectively avoid certain nest predators such as squirrels, jays, crows and other predators that are more frequently encountered in habitats with taller vegetation. The predator load in more mature habitats, if coupled with the relatively long Black-capped Vireo incubation times (i.e., 14–16 days vs. 11–13 days for many other similar-sized passerines; Gruber 1961, Ehrlich et al. 1988; Grzybowski, pers. observ.), could result in a vireo fecundity level below that needed to sustain a viable population. The extended vireo incubation period may be possible only because selective predation pressures on average are lower in the early successional habitats now occupied by Black-capped Vireos.

FLORISTIC AND ABIOTIC ATTRIBUTES OF HABITATS OCCUPIED

While structural elements have been commonly and successfully used to characterize avian habitats, several studies have shown strong associations between the presence of particular bird

species and floristic composition (Beals 1970, Abbott et al. 1977, Collins 1983b, Wiens 1985). In northern hardwood forests, bird species that glean prey from leaves generally have stronger preferences for tree species than do avian species that typically hover when seeking food items (Holmes and Robinson 1981). In addition, Robinson (1981) found that Red-eyed Vireos utilize tree species for foraging roughly in proportion to the relative occurrences of the tree species, while Philadelphia Vireos showed strong preferences for particular tree species. The scale of one's perspective (e.g., local vs. regional) may well alter the degree to which data indicate a bird species is associated with a given tree species.

Because different plant species occur in different portions of the Black-capped Vireo's range, we assessed vireo habitat essentially on the basis of vegetational life forms. We found blackjack and post oaks to be the dominant (almost exclusive) deciduous scrub species in the Wichita Mountains. On the Lampasas Cut Plains, two oak species (shin oak [*Q. sinuata*] and Spanish oak [*Q. texana*]) and two sumac species (lanceleaf sumac [*Rhus lanceolata*] and evergreen sumac [*R. virens*]) were important. On the Edwards Plateau, shin oak and Edwards Plateau live oak (*Q. fusiformis*) were the primary tree species present in vireo territories. Gruber (1961) found still other deciduous species in some areas occupied by Black-capped Vireos. In our study areas, Black-capped Vireos clearly favored relatively thick, low-level deciduous vegetation dominated, in most areas, by oaks. Many of the dominant deciduous species are fire adapted, with considerable resprouting occurring after disturbance by fire (Wright and Bailey 1982; see below).

The suitability of a particular area for Black-capped Vireos can be influenced by edaphic factors (Gruber 1961). Some locales may remain suitable for Black-capped Vireos for long periods due to abiotic structural components (e.g., boulders) or persistent disturbance (e.g., erosive forces resulting in gullies). C. W. Sexton (unpubl. data) has shown that occupied Black-capped Vireo habitats in Texas tend to occur on certain geologic substrates, specifically limestones of the Late Cretaceous. These substrates contain shallow soils and, for extended time periods, foster plant species and spatial heterogeneity considered to be typical Black-capped Vireo habitat. However, even on these substrates, habitats may not always be suitable (Shaw 1989), underscoring

that Black-capped Vireos are restricted to a successional habitat window.

As with Graber's (1961) investigation, many of the areas supporting Black-capped Vireos that we studied had a history of severe disturbance. The larger groupings of vireos in the Wichita Mountains proper, Kerr Wildlife Management Area (part of Edwards Plateau region), and Davenport Ranch (part of Lampasas Cut Plains region) were burned by hot fires 10 to 20 years before our study. The South Fork Ranch (Edwards Plateau region) was heavily grazed by goats until 1978 (E. Fuchs, pers. comm.). Goats, given their reach, can denude the woody vegetation up to 2 m above the ground. However, deciduous vegetation resprouted after the goats were removed. One area used by Black-capped Vireos on the Fort Hood Military Reservation (Lampasas Cut Plains) was bulldozed and significantly disrupted several years earlier. Other vireo territories were within or on the perimeters of impact zones designated for artillery or tank shelling; these incur periodic burning as a result of exploding ordinance. In general, the resprouting of vegetation (primarily oaks and sumac) after disturbance events can be prolific, creating dense bushes of leafy material (Wright and Bailey 1982). Periodic disturbance often appears to have beneficial effects on Black-capped Vireos and represents an important tool (if used properly) for management of vireo habitats.

MANAGEMENT IMPLICATIONS

Because the Black-capped Vireo is endangered, and vireo habitat is successional in nature, management may be necessary to enhance and maintain suitable habitat. An important finding of our investigation, from a management perspective, is that there is geographic variation in habitats available and habitats used by Black-capped Vireos. In the different regions, the vireos were selecting somewhat different portions of the habitat continuum, and the range of available habitats also varies among regions. Thus, it is unrealistic to expect that a given set of rigidly defined management techniques would be appropriate for all localities. Some management techniques may be useful at most localities, while others may be applicable at only one or a few locations.

Our results for ASY males indicate a requirement for dense deciduous vegetation at lower height intervals. This occurs in areas with approximately 35 to 55% dispersed scrub cover

(i.e., sum of PERCDECI and PERCJUNI; see Table 10), most of which should be deciduous. Cover values of 35 to 55% provide a useful goal for managers. These percentages allow for spacing among vegetation components, which permits light to penetrate to the lowest levels and promotes an "apron" of vegetation extending to ground level under the existing trees and shrubs.

In order to maintain or enhance habitat for Black-capped Vireos, reduction of junipers in many areas will be necessary and is recommended. Where there is considerable encroachment by junipers, they may replace the important deciduous component. As a result, spacing will increase between vireo territories, and vireos may become increasingly separated in habitat fragments where vegetation cover still has a significant low-deciduous component. This condition has been noted at Fort Hood in Texas (Tazik 1991), in western Travis County, Texas (D. L. Steed, unpubl. data), and in Blaine County, Oklahoma (Grzybowski, unpubl. data).

For most areas, juniper cover (i.e., PERCJUNI) should be kept well below 10%. Furthermore, PERCJUNI should not exceed one-fourth of deciduous cover (PERCDECI). In fact, junipers may not be necessary, as they are typically killed by hot fires and may not invade until substantially after vireos have occupied the resprouting deciduous vegetation. However, on some tracts, junipers actually may contribute important cover where amounts of deciduous vegetation are marginal or deficient (i.e., Edwards Plateau region and areas to the southwest). Values in Table 10 for the Edwards Plateau may provide reasonable targets in such cases. Thus, site and regional characteristics need to be considered before a management decision is made to control for junipers.

The overall heights of the vegetation in many areas judged suitable by vireos are typically 2 to 3 m tall. As areas mature, many bushes coalesce and, thus, lose the apron of dense low-level deciduous vegetation. However, some relatively tall areas (up to 6 m) dissected by paths or roads, etc., may provide an abundant edge component and may be selected by Black-capped Vireos. The needed spatial heterogeneity in vegetation cover may be encouraged by active management, or may naturally occur as a result of inherent site characteristics (e.g., on sites with relatively poor soils or other edaphic conditions that promote vegetational heterogeneity).

In general, vegetation densities (for lower-level height intervals) in Black-capped Vireo territories were greater than those found for nonvireo plots. This suggests that managers should employ techniques that will encourage thick regrowth of deciduous vegetation in the lower height intervals. In managing for other species, wildlife specialists often use prescribed burns. For Black-capped Vireos, very hot fires are more likely to mimic the historical conditions that resulted in establishing suitable habitat than will burns characterized by lower temperatures. However, cooler prescribed burns (which typically are safer) may prove useful when applied during the nonbreeding season in actively used vireo habitats to retard the maturing processes of the vegetation, and maintain the habitat in the appropriate successional window for a longer period of time, perhaps indefinitely.

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