

GEOGRAPHIC PATTERNS IN SPECIES OCCURRENCE OF TENNESSEE'S BREEDING BIRDS

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ABSTRACT

Distributional information on the breeding birds of Tennessee, obtained from preliminary results of the Tennessee Breeding Bird Atlas Project, was analyzed with clustering and ordination techniques to define bird communities and correlated environmental factors. After elimination of unevenly sampled, very rare, and ubiquitous species, information on 107 bird species in 472 sample blocks of 5.5 x 4.5 km, systematically distributed across the state, was available. Four distinctive communities were identified: at high elevations along the eastern border, in extreme northeast Tennessee, in the Cumberlands/low Blue Ridge, and in the Mississippi River Floodplain/Coastal Plain. The remaining community consisted of most of the Ridge and Valley, Highland Rim, Central Basin, and West Tennessee Uplands. Ordination showed a distinct west to east gradient inversely related to maximum July temperature and directly related to increasing precipitation and elevation. The number of species in a sample block ranged from 20 to 87 (mean = 64) and was lowest within the spruce-fir vegetation type.

INTRODUCTION

Most studies of bird communities in Tennessee have been conducted within a single physiographic area or smaller study unit. There has been little attempt to define, on a statewide basis, the breeding bird communities of the state, or the climatic factors associated with them. The availability of detailed distributional information from the nearly complete Tennessee Breeding Bird Atlas Project provides the first data set allowing such an analysis. This paper presents a preliminary analysis of Tennessee breeding bird communities and their associated environmental factors.

METHODS

Bird Distribution Information

Preliminary results of the Tennessee Breeding Bird Atlas Project provided bird distributional information. Field work for this project was begun in 1986, and is scheduled to be completed in 1991. Skilled field workers visit sample blocks equal to 1/6 the area of a USGS 7.5-min. topographic map (3.75x2.5 minutes, or approximately 5.5x4.5 km) (Nicholson and Hamel 1986). Ideally all 4300 blocks in the state would be surveyed; but because of the limited number of field workers, field work has been concentrated on 700 priority blocks, one per topographic map, systematically distributed across the state. All bird species observed in the block are recorded and assigned to one of three qualitative categories of breeding evidence: possible, probable, and confirmed breeding.

Results from 472 priority blocks judged to have reasonably complete species lists were available for this analysis. This data set contained information on 161 bird species. Because nocturnal birds (owls, goatsuckers, et al.) were not uniformly sampled in all blocks, they were deleted from the data set. Twenty-six species occurring in less than 1% of the samples, and 17 occurring in more than 95% of the samples were also deleted: the rare species were often inadequately sampled,

and ubiquitous species contribute little to the statistical analyses used (Gauch 1982). A few other species (mostly herons) which were uncommon and represented mostly by summering, nonbreeding individuals, were also deleted. This resulted in a data matrix of 107 bird species and 472 sample blocks. The rare species and ubiquitous species were included in the data set used in the analysis of environmental correlates with the total number of species observed in a block, resulting in a maximum possible number of 150 species in a block. A list of all species used in these analyses is available from the author.

Environmental Factors

A limited set of environmental variables was used to investigate their correlation with the bird community. Mean annual precipitation and maximum July temperature were taken from Dickson (1978). Minimum, maximum, and average elevation in each block was calculated from 1:250,000 USGS Digital Terrain Models. Because of the lack of a detailed map of forest or other vegetative cover, blocks were categorized by their potential natural vegetation (Kuchler 1964). Other potentially useful information, such as detailed land use/land cover information and human population density in each block, was either not available or converting it to a usable format was beyond the scope of this study.

Statistical Analysis

To identify areas with homogeneous bird communities, the bird data matrix was first analyzed with COMPCLUS, a non-hierarchical, composite clustering program (Gauch 1979, 1982). Percentage dissimilarity was used as the distance measure, and the maximum within-cluster distance was 60. Two-way Indicator Species Analysis (TWINSPAN) (Hill 1979) was then used to form a hierarchical arrangement of the samples or clusters. The TWINSPAN program uses reciprocal averaging ordination to arrange the clusters so that those with the least-similar species lists are at the extremes. The gradient is then broken into two groups of clusters, with clusters near the point of division considered to be borderline. This procedure is repeated for the desired number of levels. At each division, a list is formed of species characteristic of each grouping (preferentials), as well as a list of non-preferential species. Detrended correspondence analysis (DECORANA) (Hill and Gauch 1980) was used to form an ordination of the clusters based on their composite species scores.

The correlations of environmental variables with bird communities were investigated with canonical correspondence analysis using the program CANOCO (Ter Braak 1988). This program combines regression and ordination techniques to perform a direct gradient analysis of relationships between species and environmental variables. Because of limitations on the size of the data matrix in CANOCO, a stratified random sample of 167 blocks, picked to give approximately equal representation of the different physiographic regions, was used. Regression techniques were used to examine effects on the number of species per block, and differences in species numbers between poten-

tial natural vegetation types was examined with analysis of variance.

RESULTS

Community Classification

The initial composite clustering reduced the species data matrix from 472 sample blocks to 28 composites. Eleven of these composites were composed of one block each. These blocks, 10 of which were located along the eastern border of the state (Figure 1a), were considered outliers because of their distinctive species lists and were excluded from the TWINSpan analysis. The remaining 17 composites ranged in size from 3 to 116 blocks.

Results of the first three levels of the TWINSpan classification are shown in Figure 1. The groups formed at these levels contained composites which, usually, were geographically clumped. Group IB contained one composite of three blocks, all located on the eastern border. The 10 preferential species for these blocks were all typical of high elevations, and included the Common Raven (*Corvus corax*), Red-breasted Nuthatch (*Sitta canadensis*), Veery (*Catharus fuscescens*), Blackburnian Warbler (*Dendroica fusca*), Black-throated Blue Warbler (*D. caerulescens*), and Canada Warbler (*Wilsonia canadensis*). Division at level 2 split out group IIB, made up of five composites (Figure 1b) composed mostly of blocks in the Blue Ridge and Cumberland Plateau and Mountains, as well as a few on the Highland Rim.

The preferential species for this group were typical of middle to high elevations; the preferential species for the other group at this level (IIA) included species of agricultural habitats such as the Horned Lark (*Eremophila alpestris*) and Dickcissel (*Spiza americana*), and western and wetland species such as the Yellow-crowned Night-Heron (*Nycticorax violacea*), Tree Swallow (*Tachycineta bicolor*), Fish Crow (*Corvus ossifragus*), and Warbling Vireo (*Vireo gilvus*).

Group IIA (Figure 1c) was split into group IIIB, whose blocks were mostly on the Mississippi Coastal Plain and Mississippi River Floodplain, and a large group IIIA whose blocks were mostly to the east of the Coastal Plain in the Highland Rim, Central Basin, and Ridge and Valley. Preferential species for the Coastal Plain grouping (IIIB) were the Brown Creeper (*Certhia americana*), Fish Crow, Least Tern (*Sterna antillarum*), Mississippi Kite (*Ictinia mississippiensis*), and Swainson's Warbler (*Limothlypis swainsonii*). The 20 preferential species for group IIIA breed in a variety of habitats and were difficult to characterize as a group except for their low frequency of occurrence in the Coastal Plain. Further divisions of group IIIA did not produce geographically contiguous groups.

Figure 1d shows the division of the Blue Ridge/Cumberlands group IIB formed at the second level. This division split off 11 blocks (IIID), 10 of them located in the northeast corner of the state and 1

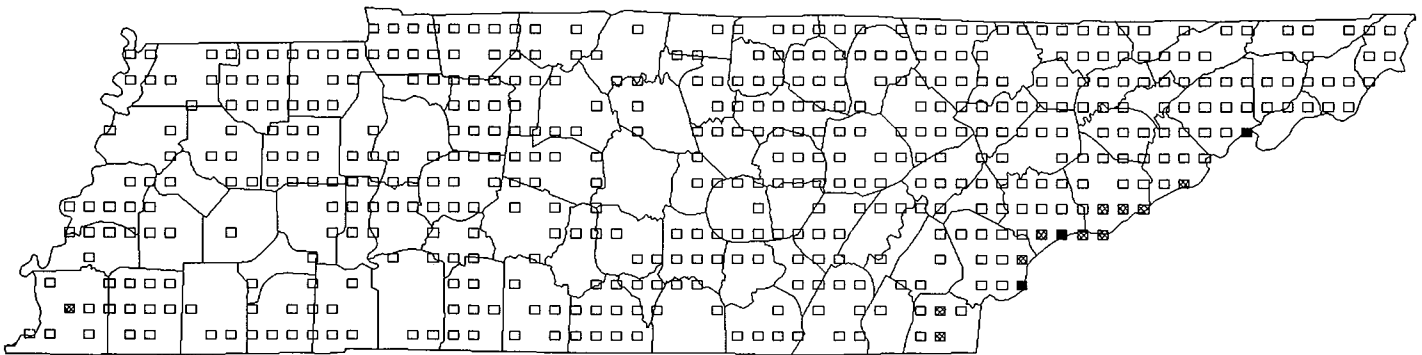
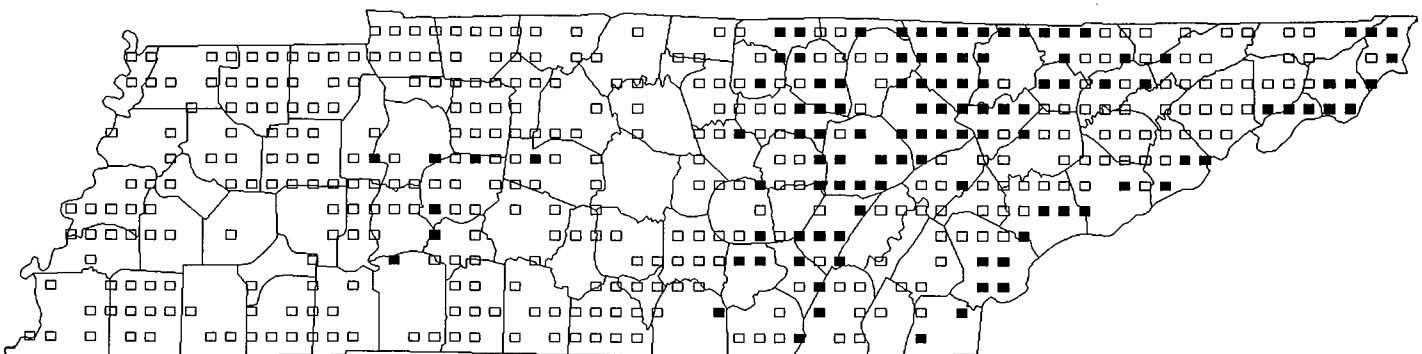
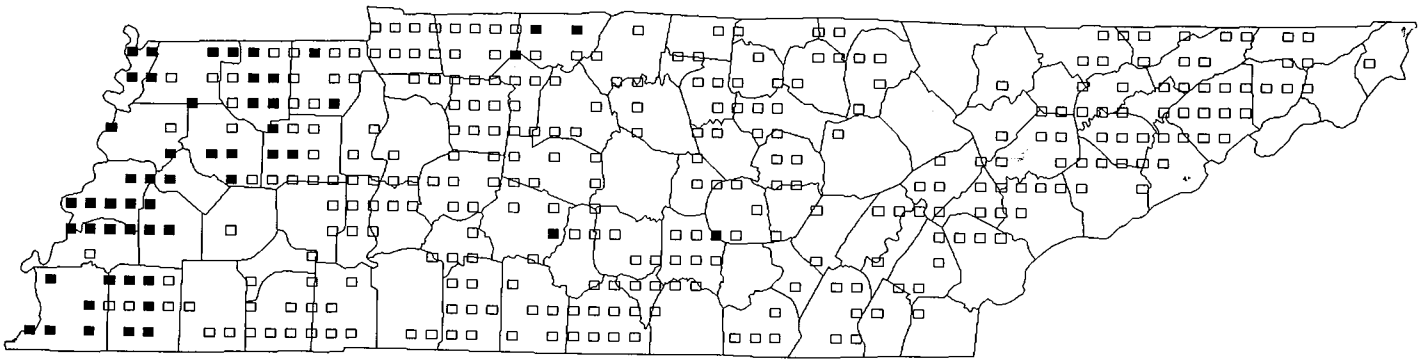


Figure 1. Groupings resulting from TWINSpan divisions.

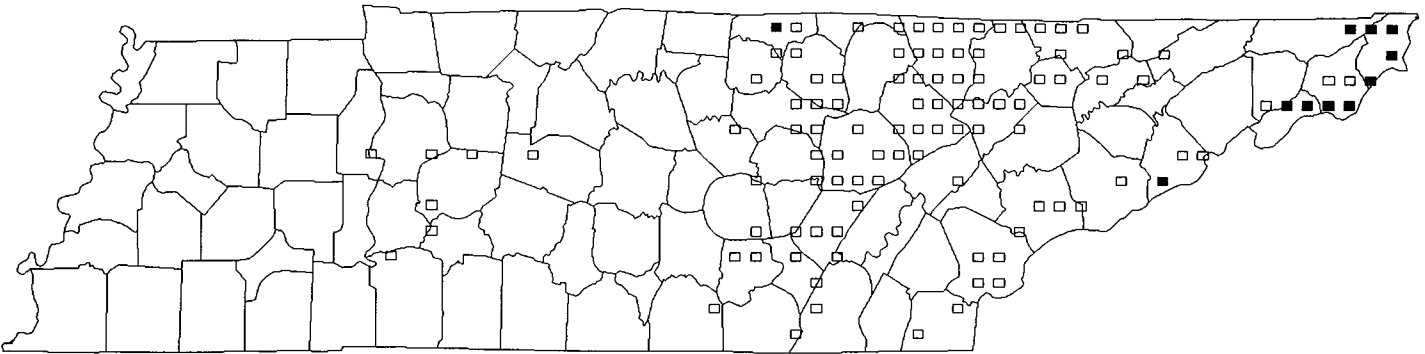
1a) Results from first division into groups IA (open blocks) and IB (solid blocks). Outliers resulting from composite clustering and excluded from TWINSpan analysis are also shown as cross-hatched blocks.



1b) Division of group IA into groups IIA (open blocks) and IIB (solid).



1c) Division of group IIA into groups IIIA (open blocks) and IIIB



1d) Division of group IIB into groups IIIC (open blocks) and IIID

on the Highland Rim. The blocks in this northeast cluster differed from other high-elevation Blue Ridge blocks further south in having a more heterogeneous landscape—from open habitats in the farmed valleys to high elevation forest. The Highland Rim block of the IIID group contained several bird species [including the Willow Flycatcher (*Empidonax traillii*) and House Wren (*Troglodytes aedon*)] more common in the northeast corner of the state.

Figure 2 shows the relationships between the clusters and groups, based on an ordination of the clusters' species lists. On both plots, the clusters are loosely grouped, and Axis 1 shows a gradient from west to east. Composite 14, in the Coastal Plain group, was made up entirely of blocks in the Mississippi River Floodplain. Most of the blocks forming composite 8, in the Cumberlands/low Blue Ridge group IIIC, were heavily wooded blocks in the Cumberlands, with somewhat lower

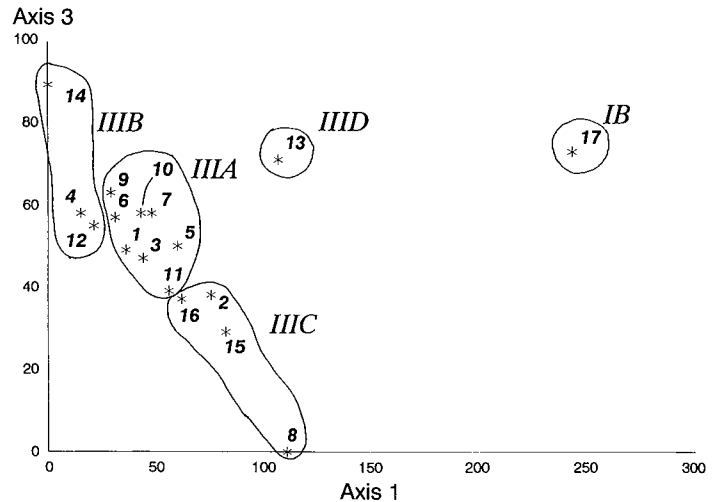
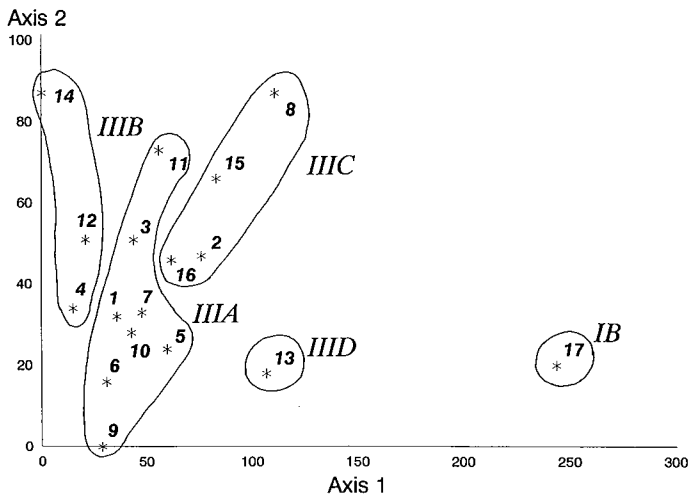


Figure 2. Ordination diagrams showing position of groups IB and IIIA-IIID produced by TWINSpan analysis and of the composite samples (1-17) forming each group. Sample scores are calculated as weighted averages of the species scores, standardized to give a within-sample variance of 1. Lengths of the axes are defined by the range of sample scores, expressed in standard deviation units (x100). Samples further apart have fewer species in common. Axis 1 represents a west to east longitudinal gradient.

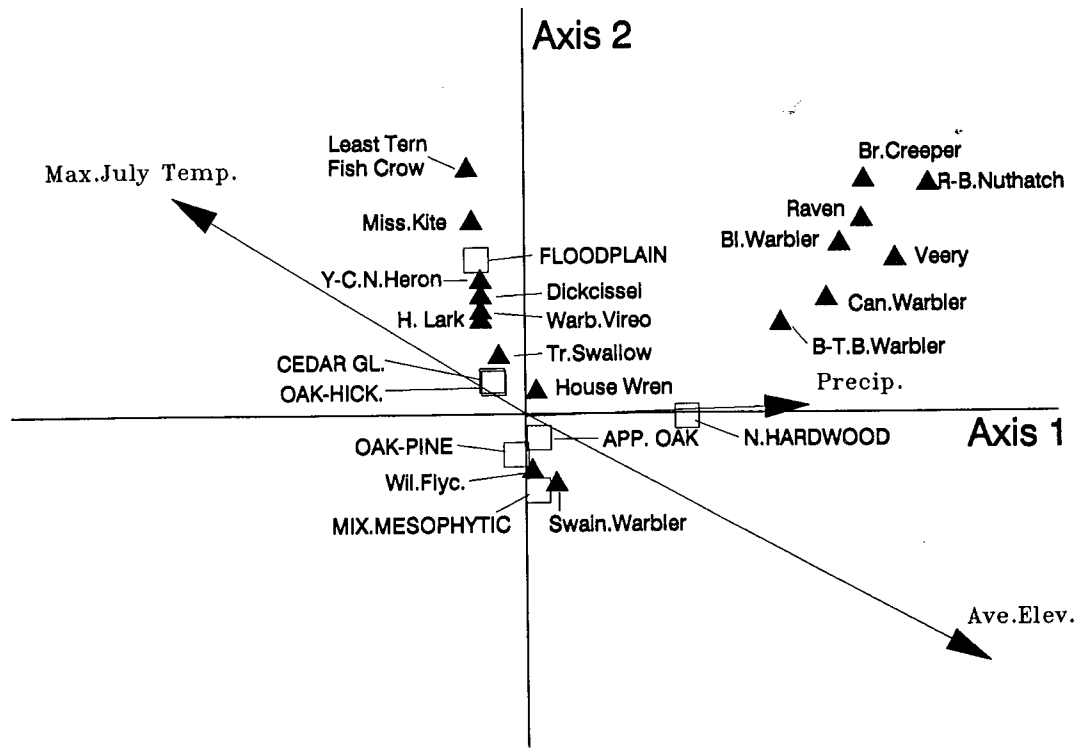


Figure 3. Ordination diagram based on canonical correspondence analysis of subsample of bird species data with continuous environmental variables (arrows: maximum July temperature, precipitation, and average elevation) and potential natural vegetation types (open boxes). Arrows show the direction and rate of change of environmental variables. Centroids of vegetation types are plotted. See text for full species names.

than average numbers of species and mid-elevation forest species such as the Solitary Vireo (*V. solitarius*) and Black-throated Green Warbler (*D. virens*).

Environmental Correlations with Species Occurrences

Canonical correspondence analysis was carried out on a subsample of the species data set (see above under METHODS). Figure 3 shows the distribution of species along the first two ordination axes. For simplicity, only selected species mentioned elsewhere as preferential in the TWINSPAN analysis are illustrated. The three elevation variables

were strongly correlated, and only average elevation is illustrated. The first axis of the species-environment plot accounted for 52% of the variance in the weighted average of the species scores. The addition of the second axis accounted for 72% of the variance, and the first three axes accounted for 83% of the variance.

Environmental Correlations with Number of Species/Block

The adjusted number of species per block, which ranged from 20 to 87 (mean = 64.0), is mapped in Figure 4. The fewest species were found in the central and southern portions of the Blue Ridge. Areas

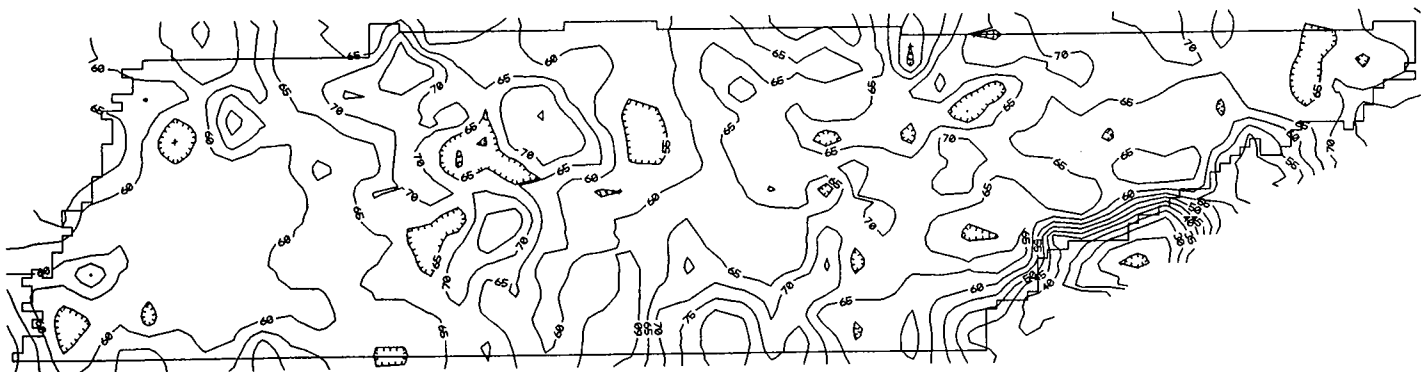


Figure 4. Contour map of number of species per block. Nocturnal species and nonbreeding waders are not included in species numbers. Contour interval is five species.

of high species numbers were scattered across the state, occurring in the extreme northeast corner, the Cumberlands, and the Western Highland Rim. The environmental variables used were weak predictors of the number of species. Precipitation and average elevation both had a significant negative correlation ($p < 0.001$) with the number of species. The slope of the regression equation for elevation ($y = 66.3 - 0.0077x$) was almost flat. Maximum July temperature was not related to the number of species. Analysis of variance showed potential natural vegetation had a significant effect ($F = 9.52$, $p < 0.01$). Bird species richness in spruce–fir blocks was significantly less than it was in the other types; the mean number of species in spruce–fir blocks (33) was almost half that of the other types.

DISCUSSION

Breeding bird communities of various degrees of distinctiveness were identified from the Blue Ridge, Cumberland Plateau and Mountains, and the Mississippi River Coastal Plain and Floodplain. The avifauna of the Ridge and Valley, Highland Rim (especially the eastern portion), Central Basin, and West Tennessee Uplands was, by comparison, relatively indistinct. The most distinctive community consisted of high elevation blocks in the Blue Ridge. These blocks had a relatively homogeneous, heavily forested landscape, and therefore lacked bird species found in open agricultural habitats. Their total number of species was low. Most of the outliers possessed these same qualities.

Mengel (1965) described five avifaunal regions in Kentucky, based on species whose ranges have presumably not changed greatly due to human activities. Four of Mengel's regions—the Cumberland Crest, Cumberland Uplands, Limestone Plateau, and Alluvial Forest—border Tennessee. The Cumberland Crest avifaunal region includes the Cumberland Mountains above 914 m elevation. I did not find this area to be distinctive in Tennessee, probably because the sample blocks where it is best represented, in Frozen Head State Natural Area (Nicholson 1987, and pers. unpubl. data), were not included in the priority blocks used in this analysis. None of the Cumberland Mountain blocks used in this analysis had all the high–elevation species found at Frozen Head. The Cumberland Uplands avifaunal region is analogous to the Cumberlands/low Blue Ridge group identified here. Boundaries of the Limestone Plateau avifaunal region closely match the large group IIIA formed here, except along the Lower Tennessee River Valley, which Mengel (1965) included in the Alluvial Forest avifaunal region. The lower Tennessee River Valley, which was not differentiated in this study, has been greatly modified by reservoir construction. My Coastal Plain group (IIIB) corresponds to the western portion of the Alluvial Floodplain avifaunal region of Mengel (1965). Some of the preferential species for the Coastal Plain group (Mississippi Kite, Fish Crow) did not regularly occur in Kentucky when Mengel (1965) described his regions. These species, as well as the Least Tern, are also absent from the lower Tennessee River Valley.

With the exception of the upper East Tennessee cluster, the bird communities revealed by my analysis are arrayed along the state's

east–west axis. Given the length of the state, the predominantly east–west arrangement of the state's physiographic regions, and the fact that relatively few Tennessee birds show range limits on a north–south axis in comparison to the east–west axis (pers. unpubl. data), this is not surprising. Many of the species showing range limits (or at least differences in frequency of occurrence) along the east–west axis, independent of physiographic regions, are recently established breeders in the state; examples include the Willow Flycatcher and House Wren (Tanner 1988).

The ordination of environmental factors with individual species also showed a west–to–east trend along Axis 1, which showed a gradient of decreasing temperature and increasing precipitation and elevation. Lowland western species were plotted toward the left, and mountain species toward the right. The total number of species in a block was significantly related to precipitation, elevation, and potential natural vegetation. More species were found in areas of lower rainfall and lower elevations. The spruce–fir blocks, which had the highest rainfall and elevation of all blocks, had fewer species than did blocks characterized by other vegetation classes.

ACKNOWLEDGMENTS

This study was possible because of the thousands of hours of field work contributed to the Tennessee Breeding Bird Atlas Project by Tennessee Ornithological Society members and others. I am indebted to them. Douglas B. McNair and an anonymous reviewer provided valuable comments on the manuscript. I also acknowledge the tolerance of my colleagues at the Tennessee Valley Authority while I worked on the atlas project.

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