AN ABSTRACT OF THE THESIS OF

Michael D. Warriner for the Master of Science Degree in Biology presented on _____

Title: Biogeographic Patterns of Passerines During the Breeding Season

Abstract Approved: _____

The results of numerical analyses examining biogeographic patterns are often the delineation of distinct regions or provinces based upon the cumulative distributional limits of each member of a respective taxon. Resulting patterns among groups of species, or assemblages, can then be used to shed light on how species assemblages correspond to broad-scale environmental and habitat features. These same biogeographic patterns also provide opportunity to examine how historical factors such as climate change and vicariant events have shaped species distributions.

By virtue of their mobility and conspicuous behaviors, birds represent an easily observed and recognizable group. As a result, a great deal of information has been collected regarding the geographic occurrence of most North American bird species. The objective of my study was to examine the

major biogeographic patterns of passerines during the breeding season across the continental United States.

Data regarding the breeding distribution of nesting passerines were collected from checklists obtained from the extensive National system of parks, refuges, and reserves scattered across the contiguous United States. Presence/absence data compiled from checklists were converted to a standardized data matrix based on the Coefficient of Jaccard. The data matrix was then submitted to cluster analysis and principal components analysis.

Results of these numerical analyses revealed five major avifaunal regions based upon passerine distribution in the continental United States. These regions are largely coincident with certain broad physiographic regions; 1) northern hardwood/coniferous forests and associated grasslands, 2) eastern and southeastern forests and associated grasslands, 3) the Great Plains, 4) mountain ranges and intermontane regions of the western United States, and 5) the southwest. The fourth and fifth areas are relatively species-rich and, along with central and southern sections of the Great Plains, form one of the three major branches of the block dendrogram produced by cluster

analysis. The passerine avifaunas of the central and southern plains were most similar to those of the American southwest and west. The northern plains, in contrast, grouped more closely with the passerine avifaunas of the northern/northeastern United States, comprising a second branch in the dendrogram. The third branch consisted of the southeastern United States and southern Texas. Differences among these regional passerine avifaunas were largely based upon similarities in distribution among several species adapted to gradients in regional environmental and ecological conditions.

Biogeographic Patterns of Passerines During the Breeding Season

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Approved by Major Advisor

Approved by Committee Member

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Approved for Major Department

Approved for Graduate Council

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Introduction

The ecological requirements of species dictate the environmental conditions they can occupy, and how these requirements are met in space determine where species can occur (Wiens, 1992). To meet these requirements, species seek out certain habitats that are the result of the interaction between climate and topography (MacDonald and Sertorio, 1991). As a consequence of evolutionary change, all species will not share an affinity for the same habitat. Instead, due to differences in morphology, physiology, genetic adaptability, and other factors (Hengeveld, 1992), each species will have its own habitat requirements. As habitat types grade and vary across a landscape in accordance with differences in climate and terrain, so too are there compositional changes in the complement of species that occur in each habitat (Rotramel, 1973). Across a heterogeneous landscape these changes can result in distinctive patterns of species assemblages (Hansen, 1992). According to Dice (1943), a basic premise of most biogeographical studies has been that there are distinct provinces or regions characterized by ". . . the occurrence of one or more important ecological associations that

differ, at least in proportional area covered, from the associations of the adjacent provinces."

The biogeographic patterns of various North American animal taxa have been examined, including Savage (1960) with reptiles and amphibians, Rostlund (1952) with fishes, and Van Dyke (1939) with beetles. The results of such studies are often the delineation of distinct regions or provinces based upon the analysis of the cumulative distributional limits of each member of respective taxa (Darlington, 1957). Analyzing the distributional patterns of 242 North American mammal species, Hagmeir and Stults (1964) developed a geographic division of the continent into 24 faunal provinces each characterized by a unique assemblage of mammal species. In their investigation, Hagmeir and Stults (1964) defined biogeographic units as those areas with a relatively homogeneous fauna separated from adjacent areas by zones of faunal heterogeneity.

To investigate patterns of association among different species and interpret them in light of landscape and historical factors requires accurate information regarding

the geographic occurrence of each species (Myers and Giller, 1988; Maurer, 1994). This information is typically based upon the presence or absence of a species from a specific location and can be derived from a variety of sources including range maps of species distributions (Smith and Fisher, 1970; Cook, 1968), records of collection localities (Echelle and Schnell, 1976; Stevenson et al., 1974), and species censuses (Bock et al., 1978; Tramer, 1974). The quantity, and to some extent the reliability, of these data are dependent upon the conspicuousness of the species under consideration and the level of interest and activity of observers (Darlington, 1957). Consequently, relatively more is known regarding the distributional patterns of ubiquitous or active taxa, than groups with secretive or cryptic habits (Simpson, 1960).

Delineation of biogeographic units based on species assemblages does not, however, connote any degree of actual interdependence among the species involved (Hengeveld, 1992). Instead, these units reveal the degree of similarity in ecological affinity among species. Ultimately, species do not respond to changes in their environment as parts of

any particular community but, due to their unique biological requirements, they behave individualistically (Connor and McCoy, 1979). Biogeographic units can then be thought of as the result of the cumulative ecological responses of an assemblage of species adapted to live under prevailing environmental conditions.

By virtue of their mobility and conspicuous behaviors, birds represent an easily observed and recognizable group. As a result, a great deal of information has been collected regarding the geographic occurrence of most North American bird species (Best, 1981). However, unlike most other North American terrestrial vertebrates, patterns of occurrence for most native bird species are highly seasonal. Many bird species are not resident on the continent year round, being present only at certain times of the year (Berthold et al., 1994). In North America, bird species diversity fluctuates predictably and markedly between winter and summer seasons (Cox, 1985). Species diversity swells during the summer as large numbers of nonresident species migrate from wintering grounds in Central and South America to take advantage of hospitable breeding grounds to the north (DeGraaf and

Rappole, 1995). Diversity subsequently diminishes as these neotropical migrants depart to the south with the onset of winter.

The steep environmental gradients of winter and summer exert different and varying adaptive pressures upon bird species resulting in differing responses in habitat selection (Cody, 1986). Consequently, for many species, habitat needed for wintering can be quite different from that required during the breeding season. Because most birds are migratory, and the rest sufficiently mobile to take advantage of changing conditions, the assumption can be made that birds breed and winter where it is most adaptive to do so. Birds, therefore, represent one of the few groups in which the influence of seasonal changes upon biogeographic patterns can be determined.

To construct an accurate interpretation of the biogeographic patterns of birds, or any taxon, the distributional limits of many species must be examined. Hypotheses about geographical patterns and processes can never be generated from a single individual or species (Hengeveld, 1992).

Instead, biogeographic investigations require the analysis of large data sets. These data, however, can prove to be difficult and expensive to procure (Echelle and Schnell, 1976). In many instances, range maps have provided the basic material to quantify species distributions. Kaiser et al. (1972) and Cook (1968) utilized the Checklists of North American Birds (A.O.U., 1957) to map the range limits of bird species across their respective study areas. Data from the Audubon Christmas Bird Count, an annual census conducted each winter by large numbers of volunteers, has been analyzed by Root (1988), Bock et al. (1978), and Bock and Lepthian (1976). Both types of data, range map and census, have been analyzed by several workers and produced meaningful and biologically realistic results (Wilson, 1974; Maurer, 1994).

Whatever form of distributional data analyzed, methodology in biogeographic studies remains mainly inductive, therefore, it is important to adopt explicit inductive reasoning (Myers and Giller, 1988). Essentially this implies that processes studied in biogeography are defined statistically. A variety of numerical techniques have been

applied in studies of biogeographic patterns, including cluster analysis (Bock et al., 1978), principal components analysis (Bock et al., 1981), and correspondence analysis (Greenacre and Vrba, 1984). Regardless of the statistical technique applied, the ultimate aim of any numerical analysis is to objectively define patterns that exist among species, or groups of species.

The objective of my study was to examine the major biogeographic patterns of passerines during the breeding season across the continental United States. The breeding status of passerines on national parks, forests/grasslands, and wildlife refuges was analyzed. This national system of protected habitats and managed natural areas represent important, and in many instances, vital nesting habitat for a number of bird species. To a certain extent, remnants of native habitats that have been degraded throughout the rest of the United States are preserved in the National Park and Refuge system. These areas also serve as sites for biological research, as well as being popular for birdwatching activities.

Since most birds are relatively conspicuous and there is such interest in observing them, parks and refuges produce checklists that summarize species that occur in these areas. Information contained within bird checklists includes when certain species are present and if they are known to nest there. The checklist data are compiled and updated by park or refuge personnel from information collected by wildlife biologists, ornithologists, and bird-watchers. Although these data do not posses the intrinsic immediacy of yearly census efforts, it provides a realistic record of the geographic occurrence of breeding passerines from a number of well-distributed sites across the study area.

Checklist data are sufficient for my study in that periodic fluctuations that would be revealed by yearly censuses occur at a shorter temporal scale than that examined herein (Maurer, 1994). This study, in contrast, attempts to examine a more long-term process of adaptation by passerines to their environment as expressed by similarities in species occurrence during the breeding season. The resulting patterns of occurrence can then be used to determine how species assemblages correspond to broad-scale environmental

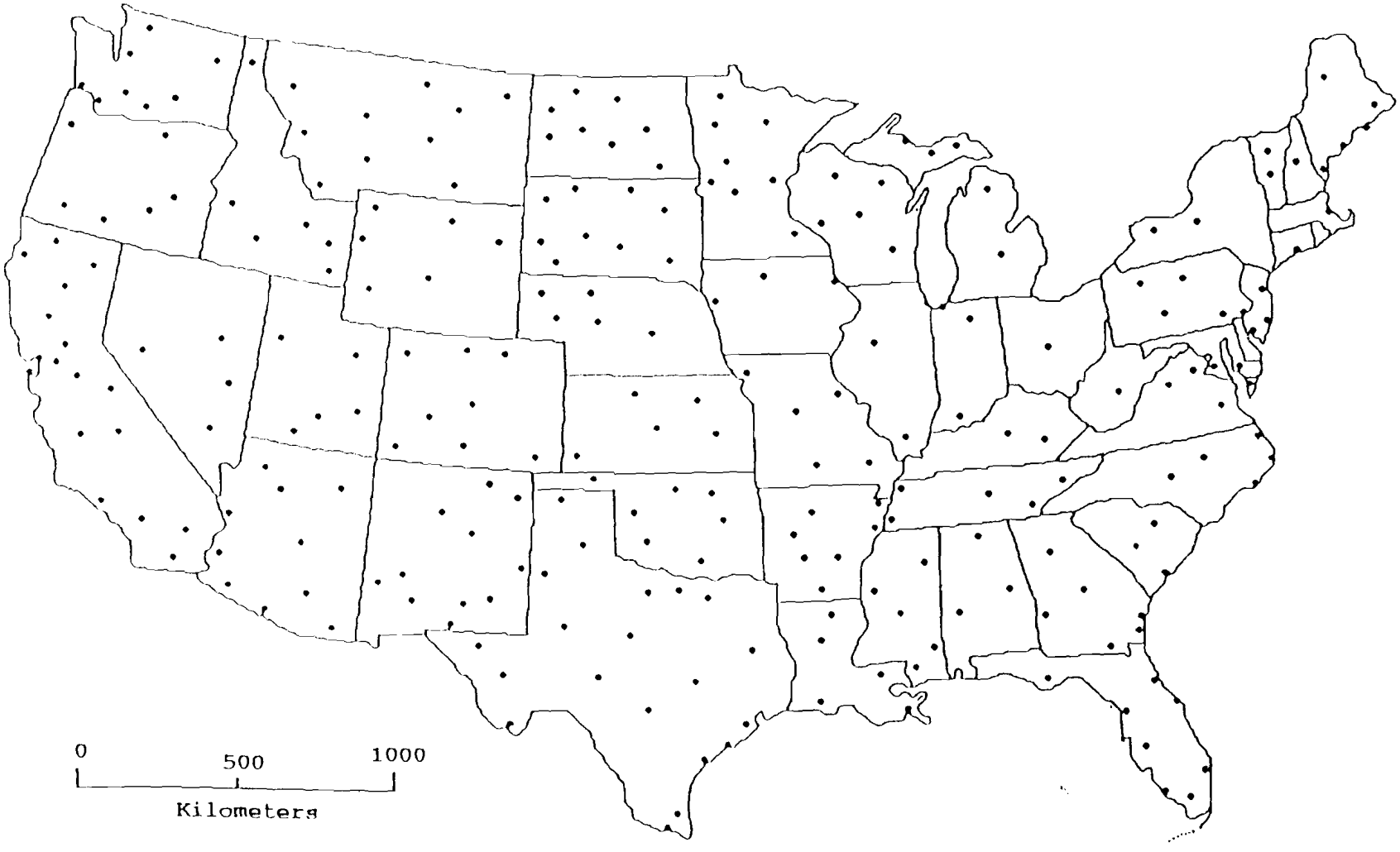
and habitat features. Ultimately, these patterns can shed light on how species have adapted and evolved in response to landscape patterns and how climatic conditions, vegetational formations, and geographical barriers have affected them.

Methods

The geographic distributions of breeding passerines were derived from bird checklists obtained from parks and refuges across the continental United States. Checklists were obtained from 167 National Wildlife Refuges, 40 National Forests, 13 National Grasslands, 29 National Parks, 15 National Monuments, nine National Recreation Areas, four National Preserves, and 18 state parks. Total sample size was 295 checklists. Figure 1 depicts the distribution of these points across the continental United States. The breeding status of passerines occurring at each site was indicated within each checklist. Checklists followed a relatively consistent criterion, as most based breeding status on observation and/or actual evidence of nesting activity. A total of 236 passerine species was determined to breed across the study area. For each site, the presence or absence of breeding activity by each of the 236 passerines was recorded, with one indicating breeding activity and zero the lack thereof.

Presence/absence data for each site were then compiled and grouped into 5-degree blocks of latitude and longitude, with

Figure 1: Distribution of points from which checklists were collected.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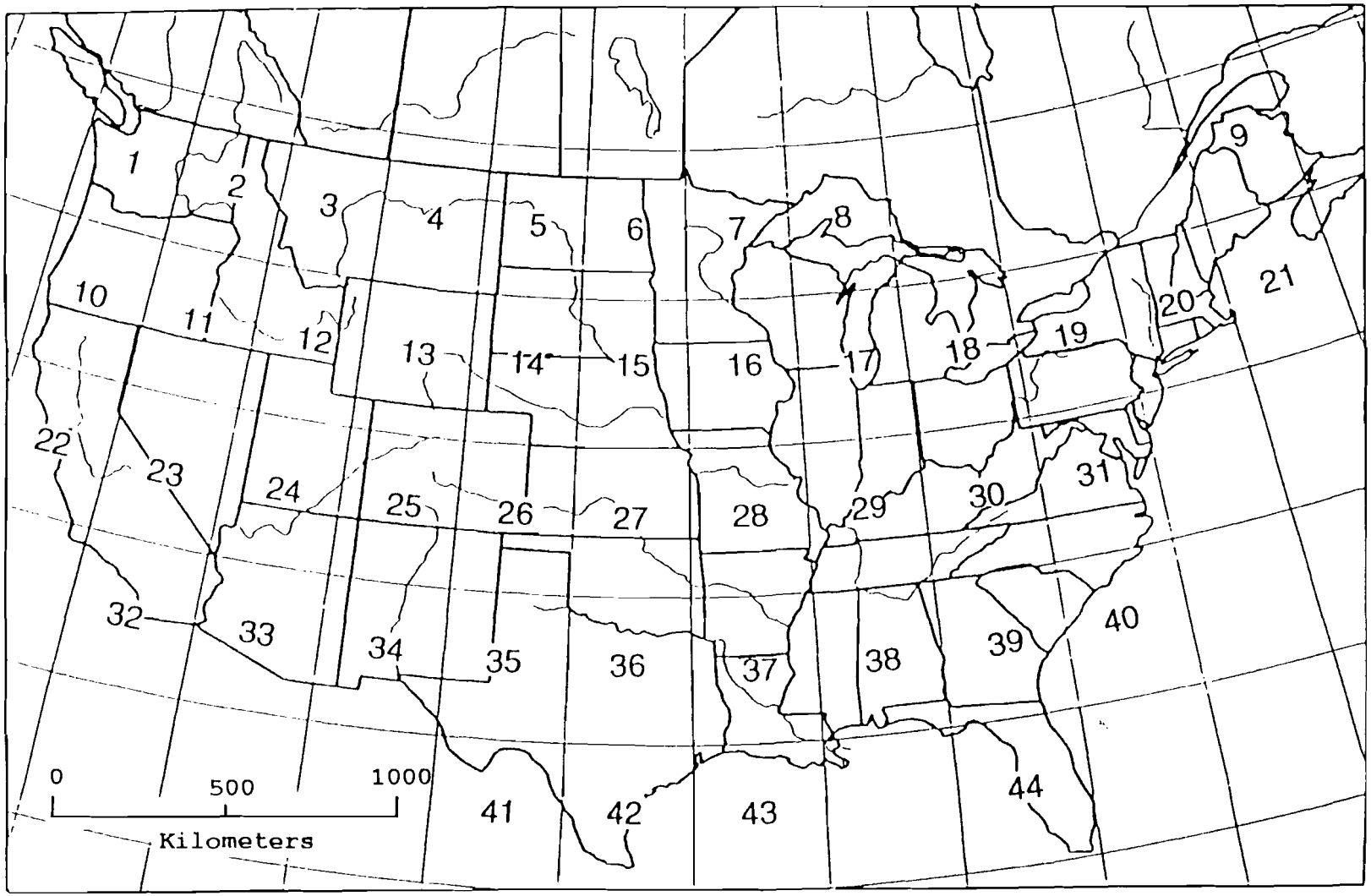
a total of 44 blocks containing verifiable species lists (Figure 2). These blocks then served as operational taxonomic units (OTUs) for analysis by the numerical taxonomy system NT-SYS (Rohlf et al., 1982). From the raw data matrix of 236 species and 44 blocks, a second matrix of similarity coefficients, based upon the Coefficient of Jaccard, was calculated by using the program SPASSOC from Ludwig and Reynolds (1988) and comparing all pairs of blocks based upon presence/absence of breeding passerines. A variety of formulae have been proposed for measuring the faunal similarities of pairs of geographic regions (Bock et al., 1981). Generally, similarity measures fall into two groups, those that include negative matches and those that exclude them. A negative match would be the mutual absence of a species from two geographic locations being compared. For presence/absence data, the Coefficient of Jaccard gives few problems and much is known regarding its properties in such applications (Hengeveld, 1992). Jaccard's coefficient excludes negative matches, therefore no two regions would be considered similar due to a mutual absence of a species.

Figure 2: Distribution of 44 latitude-longitude blocks across the contiguous United States of America.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The Coefficient of Jaccard is calculated as follows:

$$S_j = a / a + u$$

where a is the number of species occurring in both blocks being compared and u is the number of species present in one but not both blocks.

Cluster analysis and principal components analysis were the numerical techniques employed as they have been used in similar numerical analyses of avian biogeography (Bock et al., 1978; Bock and Lepthian, 1976). In cluster analysis, blocks are placed into groups according to a measure of similarity. The two most similar blocks are grouped, and the similarities of this group are then compared to that of other groups. This process is repeated until only a single group remains. This information is typically expressed as a dendrogram depicting hierarchical relationships among the blocks. Cluster analysis was performed on the S_j similarity matrix by using the unweighted pair-group method with arithmetic averaging (UPGMA). The program MXCOMP was then used to compute correlation coefficients between the S_j similarity matrix

and the dendrogram matrix produced by UPGMA clustering as a measure of congruence, or goodness of fit, between the two.

Geographic relationships among the blocks and species were also examined by principal components analysis (PCA). Principal components analysis was performed on the S_j matrix with standardized data. This analysis reduces the dimension of a group of data by producing smaller abstract variables (components), that describe the relationships among the data. Relationships among the blocks then were examined by projecting them onto the first three components of the PCA.

As a basis for analyzing the biogeographic affinities of the 236 passerines, species were assigned to one of six categories based upon the geographic boundaries of their breeding distributions. Range limits for each species were examined and a determination was made as to whether a species breeding distribution was centered in one particular geographic region of the continental United States. The geographic distribution of each passerine was delineated based upon distributional information obtained from the Checklist of North American Birds (A.O.U., 1983) and

Johnsgard (1979). The categories assigned, modified from Johnsgard (1979), are as follows:

CENTRAL: Breeding distribution generally limited to the central United States in the vicinity of the Great Plains.

EASTERN: Breeding distribution generally limited to the eastern or southeastern United States.

NORTHERN: Breeding distribution generally limited to the northern or northeastern United States.

PANDEMIC: A large continuous or disruptive breeding distribution not confined to one specific area of the United States.

SOUTHERN: Breeding distribution generally limited to the southern or southwestern United States.

WESTERN: Breeding distribution generally limited to the western or northwestern United States.

Table 1 lists the geographic affinities of the 236 passerines that breed across the study area. Passerines with eastern geographic affinities represent the largest contingent with 51 species. Western (49), southern (48), and northern (44) passerines followed comprising comparable

TABLE 1

Geographic Affinities of Passerines Nesting in the Contiguous United States During the Breeding Season as Taken from Johnsgard (1979)

Pandemic	Western	Eastern	Northern	Southern	Central
Eastern Kingbird	Western Kingbird	Gray Kingbird	Least Flycatcher	Thick-billed Kingbird	Chihuahuan Raven
Willow Flycatcher	Ash-throated Flycatcher	Great Crested Flycatcher	Alder Flycatcher	Cassin's Kingbird	Sprague's Pipit
Horned Lark	Western Wood Pewee	Eastern Wood Pewee	Yellow-bellied Flycatcher	Tropical Kingbird	Baird's Sparrow
Tree Swallow	Say's Phoebe	Eastern Phoebe	Gray Jay	Couch's Kingbird	Cassin's Sparrow
Purple Martin	Gray Flycatcher	Acadian Flycatcher	Boreal Chickadee	Scissor-tailed Flycatcher	Clay-colored Sparrow
Bank Swallow	Dusky Flycatcher	Blue Jay	Brown Creeper	Great Kiskadee	Chestnut-collared Longspur
Northern Rough-winged Swallow	Hammond's Flycatcher	Fish Crow	Winter Wren	Brown-crested Flycatcher	McCown's Longspur
Cliff Swallow	Western Flycatcher	Tufted Titmouse	Golden-crowned Kinglet	Dusky-capped Flycatcher	Dickcissel
Barn Swallow	Violet-green Swallow	Carolina Chickadee	Ruby-crowned Kinglet	Greater Pewee	Lark Bunting
American Crow	Scrub Jay	Brown-headed Nuthatch	Veery	Black Phoebe	
Common Raven	Pinyon Jay	Carolina Wren	Swaninson's Thrush	Vermillion Flycatcher	
Black-capped Chickadee	Steller's Jay	Sedge Wren	Gray-cheeked Thrush	Northern Beardless-Tyrannulet	
White-breasted Nuthatch	Clark's Nutcracker	Blue-gray Gnatcatcher	Hermit Thrush	Rose-throated Becard	
House Wren	Black-billed Magpie	Eastern Bluebird	Cedar Waxwing	Cave Swallow	
Bewick's Wren	Yellow-billed Magpie	Wood Thrush	Solitary Vireo	Gray-breasted Jay	
Marsh Wren	Wrentit	Gray Catbird	Philadelphia Vireo	Green Jay	
American Robin	Plains Titmouse	Northern Mockingbird	Tennessee Warbler	Bridled Titmouse	
Loggerhead Shrike	Mountain Chickadee	Brown Thrasher	Orange-crowned Warbler	Mexican Chickadee	
Warbling Vireo	Chestnut-backed Chickadee	White-eyed Vireo	Nashville Warbler	Verdin	
Yellow Warbler	Bushtit	Yellow-throated Vireo	Black-throated Blue Warbler	Cactus Wren	
Common Yellowthroat	Pygmy Nuthatch	Bell's Vireo	Blackburnian Warbler	Black-tailed Gnatcatcher	
Yellow-breasted Chat	Canyon Wren	Red-eyed Vireo	Chestnut-sided Warbler	Long-billed Thrasher	
Rufous-sided Towhee	Rock Wren	Prothonotary Warbler	Cape May Warbler	Curve-billed Thrasher	
Grasshopper Sparrow	Western Bluebird	Blue-winged Warbler	Magnolia Warbler	Crissal Thrasher	
Vesper Sparrow	Mountain Bluebird	Golden-winged Warbler	Yellow-rumped Warbler	Phainopepla	
Savannah Sparrow	Townsend's Solitaire	Northern Parula	Black-throated Green Warbler	Black-capped Vireo	
Song Sparrow	Sage Thrasher	Black and White Warbler	Bay-breasted Warbler	Virginia's Warbler	
Lark Sparrow	California Thrasher	Cerulean Warbler	Blackpoll Warbler	Lucy's Warbler	
Chipping Sparrow	American Dipper	Yellow-throated Warbler	Palm Warbler	Golden-cheeked Warbler	
Bobolink	Hutton's Vireo	Prairie Warbler	Mourning Warbler	Grace's Warbler	
Red-winged Blackbird	Black-throated Gray Warbler	Pine Warbler	Connecticut Warbler	Painted Redstart	
Brown-headed Cowbird	Townsend's Warbler	Kentucky Warbler	Canada Warbler	Red-faced Warbler	
Northern Oriole	Hermit Warbler	Hooded Warbler		Olive Warbler	
American Goldfinch	MacGillivray's Warbler	Worm-eating Warbler			
House Finch	Black-headed Grosbeak	Swainson's Warbler			
	Lazuli Bunting	Ovenbird			

TABLE 1 (continued)
Geographic Affinities of Passerines Nesting in the Contiguous United States During the Breeding Season as Taken from Johnsgard (1979)

Pandemic	Western	Eastern	Northern	Southern	Central
	Green-tailed Towhee	Louisiana Waterthrush	Wilson's Warbler	Pyyrhuloxia	
	Sage Sparrow	American Redstart	Northern Waterthrush	Blue Grosbeak	
	Brewer's Sparrow	Rose-breasted Grosbeak	Le Conte's Sparrow	Painted Bunting	
	White-crowned Sparrow	Northern Cardinal	Sharp-tailed Sparrow	Varied Bunting	
	Fox Sparrow	Indigo Bunting	Dark-eyed Junco	Brown Towhee	
	Western Meadowlark	Henslow's Sparrow	White-throated Sparrow	Abert's Towhee	
	Yellow-headed Blackbird	Seaside Sparrow	Lincoln's Sparrow	Five-striped Sparrow	
	Tricolored Blackbird	Bachman's Sparrow	Rusty Blackbird	Botteri's Sparrow	
	Brewer's Blackbird	Field Sparrow	Pine Siskin	Rufous-winged Sparrow	
	Western Tanager	Swamp Sparrow	Red Crossbill	Rufous-crowned Sparrow	
	Lesser Goldfinch	Eastern Meadowlark	White-winged Crossbill	Black-chinned Sparrow	
	Rosey Finch	Boat-tailed Grackle	Pine Grosbeak	Yellow-headed Junco	
	Cassin's Finch	Orchard Oriole		Bronzed Cowbird	
		Scarlet Tanager		Great-tailed Grackle	
		Summer Tanager		Scott's Oriole	

numbers of species. Thirty-five passerines were pandemic in distribution, 13 of which occurred in all nine primary regions including the Cliff Swallow (*Hirundo pyrrhonota*), American Crow (*Corvus brachyrhynchos*), Common Yellowthroat (*Geothlypis trichos*), and Brown-headed Cowbird (*Molothrus ater*). Those passerines with central geographic affinities constituted the smallest proportion of the passerine fauna with nine species having breeding distributions centered in the interior of the United States.

Recent distributional data indicate that a few bird species have undergone range contractions or expansions. However, this should not significantly affect these analyses as the magnitude of change is small and involves relatively few species. In this and other numerical analyses, patterns are defined polythetically in that members of an assemblage share most properties in common, and the lack of one or a few is largely irrelevant (James and McCulloch, 1990).

Results and Discussion

Figure 3 is the dendrogram generated by UPGMA cluster analysis from the S_j similarity matrix; it illustrates the hierarchical relationships among the 44 blocks. The thin vertical line transecting the dendrogram is a conservative delineation of nine distinct biogeographic areas based upon compositional similarities in their respective passerine assemblages. Figure 4 depicts the geographic location of these areas, or as they will be referred to hereafter as "Primary Regions." For the most part, primary regions included groups of adjacent blocks, which in turn clustered into larger contiguous areas.

The cophenetic correlation between the S_j and dendrogram matrices was 0.85 indicating a relatively high degree of congruence. Besides UPGMA, two other clustering methods were also performed on the S_j matrix. In studies employing only UPGMA cluster analysis it is generally advised to also perform single-linkage and complete-linkage clustering on the data matrix (Rohlf et al., 1982). This was done to determine if the chosen clustering method was the most effective in depicting relationships within the data. The

Figure 3: Dendrogram depicting relationships among 44 latitude-longitude blocks, revealed by UPGMA cluster analysis of passerine presence/absence data during the breeding season. The vertical line transecting the dendrogram delineates Primary Regions. Nine Primary Regions are identified (A-I). Cophenetic correlation = 0.85

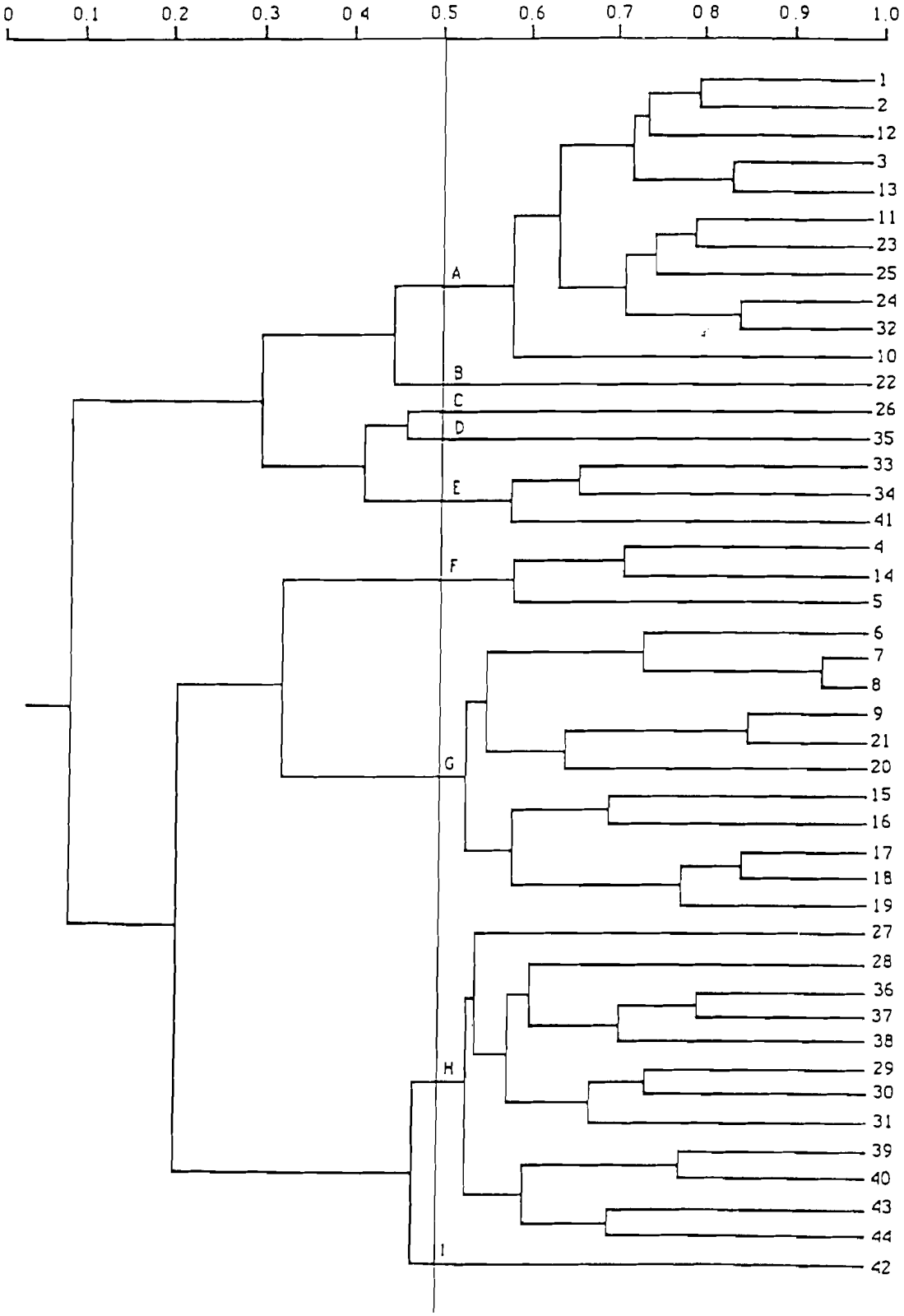
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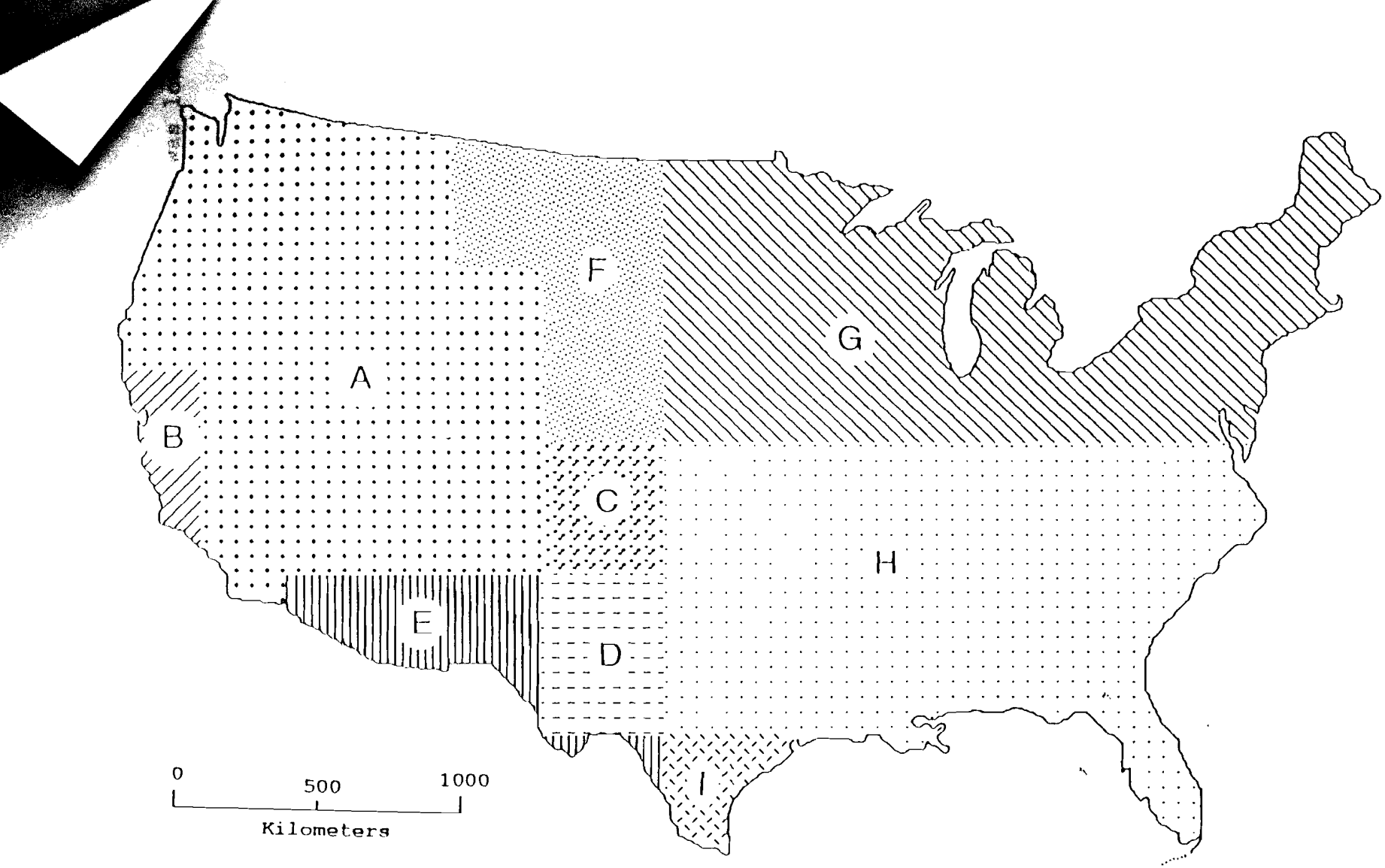
Figure 4: Map of the nine passerine avifaunal regions (Primary Regions) identified by cluster analysis of passerine presence/absence data.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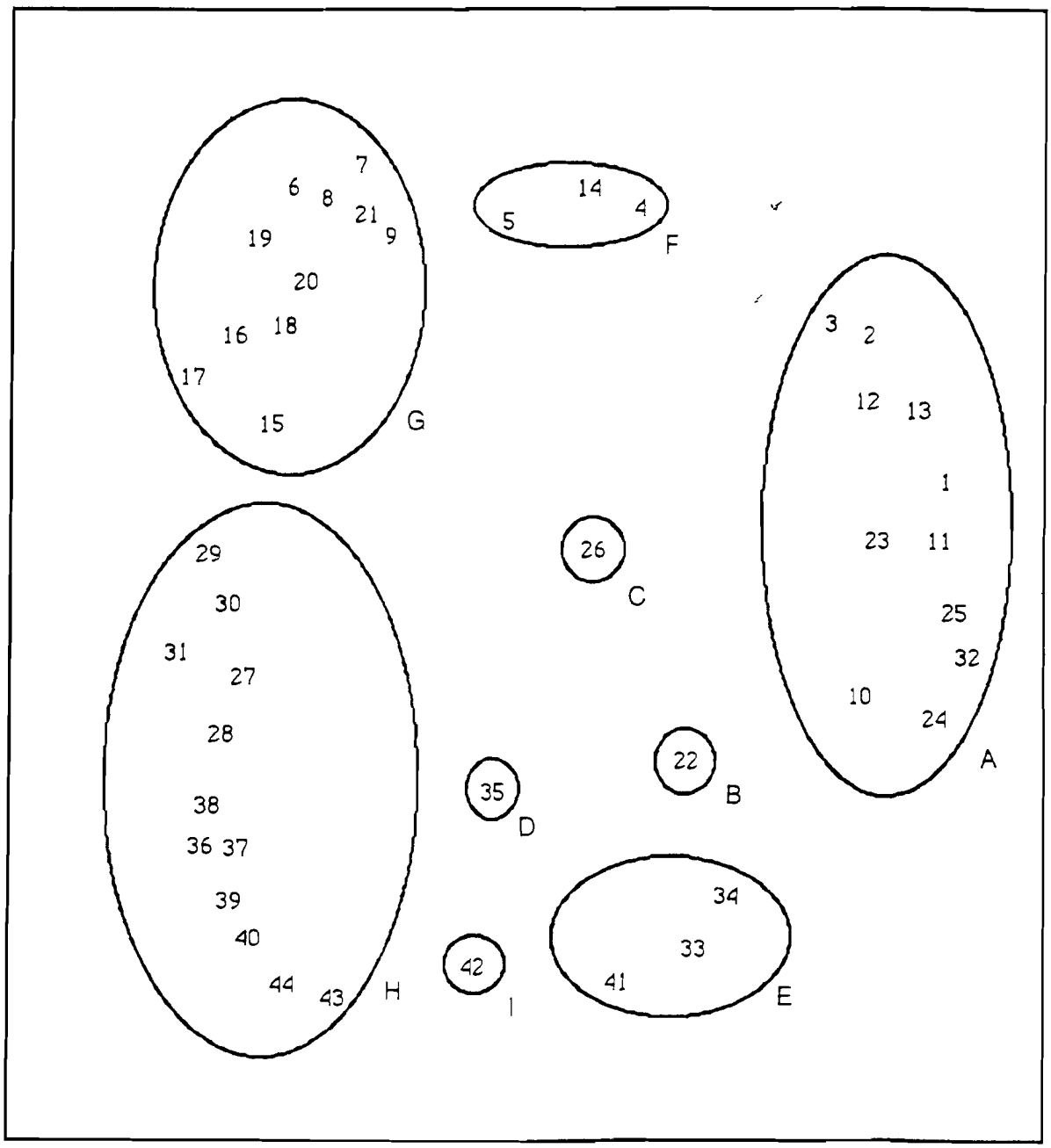
cophenetic correlation for single-linkage clustering was low at 0.54, and only relatively higher at 0.68 for complete-linkage. Subsequently, UPGMA cluster analysis was determined to be more effective in deriving relationships within the similarity matrix.

Figure 5 is a projection of the 44 blocks onto the first three axes of the principal components analysis of the S_j matrix. The first two principal components accounted for 79.3% of the variation in the similarity matrix. Those blocks that did not group closely with others stand as individual primary regions. The projection, and subsequent clumping, of blocks onto the PCA axes compare favorably to the groups depicted in the aforementioned dendrogram produced by UPGMA cluster analysis. The circled sets of labeled points within the projection represent primary regions as defined by cluster analysis.

The relative merits of using both cluster and principal components analysis have been subject to some criticism (Gauch et al., 1977). However, in studies of numerical biogeography they have proved to be useful in elucidating

Figure 5: Projection of 44 latitude-longitude blocks on to the first two axes of a principal components analysis of passerine presence/absence data. Circled points represent Primary Regions.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patterns among groups of species (Myers and Giller, 1988). An advantage of cluster analysis is that it results in easy recognition of distinct geographic regions, but it can give an unrealistic impression of their clarity. Principal components analysis is used, in many instances, to provide a basis of comparison to determine if patterns described by cluster analysis actually exist (Rohlf et al., 1982). Although primary regions were delineated based upon groups of blocks obtained through cluster analysis, these same groupings are evident in the plot derived by PCA.

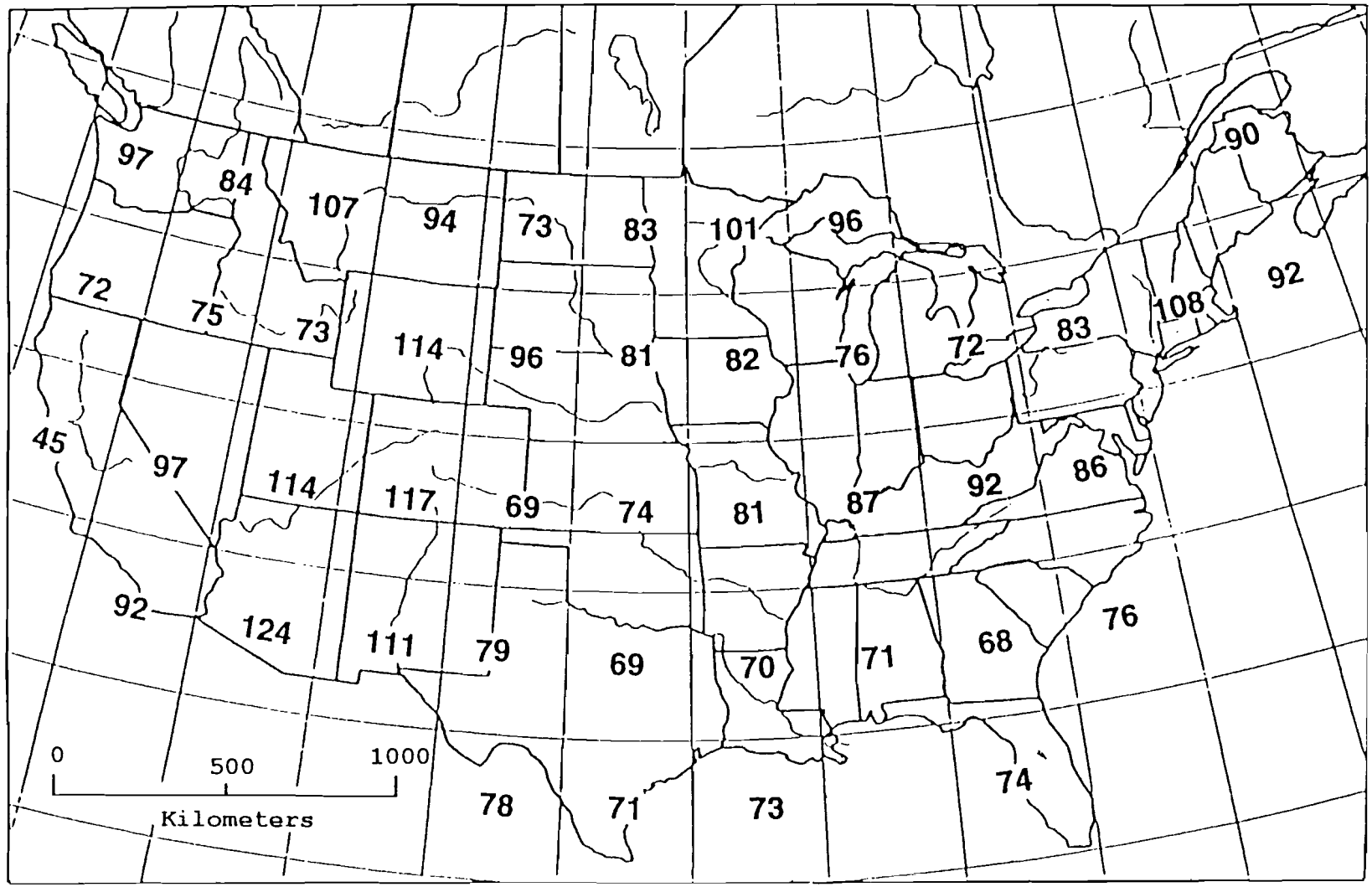
Examination of the results of both cluster and principal components analyses reveals an east-west separation in passerine assemblages across the United States. Upon inspection of the geographic location of the nine primary regions (Figure 4), it is evident that the continental United States is divided into large eastern and western sections by three distinct groups of blocks. Primary Region A is the single largest group, encompassing much of the United States west of and including the Rocky Mountains. To the east, Primary Regions G and H comprise northern and southern sections of the eastern United States,

respectively. Primary Regions C, D, and F divide eastern and western groups of blocks in the vicinity of the Great Plains. The three remaining primary regions (B, E, and I) comprise small areas along the margin of the United States.

Figure 6 depicts the number of breeding species present in each of the 44 blocks. Passerine species richness is greatest in the southwestern and western United States and declines to the east towards the Great Plains. The eastern United States also supports a number of passerines, particularly the northeast, with diversity declining toward the south-southeast. Overall, the average passerine occupied 12.2 of the 42 blocks, while the nine primary regions averaged only 4.7 blocks. That is, while each primary region or group of regions was characterized by a unique set of species, most species ranged in individually distinctive ways beyond these regional boundaries.

Primary regions proved not to consist of homogeneous complements of passerines with affinities to one particular geographic region. For example, western blocks of Primary Region A were not entirely comprised of passerines with

Figure 6: Total number of breeding passerine species present in each of the 44 latitude-longitude blocks.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500
1000
Kilometers

western geographic affinities. Instead, species assemblages were geographically heterogeneous, composed of combinations of passerines with various geographic affinities. This can partly be attributed to the extensive or widespread breeding distributions of many passerines. These passerines typically had distributions centered elsewhere and often met north-south or east-west limits in primary regions other than those encompassed by the majority of their breeding distribution. Species with extensive breeding distributions include the Brown Thrasher (*Toxostoma rufum*), Red-eyed Vireo (*Vireo olivaceus*), American Redstart (*Setophaga ruticilla*), Eastern Meadowlark (*Sturnella magna*), Western Meadowlark (*Sturnella neglecta*), and Indigo Bunting (*Passerina cyanea*).

Fifty-two of the 256 species were endemic to one primary region, with two regions of the study area exhibiting much higher levels of endemism than the others. Across the United States, the southwest (Primary Region E) and northeast (Primary Region G) contained more locally distributed passerines than any other region of the country. The Great Plains primary regions were the only areas devoid of locally distributed passerines. For the purposes of this

investigation, species were considered "endemic" to a region if the limits of their breeding distribution were confined to one particular portion of the continental United States. However, on a broad scale many of these passerines could be considered as locally distributed as the breeding distributions of many extend outside the bounds of the continental United States into either Mexico or Canada. However, 17 passerines are truly unique to the United States, at least during the breeding season. These species are the Gray Flycatcher (*Empidonax wrightii*), Acadian Flycatcher (*Empidonax virescens*), Pinyon Jay (*Gymnorhinus cyanocephalus*), Yellow-billed Magpie (*Pica nuttalli*), Carolina Chickadee (*Parus carolinensis*), Brown-headed Nuthatch (*Sitta pusilla*), Blue-winged Warbler (*Vermivora pinus*), Hermit Warbler (*Dendroica occidentalis*), Golden-cheeked Warbler (*Dendroica chrysoparia*), Kirtland's Warbler (*Dendroica kirtlandi*), Kentucky Warbler (*Opornis formosus*), Hooded Warbler (*Wilsonia citrina*), Worm-eating Warbler (*Helmitheros vermivorus*), Swainson's Warbler (*Limnothlypis swainsonii*), Louisiana Waterthrush (*Seiurus motacilla*), Green-tailed Towhee (*Pipilo chlorurus*), and Tricolored Blackbird (*Agelaius tricolor*).

For the most part, the nine primary regions correspond with certain patterns of climate and vegetation as described by Varkat (1992), Barbour and Billings (1988), and Kuchler (1964). This would be expected as vegetative characteristics are an important factor in habitat selection by birds, especially during the breeding season (Cody, 1986). It follows then that avian distributional patterns are in some measure related to patterns of climate, terrain, and vegetation from local to continental levels (Wiens, 1992). Since vegetational formations are largely reflections of temperature, moisture, and geologic structure, they provide a basis from which to interpret patterns in species distributions (Hengeveld, 1992). In particular, they provide a basis for those species that are good indicators of phytogeographic boundaries, as birds appear to be.

Primary Region A corresponds to the mountain ranges and intermountain regions of the western United States. Kuchler (1964) described a number of vegetational formations characteristic of the west. On a broad scale, forest types largely consist of coniferous-dominated associations of

pinyon-juniper, pine-oak, fir-aspen, and spruce-fir. For example, coniferous forests of Douglas fir-quaking aspen and Englemann spruce-subalpine fir characterize higher elevations of the central and southern portions of the Rocky Mountains, as well as the Sierra Nevada, Cascade Range, Transverse Range, and scattered peaks of the intermountain region. At mid-elevations, stands of pinyon-juniper and ponderosa pine-Gambel oak dominate. Below these uplands, temperature and aridity increase with desert scrub, sagebrush steppe, and grassland characterizing the intermontane regions of the Great Basin, Columbia and Colorado Plateaus, and Wyoming Basin.

Areas with increased relief, such as the western United States, tend to be more complex and varied ecologically and support more species. Consequently, habitat diversity is correspondingly high and is reflected in the large number of passerines that nest here during the breeding season. Passerine diversity is highest at points along the southern Rocky Mountains in the vicinity of western Wyoming, west-central Colorado, and eastern Utah (Figure 6). Species diversity decreases in those parts of the west where

elevation declines and vegetational structure is reduced, as in the Great Basin region of Nevada and the Columbia Plateau of southwestern Idaho and eastern Oregon. Species with western (41.0%) affinities characterize a large portion of the avifauna of Primary Region A (Table 2). Of these western passerines, woodland species with affinities to open coniferous/deciduous forests comprise the majority, including the Dusky Flycatcher (*Empidonax oberholseri*), Western Flycatcher (*Empidonax difficilis*), Steller's Jay (*Cyanocitta stelleri*), Mountain Chickadee (*Parus gambeli*), and Townsend's Solitaire (*Myadeotes townsendi*). The remaining western passerines are birds of sagebrush, desert scrub, chaparral, or grassland such as the Rock Wren (*Salpintes obsoletus*), Black-tailed Gnatcatcher (*Polioptila melanura*), Sage Thrasher (*Oreoscoptes montanus*), and Bell's Vireo (*Vireo bellii*). Northern (18.7%) passerines also comprise a group mainly composed of woodland species. These northern species are more characteristic of montane coniferous forests of the Rockies and include several species whose distributions follow this forest type south from Canada along the Rockies; Olive-sided Flycatcher (*Contopus borealis*), Gray Jay (*Perispreus canadensis*),

TABLE 2
Breeding Passerines of Primary Region A Organized by Geographic Affinity

Pandemic	Western	Eastern	Northern	Southern	Central
Eastern Kingbird	Western Kingbird	Gray Catbird	Olive-sided Flycatcher	Curve-billed Thrasher	Chihuahuan Raven
Willow Flycatcher	Cassin's Kingbird	Red-eyed Vireo	Least Flycatcher	Crissal Thrasher	Baird's Sparrow
Horned Lark	Ash-throated Flycatcher	Ovenbird	Gray Jay	Phainopepla	Clay-colored Sparrow
Tree Swallow	Western Wood Pewee	American Redstart	Common Raven	Lucy's Warbler	
Purple Martin	Black Phoebe	Indigo Bunting	Boreal Chickadee	Grace's Warbler	
Bank Swallow	Say's Phoebe	Common Grackle	Brown Creeper	Black-chinned Sparrow	
Northern Rough-winged Swallow	Gray Flycatcher		Winter Wren	Bronzed Cowbird	
Cliff Swallow	Dusky Flycatcher		Golden-crowned Kinglet	Great-tailed Grackle	
Barn Swallow	Hammond's Flycatcher		Ruby-crowned Kinglet	Hooded Oriole	
American Crow	Western Flycatcher		Veery		
Black-capped Chickadee	Violet-green Swallow		Swainson's Thrush		
White-breasted Nuthatch	Scrub Jay		Varied Thrush		
House Wren	Pinyon Jay		Water Pipit		
Marsh Wren	Steller's Jay		Solitary Vireo		
Blue-gray Gnatcatcher	Clark's Nutcracker		Orange-crowned Warbler		
Hermit Thrush	Black-billed Magpie		Nashville Warbler		
American Robin	Plains Titmouse		Magnolia Warbler		
Loggerhead Shrike	Mountain Chickadee		Townsend's Warbler[a]		
Cedar Waxwing	Chestnut-backed Chickadee[a]		Wilson's Warbler		
Warbling Vireo	Bushtit		Northern Waterthrush		
Yellow-rumped Warbler	Red-breasted Nuthatch		Dark-eyed Junco		
Yellow Warbler	Pygmy Nuthatch		Fox Sparrow		
Common Yellowthroat	Canyon Wren		Red Crossbill		
Yellow-breasted Chat	Rock Wren		White-winged Crossbill		
Blue Grosbeak	Cactus Wren		Pine Grosbeak		
Rufous-sided Towhee	Black-tailed Gnatcatcher		Purple Finch		
Grasshopper Sparrow	Western Bluebird				
Vesper Sparrow	Mountain Bluebird				
Savannah Sparrow	Townsend's Solitaire				
Song Sparrow	Sage Thrasher				
Lark Sparrow	Bendire's Thrasher				
Chipping Sparrow	LeConte's Thrasher[a]				
Red-winged Blackbird	California Thrasher[a]				
Brown-headed Cowbird	American Dipper				
Northern Oriole					

TABLE 2 (continued)
Breeding Passerines of Primary Region A Organized by Geographic Affinity

Pandemic	Western	Eastern	Northern	Southern	Central
Pine Siskin	Bell's Vireo				
American Goldfinch	Hutton's Vireo				
	Gray Vireo				
House Finch	Virginia's Warbler				
Evening Grosbeak	Black-throated Gray Warbler				
	Hermit Warbler[a]				
	MacGillivray's Warbler				
	Black-headed Grosbeak				
	Lazuli Bunting				
	Green-tailed Towhee				
	Brown Towhee				
	Abert's Towhee				
	Black-throated Sparrow				
	Sage Sparrow				
	Brewer's Sparrow				
	White-crowned Sparrow				
	Western Meadowlark				
	Yellow-headed Blackbird				
	Brewer's Blackbird				
	Scott's Oriole				
	Western Tanager				
	Rosy Finch				
	Cassin's Finch				

[a] Passerines unique to Primary Region A

Winter Wren (*Troglodytes troglodytes*), Magnolia Warbler (*Dendroica magnolia*), and Red Crossbill (*Loxia curvirostra*), for example. The few southern and central passerines present are nesting species of open country, desert scrub, and semiarid woodland. Interestingly, central California (Primary Region B) cannot be readily clumped with the rest of the western United States as indicated by this distributional analysis. Delineation of this region as distinct is primarily due to the absence of species that breed throughout much of the western United States (Table 3). Paucity in nesting passerines is most likely a function of the low vegetational diversity of the Central Valley region of California, which is largely dominated by grassland and chaparral (Barbour, 1977).

Passerine diversity in the western United States can be considered reflective of the diversity in habitat types, but is also an artifact of historical events. During the Miocene and four successive glaciations of the Pleistocene, climatic regimes shifted and, in combination with the great relief of the west, resulted in geographical and ecological isolation of small populations, increasing the chance for

TABLE 3
Breeding Passerines of Primary Region B Organized by Geographic Affinity

Pandemic	Western	Eastern	Northern	Southern	Central
Horned Lark	Western Kingbird			Blue Grosbeak	
Tree Swallow	Ash-throated Flycatcher			Hooded Oriole	
Northern Rough-winged Swallow	Black Phoebe				
Cliff Swallow	Say's Phoebe				
Barn Swallow	Scrub Jay				
American Crow	Yellow-billed Magpie				
White-breasted Nuthatch	Plains Titmouse				
House Wren	Bushtit				
Marsh Wren	Western Bluebird				
American Robin	California Thrasher				
Loggerhead Shrike	Hutton's Vireo				
Warbling Vireo	Black-headed Grosbeak				
Yellow Warbler	Lazuli Bunting				
Common Yellowthroat	Brown Towhee				
Yellow-breasted Chat	Sage Sparrow				
Rufous-sided Towhee	Western Meadowlark				
Savannah Sparrow	Yellow-headed Blackbird				
Song Sparrow	Brewer's Blackbird				
Lark Sparrow	Lesser Goldfinch				
Chipping Sparrow					
Red-winged Blackbird					
Brown-headed Cowbird					
Northern Oriole					
American Goldfinch					

speciation. Increased species diversity is evident within certain families, particularly those comprised of nonmigratory, permanent residents. For example, Corvids and Mimids are more diverse in the western United States, and contain more representative species, than in any other region of the United States, or continent for that matter. For example, six species of thrasher occur in various portions of the west, as opposed to a single species in the eastern United States. Speciation of these thrasher species in the west occurred sometime during the Miocene as the climate began to deteriorate and western mountain systems rose, resulting in climatic zones and their biota being pushed southward. As these zones were forced south, Madro-Tertiary flora, composed of various vegetation types such as chaparral, arid woodland, and desert scrub, spread throughout much of the west. Subsequently, the geographic isolation of local thrasher populations resulted in the formation of species adapted to these arid vegetational formations. For example, the Sage Thrasher, as its name implies, is associated with sagebrush communities, Bendire's Thrasher (*Toxostoma bendirei*) has associations to creosote bush scrub, and Le Conte's Thrasher (*Toxostoma lecontei*) to

desert scrub. A similar instance of geographic isolation and adaptation to different environmental and habitat conditions occurred in the Pleistocene, most notably among wood warblers of the *Dendroica* complex.

Primary Region E includes the aridlands of the American southwest, specifically the creosote bush-desert scrub of the Chihuahuan and Sonoran deserts, southern elements of pinyon-juniper woodland, along with montane coniferous forest at higher elevations. In addition, oak-pine woodlands, typical of the Mexican Plateau, reach northern distributional limits in southern Arizona and New Mexico. This southwestern region is characterized by some common, pandemic species (25.4%) but by a larger number of western (36.5%) and southern (26.4%) species (Table 4). The western complement of passerines includes a number of species adapted to the semiarid brushlands of the southwest; Curve-billed Thrasher (*Toxostoma curvirostre*), Crissal Thrasher (*Toxostoma crissale*), Phainopepla (*Phainopepla nitens*), and Brown Towhee (*Pipilo chlorurus*), for example. Many of the passerines with southern affinities are subtropical species that reach the northern limits of their

TABLE 4
Breeding Passerines of Primary Region E Organized by Geographic Affinity

Pandemic	Western	Eastern	Northern	Southern	Central
Willow Flycatcher	Western Kingbird	Bewick's Wren	Olive-sided Flycatcher	Tropical Kingbird[a]	Chihuahuan Raven
Horned Lark	Cassin's Kingbird	Northern Cardinal	Common Raven	Sulphur-bellied Flycatcher[a]	Cassin's Sparrow
Tree Swallow	Ash-throated Flycatcher	Indigo Bunting	Brown Creeper	Brown-crested Flycatcher	Lark Bunting
Purple Martin	Western Wood Pewee	Eastern Meadowlark	Golden-crowned Kinglet	Dusky-capped Flycatcher[a]	
Bank Swallow	Black Pewee	Summer Tanager	Ruby-crowned Kinglet	Greater Pewee[a]	
Northern Rough-winged Swallow	Say's Phoebe		Solitary Vireo	Vermillion Flycatcher	
Cliff Swallow	Gray Flycatcher		Orange-crowned Warbler	Northern Beardless Tyrannulet	
Barn Swallow	Dusky Flycatcher		Dark-eyed Junco	Rose-throated Becard	
American Crow	Western Flycatcher		Red Crossbill	Cave Swallow[a]	
White-breasted Nuthatch	Violet-green Swallow			Gray-breasted Jay[a]	
House Wren	Scrub Jay			Bridled Titmouse[a]	
Blue-gray Gnatcatcher	Pinyon Jay			Mexican Chickadee[a]	
Hermit Thrush	Steller's jay			Verdin	
American Robin	Clark's Nutcracker			Curve-billed Thrasher	
Loggerhead Shrike	Plains Titmouse			Crissal Thrasher	
Northern Mockingbird	Mountain Chickadee			Phainopepla	
Warbling Vireo	Bushtit			Lucy's Warbler	
Yellow-rumped Warbler	Red-breasted Nuthatch			Grace's Warbler	
Yellow Warbler	Pygmy Nuthatch			Painted Redstart[a]	
Common Yellowthroat	Canyon Wren			Red-faced Warbler[a]	
Yellow-breasted Chat	Rock Wren			Olive Warbler[a]	
Blue Grosbeak	Cactus Wren			Pyrrhuloxia	
Rufous-sided Towhee	Black-tailed Gnatcatcher			Varied Bunting	
Song Sparrow	Western Bluebird			Botteri's Sparrow[a]	
Lark Sparrow	Mountain Bluebird			Rufous-winged Sparrow[a]	
Chipping Sparrow	Townsend's Solitaire			Black-chinned Sparrow	
Red-winged Blackbird	Bendire's Thrasher			Yellow-eyed Junco[a]	
Brown-headed Cowbird	American Dipper			Bronzed Cowbird	
Northern Oriole	Bell's Vireo			Great-tailed Grackle	
Pine Siskin	Hutton's Vireo			Hooded Oriole	
House Finch	Gray Vireo			Hepatic Tanager[a]	
Evening Grosbeak	Virginia's Warbler				
	Black-throated Gray Warbler				
	MacGillivray's Warbler				
	Black-headed Grosbeak				

TABLE 4 (continued)
Breeding Passerines of Primary Region E Organized by Geographic Affinity

Pandemic	Western	Eastern	Northern	Southern	Central
	Lazuli Bunting				
	Green-tailed Towhee				
	Brown Towhee				
	Abert's Towhee				
	Black-throated Sparrow				
	Rufous-crowned Sparrow				
	Western Meadowlark				
	Brewer's Blackbird				
	Scott's Oriole				
	Western Tanager				
	Lesser Goldfinch				

[a] Passerines unique to Primary Region C; the majority of passerines are Mexican species at the northern limits of their breeding distribution

breeding distributions in Arizona, New Mexico, and portions of southwest Texas. For the most part, these are Mexican species such as the Tropical Flycatcher (*Tyrannus melancholicus*), Brown-crested Flycatcher (*Myiarchus tyannulus*), Rose-throated Becard (*Pachyramphus aglaiae*), Bridled Titmouse (*Parus wollweberi*), Red-faced Warbler (*Cardellira rubrifrons*), and Pyrrhuloxia (*Cardinalis sinuatus*) that nest in appropriate habitat in southern Arizona and New Mexico. Although the species assemblage of Primary Region E contains many of the same passerines found throughout the western United States, the distinctiveness of this region is largely predicated upon the presence of species with southern (Mexican) affinities. A few passerines with northern affinities (7.1%) reached the southern limits of their breeding distributions in Primary Region E and were mostly species that occurred in the coniferous forests and mixed woodlands typical of higher elevations, such as the Ruby-crowned Kinglet (*Regulus calendula*), Solitary Vireo (*Vireo solitarius*), and Orange-crowned Warbler (*Vermivora celata*).

Flycatchers (Tyrannidae) reach their greatest diversity in Primary Region E with 19 of the 33 species that breed in the continental United States occurring in this region. This high diversity is reflective of the warm, arid conditions of the American southwest and its subsequent effect on food availability. Tyrannids are almost completely insectivorous, and as such are highly dependent upon areas with reliable food resources (Bent, 1989). In the southwest, as a result of climatic conditions, summers are long and offer longer and less fluctuating periods of insect abundance. Consequently, most tyrannids remain closely associated with arid to subtropical areas that can support stable sources of insect prey. This tie would be expected as this group had its origins in South America and subsequently underwent a secondary radiation in Central America. According to Mengel (1964), it has been only within the recent past that tyrannids are thought to have moved north into more temperate areas, and as of yet only a small number of species have done so.

Three distinct primary regions divide the aforementioned western and southwestern regions from those to the east.

Primary Regions C, D, and F correspond to the Great Plains physiographic province in the interior of the United States. This is one of the more physically uniform regions of the continent, being east of the Rocky Mountains yet west of the mixed deciduous forests of the eastern United States. Although largely corresponding to the shortgrass prairie and western margins of the transitional mixed-grass prairie, these primary regions contain elements of vegetational formations characteristic of other regions of the United States. To the north, ponderosa pine woodlands, typical of the Rocky Mountains, occur in the Black Hills of western South Dakota, southwestern North Dakota, south-central Montana, and parts of western Nebraska. In addition, other elements of western vegetation, such as chaparral and pinyon-juniper woodland intergrade with grassland vegetation across the plains. Vegetation typical of eastern deciduous forests also invades the plains along river valleys and floodplains. In addition, in the warmer, more xeric portions of the plains, mesquite, creosote bush and other elements of desert scrub extend throughout eastern New Mexico and west-central Texas.

The blocks that compose these plains primary regions did not group closely with any other block or set of blocks, an indication that these primary regions contain unique assemblages of passerines. Although delineated as unique, the passerine faunas of the central primary regions actually contain few species that can be considered unique to the plains. According to Johnsgarrd (1979), only five percent of the bird species occurring on the Great Plains are restricted to them. Concomitantly, the results of this study indicate that Primary Regions C, D, and F are not distinct due to the presence of locally endemic or geographically confined passerines. Instead, passerines that breed throughout Primary Regions C, D, and F are species generally distributed beyond this part of the continent and are not typical of it.

The Great Plains represents a relatively young ecosystem and, as a consequence, contains few unique passerine species. Lack of avian endemism can most likely be considered a reflection of the corresponding absence of endemism in the flora of the Great Plains. Nearly all the plant species that occur on the plains have extensive ranges

and appear to have colonized from elsewhere, particularly the southeast and southwest (Dort and Jones, 1970). As mentioned earlier, many western plant species extend east onto the plains, as do many eastern species westward. According to Axelrod (1985), the flora of the Great Plains is a combination of elements in the early stages of differentiation into a distinctive flora. In terms of avian distributional patterns, the Great Plains represent an area in which the avifaunas of the boreal forests, deciduous forests of the eastern and southeastern United States, Rocky Mountain coniferous forests, and aridlands of the southwest come into contact. For example, eastern and western passerines meet along strands of riparian vegetation within the floodplains of the Missouri, Platte, Arkansas, Canadian, and Red River systems. Similarly, passerines with southern affinities nest in the warmer, xeric mesquite-scrub and semideserts of eastern New Mexico and western Texas. On the whole, these other vegetational formations support more diverse species assemblages than the surrounding grassland and are partly responsible for defining each of the three plains regions. The Great Plains passerine fauna can,

therefore, be viewed as a heterogeneous assortment of species characteristic of several regional avifauna.

The passerine assemblages of Primary Regions C, D, and F share a number of species in common, the largest portion of which are pandemic (48.6%) species (Table 5). Western (25.7%) and eastern (20%) passerines comprise the next largest components. Only two of the shared passerines, the Dickcissel (*Spiza americana*) and Lark Bunting (*Calamospiza melanocorys*), have breeding distributions centered primarily within the plains, a testament to these regions low avian endemism. Table 6 lists the habitat affinities of those passerines present in all three plains primary regions. Over half of these species (57%) have habitat affinities to forest edge, open woodlands, or riparian vegetation. The remainder (43%) comprise species typical of open grassland, shrubland, or desert scrub. No eastern representatives are present in this latter group and would suggest that the xeric, open habitats of the Great Plains are a more effective boundary to the distribution of eastern as opposed to western passerines.

TABLE 5

Breeding Passerines Shared by Primary Regions C, D, and F (Great Plains) Organized by Geographic Affinity

Pandemic	Western	Eastern	Northern	Southern	Central
Eastern Kingbird	Western Kingbird	Great Crested Flycatcher			Dickcissel
Horned Lark	Western Wood Pewee	Eastern Phoebe			Lark Bunting
Northern Rough-winged Swallow	Say's Phoebe	Blue Jay			
Cliff Swallow	Canyon Wren	Eastern Bluebird			
Barn Swallow	Rock Wren	Indigo Bunting			
American Crow	Bell's Vireo	Common Grackle			
House Wren	Black-headed Grosbeak	Orchard Oriole			
American Robin	Green-tailed Towhee				
Loggerhead Shrike	Western Meadowlark				
Warbling Vireo					
Yellow Warbler					
Common Yellowthroat					
Yellow-breasted Chat					
Rufous-sided Towhee					
Chipping Sparrow					
Song Sparrow					
Grasshopper Sparrow					
Vesper Sparrow					
Red-winged Blackbird					
Brown-headed Cowbird					
House Finch					

TABLE 6
Habitat affinities of those passerines shared by Primary Regions C, D, and F (Great Plains)

Woodland: Riparian Vegetation, Deciduous Forest Edge, and Open Woodland[a]

Pandemic	Western	Eastern	Central
House Wren	Western Wood Pewee	Great Crested Flycatcher	
Warbling Vireo	Say's Phoebe	Eastern Phoebe	
Yellow Warbler	Bell's Vireo	Blue jay	
Common Yellowthroat	Black-headed Grosbeak	Eastern Bluebird	
Yellow-breasted Chat		Indigo Bunting	
Rufous-sided Towhee		Common Grackle	
Chipping Sparrow		Orchard Oriole	
Northern Oriole			
House Finch			

[a] The American Crow, American Robin, and Brown-headed Cowbird are not included as they have broad habitat affinities. The Red-winged Blackbird is also not included as it is a marsh-nesting species.

Open Country: Scattered Trees, Grassland, Shrubland, and Scrub[a]

Pandemic	Western	Eastern	Centralp450X
	Western Kingbird		Dickcissel Eastern Kingbi
Horned Lark	Canyon Wren		Lark Bunting
Northern Rough-winged Swallow	Rock Wren		
Cliff Swallow	Green-tailed Towhee		
Barn Swallow	Western Meadowlark		
Loggerhead Shrike			
Grasshopper Sparrow			
Vesper Sparrow			

[a] The American Crow, American Robin, and Brown-headed Cowbird are not included as they have broad habitat affinities. The Red-winged Blackbird is also not included as it is a marsh-nesting species.

The loss of eastern passerines westward is most likely the result of a reduction in habitat diversity. Two environmental gradients characterize the plains, one of increasing temperatures from north to south, the other of increasing precipitation from west to east (Baldwin, 1973). Vegetatively, this moisture gradient is reflected in the tallgrass prairie, and its intergradation with oak-hickory forest to the east, to shortgrass prairie in the west. As deciduous forest becomes less extensive along this gradient, reduced structural complexity of the forest, in particular the loss of understory vegetation, is probably critical to many eastern passerines including the Northern Cardinal (*Cardinalis cardinalis*), Wood Thrush (*Hylocichla mustelina*), Kentucky Warbler, American Redstart, and Rufous-sided Towhee (*Pipilo erythrophthalmus*). In contrast, the western United States is characterized by several arid vegetational formations. Consequently, the boundary between the west and the Great Plains is vague and not as sharp as that between the plains and the more mesic communities of the eastern United States. Xeric-adapted western passerines, such as the Canyon Wren (*Catherpes mexicanus*), Green-tailed Towhee, and Western Meadowlark might, therefore, face fewer

ecological constraints than their more mesic-adapted eastern counterparts.

Although possessing species in common, the delineation of the passerine assemblages of Primary Regions C, D, and F as distinct from one another is primarily due to the passerines unique to each. These differences, largely, reflect the changing regimes in temperature and moisture that occur across the plains. These changes are most demonstrable in the various vegetational formations that encroach along the margins of, as well as intergrading with, the grassland itself. The inclusion of these aforementioned vegetational types serve to increase habitat diversity across the Great Plains. A direct result of which is an accompanying increase in avian diversity and the formation of more complex regional avifaunas.

Of the passerines unique to Primary Region F, the largest components are species with pandemic (34.0%) and western (29.2%) geographic affinities (Table 7). Most of these passerines are woodland species typical of open coniferous forests and, to a lesser extent, deciduous or mixed

TABLE 7
Breeding Passerines of Primary Region F Organized by Geographic Affinity

Pandemic	Western	Eastern	Northern	Southern	Central
Eastern Kingbird	Western Kingbird	Great Crested Flycatcher	Least Flycatcher[a]		Sprague's Pipit
Willow Flycatcher[a]	Cassin's Kingbird	Eastern Wood Pewee	Gray Jay[a]		Baird's Sparrow
Horned Lark	Western Wood Pewee	Eastern Phoebe	Brown Creeper[a]		LeConte's Sparrow[a]
Tree Swallow[a]	Say's Phoebe	Blue Jay	Golden-crowned Kinglet[a]		Clay-colored Sparrow[a]
Purple Martin	Dusky Flycatcher[a]	Sedge Wren	Ruby-crowned Kinglet[a]		Chestnut-collared Longspur[a]
Bank Swallow	Violet-green Swallow	Eastern Bluebird	Veery[a]		McCown's Longspur[a]
Northern Rough-winged Swallow	Pinyon Jay	Wood Thrush[a]	Swainson's Thrush[a]		Dickcissel
Cliff Swallow	Steller's Jay	Gray Catbird	Solitary Vireo		Lark Bunting
Barn Swallow	Clark's Nutcracker[a]	Brown Thrasher	Wilson's Warbler[a]		
American Crow	Black-billed Magpie	Yellow-throated Vireo	Sharp-tailed Sparrow[a]		
Black-capped Chickadee	Red-breasted Nuthatch[a]	Red-eyed Vireo	Dark-eyed Junco[a]		
White-breasted Nuthatch[a]	Pygmy Nuthatch	Black and White Warbler	Red Crossbill[a]		
House Wren	Canyon Wren	Ovenbird[a]			
Marsh Wren	Rock Wren	American Redstart[a]			
Hermit Thrush[a]	Western Bluebird[a]	Indigo Bunting			
American Robin	Mountain Bluebird[a]	Field Sparrow			
Loggerhead Shrike	Townsend's Solitaire	Eastern Meadowlark			
Cedar Waxwing[a]	Sage Thrasher[a]	Common Grackle			
Yellow-rumped Warbler[a]	American Dipper[a]	Orchard Oriole			
Yellow Warbler	Bell's Vireo				
Common Yellowthroat	MacGillivray's Warbler[a]				
Yellow-breasted Chat	Black-headed Grosbeak				
Blue Grosbeak	Lazuli Bunting				
Rufous-sided Towhee	Green-tailed Towhee				
Grasshopper Sparrow	Brewer's Sparrow				
Vesper Sparrow	White-crowned Sparrow[a]				
Savannah Sparrow	Western Meadowlark				
Song Sparrow	Yellow-headed Blackbird				
Lark Sparrow	Brewer's Blackbird[a]				
Chipping Sparrow	Western Tanager				
Red-winged Blackbird	Cassin's Finch[a]				
Brown-headed Cowbird					
Northern Oriole					
Pine Siskin[a]					
American Goldfinch					
House Finch					

[a] Passerines that occur in adjacent regions but unique to this section of the Great Plains

coniferous/deciduous forests. The western species provide the most typical Rocky Mountain avifauna to be found in this region and are primarily restricted to the Black Hills of South Dakota and surrounding "islands" of coniferous forest. Passerines generally associated with the avifauna of the central Rocky Mountains include the Dusky Flycatcher, Western Flycatcher, Red-breasted Nuthatch (*Sitta canadensis*), Pygmy Nuthatch (*Sitta pygmae*), American Dipper (*Cinclus mexicanus*), Townsend's Solitaire, and MacGillivray's Warbler (*Opornis tolmiei*). Similarly, many northern passerines (11.3%) have affinities to these same coniferous woodlands, including the Least Flycatcher (*Empidonax minimus*), Gray Jay, Brown Creeper (*Certhia americana*), Golden-crowned Kinglet (*Regulus satropa*) and Ruby-crowned Kinglet. Only a small number of central passerines (7.5%) can be considered endemic to this region of the Great Plains. For the most part, these are sparrow or sparrow-like species adapted to the short-grass of the northern Great Plains, including Sprague's Pipit (*Anthus spragueii*), Baird's Sparrow (*Ammodramus bairdii*), Chestnut-collared Longspur (*Calcarius ornatus*)and McCown's Longspur (*Calcarius mccownii*). The presence of coniferous forest,

and to a lesser extent, deciduous forest plays an important role in augmenting the passerine diversity of this region. Woodland passerines comprise a large portion of the species assemblage, yet the habitat types in which they nest represents a small fraction of the area encompassed by Primary Region F. Although the coniferous forests of the Black Hills and surrounding areas do comprise a small proportion of the habitats of the northern plains, these woodlands provide important breeding habitat for a number of passerines. Specifically, these woodlands provide nesting habitat for an assemblage of passerines more typical of the montane forests of the western United States and Canada than of the plains themselves.

The delineation of the block that comprises Primary Region C as distinct from the rest of the Great Plains, as well as surrounding regions, is primarily due to the absence of species that breed in adjacent regions. This central region of the plains is devoid of endemic or locally distributed species, and instead derives its distinctiveness from the absence of species that breed in adjacent regions. This plains region represents the center of the

shortgrass/mixed-grass prairie in the continental United States and lacks the vegetational diversity that characterizes much of the northern and southern extent of the Great Plains. Subsequently, habitat diversity here is correspondingly low and is reflected in the assemblage of breeding passerines (Table 8). For the most part, those species that do occur here are also found in the passerine assemblages of one or both of the other plains primary regions.

Primary Region D represents the southern extent of the Great Plains and includes the Staked and Rolling Plains physiographic regions of west-central Texas. In as much as Primary Region D represents the semiarid to subtropical extent of the Great Plains, many passerines that are adapted to and typical of the semiarid habitats of the western and southwestern United States breed in this region. This group includes western passerines (37.8%) not found in any other plains primary region, such as the Scrub Jay (*Aphelocoma coerulescens*), Black-tailed Gnatcatcher, Black-throated Sparrow (*Amphispiza bilineata*), and Lesser Goldfinch (*Carduelis psaltria*) (Table 9). In addition, other aridland

TABLE 8
Breeding Passerines of Primary Region C Organized by Geographic Affinity

Pandemic	Western	Eastern	Northern	Southern	Central
Eastern Kingbird	Western Kingbird	Great Crested Flycatcher		Scissor-tailed Flycatcher	Chihuahuan Raven
Horned Lark	Cassin's Kingbird	Eastern Phoebe		Curve-billed Thrasher	Cassin's Sparrow
Bank Swallow	Ash-throated Flycatcher	Blue Jay		Great-tailed Grackle	Dickcissel
Northern Rough-winged Swallow	Western Wood Pewee	Bewick's Wren			Lark Bunting
Cliff Swallow	Say's Phoebe	Eastern Bluebird			
Barn Swallow	Pinyon Jay	Gray Catbird			
American Crow	Black-billed Magpie	Brown Thrasher			
Black-capped Chickadee	Plains Titmouse	Red-eyed Vireo			
House Wren	Bushtit	Northern Cardinal			
Blue-gray Gnatcatcher	Canyon Wren	Indigo Bunting			
American Robin	Rock Wren	Common Grackle			
Loggerhead Shrike	Bell's Vireo	Orchard Oriole			
Northern Mockingbird	Black-headed Grosbeak				
Warbling Vireo	Lazuli Bunting				
Yellow Warbler	Green-tailed Towhee				
Common Yellowthroat	Rufous-crowned Sparrow				
Yellow-breasted Chat	Brewer's Sparrow				
Blue Grosbeak	Western Meadowlark				
Rufous-sided Towhee	Yellow-headed Blackbird				
Grasshopper Sparrow					
Vesper Sparrow					
Savannah Sparrow					
Song Sparrow					
Lark Sparrow					
Chipping Sparrow					
Red-winged Blackbird					
Brown-headed Cowbird					
Northern Oriole					
American Goldfinch					
House Finch					

TABLE 9
Breeding Passerines of Primary Region D Organized by Geographic Affinity

Pandemic	Western	Eastern	Northern	Southern	Central
Horned Lark	Western Kingbird	Eastern Wood Pewee	Olive-sided Flycatcher	Scissor-tailed Flycatcher	Chihuahuan Raven
Northern Rough-winged Swallow	Cassin's Kingbird	Eastern Phoebe		Black Phoebe[a]	Cassin's Sparrow
Cliff Swallow	Ash-throated Flycatcher	Blue Jay		Vermillion Flycatcher	Dickcissel
Barn Swallow	Western Wood Pewee	Tufted Titmouse		Verdin	Lark Bunting
House Wren	Say's Phoebe	Carolina Wren[a]		Black-tailed Gnatcatcher[a]	
Blue-gray Gnatcatcher	Scrub Jay[a]	Bewick's Wren		Curve-billed Thrasher	
American Robin	Steller's Jay	White-eyed Vireo		Crissal Thrasher	
Loggerhead Shrike	Bushtit[a]	Northern Cardinal		Phainopepla[a]	
Northern Mockingbird	Canyon Wren	Indigo Bunting		Black-capped Vireo	
Warbling Vireo	Rock Wren	Eastern Meadowlark		Pyrrhuloxia	
Yellow Warbler	Cactus Wren	Orchard Oriole		Painted Bunting	
Common Yellowthroat	Bell's Vireo	Summer Tanager		Varied Bunting[a]	
Yellow-breasted Chat	Hutton's Vireo			Bronzed Cowbird[a]	
Blue Grosbeak	Gray Vireo			Great-tailed Grackle	
Grasshopper Sparrow	Black-throated Gray Warbler				
Lark Sparrow	Brown Towhee[a]				
Chipping Sparrow	Black-throated Sparrow[a]				
Red-winged Blackbird	Rufous-crowned Sparrow[a]				
Brown-headed Cowbird	Western Meadowlark				
Northern Oriole	Western Tanager				
House Finch	Lesser Goldfinch				

[a] Passerines unique to Primary Region D

passerines typical of the southwestern United States and northern Mexico also breed here. Many of these southern passerines (17.7%) meet northern limits of their breeding distributions in Primary Region D, including the Crissal Thrasher, Phainopepla, Pyrrhuloxia, Varied Bunting (*Passerina versicolor*), and Bronzed Cowbird (*Molothrus aeneus*). Many eastern passerines (15.2%) occur in Primary Region D to the exclusion of the other plains regions. These eastern passerines are species more typical of the subhumid, southeastern United States, such as the Carolina Chickadee, Carolina Wren (*Thryothorus ludovicianus*), and White-eyed Vireo (*Vireo griseus*), whose distributions follow riparian vegetation and oak-juniper scrub westward onto the Great Plains.

A number of authors have commented upon the role of the Great Plains as an isolating agent or biogeographic barrier, (Bock et al., 1977; Rising, 1983), specifically that region of the plains in the vicinity of the 100th meridian. Rising (1983), in particular, noted that climate might directly affect distributional patterns and/or gene flow in bird populations across the Great Plains. In numerical

analyses, Bock et al. (1977; 1978) observed that changes occurred in both avian distribution and abundance as one moved from the 95th to the 105th meridians across the Great Plains. Bock et al. (1977) postulated that these distributional changes occurred as a result of the indirect influence of changing moisture regimes upon vegetational formations across the plains. Climatic maps indicate a marked gradient of decreasing annual precipitation, decreasing relative humidity, and increased frequency of prolonged droughts from east to west across the plains, (Baldwin, 1973), with the 100th meridian representing approximately where western semiarid and eastern subhumid climates replace one another. The 100th meridian is also approximately where mixed grass prairie gives way to the short grass of the high plains. For birds, some species appear to respond to the changing nature of the grassland itself, while others, such as western species, become less common to the east as a result of a decrease in grassland past the 100th meridian. In contrast, eastern species become scarce to the west due to a corresponding loss in vegetational complexity west of the 100th meridian. The patterns depicted by my analysis support the contention that

the Great Plains is an area of significant biogeographic change, at least for birds. For passerine species, many of whom are neotropical migrants, the influence of shifting moisture gradients would, understandably, be most noticeable during the summer when reliance upon vegetation for nesting and feeding would be the strongest.

South of the plains, Primary Region I comprises the Gulf prairies and marshes along the Texas coast, oak-pine flatwoods inland, and the shrub-grassland of south Texas. In this corner of Texas, as eastern woodlands give way to grassland and semiarid scrub to the west, passerines of the eastern and southwestern United States meet and are separated from one another as a result of decreasing moisture from east to west. The largest component of this region's avifauna are eastern passerines (35.1%), many meeting westward limits of their breeding distributions (Table 10). This group includes widespread eastern species such as the Acadian Flycatcher, Blue Jay (*Cyanocitta cristata*), Carolina Chickadee, Wood Thrush, and Brown Thrasher. Southern passerines (29.7%) comprise the next largest component and include many subtropical species that

TABLE 10
Breeding Passerines of Primary Region I Organized by Geographic Affinity

Pandemic	Western	Eastern	Northern	Southern	Central
Horned Lark	Ash-throated Flycatcher	Great-crested Flycatcher		Couch's Kingbird[a]	Chihuahuan Raven
Purple Martin	Cactus Wren	Eastern Phoebe		Scissor-tailed Flycatcher	Cassin's Sparrow
Bank Swallow	Rufous-crowned Sparrow	Acadian Flycatcher		Great Kiskadee[a]	Dickcissel
Northern Rough-winged Swallow		Blue Jay		Brown-crested Flycatcher	
Cliff Swallow		Tufted Titmouse		Northern Beardless Tyrannulet	
Barn Swallow		Carolina Chickadee		Rose-throated Becard	
American Crow		Carolina Wren		Green Jay[a]	
Marsh Wren		Bewick's Wren		Verdin	
Blue-gray Gnatcatcher		Eastern Bluebird		Long-billed Thrasher	
Loggerhead Shrike		Wood Thrush		Curve-billed Thrasher[a]	
Northern Mockingbird		White-eyed Vireo		Tropical Parula[a]	
Common Yellowthroat		Yellow-throated Vireo		Golden-cheeked Warbler	
Yellow-breasted Chat		Red-eyed Vireo		Pyrrhuloxia	
Blue Grosbeak		Prothonotary Warbler		Blue Bunting[a]	
Grasshopper Sparrow		Northern Parula		Painted Bunting	
Lark Sparrow		Black and White Warbler		Varied Bunting	
Chipping Sparrow		Kentucky Warbler		Olive Sparrow[a]	
Red-winged Blackbird		Hooded Warbler		Botteri's Sparrow	
Brown-headed Cowbird		Northern Cardinal		Bronzed Cowbird	
House Finch		Indigo Bunting		Great-tailed Grackle	
		Seaside Sparrow		Hooded Oriole	
		Eastern Meadowlark		Altamira Oriole[a]	
		Common Grackle			
		Boat-tailed Grackle			
		Orchard Oriole			
		Summer Tanager			

[a] Passerines unique to Primary Region I

meet northern limits of their breeding distribution in the mesquite-acacia shrubland of south Texas. In particular, such Mexican species as Couch's Kingbird (*Tyrannus couchi*), Great Kiskadee (*Pitangus sulphuratus*), Green Jay (*Cyanocorax yncas*), Long-billed Thrasher (*Toxostoma longirostre*), and Tropical Parula (*Parula pitiayumi*) are unique to Primary Region I.

The eastern half of the United States represents the remaining primary regions which, collectively, correspond to the temperate forest formations of eastern North America along with tallgrass prairie and its intergradation with eastern deciduous forests. The forests of the eastern United States are widespread and include several regional types (Varkat, 1992). Primary Region G comprises northern hardwood forest associations and the ecotone with boreal coniferous forest in the northeast. Typical associations include aspen-birch, maple-beech-birch, and spruce-fir. Spruce-alder swamps, cedar-tamarack bogs, wet meadows, and grassland also occur sporadically throughout the area encompassed by this region. Primary Region H represents mixed deciduous forest types, such as oak-hickory and

oak-hickory-pine, as well as southeastern evergreen associations of loblolly-shortleaf and longleaf-slash pine along the Gulf Coastal Plain. Also in Region H, forest types reminiscent of the northeastern United States, most notably spruce-fir, reach their southernmost extension at higher elevations in the Blue Ridge, Great Smoky, and Allegheny mountain ranges.

Though much of the Great Plains physiographic region proved to represent a distinct area of avian biogeographic change in my analysis, its eastern margin, the tallgrass prairie, exhibited no such distinctiveness. On a broad-scale, the tallgrass prairie does not differ significantly in composition of breeding passerines from the rest of the eastern United States. This lack of distinctiveness is largely attributable to the fact that most of the species that breed on the tallgrass prairie are also present in several communities further east; Horned Lark (*Eremophila alpestris*), Grasshopper Sparrow (*Ammodramus savannarum*), Vesper Sparrow (*Pooecetes gramineus*), Dickcissel, and Eastern Meadowlark, for example. These results show the strong affinities of this section of the plains to the

passerine avifaunas of the east. Therefore, in terms of the passerine distributional patterns revealed by my analysis, the eastern margins of the Great Plains as well as the prairie peninsula of Illinois and Indiana can more appropriately be considered as parts of eastern woodlands.

The passerine avifaunas of both Primary Region G and H are largely characterized by forest/forest-edge species, and to a lesser extent open country, grassland, and marsh species. Primary Regions G and H share a number of species in common, a few of which are endemic to the eastern United States during the breeding season, including the Blue-winged Warbler, Cerulean Warbler (*Dendroica cerulea*), Prairie Warbler (*Dendroica discolor*), Louisiana Waterthrush, Henslow's Sparrow (*Ammodramus henslowii*), and Scarlet Tanager (*Piranga olivacea*). Several passerines occur throughout the eastern forests, giving it considerable uniformity. Species not necessarily restricted to the eastern United States, but common to both regions include a number of passerines typical of deciduous, mixed deciduous/coniferous forests, and forest edge habitat types. By and large, these are species with either pandemic or

eastern geographic affinities such as the Acadian Flycatcher, Wood Thrush, Tufted Titmouse (*Parus bicolor*), Yellow-throated Vireo (*Vireo flavifrons*), Hooded Warbler, and Summer Tanager (*Piranga rubra*). These species are strongly representative of the deciduous forests biome of the eastern United States and serve to define this region of the country from the more semiarid regions of the western United States and Great Plains.

Although similar in many respects, Primary Region G and H comprise distinct northern and southern passerine communities that occur in the eastern United States. This division of passerine avifaunas is most likely a reflection of latitudinal changes in climate and vegetation that occur across the eastern United States on a gradient from north to south. On a broad scale, boreal to cool temperate conditions characterize much of Primary Region G. As one moves south, these cooler climates are replaced by warm temperate and ultimately subtropical conditions in the vicinity of Primary Region H. The vegetational formations of these regions, in turn, reflect these climatic shifts. As a result, each region contains locally distributed

passerines, unique to each, which have habitat associations to one or more regionally characteristic vegetational formation.

Primary Region G is the most species-rich of the two eastern regions with 135 breeding species. Passerines with northern (31.8%) geographic affinities represent the single most distinctive group in this region species assemblage (Table 11). Pandemic (31.1%) and eastern (29.6%) passerines comprise large portions of the species assemblage yet, for the most part, are species that also breed throughout Primary Region H. Most of the northern passerines have habitat associations to the coniferous, mixed coniferous/deciduous forests of Canada and northeastern United States. Species typical of northern, boreal avifaunas include the Yellow-bellied Flycatcher (*Empidonax flaviventris*), Boreal Chickadee (*Parus hudsonicus*), Gray-cheeked Thrush (*Catharus minimus*), Tennessee Warbler (*Vermvora peregrina*), and White-throated Sparrow (*Zonotrichia albicollis*). A second group of northern passerines are species whose breeding distributions also extend to montane areas of the western United States.

TABLE 11
Breeding Passerines of Primary Region G Organized by Geographic Affinity

Pandemic	Western	Eastern	Northern	Southern	Central
Eastern Kingbird	Western Kingbird	Great-crested Flycatcher	Olive-sided Flycatcher		Sprague's Pipit
Willow Flycatcher	Red-breasted Nuthatch	Eastern Wood Pewee	Least Flycatcher		Baird's Sparrow
Horned Lark	Bell's Vireo	Eastern Phoebe	Alder Flycatcher[a]		Le Conte's Sparrow
Tree Swallow	Western Meadowlark	Acadian Flycatcher	Yellow-bellied Flycatcher[a]		Clay-colored Sparrow
Purple Martin	Yellow-headed Blackbird	Blue Jay	Gray Jay		Chestnut-collared Longspur
Bank Swallow	Brewer's Blackbird	Fish Crow	Common Raven		Dickcissel
Northern Rough-winged Swallow		Tufted Titmouse	Boreal Chickadee		Lark Bunting
Cliff Swallow		Carolina Wren	Brown Creeper		
Barn Swallow		Sedge Wren	Winter Wren		
American Crow		Eastern Bluebird	Golden-crowned Kinglet		
Black-capped Chickadee		Wood Thrush	Ruby-crowned Kinglet		
White-breasted Nuthatch		Gray Catbird	Veery		
House Wren		Brown Thrasher	Swainson's Thrush		
Marsh Wren		White-eyed Vireo	Gray-cheeked Thrush[a]		
Blue-gray Gnatcatcher		Yellow-throated Vireo	Solitary Vireo		
Hermit Thrush		Red-eyed Vireo	Philadelphia Vireo		
American Robin		Prothonotary Warbler	Golden-winged Warbler		
Loggerhead Shrike		Blue-winged Warbler	Tennessee Warbler[a]		
Northern Mockingbird		Northern Parula	Nashville Warbler		
Cedar Waxwing		Black and White Warbler	Black-throated Blue Warbler		
Warbling Vireo		Cerulean Warbler	Blackburnian Warbler		
Yellow-rumped Warbler		Prairie Warbler	Chestnut-sided Warbler		
Yellow Warbler		Pine Warbler	Cape May Warbler[a]		
Common Yellowthroat		Kentucky Warbler	Magnolia Warbler[a]		
Yellow-breasted Chat		Hooded Warbler	Black-throated Green Warbler		
Blue Grosbeak		Worm-eating Warbler	Bay-breasted Warbler[a]		
Rufous-sided Towhee		Ovenbird	Blackpoll Warbler[a]		
Grasshopper Sparrow		Louisiana Waterthrush	Palm Warbler[a]		
Vesper Sparrow		American Redstart	Mourning Warbler[a]		
Savannah Sparrow		Rose-breasted Grosbeak	Connecticut Warbler[a]		
Song Sparrow		Northern Cardinal	Canada Warbler		
Lark Sparrow		Indigo Bunting			
Field Sparrow		Henslow's Sparrow			
Chipping Sparrow		Seaside Sparrow			
Bobolink		Eastern Meadowlark			
Red-winged Blackbird		Common Grackle			

TABLE 11 (continued)

Breeding Passerines of Primary Region G Organized by Geographic Affinity

Pandemic	Western	Eastern	Northern	Southern	Central
Brown-headed Cowbird		Orchard Oriole	Wilson's Warbler		
Northern Oriole		Scarlet Tanager	Northern Waterthrush		
Pine Siskin		Summer Tanager	Sharp-tailed Sparrow		
American Goldfinch			Dark-eyed Junco		
House Finch			White-throated Sparrow[a]		
Evening Grosbeak			Lincoln's Sparrow		
			Swamp Sparrow		
			Rusty Blackbird		
			Red Crossbill		
			White-winged Crossbill		
			Pine Grosbeak		
			Purple Finch		

[a] Passerines unique to Primary Region G

For the most part, these are passerines whose breeding distributions follow the coniferous forest from the west, northward around the Great Plains, through Canada, and finally down into the northeast United States; Olive-sided Flycatcher, Swainson's Thrush (*Catharus ustulatus*), Solitary Vireo, and Red Crossbill, for example. Thirteen of the northern passerines can be considered endemic to this region, however, these species' breeding distributions are not limited solely to the northeastern United States. Most northern passerines of this corner of the country have extensive distributions that range throughout parts of Canada, and simply meet southern limits in northeastern portions of the United States. Other northern species present in the assemblage, such as Swainson's Thrush, Nashville Warbler (*Vermivora ruficapilla*), Palm Warbler (*Vermivora palmatum*), Northern Waterthrush (*Seiurus noveboracensis*), and Lincoln's Sparrow (*Melospiza lincolnii*) have habitat associations with more open habitats, spruce/tamarack bogs and palustrine woodlands.

Primary Region H contains fewer breeding species (109) and, in particular, lacks most of the passerines that breed in

the cool, coniferous forests and open country of the northeast. Consequently, part of this region's distinctiveness is derived from the absence of passerines that breed further north. Eastern (44.0%) passerines comprise the largest component of this region species assemblage, with seven breeding species endemic to the southeastern United States (Table 12). This group includes three species of coastal marshes and woodlands; the Gray Kingbird (*Tyrannus dominicensis*), Black-whiskered Vireo (*Vireo altiloquus*), and the Boat-tailed Grackle (*Quiscalus quiscula*). The remaining endemic passerines, Brown-headed Nuthatch, Yellow-throated and Swainson's Warblers, and Bachman's Sparrow, are species typical of mixed pine-oak woodlands and pine scrub along the Gulf Coastal Plain. Although not necessarily endemic, but unique to this portion of the east, a few western and southern passerines occur as breeding species in the oak scrub and open country of eastern Oklahoma, western Arkansas and east-central Texas. These passerines, at distributional limits for the most part, include the Scissor-tailed Flycatcher (*Tyrannus forficatus*), Black-capped Vireo (*Vireo atricapillus*), Rufous-crowned Sparrow (*Aimophila ruficeps*), and

TABLE 12
Breeding Passerines of Primary Region H Organized by Passerine Geographic Affinity

Pandemic	Western	Eastern	Northern	Southern	Central
Eastern Kingbird	Bell's Vireo	Gray Kingbird[b]	Olive-sided Flycatcher[a]	Scissor-tailed Flycatcher	Clay-colored Sparrow
Willow Flycatcher	Rufous-crowned Sparrow	Great-crested Flycatcher	Least Flycatcher[a]	Black-capped Vireo	Dickcissel
Horned Lark	Western Meadowlark	Eastern Wood Pewee	Acadian Flycatcher	Golden-cheeked Warbler	
Tree Swallow		Eastern Phoebe	Winter Wren[a]	Painted Bunting	
Purple Martin		Blue Jay	Golden-crowned Kinglet[a]	Great-tailed Grackle	
Bank Swallow		Fish Crow	Veery[b]		
Northern Rough-winged Swallow		Tufted Titmouse	Solitary Vireo[a]		
Cliff Swallow		Carolina Chickadee	Golden-winged Warbler[a]		
Barn Swallow		Brown-headed Nuthatch[b]	Black-throated Blue Warbler[a]		
American Crow		Carolina Wren	Blackburnian Warbler[a]		
Black-capped Chickadee[a]		Bewick's Wren	Chestnut-sided Warbler[a]		
White-breasted Nuthatch		Sedge Wren	Black-throated Green Warbler[a]		
House Wren		Eastern Bluebird	Canada Warbler[a]		
Marsh Wren		Wood Thrush	Swamp Sparrow[a]		
Blue-gray Gnatcatcher		Gray Catbird	Purple Finch		
American Robin		Brown Thrasher			
Loggerhead Shrike		White-eyed Vireo			
Northern Mockingbird		Yellow-throated Vireo			
Cedar Waxwing		Red-eyed Vireo			
Warbling Vireo		Black-whiskered Vireo[b]			
Yellow Warbler		Prothonotary Warbler			
Common Yellowthroat		Blue-winged Warbler			
Yellow-breasted Chat		Northern Parula			
Blue Grosbeak		Black and White Warbler			
Rufous-sided Towhee		Cerulean Warbler			
Grasshopper Sparrow		Yellow-throated Warbler[b]			
Song Sparrow		Prairie Warbler			
Lark Sparrow		Pine Warbler			
Field Sparrow		Kentucky Warbler			
Chipping Sparrow		Hooded Warbler			
Bobolink		Worm-eating Warbler			
Red-winged Blackbird		Swainson's Warbler[b]			
Brown-headed Cowbird		Ovenbird			
Northern Oriole		Louisiana Waterthrush			
American Goldfinch		American Redstart			
House Finch		Rose-breasted Grosbeak			

(continued)

TABLE 12 (continued)
Breeding Passerines of Primary Region H Organized by Passerine Geographic Affinity

Pandemic	Western	Eastern	Northern	Southern	Central
		Northern Cardinal			
		Indigo Bunting			
		Henslow's Sparrow			
		Seaside Sparrow			
		Bachman's Sparrow[b]			
		Eastern Meadowlark			
		Common Grackle			
		Boat-tailed Grackle			
		Orchard Oriole			
		Scarlet Tanager			
		Summer Tanager			

[a] Passerines primarily associated with the Southern half of the Appalachian Mountains in this region
[b] Passerines unique to the Southeastern United States

Great-tailed Grackle (*Quiscalus mexicanus*). The breeding distributions of the few northern passerines present in this southern portion of the eastern U.S. are limited and primarily commensurate with remnant spruce-fir forests at higher elevations of the southern Appalachians. Most are species of northern coniferous and include the Olive-sided Flycatcher, Common Raven (*Corvus corax*), Winter Wren, Solitary Vireo, and Blackburnian Warbler (*Dendroica fusca*), and Canada Warbler (*Wilsonia canadensis*).

With the abundance of vegetative types present throughout the east as a whole, insect diversity and abundance are correspondingly high. Since northeastern forests are almost entirely composed of deciduous tree species they are often susceptible to severe outbreaks of defoliating insects. Consequently, such species as the eastern spruce budworm (*Choristoneura fumifererana*) and *Cercopia* spp. larvae form a large portion of the avian diet during the breeding season (Mitchell, 1952). In particular, wood warblers (Parulidae) form an extensive consumer population, comprising the largest proportion of insectivorous passerines present in the eastern forests of the United States during the summer

(MacArthur, 1958). Of the 50 species of wood warblers that occur across the continental United States during the breeding season, 37 breed in the east with 26 of these unique to this part of the country. The western United States, including the Great Plains, by comparison has a general paucity of warbler species, with only 22 breeding species, 12 of which can be considered endemic. Although the western United States does have a number of distinctive species, such as Townsend's and Hermit Warblers, most are adapted to other vegetation types (Curson et al., 1994). In the west, the foliage-gleaning niches of the warblers are largely occupied by various species of chickadee, nuthatch, and kinglet. Consequently, wood warblers appear to be distinctly eastern in distribution. This high diversity in the east primarily coincides with the coniferous and coniferous/deciduous forests of the northeastern United States. The northeast contains the largest contingent of wood warblers during the breeding season with 34 species. Regionally endemic species include the Tennessee, Cape May, Magnolia, Bay-breasted, Blackpoll, and Connecticut Warblers.

Mengel (1964) suggested a possible mechanism for the speciation and present distributional pattern of wood warblers in North America. According to Mengel (1964), between 22% and 27% of the 50 species of continental wood warblers achieved specific status as a result of Pleistocene events. He postulated that for each of several wood warbler species there existed an ancestral form adapted to the broad-leaved Arcto-tertiary forests of eastern North America. At the end of the Pliocene, with the first of the Pleistocene glaciations (Nebraskan), these ancestral species were forced into the southeast by the arid plains to the west and the climatic deterioration to the north. As the temperate deciduous forest elements of the southeast were displaced by glacial advance, boreal coniferous forests were forced farther south in their place. Some of these ancestral species adapted to coniferous forest, or their seral stages. With glacial retreat, a broad transition zone of coniferous forest developed allowing these coniferous-adapted warbler species to spread throughout Canada and down the montane coniferous forests of the west. During the second glacial advance (Illinoisan), species became isolated in the western mountains and the

southeastern United States. Speciation occurred and during the subsequent glacial retreat newly formed western species reinvaded the northeast. With each subsequent glacial retreat the temperate-adapted warblers were drawn further into association with the moist coniferous forests of the northeast. As they were drawn farther north, these species were not replaced in the south by wood warblers from tropical Central America due to the barrier presented by the arid plains to the west. Subsequently, the center of diversity for wood warblers shifted to its present location in the northeast.

This history of Pleistocene glaciation and climate change in eastern North America appears to have had an overall influence upon avian diversity in the southeastern United States. Passerine diversity is noticeably higher in the northeast and declines toward the southeastern United States. Although the southeast supports a wider range of forest types than the northeast, it contains fewer breeding passerines. A number of studies have demonstrated this regional paucity in avian species distribution, (Tramer, 1974; MacArthur, 1972), but only Cook (1968) presented a

possible explanation. Cook (1968) proposed that during the Pleistocene glacial cycles the southeast lost many subtropical species because of cooling climates. Specifically, as boreal elements shifted south during glacial advance, many avian species in the west, adapted to subtropical and tropical forests, retreated south to Central and South America. In the east, subtropical species found refuge in the southeast and became isolated by the arid plains to the west. With each successive glacial advance these subtropical species were further isolated and slowly became extinct, leaving only temperate-adapted species. During glacial retreat, temperate-adapted species, particularly coniferous-adapted species, shifted northward resulting in a gradual decrease in species diversity. As these species shifted northward, no subtropical species replaced them. Reinvasion by subtropical species from Mexico and Central America did take place in other regions, most notably the western United States. The arid, open habitats of Texas and the water gap presented by the Gulf proved to be effective barriers to reinvasion of the southeast.

Although modern communities cannot be considered directly analogous to past ones, present distributional patterns can provide important information about past environments (Mayr, 1963). The environmental changes that occurred during the late Quaternary played an important role in shaping the species composition, diversity, and structure of passerine communities of the United States as a whole. With the formation of the plains, extensive forests were replaced by grasslands thus separating eastern and western passerine avifaunas. Climatic deterioration and shifting vegetational formations in the southeast resulted in a general depression in species diversity, with the arid plains preventing recolonization from the tropics. To the west, glaciation and climate changes brought about isolation of small populations increasing chances for speciation, with the southwest possibly serving as refugia for subtropical species as well as a corridor for reinvading species from Mexico and Central America.

Conclusions

Due to its broad-scale, my study permits only the recognition of large regions. Numerical analysis reveals five major avifaunal regions based upon passerine distribution in the continental United States. These regions are largely coincident with certain broad physiographic regions; 1) northern hardwood/coniferous forests and associated grasslands, 2) eastern and southeastern forests and associated grasslands, 3) the Great Plains, 4) mountain ranges and intermontane regions of the western United States, and 5) the southwest. The fourth and fifth areas are relatively species-rich and, along with central and southern sections of the Great Plains, form one of the three major branches of the block dendrogram (Figure 3). The passerine avifaunas of the central and southern plains are most similar to those of the American southwest and west, with 30% of the breeding passerines of the United States restricted to parts or all of it. The northern plains, in contrast, grouped more closely with the passerine avifaunas of the north/northeast United States, comprising a second branch in the dendrogram. The third branch consists of the southeastern United States and south Texas.

Regionally distinct western arid and eastern temperate passerine avifaunas characterize most of the United States and are separated from one another by the Great Plains. In general, the passerine avifauna becomes progressively depauperate across the plains as a result of the replacement of climatic regimes within the vicinity of the 100th meridian. Differences among these regional passerine avifaunas are largely based upon similarities in distribution among several species adapted to gradients in regional environmental and ecological conditions. These results suggest that, to a certain degree, patterns in passerine distribution at the continental level are related to regional climatic regimes and vegetational formations. Of course, competition, food availability, predation, and many other factors must be considered when examining patterns in species distributions (Cody, 1981). How well the effects of such factors can be quantified, or evaluated, at such a broad-scale is questionable and probably not practical when considering large numbers of species.

Literature Cited

American Ornithologist's Union. 1957. *Checklist of North American Birds.* 5th ed. American Or. Union, Washington, D.C.

American Ornithologist's Union. 1983. *Checklist of North American Birds.* 6th ed. American Or. Union, Washington, D.C.

Axelrod, D.I. 1985. Rise of the grassland biome, central North America. *Bot. Rev.*, **51**:163-201.

Baldwin, J.L. 1973. *Climates of the United States.* U. S. Department of Commerce, Washington, D. C.

Barbour, M.G. 1977. *Terrestrial vegetation of California.* John Wiley & Sons, New York, NY.

Barbour, M.G., and D.W. Billings. 1988. *North American terrestrial vegetation.* Cambridge University Press, Cambridge, MA.

Bent, A.C. 1989. *Life histories of North American flycatchers, larks, swallows, and their allies.* Dover Publ., New York, NY.

Berthold, P., H. Bauer, and T. Tomlinson. 1994. *Bird migration: a general survey.* Oxford University Press, New York, NY.

Best, L.B. 1981. Seasonal changes in detection of bird species. *Studies in Avian Biology* **6**:252-261.

Bock, C.E., and L.W. Lepthian. 1976. A Christmas count analysis of the Fringillidae. *Bird-Band.*, **47**:263-272.

Bock, C.E., J.H. Bock, and L.W. Lepthian. 1977. Abundance patterns of some bird species wintering on the Great Plains of the U.S.A. *J. Biogeogr.*, **4**:101-110.

Bock, C.E., J.B. Mitton, and L.W. Lepthian. 1978. Winter biogeography of North American Fringillidae (Aves): A numerical analysis. *Syst. Zool.*, **27**:411-420.

Bock, J.H., C.E. Bock, and R.J. Fritz. 1981. Biogeography of Illinois reptiles and amphibians: A numerical analysis. *Am. Midl. Nat.*, **106**:258-270.

Cody, M.L. 1981. Habitat selection in birds: The roles of habitat structure, competition, and productivity. *Bioscience* **31**:107-113.

Cody, M.L. 1986. *Habitat selection in birds.* Academic Press, San Diego, CA.

Connor, E.F., and D. McCoy. 1979. The assembly of species communities: Chance or competition? *Ecology*, **60**:1132-1140.

Cook, R.E. 1968. Variation in species density of North American birds. *Syst. Zool.*, **17**:63-84.

Cox, G.W. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. *Am. Nat.*, **126**:451-474.

Curson, J., D.E. Quinn, and D.M. Beadle. 1994. *Warblers of the Americas.* Houghton Mifflin Company, New York, NY.

Darlington, P.J. 1957. *Zoogeography: The geographic distribution of animals.* John Wiley & Sons, New York, NY.

DeGraaf, R.M., and J.H. Rappole. 1995. *Neotropical migratory birds: Natural history, distribution, and population change.* Cornell University Press, Ithaca, NY.

Dice, L.R. 1943. *The biotic provinces of North America.* Univ. Michigan Press, Ann Arbor, MI.

Dort, W., Jr., and J.K. Jones, Jr. 1970. Pleistocene and Recent Environments of the Central Great Plains. University of Kansas Press, Lawrence, KS.

Echelle, A.A., and G.D. Schnell. 1976. Factor analysis of species associations among fishes of the Kiamichi River, Oklahoma. *Trans. Am. Fish. Soc.*, **105**:17-31.

Gauch, H.G., R.H. Whittaker, and T.R. Wentworth. 1977. A comparative study of reciprocal averaging and other ordination techniques. *J. Ecol.*, **65**:57-174.

Greenacre, M.J., and E.S. Vrba. 1984. Graphical display and interpretation of antelope census data in African wildlife areas, using correspondence analysis. *Ecology*, **65**:984-997.

Hagmeier, E.M., and C.D. Stults. 1964. A numerical analysis of the distributional patterns of North American mammals. *Syst. Zool.*, **13**:125-155.

Hansen, A.J. 1992. *Landscape boundaries: Consequences for biotic diversity and ecological flows*. Springer-Verlag, New York, NY.

Hengeveld, R. 1992. *Dynamic Biogeography*. Cambridge University Press, Cambridge, MA.

James, F.C. and C.E. McCulloch. 1990. Multivariate analysis in ecology and systematics: Panacea or Pandora's Box? *Annu. Rev. Ecol. Syst.*, **21**:129-166.

Johnsgard, P.A. 1979. *Birds of the Great Plains: Breeding Species and their Distribution*. University of Nebraska Press, Lincoln, NE.

Kaiser, G.W., L.P. Lefkovitch, and H.F. Howden. 1972. Faunal provinces in Canada as exemplified by mammals and birds: A mathematical consideration. *Can. J. Zool.*, **50**:1087-1104.

Kuchler, A.W. 1964. *Potential natural vegetation of the conterminous United States*. Am. Geo. Soc., New York, NY.

Ludwig, J.A. and J.F. Reynolds. 1988. *Statistical Ecology*. John Wiley and Sons, New York, NY.

MacArthur, R.H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology*, **39**:599-619.

MacArthur, R.H. 1972. *Geographical Ecology*. Harper and Row, Publ., New York, NY.

MacDonald, G.J. and L. Sertorio. 1991. *Global climate and ecosystem changes*.

Maurer, B.A. 1994. *Geographical population analysis: tools for the analysis of biodiversity*. Blackwell Scientific Publ., Boston, MA.

Mayr, E. 1963. *Animal species and evolution*. Harvard University Press, Cambridge, MA.

Mengel, R.M. 1964. The probable history of species formation in some northern wood warblers (Parulidae). *The Living Bird*, **3**:1-27.

Mitchell, R.T. 1952. Consumption of spruce budworms by birds in a Maine spruce forest. *J. For.*, **50**:387-389.

Myers, A.A. and P.S. Giller. 1988. *Analytical Biogeography*. Chapman and Hall, New York, NY.

Rising, J.D. 1983. The Great Plains hybrid zones. *Curr. Ornith.*, **1**:131-157.

Rohlf, F.J., J. Kishpaugh, and D. Kirk. 1982. *NT-SYS. Numerical Taxonomy System of Multivariate Statistical Programs*. State University of New York, Stony Brook, NY.

Root, T. 1988. Energy constraints on avian distributions and abundances. *Ecology*, **69**:330-339.

Rostlund, E. 1952. Freshwater fish and fishing in native North America. *Univ. Calif. Publ. Geography*, **9**:1-313.

Rotramel, G.L. 1973. The development and application of the area concept in biogeography. *Syst. Zool.*, **22**:227-232.

Savage, J.M. 1960. Evolution of a peninsular herptofauna. *Syst. Zool.*, **9**:184-212.

Simpson, G.G. 1960. Notes on the measurement of faunal resemblance. *Am. J. Sci.*, **258**:300-311.

Smith, G.R., and D.R. Fisher. 1970. Factor analysis of distribution patterns of Kansas fishes. Pp. 259-270 in *Pleistocene and recent environments of the Central Great Plains*, Dep. Geology, Univ. Kansas, Lawrence, Spec. Publ. 3.

Stevenson, M.M., G.D. Schnell, and R.B. Lack. 1974. Factor analysis of fish distribution patterns in western and central Oklahoma. *Syst. Zool.*, **23**:202-218.

Tramer, E.J. 1974. An analysis of species density of U.S. landbirds during winter using 1971 Christmas bird counts. *Am. Birds*, **28**:563-567.

Van Dyke, E.C. 1939. The origin and distribution of the coleopterus insect fauna of North America. *Proc. 6th Pacific Sci. Congr.*, **4**:255-268.

Varkat, J.L. 1992. *The natural vegetation of North America: An introduction*. Krieger Pub. Co., Malabar, FL.

Wiens, J.A. 1992. *The ecology of bird communities*. Cambridge University Press, Cambridge, MA.

Wilson, J.W. 1974. Analytical zoogeography of North American mammals. *Evolution*, **28**:124-140.

Appendix A

APPENDIX A
Localities From Which Checklists Were Collected

Block Number	Checklist Source
1	North Cascades National Park, Dungeness National Wildlife Refuge, Mount Rainier National Park, Ridgefield National Wildlife Refuge, Wilapa National Wildlife Refuge, Yakima River Canyon National Recreation Area, Olympic National Forest, Umatilla National Wildlife Refuge
2	Colville National Forest, Turnbull National Wildlife Refuge, Columbia National Wildlife Refuge, Umatilla National Forest, Kootenai National Wildlife Refuge, Clearwater National Forest
3	Benton Lake National Wildlife Refuge, Medicine Lake National Wildlife Refuge, Red Rock Lakes National Wildlife Refuge, Glacier National Park, National Bison Range National Wildlife Refuge, Gallatin National Wildlife Refuge
4	Charles M. Russell National Wildlife Refuge, Bowdoin National Wildlife Refuge, Bighorn Canyon National Recreation Area, Medicine Lake National Wildlife Refuge, Custer National Forest
5	Theodore Roosevelt National Park, Lake Ilo National Wildlife Refuge, Lostwood National Wildlife Refuge, Audobon National Wildlife Refuge, J. Clark Sawyer Complex, Upper Souris National Wildlife Refuge, Little Missouri National Grassland, Grand River National Grassland
6	Arrowwood National Wildlife Refuge, Crosby Wildlife Management District, Tewaukon Complex, Lake Alice National Wildlife Refuge, Sheyenne National Grassland, Sand Lake National Wildlife Refuge, Waubay National Wildlife Refuge, Agassiz National Wildlife Refuge, Tamarac National Wildlife Refuge, Big Stone National Wildlife Refuge
7	Chippewa National Forest, Rice Lake National Wildlife Refuge, Voyageurs National Park, Sherburne National Wildlife Refuge, Litchfield Wildlife Management District, Chequamegon National Forest
8	Nicolet National Forest, Seney National Wildlife Refuge, Huron National Wildlife Refuge
9	Moosehorn National Wildlife Refuge, Petit Manan National Wildlife Refuge

APPENDIX A (CONTINUED)
Localities From Which Checklists Were Collected (continued)

Block Number	Checklist Source
10	Hart Mountain National Wildlife Refuge, Crater Lake National Park, Bandon Marsh National Wildlife Refuge, Ankeny National Wildlife Refuge, Umpqua National Forest, Fremont National Forest, Redwood National Park, Modoc National Wildlife Refuge, Lassen Volcanic National Park, Humboldt Bay National Wildlife Refuge, Klamath Basin National Wildlife Refuge
11	Malheur National Wildlife Refuge, Deer Flat National Wildlife Refuge, Boise National Forest, Sheldon National Wildlife Refuge
12	Bear Lake National Wildlife Refuge, Camas National Wildlife Refuge, Grays Lake National Wildlife Refuge, Minidoka National Wildlife Refuge, Fish Springs National Wildlife Refuge, Ouray National Wildlife Refuge, Grand Teton National Park, Yellowstone National Park, National Elk Refuge
13	Pathfinder National Wildlife Refuge, Seedskadee National Wildlife Refuge, Bighorn National Forest, Shoshone National Forest, Dinosaur National Monument
14	Black Hills National Forest, Custer National Forest, Thunder Basin National Grassland, Nebraska National Forest, Badlands National Park, Wind Cave National Park, Crescent Lake National Wildlife Refuge, North Platte National Wildlife Refuge, Pawnee National Grassland
15	Fort Pierre National Grassland, Lake Andes National Wildlife Refuge, Madison Wildlife Management District, Fort Niobrara National Wildlife Refuge, Valentine National Wildlife Refuge, Rainwater Basin Wildlife Management District, DeSoto National Wildlife Refuge
16	Union Slough National Wildlife Refuge, Effigy Mounds National Monument, Minnesota Valley National Wildlife Refuge, Upper Mississippi River National Wildlife and Fish Refuge, Windom Wildlife Management District, Trempealeau National Wildlife Refuge, Necedah National Wildlife Refuge
17	Horicon National Wildlife Refuge, Chautauqua National Wildlife Refuge, Indiana Dunes National Lakeshore, Huron-Manistee National Forest
18	Shiawasee National Wildlife Refuge, Ottawa National Wildlife Refuge, Cuyahoga Valley National Recreation Area
19	Erie National Wildlife Refuge, Allegheny National Forest, Iroquois National Wildlife Refuge

APPENDIX A (CONTINUED)
Localities From Which Checklists Were Collected (continued)

Block Number	Checklist Source
20	Great Meadows National Wildlife Refuge, White Mountains National Forest, Green Mountain National Forest, Missiquoi National Wildlife Refuge, Great Swamp National Wildlife Refuge
21	Acadia National Park, Rachel Carson National Wildlife Refuge
22	Sacramento National Wildlife Refuge, Kern National Wildlife Refuge, El Dorado National Forest, San Francisco Bay National Wildlife Refuge, Merced National Wildlife Refuge, Salinas River National Wildlife Refuge, Yosemite National Park, Sequoia and Kings Canyon National Park, Pinnacles National Monument, San Luis National Wildlife Refuge, Los Padres National Forest
23	Death Valley National Monument, Pahranagat National Wildlife Refuge, Ruby Lake National Wildlife Refuge, Stillwater National Wildlife Refuge, Toiyabe National Forest
24	Great Basin National Park, Bryce Canyon National Park, Capitol Reef National Park, Zion National Park, Fishlake National Forest, Grand Canyon National Park, Kaibab National Forest, Glen Canyon National Recreation Area
25	Arches National Park, Canyon de Chelly National Monument, Curecanti National Recreation Area, Florissant Fossil Beds National Monument, Great Sand Dunes National Monument, Alamosa National Wildlife Refuge, Mesa Verde National Park, Bandelier National Monument
26	Comanche National Grassland, Cimarron National Grassland, Kiowa National Grassland, Rita Blanca National Grassland, Muleshoe National Wildlife Refuge, Caprock Canyon State Park, Optima National Wildlife Refuge
27	Kirwin National Wildlife Refuge, Quivira National Wildlife Refuge, Flint Hills National Wildlife Refuge, Salt Plains National Wildlife Refuge, Washita National Wildlife Refuge, Wichita Mountains National Wildlife Refuge, The Tallgrass Prairie Preserve, Black Kettle National Grassland
28	Sequoyah National Wildlife Refuge, Squaw Creek National Wildlife Refuge, Swan Lake National Wildlife Refuge, Mingo National Wildlife Refuge, Mark Twain National Forest, Ozark National Forest, Big Lake National Wildlife Refuge, Buffalo National River, Cache River National Wildlife Refuge, Wapanoca National Wildlife Refuge

APPENDIX A (CONTINUED)
Localities From Which Checklists Were Collected (continued)

Block Number	Checklist Source
29	Crab Orchard National Wildlife Refuge, Shawnee National Forest, Muscatatuck National Wildlife Refuge, Mammoth Cave National Park, Cherokee National Forest, Tennessee National Wildlife Refuge, Hatchie National Wildlife Refuge, Reelfoot National Wildlife Refuge
30	Daniel Boone National Forest, Great Smoky Mountains National Park, Cherokee National Forest
31	Back Bay National Wildlife Refuge, Chincoteague National Wildlife Refuge, Great Dismal Swamp National Wildlife Refuge, Mason Neck National Wildlife Refuge, Eno River State Park, Mattamusket National Wildlife Refuge, Cedar Island National Wildlife Refuge
32	Joshua Tree National Monument, San Bernadino National Forest, Salton Sea National Wildlife Refuge, Tijuana Slough National Wildlife Refuge, Santa Monica Mountains National Recreation Area
33	Cibola National Wildlife Refuge, Havasu National Wildlife Refuge, Imperial National Wildlife Refuge, Kofa National Wildlife Refuge, Cabeza Prieta National Wildlife Refuge, Saguaro National Monument, Buenos Aires National Wildlife Refuge, Prescott National Forest, Organ Pipe Cactus National Monument
34	Chiricahua National Monument, Petrified Forest National Park, Apache National Forest, Bandelier National Monument, Cibola National Forest, Gila National Forest, Lincoln National Forest, Las Vegas National Wildlife Refuge, Bosque del Apache National Wildlife Refuge, White Sands National Monument
35	Bitter Lake National Wildlife Refuge, Carlsbad Cavern National Park, Guadalupe Mountains National Park, Abilene State Park, Copper Breaks State Park, Lake Brownwood State Park, Big Spring State Park, Monahans Sandhills State Park, Balmorhea State Park, Davis Mountains State Park, South Llano River State Park
36	Hagerman National Wildlife Refuge, Caddo and LBJ National Grasslands, Dinosaur Valley State Park, Fairfield Lake State Park, Huntsville State Park, Bonham State Park, Colorado Bend State Park, Tishomingo National Wildlife Refuge

APPENDIX A (CONTINUED)
Localities From Which Checklists Were Collected (continued)

Block Number	Checklist Source
37	Ouachita National Forest, Felsenthal National Wildlife Refuge, White River National Wildlife Refuge, Catahoula National Wildlife Refuge, D'Arbonne National Wildlife Refuge, Upper Ouachita National Wildlife Refuge, Bogue Chitto National Wildlife Refuge, Atchafalaya National Wildlife Refuge, Big Thicket National Preserve, Yazoo National Wildlife Refuge
38	Mississippi Sandhill Crane National Wildlife Refuge, Noxubee National Wildlife Refuge, Morgan Brakes National Wildlife Refuge, Panther Swamp National Wildlife Refuge, Bon Secour National Wildlife Refuge, Eufaula National Wildlife Refuge, Wheeler National Wildlife Refuge
39	Piedmont National Wildlife Refuge, Okefenokee National Wildlife Refuge, Savannah Coastal Refuges, Santee National Wildlife Refuge, Chattahoochee National Forest, Cape Romain National Wildlife Refuge, Carolina Sandhills National Wildlife Refuge
40	Cedar Island National Wildlife Refuge, Lake Waccamaw State Park, Pee Dee National Wildlife Refuge, Weymouth Woods Sandhill Preserve
41	Big Bend National Park, Amistad National Recreation Area
42	Aransas National Wildlife Refuge, Laguna Atascosa National Wildlife Refuge, Santa Ana National Wildlife Refuge, Matagorda National Wildlife Refuge, Attwater Prairie Chicken National Wildlife Refuge, San Bernard National Wildlife Refuge, Brazoria National Wildlife Refuge, Anahuac National Wildlife Refuge
43	Sabine National Wildlife Refuge, Lacassine National Wildlife Refuge, Cameron Prairie National Wildlife Refuge, Breton National Wildlife Refuge, Delta National Wildlife Refuge
44	St. Marks National Wildlife Refuge, Chassahowitzka National Wildlife Refuge, J.N. "Ding" Darling National Wildlife Refuge, Loxahatchee National Wildlife Refuge, Merritt Island National Wildlife Refuge, Lake Woodruff National Wildlife Refuge, National Key Deer Refuge, Biscayne National Park, Everglades National Park, Big Cypress National Preserve

Signature of Graduate Student

Signature of Major Advisor

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