Winter abundance patterns of landbirds in the United States and southern Canada

A study of relative abundances of 303 species, using 10 years of data from Audubon Christmas Bird Counts

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MEASUREMENT OF SPECIES' numbers in different parts of their ranges is an important but often neglected aspect of geographical ecology (Pitelka 1941, Udvardy 1969, Rotramel 1973). Even if the range limits of a bird species were the best measure of its zoogeography, these limits are difficult to study objectively because of occurrences of stragglers outside "normal" ranges (Grinnell 1922, MacArthur 1972). This would be especially true of the winter season, when many species are nomadic or slow to settle in one area.

With Christmas Bird Count (hereafter, CBC) data we can plot regional species' abundances. We can then correlate and compare these abundance patterns with one another, and thereby describe geographic regions and boundaries revealed by those abundance patterns (Bock *et al.* 1977, 1978). The problem of extra-limital records is eliminated, because we are interested in comparing species' centers of abundance and not their absolute range limits.

We combined CBC results into 51 five-degree latitude-longitude blocks encompassing the conterminious United States and southern Canada (Fig. 1), and computed abundances of 303 landbird species for each block. This data matrix (51 blocks x 303 species) then was subjected to a mathematical treatment called cluster analysis, with the goal of describing in an objective manner the regional abundance patterns of winter landbirds. The objective of the study was to answer two related questions. First, how can winter landbirds be grouped into assemblages of species with similar abundance patterns? Second, how are the blocks related to one another in terms of their winter landbird populations, and what are the major biogeographic boundaries between such assemblages of blocks?

METHODS

Data—CBC results for 1962-63 through 1971-72 were extracted from *Audubon Field Notes* (1963-1970) and *American Birds* (1971-73). We grouped counts into 5-degree blocks (Fig. 1) and computed for each the average numbers of each species seen per party-hour of count effort. There were 7891 counts, distributed unevenly across blocks and ranging from 11 in Block 48 (a small land mass) to 864 in Block 16 (Fig. 1). The small number of counts in certain areas, especially in the Rocky Mountains and the high plains, did not permit confident resolution of nationwide abundance patterns below the level of the 5-degree blocks.

The 303 landbirds used were those counted at a 10-year mean density of at least 0.01 birds/party-hour in at least one block. A small percentage of these species are not normally considered winter birds in North America, but nevertheless remained north long enough to be counted above the minimum level in one or more blocks Exclusion of these species would have been arbitrary. Birds included in the study were those in the following orders: Falconiformes, Galliformes,

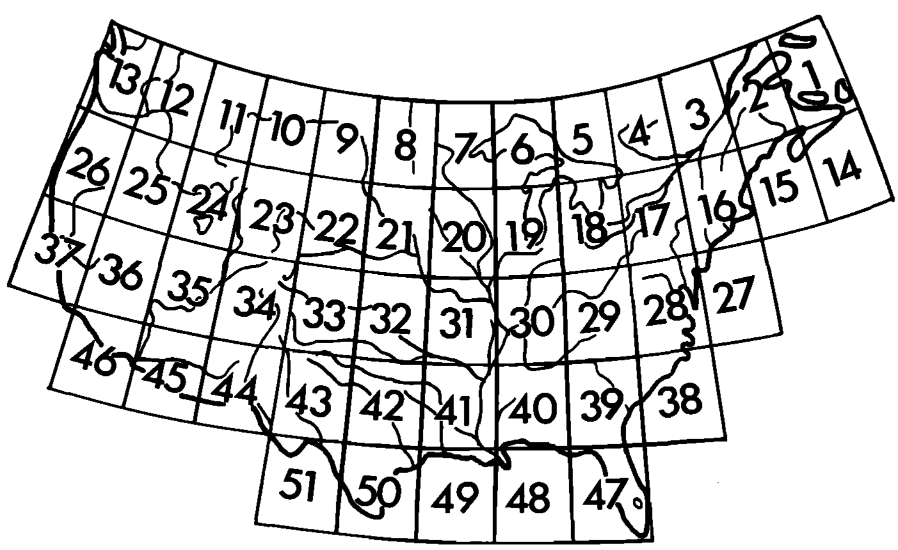


Figure 1. *Fifty-one latitude-longitude blocks used in cluster analysis, numbered in order for comparison with Figures 3 and 4.*

Columbiformes, Cuculiformes, Strigiformes, Caprimulgiformes, Apodiformes, Piciformes, and Passeriformes.

We have described elsewhere (Bock and Lepthien 1974, Bock and Root 1981) the nature, and some of the strengths and limitations of CBC data, and our methods of computerized information storage and retrieval.

Analysis—The purpose of cluster analysis is to mathematically separate large numbers of objects into groupings of those objects which are similar to one another. In the present study, we started with information about the winter abundances of 303 bird species in 51 geographic blocks (Fig. 1). The clustering process begins by determining highly similar pairs of objects, and then proceeds to combine more and more objects with these original pairs on the basis of similarity, to produce larger and larger groups (or "clusters"). The resulting clusters will be represented by a dendrogram, which gets its name because it resembles a branching tree lying on its side (Fig. 2). To answer the two questions posed at the end of the introductory section, we applied cluster analysis to the CBC data in two ways. First, for the regional analysis, we clustered the *blocks,* based upon their winter landbird populations. Second, for the avifaunal analysis, we clustered the *species* into assemblages, based upon their abundances in the 51 blocks.

The following is a technical description of our clustering methods. General interest readers may wish to skip over this and proceed directly to the "results" section.

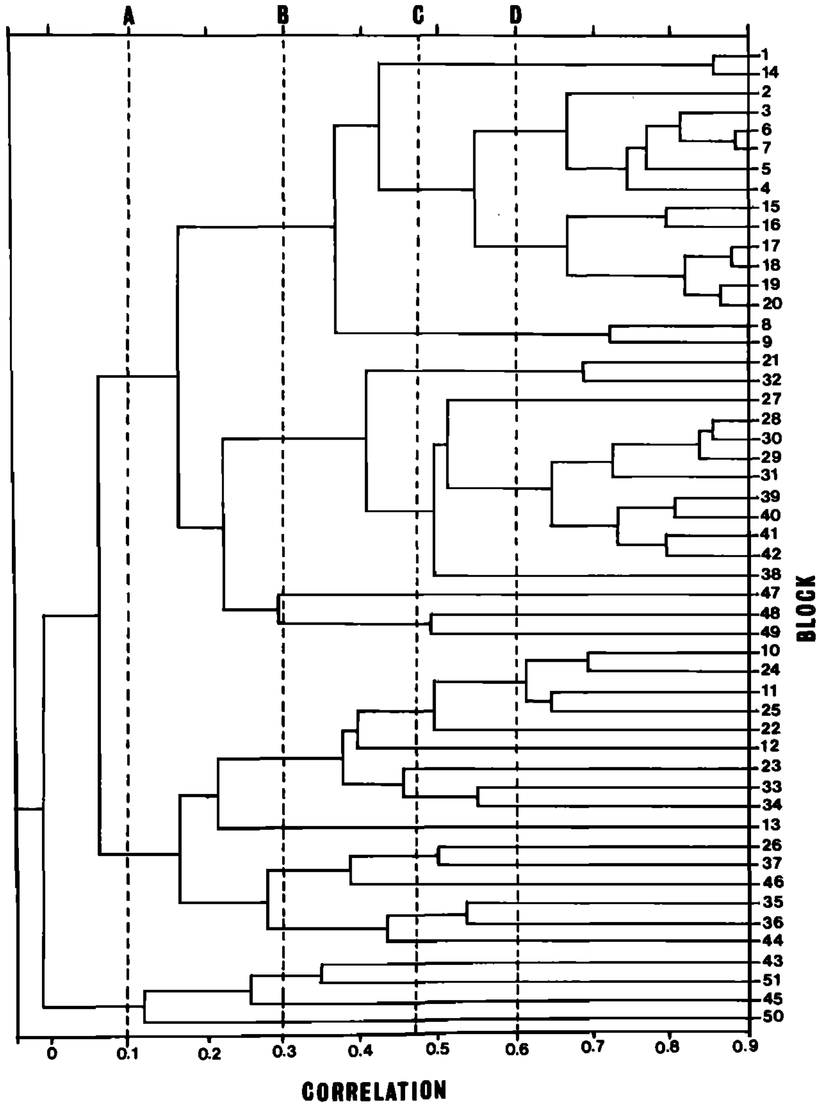


Figure 2. *Dendrogram showing relationships among 51 5-degree latitude-longitude blocks (see Fig. 1), based upon winter abundance patterns of 303 landbird species. Matrix correlation = 0.831.*

We have used the techniques of numerical taxonomy in this study, as available in the computer program package NT-SYS (Rohlf *et al* 1972). All data were standardized by ranging (Gower 1971). This gave the lowest block abundance of each species a value of zero (in blocks where it was absent) and the largest abundance a value of 100. This was accomplished by dividing the abundance of each species in each block by its abundance in the block where it was most common.

For the regional analysis the 51 blocks were the operational taxonomic units (OTU's; Sneath and Sokal 1973) to be clustered, while the abundances of the 303 landbird species constituted the characters by which each block was described. Thus, each block was characterized by 303 variables—the standardized abundances of each of the 303 landbird species in it. First, a matrix of Pearson product-moment correlation coefficients was computed comparing each block to all others. Sample size of each correlation coefficient was 303. Next, this similarity matrix was subjected to single-linkage cluster analysis, using the unweighted pair-group method with arithmetic averaging (UPGMA; Rohlf *et al.* 1972). The resulting dendrogram revealed groups of blocks with similar winter bird faunas.

Avifaunal analysis involved procedures identical to those just described, except that we began with a similarity matrix comparing species rather than blocks, and thereby generated a dendrogram revealing groups of birds rather than groups of blocks. In this case. sample size for each correlation coefficient was 51, the number of block abundances used to characterize each species.

There is much controversy over which sorts of numerical techniques are most appropriate for data such as ours. Bock *et al.* (1978) compared a variety of these methods in a preliminary CBC study restricted to the Fringillidae, and it is not our intention to review them in detail here. Nevertheless, a few comments are in order. The first concerns data standardization.

If we had used raw data (birds/party-hour) to compute similarity matrices comparing blocks, resulting patterns would have been driven almost totally by a handful of widespread and superabundant species (*e g* , Red-winged Blackbird, Starling). A common method of data standardization designed to eliminate this problem is to adjust each variable to have a mean of zero and a standard deviation of one (Sneath and Sokal 1973). We applied this to CBC data with disastrous consequences, since it resulted in large "negative abundances" being computed for the very common species, in the blocks where those species were rare or absent These blocks then would appear highly similar by virtue of sharing large "mutual absences" of the common species. Standardization by ranging eliminated this problem, since no species' abundance values could be less than zero. *All* pairwise comparisons of blocks included zero-zero matches (mutual absences of species), so that correlation coefficients between blocks almost always were positive, but the highest correlations were between those blocks which supported equivalent numbers (as standardized by ranging) of the same species. This is a biologically reasonable result. Bock *et al.* (1978) found for the Fringillidae that a similarity matrix of correlation coefficients was virtually the same as a matrix derived from a similarity measure which excluded the negative (zero-zero) matches (Legendre and Chodorowski 1977).

RESULTS

Cluster analysis of blocks—Figure 2 is a computer-generated cluster analysis of the 51 latitude-longitude blocks, based upon their winter landbird abundance patterns. The branch tips at the right of the dendogram represent individual blocks, while the branches include increasing numbers of blocks as one moves toward the "trunk" of the tree on the left.

The dendrogram shows similarities between blocks and groups of blocks in a hierarchical fashion. For example, Blocks 1 and 14 (top of Fig. 2) combine to form a common branch at a high level of similarity and then, at a lower level of similarity, they combine with another branch consisting of Blocks 2-7 and 15-20. Soon this assemblage combines with a branch including Blocks 8 and 9. At this point Blocks 1-9 and 14-20 have combined into one of the major stems of the dendrogram. Inspection of Figure 1 shows that these particular blocks include the northeastern quarter of the study area.

The best way to visualize groups of blocks comprising branches of the dendrogram is to draw lines bisecting the branches of the dendrogram at various points (or similarity levels) and determine those blocks included in each branch transected by those lines. Four such lines (A to D) are shown on Figure 2. Next, maps are constructed showing locations of the groups of blocks. In Figures 3A-D, solid lines enclose clusters of blocks transected by the dashed vertical lines A-D in the block dendrogram (Fig. 2). Arrows help clarify groups of blocks which were not in geographic contact but with similar bird faunas.

Dashed line "A" in Figure 2 cuts the block dendrogram into its three main trunks. Map A (Fig. 3) shows that these three fundamental geographic divisions of the study comprise 1) the Southwest including south Texas, 2) the remainder of the West, and 3) the East. Figures 3B-D show geographic locations of further subdivisions of these three major clusters of blocks. The power of this technique is that it recognizes, in an objective fashion, geographic regions with generally similar winter bird populations, and the boundaries between them.

Winter landbird species assemblages—The dendrogram showing relationships among the 303 landbird species is far too large for publication. However, inspection of that dendrogram revealed eight clear assemblages of species, each with characteristic sorts of winter abundance patterns. We have named these after the regions of the country where the groups of species reached their greatest relative abundances. These assemblages, and the numbers of species occurring in

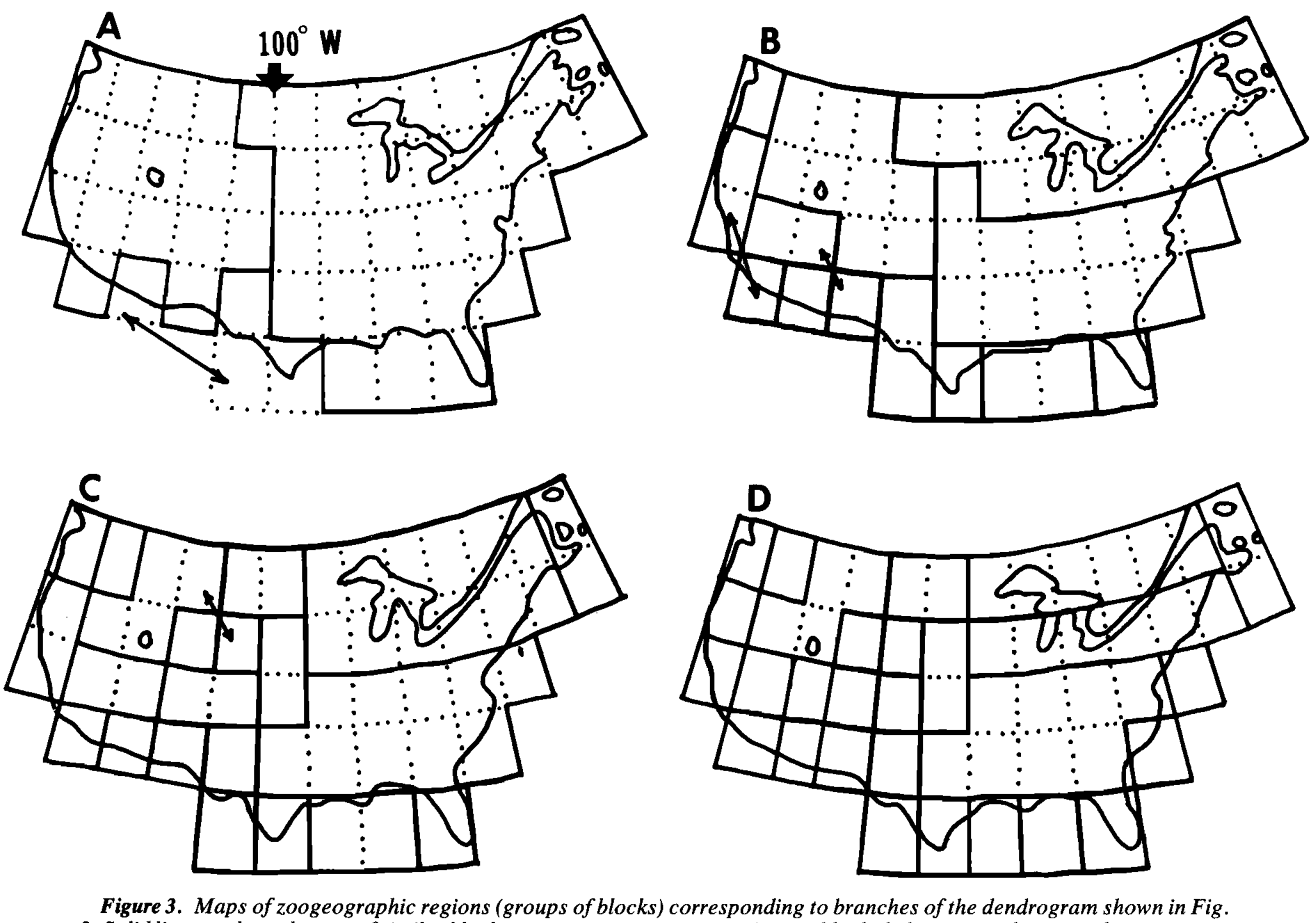


Figure 3. Maps of zoogeographic regions (groups of blocks) corresponding to branches of the dendrogram shown in Fig. 2. Solid lines enclose clusters of similar blocks; arrows connect non-contiguous blocks belonging to the same clusters. Maps A-D show geographic positions of clusters of blocks corresponding to branches of the dendrogram transected by dashed vertical lines A-D in Fig. 2.

each, are as follows:

1 Southeastern Assemblage (83 species)
2. South Texan Assemblage (20 species)
3 Central Assemblage (19 species)
4. Southwestern Assemblage (113 species)
5 Northern Montane-Steppe Assemblage (30 species)
6 Southern Montane-Steppe Assemblage (8 species)
7. Northwestern Assemblage (8 species)
8. Boreal-Northeastern Assemblage (22 species).

Figure 4 shows the winter abundance patterns of representative species from each of these assemblages. Particular species maps were chosen by inspection to illustrate the variety of patterns occurring in the assemblage. Note that some species joined assemblages because they were restricted to the geographic area in question. (*e.g.*, Brown-headed Nuthatch in the Southeast), while other widespread forms joined assemblages by virtue of the locations of their centers of abundance (*e.g.*, Hairy Woodpecker in the Boreal-Northeastern Assemblage).

DISCUSSION

OUR STUDY resulted in two different similarity groupings, one of species and one of blocks. However, both were derived from the same data matrix, and most of the species assemblages were associated in obvious ways with particular geographic regions. For example, the Boreal-Northeastern Assemblage included species most abundant in Blocks 1-9 and 14-20. The distinctness of these blocks can be seen in Figure 3B. Most species of the Central Assemblage reached maximum densities in Blocks 21 and 32. Note from Figure 2 that Blocks 21 and 32 were more similar to one another than to any other blocks. Other faunal assemblages showing relationships with particular groups of blocks are as follows: Northern Montane-Steppe Assemblage (Blocks 10-11 and 24-25); Southern Montane-Steppe Assemblage (Blocks 34, 35, and 36); Northwestern Assemblage (Block 13); and South Texas Assemblage (Block 50).

Species assemblages — Udvardy (1963) described 17 breeding season

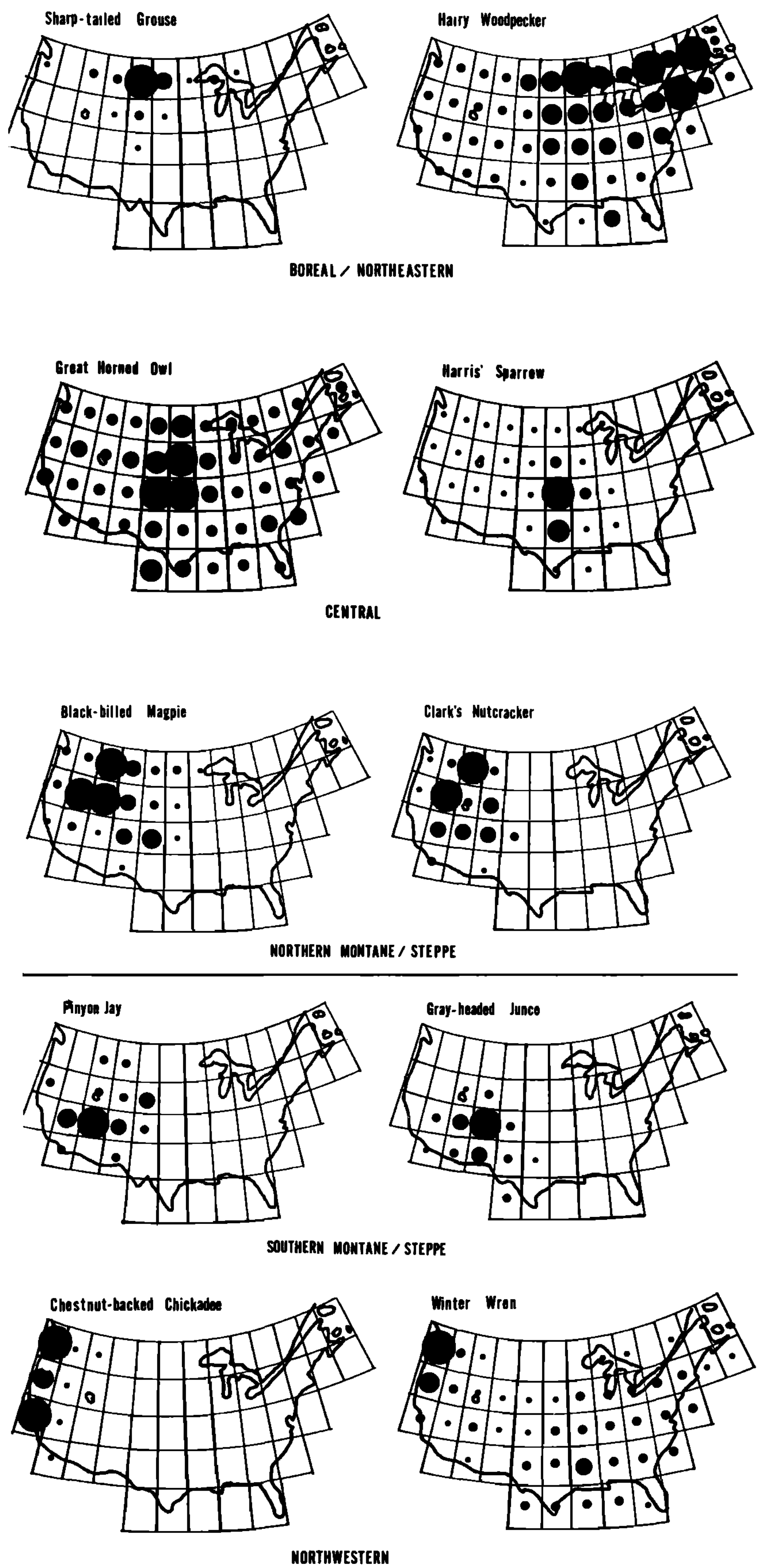
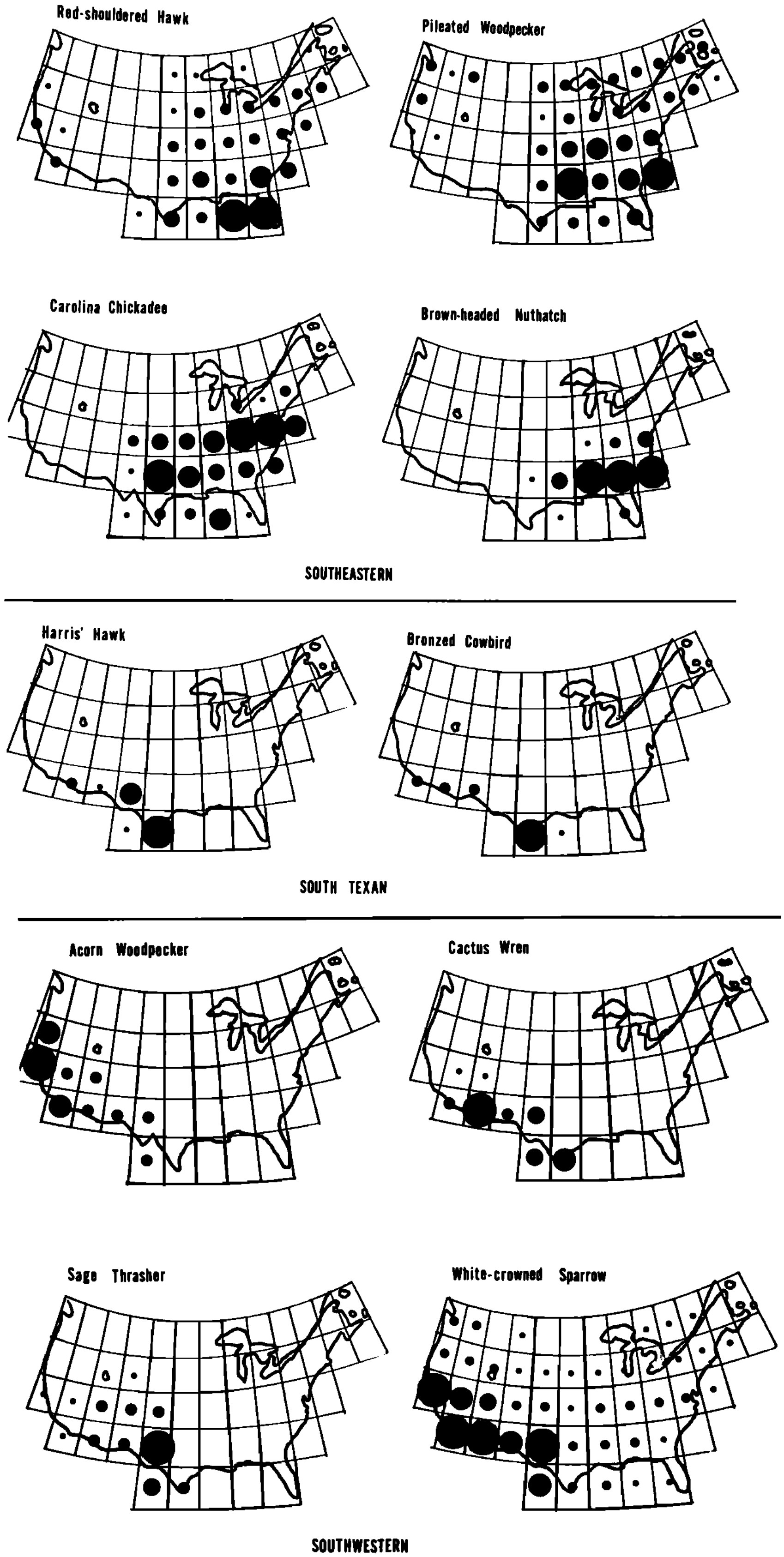


Figure 4. *Winter abundance patterns of representative species belonging to eight winter landbird avifaunas. Five sizes of dots represent > 0-20, 21-40, 41-60, 61-80, and > 80 percent of the maximum number seen per party-hour in one block for each species.*



avifaunas in North America by superimposing range maps of songbird species. His results and ours can be compared only in the most general way, since they represent different methods, with different species, during different seasons, covering different geographic areas. We both found boreal, northeastern, southeastern, and central (prairie) faunas. Udvardy *(op. cit.)* recognized a much larger number of western United States avifaunas than we have, but that is more a matter of the degree of resolution in our two studies than of any real difference in summer *vs.* winter patterns. Our Southwestern Assemblage is a very large one and includes groups of species with very different winter abundance patterns (*e.g.*, interior California, Sonoran Desert, west Texas).

Certain of the eight avifaunal assemblages (*e.g.*, Southwestern, Southeastern, Boreal-Northeastern) were to be expected, and could easily have been predicted from casual inspection of field guides. Others deserve more comment. Perhaps most interesting was the Central Assemblage. Among the 19 species in this group were a few with restricted ranges (*e g*, Greater Prairie Chicken and Smith's Longspur). However, there was a much larger group of very widespread "All-American" species such as the Red-tailed Hawk, Marsh Hawk, Downy Woodpecker, Red-headed Woodpecker, White-breasted Nuthatch, Common Crow, and Tree Sparrow. These species all joined the Central Assemblage by virtue of their high densities in Blocks 21 and 32 (Fig. 1)—the heart of the eastern plains. Evidently the mosaic of deciduous woodlands, agricultural lands, and tallgrass prairie in this region includes the preferred habitat of some of our most widespread winter birds.

The most distinctive winter assemblage of species included those which concentrated in southern Texas (Block 50). This area is characterized by many essentially Mexican species, including Harris' Hawk, Chachalaca, Tropical Kingbird, Green Jay, and Olive Sparrow.

The Rocky Mountain region, including the high plains and Great Basin deserts, appears to support two avifaunal assemblages, separated in winter by latitude. Northern species included the Goshawk, Sage Grouse, Steller's Jay, and Cassin's Finch The smaller southern assemblage included Piñon Jay, Brown-capped Rosy Finch, and Gray-headed Junco.

Biogeographic boundaries — From Figure 3A, we can see that a major biogeographic boundary separates the United States into an eastern and a western half. Much of this boundary lies near 100° W longitude. Climatic variables and certain ecological classifications show a similar pattern (*e.g.*, Thornethwaite 1941, Bailey 1978). The 100th meridian generally coincides with the division of the short- and tallgrass prairies, but plant ecologists usually would treat the central plains as a single unit to be distinguished from deciduous forest to the east and coniferous forest to the west. Our study suggests that the distinction between the short- and tallgrass prairies, or their modern agricultural equivalents, is much more important to birds than some grassland/forest boundaries more striking to the human eye (Bock *et al.* 1977, 1978). This east-west separation has an important historical component related to separation of forests during Tertiary formation of the Great Plains, and further isolation during Pleistocene glaciation (Daubenmire 1978). Its ornithological importance was recognized in the preparation of avian field guides (Peterson 1947).

Our study reveals a number of major zoogeographic patterns besides the east-west boundary just described. By cluster analysis of species or blocks, the most unusual winter landbird assemblage occurred in southern Texas (Block 50), which from an ornithological perspective should be considered part of Mexico. The Mediterranean climate of the Pacific Coast (Blocks 13, 37, and 46) has created an environment suited to a highly distinctive winter bird fauna. The comparatively mild winters of peninsular Florida (Block 47) have had a similar effect.

Finally, western and southeastern coastal blocks differed from one another much more than did inland eastern blocks, a result best shown in Figure 3D. Eastern blocks clustered into broad latitudinal bands at similarity levels where topographically and climatologically heterogeneous western blocks remained distinct from one another. This result conforms with many vegetation patterns (*e.g.*, Küchler 1964), and also with mammalian provinces recognized by Hagmeier (1966) and Hagmeier and Stults (1964).

CONCLUSIONS

It would be traditional to conclude this paper by naming winter avifaunal provinces of the United States. Bock *et al.* (1978) declined to do this in a pilot study restricted to the Fringillidae, pending analysis of all landbirds. We have now completed that task, but for two reasons we remain reluctant to name provinces. The first is that such names, with the possible exception of Wallace's realms, rarely have become widespread or useful parts of biogeographers' vocabularies. Second, we believe that our geographic units (the blocks) relate to one another in a continuum of similarity levels, rather than by falling into discrete groupings (Fisher 1968). Nevertheless, some clear patterns of avian zoogeography can be seen. First, we must recognize the southwestern part of the United States as fundamentally different from the rest of the country. Second, the remaining blocks fall into eastern and western groups, with the tension zone between them lying centrally on the Great Plains. Eastern blocks change as a continuum from north to south, with peninsular Florida being the only truly distinctive eastern area. Western blocks have much less in common than their eastern counterparts.

SUMMARY

Relative abundances of 303 landbird species were computed for 51 latitude-longitude blocks encompassing The United States and southernmost Canada, using 10 years of Audubon Society Christmas Bird Count data. Cluster analysis was used to group species into eight assemblages with similar winter abundance patterns, and to group the blocks into regions with similar species. Our study of landbird abundance patterns showed the distinctness of southwestern latitude-longitude blocks. Remaining blocks clustered into an eastern and a western group, with the boundary between them lying centrally on the Great Plains. Within the eastern group, blocks combined into latitudinal bands of high internal homogeneity. Western blocks were much more individually distinctive, especially those encompassing south Texas, southern Arizona, California and the Pacific Northwest.

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Appendix I. Scientific names of bird species listed in the text and figures.

Goshawk *(Accipiter gentilis)*
Red-tailed Hawk *(Buteo jamaicensis)*
Red-shouldered Hawk *(Buteo lineatus)*
Harris' Hawk *(Parabuteo unicinctus)*
Northern Harrier *(Circus cyaneus)*
Chachalaca *(Ortalis vetula)*
Greater Prairie Chicken *(Tympanuchus cupido)*
Sharp-tailed Grouse *(Pedioecetes phasianellus)*
Sage Grouse *(Centrocercus urophasianus)*
Great Horned Owl *(Bubo virginianus)*
Pileated Woodpecker *(Dryocopus pileatus)*
Red-headed Woodpecker *(Melanerpes erythrocephalus)*
Acorn Woodpecker *(Melanerpes formicivorus)*
Hairy Woodpecker *(Picoides villosus)*
Downy Woodpecker *(Picoides pubescens)*
Tropical Kingbird *(Tyrannus melancholicus)*
Steller's Jay *(Cyanocitta stelleri)*
Green Jay *(Cyanocorax yncas)*
Black-billed Magpie *(Pica pica)*
Common Crow *(Corvus brachyrhynchos)*
Piñon Jay *(Gymnorhinus cyanocephala)*
Clark's Nutcracker *(Nucifraga columbiana)*
Carolina Chickadee *(Parus carolinensis)*
Chestnut-backed Chickadee *(Parus rufescens)*
White-breasted Nuthatch *(Sitta carolinensis)*
Brown-headed Nuthatch *(Sitta pusilla)*
Cactus Wren *(Campylorhynchus brunneicapillum)*
Winter Wren *(Troglodytes troglodytes)*
Sage Thrasher *(Oreoscoptes montanus)*
Starling *(Sturnus vulgaris)*
Red-winged Blackbird *(Agelaius phoeniceus)*
Bronzed Cowbird *(Molothru aeneus)*
Cassin's Finch *(Carpodacus cassinii)*
Brown-capped Rosy Finch *(Leucosticte australis)*

Olive Sparrow *(Arremenops rufivirgatus)*
Gray-headed Junco *(Junco caniceps)*
Tree Sparrow *(Spizella arborea)*
Harris' Sparrow *(Zonotrichia querula)*
White-crowned Sparrow *(Zonotrichia leucophrys)*
Smith's Longspur *(Calcarius pictus)*

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