PATTERNS OF BIRD SPECIES DIVERSITY REVEALED BY CHRISTMAS COUNTS VERSUS BREEDING BIRD SURVEYS

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Continent-wide patterns of avian species diversity have been the subject of much recent attention, especially in comprehensive studies by Cook (1969) and Tramer (1974a). The objective of these and similar studies is to determine what factors of earth history, climate, vegetation structure, resource availability, and population interaction conspire to limit the number of bird species occupying a given region at a given time (see MacArthur 1965, 1972, and Tramer, op. cit., for reviews).

Earlier, we examined the winter pattern of bird species diversity revealed by National Audubon Society Christmas Count data (Bock and Lepthien 1974); Tramer (1974b) conducted a similar analysis for small landbird species. Here we include analysis of the equivalent nesting season endeavor—the U.S. Fish and Wildlife Service's North American Breeding Bird Survey. The objectives of this paper are:

1. to contrast patterns of diversity revealed by the Christmas Counts and Breeding Bird Surveys;

2. to correlate these patterns with climatic variables in a stepwise regression analysis.

METHODS

We grouped Christmas Counts and Breeding Bird Surveys by blocks of 5 degrees of latitude and longitude, and computed the mean number of species seen per census within each block (Figure 1). Data were taken from the 1974 Breeding Bird Survey (n=1563 for the blocks analyzed) and a combination of the 1969-70, 1970-71, and 1971-72 Christmas Counts (n=2743).

Although the effort made on individual Christmas Counts is highly variable, the mean number of species seen per census per block appears to be a reasonable index of diversity (Bock and Lepthien 1974). Tramer (1974b) divided total species by the log of total party hours on each Christmas Count. This probably is the superior method, but his results for small landbirds and ours for all birds were so similar that recalculation of our data seemed unnecessary. Each Breeding Bird Survey is a standardized 2.5 hour roadside census; therefore the number of species recorded should be a good index of relative diversity.

Throughout the study we have analyzed data for all species of birds, because they are so readily available in this form. Cook (1969) ex-

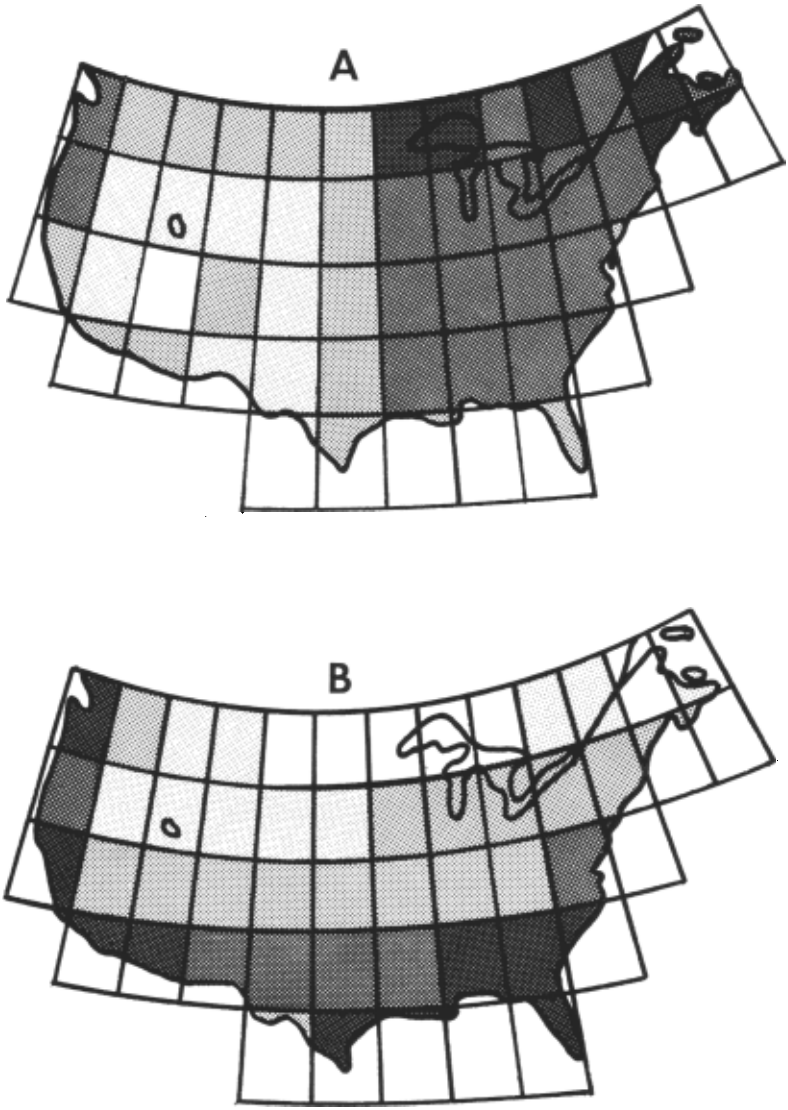

Figure 1A. Average number of bird species observed per Breeding Bird Survey (n=1563), grouped by latitude-longitude blocks. Five degrees of shading represent averages of 20-29, 30-39, 40-49, 50-59, and >60 species per census. Figure 1B. Average number of species observed per Christmas Count (from Bock and Lepthien 1974; n=2743). Five degrees of shading represent <30, 30-49, 50-69, 70-89, and >90 species per census.

cluded strictly marine species, while MacArthur and Wilson (1967) and Tramer (1974a, 1974b) apparently excluded at least marine and freshwater birds. Equivalent studies (Bock and Lepthien 1974 vs. Tramer 1974b for winter diversity; MacArthur and Wilson 1967 vs. Cook 1969 for breeding birds) suggest that the diversity patterns revealed by these species combinations are generally similar.

The patterns shown in Figures 1A and 1B undoubtedly are realistic, but the actual numbers of species seen are comparable only within each census type (see legend), since the effort on nearly all Christmas Counts exceeds that on a Breeding Bird Survey.

Results of the censuses were compared with maps of 50-year climatic means, adapted from the U. S. Department of Agriculture (1941). Correlation coefficients and stepwise regression statistics were computed using the program BMD-02R (Dixon 1971).

RESULTS

Patterns of diversity. Figures 1A and 1B show summer and winter patterns of bird species diversity, as revealed by Breeding Bird Surveys and Christmas Counts. There is a statistically insignificant negative correlation between the two seasons ($r=-.10$). Some salient features of these maps are:

1. the range of variation is much greater in winter than in summer (see legend);
2. breeding season diversities are highest in the East and Northwest, while in winter, species are concentrated in the Southeast, Southwest, and along the Pacific Slope.

Correlation with climate. Table 1 shows correlation coefficients between total species in winter and summer, and various climatic variables. The winter diversity pattern is strongly correlated with temperature regime, while breeding season diversity is similar to patterns of humidity and precipitation. Stepwise regression was not especially illuminating, probably because of the high inter-correlations between many of the climate variables in the matrix (Table 1); see Mauriello and Roskoski (1974) for a discussion of this problem. For winter bird species diversity, minimum temperature alone gave a coefficient of determination (R^2) of 0.81, with no other variables significantly increasing this value. For breeding birds, mean July humidity entered the regression equation first, giving an R^2 of 0.53; mean January temperature (negative correlation) entered the equation next, and made the only other significant contribution, raising the R^2 value to 0.66. Annual precipitation was highly correlated with breeding bird diversity (Table 1), but did not make a significant contribution to the regression equation because of its high correlation with July humidity ($r=0.81$).

Table 1. Correlation coefficients between the mean number of species per latitude-longitude block and 50-year means of climatic data, for all blocks at least partially within the United States (N=47); see Figure 1.

CLIMATIC VARIABLE	TOTAL SPECIES COUNTED	
	WINTER	BREEDING SEASON
Mean annual temperature	0.85*	–0.21
Maximum temperature	0.44*	–0.48*
Mean July temperature	0.60*	–0.37*
Minimum temperature	0.90*	–0.15
Mean January temperature	0.87*	–0.25
Number frost-free days	0.89*	–0.14
Annual precipitation	0.42*	0.62*
Summer precipitation	0.21	0.50*
Winter precipitation	0.46*	0.44*
Mean January relative humidity	–0.34**	0.59*
Mean July relative humidity	0.22	0.73*

* p<.01
** p<.05

DISCUSSION

Originally, we (Bock and Lepthien 1974) carried out a regression analysis of the Christmas Count results using environmental data measured by observers during the counts (e.g., high and low temperatures during the count period). Results showed a strong positive correlation between temperatures and total species seen, but the regression equation accounted for less than 50% of the variation in bird species diversity. In this study we have accounted for 81% of the variation in Christmas Count species totals (averaged by blocks), using the 50-year climatic means of minimum temperature. These results better show the overwhelming impact of general temperature regime upon winter patterns of bird diversity in the United States and southern Canada. This relationship probably is due to the combination of ways in which temperature can affect bird populations. Tramer (1974a:129) correctly stressed "the effects of winter climate regimes on the availability of food." In addition, temperature will affect the energy required for thermoregulation, as well as the diversity and productivity of ecosystems where birds spend the winter.

Moisture regime appears of more critical importance to summer species diversity, as revealed by Breeding Bird Surveys (Table 1).

Humidity and precipitation probably influence breeding bird species diversity largely by increasing the productivity and/or structural complexity of stands of vegetation. This explains the strong east-west gradient seen in Figure 1A, and the high diversities in the moist Pacific

Northwest. The negative correlations between breeding bird diversity and temperature (Table 1) undoubtedly are a reflection of a weak tendency toward higher diversity with higher latitudes in the eastern half of the continent (Figure 1A). Cook (1969) and Tramer (1974a) have discussed possible ecological and historical reasons for this unusual relationship.

Cook (1969), MacArthur and Wilson (1967), and Tramer (1974a) calculated species density patterns across North America using distributional limits to compute the number of species hypothectically occurring in large geographical areas. Both in winter and summer, these diversities appear very high in the mountainous western United States. However, at the level of Christmas counts (15 mile diameter circles) and Breeding Bird Surveys (2.5 hour roadside censuses) these effects largely disappear (Figure 1). Clearly, the high bird species diversities of interior western North America emerge only when vast regions are lumped together.

ACKNOWLEDGMENTS

We are grateful to the University of Colorado Computer Center and Taximetrics Laboratory, and to the many students who helped to build the Christmas Count data banks. Chandler S. Robbins and Danny Bystrak of the Migratory Bird and Habitat Research Laboratory, U. S. Fish and Wildlife Service, kindly provided data from and information about the North American Breeding Bird Survey. This project was supported by grant GB 36860 from the National Science Foundation.

SUMMARY

Bird species diversity patterns in the United States and southern Canada were compared using Audubon Society Christmas Counts and data from the North American Breeding Bird Survey. In winter, diversity is highest in the Southeast, Southwest, and on the Pacific Slope; geographical variation is lower in summer, but diversities are higher in the East and the Pacific Northwest. Correlation of bird diversities with climate variables, and regression analysis of these data show winter patterns to be strongly related to temperature regime, while breeding season diversities are more clearly tied to humidity and precipitation variables.

LITERATURE CITED

Bock, C. E. and L. W. Lepthien. 1974. Winter patterns of bird species diversity and abundance in the United States and southern Canada. Am. Birds 28:556-562.

Cook, R. E. 1969. Variation in species density of North American birds. Syst. Zool. 18:63-84.

Dixon, W. J., ed. 1971. BMD Biomedical computer programs. Univ. Calif. Publ. in Automatic Computations no. 2.

MacArthur, R. H. 1965. Patterns of species diversity. Biol. Rev. 40:511-533.

MacArthur, R. H. 1972. Geographical ecology. Harper and Row, New York.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N. J.

Mauriello, D. and J. P. Roskoski. 1974. A reanalysis of Vuilleumier's data. Am. Nat. 108:711-714.

Tramer, E. J. 1974a. On latitudinal gradients in avian diversity. Condor 76:123-129.

Tramer, E. J. 1974b. An analysis of species density of U. S. landbirds during winter using the 1971 Christmas Bird Count. Am. Birds 28:563-567.

U.S. Dept. of Agriculture. 1941. Climate and Man. U.S.D.A. yearbook. U. S. Gov. Printing Office, Washington, D. C.

Sketch by Narca Schor