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Geographic Ranges of North American Birds

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ABSTRACT

The sizes of geographic ranges of North American birds form a "hollow curve" frequency distribution with most species having relatively small ranges. In this they agree with mammals, but the average range-size (geometric mean of 2×10^6 km²) is larger for birds; also the distribution is lognormal for birds but not for mammals. There are more species of birds than of mammals; 1370 species of North American birds and 842 of mammals conformed to the requirements of the analysis. Birds and mammals have similar patterns of general distribution such as roughly parallel latitudinal gradients in diversity and the hollow curve frequency distribution noted above. Because of these similarities and because birds have larger ranges, a larger percentage of the continent's avian species than of its mammalian species may be found in any one local area. Birds differ from

mammals in greater prevalence of seasonal migration. However, more birds migrate short distances or not at all than longer distances. A larger percentage (50%) of North American avian species than of mammalian species (13%) occur also outside of North America. Present hypotheses relating sizes of geographic ranges to competition, diversity, age of taxa, eurytopy, niche width, vagility, latitude, abundance, sizes of individuals, and trophic levels are briefly noted. No hypothesis is very satisfactory. However, little attention has been devoted to studies describing or explaining patterns of frequency distributions of areas of different sizes in any group of organisms. The present paper describes the pattern for North American birds, compares them with mammals, and suggests some hypotheses for further testing.

INTRODUCTION

The distribution of the sizes of ranges of avian species has never been explicitly examined for North America, nor for any other continent. Such a frequency distribution has been studied for terrestrial mammals in North America (Anderson, 1977; Rapoport, 1982). The Mammalia exhibit a regular decline in the number of species having ranges in successively larger size-classes. The comparison of other major taxonomic groups is needed

in order to test the hypothesis that the regular decline in numbers mentioned is a general phenomenon, to see what similarities and differences between different groups exist in patterns of sizes of ranges, and to see what ecological, evolutionary, and biogeographic hypotheses may be tested by the data. This study of birds is the first such comparison to be made.

The paucity of such studies is mainly due

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to inadequate data on ranges for entire groups over sizable areas. Also, few persons have been interested, which relates to a dearth of theory that might lead to examination of the data.

Space occupied may be considered at different conceptual levels, from an alpha level for the space physically occupied by the individuals of a species at one time to a delta level for total geographic range of a species over a period of years (Anderson, 1977).

AREOGRAPHY: The topic of areography occupied 10 chapters in Cain's (1944) book on plant geography. Udvardy (1969) also discussed areography, and considered it to be the basic branch of zoogeography. Most general works on biogeography, however, scarcely mention areas, beyond noting that some species occupy large areas and some species occupy small areas. As early as 1902, C. C. Adams (quoted by Cain) had noted that "it is a very fundamental law that most forms of life are confined to restricted areas and only a small number have extensive distributions." The first major explication in English of areography in general was presented by Rapoport (1982; a Spanish edition, published a few years earlier, did not receive wide notice). The roles of barriers and of geographical and ecological factors (beyond those considered in this paper) were discussed, using data from birds and other groups. Special attention was given to North American mammals because of the data conveniently available in Hall and Kelson (1959). Rapoport considered the entire topic of areography as controversial, little studied, and not well established in either methodology or theory. He dealt with the areas of and locations of subspecies as well as of species. Most of his presentation is descriptive, or a search for patterns. The search and the development of explanations or hypotheses for further testing have barely begun.

ACKNOWLEDGMENTS

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gestions were followed. I am grateful to these persons and to the ornithology luncheon discussion group at the American Museum of Natural History for their interest and time. I am grateful also to the students and other volunteers, too numerous to list, who helped in the tedious measurements of ranges on hundreds of maps, in calculations, and in other ways.

METHODS AND BASIC DATA

In the analysis of distributional data for North American birds, the continental limits were arbitrarily defined following Hall and Kelson (1959) to include Greenland and to extend southward through Panama and through Grenada in the Lesser Antilles. There is no single source of information or of maps for birds so I prepared a set of maps by consulting the following sources: A.O.U. checklist (1957) for area north of Mexico; Friedmann, Griscom, and Moore (1950) for Mexico; Davis (1972) for Mexico and Central America; Eisenmann (1955) for middle America; Bond (1956) for West Indies; Robbins, Bruun, and Zim (1966) for range maps; Mayr and Short (1970) for comments on status of species; and Meyer de Schauensee (1966) for supplementary data on South American birds.

The areas (in km²) occupied by different species of birds in North America vary over at least five orders of magnitude. Measurements were made by counting squares on a transparent grid laid over a rough map that I drew of the range for each species, as described earlier (Anderson, 1977). The calculated values were rounded to one significant figure, for example an estimated value of 1650 became 2000 and 64,500 became 60,000. The picture is, therefore, being painted with a very broad brush. Corrections of errors in measurement of less than 5 percent would not have changed any value used, and for some measurements corrections of errors of up to 50 percent would have produced no change (for example an actual range of 14.9 that had been measured as 9.6 would be expressed as 10 in either case).

In mapping and measuring ranges, the North American part of the range only was measured; breeding range and wintering range

were included. Any migratory range between the breeding and wintering ranges was not included. Accidental or casual occurrences were not included in ranges.

The following groups of oceanic birds, including 54 species, were excluded from further analysis: Diomedidae (albatrosses), Procellariidae (shearwaters), Hydrobatidae (storm-petrels), Phaethontidae (tropic-birds), Sulidae (boobies), Fregatidae (frigate birds), and Stercorariidae (jaegers and skuas).

The following seven extinct species were also excluded, in order to limit the study to the contemporary fauna: *Ectopistes migratorius*, *Pinguinus impennis*, *Conuropsis carolinensis*, *Caracara lutosus*, *Camptorhynchus labradorius*, *Campephilus principalis*, and *Ara tricolor*.

Other exclusions were:

- 86 species with part of the range in Eurasia and not extending into North America beyond Alaska or Greenland,
- 243 species with part of the range in South America and not extending into North America beyond the Lesser Antilles or Nicaragua,
- 13 introduced species, and any accidental or casual records in North America of birds from other continents.

In all, 476 of 1846 species were excluded from the analysis of geographic ranges and 1370 species were used.

Some figures (from Robbins, Bruun, and Zim, 1966) for background and for comparison with my figures are:

- 1780 species of 97 families breed in North America,
- 645 of these species breed north of Mexico,
- 50 additional species are migratory and are regular or casual visitors,
- 100 additional species occur accidentally.

The 645 species comprise less than 8 percent of the world's 9000 or so species, and North America comprises 17 percent of the world's land.

The 1370 species included in my sample for the analysis of ranges belong to the following groups:

- 819 North American endemics,

398 species that occur also in South America as breeders or winterers,

120 species that occur also in Eurasia as breeders or winterers,

33 species that occur also in both Eurasia and South America (some also occur in other continents).

All notes and maps showing ranges and other data used in this analysis have been collected and bound and are in the archives of the Department of Mammalogy at the American Museum of Natural History.

FREQUENCY DISTRIBUTIONS OF SIZES OF GEOGRAPHIC RANGES

To examine whether the sizes of species' ranges are spread evenly among possible ranges, used as a null hypothesis in this context, the numbers of species having ranges in each 100 km² size-class, averaged over each order of magnitude, are plotted in figure 1. (Log scales are used because each variable ranges over at least five orders of magnitude and a table of numbers or a graphical plot such as a simple frequency histogram on an arithmetic scale fails completely to make visible the significant pattern under discussion. See fig. 2 in Anderson, 1974, for an illustration of this problem of scale.) A line on figure 1 conforming to this null hypothesis would be horizontal, and the more species there are in the faunal group being considered the higher the line would be on the graph. Visual inspection alone convinces me that the null hypothesis can be rejected. As with mammals, the bird species with ranges of a given size are about an order of magnitude (10 times) less concentrated in each successively larger order of magnitude of range. The exact multiple is not so important; the consistent trend is important. For comparison, the data for mammals are also plotted. (These mammalian points have been recalculated on the basis of 714 species of mammals, rather than the sample of 674 species used in the graph published earlier, Anderson, 1977, p. 12.)

These data are plotted, with insular (occurring only on islands) and "mainland" species separated, as a cumulative frequency graph in figure 2. Again the curve for mammals is included. The generally larger size of

avian ranges is illustrated by the position of the avian curve above the mammalian curve. The curve for insular mammals (not shown) also lies below the curve shown for insular birds. The relatively smaller ranges of insular birds are known ("absurdly obvious" as a reviewer noted), but this has not been presented quantitatively and graphically (as in figs. 1 and 2).

The data for insular species and those for mainland species both fit well with a straight line when plotted on a probability scale (fig. 3). Linearity on these scales indicates that the distributions are nearly lognormal. This contrasts to the distributions for mammals (fig. 5, in Anderson, 1977).

Some taxonomic groups of birds have larger average geographic ranges than other groups. The arithmetic and geometric means in millions of km² and the numbers of species used for groups in North America are as follows:

| Arith- metic Mean | Geo- metric Mean | Num- ber of Species | Group |
|-------------------------|------------------------|------------------------------|---------------------------------|
| 4.6 | 3.9 | 10 | Gaviiformes |
| 6.3 | 3.7 | 18 | Strigiformes |
| 5.1 | 3.2 | 33 | Falconiformes |
| 3.0 | 2.7 | 6 | Caprimulgiformes |
| 3.7 | 2.4 | 21 | Piciformes |
| 3.5 | 2.1 | 4 | Trogoniformes, Coraciiformes |
| 3.4 | 2.1 | 42 | Anseriformes |
| 1.9 | 2.1 | 287 | Passeriformes |
| 2.4 | 1.6 | 17 | Galliformes |
| 2.0 | 1.0 | 26 | Pelecaniformes |
| 2.2 | 0.92 | 22 | Apodiformes |
| 1.8 | 0.85 | 12 | Columbiformes |
| 1.6 | 0.61 | 101 | Gruiformes, Charadriiformes |

The geometric means and ranges of two standard errors above and below these means are plotted in figure 4. Log values were used in calculating the standard errors since the distributions of ranges fit lognormal curves better than arithmetic-normal curves. The scale on the graph, however, is converted to arithmetic unit.

These groups may also differ in other ways. Differences in degree of separation of breeding and wintering ranges are discussed below. The differences in range sizes and seasonal

ranges raise interesting ecological and evolutionary questions. For example, why should pigeons and doves have smaller ranges than woodpeckers or passeriform birds? Answers to such questions should be formulated in ways that can be tested further with other data or that lead to the formulation of other hypotheses or predictions that can be tested. To illustrate what I mean by this general comment, in relation to the question given as an example, it may be noted that pigeons and doves are mostly frugivorous and tropical and hence "available space" may cause the differences. As an "explanation" I do not find this satisfying. As a hypothesis for testing it is interesting. We should then ask—are there other groups of birds, or other organisms, with these properties and are their ranges correlated in the same way?

Data for Eurasian birds from Voous's work (1962, and other papers cited by Rapoport) were also analyzed by Rapoport (1982). The families were arranged in order of decreasing sizes of geographic ranges of species as follows (although numerical values were not given): Falconidae, Ardeidae, Strigidae, Cuculidae, Podicipedidae, Corvidae, Accipitridae, Gaviidae, Columbidae, Anatidae, Phasianidae, Turdidae, Threskiornithidae, and Phalacrocoracidae. Rapoport (1982, p. 11) suggested that "predators of vertebrates seem to have a larger geographical extension than predators of invertebrates, seed eaters and herbivores in general."

Data on South American birds of 10 selected families were analyzed by M. Esteman and E. H. Rapoport (Rapoport, 1982). Arithmetic means for ranges of species were 1.3×10^6 km² for Accipitridae, the widest ranging family, and 4.5×10^5 for Trochilidae, those with the smallest ranges.

DISCUSSION

The areographic data presented here have relevance to several topics and the discussion is organized around the following: hypotheses and correlations relating to sizes of geographic ranges, species density in birds and mammals, predicting range-sizes from local data, avian cosmopolitanism, continental differences, a competition hypothesis, and breeding and wintering ranges.

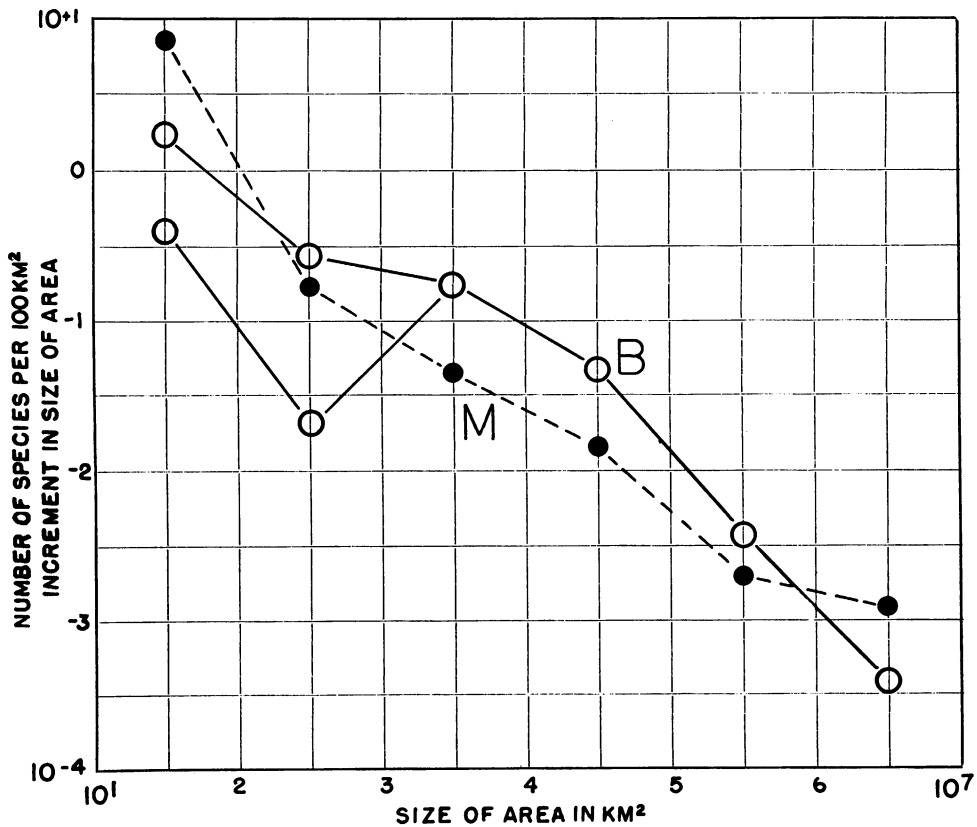


FIG. 1. Graph for North American birds showing the number of species (averaged for each succeeding order of magnitude) having ranges of any given size. Counts are grouped in 100 km² increments. The negative values on the ordinate are powers of 10, thus 10⁻⁴ or .0001 species per 100 km² increment for a range of 10⁷ (10,000,000) would mean that there are so few species with ranges of this size that most increments are unoccupied and, on the average, there is one species for each 100,000 size-classes. Data on mammals are included for comparison. The lower of the two values for birds at both sizes 10² and 10³ is for non-insular birds only. The upper values are for all birds.

HYPOTHESES AND CORRELATIONS: Various ecological, evolutionary, and biogeographic hypotheses may lead to predictions that can be tested by data on sizes of ranges. Correlations have been hypothesized or shown to exist in certain samples between distributions (area or range-size) and (1) diversity of fauna; (2) elapsed time since origin of taxon or geological duration; (3) breadth of ecological niche or degree of eurytopy; (4) vagility or ability of individuals to disperse; (5) latitude; (6) sizes of individuals; (7) abundance, and (8) predatory habits.

1. A negative correlation between area (mean of geographic ranges of species in a

sample) and faunal diversity (number of species or richness) was demonstrated for North American bats and non-marine turtles (Rosenzweig, 1975). The possibility that this might result from interspecific competition was suggested. This and alternative hypotheses were discussed by Anderson and Koopman (1981) who extended the data to include South American bats and North American rodents. The additional information did not support the "competition hypothesis." The correlation for North American passeriform birds resembles that for mammals, and, as for mammals, available space probably is more important than competition as a cause

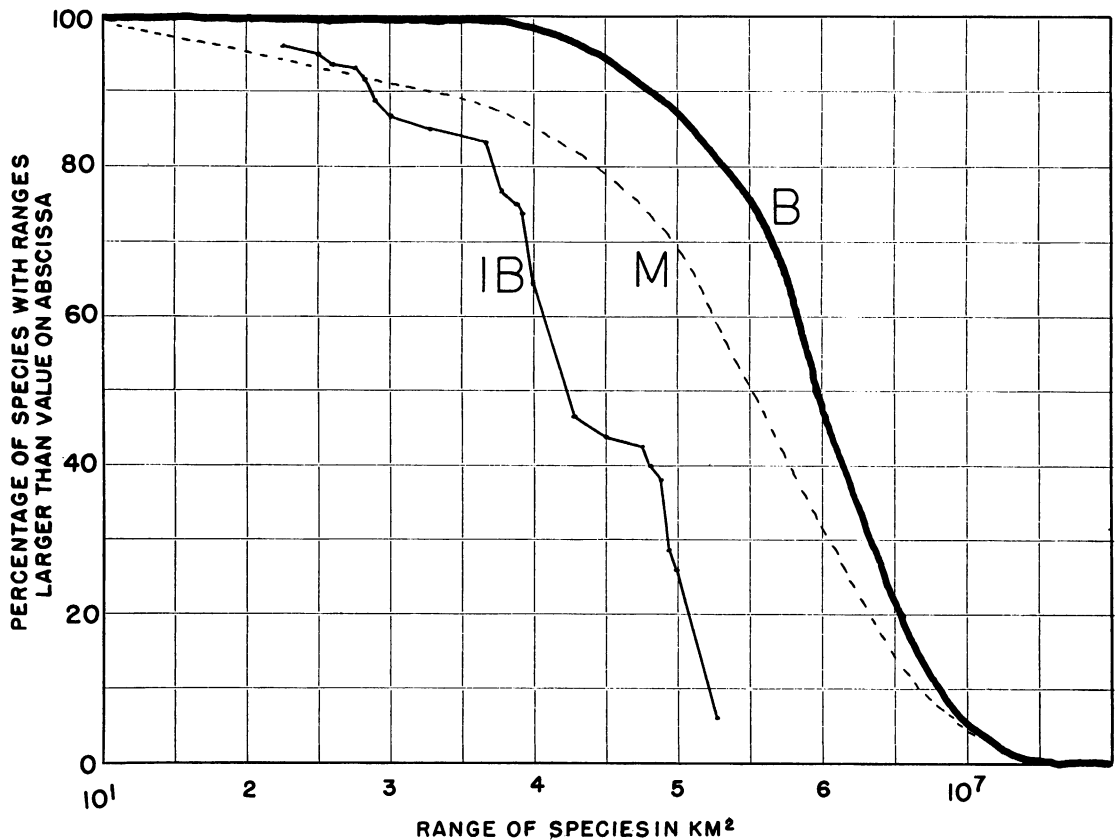


FIG. 2. Cumulative plots of ranges of North American birds, insular (IB) and non-insular (B) birds separately, and data on mammals (M) for comparison.

of the correlation. A competition hypothesis is discussed in greater detail below.

2. A positive correlation between area and age of taxa was presented for plants by Willis (1949, and earlier papers). His phraseology was mechanistic but certain stochastic elements are involved, as discussed earlier (Anderson, 1974). If information on the ages of bird species were available it would be possible to examine the correlation of age and area. Taxa with larger geographic ranges seem to have longer geological records (Boucot, 1975).

3. A positive correlation of area and degree of ecotopy (or breadth of ecological niche) has been suggested by many authors. Hesse, Allee, and Schmidt (1937) discussed this and other of the hypotheses briefly outlined here. One hypothesis, the "seasonal stability hy-

pothesis," assumes that competition among species limits the number that can coexist. According to this hypothesis, the degree of seasonal fluctuation in the environment controls the degree of specialization and this in turn controls species richness (Askins, 1983). In testing this hypothesis with data on tropical and temperate woodpeckers in North America, Askins examined the prediction that wood-excavators are buffered against seasonal change more than most birds and therefore specialization and species richness should not be different in tropical and temperate areas. Study of foraging methods and perches revealed no consistent tendency for tropical species to be more specialized; however, the tropical fauna had twice as many species as either of two temperate faunas studied.

4. A positive correlation between vagility

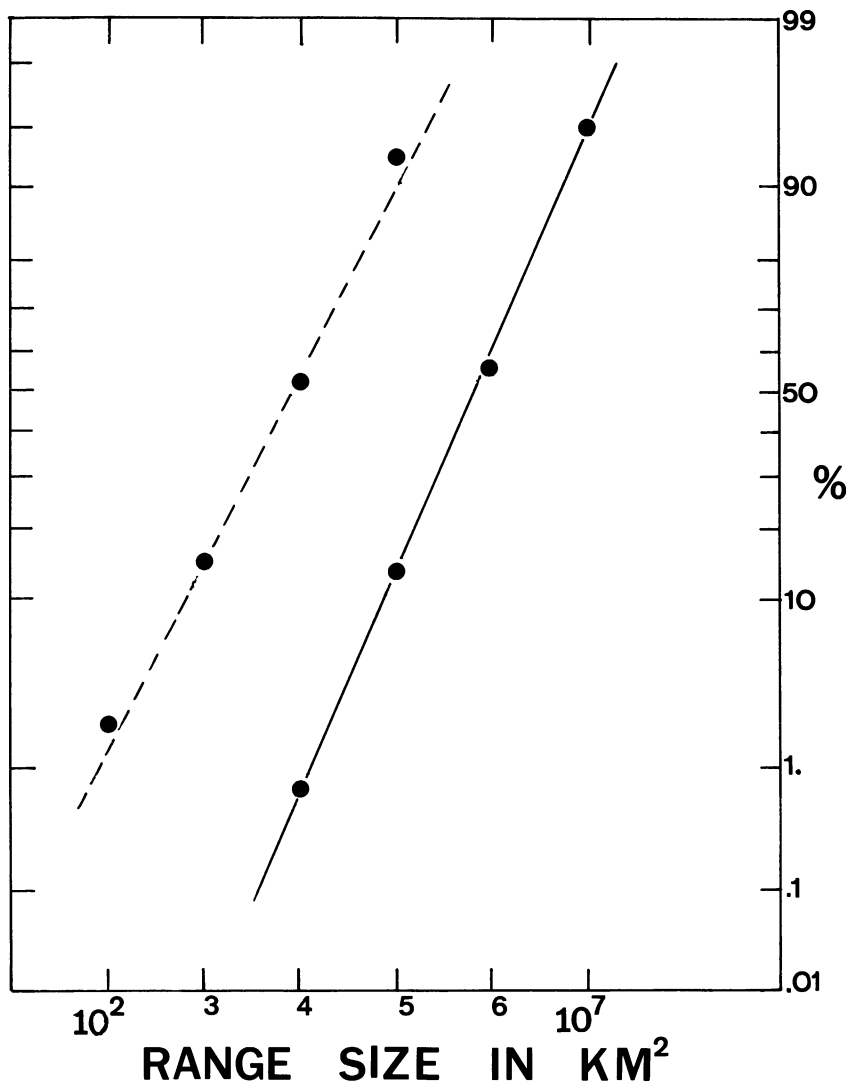


FIG. 3. Graph showing the nearly lognormal distributions of sizes of ranges among insular birds (broken line) and among mainland birds (line). A straight line on a plot of species in $\times 10$ (11–100, 101–1000, etc.) log classes of sizes of geographic ranges in km^2 (abscissa) against cumulative percentages on a probability scale (ordinate) indicates a lognormal distribution.

and area has been suggested by many authors. Flessa (1981), for example, noted that the faunal similarity among continents is greater at the generic level when bats are included in the mammalian fauna analyzed than when terrestrial mammals other than bats are analyzed. The reason for treating bats separately was that “the relatively great dispersal ability of the bats would be expected to increase cos-

mopolitanism.” As shown earlier (Anderson, 1977, fig. 3), North American species of bats do have larger ranges than rodents or insectivores, but bat ranges are about the same as those of lagomorphs and are less than those of carnivores and artiodactyles. How many of these differences should be attributed to “dispersal ability?” Are there independent measures of this ability that could be corre-

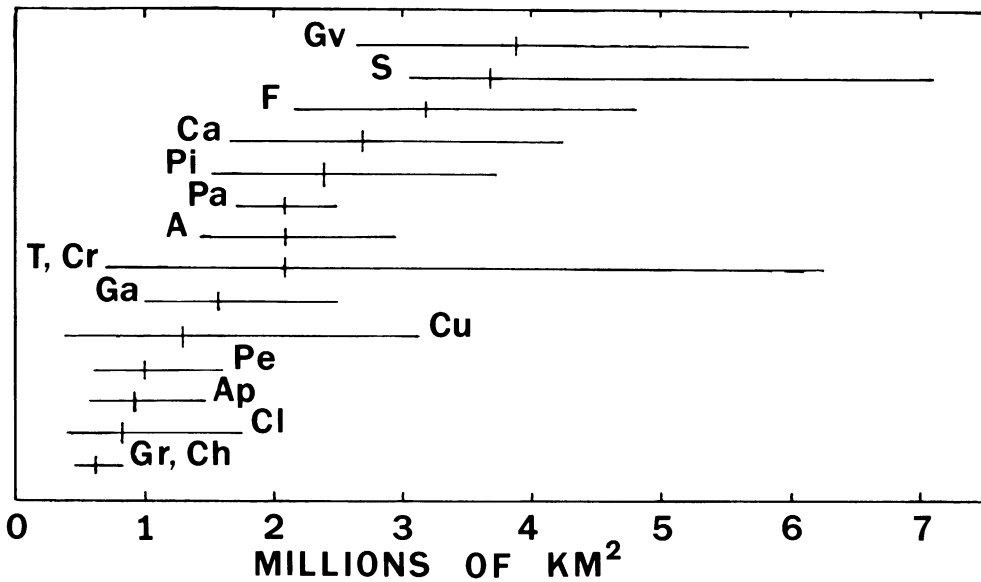


FIG. 4. Graph showing differences in sizes of geographic ranges of birds of different orders in North America. The geometric mean and a range of ± 2 S.E. are given (for reasons explained in text). The groups are: A, Anseriformes; Ca, Caprimulgiformes; Ch, Charadriiformes (grouped with Gr, Gruiformes); F, Falconiformes; Ga, Galliformes; Gv, Gaviiformes; Pa, Passeriformes; Pe, Pelecaniformes; Pi, Piciformes, and S, Strigiformes.

lated with ranges as a test of the hypothesis? Do birds have larger ranges than terrestrial mammals because birds can fly? Why do birds of different orders have different ranges? Does this have anything to do with locomotor abilities? How should we try to test such questions?

5. In North America, positive correlations have been reported for many groups of plants and animals between latitude and diversity, but rarely has the relationship between latitude and area been considered.

6. Species of larger body size may have larger areas (Anderson, 1977; Brown, 1981, and Rapoport, 1982, gave some data for mammals; a similar study for birds would be interesting).

7. The relationship between abundance and distribution was the subject of a book by Andrewartha and Birch (1954); the relationship was examined on an ecological scale of a few years and is most important in local areas at the edges of ranges. Recently, Bock and Ricklefs (1983) have demonstrated a positive correlation between range-size and local abundance in North American songbirds, based

on data from Christmas bird counts of Emberizinae and Carduelinae in 5-degree quadrats.

8. Among birds, predation and especially predation on vertebrates was positively correlated with area by Rapoport (1982, p. 11), who hypothesized that "while the herbivores are limited by the geographical distribution of the plants they eat, the predators would have less feeding specificity and therefore more freedom to extend their geographic range." If predators really are more eurytopic in dietary habits than herbivores, this is an example of hypothesis 3 above.

These and other hypotheses about sizes of geographic ranges need to be formulated and tested more carefully. They are noted here merely to suggest possibilities for research and to provide some relevant references.

SPECIES DENSITY: One important aspect of the general pattern of geographic distribution is species density. The number of species present at some time during the year in a given local area decreases with increasing latitude in North America for many groups of organisms, including birds and mammals. In

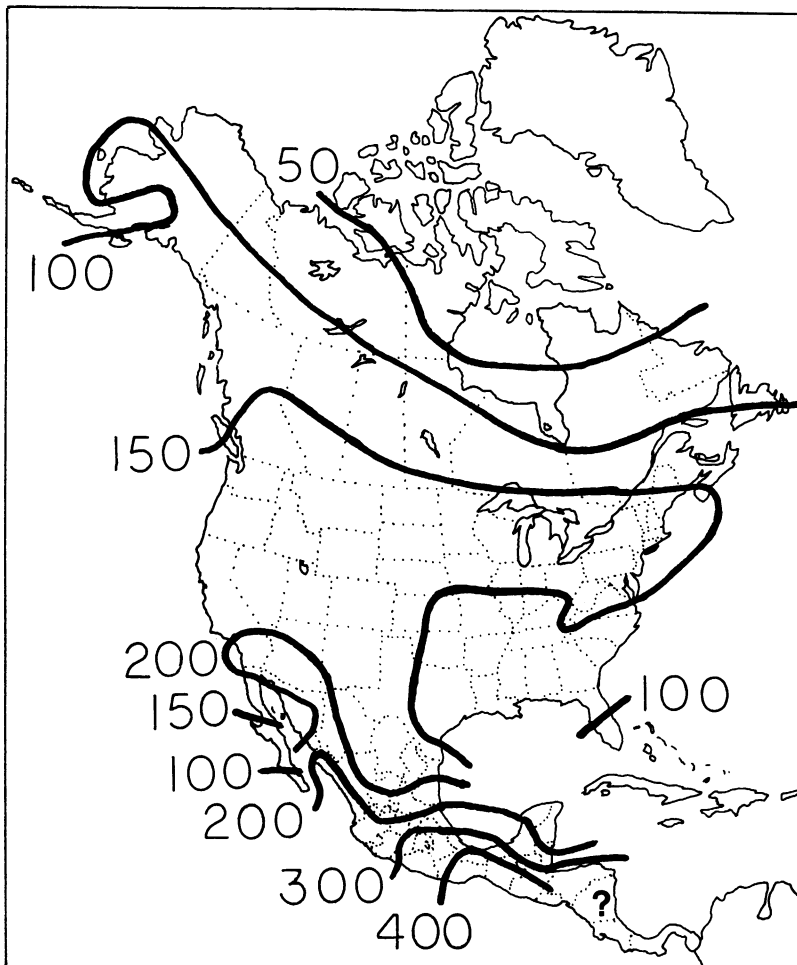


FIG. 5. Species densities of birds breeding in North America, from Cook (1969).

figure 5 the species density of breeding birds is illustrated, and in figure 6 the density of North American endemic passerines alone is illustrated. The endemic passerines make up about half of the avifauna over much of the continent. In both maps a clear latitudinal gradient is evident. North American endemics show the greatest species density in California and northern Mexico instead of farther south. There are more species of passerines farther south, but many of these extend into South America and hence are not North American endemics.

There are more species of birds (1370 as restricted above) than of mammals (842 using the same restrictions) in North America,

and the ranges of birds (fiftieth percentile at $9 \times 10^5 \text{ km}^2$) are larger than those of mammals (fiftieth percentile at $4 \times 10^5 \text{ km}^2$). The difference in total ranges would be even greater if world ranges were used instead of restricting the measurement to the North American part of the range. Half (880 of 1760, as explained below) of North American species of birds occur also on one or more other continents.

The percentage of North American species of birds present in any one local area will depend on (1) the sizes of their geographic ranges, and (2) how the ranges are distributed relative to each other. In theory, each species could occupy the entire continent, and in this

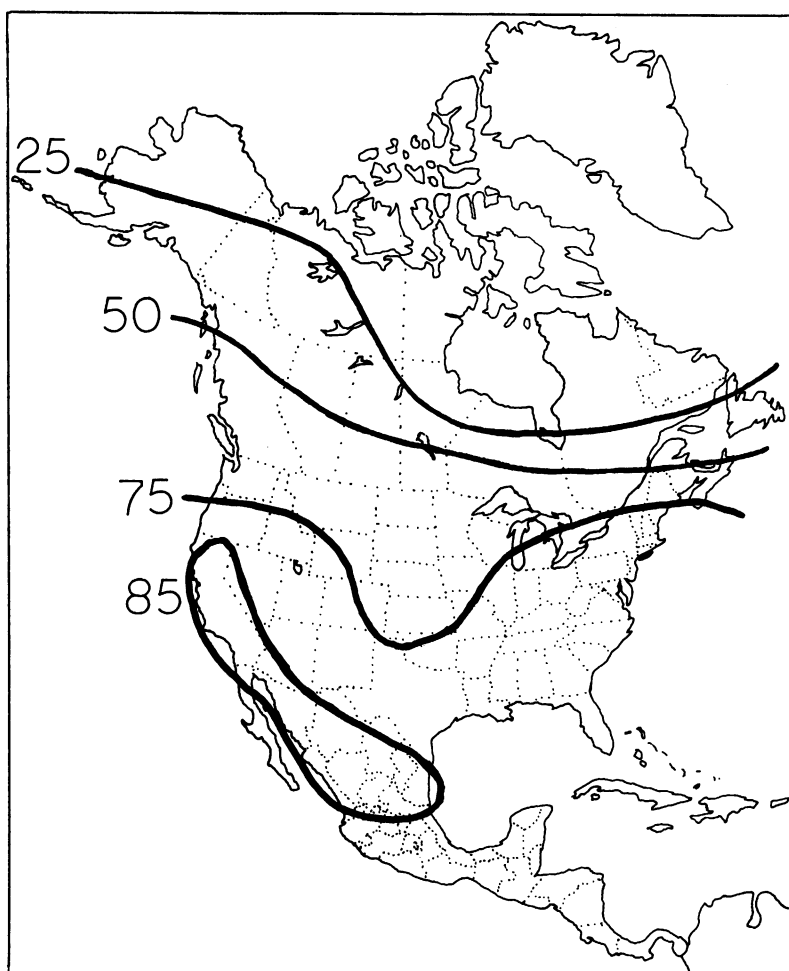


FIG. 6. Species densities of North American endemic passerine birds.

extreme case 100 percent would be present in every local area. At another extreme all species (as an example consider a fauna of 1000 species) could occupy small areas and these could be mutually exclusive (precisely parapatric and non-overlapping), in which case the number present at any one place would be one and the percentage 0.1. At another extreme the species could all occupy the same small part of the continent, in which case the percentage would be 100 percent in that small part and zero elsewhere. Neither birds nor any other group with which I am familiar tend to fit any of these extreme cases, but examination of the theoretical extremes defines limits for the parameters under con-

sideration and helps us visualize how changes in both sizes of ranges and relative positions of ranges will affect the percentage present in any one area. Birds and mammals have the same latitudinal gradients, there being fewer species farther north, so to some degree they approach the third extreme case given above.

Comparison of the species densities shown in figure 5 with the total avifauna of North America and similar comparison for mammals using earlier data (Anderson, 1977) show clearly that a larger percentage of all North American species are present in any one local area for birds than for mammals. The concept here of "present in any one local area" means that the area lies within the geographic

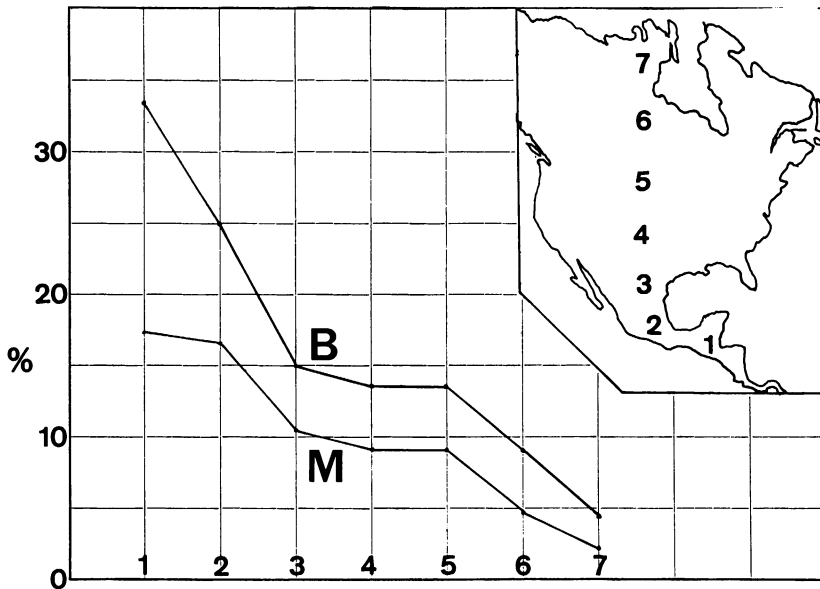


FIG. 7. Graph comparing latitudinal gradients of species density in birds (B) and mammals (M) along the transect shown on the inset map of North America. At all places, the local avifauna includes a higher percentage (%) on ordinate) of the species in the total continental fauna than does the mammalian fauna. The slope of the gradient is nearly parallel for birds and mammals except in the Neotropical area (sample areas 1 and 2).

range of the species, not that an individual bird or mammal is present at a given spot or that a population is necessarily resident at all times of the year.

PREDICTING RANGE-SIZES FROM LOCAL DATA: Figure 7 compares percentages (of the continental fauna present at any one place) for birds and mammals. I hypothesize that the higher percentages for birds than for mammals are a function of larger range-sizes for birds and not a function of different patterns of distribution of geographic ranges relative to each other in the two groups. Possibly some difference in the distributional pattern of birds other than larger ranges could explain or predict the higher percentages for birds, but I have not thought of any such difference.

This relationship between percentages and range-sizes has significance beyond the immediate comparison of birds and mammals. It means that for groups without enough data to draw a complete set of range maps for all species, it may be possible to compare sizes of such ranges by examining the percentages of the continent's species present at one or several places.

To illustrate, in Douglas County, Kansas, a small area with well-known faunas of both birds and mammals, a larger proportion of the continental fauna of birds is represented than of mammals. Figures and sources are:

| Group | No. of species | Continental fauna | % |
|----------------|-------------------------|-------------------|---|
| Breeding birds | 122 (Johnston, 1964) | 1370 | 9 |
| Mammals | 53 (Hall, 1955) | 842 | 6 |

Considering the entire state of Kansas, figures are:

| | | | |
|----------------|-------------------------|------|----|
| Breeding birds | 184 (Johnston, 1965) | 1370 | 13 |
| Resident birds | 234 | 1846 | 10 |
| Mammals | 79 | 842 | 9 |

The generality of this hypothesized correlation should be tested with other sets of data for other localities and other groups.

In order to relate percentages and range-sizes in the above manner, it is necessary to have a reasonably good estimate of the total number of species in the continental fauna

and a few reasonably good samples from local areas. The general patterns of distribution must also be alike in groups to be compared. Since the patterns will never be exactly alike, the differences need to be taken into account in deciding how to select samples, how to measure variables, and how to incorporate differences into explanations and formulation of hypotheses for further study.

AVIAN COSMOPOLITANISM: After excluding introduced species and accidental and casual occurrences of birds from other continents from consideration, 880 of 1760 species in North America also occur in one or more other continents. Thus, a larger percentage (50%) of species of birds than of terrestrial mammals (118 of 929 species, or 13%) extend beyond North America. In other words, bird species are more cosmopolitan in distribution. A quantitative measure of cosmopolitanism was discussed by Rapoport (1982), who summarized data from Voous (1962) for Eurasian birds.

CONTINENTAL DIFFERENCES: Whether there are differences (and, if so, how they may be explained) between continents in the proportions of endemic species or migratory species is an interesting question. Dorst (1974) noted that the Nearctic region does not include a high proportion of endemic forms, is relatively poor in number of species, and includes many migrants. Comparative measurements were not given, however. My data on endemism indicate that 50 percent of the species occurring in North America occur only there. I do not have comparable figures for other continents. Keast, Crocker, and Christian (1959) gave the following comparative figures for numbers of species on different continents: Africa 1750, South America 2500, North America 750, Eurasia 1110, and Australia 651. I know of no quantitative comparative summary of data on migratory species in different continents, beyond Rapoport's (1982) comparisons of African and Eurasian avifaunas.

A COMPETITION HYPOTHESIS: The hypothesis that species of more diverse faunas have smaller geographic ranges than those of less diverse faunas because of competition or narrower ecological niches, was elaborated in some detail and tested with data from North

American bats and rodents and South American bats by Anderson and Koopman (1981). These data weaken the "competition hypothesis" and support an alternative "available space hypothesis." In fact, we found no effect of competition whatsoever in the residuals after we removed the effect of available space from consideration. The concept of competition up to now has not helped in predicting or explaining continental faunal patterns.

I have analyzed data for North American endemic passerine birds, using the same sample sites in North America used in the study of mammals (Anderson, 1977). The restriction to North American endemics was to eliminate the problem of how to handle the parts of ranges outside of North America for species that range beyond this continent. The geometric means for the sizes of geographic ranges of the species present at each sample site have been calculated and are plotted in figure 8 against the number of species present at each site or local area (as defined on p. 8). If the Latin American sites are not considered, there is a negative correlation: the species in more diverse faunas tend to have smaller ranges (for the points other than those labeled L, $r = -0.8635$, and the regression line is: geometric mean = $8.3 \times 10^6 - \text{number of species times } 3.594 \times 10^4$, calculations used arithmetic values rather than logs and the regression line is therefore curved when plotted on a log scale in fig. 8). Whether a correlation such as this has anything to do with "competition" or "niche width," was discussed in greater detail in relation to mammals earlier (Anderson and Koopman, 1981). The birds at Latin American sites in figure 8 may have smaller average geographic ranges because there is less available terrestrial space than farther north rather than because of interspecies competition. The outliers at the left of the Latin American group are two localities in Panama (localities 35 and 36 of fig. 1, in Anderson and Koopman, 1981), and the small number of species here results from the restriction to considering endemic North American species. The inclusion in such an analysis of species occurring also in South America and the South American parts of their ranges probably would result in a pat-

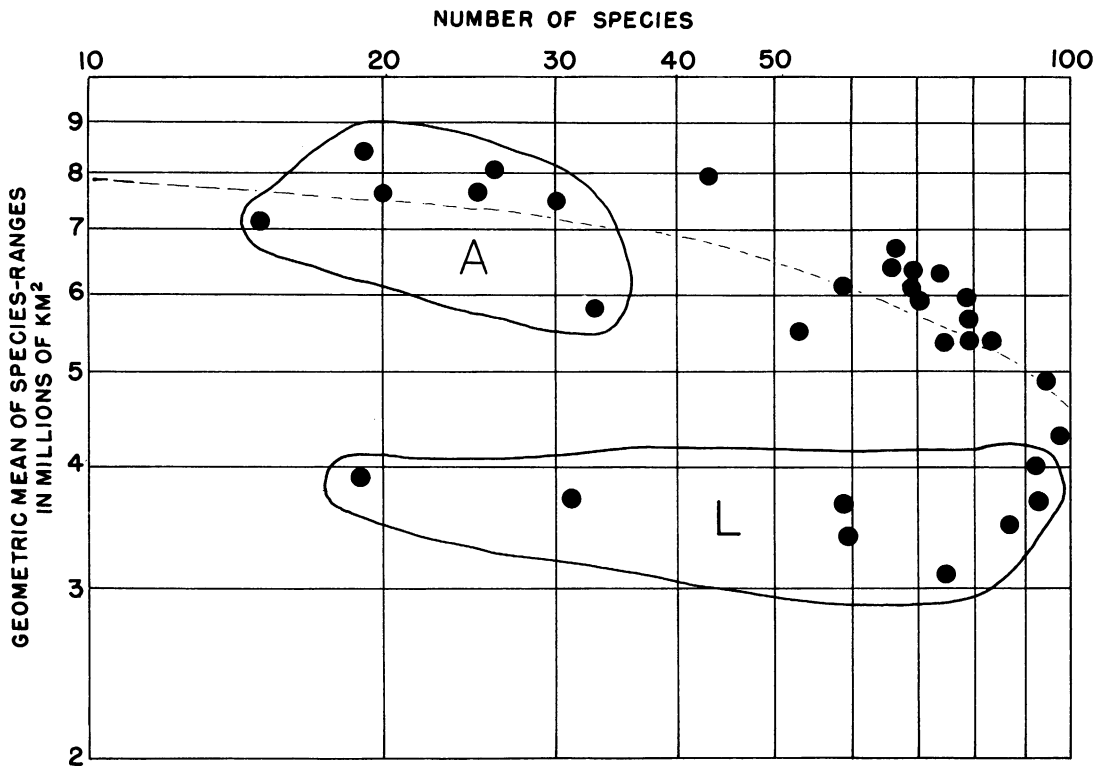


FIG. 8. The relation between diversity and distribution in North American endemic passerine birds. Each point represents a different sample site. The geometric mean of the sizes of the geographic ranges of all species present at the site is plotted against the total number of species present at that site. Sites in the Arctic are marked A and sites south of the United States (Latin America) are marked L. The regression line is for description only and is explained in text.

tern similar to that found for bats when we extended our North American analysis into South America (see fig. 2, in Anderson and Koopman, 1981). This is an interesting hypothesis for future testing (it would, incidentally, take a year of work and would be more difficult than for North America because the detailed ranges of South American birds are poorly known).

In addition to the considerations discussed by Anderson and Koopman, it should be noted that the data for the different points (in fig. 8) are not completely independent, because most species have ranges large enough to occur at more than one sample site.

On one hand, the competition hypothesis (under the conditions discussed by Anderson and Koopman) might predict that birds, having more species, should have smaller ranges

than mammals. If one accepts this hypothesis as relevant at all, the present data do not support the hypothesis. On the other hand, my ornithological colleagues, especially those with ecological orientations, are quick to point out differences between birds and mammals such as three dimensional habitats of birds, more seasonal migration, and, therefore, more "eco-space," that will either "explain" differences in ranges of birds and mammals or discourage any comparison whatsoever of their ranges. I will not attempt to resolve these differences now, but will note that I know of no discussion comparing ranges of birds and mammals, noting the gross difference in range-sizes or the similarity in prevalence of smaller ranges in both groups, or explaining the differences or similarities. Anyone interested in the present status of the general eco-

logical theory of diversity should read Brown's (1981) summary.

Stronger tests of hypotheses of competition may be obtained by studying pairs of selected species or other phenomena at a lower level of generality than the level studied here. Nonetheless, if one is interested in the possible effects of competition at a general level of continental faunas, continental faunas should be examined. Would any amount of study of selected pairs of competing species lead to a prediction of the continental pattern described in this paper? I personally doubt it, but would welcome such a connection if it could be demonstrated. For a recent discussion of the problems and concepts of organizational or phenomenological levels (which is the issue here) see Eldredge (1983).

BREEDING AND WINTERING RANGES: Birds differ from the vertebrates of other classes in North America in the higher proportion of species that migrate and in the relatively greater distances of migration. This raises a question as to whether bird ranges are fundamentally different from ranges of mammals or of other groups of animals. If so, then how should the differences be taken into account in analyses and comparisons of geographic ranges between groups? Do most species of birds have two separate ranges, a breeding and a wintering range? Many birds do migrate, and some groups of birds are more migratory than others; this may require no special documentation. However, I am not aware of any attempt to summarize graphically these generalities or to consider quantitatively the frequencies in general or in particular groups of birds. I therefore examine the frequencies among species of different taxonomic groups (such as orders) of the different degrees of separation of breeding and wintering ranges.

The degree of separation of wintering (W) and breeding (B) ranges was treated as follows: Visual inspection of the mapped ranges shows that W and B are in many cases roughly rectangular or ovoid and the distance of each range from east to west is about twice the distance from north to south. (A greater longitudinal than latitudinal range in many species was noted by Cain, 1944; some data for birds in South America summarized by

Rapoport, 1982, show this less clearly or not at all.) There are many exceptions to this general pattern. These include: (1) species that winter mostly at sea (such as Alcidae), (2) shore birds with highly restricted (narrow) wintering ranges along coasts, especially those restricted to salt water shores (principally Scolopacidae), (3) species that breed only along coastlines (such as some species of gulls and terns), (4) unusually irregular shapes of some ranges. A few species (in the above categories) that did not resemble the general model, some for which I lacked adequate North or South American data, and others occurring also in Eurasia were omitted in the tallies. The number of species included is 458, and all were drawn from the 645 species of birds breeding north of Mexico. The analysis was expanded to include entire species' ranges for species that occur also in South America, but this was not done for species that occur also in Eurasia.

Inclusion of species breeding in North America only south of the United States would have about doubled the number of species in the analysis and would have tended to increase the values at the left of the graph (fig. 9) to even higher levels.

Let R_1 and R_2 represent the smaller and the larger of the seasonal ranges (B and W); let o be the amount of overlap of R_1 and R_2 ; and let d be the distance between R_1 and R_2 . The degree of overlap varies continuously from complete to none as B and W separate and then the possible distance of separation increases from 0 to half the circumference of the globe (in theory if not in fact). This continuum was arbitrarily divided into five classes A through E, as follows:

- A, $o > .5 R_1$
- B, $.5 R_1 > o > 0$
- C, $\sqrt{R_1} > d > 0$
- D, $\sqrt{R_1 + R_2} > d > \sqrt{R_1}$
- E, $d > \sqrt{R_1 + R_2}$

In figure 9 the percentages of species in each of several different orders of birds that fit each of the classes are shown. Clearly, for most species in most groups the breeding and wintering ranges tend to overlap, and greater degrees of separation of these seasonal ranges occur in fewer and fewer species. Although

some of the five orders pooled at the top of the graph (to simplify it) are represented by few species in the analysis, there are differences between these orders. The modal class is B, with C nearly as large, for Anseriformes; the modal class is C for Gaviiformes (four species) and for Podicipediformes (four species); the modal class is B for Pelecaniformes (four species); and the modal class is A for Ciconiiformes (18 species). The Charadriiformes and Gruiformes differ conspicuously from the general pattern. Most species of these orders have separate breeding and wintering ranges.

The major point of this examination of the degree of overlap of summer and winter ranges was to see how nearly bird ranges corresponded to mammal ranges in a general way. Most birds in most orders do not have two separated ranges (but fall in class A as shown in fig. 9). Therefore, it seems reasonable to make general comparisons of avian and mammalian ranges (such as shown in figs. 1 and 2).

Two reviewers suggested that the information shown in figure 9 is well known and that the figure and discussion be deleted. (I am generally skeptical of statements that begin with "It is well known that . . ." Often, closer study indicates that it is difficult to find clear documentation to cite, that there is some reasonable doubt, or that it is not well known.)

It is said to be well known that there are more species with small ranges than with larger ranges as shown in figures 1 and 2. I tested this "hypothesis of well-knownness" by asking several mammalogists to draw graphs (as simple histograms on arithmetic scales) of the distribution of range-sizes and comparing these graphs with a graph of measured values. There is a consistent bias in underestimating the numbers of smaller ranges. I illustrated this (in fig. 1, Anderson, 1977). This part of the graph was included over the objection of reviewers who thought that it was not interesting to know how mammalogists can be wrong. I have recently tested ornithologists in the same way in regard to their understanding of sizes of bird ranges, and ornithologists misjudge the smallness of ranges in the same direction and to roughly the same degree as do mammalogists.

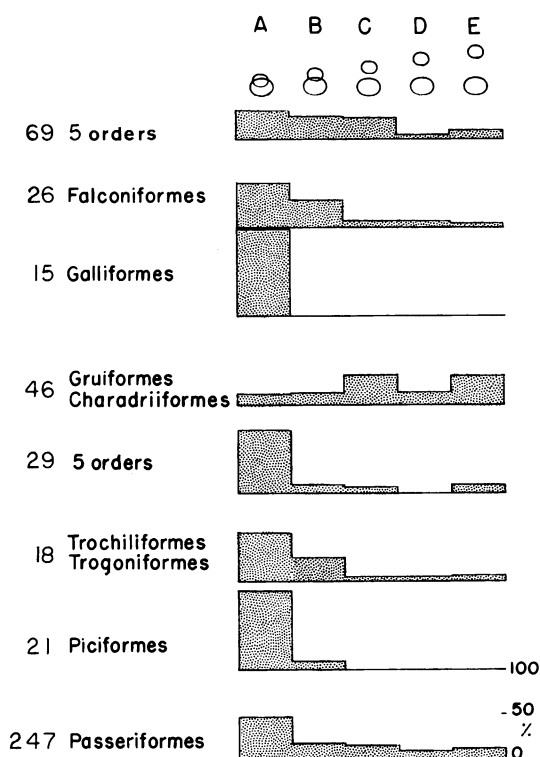


FIG. 9. Graph of various degrees of overlap or separation of breeding and wintering ranges among the species of different orders of North American birds. The diagram at the top suggests the degree of overlap represented in each column lettered (criteria are defined in text). Vertical scales are percentages. Numbers of species are given at the left. The "5 orders" at the top of the graph are Gaviiformes, Podicipediformes, Pelecaniformes, Ciconiiformes, and Anseriformes; the "5 orders" in the middle of the graph are Columbiformes, Cuculiformes, Strigiformes, Caprimulgiformes, and Apodiformes. A graph for all of these groups combined would not be distinguishable from the graph for the passeriforms alone.

EPILOGUE

I have prepared sets of data on sizes of geographic ranges of reptiles, amphibians, and non-marine fish in North America north of Mexico to compare with those of birds and mammals later. After these have been published, I hope to consider some general models relating expansions and contractions of ranges, range-sizes, speciation patterns, ex-

tinctions, and other relevant biological properties of populations and species. I hope, in the meantime, that I have raised some questions here that will encourage others in related investigations.

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