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PATTERNS OF ALPHA-DIVERSITY AND ABUNDANCE IN BREEDING BIRD COMMUNITIES ACROSS NORTH AMERICA

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Community diversity can be examined by noting the number of species within a single habitat of known area (alpha-diversity), the changes in species composition along a series of habitats (beta-diversity), or the total species richness of a large geographic region (gamma-diversity; Whittaker 1960, 1972). The diversity of breeding birds in a community is closely related to the structure of the vegetation (MacArthur and MacArthur 1961, MacArthur et al. 1962, 1966, Tramer 1969, Karr and Roth 1971, Peterson 1975, Roth 1976). Studies of beta-diversity in birds have focused on species composition or rates of species turnover between adjacent habitats (Cody 1970, 1975, Tramer 1974a, Karr 1976). Gamma-diversity patterns have been examined for breeding birds (MacArthur and Wilson 1967, Cook 1969, Bock and Lepthien 1975) and wintering birds (Bock and Lepthien 1974, 1976, Tramer 1974a, b) but these studies based their comparisons on extensive areas which obscured fine patterns of diversity. Since birds respond to the proximate releasers of their habitat (James 1971), not arbitrary geographic blocks, an analysis of local avian communities could provide insights into diversity pertaining to the structure of breeding bird populations.

Cook (1969), Tramer (1974a), and Bock and Lepthien (1974, 1975, 1976) have traced the diversity of North American birds to changes in earth history and its subsequent effects on climate, vegetation, and resource availability. These analyses considered relative species richness and disregarded the effects of relative species abundance, or species equitability. My objectives here are to describe and interpret patterns of species frequency distribution within breeding bird communities in North America.

METHODS

Maps were prepared for the United States and southern Canada depicting breeding bird population density, the number of species, species diversity, and species equitability. These maps show isopleths, lines connecting points along which a given variable has a specified constant value. They are based upon data gleaned from 445 Breeding Bird Censuses (in National Audubon Society publications) conducted between 1936 and 1973. Generally, these censuses are carefully planned and executed; in each census, participants who are familiar with their area follow standardized methods to evaluate the birds within a relatively uniform habitat. They accurately list all species present but are less accurate in estimating the number of pairs present (MacArthur 1965).

I screened individual censuses to ensure that the census plots had mature, relatively homogeneous vegetation. Those censuses containing early seral stages, such as the "old field" of eastern forests, were excluded. The censuses were classified into twelve categories according to the dominant vegetation, closely following those recognized by Küchler (1964). Since the censuses varied considerably in size, only those with areas between 8 and 40 ha (15 to 100 acres) were used in the analysis, to minimize the introduction of bias when calculating population densities. All densities were standardized to the number of territorial males per 40 ha, an estimate of the number of breeding pairs.

Breeding Bird Censuses use the spot-map method (Williams 1936, Kendeigh 1944), which is most effective when censusing landbirds with limited territories. Therefore, I excluded all species that inhabit large bodies of water and certain landbirds such as owls, hawks, or vultures, which have very large territories. Some species that do not establish territories, such as the Brown-headed Cowbird (*Molothrus ater*), were included because they were present in a majority of habitats. The analysis included 310 species.

Alpha-diversity for each census was calculated using the Shannon and Weaver (1963) information theorem,

$$H' = -\sum_{i=1}^{s} p_i \log_e p_i,$$

where p_i is the proportion of species i of the total number of individuals in the population. This is the index most used to calculate alpha-diversity (Pielou 1969). Tramer (1974a) suggested that patterns of resource partitioning within avian communities could be compared on the basis of the relative frequencies of each species in the population. To measure the evenness of species distribution (equitability), I used,

$$J' = H'/\log_e S,$$

where H' is the species diversity of a census with S species, because it allows cross-comparisons of communities that support different species or disparate proportions of species. Logically, if the species are equally distributed, then the habitat and resources necessary for each species should also be equitably distributed.

I used several different mapping programs to confirm results, but will present only maps created by CONTOUR (University of Calgary). The data were analyzed with the CDC 6400 at the University of Arizona. The maps were drawn by a CALCOMP 665 Plotter. Many of the censuses used covered the same plot in different years, hence, the spatial coordinates of their plots were identical. CONTOUR was unable to assimilate these duplications so I averaged cen-

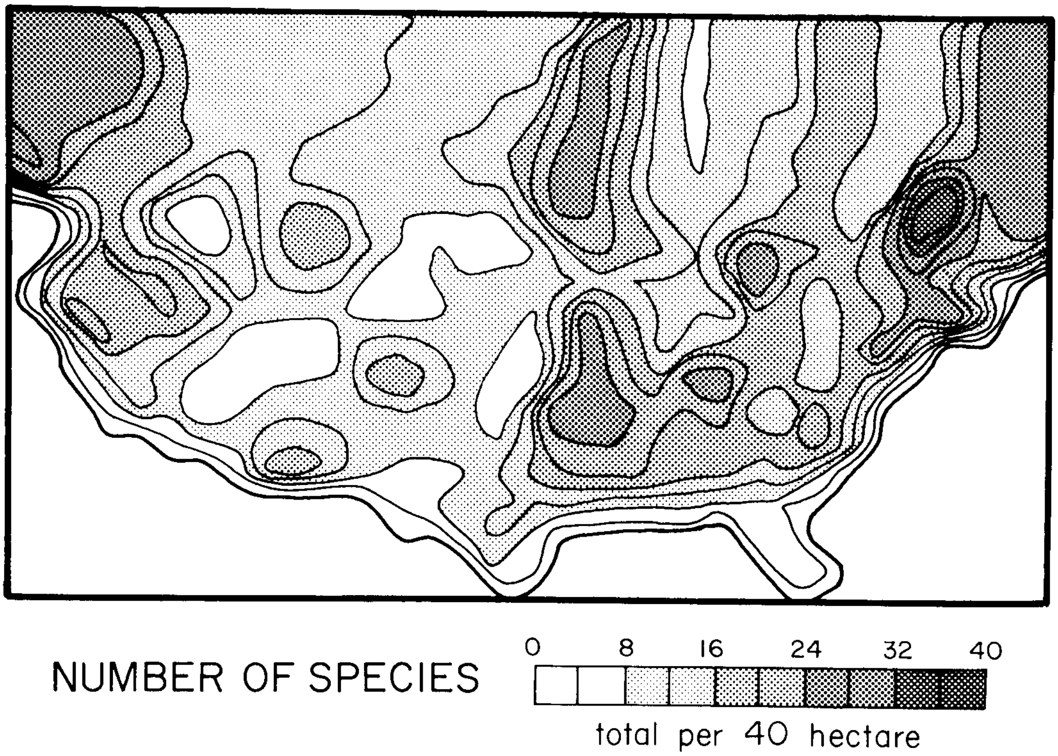

FIGURE 1. The species richness, or simple species count, within homogeneous habitats across North America (based on 445 Breeding Bird Censuses).

suses with the same location to obtain a mean for each of the four indices. A continental outline was drawn by CONTOUR by assigning a zero value to the coordinates of 50 coastal and border cities. This produced a steep border on the maps due to the increment differences between the nearest grid values (calculated by CONTOUR) and the zero value along the outline.

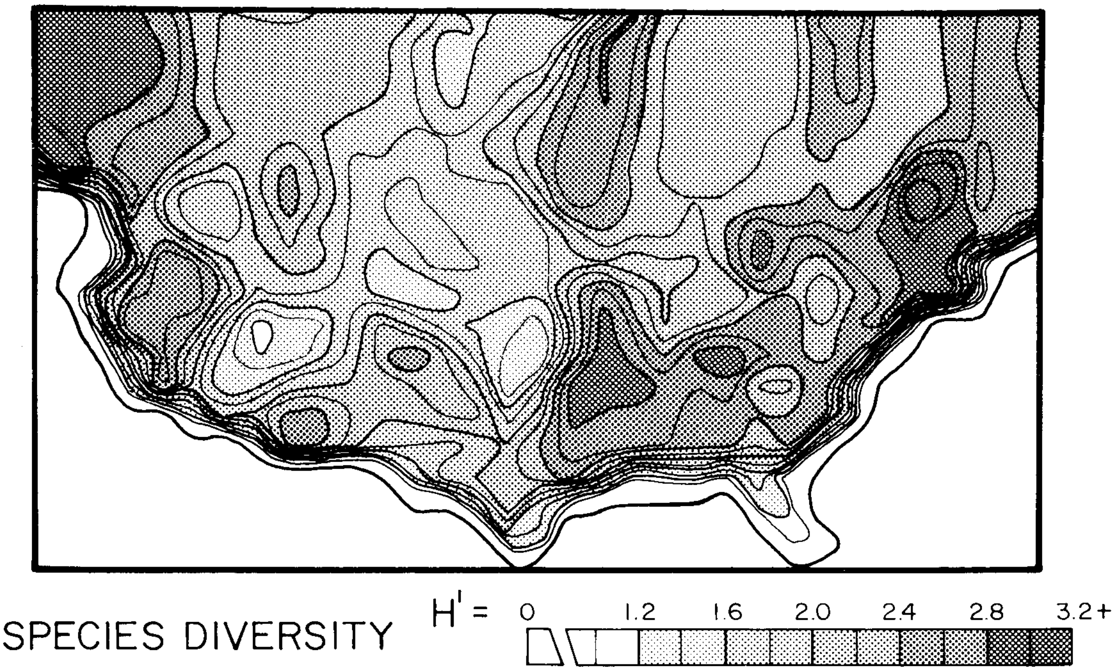

FIGURE 2. Species diversity of breeding birds (see text for explanation), within homogeneous habitats across North America.

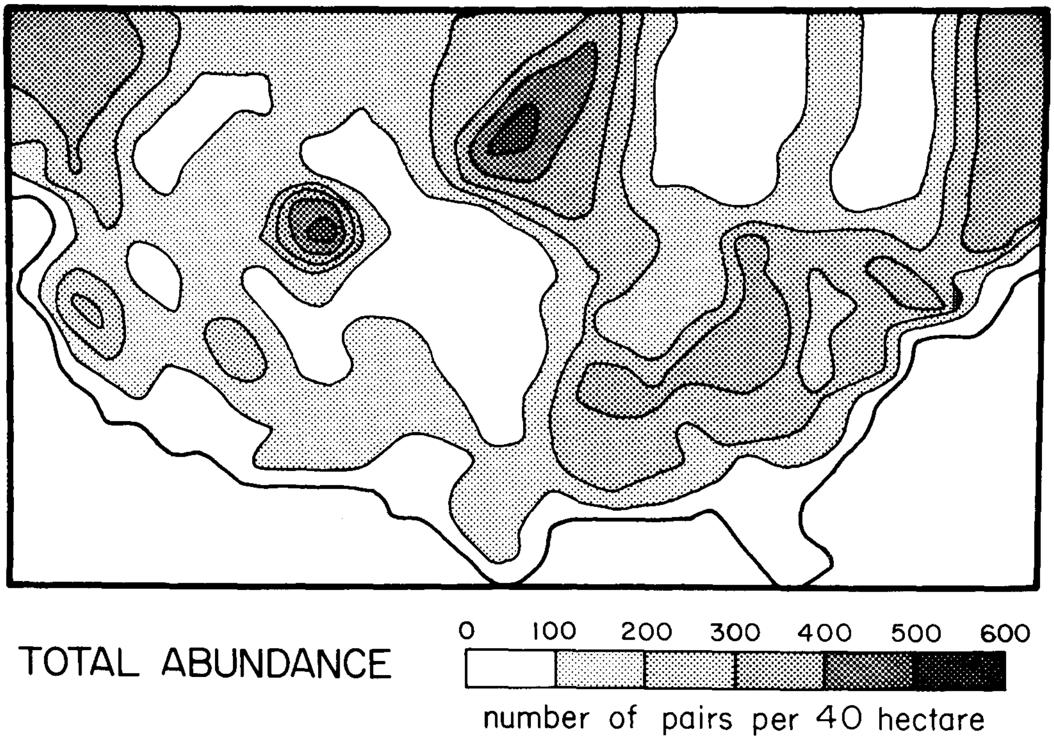

FIGURE 3. Total abundance, or density, of breeding pairs within homogeneous habitats across North America.

RESULTS

Figures 1 and 2 show the similarity between species diversity (*H′*) and the raw number of species present in a community. These maps indicate that diversity is highest in the northeastern forests, mid-continentally along the western Mississippi River drainage and to a lesser extent in the Pacific northwest. Diversity declines westward in the prairie biome.

Landbirds are generally more abundant west of the Appalachian region than in the rest of the eastern forests (Fig. 3). Prairies support the smallest total bird populations. Densities in the west are approximately half those found in the east. Birds are especially numerous in two parts of the north-central region, reflecting the many censuses from marshes there.

Breeding bird equitabilities (Fig. 4) were highest across the southern tier of states, with northward extensions up both coasts. The avifauna was evenly distributed throughout the mid-continental region. Table 1 subdivides the avian populations by habitat type and confirms the geographic patterns shown by the maps.

DISCUSSION

Figures 1 through 4 depict the character of small communities of nesting landbirds across North America. Comparisons with similar studies based on species range maps (MacArthur and Wilson 1967, Cook 1969) or wintering birds (Bock and Lepthien 1974, Tramer 1974a, b) are difficult, since these studies include some waterfowl, or their samples spanned many types of habitats. Breeding Bird Surveys evaluate the avifauna along a changing habitat which has considerable edge effect (24½ × ¼ mi) resulting in an estimate of diversity between habitats. However, Figures 1 and 2 show diversity patterns that are comparable with those in the map constructed by Bock and Lepthien (1975) based upon Breeding Bird Surveys. Table 1 likewise yields interpretations that parallel Peterson's (1975) analysis of species diversity by habitat type. Thus, patterns of alpha-diversity and beta-diversity appear to be similar, differing from gamma-diversity (Cook 1969) primarily in the west because the ranges of many species overlap there (Bock and Lepthien 1975). Combining the species found across vast distances or sampling areas with the propensity for many species creates patterns of more diversity than when considering relatively local populations in homogeneous habitats (this study).

Alpha-diversity in birds can be simply expressed as the number of species present in

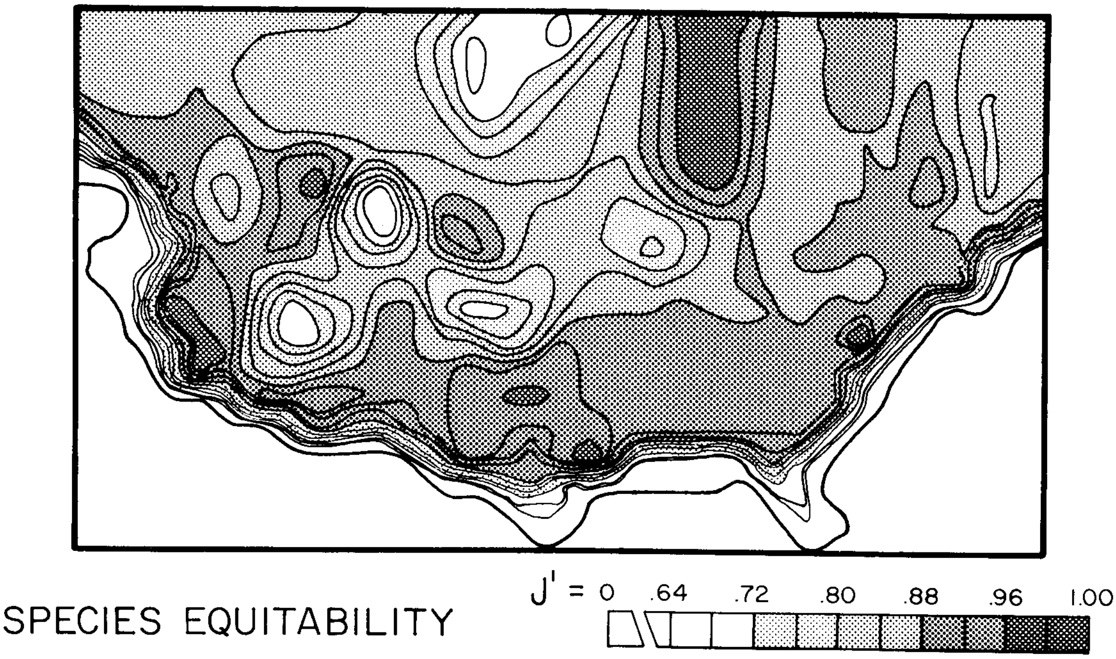

FIGURE 4. The evenness of species distribution (see text for explanation), within homogeneous habitats across North America.

a community (Tramer 1969). Although *H'* (Fig. 2) appears to be more sensitive to small variations than the simple species count (Fig. 1), their isopleths match almost exactly, indicating that these two measures are analogous.

Tramer (1974a) reported that avian alpha-diversity was "virtually constant" throughout the eastern forests. Figures 1 and 2 show no distinct latitudinal gradients in the east, but suggest that this region contains areas of high and low diversity. Birds are most diverse (Figs. 1 and 2) in the vegetationally complex eastern forest communities, not only because of the high numbers of species breeding there, but also because of the dense and evenly distributed populations (Table 1). The areas of slightly lower diversity in the southeast are due to the relatively sterile coniferous forests (Tramer 1974a). These are less complex than

TABLE 1. Means ± standard deviations of four avian population characteristics (based on 445 Breeding Bird Censuses) in twelve habitat types in North America.

Vegetational type (and region)	n	Density (pairs/40 ha)	Number of species	Species diversity*	Species equitability*
Prairie (central)	43	82 ± 37	7.51 ± 3.61	1.626 ± .340	0.845 ± .082
Marshland	33	249 ± 177	8.51 ± 6.12	1.506 ± .667	0.759 ± .166
Dry scrubland (west)	33	141 ± 76	11.45 ± 4.49	2.069 ± .414	0.877 ± .071
Riparian forest (west)	13	360 ± 184	20.46 ± 4.96	2.547 ± .496	0.852 ± .121
Montane coniferous forest (west)	55	201 ± 122	16.03 ± 6.80	2.381 ± .491	0.894 ± .102
Western mixed forest	9	227 ± 127	15.78 ± 8.17	2.066 ± .692	0.797 ± .204
Northern deciduous forest (northeast)	39	253 ± 162	20.53 ± 8.19	2.614 ± .446	0.886 ± .064
Northern coniferous forest (northeast)	48	225 ± 104	18.25 ± 6.10	2.463 ± .382	0.867 ± .079
Northern mixed forest (northeast)	39	220 ± 83	22.64 ± 5.36	2.637 ± .332	0.854 ± .075
Southern deciduous forest (southeast)	62	335 ± 174	20.82 ± 7.55	2.651 ± .384	0.894 ± .043
Southern coniferous forest (southeast)	22	250 ± 85	18.50 ± 4.99	2.515 ± .350	0.879 ± .084
Southern mixed forest (southeast)	49	223 ± 138	18.63 ± 6.35	2.535 ± .435	0.890 ± .064

* See text for explanation.

the deciduous floodplain forests in the Mississippi River basin (pers. observ.), which have relatively more diversity but similar equitability (Fig. 4). The seasonal influx of breeding birds into northern communities probably is responsible for the high diversities in these regions (MacArthur 1959, Tramer 1974a). Higher equitabilities in the eastern forests (Table 1) suggest that resources (nesting sites, food, and mates) are more evenly distributed here than in the west.

Communities with dense, evenly distributed populations would tend to restrict "niche-breadth compensation for low alpha-diversity" (Cody 1975) which is niche expansion by species into depauperate habitats. This restriction apparently is diminished along the ecotone between the eastern forests and the grasslands, where Shugart and James (1973) found typical woodland birds inhabiting grassy successional stages. They believed that this represented an historic adaptation of the forest species to the previous prairie "interdigitations" in northwestern Arkansas, that was not available to the birds in comparable eastern studies (Johnston and Odum 1956). The high diversity found by Shugart and James in the grassy seres represents a type of niche-breadth compensation by the woodland birds in this region.

Cook (1969) and Peterson (1975) found that species diversity increased with an increase in latitude in the mid-continental grasslands. Figures 1 and 2 do not support their findings but show lowered diversity within habitats throughout the prairies, with corresponding low densities (Fig. 3). Cody (1966, 1970) and Wiens (1969, 1973) noted this phenomenon, which results from a combination of environmental and vegetational factors there. The uneven distribution of the avifauna (Table 1) suggests that a few species are dominating these communities. Wiens (1974) reported a dominance of medium-sized birds in shortgrass prairies and Tramer (1969) showed that marshland aggregations of breeding birds are often unevenly distributed because of behavioral differences in nesting and feeding. The marshland censuses used in my study typically contained high numbers of Red-winged Blackbirds (*Agelaius phoeniceus*) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), whose gregarious behavior created peaks of high nesting density in the northern grasslands (Fig. 3) with less equitable distribution of the species (Fig. 4) in the same regions.

Species diversity is steeply graded in the west (Figs. 1 and 2) with less overall change in densities (Fig. 3) from place to place. Diversity within habitats decreases eastward in response to the high north-south mountain ranges. MacArthur and Wilson (1967), Cook (1969) and Bock and Lepthien (1975) found similar patterns of gamma-diversity, especially in the Great Basin region. Habitats having mostly evenly-spaced vegetation (montane coniferous forests and dry shrubby communities) also have evenly distributed avifaunas (Table 1).

Historical explanations have been offered not only for avian speciation (Miller 1951, Mengel 1964, 1970), but also gamma-diversity of wintering birds (Tramer 1974a) or breeding birds (Cook 1969), and avian alpha-diversity in Florida (Noel Wamer, pers. comm.). Regional patterns of avifaunal richness doubtless persist as a result of Pleistocene glaciation that repeatedly separated and reunited large tracts of habitat and the birds that lived there. However, local populations of birds probably are more responsive to short-term environmental fluctuations than to geologic events which take thousands of years. Bock and Lepthien (1975) found that breeding bird diversity in North America was correlated primarily with relative moisture and to a lesser degree with temperature. Figures 1 and 2 show the same patterns in diversity, which reflect the moisture patterns in North America described by Visher (1966). The mountain ranges in the Great Basin region influence avian diversity by their effects on the type and availability of moisture and habitat.

Winter environmental conditions can also affect diversity during the breeding season (MacArthur 1959, Fretwell 1972, Tramer 1974a) by limiting resources which might affect the evenness of species distribution. My map of breeding bird equitability (Fig. 4) resembles Bock and Lepthien's (1974, 1975) diversity map of wintering birds; therefore, I visually compared my map to the climatic maps in Visher (1966). Figure 4 resembles the maps of temperature patterns more than those of precipitation-humidity regimes, which are more longitudinal. The equitability of breeding birds also bears a remarkable likeness to various temperature-related patterns such as: (1) regions with hot summers and cold winters, (2) a decreasing probability of frost during late spring, (3) the proportion of moisture falling as snow, (4) the date when the mean daily temperature rises above or, (5) falls below 35°F, the temperature at which some vegetative growth occurs.

The region of low equitabilities (Fig. 4) also resembles Mengel's (1964) composite picture of the maximum extent of the Pleistocene glaciation, especially the subarctic components. This may indicate a historic relationship between temperature and avian equitability.

Avian communities with high diversity usually occupy diverse habitat which is closely related to the amount of available moisture. High equitability of breeding birds implies equal distribution of the habitat and its resources among the species. Those communities with high equitability probably reflect more stable year-round production of resources than those with large oscillations of the avifauna. Overall annual production of resources is higher in the south than the north, due to more solar input. Although southern communities have fewer neotropical migrants (MacArthur 1959) to exploit the resources than northern communities, both the northeast and northwest display very high equitabilities (Fig. 4) along with the southern deserts and swamps. This appears to be contradictory unless the stabilizing effect of moisture on temperature is considered; the northwestern and northeastern regions receive maritime buffering which moderates temperatures. Evidently, breeding bird diversity depends on the habitat of the community, which reflects the moisture regimes of a region. The evenness of species distribution appears to be related to resource availability and stability, which reflect temperature regimes and glacial history.

SUMMARY

Isopleth analysis of Breeding Bird Census data was used to examine patterns of within-habitat species richness, diversity, and abundance in North America. Richness and diversity were parallel measures; they were high in the east and northwest and low in the prairie and intermountain regions. Densities in the east were approximately twice those of the west, with a large mid-continental trough. The species were evenly distributed across the south and northward along both coasts. The equitability of species abundance appears closely tied with weather patterns relating to temperature and its effects on resource equilibrium.

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RECENT PUBLICATIONS

Ducks, Geese & Swans of North America.—Frank C. Bellrose. 1976. Stackpole Books, Harrisburg, PA. 540 p. $15.00. Here is a completely new and expanded version of the classic work by F. H. Kortright, which first appeared in 1942. Introductory chapters treat classification, molts and plumages (by Milton W. Weller), migration, conservation (by Glen C. Sanderson), hunting regulations (by Arthur S. Hawkins), identification technique, and mortality and disease. The species accounts cover measurements, identification, populations, distribution, migration, breeding, postbreeding activity, and food habits. Virtually the only unchanged elements of the original are T. M. Shortt's color plates, and even these are now grouped together and some of them are not well printed. New additions are many maps of ranges and migration corridors and the graphs of seasonal/geographic population changes. List of references, appendixes, index. This book contains a wealth of clearly-organized information, especially on migration and populations. It will be invaluable to ornithologists as well as waterfowl researchers, managers, and hunters. For an in-depth comparison of this work with those by Paul A. Johnsgard and by Ralph S. Palmer, see the special review by Milton W. Weller (1977. Auk 94:172–177).

Ducks, Geese, and Swans of the World.—Paul A. Johnsgard. 1978. University of Nebraska Press, Lincoln. 404 p. $35.00. The indefatigable Dr. Johnsgard has provided here a systematic review of the biology of every recent species (148) in the family Anatidae. No such comprehensive work in English has appeared since the classic multi-volume treatises by Phillips and by Delacour, which have long been out of print and are very scarce. This book complements the author's previous ones on waterfowl and summarizes his long-term studies on their comparative behavior and relationships. Each species account gives vernacular names, a list of subspecies, if any, measurements and weights, identification and field marks, natural history, status, relationships, and suggested readings. The book is attractively designed and generously illustrated with drawings, distribution maps, and color photographs, all by the author. It will be an invaluable starting reference on waterfowl, particularly for those species that are not covered in regional works on these birds.