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HOW MANY SPECIES OF BIRDS HAVE EXISTED?

PIERCE BRODKORB [1]

SYNOPSIS: The present world avifauna is composed of about 8650 species. During the Pleistocene and late Tertiary the avifauna was larger, with about 11,600 species living at any given time. Before the adoption of the granivorous habit in the mid-Tertiary, the avifauna was smaller, with an estimated 10,200 contemporaneous species. The Crataceous avifauna consisted mainly of aquatic birds and contained about 1000 contemporaneous species. In the late Jurassic the avifauna was negligible, with probably not more than 100 species existing at any one time.

The average longevity of avian species is considered to be the equivalent of the time needed to replace half the fauna. Based on the rate of extinction in Pleistocene faunas, the average longevity is estimated at about 500,000 years.

Multiplying the number of contemporaneous species by the duration of a given epoch and dividing by the average species longevity gives the number of species evolved during that epoch. Addition of the epochal totals gives the number of species that have existed since the origin of class Aves. This is estimated to be about 1,634,000 species. The described living and fossil birds total about one-half of one percent of those potentially knowable.

The living birds are a numerous and well-known group, but knowledge of their fossil history is still fragmentary. It is nevertheless of interest to speculate on the number of species of birds that have existed throughout time, and to estimate the ratio of presently known to potentially knowable species of birds.

The most recent counts or estimates of the number of known living species of birds total 8590 (Mayr and Amadon, 1951), 8809 (Brodkorb, 1957b), and 8548 (Van Tyne and Berger, 1959). The mean of these three estimates is 8649 species, and they differ by less than 3 percent. As the number of living species still unknown is negligible and probably amounts to less than 100 undescribed species (Mayr, 1946), we may use the figure of 8650 as the approximate number of living species of birds, described and undescribed. It is doubtful that this figure will change radically.

The quarter-century since the publication of Lambrecht's "Handbuch der Palaeornithologie" (1933) has been a prolific one in the description of new species, but a recently completed manuscript catalog of the known fossil birds of the world includes only 834 species ex-

[1] The author, Professor of Biological Sciences at the University of Florida, first presented this paper at the Seventy-seventh Stated Meeting of the American Ornithologists' Union at Regina, Saskatchewan, 26 August 1959. Manuscript received 1 November 1959.

tinct prior to the technical description of the living fauna. Although in other classes of tetrapods the number of known extinct species exceeds the number of living ones, in birds the known extinct species total less than one-tenth those living today.

Methods

Three types of information are needed to form an estimate of how many species of birds have existed. First, we need an estimate of the number of environmental niches available to and used by birds during the different epochs. This gives the approximate number of species living simultaneously in any given epoch. Second, we need an estimate of the longevity of avian species, the time needed for one species to be replaced by another. The average longevity of species gives a figure on the rate of replacement or turnover of species. Third, we need an estimate of the duration of the various epochs in years.

For a given epoch, the number of contemporaneous species multiplied by the duration of the epoch in years, divided by the average species longevity, gives the total number of avian species that originated during that epoch. This may be expressed by the following formula:

$$\frac{SD}{L} = N$$

where

S = number of contemporaneous species per epoch;
D = duration of epoch in years;
L = longevity of species in years;
N = number of species evolved during the given epoch.

The totals for the various epochs may then be added to obtain the approximate number of species evolved since the class Aves appeared.

Pleistocene Avifaunas

All living species of birds are thought to have been in existence during the Pleistocene (Howard, 1950; Wetmore, 1959), and about 732 living species are already recorded from that epoch. As 272 extinct Pleistocene species are also recognized, the avifauna during the Pleistocene was larger than now, and the birds as a group have passed their climax (Wetmore, 1951).

An estimate of the size of past avifaunas, to be meaningful, must include an analysis of past environmental conditions. Those that contributed to extinction during the Pleistocene include changes in temperature, rainfall, sea level, and vegetational types.

Lowered temperatures during the glacial ages of the Pleistocene and elevated temperatures during the interglacial ages undoubtedly caused some shifting of the ranges of bird species, either directly or, more probably, indirectly through changes in vegetational zones. Yet effectually lowered temperatures apparently did not extend far beyond the southern limits of glaciation. In North America, the most heavily glaciated area in the world, effectual cooling during times of glaciation reached only about 700 miles south of the southern limits of the ice sheets, for many warm-adapted species remained that close to the ice front (Brodkorb, 1957a, 1959a). Furthermore, in the tropics temperature changes must have been negligible, for while a northern crane is known to have crossed the equator to Java (Wetmore, 1940), most species recorded from Pleistocene sites in the Greater Antilles (Wetmore, 1922, 1937), Brazil (Winge, 1887), and India (Lydekker, 1886) are of species living in exactly the same places today, with little or no indication of an influx of temperate zone types. Therefore it is concluded that refrigerative effects in the Pleistocene were confined to relatively narrow bands in the temperate zones, and the tropics were of minor importance as refugia for species fleeing lowered temperatures during times of glaciation.

Other environmental factors may have been of more importance and seem to have operated on a world-wide basis. The repeated pluvial and interpluvial stages must have had profound effects on the vegetation, both in the tropics and in the temperate zones. Low-lying lands experienced repeated submergence and emergence with fluctuations in ocean levels, which retarded or altered the seral succession of the vegetation (Brodkorb, 1959a). The exposure of the continental shelves during the glacial stages afforded broader connections between formerly isolated areas and allowed entrance of competitors and predators at the expense of less aggressive types. The effects of fluctuating ocean levels must have been greatest on islands such as the Bahamas, where the extinction of the Pleistocene fauna is thought to have resulted from a rising sea which so fragmented and inundated the former large land mass that insufficient area remained to support the fauna (Brodkorb, 1959b). All these factors must have contributed to the extinction of forms in the tropics as well as elsewhere during the Pleistocene.

In calculating the size of the avifauna living contemporaneously during the Pleistocene, the probability must be taken into account that certain species were restricted to different parts of the epoch. Thus data for the late Pleistocene alone give a more reliable estimate of the size of the contemporaneous avifauna than data for the entire epoch.

From the late Pleistocene of North America and the West Indies Wetmore (1956) lists 248 species, of which 185 are living forms and 63 extinct. Most Pleistocene avifaunas from other parts of the world are small, inadequately dated, or insular. Nevertheless, the numerous extinct species recorded from New Zealand, Australia, and Madagascar suggest that the late Pleistocene avifaunas of other parts of the world were comparably large. In the absence of adequate information from other continents, the North American ratio of living to extinct species is assumed to be typical of the world situation.

By projecting to a world-wide basis the ratio of living to extinct species in the late Pleistocene avifauna of a part of the world, such as North America, a proportion may be formed which allows approximation of the size of the late Pleistocene avifauna of the whole world. The ratio of living to total species recorded from the late Pleistocene of North America should be roughly proportional to the ratio between the number of living species in the world and the total late Pleistocene world avifauna. This relationship may be expressed by the formula:

$$NL : NT :: WL : WT$$

where

NL = North American living species recorded from late Pleistocene;

NT = North American total species recorded from late Pleistocene;

WL = world living species today (and hence in the late Pleistocene);

WT = world total species in late Pleistocene.

Substituting,

$$185 : 248 :: 8650 : WT$$
$$WT = 11{,}596$$

Thus approximately 11,600 species of birds are thought to have lived during the late Pleistocene.

Late Tertiary Avifaunas

In the history of plant evolution the major event of the Cenozoic era was the expansion of alpine and xeric habitats (Stebbins, 1947). As these habitats became established during mid-Tertiary times, there is little reason to believe that the number of species of birds existing simultaneously during any given portion of the Pliocene or Miocene was markedly less than in the Pleistocene. It may in fact have been considerably greater than the number during the Pleistocene, when the environmental factors already discussed became operative. Therefore the Pleistocene figure of 11,600 may be used as a conservative estimate of the number of contemporaneous species of birds during the late Tertiary epochs.

Early Tertiary Avifaunas

As pointed out above, the mid-Tertiary was characterized by the expansion of alpine and xeric habitats. At this time a great increase and radiation occurred among the Gramineae and certain other plant families (Stebbins, 1947). Although three genera of grasses are known from the early Tertiary (LaMotte, 1952), grasslands did not become widespread or ecologically important until the Miocene (Elias, 1942; Chaney, 1947). The expansion of the grasslands is almost universally correlated with the development of hypsodonty in mammalian evolution, a condition that appears to have been initiated in more groups during the Miocene than in any other epoch (White, 1959). It is thus reasonable to believe that grassland-inhabiting and grass seed-eating birds formed an insignificant part of the avifauna prior to the Miocene.

The granivorous birds may be divided into two sections, the primary granivores, which seem to have developed in response to the new biotype, and secondary granivores belonging to pre-Miocene families which underwent a secondary adaptive radiation as some of their members developed the habit of feeding on grass seeds.

The Fringillidae (Emberizidae of certain authors) form the most important family of primary granivores. Apparently this family was among the latest to develop and to undergo adaptive radiation, for it is structurally advanced, both externally and in the skeleton (Ashley, 1941; Wetmore, 1957; Storer, 1959). It appears to have arisen from New World insect-eating ancestors (Tordoff, 1954). In the modern fauna the family Fringillidae contains about 289 species, most of them confined to the New World.

Other primary granivorous families include the Turnicidae (14 species), Pedionomidae (1 species), Thinocoridae (4 species), Pteroclidae (16 species), and Alaudidae (75 species). These too probably did not arise or at least did not exhibit much speciation until the Miocene, with the possible exception of the Pteroclidae, which are recorded from the Oligocene.

The secondary granivores include members of seven other families of earlier origin, some of whose species adopted the grain-eating habit and thus underwent a second, mid-Tertiary radiation within each family. The leading family is the Ploceidae, which seems to have arisen in the Old World, where it is now more or less the ecological counterpart of the Fringillidae in America. No less than 342 of its 385 species have become granivorous, the exceptions lying in the subfamily Carduelinae, the only ploceid subfamily that spread to America.

The secondary group also includes representatives of six other families, most of whose members still feed largely on food other than grain. These families, with the estimated number of grain-eating species in the modern fauna, are as follows: Tinamidae (16 of 43 species), Phasianidae (71 of 149 species), Columbidae (115 of 307 species), Psittacidae (37 of 326 species), Icteridae (40 of 88 species), and Thraupidae (7 of 232 species).

Primary and secondary granivores accordingly total about 1027 species at present, or about 11.9 percent of the Recent avifauna. Prior to the Miocene, therefore, the late Tertiary number of coeval bird species should be reduced by 11.9 percent, for an estimated total of 10,200 species of birds living simultaneously during a given portion of the early Tertiary.

Mesozoic Avifaunas

The angiosperms control many of the biotypes in which land birds live, and the invasion of birds into these environments necessarily followed the development of the habitats. The angiosperms underwent their first burst of radiation in the Cretaceous, with the evolution of woody plants adapted to subtropical or tropical forest conditions (Stebbins, 1947).

A few land birds probably existed during the Cretaceous, but the species must have been limited in number before the radiation of the flowering plants and while the reptiles still dominated. All known Cretaceous birds are water birds, as *Caenagnathus* Sternberg (1940) appears to be a reptile. The water birds comprise about 1014 species in the Recent fauna. Although the land birds may have begun their expansion before the close of the Cretaceous, the average number of bird species living contemporaneously during different parts of the period is estimated as approximately 1000.

The oldest undoubted birds are of late Jurassic age, and there is little reason to suspect that the Class Aves arose much earlier, certainly not before middle Triassic time (Gregory, 1955). The number of species of birds living during the late Jurassic must have been negligible, and one-tenth the Cretaceous number, or 100 contemporaneous species, is arbitrarily assigned to the Jurassic.

Longevity of Avian Species

Students of other groups of animals have estimated the length of life of a species without, however, indicating the basis of the estimates. Teichert (1956) gives the mean length of an epoch, 12 million years, as the top limit of longevity for any animal species. Simpson (1952) estimates the average length of life of an animal species as from 500,000 to 5,000,000 years. With birds the available evidence indicates that both the top limit of longevity and the average longevity of a species are shorter than in many other groups, as might be suspected from their high rate of metabolism.

Almost no avian species are known to cross epochal lines. The few so recorded fall into two groups, those occurring on both sides of the still equivocal Pliocene-Pleistocene boundary, and a few Tertiary forms inadequately known and thus perhaps incorrectly identified at the specific level. These moot cases do not invalidate the conclusion that the top limit of longevity is less than the duration of an epoch.

Living species of birds first appear in deposits of so-called "Blancan" provincial age, assigned by different authors to the late Pliocene or to the early Pleistocene (cf. Hibbard, 1958). Records of living species of birds in older Tertiary (Merriam, 1916) or even Cretaceous deposits (Shufeldt, 1915: 25) have been shown to be misidentifications (Lambrecht, 1933: 583; Brodkorb, 1956). As the beginning of the "Blancan" is variously estimated as from 1,000,000 to 4,000,000 years ago, the top limit of longevity of avian species must fall within those limits.

Specific longevity is a variable, as evolutionary rates differ in separate phyletic lines. One line may give rise to several distinct lineal species while another line remains unchanged. Although evolutionary rates have been little studied in birds, enough data are available to indicate that the rates do differ between lines. For example, the quail *Colinus hibbardi* occurred in the latest Pliocene (Wetmore, 1944). By the third glaciation of the Pleistocene it had been replaced by *Colinus suilium*, which in turn was supplanted by the living *C. virginianus* by the fourth glaciation (Brodkorb, 1959a). Yet the living mourning dove, *Zenaidura macroura*, has persisted apparently unchanged since the late Pliocene. Because of such different rates of evolution it is thought that the average longevity, rather than the top limit of longevity, is the datum needed in calculating evolutionary rates.

When the longevities of the various phyletic lines represented in a fauna are normally distributed, the fauna will be composed of a few species of short longevity, a few species of great longevity, and a majority of species of intermediate longevity. For example, assume that a fauna consists of 12 phyletic lines whose longevities are as follows: n years for species A; $2n$ years for species B and C; $3n$ years for species D, E, and F; $4n$ years for species G, H, and I; $5n$ years for species J and K; and $6n$ years for species L. The average longevity is $3.5n$ years; in this time half the original species will have been replaced. Thus the average longevity is equal to the time needed to replace half the fauna when longevities are normally distributed. When the longevity curve is somewhat skewed, the time needed to replace half the fauna should still be roughly equivalent to average specific longevity.

In table 1 several Pleistocene avifaunas are analyzed on the basis of the time required to replace half the fauna. It is obvious that extinction rates from IV glacial time to the present are not typical of the whole Pleistocene. If these rates were applicable to earlier portions of the Pleistocene, then complete replacement of the avifauna should have occurred between III glacial time and the present, whereas about 78 percent of the III glacial birds represent living species. Complete replacement of the avifauna does not even occur during the interval between the I interglacial and the present, during which interval, on IV glacial rates, the fauna should have been entirely replaced several times. As other factors are obviously distorting the extinction rate in the IV glacial stage, data from that stage alone cannot be used to determine the extinction or evolutionary rates for longer periods.

Fifty percent extinction must have been reached between the III glacial and I interglacial stage, as extinct species comprise approximately 22 and 68 percent of their faunas, respectively. The times estimated as necessary to reach 50 percent extinction on the data from these two stages are similar, 420,091 and 518,366 years, respectively. Thus it is concluded that the average longevity of Pleistocene avian species is approximately one-half million years, and the top limit of longevity approximately one million years.

TABLE 1

LONGEVITY OF AVIAN SPECIES

Locality and stage	Years before present	Total species	Extinct species	Percent extinct	Estimated average longevity in years
Florida, mid-IV glacial [1]	17,000	63	6	9.5	89,474
California, IV glacial [2]	25,000	121	22	18.2	68,681
Florida, III glacial [3]	184,000	70	16	21.9	420,091
Idaho, I interglacial [4]	691,500	9	6	66.7	518,366

[1] Combined faunas of Seminole Field, Melbourne, and Rock Spring, Florida (Wetmore, 1931; Woolfenden, 1959). Years for stage based on radiocarbon averages (Horsberg, 1955).

[2] Combined faunas of Rancho La Brea, McKittrick, and Carpinteria, California (Miller and DeMay, 1942; with additions by A. H. Miller, 1947, and Dawson, 1948). Years for stage based on radiocarbon averages (Horsberg, 1955).

[3] Combined faunas of Reddick, Arredondo, Haile, and Williston, Florida (Brodkorb, 1953, 1957a, 1959a; Holman, 1959). Years for stage based on geological evidence (G. F. Kay, 1931).

[4] Hagerman, Idaho, fauna (Brodkorb, 1958). Years for stage based on geological evidence (G. F. Kay, 1931).

It is probable that the rate of evolution is rapid following ecological access to a new habitat, slower and more steady when physical and biological environments are more stable. In view of the environmental changes outlined previously, two phases of rapid evolution might be expected, one near the Mesozoic-Cenozoic boundary when the angiosperms were expanding, and one in the Miocene following the spread of grasslands. As data to test this hypothesis are not yet available, the Pleistocene rate is here applied to other epochs.

TOTAL SPECIES EVOLVED

As explained in the section on Methods, the number of species that evolved during an epoch may be determined by multiplying the number of contemporaneous species by the duration of the epoch and dividing by the average species longevity, according to the formula $\frac{SD}{L} = N$. Addition of the species evolved during each epoch gives the total number of species of birds which have existed since the origin of the class. The duration of the epochs are taken from M. Kay (1955) for the Mesozoic and Tertiary, from G. F. Kay (1931) for the Pleistocene.

The total number of birds, past and present, is estimated at approximately 1,634,000 species (table 2).

TABLE 2

ESTIMATED NUMBER OF AVIAN SPECIES

Epoch	Span in millions of years	Contemporaneous Species	Species evolved
Pleistocene	1	11,600	23,000
Pliocene	10	11,600	232,000
Miocene	15	11,600	348,000
Oligocene	10	10,200	204,000
Eocene	25	10,200	510,000
Paleocene	10	10,200	204,000
Upper Cretaceous	25	1,000	50,000
Lower Cretaceous	30	1,000	60,000
Upper Jurassic	15	100	3,000
Total			1,634,000

It should be emphasized that all the data used in arriving at the estimate are inexact, and future refinements in both data and methods may radically alter the total. Wherever a variable exists the more conservative choice has been selected, and future revision may result in an increase over the current estimate. For example, the land bird fauna may actually have expanded in the late Cretaceous rather than in the early Tertiary as here assumed. This would increase the total by several hundred thousand species. In any case, the 9500 living and fossil birds now known represent an infinitesimal fraction, about one-half of one percent, of the species potentially knowable.

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