ON ESTIMATES OF THE PAST NUMBERS AND OF THE AVERAGE LONGEVITY OF AVIAN SPECIES

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ESTIMATES of the numbers of avian species thought to have lived con-
temporaneously during various past geological epochs and of the average
longevity of Pleistocene avian species have been made by Brodkorb
(1960). He emphasized that: "all the data used . . . are inexact, and
future refinements in both data and methods may radically alter the
total." However, some of his results are being increasingly quoted and
elaborated (Austin, 1961; Fisher, 1964; Fisher and Peterson, 1964;
Grossman and Hamlet, 1964). It seems, therefore, worth while to point
out difficulties of using the material available and of applying statistical
methods to them in such a way as to secure valid results. In particular,
apart from any other considerations, the reasoning and the statistical
treatment depend to a great extent on a tacit assumption that the North
American and the world avifaunas, past and present, are so far homoge-
neous within themselves and between themselves as to be uniform from
the evolutionary point of view and fully comparable. There are reasons
to doubt this.

The essence of Brodkorb's arguments is contained in the following
quoted extracts, (a)-(c).

(a) [p. 44] 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. [Table 1.]

(NL and NT are derived from Wetmore's (1956) list of fossils of North
America and the West Indies. Here the geological terms used include

TABLE 1*

LONGEVITY OF AVIAN SPECIES

Locality and stage	Years before present	Total species	Extinct species	Per cent 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

* Directly from Brodkorb's table 1.

[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, 1957, 1959; 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, 93).

both "Pleistocene" and "late Pleistocene." It is understood that the former is an inclusive term, not intended to exclude the latter.)

(b) [p. 48] 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 3.5 n 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.

[pp. 48–49] 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.

(c) [pp. 49–50] . . . 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.

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

* Directly from Brodkorb's table 2.

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

THE "LATE PLEISTOCENE"

The formula quoted in extract (a) is applied to a period described as "the late Pleistocene." This is not defined in the paper under discussion, but Brodkorb kindly informs me that this period "would extend to about 500,000 b.p. [before present], although most of the late Pleistocene avian localities (i.e., deposits) in question would not be older than 25,000 years." Now the last 500,000 years are understood to cover approximately both the last two glaciations and the last interglacial periods. Brodkorb (p. 43) has held the view that "effectually lowered temperatures apparently did not extend far beyond the southern limits of glaciation,"[1] but we now know otherwise. During the glaciations the climate at even the lowest latitudes was quite 5°C cooler than it is now and during the interglacials it was up to some 2°C warmer. With these changes were associated effects on world circulation and precipitation that, though still the subject of controversy, were certainly considerable. The result was enormous fluctuations in the areas occupied by the various biomes (see reviews in Moreau, 1955, 1963). In the face of such changes it is difficult to accept as valid the generalization of a figure for "world total species

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[1] His point that "most species recorded from Pleistocene sites in the Greater Antilles . . . , Brazil . . . , and India . . . are of species living in exactly the same places today" has no cogency unless the fossils concerned can be shown to be contemporary with the height of a glacial phase (i.e., in neither an interglaciation nor an interstadial), and in any case water-birds and large raptors greatly predominate in the fossils—groups which from their especially wide geographical ranges evidently have, on average, greater temperature tolerances than most birds.

in the late Pleistocene" when this is regarded as extending over half a
million years of extreme climatic and biological fluctuation—even though
by context contemporaneous species are intended; and it is still more
difficult to accept the assumed constancy of numbers in the term "world
living species today (and hence in the late Pleistocene)." Indeed, Brod-
korb himself seems to give this point away when, in discussing his Table 1,
he writes "It is obvious that extinction rates from IV glacial time to the
present are not typical of the whole Pleistocene." The estimated "world
total of species in the late Pleistocene" is not necessarily biased by the
inconstancy of the number at different stages of the half-million years,
but the uncertainty of the estimated total is increased to a problematical
degree.

DIAGNOSIS OF THE SPECIES

   Fossil species have been described on the basis of the characters
discernible in bones, often single and often fragmentary. Existing species
have nearly all been distinguished primarily on feather characters (and
similarly ephemeral features), usually pigmental, sometimes morpho-
logical (in the strict sense), but equally irrecoverable in any but the
rarest conditions of fossilization. A large, but uncertain, proportion of
existing species would not be separable on skeletal characters, especially
given such imperfect material as usually has to serve the avian palaeon-
tologist. Wetmore (1959) has cited the species (or semispecies) of
meadowlarks and flickers as examples. Yet, in discussing Pliocene as well
as Pleistocene fossils attributed to the modern Mourning Dove, *Zenaidura
macroura*, the same author comments that "color is lacking but it seems
reasonable to hold that if bones of a dove from a Pleistocene deposit
appear identical with a modern mourning dove, they may be listed as that
species." May they not, however, equally well belong to another member
of the same genus, as in the flickers? The fact is, the palaeontologist
rarely has more than a fragmentary specimen, and practically always one
that lacks the external characteristics most important (at least in neo-
zoology) for the specific discrimination of, at any rate, small birds. Con-
sequently, if every species that had been alive at any given date in the
past had left fossil remains, the most meticulous worker could never have
diagnosed more than some fraction of them at the specific level. And to
that extent a modern avifauna and even a complete fossil avifauna could
not validly be used as terms in a single equation, without the inclusion
of a factor making allowance for this difference. When the skeletal
characters of all existing species are far better known than they are at
present, especially the range of variation within polytypic species, it may

be possible to calculate such a factor, but it is virtually certain that it will be bigger for passerines than for other groups of birds (see below).

The Composition of the Avifaunas

Table 3 analyzes into four main groups of birds the existing avifauna as listed by Mayr and Amadon (1951) and the fossil avifauna listed by Wetmore (1956), which Brodkorb took as his basis. There is of course no finality about the total arrived at in the former work; a few new species have been discovered since 1951, and personal applications of the polytypic species concept are always tending to affect the figures. These fringe effects are not, however, of importance for the present purpose. It will be seen that in terms of these groups the two avifaunas differ strikingly in composition. Among the fossils nearly half belong to water-bird families, another quarter to diurnal raptors and owls, but only about one-sixth to each of (a) other non-passerines, and (b) oscine passerines, while suboscine passerines are wholly unrepresented. In the existing avifauna the relative importance of the various families is completely reversed, so that more than half of all the species are passerines (with an appreciable proportion of suboscines), while water-birds account for no more than one-tenth and raptors and owls for one-twentieth.

There is of course good reason to suppose that most fossil faunas are far from providing a fair (random) sample of the composition of the full fauna from which they are derived. The great preponderance of water-birds is surely in part due to the fact that their habitat, far more than that of any other group, provides opportunities for fossilization. Another fac-

TABLE 3

Representation of Different Groups of Birds in the Existing World Avifauna
and in American Post-Miocene Fossils[1]

| | Existing species[2] | | Fossil species | |
	Number	Proportion of total	Number	Proportion of total
Water-birds	906	.11	150	.48
Raptors and owls	405	.05	71	.23
Other non-passerines	2207[3]	.26	39[2]	.13
Passerines				
Suboscines	1083	.13 ⎫ .59	–	–
Oscines	3990	.46 ⎭	49	.16
Total	8591		309	

[1] From Wetmore (1956).

[2] Derived from the list in Mayr and Amadon (1951).

[3] Two-thirds of the fossil "other non-passerines" are Galli (game-birds), compared with less than one-ninth in the modern list.

tor in their "favor" is that they are mostly large, and large carcasses are more likely to be preserved than small. This factor helps to explain the prevalence also of raptorial fossils, the predominance of Galli (gamebirds) among the non-passerines and also, as noted by Wetmore (1959), the prevalence of big species among the passerines.

DIFFERENCES IN EVOLUTIONARY POTENTIAL

The selectiveness of the fossilization process would not be important for the present purpose if all groups of birds could be accepted as identical or closely similar in the relevant aspects of evolutionary potential. It seems, however, that they are not—Brodkorb indeed accepts the "inequality of phyletic lines"—in particular because the passerines, especially the oscines, which are so predominant in the existing avifauna, appear to be a far more rapidly evolving group than the others, with the implication that the passerine species are, on average, likely to have much shorter "longevity" than others. Since evidence for this generally accepted view does not seem to have been marshalled, it may be worth while to do so here.

(1) The great majority of passerines breed in their first year, while many of the other species, especially among the water-birds, do not. This gives the passerines the ability to respond more rapidly to selection pressure of any given intensity and hence for isolated populations to diverge to species level in comparatively short periods. This implies a quicker turnover of passerine species.

(2) The higher categories of passerines are not so well defined as those of non-passerines. In largely independent classifications of the birds of the world, Mayr and Amadon (1951), who used subfamilies for many groups often called families, recognized 38 families of passerines and 96 of other birds, Storer (1960) 61 and 100 respectively, Wetmore (1960) 70 and 97. This shows how much more uncertainty still exists about the classification of passerines than about non-passerine families. Moreover, among the oscine passerines there are various species whose familial allocation is still uncertain.

(3) Species may be formed either by direct single-line descent (chronocline) or by the divergence of geographically isolated derivatives of a single stock. The imperfection of the fossil record of birds ensures that known examples of the former should be rare (Wetmore, however, cites the condor line *Gymnogyps amplus–californicus*); but, making all allowance for this, there can be little doubt that the second method of species multiplication is numerically the more important, and it is certainly so

TABLE 4

INDICES OF INTRASPECIFIC VARIABILITY
(FOR EXPLANATION SEE TEXT)

Group	Ethiopian Region		India	Palaearctic Region
	Sclater	White	Ripley	Vaurie
Water-birds	1.2 ; .2		1.1 ; .1	1.3 ; .3
Raptors and owls	1.5 ; .5		1.6 ; .6	2.3 ; 1.3
Other non-passerines	2.1 ; 1.1		1.6 ; .6	2.6 ; 1.6
Passerines	2.3 ; 1.3	2.6 ; 1.6	1.9 ; .9	2.7 ; 1.7

for contemporary calculations with present knowledge. Hence a comparison of the indices of current intraspecific variation in different groups of birds gives some idea of their liability to speciate. As sources, the lists of Sclater (1928–30), Ripley (1961) and Vaurie (1959–65) have been selected, because each of these authors has dealt with the entire avifauna of a large area, so that any subjective bias applies equally to all categories of birds. White's (1960–63) list has been added in order to show, by comparison with Sclater's, the effect of a more widely polytypic concept of the species than was current until recently—another aspect of the difficulties in the way of equating fossil species with existing ones.

There is of course more than one way of calculating an index of intraspecific variability from such lists and the results, shown in Table 4, give merely an indication of the degree of difference between the various groups of birds. If the total number of subspecies, including each monotypic species as 1, is divided by the total number of species, the left-hand figures in each column are obtained. They suggest that the (oscine) passerines currently show about twice as much capacity to vary as the water-birds, and that "other non-passerines" occupy the position next to the passerines in this respect. But these figures do not adequately present the differences, because the method of calculation is too favorable to the groups with low indices. For example, if the index for the Indian water-birds were only a trifle lower, 1.0 instead of 1.1, the passerine index for this area would still be barely twice as great, although an index of 1.0 means a nil variability. An alternative, and perhaps more instructive, method of calculation, therefore, is to divide the total number of species into the number of subspecies without including monotypic species in the latter. The results are the figures in the second half of each column, which suggest a passerine variability six to nine times that of the water-birds.

It may be added that, at the next taxonomic level, a similar trend will certainly be evident when enough attention has been given to the designa-

tion of superspecies[1] for statistics to be available—which would be even
more relevant to the present discussion than subspecies. In Africa
south of the Sahara it is already clear that over half the passerine species
are members of superspecies (B. P. Hall and Moreau, in preparation),
and although similar attention has not yet been given to the other birds
it is certain that the figures for water-birds and for raptors will be lower.
This indicates that the lowest grade of speciation is especially prevalent
in passerines and confirms that evolution is most active in this group.
Consequently, for estimates of "longevity" the avifauna of the world (or
of a continent) cannot be treated as homogeneous for statistical purposes
in the enquiry under consideration.

ON THE METHOD USED TO CALCULATE LONGEVITY

In the extract (b), which is quoted in the introductory part of this paper,
the conclusions are drawn that in a given sample of "phyletic lines" of
varying longevities showing a normal distribution, the "average longev-
ity" of the whole group is equal to the time needed to replace "half the
fauna," and that this would still apply roughly if the distribution curve
of longevities were "somewhat skewed." As they stand in the hypo-
thetical example, these conclusions are acceptable because the several
"phyletic lines" are assumed to be equivalent and comparable units, of
which the distribution of average longevities is unimodal. There is,
however, no evidence for this. On the contrary, Table 4 leaves no doubt
that water-birds, which number about 900 species (Table 3) have a far
greater longevity than the passerines (about 5,000), perhaps in the
ratio of 6 : 1, while the raptors and owls (400 species) have an inter-
mediate longevity. This means that the distribution of longevities will
be bimodal, not unimodal, and consequently if an "average longevity"
for a whole avifauna is thought to be meaningful it would have to be
calculated on the median of the distribution curve. The nature of the
data do not permit a precise calculation, but the median could under
the circumstances differ widely from the mean. For example, if we
consider 5,000 species of longevity $2n$ years, 2,000 of longevity $3n$, 500
of longevity $4n$, and 1,000 of longevity $12n$, as would not be unreasonable
on the basis of Tables 3 and 4, a "mean" value of this bimodal distribu-
tion would lie at approximately a longevity of $3.5n$ years, whereas the
median value (the "true" time in which 50 per cent of all the species
considered would become extinct) would lie near the value $2n$
years. It follows that for the whole fauna the mean value would be

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[1] "A monophyletic group of very closely related and largely or entirely allopatric
species" (Mayr *et al.*, 1953).

an overestimate by 75 per cent of the true "average longevity." In other words, the average longevity of the whole fauna represents the half-life of the fauna with an accuracy inversely proportional to the distance between the mean and the median longevity, which in Brodkorb's model is 0, but which in nature, as we have seen, may vary widely.

The material basis of the calculation in Table 1 is open to even graver objections. It deals with four groups of faunal evidence. The first two, radio-carbon dated to 17,000 and 25,000 years ago, give average species longevities of 89,000 and 69,000 years but are rejected as "not typical of the whole Pleistocene." The third and fourth faunas are dated as 184,000 and 691,500 years ago specifically on "geological evidence" determined as long ago as 1931. The precision of the date for the fourth fauna is the more remarkable because, according to its describer (Brodkorb, 1958), the indications are that the lake beds concerned "were formed during either the upper Pliocene or the first interglacial stage of the Pleistocene." As for the fauna itself, it consists merely of nine water-birds, six of which are extinct. This is extrapolated as 68 per cent and used as an essential element in the estimation that "the average longevity of Pleistocene avian species is approximately one-half million years, and the top limit of longevity approximately one million years."[1] Such an exercise should not have been taken seriously. Apart from the method of calculation, the crucial fauna is quantitatively minute, qualitatively as biased as it could be, and chronologically doubtful.

Nevertheless, as noted in the introduction to this paper, the result has been widely taken up. Fisher (1964) on calculations not published, but applying, it is understood, Brodkorb's methods to a larger series of bird faunas, has found ". . . an expectation of species life progressively declining from about 1,500,000 years in the early Pleistocene to about 40,000 at Rancho [La Brea] at the very end of the Pleistocene.[2] This decline was of course natural" (i.e., due to natural causes). If, for the sake of argument, the statistical basis of these calculations were regarded as acceptable and the difference of nearly 40 times in the life-expectation of species as an approximation to the truth, then the bio-

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[1] The latter conclusion is the more unaccountable in face of the nine records of modern species in the Pliocene in Wetmore (1956), including one actually in the Lower Pliocene.

[2] Fisher and Peterson (1964) give a different version of the first part of this conclusion: "Bird species probably survived an average of a million and a half years at the end of the Pliocene, before they died out . . . ." It may also be noted that Fisher (1964) gives the date of the Rancho La Brea fauna as 14,500 years ago, i.e., well after the last phase of the last glaciation had begun to relax, while Brodkorb included it in his Table 1 along with other faunas under date 25,000, which was fully glacial.

logical basis for the difference would demand the most serious considera-
tion. Fisher (1964) has offered the suggestion that as a consequence
of the successive climatic changes during the Pleistocene and the presumably
associated extinctions of species, the evolutionary rate was increased,
involving a reduced specific longevity.

Fisher goes on to calculate, on the 78[1] extinctions since A.D. 1680
(which he lists), that "the expectation of species life has become about
16,000 years." This figure was obtained by using 8,500 as the approxi-
mate number of species living today and Brodkorb's concept of "the time
needed to replace half the fauna," i.e., by multiplying 8,500 by 284 (years)
and dividing by 78 × 2. The extinctions form, however, too biased a
sample to permit of statistical treatment or of a generalized conclusion. In
the first place, 69 of the 78 extinctions have taken place on islands, mostly
on "small" ones. Secondly, of the 78, only 25 are passerines, .32 compared
with .59 of the existing world avifauna (Table 3). Now, sample counts
in various volumes of the *Check-list of the birds of the world* (J. L. Peters
et al., 1931 ff.) show that only about one-sixth of the existing species are
confined to islands, which means that about 7,000 species, including over
4,000 passerines, are wholly or partly continental in range. If the same
formula were applied to the extinct 9 out of 7,000 total "continental" species
the result would be an average longevity of some 110,000 years and if it
were applied to the extinct 1 out of 4,000 "continental" passerines the
result would be over half a million years. These figures are very different
from "about 16,000" and no doubt equally fallacious. Anyway, world
ecology has entered upon a new dimension, where it is no longer ruled by
natural forces (i.e., those exerted by agencies other than modern man).

ESTIMATION OF THE TOTAL NUMBER OF PAST AVIAN SPECIES

As shown in extract (c), the total of 1,634,000 species, which is there
reached, is based on two factors. One is essentially an extrapolation
of the 11,600 calculated in extract (a) as the number of contemporaneous
species in the "late Pleistocene." This is applied as a "conservative
estimate" to the Pliocene and Miocene, then with a minor adjustment
(to allow for the absence of granivorous species) to the periods of Oligo-
cene to Paleocene, while arbitrary figures have of necessity been inserted
for the Jurassic and the Cretaceous. The other main factor in the esti-
mation is the half-million years arrived at in Table 1 as the mean longevity
of bird species in the "late Pleistocene." Both this and the other main
factor in the estimation have, however, been shown above to be open to

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[1] Fisher inserted a comment at the proof stage which altered the total from 78
to 76, but as he used the former figure in his calculations it has been retained here.

objection, while the wisdom of applying even a "good" Pleistocene longevity figure to the Tertiary is very doubtful indeed.

Conclusion

Taxonomically, fossil species are not equivalent to modern species; the existing avifauna differs in composition from the available fossil faunas to a crucial degree; datings are inadequate; and apart from these difficulties the statistical methods applied are open to objection. The attempt to estimate average specific longevity and the total of past species must be judged at this time to have achieved only extremely unreliable results, which should not be quoted without most careful qualification. Moreover, it is necessary to conclude that on the material at present available no satisfactory results could be obtained by any modification of treatment. In any case, a full avifauna is so heterogeneous in relevant features that an "average longevity" is a concept so imprecise as to be of little value. In fact, the concept of "average longevity" for bird species in general is not more meaningful than are averages for other groupings consisting of extremely disparate aggregations or phenomena, which is to say very little.

Summary

Estimates of the average longevity of avian species and related subjects made by Brodkorb in 1960 have since then been widely quoted and also elaborated. Unless very strong reservations are made this is undesirable, for several reasons.

(1) For statistical purposes, fossil and living species are accepted as taxonomically equivalent, which they are not.

(2) Samples are too biased. Fossil avifaunas typically consist of water-birds, with or without raptors, and with few other birds, while passerine species make up two-thirds of the existing avifauna; and reasons are given for thinking that in this group evolution is much more rapid than in others. The disparity is such that the concept of "average longevity" for bird species in general has little meaning.

(3) Apart from this, the method and the basis of calculating the mean longevity as half a million years in the "late Pleistocene" are unsound.

(4) The estimate of 16,000 years as the average longevity of existing species by Fisher (1964) is made by applying Brodkorb's imperfect method to a sample that is too strongly biased to admit of simple statistical treatment.

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