KARYOTYPIC EVOLUTION AND LONG-TERM EFFECTIVE POPULATION SIZES OF BIRDS

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ABSTRACT.—Rates of karyotypic change in birds are used to estimate that, over the long-term history of a wide assortment of genera, avian effective population sizes have averaged on the order of 100. This result is consistent with the results of electrophoretic studies of geographic variation of allelic frequencies within species but is somewhat less consistent with the results obtained from demographic modeling. Three methodologically independent analyses have now corroborated the hypothesis that avian effective population sizes are typically of the order of 10^2 or larger. Received 2 February 1983, accepted 6 September 1983.

THE genetic structure of natural populations has been a subject of increasing interest in recent years. It is of fundamental importance to the understanding and interpretation of evolutionary processes. Besides being the subject of implicit assumptions in all evolutionary arguments and scenarios, the genetic structure of populations of birds has become an explicit part of interpretations of dialects (Baker et al. 1982, Petrinovich et al. 1981), speciation mechanisms (Barrowclough 1983), and the evolution of sex (W. M. Shields 1982).

Empirical investigations of population structure at the genetic level have proceeded in two fashions. Demographic modeling has been used to calculate N_e, the effective population size of demes, when quantitative estimates were available of dispersal, density, and life-history traits. Baker (1981), Barrowclough (1980), and Fleischer (1983) have followed this methodology. An alternative has been to measure directly the genetic structure of populations by means of electrophoresis to estimate F_{st}, the among-population component of genic variance. This has been the more commonly used approach. Barrowclough (1983) has reviewed such results for birds and compared them to those of other vertebrates.

Because of uncertainties associated with both methods of estimating genetic population structure, many caveats apply to their use in the interpretation of any particular evolutionary situation. For example, an underlying assumption of both procedures is that populations are in demographic and geographic equilibrium. Estimates of N_e based on demographics reflect current population structure and are informative of how evolution might proceed in the future if the environment remains constant. Electrophoretic estimates of F_{st}, on the other hand, do not reflect the genetic structure of populations today, but rather are the result of historical patterns of population structure. The simulations of Rohlf and Schnell (1971) and of Endler (1977) suggest that it takes at least 10^3 years for the genetic structure of populations to approach equilibrium when the habitat is uniform and 10^5 years or more when habitats are geographically fragmented. Thus, estimates of F_{st} made today on the basis of electrophoresis tell us something about the average population structure over the last 10^3–10^5 years. It seems unlikely that the demography and geographic distributions of many avian species have been unchanged in that period of time (e.g. Mengel 1964, Hubbard 1973).

As evolutionary biologists concerned with the details of processes of evolution, we would like to have estimates of the time course of N_e over the evolutionary history of taxa. At present there is no way to recover such information; Lande (1979), however, has shown that it is possible to estimate the long-term average effective sizes of demes using information on rates of karyotypic change. In this paper we discuss such estimates for birds.

METHODS

A fundamental assumption of Lande's procedure is that individuals heterozygous for a karyotypic

TABLE 1. Interspecific chromosomal variation in birds.

Taxon	Species studied S	Number of fissions/fusions $\hat{K}$	Age of taxon[a] $\hat{T}$	Changes/species $\hat{K}/S$
Ratites	6	0	80	0
Threskiornis	4	1	10	0.25
Anser	5	1	15	0.20
Anas	5	0	25	0
Aythya	5	0	20	0
Falco	4	1	20	0.25
Galliformes	10	6	60	0.60
Grus	5	0	10	0
Larus	5	0	25	0
Columba	5	1	3.75	0.20
Columbina	4	7	3.75	1.75
Empidonax	4	0	3.75	0
Turdus	6	3	3.75	0.50
Lanius	4	1	3.75	0.25
Vireo	4	0	3.75	0
Emberiza	4	0	3.75	0
Geospizinae	12	0	1.0	0
Carduelis	4	1	3.75	0.25
Lonchura	4	1	3.75	0.25

[a] Millions of years.

TABLE 2. Estimates of karyotypic fixation rates and long-term effective population sizes in birds and some comparative results from other taxa.

Taxon	Fission-fusion fixation rate, $\hat{R}$	Long-term effective population size $\hat{N}_e$
Avian taxa		
Ratites	$<2\cdot10^{-9}$	>100
Galliformes	$\sim1\cdot10^{-8}$	~102
Columbina	$\sim5\cdot10^{-7}$	~64
Other nonpasserines	$\sim5\cdot10^{-9}$	~106
Passerines	$\sim5\cdot10^{-8}$	~87
Nonavian taxa		
Drosophila[a]	$10^{-8}-10^{-10}$	200–800
Mammals[a]	$10^{-6}-10^{-7}$	30–200

[a] Based on results of Lande (1979).

change are at a selective disadvantage because of problems associated with meiosis. In other words, such individuals will produce some abnormal gametes not containing the proper quota of DNA. Such gametes will in turn result in defective zygotes. This loss of fitness is not dependent on crossing over (details are discussed in Lande 1979). Consequently, because of this fitness deficit, a new mutation for a reciprocal translocation or a Robertsonian fusion/fission (White 1978) can only go to fixation through a random drift process, with a probability distribution dependent upon effective population size. It is possible to work backwards, then, and estimate the long-term N_e by examining the rate of fixation of those chromosomal changes that would have resulted in reduced fitness when they were in a heterozygous state (for more details on the method and assumptions, see Lande 1979; see also Hedrick 1981).

Lande (1979) showed that if s is the selective coefficient against a heterozygous karyotype and u and R are the karyotypic mutation and fixation rates, respectively, then long-term effective population size can be estimated as

$$N_e = -(1/s)[\ln(R/u) - 1].$$

Further, he demonstrated that the order of magnitude of s and u are reasonably well known and constant across a wide array of taxa, ranging from insects to mammals. R, however, varies considerably; although there are chromosomal differences between

most species pairs in many organisms (White 1978), this is apparently not generally true of birds (G. F. Shields 1982).

Only a few estimates of the fixation rate of chromosomal changes in birds have been made (e.g. Shields 1980), and those were for all chromosomal changes, not for specific categories of rearrangements. Recently, however, one of us (Shields 1982) has reviewed the patterns of interspecific differences in avian karyotypes, and it is now possible to get preliminary estimates of R. As Lande (1979) has pointed out, both R and u enter the governing equations as logarithms, thus making the results relatively robust to minor inaccuracies in the estimates.

We used several sources to obtain estimates of the fixation rates of chromosomal mutations. These were the review of G. F. Shields (1982) of a wide variety of passerine and nonpasserine taxa, Jo's (in press) study of the Geospizinae, de Boer's (1980) report on ratites, Stock and Bunch's (1982) review of Galliformes, and de Boer and van Brink's (1982) report on Ciconiiformes. Genera were used only if four or more species had been karyotyped. The two categories of chromosomal changes of particular interest are translocations and fusion/fission events. There are no clear cases of reciprocal translocations in any of the avian data. While this lack of data could be used to set a lower limit on N_e, that limit is small (ca. 25) and not especially enlightening. Fission-fusion events that have gone to fixation are relatively common, however, and will be emphasized. Table 1 lists the taxa for which estimates of rates of karyotypic changes are available. The ages of most taxa were estimated by means of the reviews of Brodkorb (1964, 1967). Age was taken as time since first appearance in the fossil record. Pigeons and passerine genera, with poorer fossil records, were assumed to be 3.75 mil-

lion yr old, following Shields (1980). The ratite clade was assumed to be about 80 million yr old, following Cracraft (1974) and Sibley and Ahlquist (1981), and the Geospizinae were assumed to be 1 million yr old (Jo in press). All these estimates may be low but are probably of the correct order of magnitude. We followed the methodologies of Bush et al. (1977) and Shields (1980) in estimating R. For each taxon R has been estimated as

$$R = \Sigma \ (K/S)/\Sigma \ T.$$

Following Lande (1979), typical values of 10^{-4} for u and 0.10 for s were used. Values of R were computed separately for the taxa in Table 2. *Columbina* and some of the larger and older nonpasserine taxa were segregated to show the range of estimates. A better estimate of R could be obtained if complete chromosome phylogenies were available for each clade, but such data are not yet available for most taxa.

RESULTS AND DISCUSSION

The results of this analysis (Table 2) indicate that the long-term effective population sizes of birds are consistent with values on the order of 10^2; there is variation in fixation rates among the genera listed in Table 1, as G. F. Shields (1982) has pointed out, but more data will be required for establishing the reliability of these apparent differences. Some comparative data from other taxa, shown in Table 2, suggest that the avian range of population sizes is overlapped by that of mammals but is smaller than that of *Drosophila*. Chromosomal speciation is thought to be important in many mammals, such as rodents and ungulates (Bush et al. 1977), but relatively unimportant in dipterans (but see Shields and Procunier 1982).

To check the robustness of the results, we varied the value of u between 10^{-3} and 10^{-4} and the values of s between 0.05 and 0.20. For this range of parameters, estimates of long-term N_e fall approximately between 50 and 300.

The estimates obtained here are independent of other methods used recently to estimate aspects of the genetic structure of avian populations. They are in qualitative agreement with the results obtained from electrophoretic surveys of geographic variation (mean $F_{st} \doteq 0.022$, equivalent to $N_e \doteq 300$; Barrowclough 1983) and are somewhat less than the estimates obtained using demographic modeling (N_e's = 10^2–10^4; Barrowclough 1980). There are a couple of alternate interpretations of these results. First, it is conceivable that N_e's of many bird species

are constant through time and of the order of a hundred or so; this seems unlikely. Second, it is possible that N_e's fluctuate in conjunction with habitats and environments and are typically of the order of several hundreds to thousands. Occasionally, they go through bottlenecks, at which time karyotypic changes may occur, perhaps during speciation events. The frequency of such events may vary from taxon to taxon. This interpretation is consistent with all three independent estimates of avian population structure. The results described here generally reflect the long-term average but are, as Lande (1979) indicates, somewhat biased toward the size at bottlenecks. The F_{st} values from electrophoresis also would still show the effects of Pleistocene bottlenecks, while the demographic modeling results would represent estimates of present conditions.

More data, especially chromosomal banding studies (Shields 1983), and broader surveys of more families (e.g. Hobart et al. 1982) are necessary to refine these estimates. Nevertheless, it seems likely that many avian populations have long-term N_e's on the order of 10^2 or so, occasionally going through bottlenecks of smaller size. Some taxa, such as the ground-doves, may be especially prone to bottlenecking. It is unlikely, however, that these bottlenecks are very severe in length of time or in size. Such extreme events would probably have resulted in the fixation of a number of reciprocal translocations. It is clear that most avian populations are not continuously small and prone to inbreeding, the condition that has been postulated for many mammals (Bush et al. 1977).

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