

Birds, behavior, and anatomical evolution

(rates of evolution/nongenetic propagation of new habits/brain size)

JEFF S. WYLES*, JOSEPH G. KUNKEL†, AND ALLAN C. WILSON*

*Department of Biochemistry, University of California, Berkeley, California 94720; and †Department of Zoology, University of Massachusetts, Amherst, Massachusetts 01003

Communicated by Robert K. Selander, March 31, 1983

ABSTRACT Study of more than 200 species suggests that the anatomical differences among birds are as big as those among other vertebrates of comparable taxonomic rank. The result is notable because, for more than 100 years, many biologists have believed that birds are more uniform anatomically than other classes of vertebrates. Furthermore, assessment of biochemical and geological evidence suggests that the time scale for bird evolution could be quite short. Hence, birds may share with placental mammals the distinction of having had a high rate of anatomical evolution, compared to that in lower vertebrates. The rate appears to have been very high in songbirds and higher primates and extremely high in the genus *Homo*. In an attempt to explain such contrasts in rates of anatomical evolution, we advance the hypothesis that in higher vertebrates, behavior, rather than environmental change, is the major driving force for evolution at the organismal level. This hypothesis predicts accelerated anatomical evolution in species composed of numerous mobile individuals with the dual capacity for behavioral innovation and social propagation of new habits. Consistent with this hypothesis, we demonstrate a correlation between relative brain size and rate of anatomical evolution in land vertebrates.

Since the early days of evolutionary biology, vertebrate biologists have repeatedly suggested that the anatomical differences among birds (class Aves) are minor compared to those existing within other classes of vertebrates (1–3). This suggestion fostered the impression that the tempo of anatomical evolution in birds has been lower than in mammals (2) and led some authors to try to account for it in terms of functional constraints. They (4, 5) postulated that the bird body plan is so constrained by the structural requirements for flight that many anatomical changes that could be tolerated in more generalized animals would be selected against in birds. But we know of no thorough studies comparing the magnitude of the morphological differences among birds to those among species within other vertebrate classes. It is important to examine this problem quantitatively because of the bearing the result could have on our understanding of the factors that determine the rate of organismal evolution.

METHODS AND MATERIALS

Quantitative Approach. Our approach is based on the method of Cherry *et al.* (6), which has recently been shown to give an approximate measure for the intuitive concept of degree of overall morphological difference. We made use of bird skeletons in the Museum of Vertebrate Zoology at Berkeley and measured eight traits representing all major parts of the body (see Table 1). Measurements were made on 474 skeletons representing 239 species and subspecies of birds belonging to 26 of the 27 orders recognized by ornithologists (7). From these measurements, we

estimated the morphological distance between birds with the formula:

$$H = 100 \sum_{i=1}^8 |x_i - y_i|$$

in which H is the Manhattan distance, x_i is the mean value of the relative length of the i th trait in species X and y_i is the corresponding value for the homologous trait in species Y (6). The relative length of a trait is the length divided by the sum of the lengths of all eight traits. The suitability of H as an estimator of morphological distance has been shown elsewhere (6).

RESULTS

Hummingbird Versus Albatross. Table 1 shows how this method was applied to the comparison of a hummingbird with an albatross. These creatures differ greatly in head, forearm, hind limb, and backbone length measurements. The sum of the differences in relative trait length, 485 parts per thousand, corresponds to an H value of 48.5.

This particular pair of birds was chosen because of the following statement made by an eminent comparative zoologist (3):

“. . . birds of today despite their varied plumage, songs, and habits, are very similar to one another in their structure. They are divided into many orders; but the differences, for example, between a hummingbird and an albatross are much less than those between a seal and cat The different bird orders have, in general, no more differences between them than exist between families in other classes of vertebrates, and anatomical differences between bird genera are often so slight that fossils are hard to place.”

Accordingly, we compared the morphological distance (H) between these two birds with that between a seal and a cat by making use of published measurements of homologous traits (6). The results are inconsistent with the quote, the H values being 22 for the cat/seal comparison and 48 for the two birds.

Morphological Distance and Taxonomic Rank. Regarding morphological differences among birds in general, the last sentence of the quoted statement implies acceptance of the view that there is or should be a relationship between morphological distance and distance in a taxonomic classification and that birds are so uniform morphologically that they do not deserve to be classified in different orders. To test whether this is true, we conducted an extensive survey of the relationship between morphological distance (H) and taxonomic distance among birds. As shown by the points in Fig. 1, there is a strong correlation ($r = 0.98$) between morphological distance and taxonomic distance within the class Aves. More important, the bird points fall near or above the line, which is based on a similar survey of 184 other vertebrate taxa (6). These quantitative morphological results enhance respect for the collective judgment of previous

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Table 1. Morphological differences between hummingbird (*Calypte anna*) and albatross (*Diomedea immutabilis*)

Trait*	Relative trait length, parts per thousand		
	Hummingbird (x_i)	Albatross (y_i)	Difference $ x_i - y_i $
1. Head width	45	34	11
2. Head length	334	148	186
3. Eye to nostril	16	26	10
4. Nostril to lip	3	8	5
5. Shank length	118	147	28
6. Forearm length	54	224	170
7. Toe length	49	78	29
8. Backbone length	381	335	46
Sum	1,000	1,000	485

*These traits were originally chosen for their ability to discriminate among frogs (6). The corresponding traits measured on birds were: 1, greatest width across maxillae; 2, anterior edge of premaxillae to posterior edge of occipital condyles; 3, central posterior edge of lacrimal bone to anteriormost point of suture along midline of paired nasal bone; 4, center of the bottom edge of nostril opening to bottom edge of premaxilla; 5, maximal length of tibiotarsus; 6, maximal length of ulna; 7, maximal length of tarsometatarsus; 8, ventral length of articulated vertebral column, from axis to distal end of sacrum.

generations of bird taxonomists and give no support to the view that birds are oversplit taxonomically.

Table 2 gives further information about the results that are summarized in Fig. 1, allowing statistical tests to be done. From the means and standard errors for the morphological distances observed at each rank in the taxonomic hierarchy two conclusions emerge. (i) At none of the taxonomic ranks considered are the bird distances significantly below those for frogs, lizards, or mammals of comparable rank in the taxonomic hierarchy. (ii) With the exception of the one high point for mammals at the family level, the distances among bird orders are significantly greater ($P < 0.05$) than those among families and superfamilies of frogs, lizards, and mammals.

Songbirds. We compared the morphological distances among songbirds (suborder Oscines, order Passeriformes) to those among other birds. As is evident from Table 3, the morphological differences among songbirds at a given rank in the taxonomic hierarchy are nearly as big as those for other birds, although there has been doubt among ornithologists (e.g., see ref. 8) that this result would be observed.

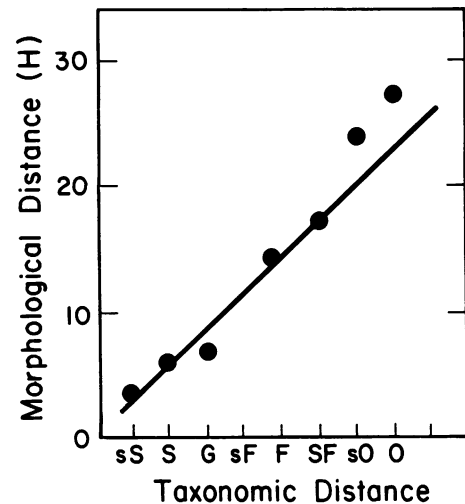


FIG. 1. Morphological distance (H) compared with taxonomic distance. The points represent the mean morphological distances among independent pairs of birds as a function of distance in the taxonomic hierarchy. The units of taxonomic distance are expressed in terms of the following categories: sS, subspecies; S, species; G, genus; sF, subfamily; F, family; SF, superfamily; sO, suborder; O, order. The line was fitted by the least-squares method to the H values calculated from the data of Cherry *et al.* (6) for frogs, lizards, and mammals shown in Table 2.

DISCUSSION

Until quantitative evidence to the contrary is presented, our measurements should be regarded as justifying the view that the anatomical differences among birds are no smaller than those among other vertebrates of comparable taxonomic rank.

Time Scale for Bird Evolution. This result has an intriguing consequence when considered in relation to our view that the time scale for the evolutionary divergence of modern birds could be quite short. The traditional view that modern birds have ancient roots is weakly based on fossil birds with teeth, from the period 135–65 million years ago. None of these fossils can be assigned convincingly to present-day orders of birds (9, 10). Hence, the possibility that the lineages leading to all modern birds stem from one of the many ancient bird species that lived about 65 million years ago deserves to be entertained.

A short history for modern birds would fit with geological evidence suggesting that there was a worldwide catastrophe 65

Table 2. Morphological distances among vertebrates at various levels in the taxonomic hierarchy

Taxonomic rank	Distance (H) (mean \pm standard error)			
	Frogs	Lizards	Mammals	Birds
Subspecies	4.2 \pm 1.7	2.8 \pm 0.0	4.0 \pm 1.4	3.7 \pm 0.4
Species	5.8 \pm 0.8	5.1 \pm 0.5	4.3 \pm 0.5	6.0 \pm 0.9
Genus	7.6 \pm 1.3	5.1 \pm 0.9	9.0 \pm 2.5	6.4 \pm 0.5
Subfamily	9.5 \pm 2.5	12.6 \pm 2.0	15.4 \pm 3.7	
Family	9.7 \pm 1.4	14.2 \pm 3.9	21.2 \pm 3.1	14.2 \pm 1.3
Superfamily	14.1 \pm 1.3	16.7 \pm 2.6	16.9 \pm 2.1	16.9 \pm 1.4
Suborder	14.4 \pm 0.7		17.7 \pm 2.7	24.2 \pm 4.8
Order		25.2 \pm 2.8	29.1 \pm 4.0	27.7 \pm 4.0

The frog, lizard, and mammal values come from Cherry *et al.* (6). The ordinal value for lizards refers to the comparison of conventional lizards (order Squamata) with the tuatara (order Rhynchocephalia). The 239 bird taxa examined and the 3,792 measurements made on them will be published elsewhere. To calculate means and standard errors, we picked independent (i.e., nonoverlapping) pairs of taxa. That is, no subspecies or species was used in more than one comparison. This allowed statistical tests to be done as described in the text. Because the Wetmore classification (7) of birds does not recognize subfamilies, we were careful in the comparisons of genera to avoid comparing representatives of what other authors would consider to be different subfamilies.

Table 3. Morphological distances among songbirds and other birds

Comparison	Distance (<i>H</i>) (mean \pm SEM)	
	Songbirds	Other birds
Interspecific	5.9 \pm 0.7	6.4 \pm 1.0
Intergeneric	7.6 \pm 0.9	8.8 \pm 0.9
Interfamilial	11.6 \pm 0.9	13.7 \pm 1.5

To facilitate statistical analysis at a given taxonomic level, we used independent pairs of species. Because the means for songbird comparisons at a given rank in the taxonomic hierarchy differ from those for other birds by 2 standard errors (SEMs), the means are not significantly different.

million years ago that caused months of darkness and mass extinctions (11). If such an event occurred, birds would have been especially vulnerable because of their high metabolic rate and extreme dependence on vision. This catastrophe hypothesis allows us to see how there could have been two rounds of bird evolution, one before and the other after the postulated mass extinctions. The second round may have started from a single species that survived the first round.

The idea that modern birds are a young group is supported by fossil evidence concerning the ages of living genera. As pointed out elsewhere (12), the average time of first known appearance in the fossil record is 3.75 million years ago for 14 songbird genera and 9.1 million for 19 genera representing 10 other orders of birds. The values are 6.5 million years for mammals and 20–26 million for lizards and amphibians (13). Thus, bird and mammal genera are younger than genera of lower vertebrates.

A short time scale also has the merit of helping to account for the small molecular differences observed among modern birds. Prager and Wilson's comparisons of proteins from all 27 orders of birds show that the accumulation of point mutations causing amino acid substitutions has been modest in birds compared with other vertebrates (12). This finding has been confirmed by more limited studies within a few bird orders (14). Point mutations are known from research on other groups of organisms to accumulate in approximate proportion to elapsed time (15). The small extent of point-mutational divergence among birds might be due largely to the short period of time elapsed since divergence.

Rates of Anatomical Evolution. Knowing that the anatomical differences among most orders of birds are not small and as-

Table 4. Brain size in relation to rate of anatomical evolution

Taxonomic group	Relative brain size*	Anatomical rate†
<i>Homo</i>	114	>10
Hominoids‡	26	2.5
Songbirds	23	1.6
Other mammals	12	0.7
Other birds	4.3	0.7
Lizards	1.2	0.25
Frogs	0.9	0.23
Salamanders	0.8	0.26

* Defined as $yx^{-0.67}$, in which *y* is brain weight in grams and *x* is body weight in kilograms; values of *y* and *x* come from refs. 16–19.

† Mean divergence in body shape per million years, based mainly on intrageneric morphological distances (*H*) computed from data in Tables 2 and 3 as well as from Cherry *et al.* (6) and unpublished data. By comparing such similar species, one tends to avoid saturation effects. The times of divergence are based on the fossil records for extant genera (12, 13) as well as on biochemical evidence in the case of hominoids (15, 20).

‡ Excluding *Homo* but including *Australopithecus*.

suming the short time scale proposed above, we must suggest that anatomical divergence among birds has been unusually fast in relation to both point-mutational divergence and to time. The only other group of land vertebrates with comparable rates of anatomical evolution are the mammals (Table 4).

We can now ask what properties the rapidly evolving vertebrates share that are lacking in more conservative groups, such as frogs, salamanders, and most lizards (6, 15). By focusing on such properties, one may gain insight into those factors, other than functional constraints on body plan, that determine the rate of evolution at the organismal level.

Behavior and the Rate of Evolution. To explain the high rate of anatomical evolution in birds and the especially high rate in songbirds, we develop Hardy's hypothesis (21) that behavior can be a major driving force for evolution at the organismal level. Our hypothesis, termed "behavioral drive" or "behavioral selection," relies on two behavioral components—innovation and social transmission—as well as on a large gene pool. Behavioral innovation refers to the nongenetic (or genetic) origin of a new skill in a particular individual, leading it to exploit the environment in a new way. Social transmission refers to the nongenetic spreading of a new skill among members of the species. Animals without the skill acquire it either by observing and imitating those who perform it or by other mechanisms of social learning (22). As a consequence of adopting a new habit, the species faces a new set of selection pressures favoring those mutations that improve the individual's effectiveness at living in the new way. The likelihood that mutants conferring such abilities are present in the population is proportional to its size.

Earlier views about the effect of behavior on anatomical evolution contain the recognition that new behaviors produce selection pressures favoring complementary anatomical mutations (21, 23, 24). Until now, however, there has not been, to our knowledge, an explicit hypothesis emphasizing the idea that nongenetic propagation of new skills and mobility in large populations will accelerate anatomical evolution by increasing the rate at which anatomical mutants of potentially high fitness are exposed to selection in new contexts and that this idea has significance for understanding rates of anatomical evolution in vertebrates other than humans.

Examples. The evidence that behavioral innovation and social transmission occur in songbirds (as well as in other birds and many mammals) has been reviewed (22, 25), the most famous example being provided by British tits. Early in this century, a few tits recognized milk bottles as a potential resource, discovered how to open them, and began drinking milk. The drinking of milk spread nongenetically, so quickly that within a few decades most of the million or so tits in Britain engaged in the practice (26). This new habit presumably exposed tits to a new set of selection pressures, ranging from selection for the biochemical ability to cope with the unusual chemicals present in milk (such as lactose and tributyrin) to selection for anatomical traits that improve the ability to open milk bottles (21).

Some human populations that have descended from cattle-raising cultures provide a possible example of the power of behavior to drive the fixation of genes for lactose utilization. Most members of these populations (i.e., Northern European and some African populations) differ from other people and animals by possessing lactase in their intestinal mucosa as adults (27). The presence of this lactose-splitting enzyme is apparently the result of a regulatory mutation whose spread through these populations was fostered by the selection pressure imposed by a new culturally transmitted behavior—namely, the consumption of cows' milk by adults. This practice presumably began only after cattle were domesticated, about 10,000 years ago.

Tests of the Hypothesis. The degree to which behavior facilitates adaptive evolution at the organismal level is expected to depend on three factors: (i) the frequency with which new habits originate, (ii) the speed at which they are transmitted horizontally to other individuals within the species and the effectiveness with which they are transmitted vertically from one generation to the next (28), and (iii) the genetically effective size of the population to which the habit is transmitted. These factors probably have high values in those vertebrates that evolve unusually rapidly at the anatomical level—namely, birds and mammals—but it is hard to measure them directly.

A quantitative, but indirect, measure of the first two factors is relative size of the brain. In relation to body weight, birds and mammals have brains that are several times bigger than those of reptiles and amphibians (Table 4). The brain is still bigger in songbirds and primates, whose rates of anatomical evolution are especially high. The individuals in these two groups are notable also for their mobility and ability to communicate over long distances, both visually and vocally (22, 23). The genus *Homo* is at the top of the scale in regard to rate of anatomical evolution, relative brain size, and the capacity for rapid behavioral shifts throughout large populations. From the strength of the correlation ($r > 0.97$) between the two sets of values in Table 4 we conclude that most of the variation in rate of anatomical evolution among vertebrates is associated with, and thus may be due to, variation in relative brain size.

In addition, molecular studies have shown recently that anatomically fast taxonomic groups have a great deal of gene flow among populations within a species (29, 30) and thus have an effectively large population size. By contrast, in anatomically conservative groups like salamanders and frogs, there is relatively little genetic (or behavioral) contact among populations (29, 30). The importance of strong selection on large populations for rapid evolution involving mutations with major effects has been emphasized in a recent theoretical study (31).

Our proposal that the incidence of cultural shifts and gene flow throughout large populations determines the pace of organismal change in higher vertebrates can be tested by extending the quantitative study of anatomical evolution to other groups of animals. Also, it will be important to examine the relationship of social learning to sexual selection (32), coevolution, speciation, karyotypic change, point-mutational evolution, and changes in genome size.

Autocatalysis. During the history of land vertebrates, the relative size of the brain has increased (16) in a manner that is reminiscent of an autocatalytic process in the lineages leading from amphibians through reptiles to birds and several mammalian groups, especially in the lineage leading to humans. In light of the strong correlation between relative brain size and rate of anatomical evolution, we propose that this rate has also been accelerating along those lineages. Our view of anatomical evolution as an autocatalytic process, mediated by social learning, contrasts with the old view that the pressure to evolve has been rather steady through geological time, owing to relentless environmental changes generated by constant geological forces.

We thank G. W. Barlow, S. M. Beverley, R. H. Crozier, K. M. Helm-Bychowski, R. L. Cann, A. Carlisle, S. M. Carr, B. S. Chapman, D. E. Dobson, H. W. Greene, M. F. Hammer, A. Larson, W. Z. Lidicker, E. Mayr, R. G. Northcutt, O. P. Pearson, E. M. Prager, U. Ritte, T. Rowell, R. D. Sage, V. M. Sarich, R. K. Selander, G. S. Stent, E. Trinka, D. B. Wake, L. S. Weisman, and R. M. Zink for discussion and the staffs of the Museum of Vertebrate Zoology (Berkeley) and the California Academy of Sciences (San Francisco) for access to specimens. This research was supported by grants from the National Institutes of Health and National Science Foundation.

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