



Bird Versus Mammal Morphological Diversity

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BIRD VERSUS MAMMAL MORPHOLOGICAL DIVERSITY

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A recent paper by Wyles et al. (1983) should provoke widespread interest among students of evolutionary zoology. Wyles and his colleagues, having compared quantitative measures of morphological diversity in certain groups of birds, mammals, reptiles, and amphibians, concluded that "... anatomical differences among birds are as big as those among other vertebrates of comparable taxonomic rank" (Wyles et al., 1983 p. 4394). According to Wyles et al., these results "... enhance respect for the collective judgment of previous generations of bird taxonomists" and lay to rest the century-old belief on the part of biologists that birds

are more uniform anatomically than are other classes of vertebrates. We believe, however, that neither the data base nor the method of analysis used by Wyles et al. is appropriate to the issue of relative morphological diversity in birds and mammals.

A long-standing belief held by many biologists and questioned by Wyles et al. is that birds, *as a class*, are remarkably uniform in structure, whereas mammals, *as a class*, are structurally diverse (Romer, 1966; Alexander, 1975; Colbert, 1980; Welty, 1982). Because this issue involves a comparison at the class level, proper falsification of the hypothesis should also focus on a comparison at this level; that

is, interordinal morphological diversity in birds should be compared to interordinal diversity in mammals. Clearly, such comparisons must include a broad taxonomic representation of both groups involved.

The mammals examined by Wyles et al. represent only three of 20 extant orders: Primates, Carnivora (including a pinniped), and Rodentia (data from Cherry et al., 1982 Appendix 1). In contrast, 26 of 27 orders of birds are represented in the bird sample (Wyles et al.). It might be assumed that the inclusion of additional orders of mammals would have little effect on the estimate of within-mammal morphological diversity. This would only be true, however, if the morphological distances among the orders used are representative of interordinal distances in mammals as a class; this has yet to be tested (consider whales vs. elephants, bats vs. aardvarks, and antelopes vs. manatees).

Wyles et al. recognized the need for interordinal comparisons when they used the morphological distance metric, H , (a statistic based on eight mensural characters originally chosen for their ability to discriminate among frogs; see Cherry et al., 1978) to demonstrate that the morphological distance between a hummingbird and an albatross far exceeds that between a cat and a seal. In Table 1 we use data presented in Wyles et al. and Cherry et al. (1982) to calculate all pair-wise comparisons of H . Although the between-bird H value (48) is much larger than the between-mammal value ($H = 22$), one will notice that all interclass comparisons (birds with mammals) result in H values that are considerably smaller than the between-bird value. If we conclude, purely on the basis of H values, that the albatross and hummingbird are more different morphologically than are the cat and seal, then we must also conclude that the albatross is more similar to the cat than it is to the hummingbird (Table 1).

Although Wyles et al. compared H values calculated within birds to those calculated within mammals, they made no actual interclass calculations of H . Before making *any* kind of interclass comparison, however, it is important to document that the H metric "sees" birds and mammals in the same way. In other words, is an H value of 10 measured within birds equivalent to $H = 10$ within mammals? Although H values may be meaningful *within* birds and *within* mammals, this does not ensure that within-bird values can be meaningfully compared to within-mammal values. We have explored this matter further.

We calculated H for the six interclass comparisons of vertebrates selected by Cherry et al. (1982 Appendix 2), and we compared these to the interordinal H values provided by Wyles et al. (1983 Table 2). The mean H value for the six interclass comparisons ($\bar{x} = 35.48$, range 20.7 – 57.2) is not significantly different ($.5 > P > .1$; Mann-Whitney U -test) from the mean interordinal values measured among three orders of mammals ($\bar{x} = 29.1$, range 15.4–40.4) and between two orders of reptiles ($\bar{x} = 25.2$, range 20.3–32.4; bird data were not

TABLE 1. Morphological distances (H values; Cherry et al., 1982) between hummingbird (*Calypte anna*), albatross (*Diomedea immutabilis*), seal (*Phoca vitulina*), and "cat" (*Lynx rufus*). Note that each of the H values in the four bird-mammal comparisons (box) is less than that measured between the hummingbird and albatross. Data from Cherry et al. (1982) and Wyles et al. (1983).

	H	A	S	C
Hummingbird (H)	—			
Albatross (A)	48	—		
Seal (S)	40	45	—	
Cat (C)	47	31	22	—

available to permit statistical comparison). Most importantly, half of the within-mammal and half of the within-reptile H calculations exceeded three of the six interclass H values. Thus, according to H , vertebrates of different classes are no more dissimilar morphologically than are two vertebrates of the same class (but in different orders). Because the interclass H values are not significantly larger than the intraclass values, it is improper to make interclass comparisons of within-class H calculations. This finding is particularly noteworthy because the H metric was specifically designed to permit interclass comparisons of morphological diversity (e.g., primates with frogs in Cherry et al., 1978; and birds with other vertebrates in Wyles et al.) Although Wyles et al. did not make direct interclass calculations of H , their conclusions rest on interclass comparisons of within-class H values. Our interclass calculations cast doubt on the justification for using H in this way.

There is a biological basis for concluding that the H statistic is invalid for interclass comparisons of vertebrate morphological diversity at *any* taxonomic level. Systematists are well aware that the set of characters that best discriminates among members of one group of organisms (i.e., is sensitive to morphological diversity within that group) may be of little value in discriminating among members of other groups; this is because certain characters that are evolutionarily labile in one group may be highly conservative in another. Thus, because of different patterns of allometric change in different groups of organisms, one's estimate of overall morphological diversity in a particular group may vary with the set of characters examined (Findley, 1979; cf. Cherry et al., 1979). If one wants an unbiased estimate of morphological diversity among several groups of organisms, one must avoid character sets that contain powerful discriminators for certain groups and only moderate or poor discriminators for others. If a character set contains variables that are particularly useful for discriminating among members of one group, then it is inevitable that the estimate of morphological diversity for that group will be inflated relative to those of other groups.

To determine if the character set used by Cherry et al. (1978, 1982) and Wyles et al. contained biases of the kind discussed above, we investigated the relative contribution of each character to the morphological distance metric, H . The metric comprises eight mensural characters including head width, head length, shank length, forearm length, and the like. Two of these eight characters (head length and forearm length) together account for more than 73% of the overall H value measured between the hummingbird and the albatross. These same characters account for an average of less than 36% of the H value in six interordinal comparisons of mammals and only 19% of the overall H value in four reptile comparisons. In birds, head length and forearm length are directly related to bill length and wing length, and it is well known that these are highly labile traits that vary conspicuously with diet and flight habits. Because the H metric contains two variables that are powerful discriminators among birds at all taxonomic levels, the metric would appear to be particularly sensitive to within-bird morphological differentiation. We suspect, therefore, that the H values measured between birds at all taxonomic levels (see Wyles et al., 1983 Table 2) are inflated relative to those of other vertebrate groups. Although Cherry et al. (1978 Footnote 13) mention that their approach "... ignores problems of allometry. . .," it is *precisely* such problems (i.e., different patterns of allometric change in different vertebrate classes) that cause the H statistic to be inappropriate for interclass comparisons.

We believe that the major problem is not the use of an H metric itself, but the application of one particular H metric to interclass comparisons among vertebrates. More basically, the question "Are the anatomical differences among birds as great or greater than those among mammals?" is unanswerable unless one specifies the particular anatomical feature of interest. For certain features, such as head length and forearm length, birds are probably more diverse than mammals, as represented by primates, carnivorans, and rodents; for a vast number

of other anatomical features, the question remains unanswered. Because the conclusions of Wyles et al. concerning bird versus mammal morphological diversity, rates of evolutionary change, and "behavioral drive" are entirely dependent on the validity of H , we feel that these conclusions are, at present, premature.

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MORPHOLOGICAL DISTANCE: AN ENCOUNTER BETWEEN TWO PERSPECTIVES IN EVOLUTIONARY BIOLOGY

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Hafner et al. (1984) question the adequacy of our data, as well as our way of measuring degree of organismal difference (i.e., morphological distance). They go on to conclude on biological grounds that morphological distances within one group of

animals cannot be compared to those within another group. We give direct answers to some of the technical points raised by Hafner et al. and then suggest that their negative conclusion be examined from two different perspectives on how to approach