

THE USEFULNESS OF BEHAVIOR FOR PHYLOGENY ESTIMATION: LEVELS OF HOMOPLASY IN BEHAVIORAL AND MORPHOLOGICAL CHARACTERS

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Abstract.—It is widely believed that behavior is more evolutionarily labile and/or more difficult to characterize than morphology, and thus that behavioral characters are not as useful as morphological characters for estimating phylogenetic relationships. To examine the relative utility of behavior and morphology for estimating phylogeny, we compared levels of homoplasy for morphological and behavioral characters that have been used in systematic studies. In an analysis of 22 data sets that contained both morphological and behavioral characters we found no significant difference between mean consistency indices (CIs, which measure homoplasy) within data sets for the two types of characters. In a second analysis we compared overall CIs for 8 data sets comprised entirely of behavioral characters with overall CIs for 32 morphological data sets and found no significant difference between the two types of data sets. For both analyses, 95% confidence limits on the difference between the two types of characters indicate that, even if given the benefit of the doubt, morphological characters could not have substantially higher mean CIs than behavioral characters. These results do not support the idea that behavioral characters are less useful than morphological characters for the estimation of phylogeny.

Key words.—Behavior, character evolution, consistency index, homoplasy, morphology, phylogeny.

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One of the basic premises of ethology is that behavior evolves in essentially the same fashion as morphology. This idea both arose from and promoted the use of behavioral characters in studies of phylogeny. Although Darwin (1859) clearly realized that instincts evolve, in modern ethology the idea that behavior and structure should be treated equivalently traces most clearly to Whitman (1899) and Heinroth (1911), whose views stemmed largely from the application of behavior to the systematics of birds. With the rise of ethology the use of behavioral characters in studies of phylogeny became relatively commonplace (Hinde and Tinbergen, 1958; Bekoff, 1977; McLennan et al., 1988). Tinbergen spoke for many ethologists when he claimed "Behaviour characters are in principle neither more nor less useful [for systematics] than morphological or other characters; they merely add characters to the total by which overall likeness is judged" (1959, p. 328).

Despite the ethological tradition of using behavior in systematics, among biologists in general it is widely believed that behavioral characters are inferior to morphological characters as indicators of phylogenetic relatedness. Two main arguments have been forwarded to support this notion. First, it is claimed that preliminary (i.e., nonphylogenetic) criteria for homologizing characters—for example, the position of the character in relation to other features—are difficult and perhaps even impossible to apply to behavioral traits (Atz, 1970; Hodos, 1976; Aronson, 1981). Second, it is held that behavior is so evolutionarily labile that it is suspect as an indicator of relationships (Atz, 1970; Urbani, 1989).

These two arguments are closely related, thus it is worthwhile to clarify the distinction between them from the outset. Both arguments imply that, following a phylogenetic analysis, behavioral characters will be found to exhibit more homoplasy—i.e., character convergence or reversal—than will morphological characters. The first argument implies that such homoplasy—or mistaken homology as some would call it—occurs because behavioral characters lack some of the properties that allow us to make reasonably good preliminary homology assess-

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