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Homoplasy, homology, and the perceived special status of behavior in evolution

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Abstract

Evolutionary biologists tend to tread cautiously when considering how behavioral data might be incorporated into phylogenetic analyses, largely because of the preconception that behavior somehow constitutes a ''special'' set of characters that may be inherently more prone to homoplasy or subject to different selection regimes than those that operate on the morphological or genetic traits traditionally used in phylogenetic reconstruction. In this review, we first consider how the evolution of behavior has been treated historically, paying particular attention to why phylogenetic reconstruction has often failed to include behavioral traits. We then discuss, from a theoretical perspective, what reasons there are—if any—for assuming that behavioral traits should be more prone to homoplasy than other types of traits. In doing so, we review several empirical studies that tackle this issue head-on. Finally, we examine how behavioral features have been used to good effect in phylogenetic reconstruction. Our conclusion is that there seems to be little justification on theoretical grounds for assuming that behavior is in any way ''special''—either particularly labile or particularly prone to exhibit high levels of homoplasy. Additionally, in reviewing historical perceptions of behavior and their links to conceptions of homology, we conclude that there is no compelling reason why behavior cannot be homologized or therefore why it should not prove phylogenetically informative. In subsequently considering several factors related to selection that influence the likelihood of homoplasy occurring in any trait system, we also found no clear trend predicting homoplasy disproportionately in behavioral systems. In fact, where studied, the degree of homoplasy seen in behavioral traits is comparable to that seen in other trait systems. Ultimately, there appear to be no grounds for dismissing behavior a priori from the class of phylogenetically informative characters.

Keywords: Behavior; Behavioral evolution; Homoplasy; Homology; Phylogenetics; Systematics

Introduction

Homoplasy—the similarity between taxa that arises from convergent or parallel evolution—is often treated differently by researchers in different fields. For phylogeneticists, homoplasy can frustrate research and is dealt with as undesirable noise, to be eliminated or controlled for in the search for *homology*—the continuity, including similarity, between taxa via descent. In contrast, homoplasy is the currency of behavioral ecology, where the appearance of similar character states under similar environmental conditions is the fundamental basis for making inferences about adaptation. Here, similarity by descent could potentially be mistaken for similarity by convergence, and thus behavioral ecologists seek evidence of homoplasy while attempting to eliminate or control for the effects of homology. Although homoplasy is treated differently, correctly identifying homoplasy is a goal common to both kinds of research.

Behavior, by which we mean the totality of an animal's ways of interacting with its physical and social environments, is often thought to present a special challenge to this goal. A common perception is that behavior is highly labile and therefore especially prone to homoplasy. In fact, some researchers have argued that behavior cannot be meaningfully homologized

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(e.g., Atz, 1970). Certainly, behavioral traits are used in phylogenetic reconstruction far less often than are morphological, molecular, and genetic characters, and this is perhaps a reflection of exactly these perceptions (Sanderson et al., 1993; Proctor, 1996). Yet, at the same time, behavioral ecologists, who otherwise tend to stress the adaptive plasticity of behavior, have frequently noted cases in which behavior has been strongly conserved within lineages over evolutionary time. Moreover, for early ethologists, the forerunners of modern behavioral ecologists, behavior was often studied expressly for its phylogenetic utility.

Such conflicting perspectives raise a number of important questions about the perceived special status of behavior in evolution. Is behavior, in fact, special? Is it particularly labile or particularly prone to homoplasy? To what extent on either theoretical or empirical grounds is behavioral homoplasy more common than homoplasy in other trait systems? Under what circumstances might behavioral traits prove useful in phylogenetic reconstruction? These questions should be of interest to phylogeneticists and behavioral ecologists alike because, whether ultimately treated as noise or as signal, both groups are united in the need for reliable identification of homoplasy.

In this paper, we will explore these questions by addressing four major subjects. First, we will consider how the evolution of behavior has been treated historically by systematists. In particular, we will examine why phylogenetic reconstruction has commonly failed to include behavioral traits because of two preconceptions about behavior that are likely to be false: (1) that behavior is inherently nonhomologizable and therefore of limited value in phylogenetic reconstruction; and (2) that, even if homologizable, behavior is too labile to be phylogenetically informative. We will then discuss, from a theoretical perspective, what reasons there are—if any—for assuming that behavioral traits should be more prone to homoplasy than other types of traits. In doing so, we will review a number of empirical studies that address this issue directly. Finally, we will examine how behavioral features have been used to good effect in phylogenetic reconstruction and offer some suggestions as to how and where they are most likely to be so used in the future. In addressing these latter issues, we will focus particularly on case studies from nonhuman primates because these are the taxa with which we are most familiar. However, we believe our points and conclusions are likely to be more broadly applicable.

Historical perspectives on homology, homoplasy and behavior

> "The essentially morphological concept of homology cannot at present be applied to behavior in any meaningful (nontrite) way."
>
> (Atz, 1970: 69)

> "To deny that homologous behavior exists would seem to deny that behavior is a characteristic of animals that is subject to evolutionary change."
>
> (Atz, 1970: 68)

These two contradictory quotes—by the same author, in the same paper—capture a familiar tension over the subject of behavior in evolution. Atz (1970) argued strenuously that behavior cannot be homologized: it is simply too labile and too far removed from *structure*, which Atz believed is the fundamental locus of homology. Yet, in making this argument, Atz was forced to admit that such an extreme claim is tantamount to saying that behavior does not evolve, which he also found unsatisfying.

What is the basis for this tension concerning behavior? Clearly behavior evolves, and if it evolves then, in principle, it could prove phylogenetically informative like any other sort of evolved trait. Yet, for Atz (1970), behavior does not seem to evolve in a manner consistent with phylogenetic diversification. Instead, it seems to change too quickly or unpredictably, in ways that preclude us from using behavioral traits to trace continuity and ancestry.

Atz (1970) is not alone in this quandary or in his basic conviction that behavior is somehow special, labile, and difficult to homologize. While Atz articulated his concerns about behavior especially baldly, the apparently special nature of behavior in evolution has been debated frequently, often with resulting skepticism concerning its phylogenetic utility (for similar views, see Klopfer, 1969; Hodos, 1976). While contemporary evolutionary biologists might not fall so readily into the sort of logical trap that Atz set for himself, the same uneasy sentiment about behavior seems to persist today, as evidenced in the numerous reviews that have appeared dealing precisely with the issue of behavioral evolution (e.g., Wcislo, 1989; Brooks and McLennan, 1991; Greene, 1994, 1999; Lauder, 1986, 1994; Wenzel, 1992; Foster et al., 1996; Proctor, 1996; Robson-Brown, 1999) and by the fact that behavior has yet to be incorporated into phylogenetic reconstruction with any regularity. In two seminal surveys, for example, Sanderson et al. (1993) and Proctor (1996) found that only 4–6% of phylogenetic studies included analysis of behavioral traits, and far fewer studies utilized behavioral traits as the primary character type.

The locus of homology: structure versus function

Part of the ambivalence toward the phylogenetic utility of behavior seems to be definitional in origin, stemming from a tendency to view homology as irrevocably tied to *structure*. Because many behaviors have only tenuous connections to underlying morphological or neural structures, there is suspicion about their phylogenetic utility:

> Until the time that behavior … can critically be associated with structure, the application of the idea of homology to behavior is operationally unsound and fraught with danger, since the history of the study of animal behavior shows that to think of behavior *as* structure has led to the most pernicious kind of oversimplification" (Atz, 1970: 69; emphasis in original).

Structural definitions of homology have a long history, dating from the nonphylogenetic origin of the concept within comparative anatomy (Owen, 1843) through their subsequent