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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.
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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

application to explicitly phylogenetic systems of taxonomy (cf. "homogeny" of Lankester, 1870). Although terminology and definitions have often varied and continue to be debated (see Hall, 1994; Bock and Cardew, 1999), structure has nevertheless been consistently placed at the core of the homology concept (see Table 1 for additional examples of the equation of homology with structure).

An additional consistent element of this history has been the importance of clearly delineating *structure* from *function* in determinations of homology. For many evolutionary biologists, homology and homoplasy are defined with respect to similarities in structure (derived from common ancestry or convergence, respectively), while the term *analogy* is reserved for those traits showing similarity of function irrespective of underlying structural similarity. This perspective was succinctly stated in the comprehensive review and clarification of phylogenetic terminology undertaken by Haas and Simpson (1946: 323):

> Homology is here defined as a similarity between parts, organs, or structures of different organisms, attributable to common ancestry. It will be noticed that … functions are not included…. It is believed that the function of organs may or may not be the same in different organisms, but that functions *as such* are never homologous…. It must be kept in mind that identity of function has been considered, from the very beginning of the terminology under discussion, to be *the* characteristic of analogy rather than homology [emphasis in original].

In phylogenetic theory, then, there has been a tendency to localize homology *within* structure and to assume that nonstructural traits, traits derived from nonhomologous structures, and the functions per se of traits are not—and *by definition* cannot be—homologous. Because behavior is often only loosely connected to structure, and because behavior is often cast *as* function rather than *as* structure, many researchers have concluded on definitional grounds alone that similar behaviors seen in different taxa are inherently nonhomologizeable and are, at best, analogous.

An illustration of exactly this sort of thinking comes from Hodos (1976), writing on the subject of homology and behavior (see also Cracraft, 1991, and quoted in Table 1). Hodos (1976) first illustrated an attraction to structural definitions of homology in the following: "I shall begin with [the] assumption that the recognition of homologous behaviors requires a structural correlate. The conclusion seems to be either implicit or explicit in virtually all discussions of the evolution of behavior" (p. 154). Illustrating the view that homologous traits require homologous underlying structures, he then wrote: "A point on which there seems to be general agreement is that behaviors that are associated with non-homologous structures cannot be regarded as homologous, no matter how similar they appear" (Hodos, 1976: 160). Finally, linking behavior to analogy (rather than to homology) he wrote: "Analogy refers to similarities in function … analogous behaviors are defined here as 'correspondence between behaviors of similar function, whether or not they can be related to homologous structures' " (Hodos, 1976: 160). Hodos's perspective, therefore, is that, while the structures that subserve behaviors might be homologized, the behaviors themselves can only ever be analogous. They are precluded from being homologous by virtue of their functionality—by virtue of their being *behavior*. This point is made even more explicitly in the following example offered to clarify his views of homology and analogy:

> The insertion of food into the mouth by a man and a monkey would be both homologous (because the hands of monkeys and humans are derived from the hands of their common ancestors) and analogous (because the behaviors serve the same purpose) (Hodos, 1976: 160).

Table 1

Statements emphasizing the structural basis of the homology concept and how it has been applied to behavioral homology

Homology	
Riedl (1978: 33)	"Homologies … are structural similarities which force us to suppose that any differences are explicable by divergence from identical origin."
Carroll (1988: 6)	"Homology refers to the fundamental similarity of individual structures."
Wagner (1989: 51)	"Only morphological equivalence in terms of relative position, structure, and connections with nerves and blood vessels counts."
Cracraft (1991: 26)	"To be sure, similarities in function sometimes parallel similarities in structure, but it is the similarity in structure that is the primary empirical basis for a hypothesis of homology.… So I conclude that functional data play no relevant role in either postulating homology or in its evaluation."
Ridley (1996: 471−472)	"First, if a character is homologous it must have the same fundamental structure."
Behavioral homology	
Atz (1970: 68)	"The extent to which behavior can be homologized is directly correlated with the degree to which it can be conceived or abstracted in morphological terms."
Hodos (1976: 165)	"The concept of behavioral homology is totally dependent on the concept of structural homology. This state of complete dependence imposes a number of limitations on the behavioral homology concept. First, behavioral homologies stand or fall with their structural correlates. If evidence comes to light indicating that structures previously thought to be homologous are not homologous, then any behaviors associated with these structures must also be redesignated non-homologous."
Cracraft (1991: 23)	"The distinction between function and behavior. The relevance here relates to the problem of defining what is meant by a systematic character. Functions of structures generally have not been thought of as characters, whereas ritualized behavior patterns have been utilized as characters for many years.… it is the behavior pattern, then, and not the function, that constitutes a systematic character."

We agree that some opposition to the use of function as a criterion for homology is justified. Functional demands commonly produce convergent adaptations, as the classic example of the wings of birds and bats clearly illustrates. However, we would argue that rigid adherence to a structural definition of homology that excludes function—and that, by extension, excludes behavior—from the class of potentially homologous traits is problematic and unwarranted for several reasons.

First, many behaviors, such as mating, dispersal, parental care, spatial navigation, range use, migration, and territorial defense, are not easily connected to structural underpinnings and are best characterized only in functional terms. Should this fact alone exclude them from the set of potentially homologous traits? We would argue most adamantly, ''No!'', if only because many behaviors with no obvious structural basis clearly show variation, are heritable, are acted upon by selection, and contain phylogenetic information, i.e., they evolve. Consider the most familiar examples of the differences in temperament and demeanor (e.g., aggressiveness, obstinacy, docility, affiliativeness, excitability) that characterize different breeds of domestic animals that result from systematic programs of selective breeding, often on the basis of these very behavioral traits. In fact, many such characteristics of domestics (e.g., the tumbler pigeon's penchant for tumbling, the pointer's penchant for pointing) featured centrally in Darwin's (1859) argument for evolution by natural selection in *The Origin of Species*. It would be ironic indeed if they were now deemed nonhomologizable.

Similar natural examples can be seen in nonhuman primates, such as in the differences in (1) levels of curiosity and behavioral responses to novelty or environmental disturbance that characterize South American titi monkeys compared to squirrel monkeys (Mason, 1990; Mayeaux and Mason, 1998); (2) the relatively despotic herding behavior of male hamadryas baboons versus the more laissez-faire herding style of male savannah baboons (Kummer, 1968); and (3) the more ''relaxed'' dominance style of stump-tailed versus rhesus macaques (de Waal and Luttrell, 1989). These behaviors have no obvious structural correlates and are best characterized only functionally, yet they are just as clearly evolved and should therefore submit to being homologized, at least in principle.

A particularly salient example of functional homology that is not clearly tied to structure is seen in the remarkable conservatism among humans and the African great apes (chimpanzees, bonobos, and gorillas) in many features of social organization, including female exogamy, weak bonds among females, and intergroup relations characterized by male hostility (Wrangham, 1987; Ghiglieri, 1987). These are social behavioral traits with no obvious underlying structural correlates. Our own work and that of others on social evolution in primates (reviewed below) has demonstrated similar conservatism in features of social organization (e.g., male dispersal, differentiated intragroup social relationships among females) among Old World monkeys. Even more generally, learned behaviors and cultural traditions in humans and other animals may have no specific connection to structure and yet undergo the same kinds of evolutionary changes (e.g., mutation, descent with modification), and thus they reflect evolutionary relationships just as well as structural

traits, even if those behaviors are not under strict genetic control (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Durham, 1991; Avital and Jablonka, 2000).

It is also relevant to note that there is a growing body of evidence from behavioral genetic studies of both primates and other mammals that suggests that some complex behavioral phenotypes, in fact, *are* directly influenced by underlying genetic (i.e., structural) variation. For example, length variation in the promoter region of the serotonin transporter gene, SLC6A4 (Heils et al., 1996), is associated with differences among peer-reared captive rhesus monkeys in the concentration of a serotonin metabolite, CSF 5-HIAA (Bennett et al., 2002). In free-ranging rhesus monkeys, CSF 5-HIAA level correlates with such behavioral traits as impulsivity, sociability, and aggressivity (Mehlman et al., 1995), and the same promoter-region polymorphism is associated with differences in the age at dispersal (Trefilov et al., 2000). More recently, variation in the length of the 5′ regulatory region of the vasopressin 1a receptor gene (avpr1a) in prairie voles has been shown to be associated with individual differences in a range of traits associated with social-bonding behavior of males towards females and with male parental care (Hammock and Young, 2005). Species differences in the distribution of avpr1a receptors within the brain have also been associated with social monogamy versus polygyny in closely related voles (Insel et al., 1994; but see Fink et al., 2006).

Second, at the opposite extreme, some behaviors show marked functional conservatism and *are* tied closely to structure but show wide variation in the actual structures that subserve them. As one such example, Striedter and Northcutt (1991) reviewed the common practice among eutherian mammals of burying the feces under a mound of earth using variously the hindfeet, forefeet, both, or neither (using, instead, the tail or dorsal scutes). In each taxon, the behavior has a clear structural correlate—the part of the body used to dig. But what is conserved across the various taxa is the function of the behavior (feces burying) rather than either the details of its performance or the morphological structures involved. If homology is to be recognized here—and we argue that it should be—it lies in the function of the behavior rather than the underlying structural components.

Similar conservatism in function vs. structure is observed at other organizational levels. For example, Lauder (1986, 1994) reviewed an example from the musculoskeletal system of ray-finned fishes (a monophyletic clade of teleost fish), concluding that ''several extremely conservative functional characteristics [of pharyngeal muscles] have been identified as retained despite extensive reorganization of musculoskeletal topology'' (Lauder 1994: 185). Additional examples include the courtship songs of Hawaiian *Drosophila*, which appear to be homologous despite variation across species in the morphological structures used in their production. The same phenomenon is seen among species of acridid grasshoppers (reviewed in Striedter and Northcutt, 1991).

These examples contradict another central assumption often associated with strictly structural definitions of homology— namely that homologous traits cannot arise from nonhomologous structures. Thus, among the criteria often articulated for

homology is the requirement that a character state present in two taxa be traceable to (1) homologous neural, physiological, or morphological underpinnings; (2) homologous developmental pathways; or (3) homologous gene sequences. For example, Ridley (1996: 472), in defining homology, wrote, "the [homologous] characters must have the same embryonic development." The same sentiment was echoed by Roth (1984: 17), who stated: "A *necessary* component of homology is *the sharing of a common developmental pathway*" (emphasis in original). However, as the examples noted above demonstrate, apparently homologous traits can stem from nonhomologous morphological structures or have no obvious underlying structure at all (see also Hall, 2007; Leigh, 2007).

This disconnect between structure and function may be relatively common, in fact, with examples available at every level of biological organization. For instance, because many nucleotide-base substitutions are silent with respect to the amino acid or protein ultimately produced, functionally homologous proteins may often derive from structurally nonhomologous genetic sequences (Doyle, 1996). Moreover, in some cases, apparently homologous structures at one level of organization can arise from nonhomologous structures at a deeper level, one example of this being the eyes of *Drosophila* fruit flies. In *Drosophila* that are homozygous for the recessive "eyeless" allele at the major genetic locus controlling eye formation, other genes from the same gene complex can sometimes assume the function of the wild-type allele and allow normal development of the eye to proceed (de Beer, 1958), a process leading to homologous phenotypes (i.e., presence of eyes) in the absence of homology at the molecular level. Indeed, the prevalence of gene complexes arising from duplication and diversification of a single ancestral gene suggests that many such examples of homologous gene products and structures arising from nonhomologous genes might be found.

Likewise, apparently homologous phenotypic structures may arise from nonhomologous developmental pathways. One example here is the neural tube of vertebrates, which develops via invagination of the neural plate in the majority of taxa but via cavitation of a neural keel in teleosts and lampreys. Despite variable embryonic precursors and developmental routes, the neural tube in the two groups is homologous (reviewed with additional examples in Striedter and Northcutt, 1991; see also de Beer, 1958). The same holds at the level of neural structure and function, where a homology criterion that attaches primacy to underlying neural structures may be difficult to reconcile with the realities of neural architecture. For instance, the same neural circuit, under different conditions of activation, can mediate several different behaviors, each of which could well have arisen independently (Lauder, 1986, reviewed in Kavanau, 1990; Katz and Harris-Warrick, 1999). It would be problematic to label these behaviors homologous simply by virtue of their common neural underpinnings. Conversely, it seems likely that homologous behaviors could be appropriated by different neural tissues in different taxa given the clear evidence that, even within an individual, substantial relocalization of the neural substrates for various behavioral tasks may occur following brain injury (Kolb and Whishaw,

1996). In such cases, homologous behaviors can, it seems, stem from nonhomologous neural structures.

In view of such ambiguities, strictly structural definitions of homology appear inadequate. In fact, numerous others have made the same point. Lauder (1986, 1994), for example, examined and thoroughly critiqued the allure of a traditional structural criterion of homology that excludes function and argued that such a view is "based on our preconceived notion that structure is solid, repeatedly observable, and definable, rather than on quantitative analyses of interspecific patterns in both structure and function" (Lauder 1994: 178). He further suggested that structural definitions of homology that have variously assigned precedence to structures at different levels (e.g., morphology, the nervous system, physiology, genes) reflect a preoccupation with identifying a single best (and structural) locus of homology, and argued (on grounds similar to those outlined above) that this search for a single locus of homology is illusory. Instead, Lauder advocated a hierarchical concept of homology, one that recognizes the potential for homology at every possible organizational level including structures, functions, behaviors, developmental pathways, and patterns of gene expression.

Others have echoed the same sentiment (for reviews, see papers in Hall, 1994; Bock and Cardew, 1999; also Hall, 2007; Leigh, 2007). Striedter and Northcutt (1991), for example, proposed an explicitly hierarchical concept of homology that they argued is intuitively appropriate for—and indeed mandated by—the inherently hierarchical organization of biological systems:

> We contend that attempts to reduce behavioral homology to morphological homologies, and morphological homology to genetic and developmental homologies, are misguided and based on a failure to recognize the hierarchical nature of biological organization (Striedter and Northcutt, 1991: 177).

Of course, this sort of hierarchical view of homology, including behavior, is not new; it is implicit (if not explicit) in the writings of many earlier writers, including preeminent evolutionary biologists like Ernst Mayr. For example, in his *Principles of Systematic Zoology*, Mayr (1969: 126) wrote that "almost any attribute of an organism might be useful as a taxonomic character" and offered a list of potential characters that includes aspects of morphology, physiology, ecology, behavior, and geographical distribution (see p. 127, Table 7-1), which he suggested may prove informative at different taxonomic levels. Elsewhere, he specifically emphasized the importance of behavioral characters in taxonomic reconstruction, reviewing numerous instances of their contribution to refining and even reformulating phylogenies originally generated using morphological traits. Mayr even went so far as to say: "If there is a conflict between the evidence provided by morphological characters and that of behavior the taxonomist is increasingly inclined to give greater weight to the ethological evidence" (Mayr, 1958: 345). In the updated version of *Principles*, he wrote: "Behavior is undoubtedly one of the most important sources of taxonomic characters" (Mayr and Ashlock, 1991: 175). Likewise, G.G. Simpson, in a review of methodological

advances in phylogenetic research, emphasized the phylogenetic utility of behavior: "Morphological characters still are the most used data in phylogeny.… There are nevertheless many relevant data of other sorts, mostly behavioral and distributional" (Simpson, 1975: 8, 9).

Why, then, is behavior still regarded skeptically and seldom used in phylogenetic research? One answer may be that formal opinion and practical implementation often diverge, causing even leading evolutionary biologists to be equivocal. For example, while Simpson fully acknowledged the potential phylogenetic utility of behavioral characters, he adhered in practice to the traditional structuralist view, expressly excluding function from the class of homologous traits unless it is closely linked to structure:

That functions *as such* are never homologous the one to the other is a matter of definition, only. I agree that such a definition is desirable if phrased that functions, considered as abstractions and without consideration for the structures that perform these functions, should not be spoken of as homologous, but that homology frequently involves both function and structure and in this combined sense it is proper to speak of the homologous functions performed by homologous structures (Simpson, in Haas and Simpson, 1946: 323; emphasis in original).

He later followed this instinct for rejecting behavioral homologies on structural grounds in the following example from a symposium specifically on the subject of behavior in evolution:

Divergence and lack of homological behavior between insects and vertebrates are again illustrated, for the external skeleton-internal muscle apparatus of an insect obviously had independent origin from the internal skeleton-external muscle apparatus of a vertebrate (Simpson, 1958: 509).

Here, Simpson's rejection of behavioral homologies was based on the assumption that homologous traits cannot arise from nonhomologous morphological structures. Thus, while formally acknowledging the potential homology of behavior, Simpson's attraction to the primacy of structural data led him to exclude behavior in practice. Complicating this already confusing picture, however, Simpson wrote the following in a footnote to the *same* paper acknowledging debate over phylogenetic terminology:

A few years ago there was a flare-up of highly polemic discussion on the definitions of these terms, especially "homology".… There did seem to be a consensus among morphologists and systematists that "homology" applies to similarity of structure only, *not* of function or behavior. Nevertheless several authors in this symposium, including systematists (e.g., Mayr, Emerson), have applied the term "homology" to behavior with tacit assumption that the usage is acceptable and will be understood, and no conference member objected. As a personal opinion, I maintain that the concept of homology applies to behavior as well as to structure (Simpson, 1958: 533; emphasis in original).

Given such equivocation from authorities like Simpson, it is perhaps not surprising that doubts and ambiguity remain over the potential homology of nonstructural traits and traits—such as behaviors—that are perceived to be more closely associated with function than with structure.

Behavioral lability

Another source of outstanding ambivalence toward behavior and its potential phylogenetic utility stems from notions of its inherent lability. Such notions may have been inspired by a number of sources, the most basic among them being the behavioral variation that is observable both among and within individuals of the same species. Another important influence may have been the behaviorist tradition of comparative psychology, which was the predominant theoretical framework for the study of behavior in North America through the middle twentieth century. Behaviorists focused on the experiential (nonheritable) bases of behavior and tended to stress the malleability of behavior in response to variable environmental input.

More recently, and perhaps ironically, the rise of behavioral ecology may have reinforced the view that behavior is especially labile. Born of sociobiology, behavioral ecology examines behavior within an explicitly evolutionary framework. The focus in behavioral ecology is on *adaptation* and on the current fit of an organism's behavior to local environmental conditions. Behavioral ecology has been enormously successful, demonstrating how ecological conditions influence a wide range of behaviors—foraging decisions and habitat selection, mate assessment and mating patterns, parental investment strategies, and grouping behavior—and how behavior can sometimes be exquisitely adjusted to subtle variations in environmental conditions. As a result, however, individual animals are now often cast as adaptive reservoirs capable of modifying their behavior almost without limit to accommodate changing environmental conditions, a view that tends to reinforce the notion that behavior is evolutionarily labile. In fact, behavioral ecologists' emphasis on the current functional utility of behavior is sometimes so complete that some tend to reject or be skeptical of evidence for behavioral conservatism (i.e., behavioral phylogenetic inertia), seeming to equate evolutionary stability with nonadaptation (adaptive neutrality) or maladaptation (e.g., van Schaik, 1996; Sterck et al., 1997). Wilson (1975: 32), one of the founders of sociobiology and behavioral ecology, defined phylogenetic inertia as "the deeper properties of the population that determine the extent to which its evolution can be deflected in one direction or another, as well as the amount by which its rate of evolution can be speeded or slowed." Phylogenetic inertia, so defined, could be interpreted as adaptive resilience (a low broad peak in a shallow adaptive landscape) just as easily as it could be viewed as nonadaptation or maladaptation. Nevertheless, *conservatism* often seems to be read as *constraint* and thus as anathema to the behavioral ecologist's focus on the current adaptive utility of behavior, as evidenced in the curious tendency to label the same behavioral pattern when observed in distantly related taxa as *adaptation* but when observed among closely related taxa as *constraint*.

Furthermore, the primary evidence for adaptive inference in behavioral ecology is convergent evolution, or homoplasy, cases in which similar behaviors (or structures) have arisen in response to similar ecological conditions from ancestors that did not have these behaviors (or structures). And because the strength of any inference of adaptation hinges on the frequency with which convergent character states have arisen, focal traits are often defined loosely—in functional terms—so as to incorporate a larger number of possible convergence events, thereby increasing the power of statistical tests of adaptation. However, this practice risks inflating estimates of behavioral similarity and, by extension, homoplasy among focal taxa. Pellis (1988), for example, studying muriod rodents, found that loosely defined behaviors lumped functionally under the rubric of "play" actually constituted a constellation of numerous distinct elements, and that lumping the behaviors functionally with respect to play not only obscured important (and even functional) differences between them (e.g., having to do with targets of agonistic versus amicable playful attack) but also ultimately obscured the evolutionary pathways through which different elements arose.

Thus, although behavioral ecology is decidedly evolutionary in its approach to behavior, its focus on the current adaptive function or utility of the trait under consideration and the practice of defining traits in functional terms may have conspired to minimize the historical component of behavior, as well as to emphasize its apparent lability.

It is a further bit of irony that the intellectual predecessors of contemporary behavioral ecologists—the classic ethologists—specifically *stressed* the phylogenetic component of behavior. Ethologists like Tinbergen and Lorenz and their many contemporaries saw behaviors as clear markers of phylogenetic affinity, one of the explicit goals of ethology being to illuminate patterns of evolutionary relatedness as revealed through behavior. Classic studies, like those on ducks by Lorenz (1941), gulls by Tinbergen (1959), and pelicaniforms by van Tets (1965), used detailed analyses of movements and courtship displays to determine both the likely patterns of evolutionary relatedness among species and the evolutionary processes responsible for producing behavioral diversification from common origins. The goals of what would become ethology under Tinbergen and Lorenz by the middle of the twentieth century were, in fact, formally articulated much earlier by ethology's founders, Oscar Heinroth and Charles Whitman. In 1898, Whitman wrote that both "instincts and structure are to be studied from the common viewpoint of phyletic descent" (p. 328). Hence, ethology was founded on the disciplinary assumption that behavior, like structure, could be homologized and could provide evidence of phyletic relationships. Of course, this ethological approach to behavior was undoubtedly influenced by the writings of Darwin, who clearly embraced the historical element of behavior: "He who understands baboon would do more toward [human] metaphysics than Locke" (Darwin, 1838: 84).

It is important to note that, although focused primarily on current adaptive utility, behavioral ecologists have often been confronted with the historical component of behavior.

Broad-scale efforts to identify the ecological correlates of behavior have frequently been frustrated by phylogenetic influences. For example, comparative studies of adaptation have been complicated by cases in which closely related species inhabiting different environments or occupying different ecological niches nevertheless behave similarly, presumably owing to their recent common ancestry. An early example comes from Eisenberg's (1963) study of the ecological correlates of social behavior in heteromyid rodents (a family that includes the kangaroo rats and pocket mice). He found that species' social systems tracked phylogenetic history as, or more, strongly than ecology, concluding that, "it appears that the phylogenetic background has been very important in the expression of the social organization in the family (Heteromyidae)" (Eisenberg, 1963: 86). Struhsaker (1969: 114) reached a similar conclusion in early field studies of Old World primates. Studying the relation between ecology and social organization in cercopithecines, he noted an extremely consistent pattern of one-male (harem) social systems among the otherwise diverse and speciose guenon clade, writing: "This appears to be a case in which phylogenies are at least as important as ecology, if not more so, in understanding an aspect of the social structure."

In fact, observations of exactly this sort stimulated refinements in the comparative method that coincided with the blossoming of behavioral ecology in the late 1970s and have featured centrally in the field ever since. The key development in comparative research was the realization that, due to their recent common ancestry, species cannot necessarily be considered independent data points in statistical tests of adaptation. This proscription has become a familiar refrain, and a host of comparative methods have been developed to overcome the problem and are now routinely used. However, the underlying rationale for the proscription, namely that behavior has a historical component, often seems to have faded from our collective memories, replaced with the simplicity (and sterility) of the proscription itself. Research still continues to stress current adaptive utility with little or no emphasis on how current adaptive solutions are influenced by a species' phylogenetic history, and (surprisingly!) evidence for behavioral conservatism in the face of ecological diversification meets with skepticism and incredulity.

It is perhaps not surprising, then, that despite observations like those above by Eisenberg and Struhsaker confirming the historical component of behavior, and despite major developments in the comparative method formally acknowledging this point, and even despite claims to the contrary by systematists (see Proctor, 1996), the sentiment today remains frustratingly like that expressed by Atz some 30 years ago—that behavior is special, labile, and prone to extreme levels of homoplasy and thus of dubious phylogenetic utility.

Is behavior "special"?

This brief look at recent historical perceptions of behavior illustrates several conflicting perspectives, with some researchers arguing that it is special and not capable of being

homologized (e.g., some systematists), others arguing just the opposite (e.g., ethologists and other systematists such as Mayr), and still others formally committed to its evolutionary basis, but oddly ambivalent about the historical element thus implied (e.g., behavioral ecologists). How can these contradictory perspectives toward behavior be reconciled?

In what follows, we explore the potential theoretical and empirical bases for assuming that behavior is subject to different interpretation than other classes of traits. We begin from the theoretical standpoint for two reasons. First, because the widespread ambivalence towards the use of behavioral traits in phylogenetic analyses seems to stem more often from a priori assumptions about its lability than from specific empirical evidence (de Queiroz and Wimberger, 1993), it seems appropriate to examine from the outset what might be the theoretical basis for such assumptions about lability in behavioral as opposed to other trait systems. Second, it seems valuable to try to arrive at a set of theoretical predictions about the relative levels of homoplasy we might reasonably expect in different trait systems, which would contribute to making phylogenetics a more predictive and less descriptive science. If nothing else, appeal to such predictions could help researchers resolve the conflicting but equally parsimonious trees so often encountered in phylogenetic analyses. Thus, the following basic question will guide our inquiry: What conceptual or theoretical basis is there for assuming that behavioral traits should be more homoplastic than other types of traits?

Theoretical considerations

Perceptions about the relative lability of behavioral traits may depend in part on how precisely such traits typically have been defined or characterized, as we have already intimated. The importance of precisely defining characters and character states has long been a central concern of systematists trying to homologize traits, and it should be equally important to behavioral ecologists because loosely defined traits that are not truly the same—even functionally—risks generating false conclusions about adaptation. Problems of trait definition and characterization are not unique to behavioral systems, of course. However, the potential for imprecise trait definition certainly may be greater for behavioral than for other trait systems, if only because less effort has been expended on trying to identify the appropriate units of behavior. This is a key methodological concern, then, that needs always to be borne in mind. However, because currently there is no consensus on the "right" units of behavior (or even on a method to identify them), we will sidestep this issue (as morphologists are often also forced to do) and ask whether appropriately identified behavioral traits *should* be more homoplastic than other types of traits, for example morphology, to which comparisons of behavior are often made.

We will pursue this question by separating it into a few relevant factors concerning the strength, timing, type, and possible outcomes of the selection process that should, theoretically, affect the likelihood of homoplasy in any trait system. The first factor concerns the strength and timing of selection, with the

assumption being that traits under strong selective pressure—highly functional traits—or traits more commonly exposed to selection will change more or more often and show higher levels of homoplasy than traits under weak selection pressure or those that are buffered from selection [see also Lockwood (2007) and Masters (2007), who consider these factors with respect to morphological and behavioral data, respectively].

Does selection act more readily, or more strongly, on behavior than on morphology?

This question immediately raises the bedeviling problem of how to characterize the relationship between an organism, its behavior and morphology, and the environment. Clearly, the influences can flow in both directions. In theory, there are at least two ways to view this relationship. First, we might imagine that, because behavior is the medium through which an organism confronts its environment, behavioral traits may be exposed to selection pressures more readily or more directly than morphological traits. In this view, behavioral change can effectively buffer the organism from its environment, precluding (or at least forestalling) the need for morphological change. Alternatively, we might imagine that, because behavior is to varying degrees liberated from morphology, it is resistant to, or independent of, underlying morphological change, so that morphological change induced by environmental demands need not be accompanied by behavioral change.

The first of these scenarios, in which behavior provides an adaptive buffer between organism and environment, is by far the more commonly held view and accords well with neo-Darwinian notions of evolutionary change, in which behavioral plasticity often introduces the organism to slightly different selection regimes that may then subsequently act on morphology (Mayr, 1963; West-Eberhard, 1989; Mayr and Ashlock, 1991). For example, modifications of habitat choice or feeding behavior may be a common means by which organisms are introduced to novel physical environments that subsequently select for changes in structural anatomy. The inference here is that behavioral change often precedes, and in some sense drives, structural change. Especially good evidence for this pattern of evolutionary process derives from the concept of *ethospecies*—species distinguishable only on the basis of behavioral differences. How common ethospecies may be is unclear, though they have been reported in several invertebrate taxa [e.g., wasps that differ only in larval diet (Adriaanse, 1947) or in their mode of hunting and prey choice (Evans, 1953); nematodes differing only in host selection (Brooks and Wiley, 1986); fireflies differing only in flash pattern (Barber, 1951; Lloyd, 1983); and additional examples reviewed in Mayr (1958)], and certainly many previously unrecognized sibling species among diverse animal taxa have been identified on the basis of behavioral characters. Song patterns, for example, have been instrumental in species identifications in crickets (e.g., Otte, 1989), frogs (e.g., Gerhardt, 1974), and birds (reviewed in Payne, 1986). The applicability of the ethospecies concept among primates is uncertain, though it may well help to account for problematic species affinities in

some clades (e.g., South American tamarins and African guenons) where relations based on physical traits such as pelage have been problematic at times, and where natural hybridization has been observed or suspected.

Thus, the view that behavioral change often precedes morphological change, and by extension is more prone to homoplasy, appears wholly intuitive. However, there are several important caveats to this generalization. First, when we think of behavioral plasticity of the sort that buffers organisms from the environment, forestalling morphological change, are we dealing with evolutionary or merely phenotypic plasticity? Certainly, there can be extensive phenotypic behavioral plasticity, but how (or even if) this plasticity translates into evolutionary lability is seldom clear. Here, we confront the thorny issue of *reaction norms* and their breadth. There is clear evidence that extensive phenotypic variation can often result from the same underlying genotype under the influence of different environmental conditions, with the variable phenotypic expressions representing the genotype's norm of reaction (Schmalhausen, 1949; Schlichting and Pigliucci, 1998). Reaction norms may be relatively broad or narrow, as dictated by the relative canalization of developmental pathways. Extreme examples among invertebrates include alternative behavioral morphs that vary with environmental conditions—solitary under some conditions and gregarious under others (reviewed in Dobzhansky, 1970). This is a difficult problem because for most behaviors in most organisms it is often impractical to establish reaction norms quantitatively. Nevertheless, it is important to bear in mind that a large measure of the phenotypic variation believed to buffer organisms from the environment and used to support a priori judgments about behavioral plasticity may be epigenetic in origin and not indicative of evolutionary lability at all. Of course, the same problem applies perforce to morphological systems, where activity-dependent growth or atrophy in bone, muscle, and organ tissue is commonplace, and to neural systems, where synaptic growth and dendritic arborization occur in response to neural stimulation.

The second caveat to bear in mind is that the extent to which behavioral change will precede and be more common than morphological change may depend a great deal on the level of behavioral organization concerned. As reviewed above, there has been a tendency to equate homology with structure. Taking this view, we might predict that behaviors that are, in fact, closely tied to structural underpinnings should retain greater phylogenetic value. That is, lower-order behaviors, such as the individual elements of a motor sequence (e.g., axial rotation of the forearm in food-harvesting) or those closely tied to physiological processes, should show less homoplasy than higher-order behaviors (e.g., social relationships, grouping, and dispersal patterns). In fact, just this sort of assumption may have motivated the early ethologists' commitment to the phylogenetic utility of behavior, because they tended to focus on low-level, ritualized motor routines (fixed-action patterns) and display behaviors that were highly stereotyped and species-specific.

However, the degree of homoplasy in low-level behavioral traits tightly leashed to underlying structures will obviously depend entirely on the degree of homoplasy in those underlying structures, which raises an important issue: Might, in fact, higher-order behaviors sometimes be *less* homoplastic than lower-order behaviors because they are not leashed to structural underpinnings that are themselves homoplastic? That is, would some behavioral patterns (e.g., social behavior, mating) be relatively independent of morphology and environmental context, and therefore relatively immune to variation in them, and thus be more conservative? In this way, the adaptive buffer that behavior provides can be viewed as a capacity to resist change at the behavioral level in response to environmental variation that is superficial with respect to critical behavioral functional systems.

Although this possibility has yet to be explored extensively, there is increasing evidence from a variety of different taxa (e.g., insects, lizards, frogs, birds, and mammals) that aspects of behavior at higher organizational levels can be evolutionarily conserved (reviewed in Brooks and McLennan, 1991). For example, Carothers (1984) mapped two features of iguanid lizard social organization (the presence/absence of male territoriality and male dominance hierarchies) onto an established phylogeny and found that both traits had as high or higher consistency indices than did morphological traits related to sexual dimorphism in body size. Similarly, McLennan et al. (1988) found that a reconstructed phylogeny of stickleback fish based on behavioral traits, including behaviors removed from structural underpinnings (e.g., male territoriality, parental care), was less ambiguous and had a higher consistency index than one based on morphological traits (for additional examples, see below section on primate social behavior). Observations like these tend to support the second scenario above, namely that behavioral traits may, at times, be resistant to, or independent of, change in other trait systems and thus are less prone to the convergent or parallel evolutionary change that generates homoplasy.

Is selection stabilizing, directional, or disruptive?

Together with points made earlier about functional conservatism, the examples above also serve to suggest that the strength and timing of selection are perhaps less important determinants of homoplasy than is the pattern of selection, particularly whether it is stabilizing, directional, or disruptive. Clearly, when selection is stabilizing, regardless of its strength or timing, the result is stasis, and the probability of homoplasy is minimized. Conversely, it is also clear that similarly strong directional selection in different taxa may lead to functional convergence and homoplasy. Disruptive, or diversifying, selection too is more apt to yield homoplasy because the potential for recurrent evolution of similar traits (even just by chance) is requisitely increased with diversification.

Broad generalizations about the propensity for different selection regimes to act in different trait systems are difficult to make, but all trait systems appear to be subject at times to very strong stabilizing selection. Certainly, some genetic mechanisms are known to be conserved over vast periods of time, as in the example of homeotic genes controlling the development

of the central nervous system (CNS), which are shared across invertebrates and vertebrates (reviewed in Reichert and Simeone, 1999). The conservatism here evidently stems from the extreme functional importance of certain regulatory mechanisms governing basic aspects of brain organization. Similarly, some aspects of CNS structure are known to be highly conserved. Entire circuits, for instance, can be conserved across phylogenetic orders seemingly due to their multifunctional design. Thus, selection against individual neurons of a circuit that mediate one function may be inhibited by the role of those same neurons in mediating other functions that are selectively favored, contributing to a stabilizing effect on overall circuit structure (Kavanau, 1990). Likewise, certain aspects of morphology such as overall body plans (bauplans) are highly conservative, in this case due to the extreme functionality of basic designs for locomotion. In addition, as reviewed above, some aspects of behavior also show strong conservatism and thus appear to be subject to very strong stabilizing selection.

With respect to other selective regimes, one feature of behavioral systems may seem to predispose them to diversifying selection and hence homoplasy—their frequency-dependent nature. Often in behavioral systems, what is optimal for one individual depends greatly on what others in the population are doing. This kind of frequency dependence can and often does produce alternative behavioral "strategies," where some individuals in the population display one behavioral phenotype, while others display another. Frequency-dependent behavioral variation has become a popular subject of behavioral ecology recently, where research focuses on the optimality and evolutionary stability of alternative phenotypes. However, it would be premature to conclude that this feature of behavioral systems might contribute to the increased probability of homoplasy because in few cases do we actually know whether the observed alternative behavioral strategies are a product of genotypic differences, different life-history stages, or variable reaction norms. Therefore, we cannot be certain that intraspecific phenotypic variation in behavior produces interspecific behavioral diversity of the sort that might increase homoplasy disproportionately in behavioral systems.

Moreover, although frequency-dependent alternative phenotypes might be less common in other trait systems where selection with respect to some external pressure (itself variable or not) more often seems to favor a single optimal phenotype, it is not clear that either frequency dependence or diversifying selection are unique to behavioral systems. Certainly there are morphological structures shaped by sexual selection that stem from strong diversifying selection resulting from an element of frequency dependence. Thus, we see a bewildering array of elaborate physical structures (e.g., crests, long tails, brilliant colors) among males of many animal taxa selected on the basis of their function in attracting female mates. In some cases, female preferences for such male extravagances have been shown to result from sensory biases favoring novelty or supernormal stimuli (Ryan and Wagner, 1987; Basolo, 1990), with both qualities defined with respect to rarity in a population. As a result, at least some morphological traits are subject to strong diversifying selection resulting from female preferences for rare phenotypes.

Perhaps more importantly, however, diversifying selection alone will not ultimately produce homoplasy without there also being convergence of the same traits. Hence, an additional important factor in the production of homoplasy, beyond the strength, timing, or even form of selection, may be the range of possible end-states to which traits can change. After all, in the production of homoplasy, it is not the probability of change per se that is critical but whether change produces recurrent patterns.

Character-state options

"Behavior is much more difficult to treat comparatively than is structure because of its variability."
"Convergence in behavior is prevalent, probably because of intense selection pressures and limited possible responses by the animal."

(Atz, 1970: 69)

Although opinion on this matter is not consistent (and Atz's comments above show that even the same author can vacillate), it does seem reasonable to suggest that the range of possible character states to which a trait can evolve is far greater for behavioral traits than for genetic, morphological, and perhaps neural traits. In genetic systems, for instance, each nucleotide position can only exist in one of four character states (A, G, T, or C); thus, the number of possible character states to which a given base pair can change is limited (from one, if only transitions are allowed, to three, allowing for either transitions or transversions). The same sort of limitation may obtain for at least some neural and morphological traits, as illustrated in the above examples of extreme conservatism in neural-circuit design and morphological bauplans. In these cases, the observed conservatism appears to be due to the limited range of alternative possible functional designs. In contrast, while perhaps not universally true, the range of alternative possible behavioral states is almost certainly broader (see discussion of display behavior below).

Thus, although behavior may (or may not) change more readily than morphological traits and may (or may not) be more prone than morphological traits to diversifying selection, it is nonetheless likely to involve a greater range of viable alternative character states that effectively reduce the probability of homoplasy arising through recurrent convergence on a small number of end states.

Empirical evidence—Is homoplasy greater in behavioral traits?

We now turn to the important question of whether behavioral characters are, in general, more homoplastic than other sorts of traits. A number of studies from a variety of animal taxa provide data germane to this question, and some make direct comparisons of relative levels of homoplasy in behavioral versus morphological traits. The most comprehensive of these is a review by de Queiroz and Wimberger (1993; see also

Wimberger and de Quieroz, 1996; Irwin, 1996; Lockwood and Fleagle, 1999), who compared levels of homoplasy in morphological and behavioral characters from 40 different published studies on a wide range of animal taxa. These authors undertook two different comparisons for the purpose of testing the common assumption that behavioral characters are more homoplastic than morphological characters. One test involved comparing overall levels of homoplasy for all data sets involving morphological characters with those for all data sets involving behavioral characters, while the other involved comparing levels of homoplasy in morphological versus behavioral characters specifically for studies of the same taxon. In neither test were levels of homoplasy (evaluated using the consistency index) significantly higher for behavioral than for morphological characters.

Similar comparisons have been undertaken in studies of specific taxa, with similar results. For example, McLennan et al. (1988) compared levels of homoplasy in phylogenies of stickleback fish (family Gasterosteidae) reconstructed using either morphological or behavioral characters. Here, the behavioral phylogeny showed considerably less homoplasy than that based on morphology and was highly concordant with a phylogeny based on molecular characters (as well as one based on a combination of molecular, morphological and ecological characters). Likewise, Prum (1990) compared homoplasy in a phylogeny of the manakin birds of South America reconstructed solely on the basis of behavioral characters with the one obtained from a phylogeny reconstructed by combining behavioral and morphological characters. He found that the consistency index for the behavioral phylogeny was higher (indicating less homoplasy) than that of the phylogeny based on the combination of morphology and behavior (i.e., removing morphological characters from the analysis *reduced* the overall level of homoplasy on the tree).

Thus, overall, empirical findings to date offer very little evidence to suggest that behavioral traits are more homoplastic than other types of traits. In the studies cited above, a wide range of animal taxa was considered, including insects, fish, frogs, reptiles, and birds. An equally wide range of behaviors was encompassed by the analyses, ranging from low-level stereotyped movement patterns to higher-order behaviors (e.g., courtship behavior, territoriality, parental care) and even including some of the physical by-products of behavior (e.g., nest architecture and placement). Notwithstanding this variation, there may be certain limitations to these studies. First, although encompassing a diversity of animal taxa, studies to date have been biased towards arthropods and birds, and mammalian taxa (in particular, primates) have not featured in analyses of behavioral homoplasy. Second, while based on a variety of different behavioral traits, the analyses have nonetheless been biased toward lower-level behavioral patterns, such as stereotyped movements and display. As a result, the extent to which the results of these tests of behavioral versus morphological homoplasy generalize to higher-order behavioral patterns or to mammalian taxa with complex social systems remains unclear. There are, however, two studies on higher-order behavioral traits in primates that deserve mention in this regard (Spuhler

and Jorde, 1975; Di Fiore and Rendall, 1994; Rendall and Di Fiore, 1995). Although both focused only on the lability of behavioral traits and made no direct comparisons with morphology, they do provide important data on the matter of the perceived lability of behavior, particularly higher-order behaviors removed from structural underpinnings (see also Fleagle and Reed, 1996, 1999; Kappeler, 1999).

An illustrative example—primate social behavior

Spuhler and Jorde (1975) undertook a quantitative analysis evaluating the fit between various aspects of species' behavior and either their ecological or phylogenetic position. Their task was not to use behavioral traits to try to reconstruct primate phylogeny—the basic phyletic relationships of primate taxa were already worked out on the basis of both morphological and molecular data—but rather to ask whether historical factors (phylogeny) or current environmental conditions (ecology) better explained the distribution of behavioral patterns observed among extant primates. The focus of research on primate behavior at that time (and to follow) was on the deterministic influence of local ecological conditions, and it tended to emphasize the relative plasticity of behavior. Hence, in asking whether ecology or phylogeny better accounted for patterns of primate behavior, Spuhler and Jorde were undertaking an early test of behavioral lability.

They classified 21 different primate species on the basis of 19 different features of behavior, encompassing aspects of ecology, demography, and sociality. They then used quantitative statistical techniques (e.g., cluster analysis) to examine how species clustered when all traits were considered simultaneously based on categorizations either by ecological grade [according to the schemes of Crook and Gartlan (1966) and Jolly (1972), which were popular at that time] or by phylogenetic grade (roughly equivalent to superfamilies). Albeit using nonphylogenetic clustering techniques (i.e., not based on *derived* similarity), they found that species clustering on the basis of phylogenetic grade was as good as that based on ecological grade, meaning that many higher-order behaviors seemed as strongly correlated with phylogeny as with environmental factors. On the basis of these results, they concluded that "phylogenetic and environmental factors are approximately equally important determinants of primate social behavior" (Spuhler and Jorde 1975: 376).

More recently, Di Fiore and Rendall (1994; Rendall and Di Fiore, 1995) undertook a similar analysis focused specifically on higher-order behavioral traits associated with social organization. Here again, the goal was to examine the extent to which patterns of primate sociality could be accounted for on the basis of historical (i.e., phylogenetic) as opposed to ecological factors. In this analysis, both the number of taxa and behavioral traits considered were greatly expanded. The authors classified 65 species, representing 37 genera and all the major superfamilies, based on 34 different behavioral traits of social organizations (e.g., dispersal, grouping, community structure, mating patterns, social relations within and between the sexes, and reproductive investment; for a complete list of taxa and behavioral traits used see Di Fiore and Rendall, 1994). The authors first

conducted a cladistic parsimony analysis—unconstrained by information on the phylogenetic relationships among taxa—to determine how primate species clustered solely on the basis of derived similarity in social behavioral traits. In this way, they were asking how well a cladogram based only on behavioral characters could recover details of an accepted primate phylogeny. In a second analysis, they then mapped social behavioral traits onto a well-supported phylogeny to evaluate how and where details of primate social behavior changed in the evolutionary history of the primates. Some striking results emerged.

In the first of these analyses—the cladistic analysis—one very conspicuous species-cluster correlated highly with phylogeny: almost all cercopithecoid species were grouped together at the derived pole of this cladogram based only on social behavioral traits (Fig. 1). This cercopithecoid cluster was due to the sharing of a number of derived traits related to female philopatry and social relations among adult females. In the second analysis, in which social behavioral traits were mapped onto a supported phylogeny, the same aspects of cercopithecoid social organization were parsimoniously reconstructed as having arisen once in the ancestor

of all extant cercopithecoid species and conserved in most descendant taxa, despite the subsequent radiation of these taxa into a diversity of ecological niches (Fig. 2).

While neither set of results speaks directly to the issue of behavioral homoplasy, nor to the more specific issue of comparative levels of homoplasy in morphological versus behavioral traits, the two studies are consistent in finding evidence for phylogenetic conservatism in important features of primate social behavior which, of course, by extension implies low levels of homoplasy (see above). Di Fiore and Rendall's (1994) study is especially illuminating in this regard, as their phylogenetic reconstructions clearly indicate that even higher-order behavioral traits associated with social organization can be conserved over considerable evolutionary time scales (see section above on behavioral lability). In fact, this conservatism in cercopithecoid social systems has occurred in the face of considerable diversity in species' ecology and morphology. As summarized in Di Fiore and Rendall (1994: 9944):

> extant cercopithecoids are the most ecologically diverse primate taxa—they cover the largest geographical range of any nonhuman primates, occur in the most extensive variety of habitat types (including dry open savannas, tropical rainforests, and snow-covered subalpine regions), show a corresponding diversity of substrate use and locomotor patterns (from strict terrestriality to strict arboreality), and include species specialized for folivory (colobines), gramnivory (hamadryas and gelada baboons), frugivory (*Cercopithecus*), and broad omnivory (macaques).

Some of this extreme ecological diversity has yielded morphological diversification, and one good example is the relatively simple stomach of frugivorous cercopithecines compared to the complicated polygastric stomachs of the folivorous colobines. The comparative uniformity in behavioral traits associated with social organization, despite such ecological and morphological diversity, serves to confirm the conclusions (see above) that behavioral traits are not justifiably assumed to be more variable, and thus more prone to homoplasy, than morphological (or other) traits.

Behavior in phylogenetics

We can now begin to predict when behavioral traits might prove useful in phylogenetic systematics and which classes of behavioral traits are likely to be the most informative (Table 2). Given the hierarchical nature of biological systems, it seems likely that the phylogenetic utility of any given behavioral trait will depend to a large extent on (1) the selective regime to which the behavior is subject (as discussed above), (2) the type of behavior being considered and its level of organization, (3) the taxonomic level under investigation, and (4) interactions between all three (Proctor, 1996; Masters, 2007).


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                                    Outgroup
                                    Galago
                                    Mirza
                                    Perodicticus
                                    Microcebus
                                    Lepilemur
                                    Avahi
                                    Hylobates △
                                    Eulemur
                                    Indri
                                    Phaner
                                    Tarsius
                                    Varecia
                                    Aotus
                                    Callicebus
                                    Callithrix
                                    Leontopithecus
                                    Saguinus
                                    Pongo △
                                    Brachyteles
                                    Saimiri
                                    Alouatta
                                    Piliocolobus *
                                    Pan △
                                    Ateles
                                    Gorilla △
                                    Colobus *
                                    Propithecus
                                    Lemur
                                    Cercocebus *
                                    Cercopithecus *
                                    Erythrocebus *
                                    Macaca *
                                    Nasalis *
                                    Presbytis *
                                    Cebus
                                    Papio *
                                    Theropithecus *
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* Old World Monkeys
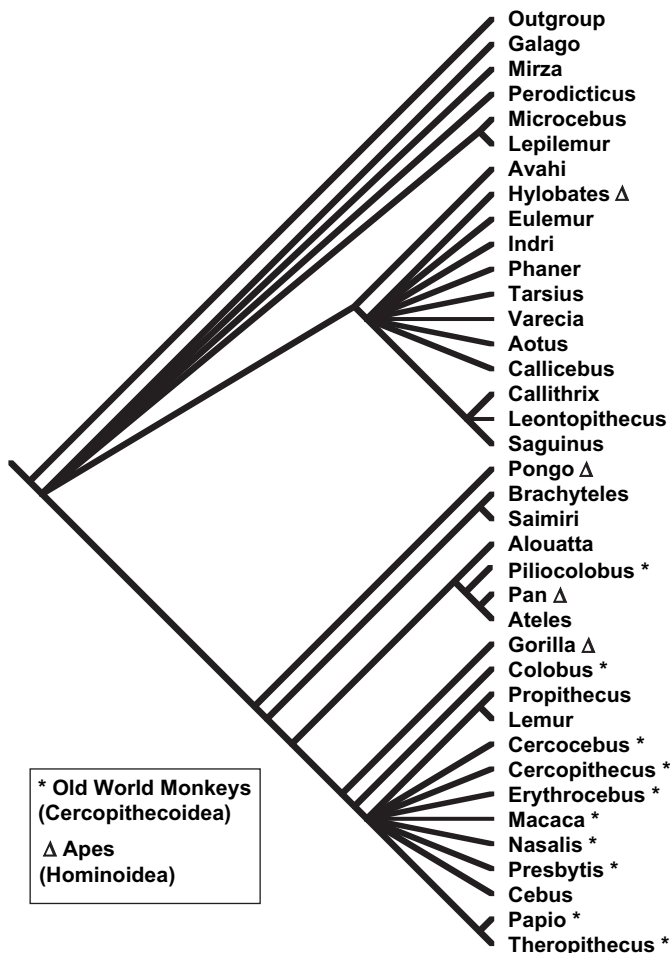(Cercopithecoidea)

△ Apes
(Hominoidea)

Fig. 1. Relationships among primate genera based on features of their social systems. Genera with similar social systems group together. Those further from the outgroup are more derived. Outgroup character states were assigned based on characteristics of extant tupaiids (commonly regarded as a likely sister group for primates) and based upon the "generalized primitive mammalian social condition" articulated by Eisenberg (1981) and Poole (1985).

Types of behavioral traits

Obviously, not all types of behavioral traits will prove useful for reconstructing phylogenies. Just as different molecular
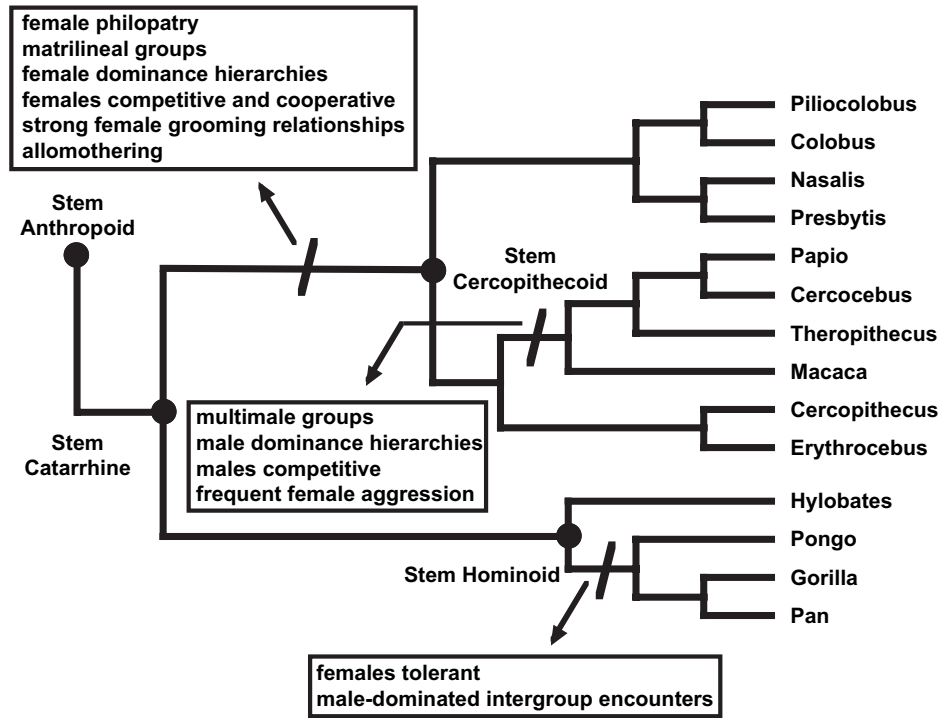
Fig. 2. Phylogeny of the Old World monkeys (Cercopithecoidea) and apes (Hominoidea) with specific social system traits marked on the branches of the tree where they are reconstructed to have arisen. Female philopatry and various traits pertaining to social relationships among females are derived characteristics of cercopithecoids that arose once in the cercopithecoid ancestor and were subsequently retained in descendant species.

traits (e.g., nuclear versus mitochondrial genes, coding versus noncoding gene regions, or first and second versus third codon base pairs) and different morphological structures (e.g., overall bauplans versus details of peripheral anatomy) may evolve at different rates and thus prove phylogenetically informative at different taxonomic levels, so, too, is it likely that certain classes of behavior will evolve at different rates and will prove better at resolving the branching patterns among lineages at different time depths within a phylogeny (Masters, 2007).

To date, behavioral traits that form elements of courtship and mating displays have been employed with great success in phylogenetic reconstruction, presumably because combinations of these traits serve as important markers for species recognition which is, of course, critical to successful reproduction. In fact, Mayr and Ashlock (1991: 175) argued that ''behavioral characters are often clearly superior to morphological characters in the study of closely related species, particularly sibling species … [because] behavioral characteristics are the most important isolating mechanisms.''

In fact, courtship and mating displays in birds featured centrally in the development of early ethologists' ideas regarding the phylogenetic utility of behavior (e.g., Lorenz, 1941; Tinbergen, 1959; van Tets, 1965; see the section above on historical perspectives). Prum's (1990) comparison of manakin phylogenies derived from courtship displays versus morphological traits (discussed above), and Irwin's (1996) reanalysis of the display data of Lorenz and van Tets for ducks and pelicaniformes, respectively, have confirmed the utility of display behaviors for estimating phylogenetic affinities at several taxonomic levels, most significantly among species and genera. More recently, Slikas (1998) examined the phylogenetic content of courtship displays in Ciconiformes (storks) and demonstrated that a phylogeny based solely on behavioral characteristics accorded reasonably well with a genus-level phylogeny based on DNA hybridization data. Similarly, other kinds of visual displays such as flash patterns used by males to attract females have been critical in distinguishing species of North American fireflies (Barber, 1951; Lloyd, 1983), and

Table 2
Summary of observed or predicted relationships regarding the use of behavioral traits in phylogenetic reconstruction

Behavior type	Examples	Connection to underlying structure	Phylogenetically informative at…
Maintenance behavior (lower order)	Autogrooming; motor patterns involved in locomotion and food acquisition	Strong	Low taxonomic levels
Display behavior (lower order)	Motor patterns involved in courtship and mating; vocal signals	Strong	Low taxonomic levels
Subsistence strategies (higher order)	Diet choice; habitat selection	Intermediate	Low to high taxonomic levels
Social strategies (higher order)	Dispersal pattern; mating system	Weak	High taxonomic levels

vocal displays and courtship songs in birds and some arthropods have featured as key taxonomic characters distinguishing closely related species (reviewed in Payne, 1986; Otte, 1989; Irwin, 1996).

For mammals in general and primates in particular, distinctive courtship and mating displays are less common and less stereotyped, perhaps due to basic differences in the social milieu in which reproduction occurs. Nevertheless, other aspects of signaling behavior may function in species identification and thus be phylogenetically informative at this taxonomic level. For example, in many primate species, individuals moving and foraging in dispersed fashion produce "contact" calls to promote group cohesion and coordinate travel direction under conditions of poor visibility. In addition, males in many species produce loud calls that function in territory advertisement and perhaps also in mate attraction. Here, selection should favor divergence in call structure between closely related, sympatric species to aid in species identification analogous to the divergence seen in avian mating displays. We might predict, then, that features of contact calls and loud calls would be especially phylogenetically informative at this level among, for example, sympatric cercopithecines in central Africa, macaques in southeast Asia, callitrichids in South America, and lemurs in Madagascar, and indeed there is some evidence in support of this prediction (e.g., Marler, 1970, 1973; Struhsaker, 1970, 1975, 1981; Waser, 1982; Oates and Trocco, 1983; Snowdon et al., 1986; Gautier, 1988, 1989; Zimmermann et al., 1988; Macedonia and Stanger, 1994).

These results suggest that display behaviors may be particularly good behavioral traits to use in phylogenetic reconstruction for resolving relationships at low taxonomic levels (e.g., species, subspecies). In fact, in a recent survey of several different nonmammalian taxa, Foster et al. (1996) found that display behaviors were more phylogenetically informative (characterized by lower levels of homoplasy) at the species level than were maintenance behaviors like foraging and locomotion, which they interpreted as being closely associated with environmental factors. They suggested that this pattern may reflect constraints on the range of forms that maintenance behaviors can take because few variations are likely to represent functional improvements. The potential functional variants of basic motor behaviors, for example, will be seriously limited by the demands of biomechanical and energetic efficiency, both of which favor economy of motion. In contrast, display behaviors are not similarly limited since their function, in many cases, is to increase the conspicuousness of the displaying individual, allowing biomechanical and energetic considerations to be relaxed and the range of potential character states for the behavior to express to be expanded.

However, not all elements of display behavior are equally phylogenetically informative. For example, some behavioral features of vocal displays have been found to be phylogenetically informative (e.g., call structure, temporal patterning, the presence/absence of particular call types in the repertoire), while other features (e.g., song repertoire size) have proven less so (e.g., Irwin, 1996). Similarly, Slikas (1998) found that when the various behavioral components of stork visual courtship displays were mapped onto a molecular phylogeny, early elements in the display sequence retained much more phylogenetic information (i.e., had higher consistency index values, indicating less homoplasy) than did behaviors from later in the display sequence or display behaviors not associated with courtship and reproduction. One way to interpret these results is as evidence of strong selection for conservatism in the early elements of a display to allow fast and accurate recognition of conspecifics. Later elements of a display may be more likely to vary between individuals of the same species (possibly providing a metric for decisions about quality variation by members of the opposite sex) and thus be more apt to show homoplasy between species. In general, then, we would predict that those features of displays that are most phylogenetically informative, at least at low taxonomic levels, are likely to be the ones most closely tied to recognition of conspecifics. Similarly, we might also predict that display features should prove to be particularly good phylogenetic characters for species living sympatrically with closely related taxa. The main caveat to these remarks is that such features may prove to be too often species-specific, in which case they would be autapomorphic and not phylogenetically informative.

Finally, a whole class of behavioral characters that may prove especially informative (at least at low taxonomic levels) would be behaviors whose form would be predicted to be under little or no selective pressure, such as scratching, sneezing, defecating, yawning, stretching, and shaking. Behaviors like these have seldom, if ever, been studied for their phylogenetic utility in primates [although they have at times in other taxa: e.g., scratching in tetrapods (Lorenz, 1958); antenna-cleaning in grasshoppers (Jacobs, 1953)]. As close to selectively neutral as behavior is ever likely to be, they are roughly analogous to noncoding regions of the genome and thus potentially useful in distinguishing at the level of species or below.

Taxonomic level

Apparent in the discussion thus far is the fact that behavioral traits have been most often applied to phylogenetic reconstruction at the species and generic levels and only rarely to phylogenetic reconstruction at higher taxonomic levels. This is most likely due to difficulties in homologizing behavior across more distantly related taxa, particularly where research has abided by the overly restrictive criterion of a *structural* locus for homology. The behavioral display traits discussed above all have clear structural underpinnings, inasmuch as displays are integrally related to the parts of the body they are performed with and to the motor patterns they involve. Hence, it is perhaps not surprising that the behavioral traits that have been used most widely and to greatest effect in phylogenetic reconstruction have been display elements.

While behavioral traits that are closely tied to underlying structures—what we have called "lower-order behaviors," such as stereotyped movements or displays that may be co-opted from such movement—undoubtedly will continue to

prove useful in phylogenetic reconstruction at the species or generic levels (or for distinguishing among evolutionarily significant population units within species), their utility for resolving deeper evolutionary relationships is still unknown. There may be reason to think that certain "lower-order" behavioral traits with close ties to structure could prove useful for phylogenetic reconstruction at higher taxonomic levels. Although few formal quantitative analyses have been performed, some aspects of primate vocal signals, such as the structure of alarm, threat, and other agonistic calls (e.g., screams), appear to be relatively conservative among congeners and perhaps at higher taxonomic levels (Gautier, 1988). This conservatism may reflect similarities in the underlying anatomy of vocal production and perception, similarities in the function of calls across taxa in the case of threat and agonistic calls, or in the case of alarm calls, perhaps similarities in the sorts of predators faced (possibly as a by-product of conservatism in the evolution of body size, body plans, or niche radiation). Nonetheless, we suspect that, in general, the ability of "lower-order" behavioral traits to resolve higher taxonomic levels may be limited, if only because the reality of relying on a structural criterion of homology means that these traits will be difficult to homologize across more and more distantly related taxa (see also Masters, 2007).

To date, few studies have examined the phylogenetic utility of what we would call "higher-order" behavioral traits—traits that are relatively divorced from underlying morphological structure or traits that other authors have referred to as "multivariate or metabehaviors" (Ryan, 1996) (e.g., dispersal patterns, foraging styles, social behaviors). We submit that this is principally due to the persistent tendency to require that homology be associated with structure, a view that we feel has unnecessarily hampered the inclusion of behavioral information in phylogenetic analyses. In those few cases where "higher-order" behaviors have been included in phylogenetic analyses (see above section on primate social behavior), the results are encouraging, and we predict that higher-order behavioral traits or metabehaviors might prove useful in resolving deeper phylogenetic relationships (although, obviously, particular care must be taken in defining these higher-order behaviors to minimize incorrect assumptions of homology).

In fact, some support for this prediction can be found within the primates. For example, while the mechanics of food harvesting may be broadly similar among species within particular clades, aspects of dietary choice or feeding strategy may provide phylogenetic information that distinguishes among clades, the way the frugivory/folivory distinction nicely (though not perfectly) separates the cercopithecine and colobine subfamilies, the way gummivory distinguishes callitrichines from the other cebids, and the way below-branch feeding distinguishes atelines from other platyrrhines. Certain aspects of social organization appear to characterize particular primate clades (Di Fiore and Rendall, 1994; Rendall and Di Fiore, 1995). For example, cooperative breeding is a synapomorphy of the Callitrichinae, and strict female philopatry is diagnostic of the Cercopithecoidea, while female dispersal is normative for all of the Hominoidea.

Conclusions

While perhaps few modern systematists would admit it, the fact that behavioral traits feature rarely in the vast majority of systematic studies reflects an inherent bias against the use of such traits in phylogenetic reconstruction. Among the common criticisms offered against the use of behavior has been the notion that behavior is *functional* rather than *structural* and therefore cannot be homologized. Additionally, behavior has been perceived as more readily subject to selection and more evolutionarily labile than other types of traits and therefore more prone to homoplasy. Some researchers have also suggested that there are few different ways in which behaviors can be performed, thereby adding to the likelihood of convergence. Taken together, such assumptions have contributed to what we feel is a mistaken impression that behavior is somehow evolutionarily "special" and thus of suspect utility in phylogenetics.

In this paper, we have touched on each of these criticisms and found them wanting. First, like several other authors in recent years, we have reviewed the ongoing controversy over definitions of homology and concluded that rigid adherence to a structural as opposed to functional criterion for homology is unjustified. Instead, we have offered our support for the hierarchical concept of homology articulated by Lauder (1994), which allows for functional homology, and we have pointed to a number of examples where functionally defined, higher-order behaviors—divorced from underlying structures—have been shown to be useful in phylogenetic analyses.

We have also discussed the perceived lability of behavior and the nature of the relationship between behavioral traits and the timing, strength, and form of selection. We have pointed out that highly functional behavioral traits subject to strong selection are not necessarily more labile or more prone to homoplasy than other types of traits. Stabilizing selection, regardless of its strength, produces conservatism in any type of trait, and we saw examples of this at the level of genes (homeotic genes for CNS development), neural systems (circuit design), morphology (bauplans), and behavior (features of social organization). Whether directional or diversifying selection should lead to more homoplasy in behavioral versus other trait systems is still an open question, although at first glance there seems to be no strong reason to expect it to. In contrast to certain past assumptions, we have suggested that behavioral traits will, in many cases, show a greater range of possible character states than other types of traits, thereby reducing the likelihood of chance (or adaptive) convergence.

Thus, we conclude that it is premature to assume that behavioral traits should be more homoplastic than other types of traits. That assumption seems to be unjustified both on a priori theoretical grounds and from our review of the empirical work to date, where the few strict comparisons of relative degrees of homoplasy in behavioral versus other traits indicate comparable levels. Behavioral traits appear to be subject to exactly the same kinds of problems that characterize homology/homoplasy determinations in other trait systems (reviewed in Lockwood and Fleagle, 1999), and interpretations of the utility

of behavioral traits ought to be evaluated using the same criteria applied to those systems.

Finally, one emerging consensus, both here and elsewhere (including several of the other contributors to this special issue), is that the lability of particular traits (behavioral, morphological, molecular, etc.) is likely to vary hierarchically (Lockwood and Fleagle, 1999). Thus, different traits even within each of these trait classes will undoubtedly prove more appropriate for examining branching patterns at different depths on an evolutionary tree (Masters, 2007). As in molecular phylogenetics, where fast-evolving genes may be informative at lower taxonomic levels but saturate at higher levels (where genes that evolve more slowly become more informative), in behavioral phylogenetics, details of behavioral patterns and performance may help to distinguish relationships among taxa at lower levels while similarities in trait function may in many cases prove to be informative characters at higher taxonomic levels. Thus, in general, behavior certainly seems to be a valuable class of character that shows phylogenetically informative variation over a range of taxonomic levels. Our conclusion here echoes that of Niko Tinbergen, stated almost 50 years ago, concerning the utility of behavior in phylogenetic studies: "Behaviour characters are in principle neither more nor less useful than morphological or other characters; they merely add characters to the total by which overall likeness is judged" (Tinbergen, 1959: 328).

Acknowledgments

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