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BEHAVIORAL HOMOLOGY AND PHYLOGENY

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INTRODUCTION

The sociobiology debates of the 1970s increased interest in the biology of behavior. At the same time, the growth of cladistics increased interest in how to do systematics and phylogenetic reconstruction. Yet, there are surprisingly few recent papers dealing explicitly with behavior from a phylogenetic perspective. Lack of communication between students of behavior and students of systematics is partly to blame. If one says to a behavioral ecologist, "Isn't it curious that there are white bears in the arctic?" he may say that there is nothing curious about it because they are white like all the other arctic mammals, and the fact that they are bears is irrelevant to the broad patterns of evolution. If one asks the same of a systematist he may reply that there is nothing curious about it because they are still bears like all the others, and the fact that they are white is irrelevant to the broad patterns of evolution. Both perspectives are partly right, and both are less than the whole story. Systematists tend to look for constraints of history, while behaviorists usually prefer to work with a warm ball of clay that lies ready to take on any shape the outside forces push upon it.

Some of what follows is review and some is more philosophical, but the point of the paper is simple. Determining homology among behaviors is no different than determining homology among morphological structures. Behavior is not special, it is only more difficult to characterize. Ethology (the study of behavior) is a relatively young science and does not yet have the benefit of centuries of debate and consensus, but that provides more reason for us to take up the challenge now. Ethology has made almost no advance with respect to a phylogenetic understanding of behavior since the late 1950s, and most

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*Current address: Department of Entomology, American Museum of Natural History, Central Park West at 79th, New York, NY 10024-5192 modern ethologists simply do not work toward that goal. To honor the proud heritage of Lorenz and Tinbergen we need only to be brave and begin.

There is an immense literature dealing with "evolution of behavior," but only a tiny fraction of ethological efforts are relevant to the question of how one postulates homology among specific elements of an animal's behavioral repertoire. The majority of studies on behavioral evolution are related to theories of the process of evolution, and they therefore compare grades to illuminate the way in which analogous transitions occur in different groups (33). The focus of these studies is the transition itself, and homology of the steps is not an issue. Also the taxonomic literature is skewed toward finding species-specific behaviors that allow identification more easily than morphological variation allows (1). Such unique traits do not assist in reconstructing phylogeny; only shared traits are useful for finding a nested hierarchy of order. I have tried to include here both classical and more recent works that illustrate explicit postulates of homology, or cases where behavioral characters were critical for defining or supporting a phylogenetic scheme, but this discussion is streamlined to serve more as an introduction to a developing field than as the conclusive study of a mature body of science.

CRITERIA OF HOMOLOGY

The distinction between homology and analogy provided the foundation for systematic biology, and the terms have been the source of disagreement for close to two centuries. Evidently the discussion is not over yet, and if the reader chooses to pursue the philosophical issue, there is plenty to do (9, 24, 36, 46, 78, 79, 86, 98). Some of these papers generate more heat than light, and the entire debate is almost completely without reference to behavior (but see 3, 54). For the present purpose, homologous behaviors are defined as those that find their origin in the same ancestor and are similar because of descent from that common ancestor. Even if two behaviors satisfy all other criteria (below), they are not homologous if they are derived independently from different ancestors.

In the past, this sort of definition was regarded as partly circular because the postulates of homology are used to generate a phylogeny that in turn informs us of ancestry. Prior to the growth of Hennigian methods (10, 43, 112), most systematists based their classifications and evolutionary scenarios upon several critical characteristics that were believed a priori to have some special importance much greater than other characters. The amnion is not a particularly flamboyant structure, nor is it even present for most of an animal's life, but its influence in taxonomy is great because it is a "good" character. To maintain the postulate of homology among all amnia, we sacrifice any other character. This amounts to saying that there is a way to tell a "true" homology from mistaken homologies (analogies) in the absence of phylogenetic information. Although this view is represented here in an extreme that would apply better to scientists of a century ago, it is presented by Wagner (98, p. 62) who felt that "self-regulatory mechanisms of organ differentiation" were the key.

Congruence with Other Data

Opposing the traditional view, the Hennigian perspective dictates that because we cannot observe the relevant ancestor directly, there is no way to know what are the "true" homologies. Because we cannot confirm or refute any hypothesis of homology for a given character directly, we have no choice but to rely on some kind of indirect method to evaluate the postulate of homology for each character. If characters are allowed to weight themselves, "true" homologies (synapomorphies for relevant clades) will be concordant and will support each other, while analogies will not form a pattern (24, 79). The correct statements of homology will win if the characters are allowed to fight among themselves for the simplest resolution of discordant evidence. First, the Hennigian systematist uses the same methods systematists have always used to infer homology (below; "primary homology" sensu de Pinna, 24), then s/he observes the most parsimonious phylogenetic tree and deduces from it, post facto, which of the a priori determinations were correct and which were incorrect. Some methods allow characters to adopt the weights suggested by the phylogeny they produce (12). The advantage of this recursive procedure is that we simply do our best and see what happens.

This Hennigian perspective on homology is applied to behavioral data with increasing frequency, both for reconstructing phylogeny and for understanding the evolution of the behavioral characters themselves (10, 13, 14, 17, 18, 26, 39, 54, 67, 83, 106). Whether the characters are used to generate a cladogram or they are simply plotted on an accepted phylogeny, derivation of the same trait in separate lineages demonstrates a false postulate of homology. Casual critics often remark on the possibility for circular reasoning because the investigator may recode his data to get the result that suits his needs, but this hazard exists in every branch of science. Of course, character coding is by far the most difficult step in the process because it requires explicit statements of how many states there are for each character, whether these states are arranged linearly or in a hierarchical fashion, why the states are polarized as they are, whether all transitions are equally likely or some are favored, whether convergence is more likely than reversal, as well as other more subtle decisions (10). When done properly, the work is repeatable by others less familiar with the taxa and characters, or the points of contention are defined clearly. For this paper, congruence with other data is regarded as the ultimate arbiter of homology, and all other criteria are merely tools to assist in forming the original postulates.

The main disadvantage of this approach is that it operates nearly in reverse of how most ethologists prefer to work. As a young biologist steps into the field to do a comparative study of several species, he usually asks himself, "How do they differ?" For success in the Hennigian paradigm he must ask himself, "How are they the same?"

Morphological Criteria

Morphology may appear to provide a more stable reference than behavior itself, but morphological criteria for homology amount to little more than a case of Remane's (84) "special quality" (below). Neuroethology has progressed to the point where certain behaviors can be mapped onto anatomy (6, 47). Unfortunately, the output of a given system can vary a great deal due to hormonal (52) or other influences. Furthermore, the cascade of neural activities that leads to, or regulates, a behavior is often discovered indirectly so that statements of causality are more inductive than deductive. Bullock (11, p. 408) remarked that "innumerable instances in the literature testify to the temptation to conclude a causal relation which turns out later to be a parallel but distinct system." For the purposes of determining homology among behaviors, the field of neuroethology appears to be not yet mature enough to lend much assistance.

Taking a more macroscopic view, Jander (49) considered motions of legs and antennae to define traits in the grooming behavior of 45 families of insects. The breadth of her study required that the characters be defined broadly, such as "antennae rubbed between upraised forelegs." Whether one leg (Planipennia, Mecoptera, Diptera, Lepidoptera) or both (Megaloptera, Trichoptera) are used is regarded as variation among homologues. Although there is no obvious causal linkage between the morphological and behavioral evolution, the general pattern of evolution of grooming across insect orders corresponds well with phylogeny based upon morphological data. In some cases, behavioral data appear to be more stable than morphological data and show lower average homoplasy across the same taxa (18, 106; A. de Queiroz, P. Wimberger, unpublished information).

More strict application of morphological criteria require that the behaviors cannot be considered homologous unless the precise motions of the same body parts are used. Atz (2) took an extreme position, "the whole neural-behavioral organization of the bird is so unlike that of the mammal that any similarities in behavior between them must be attributed to convergence" (2, p. 65), concluding that "homology is a concept inappropriate for behavioral characters." He rejected behavioral products such as architecture despite its importance in species, genus, and family-level taxonomy of many speciose groups including birds (20), spiders (81), termites (32), caddisflies (85), bees (69), and social wasps (27). Hodos (45) chose to demonstrate his position by reviving Lorenz's classic example of the homology of scratching behavior in tetrapods (also discussed by Atz—2). Following Heinroth (42), Lorenz (60) pointed out that passerine birds do not scratch the back of their heads by doing anything that would seem easy and natural, but rather they dip one shoulder, extend a wing and pass the ipsilateral foot over the back and across the opened wing to reach the head in a most awkward fashion. He proposed that the deep phyletic root of scratching is evident from the fact that birds, dogs, and most other tetrapods pass the hind foot over a shoulder to scratch the ipsilateral ear, a primitive motion which persists in passerines despite the awkwardness. Hodos (45) claimed this example shows that scratching in primates is not homologous with other tetrapods because it is performed with the front foot rather than the hind foot. According to this position, substitution of serially homologous structures for the same function inspired by the same motivation constitutes a novel character (nonhomologous) rather than a derived state of the same old character (homologous). Yet, many morphologists see that substitution of elements does not invalidate a statement of homology regarding the composite structure (3, morphology and fish behavior; 66, insect thorax), so it would be extreme to disallow morphological modification or substitution when studying behavioral traits.

The strictest application of morphological criteria alone assumes that evolution does not take separate paths for morphology and behavior. When this assumption fails, two errors are possible. First, if morphological change occurs under the mantle of homologous behaviors, the behaviors may lose the status of homologues despite the fact that they may be conserved as much as possible. This is implicit in Hodos' (45) view of substitution discussed above. The morphological variation should be seen rather as alternative states of the same character rather than two characters that have no historical connection. When spiders try to localize the sticky spiral during web construction, or they need to support a combing leg, they may use either the outer or inner leg (relative to the hub), and Coddington (18; characters 55 and 61) treated this as alternative states of homologues, not as two different characters.

The second problem with strict morphological criteria is the corollary of the first: if separate and nonhomologous behaviors evolve to take advantage of the same morphological elements, they will lose their identity as independently derived traits. This may be common because behaviors serving other purposes will have to be laid over the anatomy and motor patterns defined for primary functions (5). Barlow (4, p. 228) characterized the problems of the morphological reductionist extreme by stating " . . . it reduces all to one. Thus in the end everything is locomotion, respiration, or feeding. Clearly the motivational world of the animal is more structured than this." The fundamental problem is that there is no assurance that postulates of homology for behavior will be at a level corresponding to the meaningful postulates of homology for morphology.

Remane's Criteria

Statements of morphological homology generally use Remane's (84) classical criteria: position, special quality, and connection by intermediates. Applying Remane's criteria directly to behaviors themselves provides just as accurate, if not more accurate, an assessment of the homology among behaviors than does relying upon Remane indirectly by way of morphology. Remane's three criteria all have ethological counterparts and are already used (perhaps unconsciously) by ethologists.

POSITION Baerends (3) referred to the behavioral analogue of Remane's similarity in position as "similarity in topography" (3, p. 408). He homologized behaviors by using position relative to others in the sequence to find broad patterns common to all species. One of his better examples is that the tail wagging movements of two species of *Tilapia* look somewhat different but are assumed to be homologous because they occur in exactly the same places in courtship ceremonies. Similarly, Tinbergen (96) divided the greeting ceremony of gulls and kittiwakes into arbitrary steps of a progression, homologizing the major phases despite variation across taxa. Simple and easy to understand, this is the weakest criterion of homology. This approach is usually used in combination with other criteria.

SPECIAL QUALITY This is the most useful criterion, though it is also the most difficult to define. If the complex movements of several species take the same distinct form in the same context and appear to be largely innate, they may be thought of as homologues. A morphological criterion for homology may be considered a special case of Remane's "special quality" criterion. The more complicated and distinctive the behavior is, the stronger the postulate of homology will be. Eberhard (28) and Coddington (18) divided web weaving into qualitatively different steps of frame, radius, hub, temporary spiral, and sticky spiral construction, etc, with variants in these categories then regarded as homologues, including taxa that are so derived as to produce a web no longer recognizable as an orb (16). Prum (83) used distinctive, arbitrary portions of displays (e.g. "wing-shiver twist display," or "double-snap jump display") of 21 species of manakins. Eberhard (28), Coddington (18), and Prum (83) homologized characters across taxa, but special quality can also be used to homologize elements within the repertoire of an animal. Tinbergen

(93, 95) and Daanje (23) homologized certain ritual behaviors of territorial and sexual displays with ordinary preening, feeding, and locomotory motions.

Motivation as quality Cichlids use identical components in such different behaviors as territorial display and calling fry, and Baerends' (3) explanation relied upon the idea that these contextually different situations share a homologous special quality—motivational conflict. Although the precise functions of defense or calling differ, the animal must resolve a conflict between advertising itself (to the intruder, or the young) and departing (to flee from combat, or to relocate the young). This emphasis on motivational factors and internal "drive" was common among early ethologists (23, 93) and is retained in some recent work. Mundinger's (75) "criterion 3" explicitly considered motivation to be separate from Remane's criterion of special quality.

Function as quality As with the morphological criteria (above), the exact motions do not always allow definition of homology, but "special quality" may be fulfilled partly through distinctive function. A broadly defined attribute such as host plant choice or the like (10, 99) may have some complex physiological foundation suggesting homology by special quality despite differences in motor patterns. If the same distinct function is served by different series of acts in different species, then the composite behaviors may be worth comparing as different states of the same trait. Such cases would include mating behaviors, territorial behaviors, and other ritualized behaviors that vary in the reduced components of the ritual but serve the same function. Tinbergen's (96) implicit assumption of homology between the parts of the greeting ceremony display seems plausible because the study was constrained to identical context in closely related taxa; therefore the different behaviors are homologous at the functional level of "greeting ceremony."

However, homologizing traits of "special quality" through function is more difficult than it first appears. Identical behaviors in identical circumstances pose no problem, but what of identical behaviors in very different contexts? Beer (5) showed a table of 15 display elements and their various combinations that give rise to 12 functional behaviors in laughing gulls, demonstrating that exclusive correspondence between display and function does not exist for these birds; Beer stated that as a practical matter "ethologists have used criteria of form rather than function to decide what is to count" (5, p. 49).

Many scientists equate function with adaptation, and the latter thereby serves to identify behavioral variation and its purpose: "diverse patterns of behavior, from foraging to mating, are being understood in terms of their individual selective benefits" (87, p. 3). People studying behavioral ecology and adaptation may benefit from studying traits defined by function, but students of phylogeny and homology should be wary of such traits. Certainly, the adaptational postulates of homology will be no less vague, axiomatic, and circular than the definitions of adaptation often are (17, 38). Furthermore, behaviors are specifically believed to be more plastic than morphology and to play an important role in evolution (101, 107), suggesting that functionally defined characters may appear repeatedly and are more likely to be convergent or broadly overlapping than are morphological adaptations (30, 105).

Functional definitions of characters are sometimes difficult to rationalize. Wiggins & Wichard (111) proposed a new classification of Trichoptera (caddisflies) based upon a functional and adaptive view of the cocoon or larval case, but this view is evidently not congruent with other data (102). It should be emphasized that while one should be cautious from the point of view of homology and phylogeny about adaptively defined traits, the general aversion to using phylogenetic perspectives in adaptive story-telling (25) is without foundation. Cladistic methodology itself has nothing to say about the presumed process by which characters became what they are today; it merely states the most parsimonious resolution of the observed facts and patterns (19).

The significance of functional and adaptive information for phylogenetic studies is at best indecisive. Special quality defined by function will be no better. Bock (8, p. 12) declared that "the morphological description of taxonomic characters cannot be done in the absence of proper functional understanding because no guide would exist to the functionally and adaptively significant aspects of these features." Cracraft (22) denied the idea that functional information contributes anything to either the postulate or evaluation of homology, and wrote, "that there may be one or more functions for a structure does not imply an associated stereotypic behavior pattern for each function; it is the behavior pattern, then, and not the function, which constitutes a systematic character" (22, p. 23). Beer (5, above) would likely agree. Lauder (55, p. 322, 323) took a position in the middle, stating that "functional characters are not different from any other attribute that might contribute to our understanding of genealogy", that "functional characters may be homologous or convergent (just like morphological features)", and that "function does not take primacy in homology decisions."

CONNECTION BY INTERMEDIATES Continuity of intermediates is used widely by ethologists, usually to build an evolutionary scenario that runs between two poles. When Tinbergen (93) and Daanje (23) homologized displacement and intention movements with preening, feeding, and locomotory motions, they supplied a number of species and contexts with intermediate degrees of ritualization to connect the highly ritualized forms with their putative origins. One hazard with this approach is that even if the postulate of homology is correct, polarity may be determined incorrectly because there is no assurance that the inferred "ethocline" actually matches the path of evolution (70). Lorenz (58, 62) reminded his readers that the "intermediates" are actually evolutionary terminals in their own right. This is demonstrated by Kessel's (50) logical spectrum explaining the bizarre development of worthless (but not meaningless) nuptial offerings in balloon flies. Recent phylogenetic study (14) shows that a branching pattern is more appropriate than an ethocline for these traits. The evolution of spider webs (15) presents a similar problem in which the so-called intermediates confuse the interpretation of polarity.

If homology is suggested by different species showing intermediate forms, then it might be rejected by a single species showing both forms together. This is Patterson's "conjunction test" (79, p. 38). The test may not provide unequivocal rejection of homology even for morphological situations (24), and I do not believe that the test will prove useful for behavioral problems. As mentioned previously for displacement behaviors (93) or intention movements (23), an animal may incorporate a behavior from one part of its repertoire into another suite of behaviors. Motions derived from feeding, preening, or locomotory functions become established as part of a territorial or mating ritual, and the same animal displays both the original behavior and the behavior derived from it. Behavioral evolution does not require complete replacement.

Relative Utility of the Criteria

Those who live in the realm of pure theory often disagree with those who work with the practical problems of simply getting the job done. An example of this schism is the dispute about what criteria serve to establish homology in behavioral traits. Table 1 shows a brief list of some of the major contributions in which behavioral variation is discussed in a phylogenetic context. Although the list is not exhaustive, such papers are surprisingly rare, and one sees that the "general discussion" papers all rely primarily on morphology while those dealing with the phylogeny of a particular group use other criteria. Chronology shows no evidence of resolution of this problem except perhaps in that the most modern papers show a Hennigian focus in which the final arbiter of homology is congruence with the other data at hand.

UNITS OF BEHAVIOR

Recent developments in biology have led to a revolution in our ability to examine DNA directly and to make use of this molecular information. Because we can now read the genetic code itself, why shouldn't we focus all our attention on the molecular record of evolution? The reason we should not is that biology is full of properties that emerge in an unforeseeable manner from a combination of lesser units, properties that are not inherent to any of the constituent parts. The very breath of life itself and the living world in all its richness demonstrate that the "whole" can be much more than the sum of its parts. We may be able to explain post facto why the structure of a given

Table 1 Criteria of behavioral homology used in several studies, in chronological order, beginning 1951.

Taxa	Traits used	Homology criteria[a]	Author
Diverse birds	Locomotion, ritual motions	Remane	Daanje (23)
4 genera of Balloon flies	Courtship	Connection by intermediates	Kessel (50)
General discussion		Morphology, motivation, Remane	Baerends (3)
Many cricket species	Songs	Special quality	Alexander (1)
Red jungle fowl	Entire repertoire	Ontogeny, special quality	Kruijt (53)1
22 families of caddisflies	Architecture, weaving	Special quality, ontogeny	Ross (85)
45 families of insects	Grooming	Morphology, special quality	Jander (49)
General discussion		Morphology, Remane	Atz (2)
General discussion		Morphology	Hodos (45)
12 subfamilies of Balloon flies	Courtship	Congruence with other data	Chvála (14)
4 genera of finches	Songs	Motivation, Remane	Mundinger (75)
7 subfamilies of spiders	Architecture, weaving	Special quality, morphology	Eberhard (28)
7 genera of sunfish	Feeding	Congruence with other data	Lauder (54)
5 genera of yellow-jackets	Architecture, social traits	Congruence with other data	Carpenter (11a)
7 species of fruit flies	Courtship	Congruence with other data	Grimaldi (39)
6 genera of social wasps	Architecture, social traits	Congruence with other data	Carpenter (12a)
7 genera of stickle-backs	Courtship	Congruence with other data	McLennan et al (67)
13 species of sandpipers	Songs	Special quality	Miller et al (72)
16 families of caddisflies	Architecture	Special quality	Wiggins & Wichard (111)
19 genera of spiders	Architecture, weaving	Congruence with other data	Coddington (18)
21 species of man-akins	Courtship	Congruence with other data	Prum (83)
24 families of caddisflies	Architecture	Congruence with other data	Weaver (102)
29 genera of paper-wasps	Architecture	Ontogeny, congruence with other data	Wenzel (105, 106)

[a] Remane's criteria (placement, special quality, connection by intermediates) are listed separately unless an author used more than one, in which case only "Remane" is listed. In many cases there was no explicit statement of criteria used.

system permits a certain behavior, but knowing the structure alone is usually not enough to predict how the system will behave. Understanding oral anatomy does not predict language, and the molecular code to build that anatomy is still further away from the spoken phrase. Although we must have a certain combination of genes to permit us to speak, there is likely no gene for speech.

Contributing to the emergent nature of behavior, and hence the need to be flexible in recognizing units, is the contextual significance of the act in question. Behaviors that originate in one context may gain additional significance in a different context, perhaps leading to an appropriation of the behavior for the new function. Tinbergen (93) and Daanje (23) found that for elements of displays co-opted from other parts of the behavioral repertoire, the same motion in a different context bears a different message. An old motor pattern in a new context can reflect an historical event that is informative about phylogeny. Here, it is not the motor pattern per se that provides the synapomorphy for a given group, but rather the new context in which the borrowed behavior was expressed and its new significance. Reducing the sequence of behaviors to its smallest components may discard the epiphenomenon that is the trait.

Russell et al (88) made a bold effort to classify behaviors according to the "fixed action pattern" (4), which they redefine as "Act," in an effort to outline precise concepts about the units of behavior. The scheme requires so much knowledge about neural aspects of messages and channels that it is impractical outside a physiological study of behavior. Furthermore, defining traits according to their functions is problematic and not necessarily related to phylogenetic history (see Special Quality, above), which is more the subject of the present review. Regardless of the enthusiasm Russell et al show for conceptual issues, the main problem with our understanding of behavior is not that we lack precise concepts, but rather that we lack adequate data from enough taxa.

Far more practical and useful as a guide for recording and documenting behavior is Miller's (73) clear, sophisticated discussion richly detailed with examples from studies of avian behavior. In agreement with the theme of the present paper, Miller states that "'natural' units are as elusive in ethology as in taxonomy" (73, p. 353). We cannot rely upon fixed action patterns alone because such rigid behaviors may exist mostly in the minds of observers. In reality, the defining characteristics of a fixed action pattern (that the behavior is innate, invariant, released by an external trigger stimulus, and that it cannot be reduced to successive responses that depend on different external stimuli for modulation) are rarely satisfied under thorough experimentation (56). Barlow (4, p. 222) concluded that "there is no single case where all the criteria have been properly tested and fulfilled." In any case, reliance upon fixed action patterns differs little from reliance upon morphological criteria of homology (above), so failure to demonstrate the same neuromuscular activity is inadequate for rejection of homology (above). I agree with Barlow (4, p. 217, 218) that "any unit is appropriate if it fits the needs of the study," and that "models based on the behavior of individual neurons can only be regarded as starting points."

The problem of units then relies on the needs of the study (95, p. 189 ff). Genetical studies can help to define components of a system (7), but dissolving everything to "ethons," the smallest units of behavior, will not likely serve all purposes. At the lower limit, four or fewer amino acid substitutions in a less conserved region of the *per* locus are known to control the difference between species-specific wing rhythms in *Drosophila melanogaster* and in *D. simulans* courtship display (109). However, variation in the genetic architecture between species does not address the question of whether or not rhythmic wing motion is homologous as such across these species, hence, a synapomorphy for these flies at a higher level in Drosophilidae. Rapid wing vibration is a primitively homologous state for the related genus *Zygothrica*. (39, Table 3, Character 3), and lack of vibration is derived separately in different species (39, fig. 115). These absences of wing vibration are not homologues, regardless of what the identity of nucleotides might be.

It seems likely that the appropriate units will be larger as a study encompasses more taxa. The exact motions of pollen collection would be relevant to a study of different genera or species of bees. For distinguishing families of bees from each other, the character will become larger such that details that converge or vary among many genera do not obscure basic, gross differences such as "pollen carried in crop" or "on legs" or "on ventral scopa." Still larger, "collects pollen" is a unit adequate to distinguish all families of bees from wasps, flies, and beetles. If bees appropriated ordinary insect grooming behaviors for the purpose of manipulating pollen, then pollen carrying and grooming are homologues and synapomorphic for bees, wasps, flies, and beetles to show they share a more recent common ancestry with each other than with spiders or crabs. The appropriate unit changes with the scale of the problem. As the units become increasingly coarse, the chance of lumping analogous traits increases. Furthermore, there is nothing to exclude the possibility that individual fine motor patterns may have broad phylogenetic significance.

Several levels of units may be required in a single study. Mowry et al (74) dissect in detail the behaviors surrounding oviposition in the onion fly, drawing a flow chart with probabilities assigned for stepping from one behavior to another. The study was not searching for homology, but the results are informative about the need for units in a variety of levels. The model includes a string of five separate boxes that are linked in sequence by probabilities of 100%. Such linkage makes the sequence a candidate for "fixed action pattern" in the classical sense (above), in which case it is a meaningful unit on its own even if the components are justified as individual elements by virtue of appearing separately elsewhere in the repertoire. Mowry et al also include variables to account for emergent properties only visible from afar and not inherent to any of the reduced components of the model, such as seven separate probabilities for repeating "inter-egg subsurface probing" based on whether the female is trying to lay her second, third, fourth, or up to eighth egg. This relationship between probability of repetition and the number of times the fly has cycled through the model becomes a trait by itself. Thus, Mowry et al have found at least three levels: the individual components, the combined fixed action pattern, and the dynamic nature of these behaviors under iteration.

The meaningful level of analysis from a phylogenetic viewpoint will be the level that shows characteristics shared among several but not all taxa. The appropriate units of comparison will have to be distributed more broadly than species-specific traits unless there is a credible transition series between the traits. It may eventually prove to be the case that many so-called species-specific behavioral traits are, in fact, shared by a number of species. This is true for architectural constructs (21), a class of behavioral characters (or at least surrogates of behavioral characters) for which variation is measured more easily, and perhaps interpreted more easily, than most. In speciose groups like sweat bees (31, 89), paper wasps (103, 105), or spiders (30), intraspecific architectural variation is broad and phyletic convergence of architecture may be rampant. Eberhard (30, p. 342) wrote of spider webs: "the impression of species-specificity may usually, however, be the product of lack of information . . . . Given the long-standing and repeated documentation of substantial *intra*specific variation . . . species-specificity will be uncommon" (emphasis in original). Marler (64) pointed out that bird calls with certain functions, such as aggressive and alarm calls, should be (and appear to be) convergent rather than distinctive because they are most useful when they are understood by many species.

The search for species-specific units is not only useless from the point of view of phylogenetic analysis (assuming the species are already identified), but it may also be ill-advised on the grounds that it deliberately or inadvertently obscures phylogenetically informative elements common to several species. Repeated claims of specificity of behavioral units in such well known systems as bird courtship rely in part on a philosophical argument that the ritual "requires each step to be performed in a specific manner and in a specific place in the order, failure of an individual to follow the script will deny parenthood" (5, p. 18). Note that this opinion dictates only conservation of established ritual, not necessarily species-specificity across many taxa. Indeed, Miller and collaborators (71, 72) have found that the breeding vocalizations of certain birds are a mix of species-specific and more broadly distributed traits. Moreover, Heinroth's (42) empirical work, arguably the origin of ethology, documents a heterospecific mated pair in which the female Egyptian goose (*Alopochen aegyptaicus)* and the male Muscovy duck (*Cairina moschata*) managed to combine very different body motions and to learn those of the mate in order to form their own ritual and a bond lasting for years (42, p. 667). Clearly, these animals were not restricted to expressing or recognizing unit behaviors unique to their own species or genera, even in the most "species-specific" context.

Learning

Learning presents both empirical and theoretical problems in behavioral biology. It is outside the scope of this paper to deal with the enormous literature on learning except to examine its relevance to the definition of a phylogenetic trait. The great "nature versus nurture" debate centers on the idea that if something is learned, then it cannot be genetically based. It follows that if a behavioral trait is not strictly heritable, then it is useless in phylogenetic reconstruction or interpretation of large-scale evolution because the determinations of homology will be weak or false; learned behaviors are poor characters, innate behaviors are good. This perspective is deficient for at least three reasons: (i) "learned" and "innate" have largely evaded definition; (ii) how something is learned rather than what is learned may be phylogenetically informative; (iii) criteria of homology rely more on simple persistence of the character across taxa than on details of genetic architecture and heritability that produce it. The first two of these objections will be examined immediately below, the third is discussed above (see UNITS OF BEHAVIOR).

The great debate several decades ago about the nature of learning seems to have been largely abandoned by behavioral biologists today. Originally, the opposite of learned behaviors were the innate behaviors defined by the "fixed action pattern." Lorenz (59, 61), and in the early days Tinbergen (94) argued that animals were capable of certain behaviors that were complete and distinct from the first time they were executed. These patterns of motion were "fixed" because they were performed in the presence of specific stimuli and were not subject to change by repeated performance. Lehrman (56) and others (41) attacked this idea because under certain experimental regimes the fixed action patterns failed to be expressed according to the rigid description required by Lorenz's model. Therefore, learning, or at least some undefined process of neural ontogeny related to experience, did play a role. Lorenz (61) defended his extreme position: "The naïve ethologist's assertion that [bird flight and orientation] are 'completely innate' is less inexact than the statement that a steam locomotive or the Eiffel Tower are built entirely of metal" (61, p. 27). Nonetheless, Lehrman's critique convinced Tinbergen (44) to retreat to a middle ground that included an interaction between inherent and environmental factors, eroding from one end the dichotomy between "innate" and "learned."

Recent work refers largely to learned behaviors such as those of Pavlov's dogs or Skinner's pecking pigeons, which are subject to classical conditioning. Skinner's school of psychology proposed that anything could be learned if an appropriate reward/punishment schedule was used, and the early success of this approach helped define modern psychology (92). However, dissent includes the work of Garcia et al (35), who showed that laboratory rats (relatively intelligent animals) can learn to associate flavor of pellets with illness, or size of pellets with shock, but not flavor with shock or size with illness (outwardly simple lessons). Whether or not the animal learns is in part due to an inherent propensity to learn given tasks (44). The innate/learned dichotomy is eroded from the other side. "Innate" cannot always be separated from "learned," and thorough studies of ontogeny of behavior show continual interaction (41, p. 127; 45).

At the same time that the definition of learning presents a problem for researchers who want to exclude learned behaviors from phylogenetic analysis, the details of the learning process provide additional fodder for researchers who want to include learned behaviors. The phenomenon of imprinting (57) has long been taken as a prime example of learning outside of classical conditioning (above), and Lorenz's success at getting geese to follow him as they would their mother is legendary. Here, one might say that imprinting is a "learned" phenomenon because the cues were learned by all the goslings. Such a declaration would be inaccurate, however, because only the cues are learned, not the process by which imprinting occurs. Imprinting per se is strictly controlled such that during a certain window of time anything presented appropriately will be then and forever identified as the relevant cue. In this case, discussions of homology should consider not only "learns cue," but also "anything observed in the imprinting window is learned to be the cue." The imprinting window is brought to the foreground for study, where details of the learning process may prove to be richer in information than is the observation that something is learned. Highly canalized learning via imprinting has been demonstrated in kin recognition in many groups (34), and behavioral biologists must be careful not to confuse the rigid (innate) process with the variable (learned) end point. In an unusually clear and explicit discussion of behavioral traits from a phylogenetic viewpoint, Mundinger (75) found that vocalizations in two large clades of perching birds—the oscines and suboscines—are largely learned or innate, respectively. He concluded that learned behaviors are valuable taxonomically: "call learning" is itself a character useful at the level of subfamily, while details of the calls are useful at lower taxonomic levels.

Perhaps the best demonstration that learning does not preclude postulates of homology comes from studies of the acquisition of intellect in humans. Piaget's (82) scheme, generally taken as the most thorough, coherent, and best supported by data (97), identified four stages through which children pass during the development of adult logical intelligence: (i) ten months to two years of age: sensory-motor exploration, Copernican revolution that "I am one object among many"; (ii) two years to seven or eight years: language acquisition, semiotic and symbolic development but without deductive logic; (iii) seven or eight years to 11 or 12: chains of causality but only for objects, hypothetical propositions still often unintelligible; (iv) 11 or 12 years and later: hypothetical reasoning, ability to see necessary consequences without having to decide upon validity or falsehood of component parts of a proposition. Only very few things are learned by direct experience alone, such as that the largest object is not always the heaviest. Piaget (82) observed the same process of learning in children that are somewhat mentally handicapped, or deaf-mute, or blind, or from cultures lacking written language, and recent research (68, 80) confirms the universality of this strict process for learning language. Thus, the ontogeny of intelligence is rather strictly controlled and similar in all children despite great differences in experience or absolute sensory and mental capacity. From the point of view of behavioral homology, the universality of this developmental pattern suggests that it has been inherited from a common ancestor, that learning language is a homologous process in all humans. There is no reason to discard any trait as useless to the illumination of homology and phylogeny because learning plays a role.

Ontogeny

Ontogeny continues to be a major and controversial resource for evolutionary biologists (37, 48). Behavioral ontogeny is generally regarded as a process of maturation by which an animal's age correlates with its performance. Learning or other interactions with the environment usually play some role (40). One approach is to document behaviors that appear at each age. Kruijt (53) showed how growing chicks acquire new behaviors, and that units of this inventory later interact to become composite behaviors in the adult repertoire. In some social insects, each adult specializes in a given task that differs with age; thus the adult repertoire itself paces through a schedule of separate behaviors necessary for colony maintenance (91, 113). An alternative approach, focussed more narrowly, is to describe the development of a single behavior by showing how experience or age effects a change in the animal's reactions toward various stimuli, change in the same motor patterns, or change in the perceptual system (41). Still more reductionistic is to show how a certain perceptual system changes with time at the cellular level (65).

Another perspective is to regard the sequential components of a complex behavior as if they were developmental steps toward the larger unit. The components can be compared across taxa as homologues according to their distinctive qualities and position in the sequence. Unlike processes of maturation (above), the sequence may be repeated many times, or the units reassembled to produce another complex behavior in a different context (5). Tinbergen (96, Figure 15) homologized the component steps of the greeting ceremony of various gulls. The greeting ceremony varies across taxa but can be shown to be composed of similar elements: "Thus all the Obliques are undoubtedly of common descent, and so are all forms of Jabbing, of Choking and of Facing Away." Ross (85) used spinning and construction sequences to discuss the evolution and elaboration of larval cases and cocoons in aquatic Lepidoptera and Trichoptera. Wenzel (105, 106) used classical ontogenetic changes of deletion, compression, and terminal addition in the nests of paper wasps to demonstrate hierarchical order loosely matching major clades inferred from morphological characters. None of these authors referred to the sequences as literal ontogenies, but they treated them just as morphologists have treated true ontogenies: steps are homologized across taxa, changes in speed or position constitute a departure from the ancestral pattern. Whether or not more explicit application of ontogenetic principles to large-scale behavioral problems (104–106) will be accepted or generally useful remains to be demonstrated.

Tinbergen (95) evidently felt that knowledge of the ontogeny of behavior would provide important understanding. Judging from the labors of morphologists, this may be optimistic. Similar ontogeny is often taken as evidence of morphological homology, but Wagner (98) argued that variability in developmental patterns is so great as to make irrelevant the information regarding cellular origins or inductive stimuli. Ontogenetic patterns are sometimes used as a substitute for the now widely used outgroup criterion (100) to infer the polarity of evolutionary change ("primitive" versus "derived") in morphological characters (76, 77, 108, 110). However, the ontogenetic polarization sometimes fails to match decisions derived by other means (51, 63), as one can easily imagine if the derived condition involves a deletion of terminal stages to produce a neotenic phenotype. Cases in which strict behavioral ontogeny, sensu Kruijt (53) or Hailman (41), is used to infer polarity among alternative states are rare (but see 29), although some can be found if "ontogeny" is broadened to include long sequences toward a composite whole (33, 85, 96, 105, 106). Nonetheless, such cases are unlikely to be any less controversial than those from morphology.

CONCLUSIONS

The tools that our predecessors left for us are adequate for determination of homology, although no single one is sufficient when used alone. Congruence with other data is probably the best support for a statement of homology when many traits in many taxa are already known. Strict morphological criteria for behavioral homology are inadequate when evolution acts separately on morphological and behavioral traits. Remane's criteria of placement, special quality, and connection by intermediates are useful in postulating behavioral homology. Functional or adaptive definitions of traits can be misleading. Arbitrary units of behavior are not a major problem. Analysis of relatively more learned behaviors is more complicated than for relatively more innate behaviors, but it is still possible from a phylogenetic viewpoint. Ontogeny of behavior has not yet contributed much to our understanding of larger evolutionary issues.

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