Behavioral Phylogeny
The Evolutionary Origins of Behavior

Animal behavior is the result of millions of years of evolutionary history, but how do we study the evolutionary origins of behavior? Occasionally behavior leaves a trace in the fossil record. For example, we can tell some dinosaurs took care of their young, because we see fossilized remains of mothers close to their babies and hatching eggs. Fossil footprints also inform us that some ancient animals traveled in herds. But the fossil record tells us little about the details of behavioral evolution—whether those mothers provided food or protection from predators, or whether the herds were led by a single individual or by a group. Instead, behavioral biologists rely on the comparative method and behavioral phylogenies to understand the details of behavioral evolution.

The *comparative method* refers to any study in which differences among existing species are used to infer something about the traits of their ancestors. A *phylogeny* or *phylogenetic tree* is a visual diagram by which we describe the evolutionary relationships among species. By considering species-typical behavior in a phylogenetic context, we can learn a great deal about how behavior evolved. Let's imagine we are interested in the evolution of laughter. Because smiles and sounds do not appear in the fossil record, we use a comparative study, looking for laughter in nonhuman primates. We find that most monkeys and apes smile, but they do so as a sign of social submission (to appease a threatening animal). Other great apes—our close phylogenetic relatives—also laugh when they are tickled during rough-and-tumble play. Recent studies of humans suggest that we too use laughter and smiles to cement social bonds, and only infrequently because we have heard or seen something funny. Putting it all together, we can conclude that our primate ancestors probably smiled to pacify potential aggressors, that laughter was brought in when smiles were used in social play, and that this gave rise finally to a link between laughter and humor.

By mapping behavioral traits onto a phylogeny we can interpret their evolutionary origins more accurately. For example, we are able to determine if different animals share behavior through common ancestry (homologous behavior) or whether similar behavior has evolved via independent evolutionary events in otherwise distantly related animals (convergent behavior). Behavioral phylogenies are also essential for teasing out evolutionary pressures or constraints, such as ecological forces, that act on behavior.

Shared Behavior through Descent

Species that are closely related often share similar traits simply because both inherited those traits from a common ancestor. For example, you probably look more like your sisters and brothers than you do like random strangers simply because you and your siblings share the multitude of genes, cultural traditions, and other traits inherited from your parents. Similarly, species that arose from the same phylogenetic ancestors will often retain the behavioral characteristics of their ancestors, and consequently share those traits with other descendents.

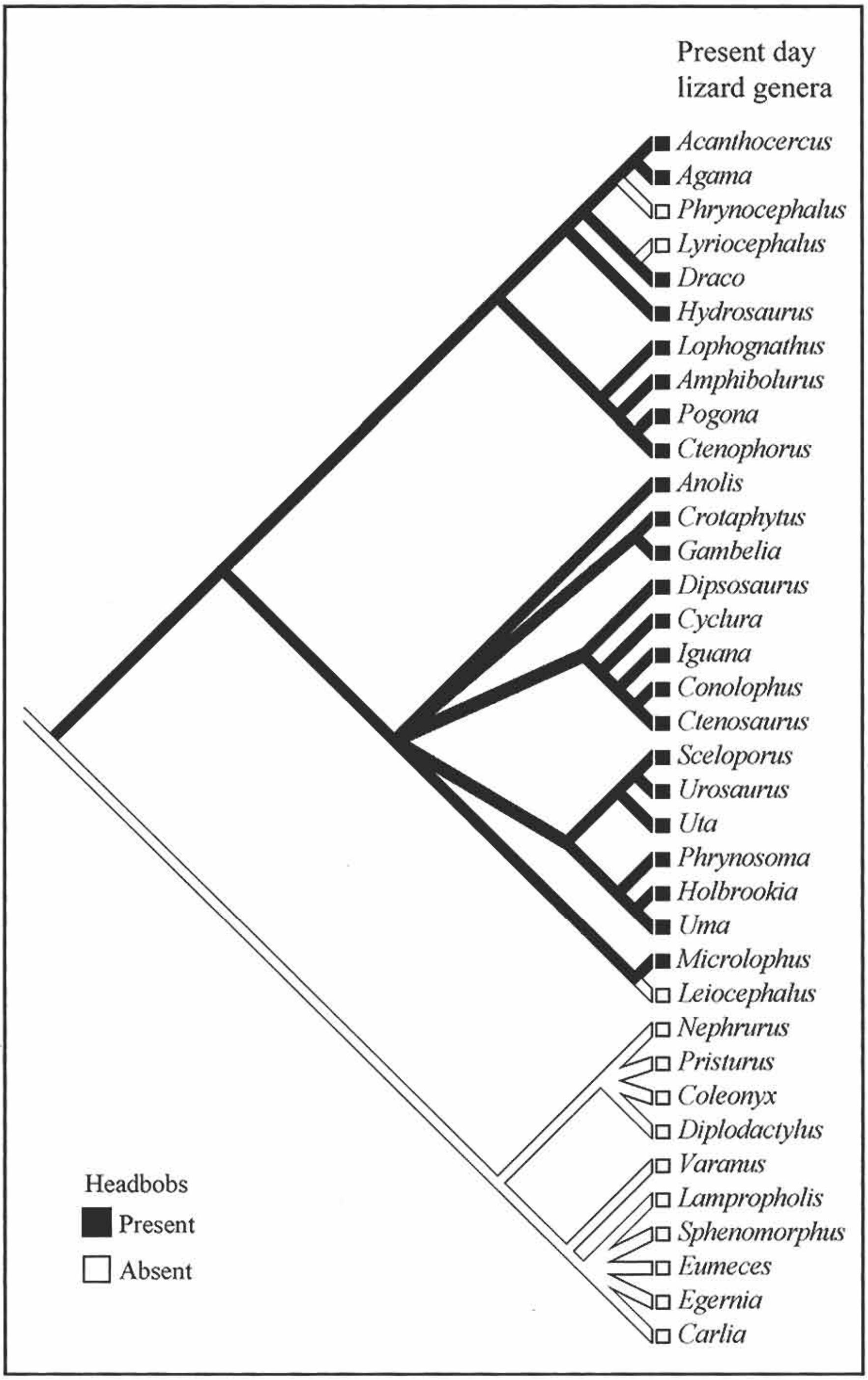
Species-typical behavior is also a product of the environment in which animals are found. Through natural selection, behavior patterns that help individuals to survive and produce offspring in the context of a particular environment will become increasingly common over evolutionary time. Thus, the properties of the physical environment (ecological habitat), predator, prey and parasite species (which are also evolving simultaneously in the same environment), and the complex web of social interactions with other animals of the same species, all shape the evolution of behavior.

Because natural selection is such a potent evolutionary force, only those behavior patterns that are important to survival and reproduction are likely to persist unchanged over evolutionary time. Using behavioral phylogenies we can identify which behavior patterns have persisted and look for explanations in terms of their importance to the animals exhibiting that behavior. Many lizards are territorial, but instead of fighting when disputes arise, they generally resolve conflicts using visual displays consisting of repeated up-and-down head movements or headbobs. Because these displays are energetically costly, animals which perform many displays are showing their opponents they are in excellent physical condition and subsequently more likely to win fights. By using displays to assess opponents before committing to combat, lizards circumvent many of the injuries and other costs associated with fighting behavior, which is especially important when they are unlikely to win. Looking at headbob displays across species, we find that the details of display structure (number, type and timing of headbobs produced) vary considerably across species, but that many, if not most, lizard species produce headbob displays of some form. Placing these behavior patterns in a phylogenetic context, we find that the details of display structure are well explained by the social and physical environments in which each species is found, being clearly the result of natural selection and offering a quick response to a constantly changing environment. But the use of headbob displays evolved very early in lizards and has therefore been retained over very long periods of evolutionary time. We can conclude from this that the risk of physical combat is considerable, and performing vigorous headbob displays is an excellent method for lizards to demonstrate superior fighting ability without having to resort to combat.

A phylogenetic approach can be particularly useful in interpreting behavior that seems unrelated to survival or reproduction. Why should a species exhibit any behavior that does not improve its ability to survive or reproduce? If possessing a behavior presents little or no additional cost to an animal, then a behavior might be passed on between parent and descendant species even though it no longer serves any function. Females of several parasitic bird species seek out nests of other species, where they lay their eggs to be cared for by the nest owner. The most notorious culprits of this brood parasitism are the Old World cuckoos (hence the term "cuckoldry"). Targeted host species often evolve methods to counter the tactics of brood parasites, such as recognizing and ejecting foreign eggs from their nests. But such ejecting behavior is puzzling when it is exhibited by species like the North American loggerhead shrike that does not occur (and never has) in regions frequented by cuckoos or any other brood parasite. How do we explain the presence of such behavior? The story becomes clearer when we look into the phylogenetic history of shrikes and see they are closely related to several Old World bird species that regularly eject cuckoo intrusions. The ejecting behavior seen in loggerhead shrikes is apparently an evolutionary "left-over" from a time when such behavior did in fact serve a valuable function.

Independent Evolution of Similar Behavior

In contrast, we expect animals derived from different ancestors to possess traits that reflect their unique evolutionary history. Yet many unrelated animals exhibit behavior remarkably similar in appearance and function despite differences in their evolutionary background. Behavioral phylogenies are imperative in, first, identifying whether these behavior patterns do indeed result from independent evolutionary events and, second, determining



A behavioral phylogeny illustrating how the comparative method can be used in conjunction with a phylogenetic tree to map the evolutionary history of a behavior, in this case the evolution of headbob displays used in territorial defense by lizards.

Courtesy of Terry Ord.

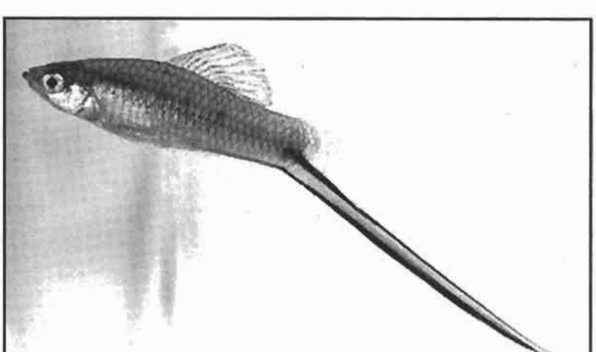
what shared evolutionary factors have facilitated the independent evolution of similar, convergent behavior.

Often, when the evolutionary relationships between animals expressing similar behavior are clearly remote, it is obvious convergence has occurred. For example, black-headed gulls and California ground squirrels have both evolved antipredatory defenses involving synchronized "mobbing" behavior to confuse and distract predators from entering nesting areas. Considering how distantly related these animals are, it is unlikely mobbing was inherited from the same common ancestor. However, with closer relatives, identifying events of true convergence can be considerably more difficult and requires careful inspection of a detailed phylogeny to ensure that the shared presence of the behavior is not the result of common descent. For example, many European songbirds (e.g., blackbirds and chaffinchs) produce a high-pitched "seet" alarm call to warn other group members of the presence of predatory hawks. Such calls need to alert nearby individuals without attracting the attention of the predator itself, a need that substantially limits the natural pool of sounds with the appropriate acoustic properties. The result are signals remarkable in their similarity across different bird species. Only by mapping these calls onto a phylogeny, can we deduce they have arisen through multiple, independent, evolutionary events (i.e., convergent evolution).

Habitat characteristics also determine the properties of animal signals. For example, denser habitats introduce obstructions between the sender and receiver of signals and reduce the distance over which signals remain effective. Many birds have increased the transmission distance of their songs by tailoring calls to the acoustic environment in which they are typically given. Birds in similar physical habitats may thus give remarkably similar calls, despite being phylogenetically unrelated.

Behavioral Sequences

Phylogenies have also been informative in determining the sequence of evolutionary changes in behavior without having to rely on an incomplete and sparse fossil record. If we believe the threat of predation (or parasitism) has led to the evolution of novel behavioral defenses, such as mobbing (or egg ejecting) behavior, this hypothesis assumes a causal factor predating the evolution of behavior. If, after tracing the evolutionary history of an animal, we find our proposed causal factor occurred *after* the development of behavior, then we would obviously have to rethink our hypothesis.



A swordtail fish from Central America.

With the development of sophisticated phylogenetic techniques in the early 1990s, biologists have been able to trace the evolutionary history of behavioral traits with greater confidence. One of the first results looking at sequences of behavioral evolution was the discovery of a fascinating phenomenon—behavioral predispositions. Several live-bearing freshwater fish in Central America are called swordtails because they possess a long filament protruding from the caudal (tail) fin. These "swords" are developed by males and are believed to attract females—the longer the sword, the more attractive a male. Males of the closely related platyfish, on the other hand, do not develop swords, yet incredibly females show preferences for males that have been experimentally manipulated to possess artificial swords. Reconstructing historical sequences of behavior onto a phylogeny reveals female preference for swords predate the evolution of the swords themselves. This "preexisting bias" hypothesis created much excitement (and its fair share of controversy) in the animal behavior community. It was some of the first evidence that psychological predispositions in animals—essentially biases resulting from the way the brain is wired—can have a profound affect on the evolution of elaborate behavioral traits.

Behavioral Phylogenies and Biological Sleuthing

There are many examples of how effective phylogenies have been in solving evolutionary puzzles, and how some patient detective work has given us profound insight into the processes that lead to the evolution of complex behavioral traits. It is becoming increasingly important to take phylogenies into account in any comparative study of behavior, otherwise it is difficult (if not impossible) to make reasonable inferences about the current function and evolutionary history of behavioral traits.

Behavioral phylogenies may also be valuable in helping to understand the ecology of rare or endangered species that are difficult to study directly because they either inhabit geographically remote areas or are hard to observe in the wild. By extrapolating from a behavioral phylogeny inclusive of closely related and better-studied species, we can gain an informed estimate of the behavioral ecology of these rarer animals. When time is of the essence, research funding limited, or detailed study impractical, this information may be extremely important in devising appropriate conservation strategies for saving endangered species.

Behavioral phylogenetics—understanding the evolutionary history of behavior—has been central to the study of animal behavior since the inception of the field. In the 1940s, Konrad Lorenz used behavioral phylogenies to show how duck displays evolved from grooming and foraging behavior. Nicholas and Elsie Collias combined behavioral phylogenies with a lifetime of data collected on nest building techniques used by different bird species to uncover the sequence of evolutionary changes leading from simple twig nests to the amazingly elaborate works of African weaver birds.

How different behaviors have evolved over time, what behaviors were likely to have been expressed by extinct ancestors, and from what forms unique behavior in present day species have evolved, are questions that have fascinated biologists for generations. By comparing and contrasting related species we can gain a window into the past and piece together the steps that have led to the behavior present in animal societies today. In revealing the pressures and constraints acting on behavior, phylogenies provide us with a unique picture of how the diversity, and similarity, of behavior has evolved in the animal world.

Further Resources

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