

Systematics, Ecology, and Behavior

Integrating phylogenetic patterns and evolutionary mechanisms

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Nature is complex. As sentient beings, we have always sought explanations for the origin and maintenance of that complexity, hoping that somewhere during the search we would discover answers to questions about who we are and where we fit in the global biosphere. The search has been conducted from many different perspectives—from religion to sociology, from art to science. One of the most controversial perspectives has been the attempt to explain human interactions by extrapolating from our knowledge of other animals (socio-biology; Wilson 1975).

This approach is founded upon the assumption that general evolutionary principles underlie all social systems, producing similar results given the same starting conditions. Results of behavioral and ecological investigations are routinely co-opted

Phylogenetic analysis is indispensable to understanding behavioral and ecological evolution

to explain human social interactions and to form the basis for ethical, moral, legal, and political decisions. For example, information about mother-infant interactions in rhesus monkeys has been applied in arguments about daycare and the issue of women in the work force, data from insects and ducks have been used to explain the occurrence of rape in humans, and observations on rats have been cited to explain a perceived increase in homicide associated with high human population densities.

The practice of explaining our behavior by extrapolation from other animals is not declining. In the popular media, sweeping conclusions about the evolution of human behaviors from homosexuality to warfare are drawn on the basis of little or no actual data from studies of human beings. To the public, what people think are conclusions from animal data often serve as political justifications. Conversely, some of the most important modern scientific debates regarding behavioral evolution are mired in political struggles.

Systematic biology, through the use of phylogenetic analysis, allows us to approach many of these issues from a scientific perspective. For example, if we had a phylogenetic tree and a detailed dataset of behavioral and ecological interactions for the great apes, we could ask questions such as: "Of all the traits humans display, which are historical legacies and which are uniquely evolved in *Homo sapiens*?" or "At what point in time did the character 'intraspecific group conflict' arise in the great apes, and were there any concurrent changes in behavior or ecology that could help us to explain the original evolutionary success of that character?" At the heart of this approach lies the assumption that we can gather more information about our evolution from close relatives than from more distantly related taxa. Think of it this way: if you want to know why you have blue eyes, would you gather eye-color data from members of your family or from your cats?

Aside from highlighting the level of comparison needed to effectively answer an evolutionary question, why should evolutionary biologists begin their search with a phylogeny? Currently, many researchers study evolution by arranging characteristics as a "plausible series of adaptational changes that could easily follow one after the other" (Alcock 1984). Although intuitively pleasing, this method relies heavily on subjective, *a priori* assumptions concerning the temporal sequence of evolutionary modifications and

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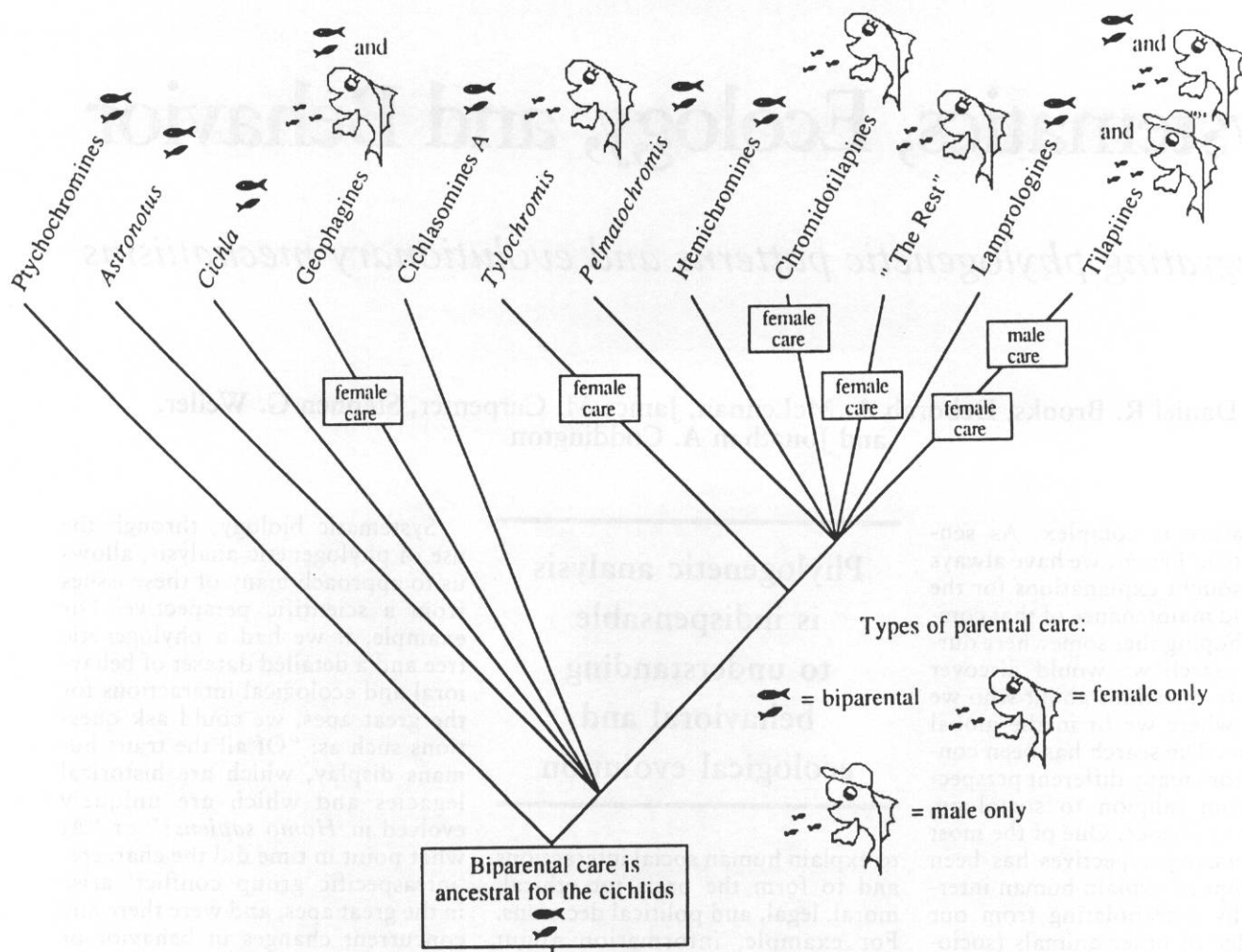


Figure 1. Evolution of parental care in cichlids. Three types of parental care—biparental, female only, and male only—are mapped above a simplified phylogenetic tree for the cichlids. The analysis indicates that female-only care originated a number of times from biparental care and that male-only care originated once from either biparental or female-only care (modified from McLennan 1994).

dissociates character evolution from underlying phylogenetic relationships.

The dissociation of history from evolution has had an important impact on both the nature and direction of behavioral and ecological research (Brooks and McLennan 1991, Greene 1994, Lauder 1986, McLennan et al. 1988, Ricklefs 1987, Wenzel 1992). For example, researchers questioning why a behavioral or ecological trait evolved, or why two or more traits are correlated, frequently search for the answers via sophisticated cost-benefit analyses within a single species. This approach may produce confusing results, because it does not differentiate between mechanisms affecting the evolutionary origin of a charac-

ter and those involved in its maintenance, once established. Investigating evolution within a phylogenetic framework allows us to disentangle the complex questions involving character origin and character maintenance.

Fortunately, ecologists and ethologists have begun to rediscover the benefits of exploring evolutionary questions within a phylogenetic framework at precisely the time when phylogenetic systematists have begun to elucidate that framework (Brooks and McLennan 1991, Wanntorp et al. 1990). This integration of systematics, ecology, and behavior is likely to provide us with more robust explanations of evolutionary patterns and processes.

In terms of questions about our

own evolutionary history, the interaction between systematics, ecology, and behavior is likely to allow the formulation of sociobiological theories based upon biological data, not political agendas. Given a phylogenetic tree and detailed behavioral and ecological data, we can begin to search for the factors influencing the origin and maintenance of both emotionally charged characters like intergroup conflict, group identification (including racism), sexual identity, and rape, and emotionally neutral but nonetheless interesting characters like sexual dimorphism and bipedalism.

This search, in turn, is likely to advance rational discussion of social ideals based upon a knowledge of how our past has brought us to

our present. Because this discussion has an immediate and direct impact on society, as the basis for far-reaching decisions, it must be founded on the most rigorous theories about behavioral and ecological evolution that we can develop.

Temporal sequence of character changes

Theories about the evolution of behavioral and ecological characters are often based upon a presumed sequence of evolutionary change. Such character changes are generally assumed to occur across taxa; therefore, the only way we can investigate the validity of a hypothesized evolutionary sequence, or to choose among alternative hypothesized sequences, is to look for the patterns of character origin and diversification on a phylogenetic tree (Greene 1986).

The evolution of parental care in cichlids. The evolution of parental care in fishes has received considerable attention from researchers, in part due to the seemingly anomalous observation that the male is usually the primary care giver in species displaying parental behavior. Gittleman (1981) examined 18 families of fishes and concluded that transitions from no care to paternal care were the most common evolutionary phenomena, that transitions from paternal care to biparental care were the next most common, and that transitions from biparental care to maternal care or from maternal care to no care were rare. He found no evidence for the other possible parental care transition sequences. Building upon Gittleman's taxonomic survey, Gross and Sargent (1985) constructed a general evolutionary model about "the origins, transitions, and phylogenies" of the four parental care states. The model, based upon presumed trade-offs between one benefit (increased survivorship of the young) and three costs (decreases in number of matings, future survivorship, and future fertility), predicted that the dominant parental care transformation series represented a cyclical transition from no care to male-only to biparental to female-only to

no care. Consequently, Gross and Sargent (1985) proposed that "no care" may be a "phylogenetically advanced state" in some fishes. A second, but less likely, sequence involved a direct and stable transition from no care to female-only care.

Cichlids are an excellent system for investigations of parental care evolution, because they display a wide range of behavioral states—from biparental nest spawning and guarding to paternal or maternal mouth brooding (references in Keenleyside 1991)—and because they have been subjected to rigorous phylogenetic scrutiny (reviewed in Stiassny and Gerstner 1992). Although still incomplete, the phylogenetic resolution is adequate for a preliminary investigation of patterns of parental care origin and diversification in the family. Stiassny and Gerstner (1992) mapped the available data for parental care states onto the phylogenetic tree (Figure 1) and found many cases of an evolutionary transition from biparental care to female-only care. At present, it is equally parsimonious to hypothesize that male-only parental care evolved from biparental care or from female-only care. The placement of male-only care in a derived position within the family, however, does not support Gross and Sargent's (1985) prediction that male-only care is derived from no care or their proposition that parental care evolution has been cyclical through time.

The evolution of social behavior in wasps. Carpenter (1989) tested West-Eberhard's (1978) model for the origin of social behavior in wasps. West-Eberhard's polygynous-family hypothesis suggested many possible transitions in the evolution of a worker caste and the development of different types of eusocial behavior. The separate stages of West-Eberhard's scenario were defined as the possession of different suites of independent features, such as nest sharing, reproductive division of labor, and number of queens. Carpenter (1989, 1991) treated these features as characters and mapped them onto social wasp phylogenetic trees. Evidence in favor of the model was the matches

between the suites of character states of the interior nodes and the stages of the model; mismatches counted as evidence against the model.

West-Eberhard envisioned casteless groups of females as the setting for the evolution of workerlike behavior, and caste formation was held to have preceded single queens. When these data were mapped on the phylogeny, no evidence for the occurrence of a casteless, nest-sharing stage was found, but caste formation was found to precede single queens (Ross and Carpenter 1991). As for the various transitions among different types of eusocial behavior, the primary nature of behaviorally enforced dominance was corroborated, but there was no evidence of the direct evolution of multiple queens without an intervening monogynous stage.

The evolution of dimorphism in carnations. The 24 species of *Schiedea*, a shrubby member of the carnation family, share a common hermaphroditic ancestor. They are diverse in morphology and habitat, occurring in wet, mesic, and dry forest, grasslands, and dry, rocky coastal regions of the Hawaiian Islands. Breeding systems in *Schiedea* are equally diverse. Hermaphroditic species range from obligate selfers to outcrossers, while ten species are dimorphic, possessing gynodioecious, subdioecious, and dioecious breeding systems (Weller et al. 1990).

All dimorphic species of *Schiedea* occur in dry habitats in the Hawaiian Islands, while hermaphroditic species are concentrated in mesic and wet forests. This correlation suggests that colonization of dry habitats may have been important in the evolution of dimorphism, although phylogenetic information is essential for understanding how many times the transition from hermaphroditism to dimorphism occurred (Donoghue 1989). The exceptional occurrence of several hermaphroditic species in dry habitats indicates that the evolution of dimorphism followed a shift to dry habitats, but the sequence of events can be ascertained with certainty only by using phylogenetic approaches.

In *Schiedea*, phylogenetic analysis indicates that dimorphism has evolved on several occasions and the shift to dry habitats does not necessarily entail the evolution of dimorphism (Wagner et al. 1995). With this knowledge that apparently strong relationship of dimorphism and dry habitats is more than coincidence resulting from a single evolutionary transition, scientists can now develop hypotheses for the effect of dry habitats on shifts in reproductive systems.

The mechanistic basis for behaviors and ecologies

Phylogenetic analysis on its own tells us little about evolutionary processes. The strength of such analysis lies in its ability to falsify a particular evolutionary scenario based upon the patterns of character origin and diversification. Phylogenetic patterns may thus be critical for examination of hypotheses about the underlying mechanisms of evolutionary change.

The evolution of male courtship calling in frogs. When Charles Darwin (1859) first published his theory of evolution by natural selection, the presence of male characteristics like elaborate plumage, bright colors, and large antlers was a thorn in the side of the newly created research program. Fortunately, that thorn was removed by Darwin's (1871) own suggestion that the survival-threatening costs of such traits were more than balanced by the benefits in attracting mates.

Darwin's suggestion was not greeted enthusiastically by his supporters (see discussion in Ryan 1990a). However, as empirical studies documenting the existence of female choice began to accumulate, the initial controversy was replaced with debates about underlying mechanisms. Two hypotheses were originally proposed, one based upon a genetic correlation between the female preference and the male trait (runaway sexual selection; Fisher 1958), and the other upon the benefits accrued to females who mate with genetically superior males (good genes; Trivers 1972). Under both scenarios, the female prefer-

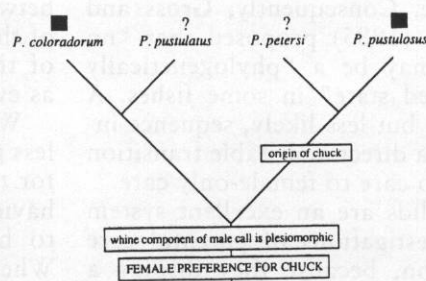


Figure 2. Female preference for males with a chuck added to their advertisement call predates the origin of the male chuck in *Physalaemus* frogs. ■ = females prefer complex calls (whine plus chucks) to simple calls (whine only); ? = female preference unknown in this species.

ence and the male trait are involved in a tight coevolutionary dynamic in which the evolution of the male trait influences the evolution of the female preference.

Ryan (1990a) approached the problem from a different angle. He proposed that intersexual selection favored male traits that exploited preexisting biases in the female's sensory system (sensory exploitation; Ryan 1990b, Ryan and Rand 1990, Ryan et al. 1990). Because the origin of the bias in the female's sensory system is influenced by selection pressures that predate the origin of the sexual selection dynamic, this hypothesis decouples the evolution of the male and the female traits. Once that dynamic is established in the population, however, female preference may continue to be favored through the simple benefit to the female of acquiring a mate in an often unpredictable world and/or through the establishment of either a runaway or a good genes coevolutionary interaction.

The sensory exploitation hypothesis makes one powerful prediction that distinguishes it from both runaway and the good genes hypotheses: The evolution of the female preference is decoupled to some extent from the evolution of the male character. This prediction can be tested directly within a phylogenetic framework.

One such test involved a group of neotropical frogs in the genus *Physalaemus*. Like many frogs, males in this clade produce an advertisement call that attracts females.

The basic *Physalaemus* call consists of a long whine. Two members of the clade, *Physalaemus petersi* and *Physalaemus pustulosus*, the Túngara frog, add a series of short chucks to the end of the whine, producing a more complex call. Research with the Túngara frog indicated that the dominant frequency of the whine matches the most sensitive frequency of the amphibian papillae in the frog's inner ear, while the dominant frequency of the chuck is close to the most sensitive frequency of the basilar papillae (reviewed in Ryan 1991). The whine alone is necessary and sufficient for species recognition, but, once a conspecific had been identified, females prefer calls with chucks (complex calls) to simple calls (Ryan 1983, Ryan and Rand 1990).

These results corroborate the hypothesis that sexual selection has influenced the evolution of call complexity in this group, but they do not allow us to differentiate among the three sexual selection mechanisms. In order to do that, Ryan and coworkers (1990) expanded the phylogenetic scope of the research to include a chuckless *Physalaemus*-species. They discovered that female *Physalaemus coloradorem*, like their Túngara cousins, preferred complex calls. In addition, the tuning in the basilar papillae of *P. coloradorem* is the same as that for *P. pustulosus* (Ryan et al. 1990), indicating that both the female preference and the sensory physiology underlying that preference existed before the evolution of the male chuck (Figure 2). This macroevolutionary pattern strongly falsifies the runaway sexual selection and good genes hypotheses, while supporting the third option, sensory exploitation.

The evolution of male nuptial coloration in stickleback fishes. Male sticklebacks undergo a striking transformation during the breeding season from inconspicuous, gray-green fishes to individuals sporting nuptial dress of species-determined colors: scarlet red and flashing cerulean blue in *Gasterosteus aculeatus*; deep, velvety black and amber in *Pungitius pungitius* and *Culaea inconstans*; and bright green-gold with contrasting black splotches

in *Gasterosteus wheatlandi*. Phylogenetic analysis indicated that origin of male nuptial coloration is buried deep within the evolutionary history of the sticklebacks (McLennan et al. 1988). As a result researchers face a dilemma in uncovering the processes responsible for the original success and spread of male nuptial coloration: Neither the ancestor in which, nor the environmental conditions under which, the character originated are available for experimental investigation. One solution is to use the information locked within the genealogical relationships among species. For example, comparing patterns of diversification for persistent ancestral characters may uncover phylogenetic associations that can be used to make predictions about underlying processes, which can then be tested experimentally (McLennan 1991).

Mapping the characters involved in male nuptial coloration and male breeding behaviors onto the phylogenetic tree for the sticklebacks revealed three types of phylogenetic association:

- Co-origination and almost complete codivergence of male color and male courtship behaviors (intersexual selection, Figure 3a). The origin of male nuptial coloration is preceded by the origin of the zigzag dance in an early ancestor. During evolution, the courtship interchange became more complicated, requiring more time in which the female waited while the male danced rapidly around her. The origin of male nuptial coloration in a later ancestor was correlated with a further increase in the complexity of stickleback courtship; males performed their zigzag dance more slowly and in front of the female, while females in the head-up position moved with the dancing male. Past that point in evolution, both the behavioral and hue components of the nuptial signal to diversify on almost a one-to-one basis.

- Incongruent patterns of origination and divergence of male color and behaviors involved in male-male interactions during territory acquisition and maintenance (intrasexual selection; Figure 3b). Color has been postulated to play a role in male-

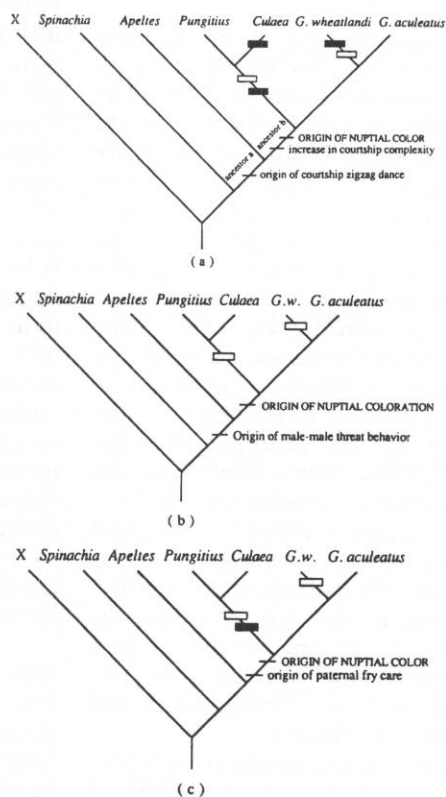


Figure 3. Evolution of male nuptial coloration in stickleback fish. □ = a change in male nuptial color; ■ = a change in male behavior. There are three types of phylogenetic associations between the origin and diversification of male color and male breeding behaviors: (a) co-origination and almost complete codivergence of color and courtship behaviors; (b) neither co-origination nor codivergence of color and male-male aggressive behaviors; and (c) co-origination and only partial codivergence of color and parental care behaviors. G.w. = *Gasterosteus wheatlandi*; X = outgroups.

male interactions as part of a threat display, allowing an individual to assess the social status, experience, and motivational state of an opponent. Once an encounter has escalated past threat, the emphasis should shift away from signals such as color to factors directly involved with fighting performance (stamina, skill, and strength). Examination of the phylogenetic tree indicates that, contrary to expectations, whole body nuptial coloration co-originated with the appearance of circle-fighting, not threat behavior. The phylogenetic patterns do not support the proposition that male color became secondarily associated with

male agonistic interactions during territory establishment, because color continued to diversify after its origin, while agonistic behaviors remained unchanged. Therefore, the characters were completely decoupled.

- Co-origination and incomplete divergence of male color and paternal care behaviors (natural selection; Figure 3c). The origin of male fry-guarding behavior is associated with the origin of male body coloration in an ancestor. If male color enhances male threat behavior, enabling a male to more effectively protect his offspring, then natural selection played a role in the origin of the color signal. Color and parental care, however, do not change together past this point in evolution. This pattern (co-origination and incomplete coupling during diversification) falls between the patterns uncovered for intersexual and intrasexual selection.

The phylogenetic patterns indicate that intersexual selection, reinforced by natural selection during fry guarding, has played the dominant role in shaping the evolution of male nuptial coloration in gasterosteids. Two predictions stem from these patterns. First, females should discriminate among males based upon differences in the intensity of male nuptial coloration. This prediction, which is not a novel by-product of the phylogenetic analysis, has been confirmed for two populations of three-spined sticklebacks (McLennan and McPhail 1990, Milinski and Bakker 1990).

Second, the intensity of male body color across the breeding cycle should be at its lowest level during territory establishment and nest building, should peak during courtship, and should reach a second, but lower peak during fry guarding. This prediction could not have been formulated outside of the phylogenetic framework. Experimental investigations of changes in male color across the breeding cycle corroborate that prediction for two members of the male-colored clade, *G. aculeatus* (McLennan and McPhail 1989) and *C. inconstans* (McLennan 1993).

These experiments demonstrate that explanations for the processes

involved in the evolution of phylogenetically old traits need not be forever relegated to ad hoc explanations about selection in the past. In some cases, it may be possible to make the transition from pattern to process by integrating experimental data within a phylogenetic context.

Origins of ecological associations

Two questions are central to ecology. First, "How do species manage to coexist?" This question is generally answered by investigating the evolution of characters involved in the interspecific interaction. Second, "How do species come to be where they are today?" or "What factors are involved in the evolution of ecological associations?" The step from understanding the evolution of a single behavioral or ecological character or suite of characters to understanding the evolution of ecological associations is a daunting one. It requires that we incorporate information from both character evolution and species formation into our explanatory framework (Brooks 1985, Brooks and McLennan 1991, 1993a, Cadle and Greene 1993, Gorman 1992, Losos 1992).

Studies to date indicate that there may be few generalizations about the way in which ecological associations are assembled. For example, parallel diversification in plants and their insect hosts has been suggested for *Phyllobrotica* leaf beetles and their hosts in the Lamiales (Farrell and Mitter 1990). A comparison of phylogenies for the two groups of organisms revealed only a few cases of discordance, perhaps best explained by host transfer. In contrast, Futuyma and McCafferty (1990, see also Miller 1987) found no congruence between phylogenies for leaf beetles (*Ophraella*) and their hosts, several genera in the Asteraceae. They concluded that host shifts in *Ophraella* occurred after divergence of the host species. The contrasting results obtained in the preceding studies indicate that the factors influencing the evolution of ecological associations may be system specific. This possibility, in turn, further emphasizes the dangers inherent in extrapolating from one

system to another.

The distribution of biodiversity is affected by two major environmental factors (Cracraft 1985). The first factor is environmental harshness. The observation that diversity in the tropics is higher than diversity in temperate or arctic regions is often attributed to differences in speciation rates. However, it is also possible that extinction rates in temperate to arctic habitats have been higher than extinction rates in the tropics due to historical increases in environmental harshness in the colder areas. For example, the Central Highland areas, which contain the most diverse freshwater ichthyofauna in the United States and Canada, have not been glaciated or inundated by advancing seas like the areas in the North or South, respectively. Nor have they suffered the aridity that has affected ichthyofaunas in the Great Plains and the desert southwest.

The second factor affecting biodiversity is the history of geological change and accompanying speciation. Biological diversity tends to be clumped in so-called hot spots corresponding to areas with historically high rates of geological change, rather than being uniformly distributed across a given habitat or zone. For example, tropical diversity is clumped in South America, the Indo-Malayan region, and the lakes of the Great Rift Valley, areas whose geological histories are extremely complicated. Remote tropical islands colonized through long-distance dispersal also represent extreme examples of biodiversity, not only because the number of species is high, but because the proportion of endemic species is high. A species may thus occur where it does today because it evolved elsewhere and subsequently dispersed into the area (colonizer), or it may be present in a given area because it evolved there (resident). It is likely that many, if not most, communities contain both resident and dispersalist elements.

Given a phylogenetic analysis, a record of geological change, and information about ecological and behavioral interactions, scientists can ask questions about the production of biological diversity within a rigorous evolutionary framework.

For example, are environmental conditions today similar to the conditions at the time of the species origin? How long has a species been in a community? What is the historical sequence of species addition to the community? Are core species usually residents, and are satellite species usually colonizers? Is there a relationship between a species' length of residence in a community and the stability of that community? Are residents or colonizers more susceptible to disturbance? Answering these questions is likely to add a macroevolutionary component to the concept of keystone species and is likely to help refine predictions about ecosystem responses to perturbations and identify the evolutionarily most vulnerable members of a community.

How old is this community? Ancestral species from many different clades, fragmented by the same isolating event, could all speciate concurrently, because the mechanism initiating speciation is independent of any particular species. If some of those species were interacting within a community, it is possible that the multiple speciation events within the ancestral community would result in descendant communities comprised, in part, of sister-species preserving these interactions.

For example, Mayden (1988) examined the historical biogeography of fishes in seven different clades of the North American Central Highland freshwater fish communities. These fishes inhabit drainage systems within the Central Highland region, including the Ozark and Ouachita Highlands, separated from each other by the floodplain of the Arkansas River, and the eastern highlands, separated by the floodplain of the Mississippi River. Before the disruptive influences of Pleistocene glaciation, these three regions were continuous.

Two hypotheses have been proposed to explain the diversity patterns of the freshwater fish fauna in this region. The first hypothesis is that much of the current diversity was produced by the fragmentation and isolation of populations during Pleistocene glaciation. The second hypothesis postulates that current

diversity existed before the Pleistocene glaciation. Mayden (1988) characterized the problem thusly:

For Central Highland fishes one may examine the origin of the fauna by comparing the history of the drainage basins involved and the history of the fishes, inferred from geologic data and phylogenetic relationships, respectively. If congruence is obtained between the phylogenetic relationships and drainage relationships existing prior to the Pleistocene then one may predict that the fish groups existed prior to glaciation and the vicariance hypothesis would be supported. However, if relationships of fishes are congruent with drainage patterns developed after glaciation, then an explanation of dispersal during and after the Pleistocene glaciation may be appropriate. (p. 340)

Mayden examined the relationships among 34 river drainages based on the phylogenetic relationships of the fish species in the seven different clades. The majority of the distributions coincide with pre-Pleistocene, rather than post-Pleistocene or contemporary, drainage patterns (for a detailed discussion of individual rivers see Mayden 1988). This result suggests that there was a diverse and widespread Central Highland ichthyofauna before the Pleistocene glaciation. Relatively recent episodes of dispersal and glaciation have also been important in this system; in seven cases, river associations in Mayden's analysis coincided with episodes of Pleistocene glacial alterations in river flow patterns that apparently resulted in faunal mixing. Current geographic distributions thus reflect a combination of ancient origins and diversification of the fauna and recent effects of large-scale environmental changes.

Identifying residents and colonizers in freshwater stingray parasite communities. Most elasmobranch species (sharks, skates, stingrays, and their relatives) are either marine or euryhaline. Marine elasmobranchs retain urea and other organic substances in their blood and tissue fluids, creating an internal osmotic environment that is similar to the surrounding sea water. The rectal

gland supplements kidney function, secreting salt in a fluid that is twice the concentration of body fluids. Euryhaline elasmobranchs function like marine species under conditions of high salinity; however, in less saline waters their urea concentration drops by 50%–80%, and rectal gland function is either reduced or stopped. Members of the stingray family Potamotrygonidae occur throughout the major river systems of eastern South America. They cannot concentrate urea, although they produce some of the necessary enzymes, and their rectal glands are small and apparently nonfunctional. The highly modified nature of stingrays relative to sharks and skates, and the absence of totally freshwater species in any other elasmobranch group, led biologists to assume that potamotrygonids were derived from a marine or euryhaline ancestor that dispersed into freshwater relatively recently (i.e., within the past 3–5 million years).

Phylogenetic and biogeographic analysis of the parasites inhabiting potamotrygonids suggests an alternative explanation (reviewed in Brooks in press). It appears that potamotrygonids are derived from Pacific ancestors that lived around the mouth of the Amazon and were trapped in fresh water by the uplifting of the Andes mountains beginning perhaps as early as the early Cretaceous and ending by the mid-Miocene, when the flow of the Amazon was changed from westward to eastward. That analysis also indicated that the freshwater stingrays' parasite communities have been assembled in different ways in each of six different areas. The Paraná, mid-Amazon, upper Amazon, Orinoco, and Magdalena systems all contain species of parasites inhabiting potamotrygonids whose phylogenetic relationships indicate that they evolved in the areas in which they are presently found. In addition to species endemic to the area, the Orinoco community contains species that have colonized from three other systems—the upper Amazon, the Paraná, and the mid-Amazon. The Orinoco community thus has the highest diversity, although it is not the oldest. The Lake Maracaibo community also has representatives

from three different source areas—the Magdalena, Orinoco, and the upper Amazon. Finally, the Paraná community contains species that have colonized from the Orinoco two different times.

The communities of helminth parasites inhabiting South American freshwater stingrays thus comprise four categories of species: those that evolved in the host they inhabit and in the geographic area where they live, those that evolved in the host they inhabit but were brought by that host into the community from the area in which they originally evolved, those that evolved in one host and colonized another within the area in which they evolved, and those that were brought into a community from the area in which they evolved and colonized a host living in the new area. Each community examined exhibits a unique profile resulting from different mixtures of these four historical influences (Brooks and McLennan 1991, 1993a,b).

Conclusions

Comparison is an indispensable tool of the trade for evolutionary biologists. This vital methodology transcends all levels of analysis, from comparing the success of alleles in a population to the reconstruction of large-scale patterns of biological diversity. The phylogenetic approach is the newest component of comparative biology. It involves using the genealogical relationships among species, in conjunction with detailed ecological, behavioral, and geological information for those species, to investigate questions concerning the sequence of character origin, the patterns of character divergence, the processes underlying those patterns, and the evolution of ecological associations from parasite host interactions to complex communities and ecosystems.

There are at least two reasons for studying ecology and behavior within a phylogenetic framework. First, in order to understand evolution fully, biologists must be able to disentangle and explore the processes involved in character origin from those involved in character maintenance. This information is

particularly important to speciation studies. A plethora of sexual-selection studies have demonstrated that behavioral differences evolving in isolation can form a powerful barrier to panmixis should allopatric populations ever develop secondary sympatry. In addition, behavioral differences evolving within a population might be a plausible mechanism underlying sympatric speciation. Understanding how species evolve and interact has a direct bearing on understanding how communities evolve, and this understanding, in turn, is an important component of policies regarding the conservation of biodiversity.

Second, the results of ecological and behavioral investigations are routinely co-opted to explain our own sociological interactions and to form the basis for moral, legal, and political decisions. Because such decisions have an immediate and direct impact on society, we must base them upon the most rigorous theories about evolution that we can muster.

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