

## CHAPTER 1

# **Phylogenetics in Behavior: Some Cautions and Expectations**

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Phylogenetics has had an interesting history in studies of animal behavior (Burghardt & Gittleman 1990; Brooks & McLennan 1991). For some of the early ethologists with backgrounds in comparative anatomy, species comparisons were the essence of their science. Coincident with the formulation of kin selection theory (Hamilton 1964), however, emphases in animal behavior shifted toward issues in population genetics and population biology, and sociobiology seemed quickly to forget its ethological (both its historical and mechanistic) roots. But another science was being revolutionized at the time (Hull 1988). Hennig's (1966) cladistic methodologies were being argued among systematists with a vigor and style that were sometimes more characteristic of theological debates (Hull 1988). Once the acrimony subsided and the smoke cleared, some scientists outside of systematics became convinced that this field offered tools critical for understanding the evolution of behavior — once again behaviorists realized that evolution is something that happened in the past and that we must resort to techniques used in historical analysis to study it fully.

This volume shows that there are now many behaviorists enthusiastic about utilizing historical approaches to address a variety of behavioral problems. Although far from universal — e.g., Reeve and Sherman (1993) refer to phylogenetics as one of the "recent challenges

to adaptationism" — there appears to be some consensus that historical investigations are a necessary supplement to the field of animal behavior.

I was asked to discuss briefly some of my expectations for the future roles of phylogenetics in animal behavior. Before doing so, however, I would like to raise some cautionary notes about what we are doing now. There are some issues that need resolution, and until they are resolved they at least need our attention. After reviewing these issues, I then offer suggestions as to some more imaginative approaches in which phylogenetics can be used to study behavior.

### *Some cautions*

#### *A. Phylogenies*

"We will first look for a taxonomy in the literature. Then, when we have found one, we will assume it is true."

(Ridley 1983, p 19)

It is obvious to at least some that a phylogenetic interpretation of behavior is only as good as the phylogeny used as the foundation for that interpretation. Thus behaviorists need to consider seriously the field of phylogenetics and the phylogenetic problems they wish to analyze. Ridley (1983) gives a rather glib methodology for discriminating among competing phylogenies. Alternatively, others behaviorists have approached this issue in a more serious manner (e.g., Lanyon 1992). But some of animal behavior is in its current state because there has been scant attention paid to historical pattern, especially by those who attest to be more interested in current processes.

Felsenstein (1985) and Harvey (e.g., Harvey & Pagel 1991) performed an important service for animal behavior in emphasizing the problem of evolutionary independence in statistical tests of adaptation. The comparative approach typically involves testing predictions of correlations of variables, these predictions being derived from hypotheses of how natural selection causes the evolution of adaptation. These predictions are tested by contrasting the variables of interest among different taxa. Since the hypotheses predict evolutionary origin rather than maintenance (but see below), one cannot necessarily use each taxon as an independent datum, since taxa might be similar in the

variables of interest due to shared ancestry rather than independent evolution. It appears to be generally accepted that a comparative approach must have a phylogenetic component to help mitigate this problem of independence. This puts behaviorists in a bind, however, if one wants to utilize the comparative approach to test hypotheses of adaptation but there is no phylogeny available for the group under study. What is the solution? Unfortunately, to employ the comparative approach, to compare species statistically, one must know whether the traits exhibited by these species are statistically independent. No phylogeny, no test.

When there is a phylogeny available, it should never be written in stone. A frustration of behaviorists, myself included, is that phylogenies are constantly being reevaluated, whatever the technique. A case in point is the studies that my colleagues and I have been conducting on the evolution of mate recognition in the túngara frog (*Physalaemus pustulosus*) and its close relatives. This study incorporates aspects of calling behavior, auditory neurophysiology, female phonotaxis, vocal morphology and, of course, phylogeny. The original description of the *Physalaemus pustulosus* species group was provided by Cannatella and Duellman (1984; Fig. 1a). This hypothesis suggested two clades within the species group, those on the western side of the Andes (*P. coloradorum*, and *P. pustulatus*) constituting one clade, and the Amazonian species (*P. petersi*) and the primarily Central American species (*P. pustulosus*) constituting the other clade. This hypothesis was derived from consideration of several morphological characters. This hypothesis also led us to interpret certain neurophysiological data as supporting the notion of sensory exploitation (Ryan 1990) — that is, that males evolve traits that exploit preexisting female preferences (Ryan et al. 1990). *Physalaemus pustulosus* and *P. coloradorum* both share the neural tuning that we suggested is responsible for female *P. pustulosus* preferring calls that have been enhanced by lower-frequency chucks. Since the chucks appeared after the divergence of the clades containing *P. pustulosus* and *P. coloradorum*, this argues for the shared neural tuning preceding the evolution of the chuck, thus supporting the hypothesis of sensory exploitation.

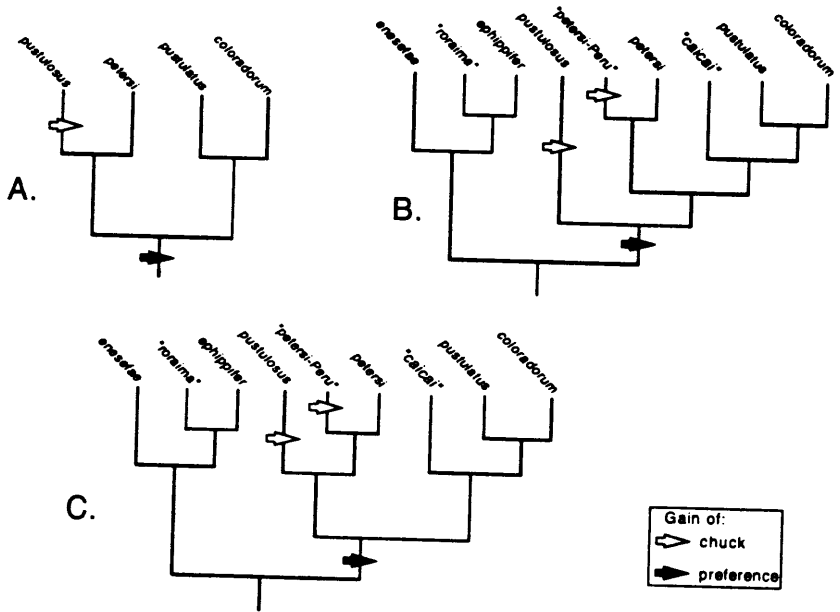


Figure 1. Various phylogenetic hypotheses and interpretations of trait-preference evolution in the *Physalaemus pustulosus* group, based on two observations: (1) Only *P. pustulosus* adds a chuck to its call; the chuck is also absent from the outgroup species and, to the best of our knowledge, in the rest of the approximately 30 species in the genus (but see *P. "petersi-Peru"*, below). (2) Females of both *P. pustulosus* and *P. coloradorum* prefer calls with chucks. (A) Phylogeny proposed by Cannatella and Duellman (1984), and the interpretation of when the chuck and the (most recent possible) preference for the chuck evolved. This phylogeny suggests two monophyletic groups within the species group. (B) Preliminary molecular analysis suggested a different tree and the discovery of a new species, *P. "petersi-Peru"* (quotes indicate undescribed species), with a suffix to its call. It is not known if this suffix is homologous to the chuck. Despite the change in phylogeny, however, parsimony still suggests that chuck preference evolved prior to the chuck (Ryan & Rand 1993). Outgroup species are also analyzed. (C) The most recent phylogenetic hypothesis is in agreement with the original hypothesis of Cannatella and Duellman (1984; A) in suggesting two monophyletic groups within the species group. It is equally parsimonious to suggest that the chuck was gained in the common ancestor of *P. pustulosus* and *P. "petersi Peru"* and lost in *P. petersi*. Nevertheless, parsimony still suggests preference for chucks evolved prior to the chuck.

Realizing that our interpretation depended on our phylogenetic hypothesis, we collaborated with several systematists (D. Cannatella, D. Hillis, and P. Chippendale) in deriving additional characters for testing the available phylogenetic hypothesis. Our preliminary analysis, which assayed 27 polymorphic allozymes and a portion (400 base pairs) of the mitochondrial 12S gene, resulted in a different tree with some additional species (Ryan & Rand 1993). This tree was pectinate with *P. pustulosus* as sister to all other taxa in the species group (Fig. 1b). These data led Pomiankowski (1994) to suggest that the revised phylogeny, although not rejecting the hypothesis of sensory exploitation, made such an interpretation less compelling. Upon completion of the DNA sequencing, which included 1200 bases of the 12S gene and flanking regions, however, our "final" phylogeny coincides with that originally proposed by Duellman and Cannatella, with strong statistical support from bootstrap estimates (Fig. 1c). But this phylogeny will be reevaluated once more when we complete our analysis of the relationships of all the approximately 40 species within the genus. If additional outgroups and data sets continue to suggest a phylogeny that supports our sensory exploitation hypothesis, we gain more confidence in our interpretation, if not, the hypothesis will need to be rejected. At no point should we be tempted by the arrogance of certainty that characterized the early debates in cladistics.

When new techniques are introduced into a field, they often assume an air of primacy. There is no question that the comparative approach, if it includes rigorous phylogenetic techniques, is a powerful method for testing hypotheses of adaptation. But it is not the only approach (Reeve & Sherman 1993). Some questions might not allow a comparative test. Consider the mammalian four-chambered heart. Few would argue against the proposition that the presence of this structure in the more than 4,000 species of mammals is due to common descent rather than 4,000 independent evolutionary events. Even if one were to have a completely resolved phylogeny of mammals, this would not aid in testing hypotheses for the adaptive significance of this structure, since there is only one evolutionary event. But all is not lost. Physiological considerations make it clear that the four-chambered heart offers advantages for circulation and correlated physiological and behavioral processes. From first principles of physiology, one could argue that the

evolution of this structure would be favored by selection. Of course, by this argument alone we could never be totally confident this assertion was correct, but the same can be said of any hypothesis supported through a comparative study. It is unfortunate, but the passage of time results in serious constraints for those interested in historical sciences. The comparative method should be added to the arsenal of techniques used to study animal behavior, not substitute for them.

A related issue concerns the use of maintenance as evidence for adaptations (Reeve & Sherman 1993). Knowledge that selection is maintaining a trait in a population does indicate that the trait is adaptive, if not an adaptation (e.g., Greene 1986). This assertion, however, cannot be made based on the mere presence of the trait. It also needs to be remembered that demonstrating maintenance is not equivalent to demonstrating the role of selection in the evolution of the adaptation.

### ***B. Reliance on parsimony***

In both phylogenetic reconstruction and in optimizing character states on reconstructed phylogenies, one makes assumptions about patterns that are most likely to occur. For many, parsimony is used as a guiding principle, for others, maximum likelihood, etc. But for all, there should be sole reliance on these methods only in the absence of other information. We cannot rely on an uncritical acceptance of parsimony, maximum likelihood, or any other single method to give us the truth or even a good estimate of it. I offer some of my own work as an example.

We had suggested that the chuck of *P. pustulosus* evolved after that lineage diverged from the lineage containing *P. coloradorum*. This conclusion was based on optimizing the character on the phylogeny using the principle of parsimony. Gardner (1990) criticized this interpretation and suggested that it was more likely that the chuck evolved at the base of the species group and was subsequently lost an additional two times. Although there is no argument that a gain and two subsequent losses is less parsimonious than a single gain, it still might be true. For example, we know that when males add chucks to their calls, they not only increase their attractiveness to females but also are more at risk from predation by the frog-eating bat (Ryan 1985). If *P. pustulosus* were found in areas with much less predation pressure than that of the closely related species, these data should justify adopting the

less parsimonious hypothesis, or at least entertaining it seriously. That happens not to be the case. In this example, *P. coloradorum* is not sympatric with the frog-eating bat, and patterns of vocal morphology (Ryan & Drewes 1990) are also consistent with our hypothesis of chuck evolution.

Carl Sagan, when discussing reports of alien beings piloting flying saucers, said that extraordinary claims require extraordinary evidence. Homoplasy (evolutionary convergence and reversal) is not an extraordinary claim. Almost all phylogenetic analyses show evidence of it. Parsimony and other assumptions are helpful guiding principles; they should not be accepted uncritically, however, but should be combined with our knowledge of the general biology of the animals we study.

A related issue regards the model of evolution we adopt. Do we have different expectations about rates of evolution if we are investigating foraging behavior on the one hand versus mate recognition signals on the other? We might expect the mode of evolution to be different in these cases, and we also know that phylogenetic reconstruction techniques are more or less sensitive to unequal rates of evolution (e.g., Hillis et al. 1994). Should that change how we interpret historical patterns? Another assumption we make is how new taxa arise. Some models of speciation might suggest divergence of two daughter species from an ancestral one. But in centripetal evolution, isolate populations achieve species status. Can we use the same methods to estimate ancestral characters in both cases?

### ***C. Total evidence***

There is a controversy in systematics in how to evaluate different data sets (e.g., morphology, behavior, DNA sequences) in phylogenetic reconstruction (Bull et al. 1993). A related issue involves using phylogenetic techniques to explore behavioral evolution; should behavioral characters under study contribute to the phylogenetic reconstruction that is then used to evaluate the patterns of behavioral evolution?

Systematists and behaviorists can have quite different goals in phylogenetic reconstruction. Systematists strive to present the most likely hypothesis of evolutionary relationships. A behaviorist,

alternatively, wants to interpret the patterns by which behavior evolves, but the success of this task is dependent on the accuracy of the phylogeny. Thus there is validity to the proposition that the behaviorist should use all the available information to reconstruct the phylogeny. But one cannot ignore the fact that inclusion of behavioral data will influence our interpretations of how that behavior evolves. de Queiroz and Wimberger (1993) demonstrated that, for the studies they evaluated, behavioral characters were as phylogenetically informative as other characters. In our studies of call evolution in *P. pustulosus*, however, morphology, allozymes and DNA sequence suggest the same major branching patterns in their independent estimates of phylogeny, but a separate analysis of call variation results in a quite different tree. In our study we have decided to use the phylogeny reconstructed without call data to interpret patterns of call evolution. We realize this approach will have its detractors and that there are strong arguments for the alternative approach. This issue needs serious debate.

#### *D. Homology*

This has always been a slippery concept, and especially so for behavior. Atz's (1970) discussion of the difficulty in homologizing behavior might have been responsible for many researchers temporarily abandoning behavior as a useful phylogenetic character. Although determining behavioral homologies is still sometimes seen as a difficult task, it is not longer viewed as offering a serious deterrent (Wenzel 1992; Greene 1994), but perhaps it should.

The most widespread use of phylogenetics in behavior is to recover independent evolutionary events. Quite often social structure is one of the "behaviors" being analyzed (see examples in Harvey & Pagel 1991). But to what degree is social structure, such as mating systems, a single behavior, a multivariate or metabehavior, or an emergent property of behavioral interactions? Consider different forces that can influence lek evolution: hotshots, hotspots, exploding leks (Emlen & Oring 1977; Wiley 1991). If these hypotheses for lek evolution are not mutually exclusive but are more or less important in different taxa, we are probably not talking about homologous "behaviors" and thus need to exercise caution when using phylogenetics to test for evolutionary



effects of leks, as an example (Höglund 1989; Oakes 1992). Homology is an old problem but that does not mean it has gone away.

## *Expectations*

I would agree with many if not most behaviorists, and certainly with the contributors to this volume, that phylogenetics has made important contributions to our understanding of animal behavior. I do have some concerns, as just mentioned. But now what to do? Certainly, we should keep doing things that we are doing right and when possible improve on them. But we might also want to make some leaps, take some chances, and try some more imaginative but not necessarily less rigorous approaches that might strain the limits of using phylogenetics in behavior. When we exceed the limit, it should be clear — if not to us, then to our critics.

### *A. Reevaluate standard examples of behavioral evolution*

Many of the earlier examples of patterns of behavioral evolution predate the cladistics revolution and rely on intuitions of how behavior patterns are most likely to evolve. Some of these examples have become embedded in our instructional heritage, being repeated to several generations of undergraduates in animal behavior courses. It would be instructive to know how many of these examples hold up to a phylogenetic analysis.

A classic example of a behavioral transition series deals with the bizarre courtship behavior of a group of empidids known as balloon flies. The initial observations reported on groups of males gathered in leklike mating arenas holding large, empty balloons of silk, and females choosing males as if they were judging male quality by the size of their balloons. This phenomenon begged for an explanation, and Kessel (1955) offered a very appealing one. He reported the behavior of a number of species of empidid flies that he classified into eight behavioral groups, which he arranged into a phylogenetic series (cited in Alcock 1975): (a) some species hunt small insects; (b) others use their insect prey as nuptial gifts; (c) in others, males with nuptial gifts gather in leks; (d) nuptial gifts are wrapped in a single strand of silk; (e) nuptial gifts are totally wrapped with silk; (f) nuptial gifts are wrapped in silk

but the males suck the juices out of the prey prior to presenting it to the female; (g) some species feed only on nectar but use a dead insect around which the balloon is formed; and finally, (h) some species present females with a large, empty balloon.

It is interesting to know why balloon flies act as they do, and surely Kessel's hypothesis of an evolutionary elaboration of nuptial gifts deserves serious consideration. But to my knowledge, no one has examined the phylogeny of empidid flies with the goal of testing Kessel's hypothesis. That might not be surprising given that there are well over 1,000 species of empidid flies and their phylogenetic relationships are poorly known. But the little work that has been done in this area suggests that balloons have evolved several times independently (Powell 1964, Marden 1989, Cumming 1994). Until we have some better evidence to support Kessel's hypothesis of behavioral transitions, we probably want to be a bit more cautious in using this example in undergraduate courses. (Alcock seems to have done just that. This example was given in the first four editions of Alcock's widely used text *Animal Behavior* [1975–1989] but is omitted from the fifth edition [1993]).

## ***B. Coevolution***

In ecology, phylogenetic patterns have become quite useful for testing hypotheses of coevolution resulting from such effects as plant-insect interactions (Maddison & Maddison 1992). A related but slightly different approach in behavior is asking how the existence of one trait biases the evolution of a second trait. Höglund (1989) and Oakes (1992) used this approach in testing the hypothesis that lek breeding in birds promotes the evolution of male sexual dimorphism.

This approach has also proven useful in sexual selection studies. Although there has been long controversy about the efficacy of runaway sexual selection versus good genes in explaining the evolution of female mating preferences, both models predict that the preference evolves as a correlated response to selection on the male trait with which it is genetically correlated (Kirkpatrick & Ryan 1991). Ryan (1990) suggested that hypotheses based on genetic correlations could be tested by reconstructing historical patterns of trait and preference evolution (cf. Fig 1). Several studies have now shown that female preferences and

male traits do not cocvolve but instead that preferences exist prior to male traits; thus males evolve traits to exploit preexisting preferences (Basolo 1990; Ryan et al. 1990; Proctor 1993; Ryan & Rand 1993; Basolo 1995). Although previous researchers had predicted preexisting preferences (e.g., West Eberhard 1983), the phylogenetic approach proposed by Ryan (1990) was the first explicit test of this hypothesis.

### ***C. Behavioral transitions.***

A major issue for evolutionary biology is explaining the evolution of complex adaptations. What were the transitions and how were they favored by selection? The ritualization of behavior was an important contribution of the early ethologists (e.g., Hinde and Tinbergen 1958) that would be worth reexamining with more recently available techniques. Irwin (chap. 8, this volume) suggests the importance of such an approach in her study of bird song.

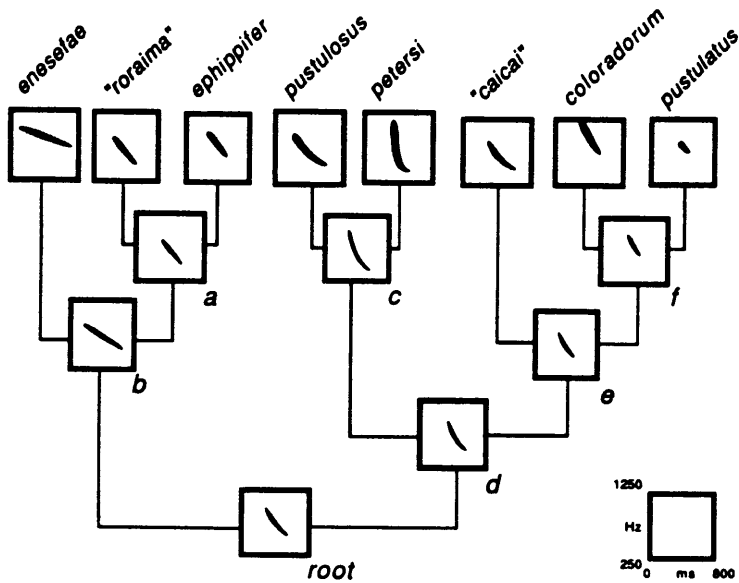
A more general consideration of behavioral transitions addresses the evolution of genetic and phenotypic correlations. Many behavior patterns are multivariate (see Arnold [1994b] for an excellent review of multivariate evolution) in that they depend upon the coordination of numerous motor patterns, certain relationships between morphology and behavior, sensory feedback, and the physiological and social context in which the behavior patterns are exhibited.

Arnold (1994a) discusses multivariate characters, including behavior, in the context of evolutionary constraints. He takes a rather broad view of constraint by defining it as any factor that biases the distribution of phenotypes exhibited by a taxa. Thus selection joins the ranks of constraints along with developmental and functional influences. He suggests that the degree to which traits are constrained can be estimated by the phenotypic and genetic correlations among them. In this paradigm, behavioral innovations can occur by breaking these constraints. If we could reconstruct phenotypic or genetic correlations at ancestral nodes, we could then determine when these constraints are broken by determining when there are changes in the character correlation matrices. Furthermore, with sufficient understanding of the animal's biology, we can gain some insights into the mechanisms involved in this reorganization.

**D. Reconstructing ancestral behavior**

In the novel and film *Jurassic Park*, the geologist observes dinosaur behavior that corroborates hypotheses about homeothermy and complex parental care. Although it is clearly fictional, is there anyone interested in the evolutionary history of behavior who did not feel an acute pang of jealousy? Most researchers who study history would like to have more direct access to the phenomena they study.

A. S. Rand and I have tried to partially circumvent this problem imposed by the passage of time in our studies of communication evolution. For members of the *P. pustulosus* species group and their close relatives, we have estimated the calls at ancestral nodes (Fig. 2),



*Figure 2.* Sonograms of the *Physalaemus pustulosus* species group and three close relatives. Also depicted are sonograms of calls reconstructed at the ancestral nodes (Ryan & Rand, 1995). Not all species indicated in Fig. 1 are used in this analysis.

synthesized these calls, and determined the degree to which these calls elicit phonotaxis from female *P. pustulosus*. We have used both local squared-change parsimony (Felsenstein 1985) and squared-change parsimony (Huey & Bennett 1987) to estimate the nodal values for each of eight individual call characters that we use to synthesize calls (see Maddison [1991] for a comparison of these techniques, and Martins and Hansen in chap. 2 of this volume as to the appropriateness of each for estimating ancestral behavior). The estimates from these techniques usually were quite similar (within 5% of one another), and future studies will determine if these differences are relevant to female call preferences.

Our results allow some insights into how call recognition evolves in this group of frogs. There is not much evidence of finely tuned coevolution. Females do not discriminate between the call of their most recent ancestor and their conspecifics, even though these calls are significantly different from one another. When females are given heterospecific calls in the absence of conspecific calls, those of both extant and ancestral species elicit phonotaxis, i.e., they are (perhaps mistakenly) recognized as signaling an appropriate mate (Fig. 3). Alternatively, the degree to which a female discriminated between a conspecific and heterospecific call is predicted by phylogenetic distance; the more distant the nodal call, and thus the longer since the signal and receiver are thought to have diverged, the weaker the female's response. Thus, in this group, signals and receivers diverge in concert over evolutionary time, but that divergence is not tightly correlated and calls of both extant and hypothesized ancestral species contain key stimuli for eliciting female responses.

It could be argued that the reconstructed ancestral nodes in this study are not likely to be accurate estimates of species past. If that were true, this approach would still offer valuable insights into evolutionary interaction of signals and receivers. We now realize that in a variety of animals, a female's preference function is broader than the distribution of conspecific-male sexually-selected traits (Ryan 1994). One approach to defining this preference function is to determine how females respond to traits absent in their own but present in other (extant) species. Thus we find that *P. coloradorum* females prefer their own calls with chucks of *P. pustulosus*; *P. pustulosus* females prefer their own calls, to which

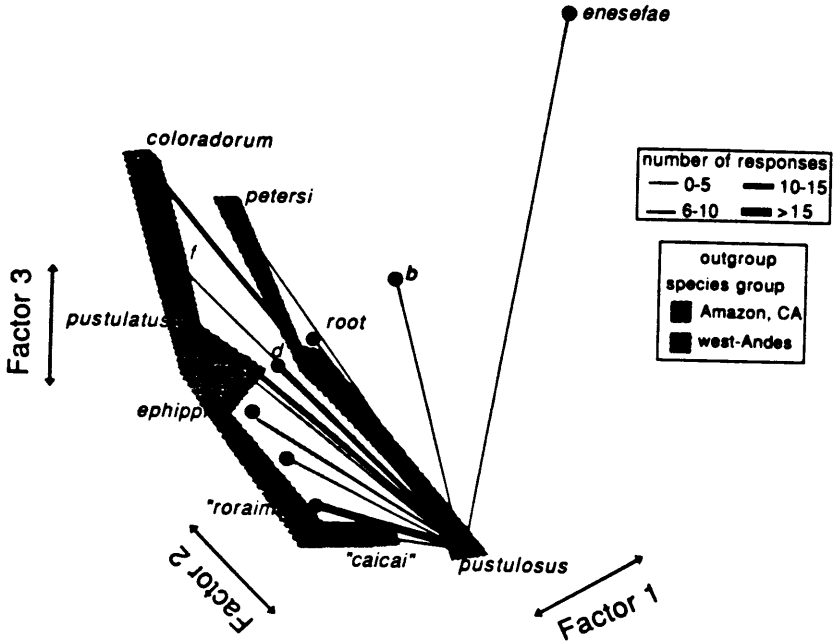


Figure 3. A plot of the first three factors of a principle component analysis of the calls shown in Fig. 2. These factors explain 87% of the variation among calls. Also depicted is the number of responses female *Physalaemus pustulosus* exhibited to each call when it was paired with a white noise stimulus (total  $N = 20$ ), and the phylogenetic groupings of the taxa and nodes being tested.

the prefix of the *P. pustulatus* call has been added (Ryan & Rand 1993), and in other taxa, female platyfish prefer males with swords over their own unsworded males (Basolo 1990), female birds prefer complex repertoires although their males produce only simple song types (Searcy 1992), and female fiddler crabs prefer males that construct pillars even though this trait is only present in closely related species (Christy & Salmon 1991).

Another axis of variation along which the preference function can be explored is historical. What were the pathways along which complex signals were likely to diverge and how does the female preference

interact with such signal variation? Thus, even if the calls at ancestral nodes are not good estimates of what ancestral species might have sounded like, these estimates still provide guidance as to the type of stimuli that can be used to probe the breadth of the female's preferences. Figure 3 shows that the axis of variation along which calls of the two clades within the *P. pustulosus* species group evolved are disjunct but parallel, and along this axis responses of *P. pustulosus* females decrease with decreasing call similarity. It appears that the outgroup species are evolving along an orthogonal axis of call evolution. How would *P. pustulosus* females respond to more fine-grained change along this axis as well as other axes of variation? Using digital call synthesis, we can determine female responses to an almost infinite array of acoustic stimuli. Phylogenetic reconstruction can guide us to those forms of stimulus variation that might be most informative in understanding female preference evolution.

### *E. Studying history as it happens*

In systematics, there has been considerable debate as to the accuracy with which various techniques reconstruct phylogenetic history. Most investigations into this problem utilize numerical simulations; Hillis et al. (1992) took a more direct approach. They used a bacteriophage, T7, that was propagated in the presence of a mutagen to construct what might be the first completely known phylogeny. Restriction-site maps of the terminal taxa were used in phylogenetic reconstruction, and these reconstructions were compared to the true phylogeny. Encouragingly, most of the commonly used phylogenetic techniques were good predictors, and parsimony also accurately predicted ancestral restriction maps.

The ability to create a known phylogeny clearly offers important potential for studies of phylogenetics and microbial evolution. But can it be applied to any central problems in animal behavior? Perhaps. One of the galvanizing issues in sociobiology is the evolution of cooperation (Wilson 1975; Dawkins 1976; Maynard Smith 1982). Bull and Molineux (1992) addressed this fundamental issue using another phage,  $\phi 1$ , in their study of "molecular sociobiology." (Some might argue that viral benevolence is hardly what most of us mean by behavior;

nevertheless, the example should be instructive.) This phage and a bacterial host were serially propagated so that the phage could increase its numbers only by increasing the growth rate of the host; infection of new hosts were not permitted, thus there was selection for benevolent or cooperating phages. Bull and Molineux then described the genetic changes that occurred under selection for cooperation. From this research, it seems that microbial selection studies can be used to address some important issues in the evolution of adaptation, and if combined with the generation of phylogenetic diversification, as described above, could provide a system for identifying the genetic changes that accompany the evolution of adaptations. Whether there are any systems in which this approach could be replicated for studies of more conventional animal behavior is not clear.

### *F. How behavior influences phylogenetic diversification*

A focus of phylogenetic studies of behavior, especially with the availability of MacClade (Maddison & Maddison 1992), has involved examining how behavior changes over a phylogenetic tree. Another issue is how behavior itself influences phylogenetic diversification. The notion that key adaptations or innovations can influence rates of diversification is an old one (e.g., Liem 1973) that generates continued interest (e.g., Craig et al. 1994). Theoreticians have suggested that the potential for divergence of mate-recognition systems influences the rate of speciation (Lande 1982; West Eberhard 1983). There is some empirical support for this notion, suggesting that accelerated speciation rates accompany increasing complexity of the frog's inner ear (Ryan 1986), evolution of syringeal structures and song learning in birds (Fitzpatrick 1988; Brenowitz 1992, but see Baptista and Trail 1992), and elaboration of complex androconia (pheromone dispersing organs) in nystaleine moths (Weller 1989).

One method of testing the relationship between behavioral evolution and speciation rates is to examine the shape of the phylogenetic trees. If all species are equally likely to speciate, then highly asymmetrical trees are unlikely. Guyer and Slowinski (1993) and Kirkpatrick and Slatkin (1994) have recently developed the statistical techniques necessary for testing such hypotheses.



### ***G. Phylogenies and conservation***

Brooks et al. (1992) discuss the contribution that phylogenetics can make to conservation. The most intriguing possibility for behaviorists is using phylogenetic information to infer the behavior and ecology of unstudied and inaccessible species. For example, it is critical to define the nesting habitat and habits of species for sensible attempts at rescue or conservation. If the species under question is nested well within a group that shares a common nesting syndrome, then one can evaluate the relative costs and benefits of relying on phylogenetic inference to assume this critical knowledge versus the alternative of disturbing the species at risk.

### ***Summary***

In an influential paper in comparative psychology, Frank Beach (1950) warns against basing the foundations of a "comparative" field on studies of the white rat conducted under unnatural laboratory conditions. Animal behaviorists were sometimes traveling down a different but similarly hazardous path by doing "comparative" biology without considering evolutionary history. This volume suggests that we now understand that history can no longer be ignored; to incorporate it we need to rely on methods developed for historical analyses. Phylogenetics offers some methods that have been utilized fruitfully to incorporate estimates of the past into evaluating how behavior evolves. It might be that these methods will need to be refined and reevaluated, but they presently offer possibilities for study not available twenty years ago. But if there is a discipline in the life sciences that needs to be multidisciplinary, animal behavior is it. Phylogenetics should be added to our methodological repertoire but it cannot substitute for all other analyses and approaches. It appears that the best behavioral studies are still those that address the general biology of behavior.

### **ACKNOWLEDGMENTS**

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