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Sexual selection and signal evolution: the ghost of biases past

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SUMMARY

The evolution of female mating preferences is an important key to understanding the evolution of signal diversity. Several hypotheses for preference evolution invoke different processes but all can produce the same end results: thus comparisons of extant traits and preferences within and among populations have made little progress in discriminating among competing hypotheses. Some of these hypotheses, however, do make different predictions as to the historical sequence of trait-preference evolution, and thus can be discriminated with appropriate phylogenetic analyses. We explore this approach in an analysis of the evolution of calls and call preferences in a monophyletic group of frogs, the *Physalaemus pustulosus* species group. In this clade there are pre-existing preferences for four call traits. These data reject hypotheses that invoke coevolution (good genes, runaway sexual selection) and females evolving preferences to choose males providing better resources, and instead support the hypothesis of sensory exploitation that suggests that males evolve traits that match pre-existing biases in the female's sensory system.

We suggest that some of the difficulty in understanding preference evolution might derive from defining a preference only by those extant stimuli that elicit the preference. Our results suggest that preferences might be more general, and that signal diversity might arise from alternative means for eliciting the same preference. Furthermore, we discuss some difficulties with utilizing both population-based comparisons and phylogenetic approaches and suggest that the greatest progress will be made by addressing the problem of preference evolution at several levels of analysis.

1. INTRODUCTION

For signals to transmit information they must differ (Shannon & Wever 1949) and signal diversity among taxa is found in the extreme when involved in communication between the sexes. In all major taxa of animals and operating through all sensory modalities, males have evolved elaborate signals that function in attracting females to mate: courtship displays with their associated bright plumage in birds; pheromones in mammals and insects; electrical discharges of some fish; and calls and songs of insects, birds and frogs. Understanding precisely how males evolve such traits and why females evolve preferences for these traits through the process of sexual selection has been a major preoccupation of evolutionary biology for the last several decades (e.g. Campbell 1972; Bradbury & Andersson 1987; Kirkpatrick & Ryan 1991; Maynard Smith 1991; Cronin 1992). In a communication context this problem can be rephrased as understanding the evolution of the signal-receiver dyad.

All signals, regardless of function, must be distinguished from background noise, which includes interference from abiotic sources as well as from conspecific and heterospecific signals that might impinge on the intended receiver. An increase in the signal to noise ratio increases the signal's conspicuous-

ness, and this does not come cheaply. Signals often involve sexually dimorphic characters, and their growth is at some expense. This is evidenced by the fact that males in poor health usually have secondary sexual characters of reduced magnitude (Møller 1990). Exhibiting the signal also requires energy, whether the animal is displaying a morphological character in a courtship dance or producing a sound, pheromone, or electrical discharge. A frog, for example, might increase its metabolic rate (at resting) by a factor of 30 while calling (Pough *et al.* 1992). Finally, conspicuousness itself has a cost as the signal can be conspicuous to both intended and unintended receivers. Parasitoids orienting toward calling crickets (Cade 1975) and bats homing in on calling frogs (Tuttle & Ryan 1981) are two examples. It was this costly aspect of secondary sexual characters, especially signals used in attracting mates, that challenged Darwin's (1871) natural selection paradigm and led him to propose the theory of sexual selection (Cronin 1992).

(a) *Signal-receiver evolution under sexual selection*

Understanding signal evolution under sexual selection is not an issue. Female choice can result in males evolving traits more attractive to females. The difficult

and quite controversial issue is why females have evolved receiver properties that make one trait more attractive than another.

In resource-based mating systems this issue is easily resolved; female preferences will evolve under direct selection if their choice of mates has an immediate effect on their fecundity or reproductive success (Kirkpatrick 1987). Females will evolve preferences for males that reliably signal the quality of the resources they can provide for females. Zahavi (1991) suggested that signals will be reliable when they are costly and can not be easily bluffed, and this is consistent with the notion that preferences, even in resource based mating systems, favour males with more costly and thus usually more extreme traits.

The controversy arises when considering the evolution of preferences in lek mating systems. In this situation females usually receive no resources from a male besides his sperm, thus her choice does not have an immediate effect on her fecundity (for exceptions see Reynolds & Gross (1990); Kirkpatrick & Ryan (1991)). The most popular explanation for this phenomenon among behavioral ecologists has been the 'good genes' hypothesis (Zahavi 1975). This hypothesis suggests that female choice is utilitarian, and that the design of the signal indicates to the female the male's underlying genetic quality in terms of his vigour or future survival ability. Males should evolve costly signals to signal genetic quality as these signals are more reliable.

Population genetic models have shown that preferences for good genes can evolve through indirect selection (Pomiankowski 1988). A genetic correlation between a female preference and a male trait will arise if there is linkage disequilibrium between the two. The good genes will increase in frequency under the influence of natural selection, and the preference genes will coevolve or hitchhike along with the good genes; females who exerted the preference will have daughters that both exhibit the preference and possess the good genes for survival. The empirical prediction is the evolution of costly traits, preferences for costly traits, and inheritance of good genes (Kirkpatrick & Ryan 1991).

Fisher's theory of runaway sexual selection offers an alternative hypothesis for the evolution of female signal preferences that also involves indirect selection. Fisher (1958) suggested that a runaway process would be initiated when a female preference becomes genetically correlated with a male trait through assortative mating. Both trait and preference could be driven to extremes with the male trait evolving under direct selection generated by female choice and the preference then evolving as a correlated response to evolution of the trait. Empirical support for runaway has been based on examining relationships between extant traits and preferences; some studies have found variation in traits and preferences correlated among populations (Houde & Endler 1990). These correlations, however, could also arise from other causes, and can even be accommodated by a good genes hypothesis (Houde & Endler 1990).

A more recent hypothesis for preference evolution is

sensory exploitation (Ryan 1990; Ryan and Rand 1990; Ryan *et al.* 1990). This hypothesis states that female preferences are manifestations between perceptual biases of the sensory system and properties of stimuli. Sensory systems are involved in mating preferences but also function in a variety of other biological tasks, and thus will evolve in response to an array of selection forces. Sexual selection will favour males that evolve signals that match these sensory biases. This process can lead to relationships between extant traits and preferences that are similar to those predicted by the good genes and runaway hypotheses; extreme traits and preferences for extreme traits.

Models have shown that all three hypotheses for the evolution of preference are internally valid; i.e. they could work (Kirkpatrick & Ryan 1991). Testing the external validity of these hypotheses, however, has proven troublesome. Most empirical tests compare extant traits and extant preferences and explicitly predict, or at least can accommodate, a correlation between extreme traits and preferences for extreme traits. A recent review of female mate choice studies shows that females prefer more extreme traits in over 150 studies of choice guided by acoustic or visual cues (Ryan & Keddy-Hector 1992). It is clear, however, that all three of the hypotheses invoke processes that can result in this outcome. Thus it has been difficult to discriminate clearly among these hypotheses by merely comparing extant traits and preferences.

(b) *Historical tests of female preference evolution*

Although the hypotheses for the evolution of preferences all predict the same end result, the historical pattern of trait-preference evolution will differ (figure 1).

In resource-based systems we would first expect males to evolve signals that indicate resource quality to females and then for females to evolve preferences for traits that indicate better resources (figure 1). A different pattern of evolution would occur in both the good genes and runaway sexual selection hypotheses because traits and preferences coevolve (figure 1). A third historical pattern would be exhibited under sensory exploitation. Initially, females would evolve sensory biases that result in preexisting preferences, and then sexual selection would favour males that evolve traits matching these biases (figure 1). Therefore, to the extent that we can reconstruct the history of trait-preference evolution, we can pursue an alternative approach to testing these hypotheses for the evolution of female mating preferences.

Figure 1 also represents a hypothetical phylogeny with the character state distributions of traits and preferences that would reject both hypotheses of direct selection on preferences in resource-based mating systems, and coevolution as would occur in runaway and good genes processes, but would be consistent with the historical pattern of trait-preference evolution predicted by sensory exploitation. In this example the sexually selected male trait is present in one taxon, absent in the sister taxon as well as in the outgroup taxa. Adopting Hennig's (1966) principle of parsimony that the evolutionary hypothesis requiring the

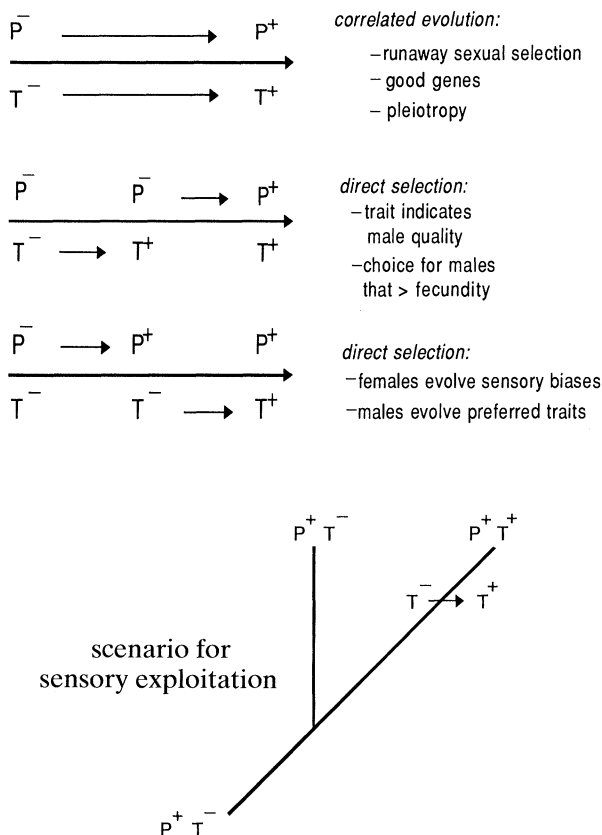


Figure 1. Top: historical patterns of trait-preference evolution predicted by various hypotheses for the evolution of female mating preferences. Bottom: example of phylogeny and character state distributions that would support the hypothesis of sensory exploitation and reject other hypotheses for the evolution of female mating preferences. P, preference; T, trait; +, present; -, absent.

fewest changes is the most likely, in this example the trait evolved once in the lineage exhibiting the trait. The preference, however, is present not only in the taxon exhibiting the attractive male trait but also in the sister taxon lacking the trait. Thus parsimony suggests that the preference was inherited through a common ancestor. This example suggests that the preference evolved prior to the attractive trait and that sexual selection favoured males with traits that matched this preexisting preference.

To utilize this phylogenetic approach to studying trait-preference evolution it is necessary to have a robust phylogenetic hypothesis for the taxa being studied, and to be able to determine if females exhibit preference for traits that are present in other taxa but lacking in their own males.

2. HISTORICAL PATTERNS IN TRAIT-PREFERENCE EVOLUTION IN THE *PHYSALAEMUS PUSTULOSUS* SPECIES GROUP

(a) The species group

The túngara frog, *Physalaemus pustulosus*, has been the subject of intense investigation in sexual selection and

animal communication (e.g. Ryan 1980, 1985; Rand & Ryan 1981, 1990; Ryan *et al.* 1990, 1992). We have extended these studies to other members of the species group to investigate patterns and processes of evolution of this communication system, including an attempt to reconstruct historical patterns of trait and preference evolution.

The *Physalaemus pustulosus* species group was first defined by Cannatella & Duellman (1984) as consisting of four species. According to their hypothesis, *P. pustulosus* and *P. petersi* are sister taxa; the former is in Central America and northern South America and the latter throughout much of the Amazon Basin. *P. pustulatus* and *P. coloradum* are sister taxa, are found on the western side of the Andes, and are geographically isolated from other congeners. This phylogenetic hypothesis resulted from analysis of a small number of morphological characters, thus we used molecular analysis to further investigate the phylogenetic relationships within the group (D. M. Hillis, unpublished data).

Our phylogenetic reconstruction, which is considered to be preliminary, was based upon allozyme variation and sequence variation of the 12S portion of the mitochondrial genome combined with the original morphological data. We used three closely related species, *P. ephippifer*, *P. enesefae* and *P. roriamia*, as the outgroups (quotations denote undescribed species). Our results show that there is at least one additional species in the group. *P. pustulatus* was originally considered to encompass populations in both Ecuador and Peru. The advertisement calls, however, differ between these populations suggesting that they should be considered different taxa; the molecular data support such a suggestion. The populations in Peru will be designated as a new species; here we refer to that taxon as *P. 'pustulatus-Peru'*. The only other difference between the original phylogeny and the one we tentatively propose is the rooting of the tree (figure 2). Our results suggests that *P. pustulosus* is sister to all other species in the group, *P. petersi* is sister to all species on the western side of the Andes, and all of these species form a monophyletic group, although the precise relationships within that smaller group are not well resolved (figure 2). All of our interpretations would be the same for the phylogenetic hypothesis originally suggested by Cannatella & Duellman (1984) as well the phylogeny we propose.

(b) Call traits

Male túngara frogs produce a call of unusual complexity. Each call contains a whine which can be followed by 0-6 chucks. The whine is necessary and sufficient for mate recognition, and phonotaxis experiments show that the chuck further enhances the attractiveness of the call to females (Rand & Ryan 1981; Rand *et al.* 1992). Most of the energy in the chuck (90%) falls within the frequency region to which one of the inner ear organs, the basilar papilla, is most sensitive; this inner ear organ is sensitive to higher frequencies, usually greater than 1.5 kHz (Ryan *et al.* 1990). Alternatively, in the whine only

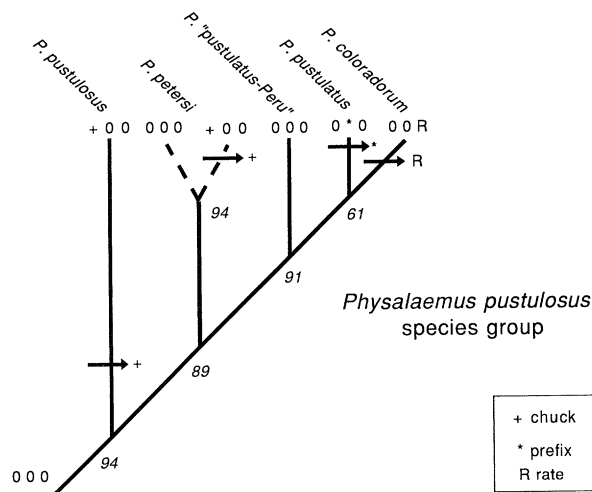


Figure 2. The distribution of call character states superimposed on a tentative phylogeny of the *Physalaemus pustulosus* species group generated from a preliminary analysis of molecular and morphological characters. '0' indicates the trait is absent. The outgroup condition (state 000) indicates that all three call characters are absent in all three species used in the outgroup analysis (*P. ephippifer*, *P. enesefae*, and *P. 'roraima'*). Numbers in italics represent bootstrap confidence intervals. (> 70 indicates that node was supported in more than 95% of the bootstrap samples (Hillis & Bull 1993).)

the lower frequencies that fall within the range of the other inner ear organ, the amphibian papilla, are used in call recognition; this inner ear organ is usually most sensitive to frequencies below 1.2 kHz. Thus recognition of the whine and chuck are processed through different inner ear organs in the auditory periphery (Rand *et al.* 1992; W. Wilczynski, unpublished data).

In nature females prefer larger males, and phonotaxis experiments show that females are attracted preferentially to the lower frequency chucks produced by these larger males (Ryan 1980, 1985; W. Wilczynski, unpublished data). This preference appears to result from a slight mismatch between the female's auditory system and the dominant frequency of the chuck. On average, females are tuned below the mean dominant frequency of the chuck in their population, and thus lower frequency chucks might elicit greater neural stimulation because they better match the tuning of the female's peripheral auditory system (Ryan *et al.* 1990; W. Wilczynski, unpublished data). Our attempt to test this hypothesis further using pure tones in place of chucks reveals a strong trend in the direction of a low-frequency preference (19 versus 11), but this trend is not statistically significant ($p=0.10$). In cricket frogs, *Acris crepitans*, females also are tuned to frequencies below the average call frequency in the population and show behavioural preferences for lower frequency calls (Ryan *et al.* 1992).

All male túngara frogs can add chucks to their calls and do so in response to vocalizations of other males (Rand & Ryan 1981). The only other case of a call with a chuck-like suffix is in populations of *P. petersi* in southern Peru (R. B. Cocroft, personal communi-

cation) and nearby western Brazil (R. I. Crombie, personal communication), and this was known to occur in only a few males. In our detailed studies of this same species in the Rio Napo area of Amazonian Ecuador, in which we analyzed over 1500 calls and heard many more, males never produced calls with chucks.

Although all males in the species group and the outgroup produce whine-like advertisement calls, there are other unique call properties besides the chuck. The call of *P. pustulatus* is preceded by an amplitude modulated (AM) component that is similar in duration to its whine (figure 3). This AM prefix is absent in all other species in both the species group and the outgroup. Another unique character is the temporal pattern of calling. In most of these species the call period (the time from the onset of one call to the onset of the next call) is fairly constant; for example, about 2 s in *P. pustulosus*. When males increase the call repetition rate they do so by uniformly decreasing the call period. In *P. coloradurum*, however, males often produce calls in doublets or triplets. The differences in temporal calling pattern can be seen when comparing the distributions of call periods between *P. pustulosus* and *P. coloradurum*; the former has a normal distribution while that of *P. coloradurum* suggests a bimodal distribution and also has a greater variance.

The character states for these three call variables, chuck, AM prefix, and call rate, were optimized on the phylogeny of the species group (figure 2). The parsimony analysis suggests that the chuck was derived twice, once in the *P. pustulosus* lineage and again in the southern part of the range of *P. petersi*, the AM prefix was uniquely derived in the *P. pustulatus* lineage, and the double and triple calls were uniquely derived in the *P. coloradurum* lineage. Any other hypothesis for the evolution of these call characters would require more evolutionary changes than the hypotheses proposed.

(c) *Female preferences*

We determined female phonotactic preferences for call characters present in heterospecifics but lacking in their own males. Female *P. coloradurum* were given a choice between the normal, whine-like call of their own males and the same call to which three chucks from a *P. pustulosus* call were appended. Females showed a significant preference for the call with chucks (Ryan & Rand 1993b; figure 4). As discussed earlier, the tuning of the basilar papilla is involved in both recognition of the chuck and, perhaps, preference for lower frequency chucks. To determine whether the auditory properties of this inner ear organ evolved in concert with the chuck or if it is a property of the species group, we compared the tuning of this organ between *P. pustulosus* and *P. coloradurum*. They were statistically indistinguishable (Ryan *et al.* 1990). Recent analysis shows that the tuning of the basilar papilla is fairly similar for all species examined, suggesting that there has been little or no evolution of this auditory property in the species group (W. Wilczynski, unpublished data). This is not surprising

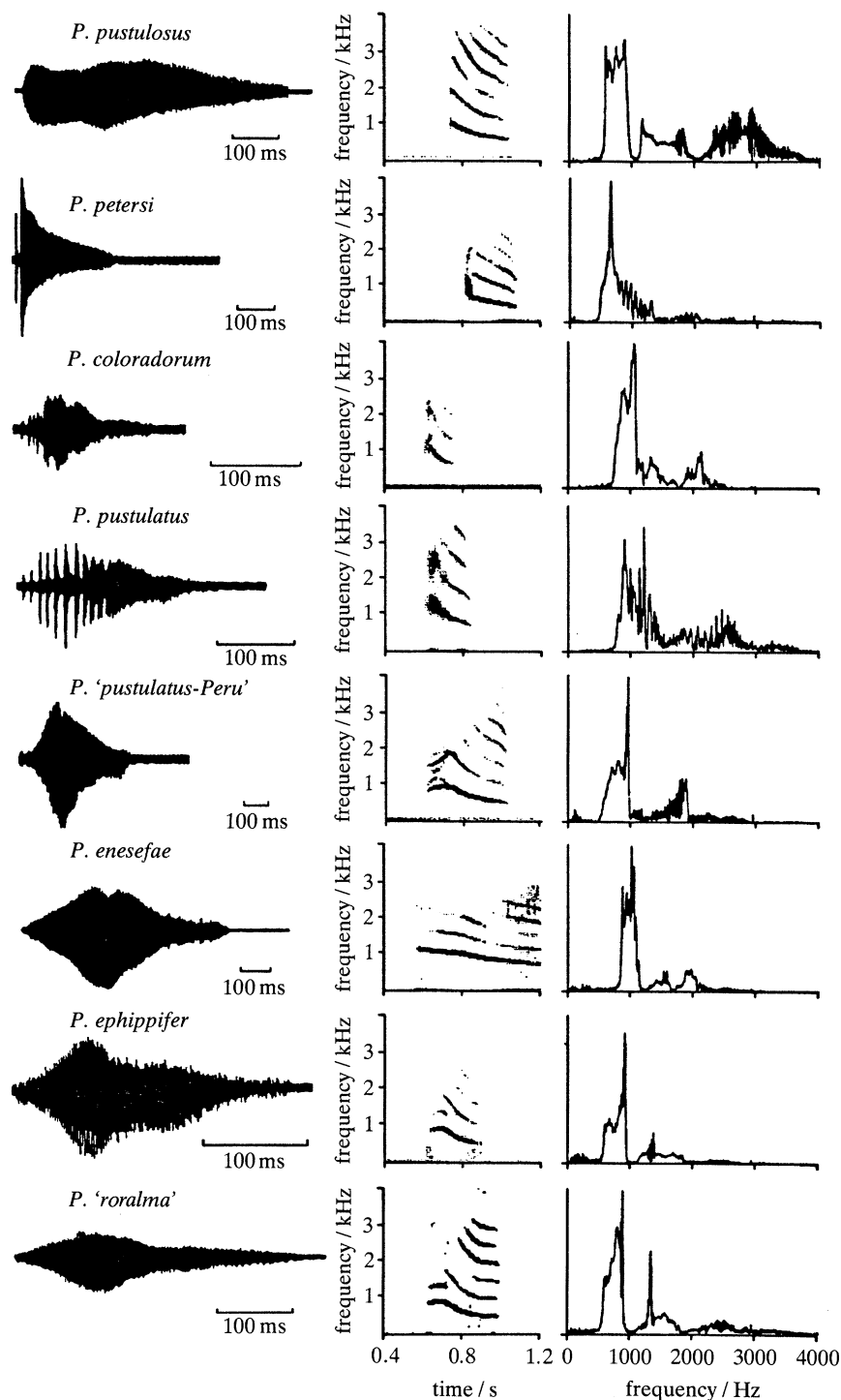


Figure 3. Advertisement calls of the species investigated showing oscillograms (left), sonograms (center), and power spectra (right). (Chucks, which can be added to the whine-like advertisement call of *P. pustulosus*, are not shown in this figure but are illustrated in figure 4.)

since most species produce only whine-like calls and these calls appear to be processed only by the amphibian papilla.

The phonotactic preferences of *P. pustulosus* were determined for the conspecific whine versus the same call to which the *P. pustulatus* AM prefix was added. Females preferred the call with the prefix (Ryan & Rand 1993a; figure 4). We also examined the response of female *P. pustulosus* to calls produced at the rate of

one call per 2 s usually exhibited by their own males versus the same calls produced at this rate but in doublets, as could be produced by male *P. coloradorum*. Female *P. pustulosus* showed a strong preference for the calling pattern of *P. coloradorum* (Ryan & Rand 1993a; figure 4). In *P. coloradorum* females showed a majority, but not a statistically significant preference for double calls versus single calls; the sample size for this experiment, however, is quite small (figure 4).

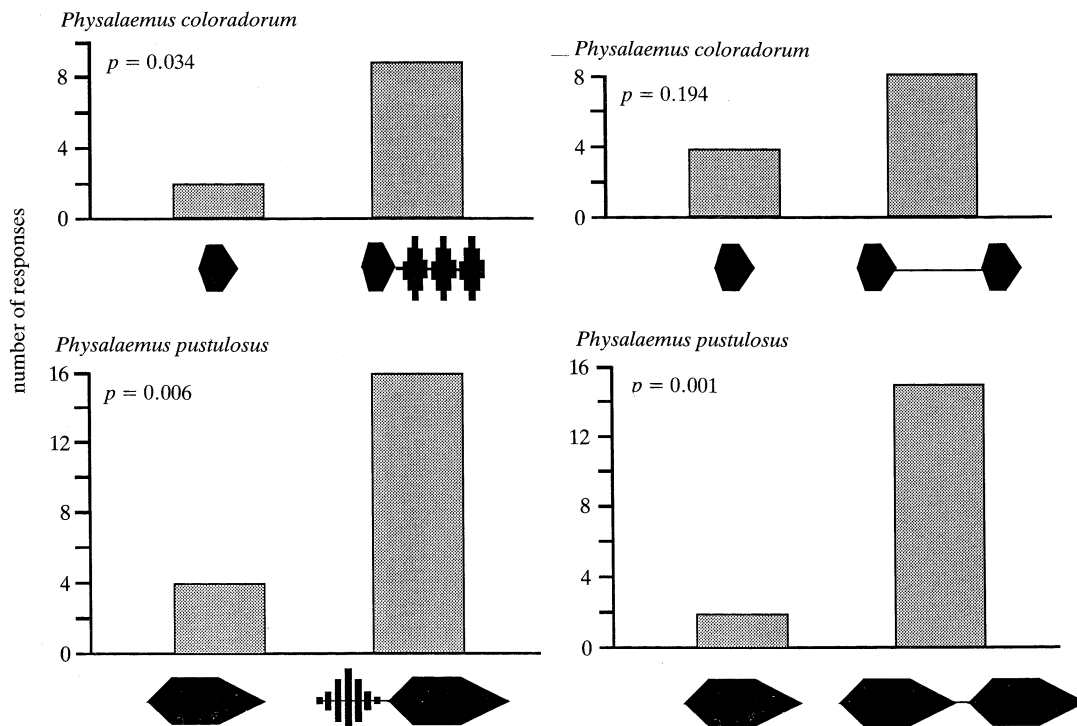


Figure 4. Top, left: responses of female *Physalaemus coloradorem* to the conspecific call and the same call to which chunks from a *P. pustulosus* call were appended. Bottom, left: responses of female *Physalaemus pustulosus* to the conspecific call and the same call to which the AM prefix from the *P. pustulosus* call was added. Responses of female *Physalaemus coloradorem* (top, right) and *P. pustulosus* (bottom, right) to the conspecific call broadcast at the normal rate exhibited by *P. pustulosus* and the same call broadcast at the calling rate often exhibited by *P. coloradorem*. All tests are by one-tailed binomial probability; the sensory exploitation hypothesis predicts the direction of the females' responses.

These phonotaxis experiments show that there are female preferences for several call features that are lacking in conspecific males: chuck, low frequency chuck (as might be suggested by the tuning bias), AM prefix, and double calls. Therefore, in this monophyletic group of frogs there appears to have been ample opportunity for sensory exploitation as all of these traits appear to have evolved after the preferences for these traits.

3. DISCUSSION

(a) Sensory exploitation in other taxa

Pre-existing preferences seem to be a common feature of frogs in the *Physalaemus pustulosus* species group. Such preferences have been reported in other taxa as well.

Swordtails and platyfish are both members of the genus *Xiphophorus*. Basolo (1990) showed that female swordtails (*X. helleri*) prefer males with longer tails, and female platyfish (*X. maculatus*) prefer males to which artificial swords were attached. In another example, Searcy (1992) showed that female grackles prefer larger song repertoires even though their males sing only single call types. In each of these cases there is either some question about the phylogenetic hypotheses available for the group studied (*Xiphophorus*) or a phylogenetic hypothesis is not presented (grackles).

Thus in each of these cases it is possible that the trait and preference coevolved and the trait was subsequently lost. This might be the case in the pygmy swordtail, *Xiphophorus pygmaeus*. These males are all small because they lack the genetic variations necessary for large size; they also lack courtship (Kallman 1989). Females in this species, however, prefer larger, courting male *X. nigrensis* to their own males (Ryan & Wagner 1987). If large size were lost in *X. pygmaeus*, suggesting that having only small size in the species is the derived condition, then it is possible that preference for courtship evolved in concert with courtship behaviour and the latter was lost along with large size in *X. pygmaeus*. (Kallman (1989) has suggested, however, that small size and lack of courtship might be the ancestral condition.) Even if preferences and traits coevolved and traits were later lost, this still creates conditions under which sensory exploitation could occur. In the pygmy swordtails, for example, if large size were to evolve then there might be a preference for large size that would promote the evolution of this trait. This preference and trait in *X. pygmaeus* would not have coevolved. It is possible that selection in the context of mate choice, such as good genes or runaway, could establish a preference which later in its history might become a pre-existing preference.

In none of the above cases has it been demonstrated why the pre-existing preferences exist, but there are some speculations. For example, in grackles, Searcy

(1992) has argued that switching among song types could release the auditory system from habituation, and he presents experimental evidence supporting this claim. If this were the case, this suggests that general neural properties could enhance the opportunity for sensory exploitation in a diverse array of taxa.

Perhaps the most complete study of sensory exploitation is Proctor's (1991, 1993) analysis of water mites. One species of mites feeds on copepods and locates prey by detecting water vibrations. Males mimic these vibrations to attract females to a close proximity at which time courtship begins. To show that males are exploiting the female's predation response, Proctor (1991) showed that food-deprived females were more likely to be mated than satiated females. Proctor (1993) also reconstructed the phylogeny of this group and showed that the hunting behaviour might have evolved prior to the males' use of vibratory cues. In this case Proctor has evidence both suggesting there are preexisting preferences and for the ecological forces responsible for the pre-existing preference.

(b) *Why pre-existing preferences exist*

Several selection forces could result in pre-existing preferences. In general, any factor that directly influences the evolution of a sensory system implicated in mate choice could consequently bias female preferences. We can consider such effects in two categories: those not related to mate choice and those related to mate choice.

Proctor's study is the best demonstration of how factors unrelated to mate choice can influence preferences. A similar example is how selection for finding small insect prey has influenced the visual system of anoline lizards and how these visual properties then favour the evolution of quick head bobs that are associated with the courtship display (Fleishman 1992). As another example, we should consider Searcy's (1992) assertion that neural properties, such as habituation, might provide some fairly general sensory biases that generate selection on male traits. If neural habituation is a ubiquitous problem in communication systems, this could explain the evolution of increasing complexity in many signalling systems.

Although only the study on water mites offers strong evidence that selection outside of the context of mate choice has influenced the evolution of pre-existing preferences, it seems possible that this might be a more common occurrence. It is important to remember that sensory systems involved in mate choice also serve other functions and thus should be subject to an array of selective forces that can influence their evolution.

Sexual selection studies usually address female mating preferences among conspecific males in the same population. But mate choice occurs in other arenas as well, and there is no doubt that there has been strong selection for females to choose appropriate mates in a variety of situations. A major emphasis of the New Synthesis was the role of behavioural isolating mechanisms in the speciation process (Mayr 1982). Ryan & Rand (1993b) recently discussed how

selection for specific-mate recognition is bound to generate mating preferences among conspecific males as an incidental consequence. If two species differ in pulse rate, one being faster and the other slower, then females of the slow-pulsed species might not only avoid heterospecific males with fast pulses, but might also tend to prefer males within their own population that exhibit slower rather than faster pulses even though females gain no advantage from making this latter discrimination. Fisher (1958) also discussed how selection for specific-mate recognition could generate sexual selection.

One of the important functions of courtship is to synchronize the physiological states of male and female (Morris 1956). Lehrman (1965) showed in a series of studies on ring doves the importance of various stimuli provided by males in influencing ovulation in females (see also Cheng 1986, 1992). Females evolve sensory biases to traits of an appropriate mate. But there is almost certain to be variation among males in these traits, and selection will favour males with traits that best match these sensory biases. The result is that the females will become more responsive to some males rather than others, even though all of these males might be appropriate mates. This preference did not evolve because of any advantage to discriminating among these appropriate mates; this discrimination is an incidental consequence. In some ways, this example could be considered one of the possible mechanisms underlying the case of species recognition discussed above.

The final example of mate choice establishing a preexisting preference brings us back to sexual selection and female mate choice. Selection could favour preference for traits indicating good genes or preference and trait could coevolve in a runaway process. As discussed above in relation to pygmy swordtails, if the trait is subsequently lost then this preference could be exploited later by males that evolve the appropriate traits. In this example, more than one process have interacted in the evolution of traits and preferences. Runaway or good genes could be responsible for establishing both the trait and the preference in one lineage and the preexisting trait in another lineage in which the trait evolves independently, not due to correlated evolution as in runaway or good genes, but because it matched an already existing preference.

(c) *How to define a preference*

The occurrence of a pre-existing preference for a character as specific as a chuck might seem more than coincidental. The problem, perhaps, is one of definition rather than evolution. We define preferences by those stimuli that elicit them. As we usually are concerned with stimuli that are components of extant communication systems, our definition of a preference might be restricted to only a small fraction of its full expression. For example, *P. pustulosus* females prefer chucks. The chuck covers a wide frequency range and 90% of the energy falls within the frequency region that stimulates the basilar papilla; this is a very

specific spectral character. But females also prefer half-chucks having either only the lower or only the higher harmonics present to calls without chucks, as long as each of the call variants has the same amount of energy as a full chuck. Furthermore, the full chuck is no more attractive than the half-chucks. It is especially surprising that the same effect can be achieved with white noise in the amplitude envelope of a chuck (Ryan & Rand 1990). It is true that females prefer chucks but these experiments suggest that the full chuck is only one of a variety of stimuli that can elicit this response.

Defining a preference becomes more complicated when we recognize that *P. pustulosus* also prefers the AM prefix of the *P. pustulatus* call when it is added to the conspecific whine, and double calls as can be produced by male *P. coloradorum*. Are there three separate preferences, one each for the chuck, AM prefix, and double calls, or is there one preference for more call energy that is not without specifications but is fairly catholic in its response to stimulus variation?

If preferences are general this suggests that the precise relationship between preference and trait might be dependent upon factors that bias males towards evolving one attractive trait rather than another that would be as attractive (e.g. chuck versus white noise). This could involve morphological constraints on males (e.g. it is easier to change the larynx to produce a chuck than to produce white noise), or different intensities of natural selection against different traits (e.g. white noise might attract more predators than chucks). More general preferences might also give us a different impression about how often preferences evolve. For example, a good genes hypothesis might suggest that males investing more energy in signals indicates better genetic quality, but males in different taxa might increase signal energy in different ways (adding chucks versus producing double calls). Thus a single preference that evolved in an ancestor could be responsible for considerable signal diversity among descendent taxa. A more general hypothesis based on signal theory (Shannon & Weaver 1949), that males should compete to increase the signal to noise ratio, would yield the same results.

(d) *Historical versus population approaches*

We have suggested adopting a phylogenetic approach to test hypotheses for the evolution of female mating preferences. Earlier we suggested that different hypotheses can result in the same relationships between extant traits and preferences within or among populations. Specifically, showing that traits are costly, that they are produced by healthier males, and even that there is heritable variation in male vigour is predicted by the good genes hypothesis but does not necessarily reject other hypotheses. We do not suggest rejecting this population-based approach, but instead that it should be combined with an historical analysis when possible because, as we discuss below, the historical approach has its own problems.

A major stumbling block to using the historical approach is the need to know the phylogeny of the

group being studied. Often this information is neither available nor can it easily be obtained. Also, not all groups have the proper character state distributions that allow determination of the sequence of preference-trait evolution (figure 1). For some systems the historical approach is not a tractable possibility.

Another problem is the principle of parsimony. When attempting to reconstruct the historical sequence of trait-preference evolution we accept the hypothesis that invokes the fewest number of evolutionary changes. If we are in error by even one change, this could cause us to revise our interpretations. We suggest that any single case can not offer strong support for a sensory exploitation hypothesis, but if this pattern appears in a variety of taxa using different sensory modalities for mate choice it should be given serious consideration (Ryan 1990).

Finally, a serious problem with the historical approach, as well as with the other approaches, is that it is difficult to determine the interaction of different processes, a possibility that Maynard Smith (1991) has recently emphasized. In sensory exploitation, preexisting preferences could initiate the evolution of the trait and then runaway could cause the further evolution of both trait and preference. Searcy (1992) suggested that this is the case in some birds. He found both a pre-existing preference for repertoire in species lacking repertoires and a stronger preference for repertoire in species in which males had larger repertoires. In many cases, however, the coevolutionary process, either good genes or runaway, could be masked by a trait-preference sequence that would cause us to reject those coevolutionary hypotheses. If a phylogenetic analysis suggests sensory exploitation (figure 1), however, it might be more prudent to invoke only a single hypothesis for which there is support rather than adding an additional process that could occur but for which there is no support.

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