# Factors Influencing the Evolution of Acoustic Communication: Biological Constraints

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**Abstract.** Numerous studies have investigated selective forces that appear to influence the evolution of acoustic communication systems. I review a number of constraints on evolution in these systems. A species' history is of undeniable importance in the analysis of any trait. However, studies have given little or no attention to phylogenetic patterns of acoustic signals. This precludes the identification of phylogenetic constraints, and should be viewed as a serious constraint on our ability to understand how communication systems evolve. Morphological constraints influence the energetic efficiency of acoustic communication. To maximize transmission distance of signals used in long-range communication, the animal's morphology favors signals with high frequencies. Thus morphology acts in opposition to properties of the environment, which favor low frequencies for use in long-range communication. Sensory receptors also play an important role in the evolution of acoustic signals. There is significant variation in the frequency range to which an inner-ear organ of the frog is sensitive. Different lineages of frogs are characterized by ear organs with different ranges of sensitivity. This variation should influence the frequency range over which calls evolved and, as a consequence, might have influenced the rate at which different lineages of anurans speciate.

## Introduction

Studies of acoustic communication have made important contributions to evolutionary biology. A number of studies have demonstrated, or at least persuasively argued for, a variety of selective forces that have shaped the evolution of acoustic signals. Prominent among these are the suggested roles of species recognition [Blair, 1964; Alexander, 1975; Littlejohn, 1981], predator pressure [Marler, 1955; Cade, 1975; Tuttle and Ryan, 1981], sexual selection [Cade, 1979; Ryan, 1980, 1983b; Payne, 1983], motivational-structural rules [Darwin, 1872; Morton, 1977],

and environmental selection on acoustic structure [Morton, 1975; Wiley and Richards, 1982; Ryan and Brenowitz, 1985]. Some of these forces will act in opposition, thus, for example, the advantage, vis-à-vis mate attraction, derived from evolving a more conspicuous signal will be opposed by disadvantages of increased predation [e.g., Ryan et al., 1982]. Thus these opposing selective forces will influence the evolution of the signal structure, and hypotheses based on optimization of traits as an evolutionary response to a single selective force often are naive.

Besides the opposition of selective forces, there are features of the organism that prohibit an optimal response to selection, and these factors are usually referred to as constraints [Oster and Wilson, 1978; Maynard Smith et al., 1985]. I define constraints as properties of the organism's biology that result in a bias in the production of variant phenotypes [this definition follows from Maynard Smith et al., 1985].

This discussion will review a variety of factors that constrain the ability of a trait to exhibit an optimum response to a single selective force. I will concentrate on those traits that are of particular importance to communication systems, and ignore some of those that are of more general significance in evolutionary biology and whose importance is better understood, such as sufficient genetic variability for evolution to occur. I will discuss the importance of the following constraints: phylogeny, morphology, acoustic coupling and energetics, and sensory receptors. I will draw examples from studies of anurans, in general, and from studies by my colleagues and me on the frog *Physalaemus pustulo-*

*sus* [summarized in Ryan, 1985b] for some specific examples.

## Phylogeny

Although in most circumstances selection appears to act at the level of the individual, hypotheses of adaptation are often tested at the level of the species. Quite often the comparative approach consists of erecting a hypothesis, predicting the occurrence of certain traits (the alleged adaptations) in certain ecological settings, and testing this prediction by asking if there is a correlation between traits and ecological settings. If there is good congruence between the trait and the ecology as predicted, then the hypothesis of adaptation is supported.

The underlying assumption to this approach is that a species is an independent data point. The potential fallacy of this assumption has been discussed by a number of authors [e.g., Clutton-Brock and Harvey, 1977; Harvey and Mace, 1982; Ridley, 1983; Northcutt, 1984; Felsenstein, 1985]. The problem of confounding results by not controlling for phylogeny is of special concern in studies of communication.

The potential role of phylogeny in explaining the diversity of anuran acoustic signals can be exemplified by asking: does a toad sound like a toad, a treefrog like a treefrog, and a dart-poison frog like a dart-poison frog? More succinctly, how much of the variation among species can be explained by variation among ancestors? Given the generally accepted importance of the anuran mating call in species isolation, it is surprising that this question has not been answered directly. For exam-

ple, in a well-known text on vertebrate biology, McFarland et al. [1979] state that '...a species-specific call is a conservative evolutionary character, and among taxa there is often considerable similarity among calls' [see also Blair, 1974; Passmore, 1981]. But when one searches the literature one finds little evidence to support or reject this contention. Tandy and Keith [1972] offer one of the few analyses that allow some glimpse of phylogenetic patterns and constraints in the evolution of frog calls [but see also discussion below of Martin, 1972]. They examined various dendograms depicting phenetic similarity using data on paratoid-gland secretions, hemoglobin, and hybrid crosses. These dendograms are highly congruent with one another, and with a dendogram based on passive pulse repetition rate. For this call character, then, something can be said about potential phylogenetic patterns. Pulse rate appears to evolve in a conservative manner relative to non-call traits because it results in dendograms similar to those derived from other traits. Other call characters were not discussed. However, I suggest that call characters which are not phylogenetically informative are more, not less, interesting and deserve rigorous phylogenetic analysis.

Clearly, there are cases where much of the variation in calls characterizes not the species but a larger monophyletic unit. The example of amplitude-modulated calls in the genus *Bufo* is the best documented case. Martin [1972] characterized calls as types I, II, and III based on patterns of amplitude modulation. He showed that call types often characterize species groups [see his table J, pp. 446–447], and that only groups possessing well-developed aretynoid valves produced the type I call.

Although a variety of studies have investigated selective forces that might influence evolution of acoustic signals, there has been little or no attention given to phylogenetic patterns of signals. Without a knowledge of history one can not evaluate the influence of phylogenetic constraints, and the lack of this information greatly constrains our ability to understand how communication systems evolve. I suggest, perhaps an extreme view, that until one addresses the question of phylogenetic influence on a characters' evolutionary history, one can not adequately test hypotheses of adaptation [see also Felsenstein, 1985]. Currently, I am attempting to address such phylogenetic patterns in the evolution of frog calls.

## Morphology

The anuran auditory system appears to be designed to extract spectral information from the call and this information is one of the primary features used in species recognition [Frishkopf et al., 1968; Feng et al., 1975; Walkowiak, 1980; Fuzessery and Feng, 1981; Ryan, 1983a]. Thus the evolution of spectral-call characters, especially dominant frequency, are crucial in discussions of the evolution of this communication system. Spectral properties of mating calls often differ among frog species, and there is usually a correlation between body size and the dominant frequency of the mating call [e.g., Blair, 1964; Duellman and Pyles, 1983]. This correlation results from a correlation between body size and the mass of the vocal cords [Martin, 1972].
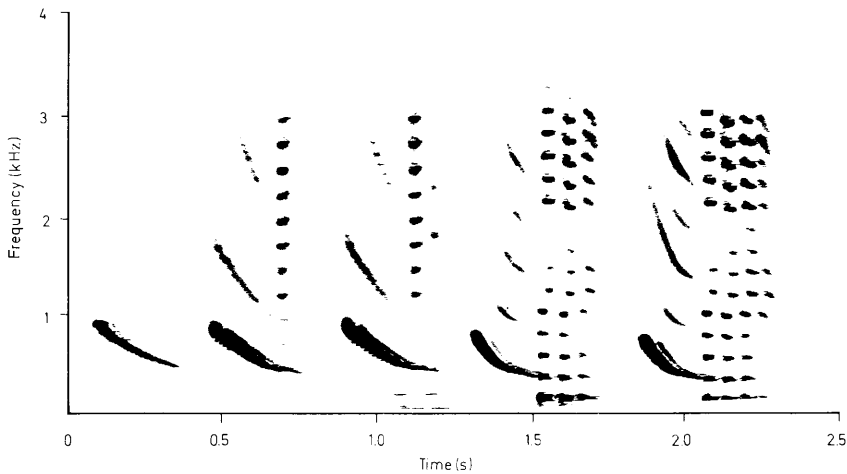
**Fig. 1.** Sonograms of the call complexity series of *P. pustulosus* [from Ryan, 1983a].

Since the frequency of vibration is a function of the tension and the mass of the cords, larger frog species usually produce mating calls with lower frequencies. Thus an important question is, how much of the variation in the dominant frequency of the call can be explained by body size? If the answer is all of it, then it would be difficult to elucidate causes of the evolution of this character since it would not be known if selection had acted on body size or on the call. In fact, Blair and Littlejohn [1960] suggested that in some cases selection on body size led to species divergence because of its secondary effect on mating calls.

The correlation between body size and frequency is of special concern in the frog *P. pustulosus*. This frog has a complex vocalization, consisting of a whine followed by 0–6 chucks (fig. 1) [Rand and Ryan, 1981]. Males call from stationary sites, and females move among males with little or no interference. A female will sit directly

in front of a calling male, often moving from one male to another before finally selecting a mate. In the field, females choose larger males as mates, and larger males produce calls in which the chuck has a lower frequency [Ryan, 1980, 1983a, 1985a]. These results suggested the hypothesis that larger males are more likely to mate because females are attracted preferentially to calls with lower-frequency chucks. Playback experiments using synthetic calls supported this hypothesis. This study demonstrates that there is selection, in the form of female choice, on call frequency in this species. However, it only demonstrates selection, not evolution. With most vertebrates it is not possible to demonstrate evolution experimentally due to long generation times. Therefore, the comparative approach becomes invaluable as a tool to test the hypothesis of evolution in response to selection.

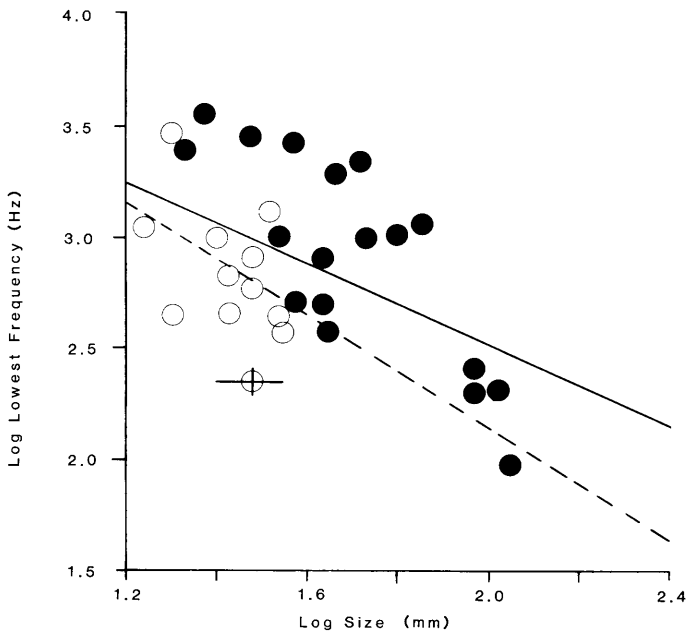I tested the prediction that sexual selection has influenced the evolution of lower

**Fig. 2.** The relationship between the logarithm of male size and the logarithm of the lowest frequency in the advertisement call for 30 species of the subfamily Leptodactylinae. Open circles represent members of the genus *Physalaemus* and closed circles represent other members of the subfamily. The solid line represents the regression of frequency on size for members of the subfamily, and the dashed line represents the regression derived from data of the genus *Physalaemus* only. The circle intersected by vertical and horizontal lines represents the midpoint and the ranges of the size and frequency for *P. pustulosus* [from Ryan, 1985b].

frequencies in the call of *P. pustulosus*. As I stated above, across species there is a correlation between body size and frequency of the mating call. Figure 2 shows this relationship between body size and the lowest frequencies of the mating call for 30 species of the subfamily Leptodactylinae. Clearly, *P. pustulosus* has a call with a very low frequency for its body size. When comparing the residuals for all these species it is seen that the call of *P. pustulosus* departs from the predicted regression in the negative direction more so than any other species. In fact, its residual is actually disjunct from the distribution of the other residuals (fig. 3). Therefore, not only is their call low for their body, they have the lowest call for their body size of all species considered. Parallel results are found if only members from the genus *Physalaemus* are used.

It is possible that *P. pustulosus* did not evolve a lower-frequency call, but all of the other species tested evolved higher-frequency calls. The direction of character evolution must be determined to elucidate whether the low-frequency call of this species is the primitive or the derived state. Cladistics suggests a method for character state polarization, outgroup comparison,
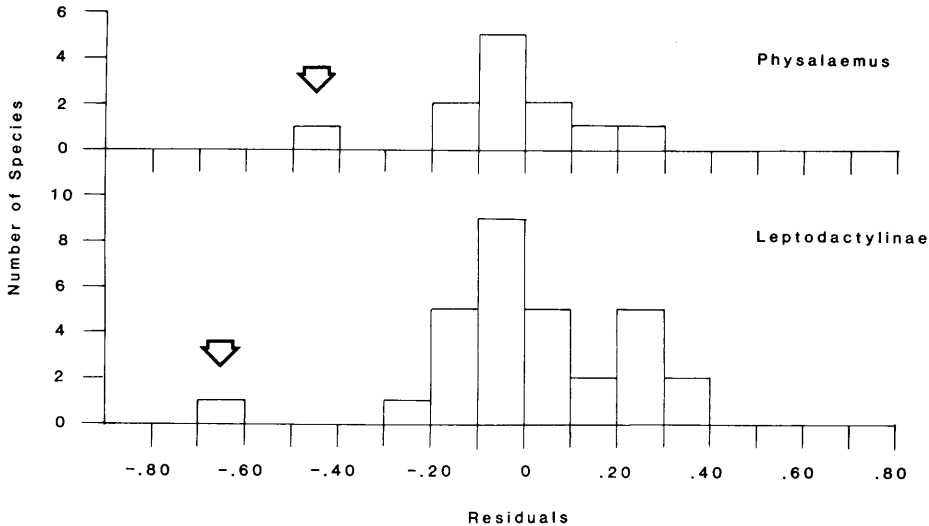
**Fig. 3.** Frequency distribution of the magnitude of the departure of the observed low-frequency of the call from that expected based on the size-frequency relationships of the subfamily Leptodactylinae and the genus *Physalaemus*. The arrow indicates the departure exhibited by *P. pustulosus* [from Ryan, 1985b].

that can be applied in this situation [Wiley, 1981]. If the regression of body size on call frequency for a closely related group better predicts the relationship between these two characters in *P. pustulosus* than does the group to which the species belongs, it would be concluded that the low-frequency call is the primitive state. Using the subfamily Telmatobiinae as the outgroup for the subfamily comparison, and the genus *Leptodactylus* as the outgroup for the genus comparison, I showed that the low-frequency call of *P. pustulosus* is the derived state (fig. 4). These phylogenetic results support the hypothesis that the selection on low frequency-calls by females has influenced the evolution of the calls.

Even though *P. pustulosus* has evolved lower-frequency calls independent of a

change in overall body size, this evolutionary change in call structure can not occur independent of morphological change. Drewry et al. [1982] identified the precise morphological innovation that has allowed these calls to evolve. *P. pustulosus* has two fibrous masses associated with the vocal cords. During production of the first component of the call, the whine, changes in the tension of muscles associated with the larynx change larynx shape, thus bringing these masses into the air flow. The vibration of these structures result in the chuck. The analysis of Drewry et al. shows a clear correlation between call structure and vocal morphology for three species in the genus *Physalaemus (gracilis, olfersi, pustulosus)*, the morphology and call of *P. pustulosus* being the most elaborated. Ryan and Drewes [in preparation]
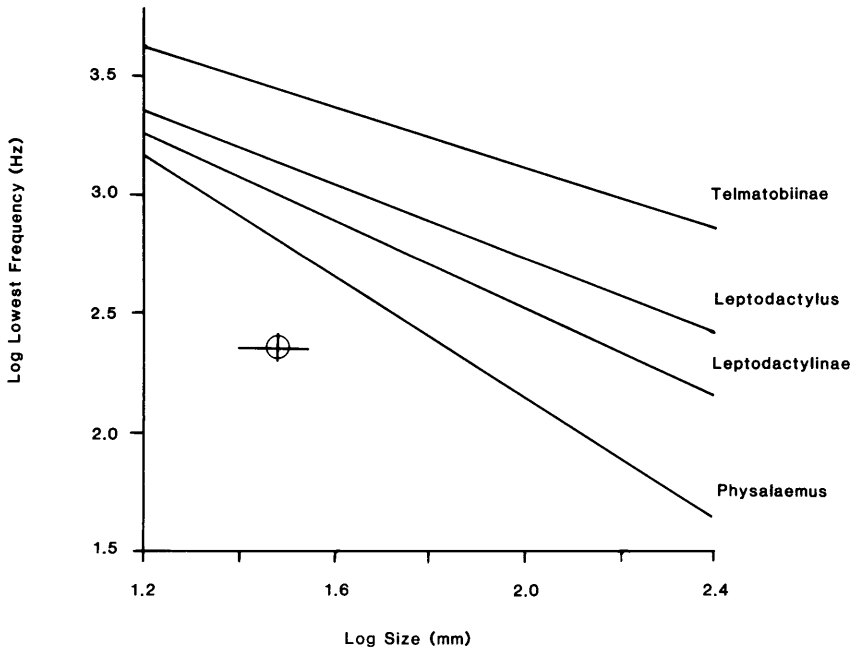
**Fig. 4.** Regression lines of the logarithm of call frequency on the logarithm of body size for species in the subfamilies Leptodactylinae and Telmatobiinae, and the genera *Physalaemus* and *Leptodactylus*. The circle represents mean body size and frequency for *P. pustulosus* and the horizontal and vertical lines intersecting the circle represent the ranges [from Ryan, 1985b].

have surveyed laryngeal morphology of the *P. pustulosus* species group and their results also suggest that the larynx of *P. pustulosus* is both complex and derived within the monophyletic unit.

### Acoustic Coupling and Energetics

The above discussion shows that call frequency can evolve independently of body size. This should be of concern not only in regard to *P. pustulosus,* in which sexual selection favors lower-frequency calls, but for all animals that use acoustic communication to transmit information

over relatively long distances. Due to atmospheric absorption, high-frequency sounds tend to attenuate at a greater rate than do low-frequency sounds. Near the ground, in a variety of habitats, there appears to be a low-frequency window; that is, a band of frequencies where attenuation is less than frequencies immediately above and below. In many cases, then, there should be selection for relatively low-frequency calls for use in long-range communication [Morton, 1975; Wiley and Richards, 1982; Ryan and Brenowitz, 1985; Brenowitz, this volume].

Increasing the mass of the vocal cords will lower the frequency of vibration at the

source, but that vibration can only serve as a functional communication signal if it is coupled to the environment with some minimum efficiency. *P. pustulosus* serves as an example of the need to evolve structures to accommodate the coupling of low-frequency sounds to the environment. The vocal sac of *P. pustulosus* is very large relative to closely related species (fig. 5). Drewry et al. [1982] showed that the call of *P. gracilis* is similar to the whine component of the *P. pustulosus* call, and the lower fundamental frequency in the frequency sweep is about 450 Hz. *P. olfersi* is characterized by a call more similar to the chuck of *P. pustulosus*. The fundamental frequency, determined by analysis of the harmonic structure, is 150–200 Hz, lower than either of the other two species examined. However, the lowest frequency of the call that appears on the sonogram is 1,500 Hz. *P. olfersi* is distinguished from *P. pustulosus* by having a very small vocal sac. Thus Drewry et al. [1982] suggested that, although the vocal cords produced a pattern of vibration with a low fundamental frequency, only the higher harmonics are coupled to the environment due to the filtering effect of the small vocal sac.

In anurans, the vocal sac appears to act as a radiator rather than a resonator. Martin [1972] punctured the vocal sac of some *Bufo*, the effect being a great reduction in amplitude and a slight detuning of the call; effects predicted for a radiator but not a resonator. Capranica and Moffat [1983] recorded the mating call of a *Hyla crucifer* placed in a helium-oxygen mixture. The resonant frequency of a resonator is a function of the size of the resonator and the wavelength of the sound. Since the speed of sound in helium is approximately



Fig. 5. A calling male *Physalemus pustulosus* [from Ryan, 1985b].

3 times that in air, the frequency of sound for a given wavelength is 3 times higher in helium than in air. Capranica and Moffat [1983] found no difference between the spectral properties of the call recorded in air and in helium. This supports Martin's contention [1972] that the vocal sac is a radiator.

A radiator is characterized by a cutoff frequency, above which sound energy is radiated with maximum efficiency. The cutoff frequency of a sphere is $f_c = c/2\pi r$, where c is the speed of sound in air (ca. 330 m/s) and r is the radius of the sphere. For *P. pustulosus* to radiate its call so that the fundamental frequency of the chuck is above the cutoff frequency, the radiator must have a diameter of 26 cm. The frog is only 3 cm long! The addition of a large vo-
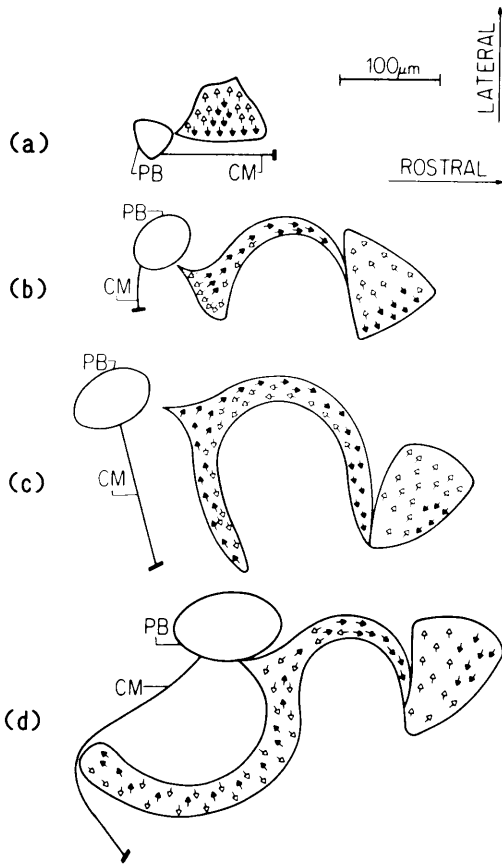
Fig. 6. Sketches of the amphibian papillae of four anurans representing four character states. a *Ascaphus truei* (Ascaphidae). b *Bombina orientalis* (Discoglossidae). c *Scaphiopus couchi* (Pelobatidae). d *Kassina senegalensis* (Hyperoliidae). PB = Transected papillar branchlet of the VIIIth nerve; CM = contact membrane separating the papillar chamber from the amphibian periotic canal [with permission from Lewis, 1984].

structures is a low efficiency in converting metabolic to acoustic energy. Bucher et al. [1982] and Ryan et al. [1983] determined the amount of aerobically and anaerobically generated energy used in vocalization by *P. pustulosus*. On average, these frogs used 24 mJ to produce a single call. The amount of acoustic energy in a single call ranged from 0.12–0.30 mJ, depending on the number of chucks in the call. This yields energetic efficiencies between 0.5–1.2% [Ryan, 1985a]. Other animals also have been shown to have low efficiencies for converting metabolic to acoustic energy [e.g., crickets, MacNally and Young, 1981]; this probably is true in many if not most animals, and results from a mismatch between the wavelength of the sounds produced and the radiating structures involved in coupling sound to the environment.

For signals used in long-distance communication, it is usually assumed that selection should favor increased signal amplitude at the receiver [e.g., Morton, 1975; Ryan and Brenowitz, 1985]. This can be accomplished in two ways: increasing signal amplitude at the source, and decreasing loss of signal amplitude during transmission. The former is best accomplished by high frequencies, while the latter is best accomplished by low frequencies. It appears that signals used in long distance communication have evolved under conflicting selective forces generated by the animal's morphology and environment.

cal sac in this species might enhance coupling of low-frequency sound, but it clearly does not maximize it.

A consequence of this mismatch between the frequency of vibration at the source and the properties of the radiating

## Sensory Receptors

The evolution of an animal communication system involves co-evolution of a

*Urodela* *Ascaphidae* *Leiopelmatidae* *Discoglossidae* *Pipidae* *Pelobatidae* *Leptodactylidae* *Dendrobatidae* *Hylidae* *Bufonidae* *Ranidae* *Hyperoliidae* *Rhacophoridae* *Microhylidae*
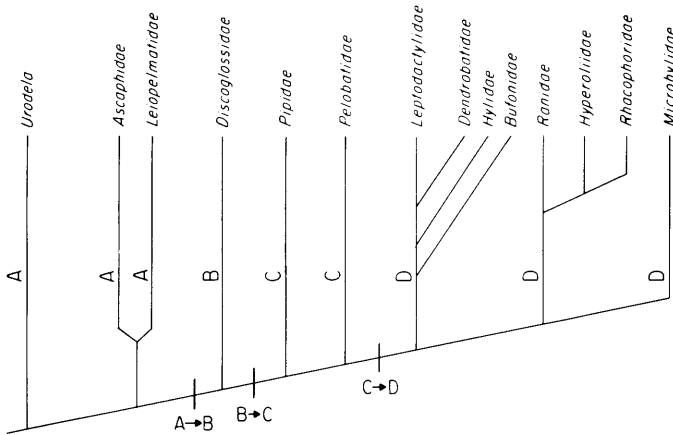
A A A B C C D D D

A→B B→C C→D

Fig. 7. The phylogeny of frog families with character states of the amphibian papilla representing each family superimposed. Hypothesized character state changes are represented [from Ryan, 1986].

signal and a receiver. Alexander [1962] suggested that both the signal and the receiver might be under control of the same genes [pleiotropy]. If so, he suggested, the evolution of the system is more likely since a mutation would concurrently influence both aspects of the system in the same manner. A number of studies [Hoy and Paul, 1973; Hoy et al., 1977; Dougherty and Gerhardt, 1983] present evidence that calls of hybrids are intermediate between calls of parental forms, and in some cases females prefer the hybrid call. Although these data are suggestive, they do not discriminate the possibility of pleiotropy from other phenomena, such as different polygenic systems controlling the signal and the receptor.

If pleiotropy is not the rule, then it is possible that either the sender or the receiver could constrain evolutionary change in the concomitant component of the communication system. For example, mutations in a signal that fall outside of the sensitivity range of the receiver will not be biologically meaningful and are unlikely to be incorporated into the genome.

Table I. Character states of the AP and the number of species in each clade, in which the clade is characterized by character state autapomorphy (see fig. 7)

| Character state | Number of species |
| --- | --- |
| A | 4 |
| B | 9 |
| C | 66 |
| D | 2,489 |

Ryan [1986] suggested this phenomenon has occurred in anurans.

Frogs possess two inner-ear organs that are sensitive to air-born sound: the amphibian papilla (AP) and the basilar papilla (BP). Neurophysiological studies, much of this work done by Capranica and his colleagues [recently reviewed in Capranica and Moffat, 1983; Capranica and Rose, 1983; Wilczynski and Capranica, 1984], have shown that the inner ear acts as a peripheral filter, and those frequencies to which the receivers are most sensitive tend to match the dominant frequencies in the species' mating call. In most

species, the AP gives rise to two populations of nerve fibers in the statoacoustic (VIIIth) cranial nerve. One population tends to have a best frequency at low frequencies while the other population tends to have its best frequency at mid-frequencies. Nerve fibers from the BP are tuned to higher frequencies.

Lewis et al. [1982] showed that the AP is tonotopically organized, with low-frequency fibers being traced to the rostral end, high-frequency (i.e., high frequencies within the AP, frequencies that are lower than those to which the BP is sensitive) fibers to the caudal end, and intermediate-frequency fibers were traced to intermediate areas. However, when Lewis [1984] surveyed the anatomy of the AP from 79 species of frogs belonging to 13 different families he found a range of complexity in AP structure that could be classified into 4 character states (fig. 6). The most simple AP consists of only a single patch of sensory epithelium (character state A), and thus is similar to the AP that characterizes salamanders. The next stage of complexity (B) incorporates a second patch of epithelium into the AP, and the last two stages (C, D) are characterized by caudal extensions of the AP. This morphological variation has a functional counterpart. From VIIIth nerve recordings [Capranica and Moffat, 1975; Capranica, pers. commun.] it seems that the increased complexity of the AP corresponds to an increased range of frequency sensitivity.

Blair and others [see especially Blair, 1964] have shown that mating-call divergence is an important component of the speciation process. Calls can diverge in the spectral and/or temporal domain. I suggested that the receptor constrains the degree to which mutations in call frequency might be incorporated into the genome, thus it should constrain the opportunity for speciation [Ryan, 1986]. There is a correlation between the complexity of the AP of a taxon and the number of species in that taxon. The number of species increases with the complexity of the AP (fig. 7, table I). Since the rate of species extinction does not appear to be greater in taxa with fewer species, the differences in species numbers should be due largely to differences in rates of speciation. I concluded, therefore, that variation in the complexity of the receptor structure seems to have some influence on the rate of speciation in anurans.

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