Chapter Twenty-Eight

CONSTRAINTS AND PATTERNS IN THE EVOLUTION OF ANURAN ACOUSTIC COMMUNICATION

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I. INTRODUCTION

The anuran auditory system differs from that of other amphibians in that it is an integral component of an acoustic communication system. In anurans, audition is the primary sensory modality for communication; it is crucially involved in mate recognition and thus is of paramount importance in speciation and sexual selection. In this chapter I consider factors that influence the evolution of the anuran acoustic communication, especially the advertisement call. I begin by discussing the function of the advertisement call and the obvious advantage of being able to communicate efficiently. I then consider a variety of factors that limit the ability of the advertisement call to exhibit an optimal evolutionary response to a given selective force. Some of these limiting factors are constraints in the sense that they bias the production of phenotypes (Maynard Smith et al., 1985; Ryan, 1986b). Other limitations result from opposing selective forces;

under these conditions an optimal response to a single selective force is not possible. I then address the question of how the communication system, including both the behavioral and sensory systems, coevolve. Finally, I consider why and how patterns of evolutionary change in advertisement calls should be investigated.

My emphasis in this chapter is integrative; an understanding of the acoustic communication system of anurans involves a variety of disciplines that too often are not considered in concert. A major goal of evolutionary biologists since Darwin has been the explanation of organic diversity, especially functional diversity. Accomplishing this task for any communication system entails considering behavior, morphology, neurophysiology, ecology, and phylogeny. The amount of information in each of these areas, and the possibility of acquiring such information in areas in which it does not now exist, suggests that anurans are an ideal system for investigations of coevolution of sensory-behavioral systems, in general, and communication, in particular (Wilczynski and Ryan, this volume). Below I review the available information from these disciplines in the hope of lending some insights into the evolution of anuran acoustic communication.

II. THE ADVERTISEMENT CALL

During the warmer seasons in the Temperate Zones and the wetter seasons in the Tropics, the din of male frogs attempting to attract females to mate is often the dominant nocturnal sound. The ways and means by which male frogs achieve syngamy are varied (Wells, 1977; Duellman and Trueb, 1985), but in most species vocalizations play an integral if not dominant role. Males produce a variety of vocalizations which achieve a variety of functions. Those vocalizations used by males to attract females over a long distance for the purpose of mating and to advertise their presence to other males are termed advertisement calls (Wells, 1977; see also Rand, this volume). The advertisement call is the most conspicuous vocalization. In terms of mate recognition, sexual selection, and speciation it is the most important vocalization, and almost all studies of neural processing of vocalizations have investigated decoding of the advertisement call (e.g., see Walkowiak, this volume).

The adaptive significance of the advertisement call is clear; there are obvious fitness benefits accrued to those males that are able to attract females for mating. From the female's perspective, the advertisement call allows her to identify those males with which effective syngamy is possible; there should be strong natural selection against those females that lose their reproductive investment by being involved in matings that do not result in efficient fertilization and development of offspring. Most important is the necessity to mate with a conspecific male, since the results of heterospecific matings often are disastrous (e.g., Blair, 1972). However,

mate choice among conspecific males also might increase a female's reproductive success and thus be favored by natural selection. For example, in *Rana catesbeiana* (Howard, 1978) and *Hyla rosenbergi* (Kluge, 1981), eggs deposited in the territories of larger males have higher survivorship, and in *Physalaemus pustulosus* (Ryan, 1983, 1985b) and *R. sylvatica* (Smith-Gill and Berven, 1980) male size influences fertilization rates.

Reliance on the vocalization for mate recognition has several consequences. The most obvious is that species of frogs differ both in their advertisement calls and in various aspects of the auditory system with the result that females are attracted preferentially to the conspecific call. I agree with Paterson (1978) and Littlejohn (1981) in emphasizing this positive aspect of male recognition—the mate recognition system has evolved to achieve efficient syngamy and a consequence is species distinctiveness in calls, as opposed to the alternative view (e.g., Dobzhansky, 1937) that the evolved function of mate recognition systems is to ensure species integrity through the avoidance of mating with heterospecifics.

Acoustic mate recognition also has consequences for intraspecific mate choice, and Littlejohn (1981) emphasizes that considerations of mate recognition must extend to notions of sexual selection. There is always intrapopulational variation in advertisement calls. Not all of this variation influences the behavior of females, but some of this variation clearly does affect female phonotaxis (Gerhardt, this volume). Thus even within a population of conspecifics, females are more attracted to some advertisement calls than to others. This has been demonstrated in *H. cinerea* (Gerhardt, 1974, 1982), *P. pustulosus* (Ryan, 1980, 1983, 1985b), *Bufo woodhousei* (Sullivan, 1983), *H. ebraccata* (Wells and Schwartz, 1984), *H. crucifer* (Forester and Czarnowsky, 1985), and *Uperoleia rugosa* (Robertson, 1986) among others (see Gerhardt, this volume). This intrapopulational variation in calls can result in sexual selection; that is, differential mating success among males due to their ability to acquire mates.

There has been some confusion in the literature regarding this aspect of female choice based on advertisement calls. The importance of female choice has been evaluated by asking what advantages might accrue to choosing females (Gerhardt, 1982; Arak, 1983a,b; Halliday, 1983). If this behavior is not demonstrated to be adaptive then its importance is often questioned. The hypothesis that female choice influences male mating success is a phenomenon that needs to be evaluated separately, and initially in isolation from speculations about why this choice has evolved. The fact that sexual selection through female choice might influence the evolution of male calls does not imply that females need gain some benefit in reproductive success by exercising mate choice. In fact, Darwin (1871), Fisher (1958), Lande (1981), Kirkpatrick (1982), and Arnold (1983) have all emphasized that this need not be the case. Female preference for various calls can evolve as the result of natural selection (due to increased reproductive success of female exercising choice, as discussed above), sexual selection

[due to genetic covariance of the preference and the trait, as envisioned by Fisher (1958)], or it might result merely as a consequence of how the auditory system perceives call variation (Ryan, 1985b). In the following sections I consider how various factors can influence the evolution of the advertisement call in order to enhance the ability of the male to attract females.

III. ENVIRONMENTAL AND ECOLOGICAL CONSTRAINTS

For the advertisement call to be effective in mate attraction it must be detected, discriminated, and localized by the female. Although the advertisement call is assumed to function over relatively long distances (relative to the body size of the frog, that is) there are few data suggesting the distances over which the mating call is effective, but these data do suggest the likelihood of long-distance communication. *P. pustulosus* is attracted to speakers broadcasting the conspecific advertisement call from distances greater than 5 m (ca. 160 body lengths) in the laboratory (Ryan, 1985b). Gerhardt (this volume) has shown that *H. cinerea* is attracted to calls from a distance of 80 m (ca. 1,600 body lengths; for perspective, this would be ca. 1.8 miles for humans), although *H. gratiosa*, which has a somewhat similar call and similar auditory sensitivities, is not attracted to its call from the same distance. Clearly, in some species females orient to the advertisement call over long distances but the extent to which this is a generalization is not known.

In a number of other species female phonotaxis is elicited preferentially by more intense calls (e.g., *H. cinerea*, Gerhardt, 1982; *B. calamita*, Arak, 1983b; *H. versicolor*, Fellers, 1979). Thus increasing the intensity of the call at the receiver is an obvious advantage for males. Although there is less evidence suggesting an advantage for increasing the distance over which the call is transmitted effectively, achieving increased transmission distance is often synonymous with increasing the intensity at the receiver. If the frog achieves one it usually achieves the other. But increasing the intensity of the call at the receiver is not the only issue. Two other factors for effective communication need to be considered: the intensity of the call relative to background noise and the ability of the female to localize the call. Thus calls should be selected to: (1) increase the intensity of the stimulus at the source; (2) decrease the amount of signal attenuation and degradation that occurs with distance; (3) increase signal to noise ratio; (4) increase the localizability of the call to the female. I will consider how environmental factors influence the evolution of the call in achieving these factors.

A. Noise

A male can increase the signal-to-noise ratio by increasing the overall intensity of the call and by calling in a less noisy environment. Narins and

Zelick (this volume) provide a comprehensive treatment of the problem faced by male frogs communicating in noise. Here, I will mention only some of the major considerations.

Noise is any extraneous sound that interferes with reception of the signal (Pierce, 1961). It can be biotically or abiotically generated. Since the focus of selection is the individual, and the signal is part of the individual's phenotype, biotic noise can be produced by conspecifics as well as heterospecifics. Conspecific calls present a special problem. These calls are very similar in structure and are directed toward the same receiver—the conspecific female. In general, the female is equally likely to detect (although not necessarily prefer) the call of any one male. Also, these calls are produced at the same time and in the same place. It is assumed that females can more easily detect and localize calls that are produced antiphonally (e.g., Alexander, 1975). Thus it is not surprising that many frogs alternate their calls, a supposed adaptation for increasing the conspicuousness of the call to the female (e.g., Lemon and Struger, 1980; Narins, 1982). However, some frogs (e.g., *Smilisca sila*; Tuttle and Ryan, 1982; Ryan, 1986d) overlap their calls in time, and the few tests of the hypothesis that overlapping calls are more difficult to localize have not supported that hypothesis (Passmore and Telford, 1981; Schwartz, cited in Narins and Zelick, this volume).

Noise generated by heterospecific calling is generally less of a problem for calling frogs because the female's auditory system tends to be biased toward properties of the conspecific call. However, when calls are similar male frogs utilize a variety of behaviors that reduce the noise generated by heterospecific calling. First, heterospecific calls often are temporally dissociated, either seasonally or through the night (Drewry and Rand, 1983). Also, as with conspecifics, males may alternate their calls with similar calls of heterospecifics (Littlejohn and Martin, 1969). Although there have been suggestions that heterospecifics partition the acoustic environment, this has not been documented extensively. Duellman and Pyles (1983) showed that in an Amazonian community, closely related species have similar calls only when they are allopatric. When they are sympatric the calls differ, suggesting divergence due to call similarity. Hödl (1977) also presents data suggesting acoustic niche partitioning in an Amazonian frog community. Drewry and Rand (1983) examined communities of *Eleutherodactylus* frogs in Puerto Rico over an altitudinal gradient. Their data suggest frequency and temporal partitioning of the acoustic environment. The frequencies of many species are disjunct, and when they are similar these species tend to call at different times during the night.

Another means of reducing heterospecific noise is evolutionary divergence of calls of syntopic (same space) and synchronic (same time) species. Divergence of advertisement calls due to heterospecific interactions can lead to reproductive character displacement (Brown and Wilson, 1956). Due to the fitness decrement involved in heterospecific matings, selection

will favor divergence of calls and preferences in situations in which mis-matings are possible. The theory of reproductive character displacement is controversial (Paterson, 1982), and the best documented case of this phe-nomenon occurs in anurans—e.g. Littlejohn's (1965; Littlejohn and Loftus-Hills, 1968) study of *H. ewingi*.

The presence of heterospecifics can also have a stabilizing effect on the evolution of conspecific advertisement calls. As Gerhardt (1982) has em-phasized, intraspecific mate choice can be constrained by interspecific in-teractions. If directional selection exerted by female choice on the conspecific call would result in the call becoming similar enough to the calls of syntopic and synchronic heterospecifics, this could result in heterospecific matings.

Although abiotic noise is of obvious importance in acoustic communica-tion, there have been few investigations of its effect on communication in any animal. Brenowitz (1982) found that the dominant frequency of the component of the red-winged blackbird song used in long-distance communication occurs in a frequency region of relatively quiet in the background noise. The lower frequencies in this noise are due to wind-generated sounds and the higher frequencies are from day active orthopterans. Ryan and Brenowitz (1985) showed that habitat-dependent differences in the emphasized frequencies in songs of Panamanian birds also could be explained by a quiet area in the background noise. This phenomenon has not been investigated in anurans, but such investigations might be especially fruitful in species calling in areas of high ambient noise, such as fast-moving streams (e.g., *S. sila*; Tuttle and Ryan, 1982).

B. Habitat Effects

Since the pioneering work of Morton (1975) and Chappius (1971), a num-ber of studies have suggested that bird song used in long-distance com-munication has evolved to reduce attenuation and degradation with dis-tance (e.g., Marten and Marler, 1977; Marten et al., 1977; Bowman, 1979, 1983; Gish and Morton, 1981; Lemon et al., 1981). Although there have been few studies addressing this problem in anurans, I review this topic here because of the potential importance of this selective force on the evolution of anuran advertisement calls.

A number of authors have reviewed this subject (Michelson, 1978; Gerhardt, 1983; Brenowitz, 1986; Wiley and Richard, 1978, 1982); the reader is referred to these papers and especially to the treatment by Wiley and Richards (1982) for a comprehensive review.

The central tenet of the environmental attenuation theory is that as sound travels through the environment the intensity and the fidelity of the sound decreases as a function of distance. Decrease in intensity is attenua-tion, and decrease in fidelity is degradation. The environmental attenua-tion hypothesis predicts that signals used in long-range communication should be structured to reduce these effects. First, I will address environ-

mental effects on spectral components, and then their effects on temporal components.

Pressure and intensity of sound decrease with increasing distance from the source. For an omnidirectional point source, sound radiates as a sphere. Sound pressure level decreases linearly with the distance from the source while intensity falls off with the square of the distance. On a decibel (dB) scale this results in both sound pressure level (dB SPL $= 20 \log (P1/P2)$) and sound intensity level (dB SIL $= 10 \log (I1/I2)$) decreasing at a rate of 6 dB per doubling of distance. Attenuation in excess of that due to spherical spreading is referred to as excess attenuation.

Excess attenuation is frequency dependent. Increased molecular interactions at higher frequencies lead to increased energy loss through heat dissipation. Thus excess attenuation is reduced by emphasizing lower frequencies. Physical obstructions, such as vegetation and atmospheric disturbances reflect, refract, and diffract wavelengths. All of these factors increase attenuation of the traveling sound. The amount of attenuation is dependent on the relationship between the size of the object and the wavelength of the sound. Given the size of interfering structures in the environment, high frequencies (short wavelengths) attenuate most rapidly.

Excess attenuation also can be habitat dependent; the most dramatic effect is the variation in calling sites due to the distance between the sound source and the ground. Destructive interference of sound waves occurs due to interaction of waves that reach the receiver by paths of different lengths. Those frequencies that are attenuated most depend on the height of the signaler. For example, at heights of 1–2 m, frequencies below 1 kHz are most drastically attenuated—the greater the height the lower are the frequencies of maximal attenuation (Brenowitz, 1986). Thus by calling at a sufficient height, the calling frog can avoid excess attenuation over considerable distances. This appears to be the case for *H. crucifer* in which excess attenuation is negligible (Brenowitz et al., 1984). Signaling on the ground is a special case—and clearly one that is important for a large number of frog species. Due to generation of ground and surface waves, frequencies below 1 kHz suffer greater excess attenuation. This effect leads to what Morton (1975) has called a frequency window—a frequency range (ca. 1.6–2.5 kHz) of low excess attenuation bordered by higher and lower frequencies with increased excess attenuation. Morton (1975) found that a frequency window near the ground occurred in forests but not in grassland or edge habitat. Marten and Marler (1977) and Marten et al. (1977) found that the frequency window existed in forest and open habitats. Morton (1975) suggested that birds singing near the ground in forest habitats match the emphasized frequency in their song to the frequency window. Ryan and Brenowitz (1985) reanalyzed Morton's data, taking into account the possible confounding factors of body size and phylogeny. They confirmed Morton's finding but indicated that ambient noise also might play an important role in the evolution of the emphasized frequency of the song of these birds.

The above discussion results in a clear prediction of how frog calls should be structured to reduce excess environmental attenuation. Frogs should call from elevated sites, and they should produce low-frequency calls. If they do call from the ground, they should emphasize frequencies in the frequency window. Surprisingly, this prediction has not been tested adequately. However, as will be discussed in Section IV, there are morphological and energetic constraints limiting the extent to which frogs can produce low-frequency calls.

There has only been one direct test of the theory of an environmental effect on call structure in anurans. *P. pustulosus* produces a call with two components, a "whine" and a "chuck" (Fig. 1). The whine is both sufficient and necessary for species recognition, while the chuck enhances the attractiveness of the call to females. I tested the hypothesis that relative to the chuck, the whine is structured to achieve greater transmission over distance by measuring attenuation of both artificially broadcast calls as well as the call produced by the frog. In both cases relative attenuation of the whine was less than that of the chuck (Fig. 2; Ryan, 1986a). Using only artificially broadcast calls this effect was present in a variety of habitats (Ryan, 1985b). The cause of differential attenuation of these call components is clear. The whine has more energy in low frequencies that attenuate less, while the energy in the chuck is concentrated in higher frequencies that are more susceptible to attenuation (Fig. 3).

For effective mate attraction the call not only must be of sufficient intensity when it reaches the receiver to be detected, it also must be discernible as the conspecific call. Habitat can differentially affect temporal aspects of the calls. Due to reflection of sound waves from structures in the environment, sound will reach the receiver over several paths of differing lengths, and this will result in reverberations that "smear" amplitude modulations in the signal. For example, the rapid trill rate of a small toad would be perceived as one continuous sound after being sufficiently smeared. The magnitude of reverberations increases with the number of paths the sound travels en route to the receiver, and the number of paths increases with the number of interfering structures in the environment. It is expected that degradation of amplitude modulations should be greater in forests than in open habitats. Furthermore, degradation will increase as the rate of amplitude modulation increases (Richards and Wiley, 1980; Wiley and Richards, 1982). Thus information coded by relatively fast call or pulse repetition rates should be more prone to degeneration in the forest than in open habitats.

Reverberations are almost completely absent in open habitats. However, signals in open habitats also are prone to degeneration of temporal cues, but of a different sort. Disturbance from wind is a more common phenomenon in open habitats than in more heavily forested ones (Ryan and Brenowitz, 1985). Turbulence introduces random amplitude fluctuations into a signal, and thus can mask low-frequency amplitude modulations
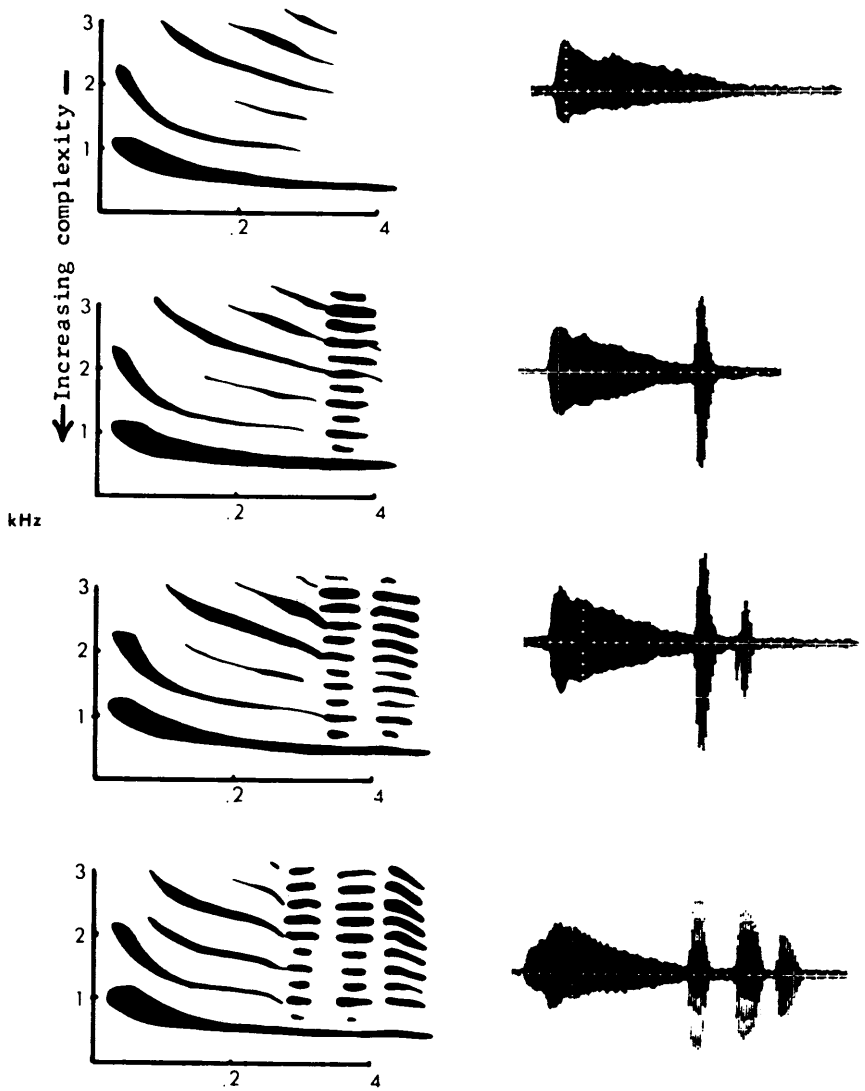
FIGURE 1. (Left) sonograms and (right) oscillograms of the call complexity series of *Physalaemus pustulosus*. Each call contains a whine with zero to four chucks (from top to bottom). (Left from Ryan, 1985b; right from Rand and Ryan, 1981.)
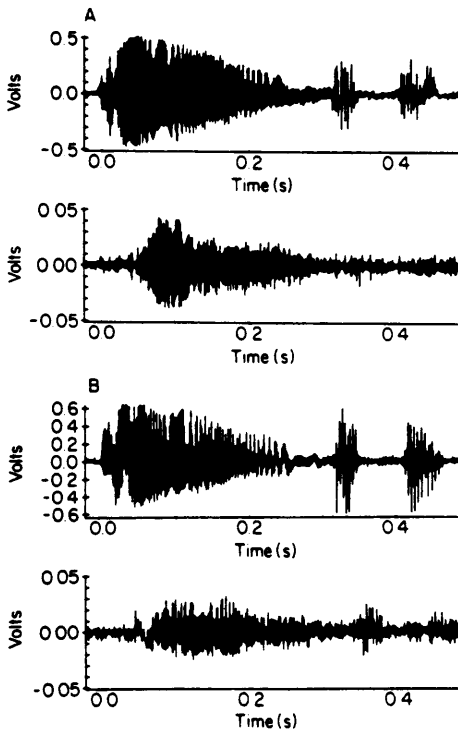
FIGURE 2. Oscillograms of a naturally (A) and artificially (B) broadcast call of *Physalaemus pustulosus* recorded over the same transmission line from 1 m (top of each pair) and 11 m (bottom of each pair) from the frog (A) and the speaker (B) (from Ryan, 1986a).

(<10–20 Hz; Wiley and Richards, 1982). These environmental effects lead to a prediction about optimal signal encoding in different habitats—low-frequency pulse rates should be more prevalent in forests and high-frequency pulse rates should be more prevalent in open habitats.

C. Temperature Effects

There is one other ecological factor that needs to be considered in discussing environmental effects on calls—temperature. First, I consider its effect on transmission, and then its effect on call production.

The speed of sound is dependent on the velocity and temperature of the air. Sound travels faster in warmer air, and if air temperature is stratified sound is refracted (Wiley and Richards, 1982). Most frogs call at night, and during the night the air near the ground cools faster than the air above the ground. Hence, air temperature tends to increase with distance above the ground, a condition referred to as a temperature inversion. The greater velocity of air at greater heights (warmer temperatures) will result in sound being refracted back towards the ground. In such circumstances, sound will attenuate less than expected to spherical spreading alone (i.e., negative excess attenuation). Although this phenomenon has not been docu-
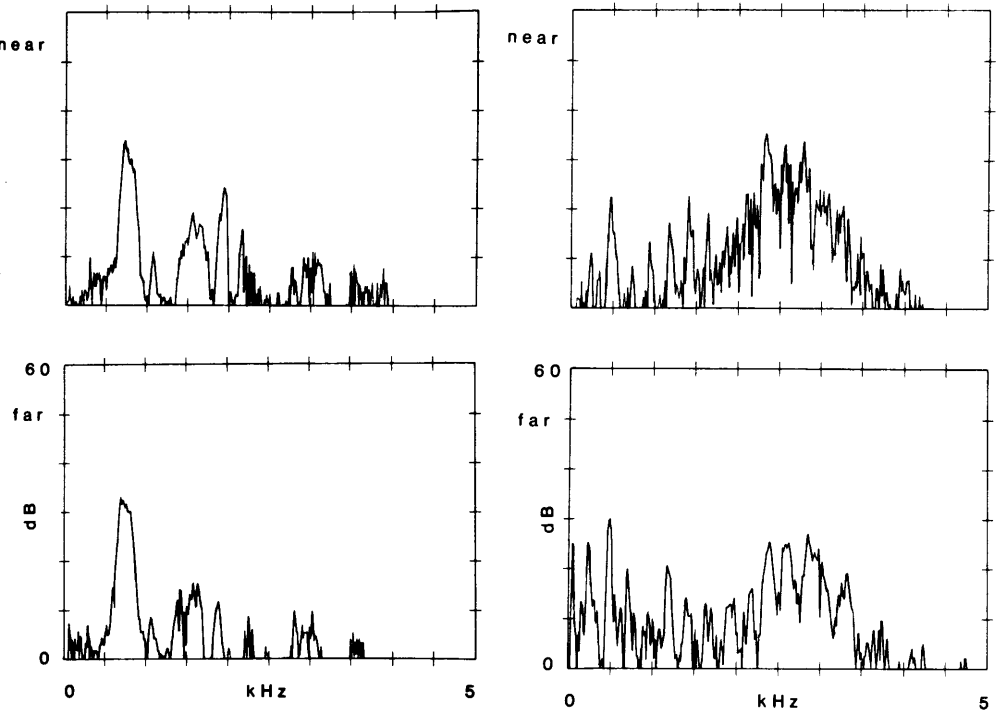
FIGURE 3. (Left) A power spectrum of the first 80 ms of the whine component of the advertisement call of *Physalaemus pustulosus* recorded at a near and far distance from a speaker broadcasting the call. (Right) A power spectrum of the chuck component of the advertisement call of *Physalaemus pustulosus* recorded at a near and far distance from a speaker broadcasting the call. (From Ryan, 1985b.)

mented in frogs, Waser and Waser (1977) have shown temperature effects on sound transmission in tropical forests in their studies of long-distance primate vocalizations. Monkeys vocalize at a time when temperature inversions enhance long-distance communication. A caution, however; although frogs may be calling at a time when excess attenuation is reduced due to temperature inversions, this obviously does not demonstrate an adaptation rather than a coincidence.

A very different effect of temperature on calls results from the general influence of temperature on behavioral performance of ectothermic vertebrates. Temperature can influence both spectral and temporal properties of calls, although the latter effect is more extreme and more general. Temperature can be especially important when it affects properties of calls used by females to discriminate among sympatric species. Gerhardt (1978, this volume) documented such an effect in the sibling species *H. versicolor* and *H. chrysoscelis*. Briefly, pulse repetition rate is important for discrimination between these two species; *H. chrysoscelis* has a faster repetition rate than

H. versicolor. Under certain conditions, a male *H. chrysoscelis* at a colder temperature can have a pulse repetition rate similar to that of *H. versicolor* at a warmer temperature. Gerhardt showed that female *H. versicolor* prefer the repetition rate produced by a conspecific male if the male's body temperature were the same as the female's. Thus temperature coupling of the signal production and signal reception mechanisms ensures conspecific mate recognition in the face of fluctuating temperatures. Dominant frequency of the call does not discriminate these sibling species. Gerhardt showed that although temperature affects the dominant frequency of the call, it does not affect the female's frequency preferences. However, in *B. variegata* and *B. bombina* the dominant frequency of the advertisement call and the best excitatory frequency of the amphibian papilla decrease concordantly with decreasing body temperature (Walkowiak, this volume).

IV. MORPHOLOGICAL EFFECTS

There may be a theoretical optimum to which an acoustic signal could evolve to minimize attenuation and degradation. However, the male frog must be capable of producing this sound effectively. Thus to understand the evolution of acoustic communication in frogs it is necessary to understand the limitations on call evolution imposed by mechanisms of vocal production. Because of the general advantage in using lower-frequency sounds for long-distance communication, it is especially important to understand how morphology might constrain the lower range of frequencies available to male frogs (see also Ryan, 1986b; Ryan, in press).

A. Determinants of Call Frequency

Schneider (this volume) provides a detailed review of how frogs produce calls. In general, air expelled from the lungs passes through the larynx where it vibrates the vocal cords and associated fibrous masses. In many species the frog possesses a vocal sac which is intricately involved in sound transmission.

The frequency of the call is determined to a large extent by the mass and tension of the vocal cords (Martin, 1972; Ryan, 1986b), and to a lesser extent by temperature (see above), and the pressure of the air as it enters the larynx (Martin, 1972). In general, the more massive the vocal cords the lower the frequency of the call. However, the frequency of the call can be actively modified by changing the tension of the vocal cords. This is accomplished by contracting or relaxing various muscles associated with the larynx. Usually, the muscles change the shape and the position of the arytenoid cartilages relative to the vocal cords (Martin, 1972), but in some species the muscles may insert directly onto the vocal cords (e.g., *Pelobates fuscus* Schmid, 1978; Schneider, this volume).

Vocal sacs characterize most calling frogs but appear to have little effect on call structure. Martin (1972) punctured the vocal sac of some *Bufo* and showed that call intensity was reduced greatly and the call was only slightly detuned. Capranica and Moffat (1983) showed that the dominant frequency of a male *H. crucifer* calling in helium was the same as the natural call. If the vocal sac were acting as a resonator as well as a radiator the call frequency should have increased. This is because a resonator will enhance certain wavelengths, depending on its size and shape. Since the speed of sound is three times greater in helium than in air, the frequency of the resonated wavelength should increase by threefold. Although the vocal sac fulfills the important function of coupling sound to the environment (Section IV.D), it does not seem to have an important effect on spectral call properties. However, it should be emphasized that anurans exhibit a variety of sizes and shapes of vocal sacs, and only a few species have been investigated.

B. Evolution of Call Frequency

Vocal cord mass increases with the size of the frog. Therefore, the most obvious mechanism for achieving a lower-frequency call is to evolve a larger body size. A correlated increase of body size and decrease in frequency complicates evolutionary interpretations of cause and effect—did body size increase because of the attendant advantages of lower frequencies, or is the lower frequency merely a consequence of an increase in body size that evolved in response to other selection forces, such as desiccation (e.g., Nevo, 1973)? In either case, an evolutionary change in the dominant frequency of the call can have important consequences whether or not this change is in response to selection. For example, Blair (1955) suggested that divergence in body size in two species of *Microhyla* (*M. carolenensis* and *M. olivacea*) in response to ecological selection is responsible for the divergence in the dominant frequency of the call and the subsequent premating isolating mechanisms evolving in these two species.

Call frequency can change independently of body size, and in these cases hypotheses of an evolutionary response to selection can be tested in a more satisfactory manner. Female *P. pustulosus* choose males and are more likely to mate with larger individuals. Females prefer calls with chucks, and all males add chucks to their calls in the presence of other calling males (Fig. 1). There is a negative correlation between the fundamental frequency of the chuck and a male's size. Phonotaxis experiments reveal a female preference for lower-frequency chucks. These data demonstrate sexual selection on the frequency of the male's call through the action of female choice (Ryan, 1980, 1983, 1985b). They do not demonstrate that the call actually evolved in response to sexual selection.

The hypothesis that sexual selection has influenced the evolution of the call predicts that call frequency in *P. pustulosus* should be lower for its body
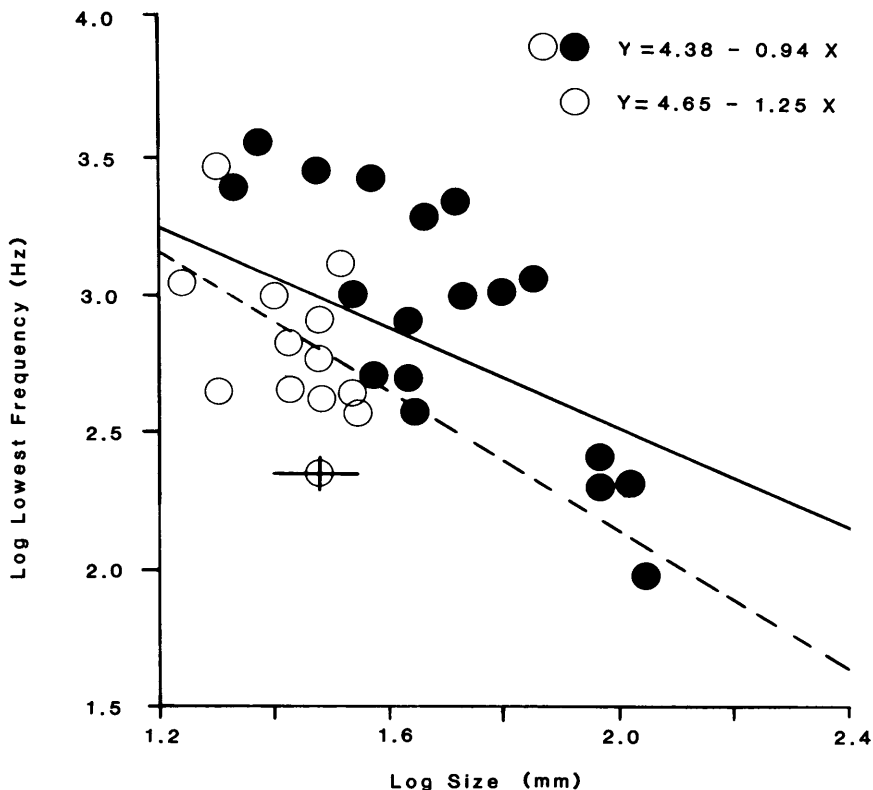
FIGURE 4.   The relationship between the logarithm of male size (log SVL) and the logarithm of the lowest frequency in the advertisement call (log Hz) for 30 species of the subfamily Leptodactylinae. Open circles represent members of the genus *Physalaemus* and closed circles represent other members of the subfamily. The solid line represents the regression of frequency on size obtained for all members of the subfamily, and the dashed line represents the regression for only members of *Physalaemus*. The circles intersected by the vertical and horizontal lines represent the midpoint and the ranges of size and frequency for *P. pustulosus*. (From Ryan, 1985b.)

size than that of other closely related species. This was tested by plotting the regression of frequency on body size for 30 members of the subfamily Leptodactylinae (Fig. 4). The selection hypothesis predicts that the call of *P. pustulosus* should fall below the regression line; that is, it should have a negative residual. Not only does *P. pustulosus* have a negative residual, it also has the lowest frequency for its body size (i.e., the largest negative residual), and its residual is actually disjunct from those of all other species (Fig. 5). Similar results are obtained if the comparison is restricted to 12 members of the genus *Physalaemus*. This comparison supports the hypothesis that in *P. pustulosus* call frequency evolved in response to sexual selection (Ryan, 1985b).
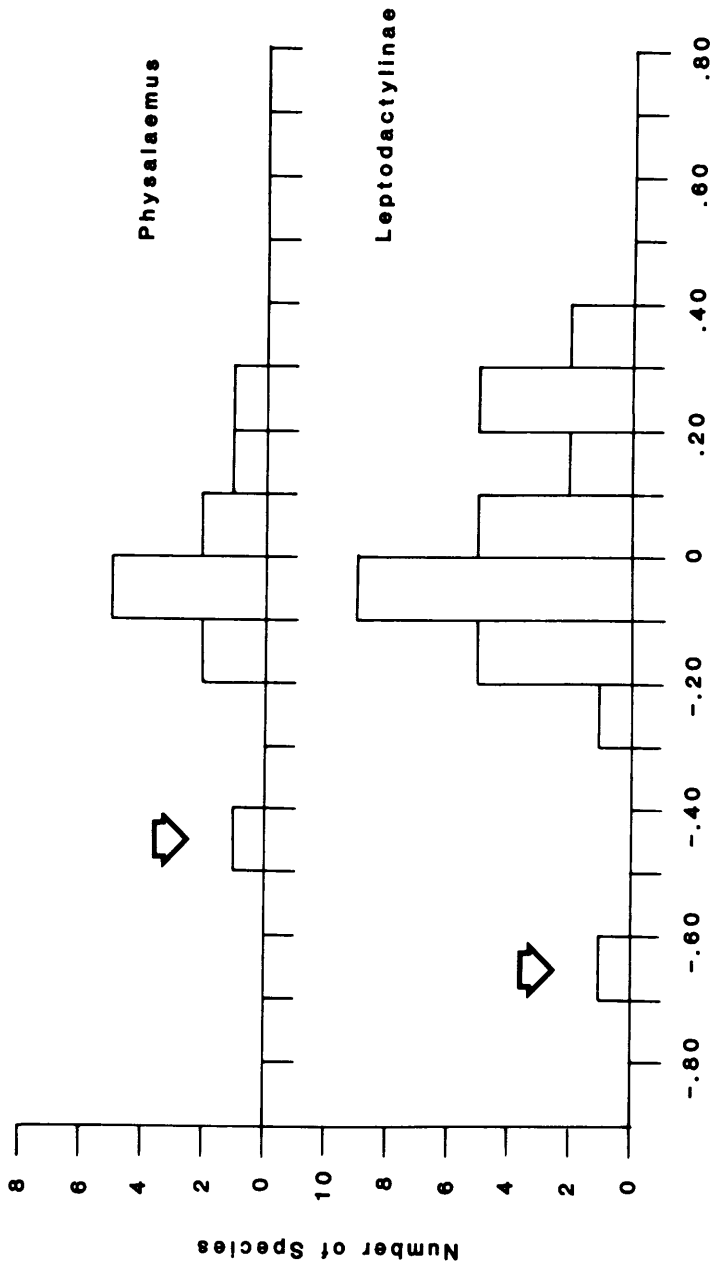
FIGURE 5. Frequency distribution of the magnitude and direction of the departure of the observed low frequency of the call from the expected based on the size-frequency relationships of the subfamily Leptodactylinae and the genus *Physalaemus*. The arrow indicates the departure exhibited by *P. pustulosus*. (From Ryan, 1985b.)

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C. Call Frequency and Call Coupling

There are lower limits to which call frequencies can evolve. As a correlated response to change in body size, the lower frequency limit is influenced by the maximum body size attainable by the frog. When call frequency evolves independently of body size, the size of the larynx is a theoretically limiting factor. Although larynx size as well as vocal cord mass can increase independently of body size, as evidenced by sexual size dimorphisms in the larynx (Trewavas, 1933), there presumably is an upper limit to the size of the larynx that can be accommodated.

There is a more subtle and perhaps more important morphological limit on the evolution of low frequencies. As discussed above, a frog can increase the intensity of its call at the receiver by both decreasing excess attenuation and increasing the intensity of the stimulus at the source. The source intensity will be influenced by the relationship between the wavelength of the sound and the size of the structures radiating the sound. As the wavelength increases relative to the size of the radiating structure, the efficiency with which the call is coupled to the environment decreases. Beranek (1954) shows that for a spherical radiator of radius r there is a cutoff frequency, above which coupling efficiency is at its maximum, and below which coupling is increasingly inefficient. The cutoff frequency (fc) is $fc = c/2 \pi r$, where c is the speed of sound. For example, the chuck in the call of *P. pustulosus* is harmonically structured with a fundamental frequency of 200 Hz. For the frog to couple this wavelength (1.65 m) with maximum efficiency the radiator would require a diameter of 26 cm. The frog's total length is only 3 cm.

The vocal sac clearly plays an important role in increasing coupling efficiencies. Again, *Physalaemus* can serve to illustrate this point. *P. pustulosus* has a very large vocal sac for its size (Fig. 6), as does its close relative *P. gracilis*. The latter species produces a call similar to the whine of *P. pustulosus*; the lowest frequency in its call is 450 Hz. *P. olfersi* produces a call that is more similar to the chuck of *P. pustulosus*, and its call has a fundamental frequency of 150–200 Hz. However, the lowest frequency that appears on a sonogram is 1500 Hz. Besides its higher-frequency call, *P. olfersi* is distinguished from *P. pustulosus* and *P. gracilis* by having a very small vocal sac. In this species, the vocal cords vibrate at low frequencies but the filtering effect of the small vocal sac results in only the higher frequencies being coupled to the environment (Drewry et al., 1982).

This review of morphological constraints on calling indicates that frogs have a restricted *Bauplan* available for evolutionary experimentation. There is a great deal of recent interest (e.g., Gould, 1977; Maynard Smith et al., 1985) in the role of constraints in evolution. Given the accessibility of morphological constraints on frog calls and the immense importance of the call in speciation and sexual selection, it is surprising that with the exception of Martin's (1972) studies of *Bufo*, there has not been another intensive
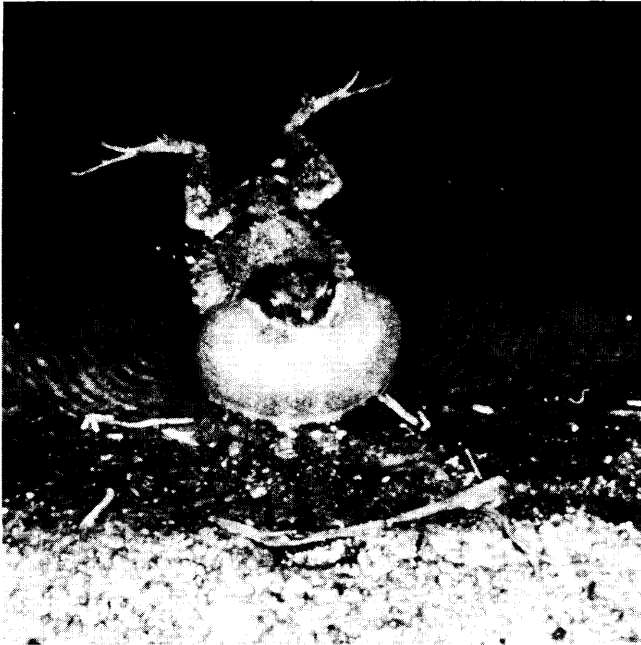
FIGURE 6.   A calling male *Physalaemus pustulosus*.

investigation of the vocal mechanics of a large group of closely related species.

V. PREDATION

As stated previously, effective mate attraction entails detection, discrimination, and localization. In anurans, perhaps more so than any other animal, there still is considerable debate as to how localization of sound is achieved (e.g., Eggermont, this volume; Rheinlander, this volume). In fact, given any two sounds it is not even possible to predict a priori which of those sounds will be easier for a female to localize. Although an efficient advertisement call should exhibit the virtue of easy localizability for the female, at this time it is not possible to predict the effect of this factor on the evolution of signal structure.

A number of animals besides frogs experience their environment through the acoustic sense. Some of these animals are predators, some of these predators eat frogs, and some of these frog-eaters locate frogs by orienting toward the frog's advertisement call. There is some evidence that predation may have influenced the evolution of frog calls in the same manner that predation is responsible for convergence in structure and

function in bird calls (Marler, 1955; Klump and Shalter, 1984). Again, *P. pustulosus* best illustrates this point.

As mentioned above, the whine component of the call is necessary and sufficient for species recognition. Males add chucks to their calls while competing for females, and females prefer calls with chucks. This leads to the question of why males do not always produce the call most attractive to the females (Rand and Ryan, 1981; Ryan et al., 1982). The benefit accrued by adding chucks is clear—thus there presumably is some cost involved. The cost is not energy. Although calling requires a surprisingly high rate of energy expenditure (see Section VI), this does not appreciate significantly when a male increases the number of chucks in the call (Bucher et al., 1982; Ryan et al., 1983). However, both the frog-eating bat (*Trachops cirrhosus*) and the philander opposum (*Philander opposum*) eat frogs, and they localize the frogs through the advertisement call (Fig. 7; Tuttle and Ryan, 1981; Tuttle et al., 1982). Like female *P. pustulosus*, the bats are attracted to the whine component only. And again like the female frogs, when given a choice the bats prefer calls with chucks (Ryan et al., 1982). These data clearly demonstrate the action of the opposing forces of natural selection and sexual selection operating through predation and female choice, respectively. The evolutionary response of *P. pustulosus* was not to evolve a fixed trait that compromised between these two opposing forces, as most genetic models of sexual selection have envisioned (e.g., Fisher, 1958; Lande, 1981; Kirkpatrick, 1982). Instead, these frogs evolved a flexible trait;


FIGURE 7.   A fringe-lipped bat, *Trachops cirrhosus*, capturing a *Physalaemus pustulosus* (photo by Merlin Tuttle).

a call of varying complexity that allows them to vary continuously their attraction to females and their risk to predators.

Bats might prefer calls with chucks because these calls are easier to localize (Ryan et al., 1982). Mammals seem to rely to a great extent on binaural cues for sound localization (e.g., Fuzessery, 1986). These cues can be based on differences in spectrum, intensity, time of arrival, or phase. Many of these differences are accentuated when the sound is short in duration, has a fast rise and fall time, and a rich frequency spectrum. There is an uncanny resemblance between the supposedly ventroloquial alarm calls of birds and the whine of *P. pustulosus*, on the one hand, and the localizable mobbing call of birds and the chuck of *P. pustulosus*, on the other hand (Fig. 8). Marler (1955) suggested that convergence in structure and function in bird calls might be due to predation. Thus predation might have similarly influenced signal structure in both bird calls and frog calls. However, it should be emphasized that studies of the frog-eating bat demonstrate preference for calls with chucks, and suggest this is because chucks are easier to localize. The greater localizability of this call component still needs to be demonstrated.

Another example of a predation effect on call structure comes from studies of the neotropical frog *S. sila* (Tuttle and Ryan, 1982). Males vary the number of notes in their call and, as in *P. pustulosus*, bats are attracted preferentially to multinote calls. Frogs are able to detect approaching bats on moonlit nights. Under both natural and artificial conditions, ambient light influences the number of notes in the call; fewer notes are produced when the frogs can not see the bats. Predation of frogs based on localizing advertisement calls probably is a general phenomenon, at least in the trop-
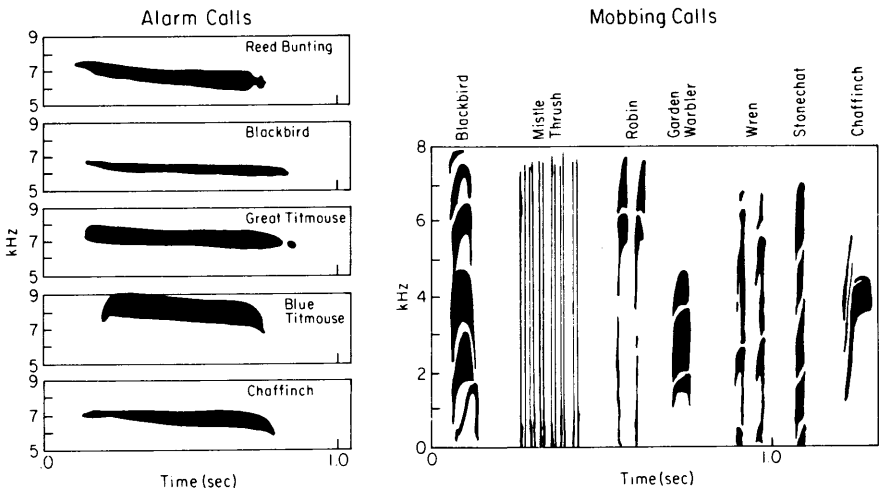
FIGURE 8.   Sonograms of avian alarm calls and mobbing calls. (From Marler and Hamilton, 1966.)

ics. Thus when a calling male enhances his attractiveness to females he does so at the risk of increasing his susceptibility to predation. Predation should have some influence on the structure of the call and the manner in which the call is used. A possible test of this prediction can come from species of frogs that are either poisonous or unpalatable to predators. These calls should have been able to evolve unencumbered by the constraints of predation. If predation has been an important evolutionary force on frog calls, then these species should be more likely to exhibit calls of greater localizability.

VI. ENERGETICS

There is no free lunch, and this is especially true for behavior (e.g., Bennett, 1980). The ability of an animal to marshal energy in support of behavior will have an important influence on the manner in which the behavior is exhibited. Our intuition does not serve us well in estimating the energetic costs of various behaviors, and a surprising result from studies of frog-calling energetics is the greatly elevated rates of oxygen consumption associated with this behavior (e.g., see discussion by Bennett, 1986). In *P. pustulosus* the rate of oxygen consumption is 450% above daytime resting levels (Bucher *et al.*, 1982), and in *H. versicolor* it is an incredible 2125% above resting (Taigen and Wells, 1985). Male *P. pustulosus* expend on average 11.8 joules per gram-hour (J/g-h) during calling, while *H. versicolor* expend energy at the rate of 32.5 J/g-h (Wells and Taigen, 1986).

Given the high cost of this behavior together with the inefficiency with which some frogs couple acoustic energy to the environment (Section IV.C), calling is perhaps one of the most energetically inefficient ventures these animals can undertake. Depending on the number of chucks present in the call of *P. pustulosus*, the energetic efficiency of calling ranged from 0.5–1.2% (Ryan, 1985a).

One characteristic of many species of frogs is that males spend a good deal of the night calling. Male *P. pustulosus*, for example, begin to call at approximately 1900 h and can continue calling past 0200 h the next morning, a time during which they might produce in excess of 7000 calls. Not surprisingly, this behavior appears to be supported primarily through aerobic metabolism (99% in *P. pustulosus*, Ryan et al., 1983); anaerobic metabolism eventually results in fatigue and can only be maintained for short periods of time. Ryan et al. (1983) and Taigen and Wells (1985) showed that there was no significant difference between lactate concentration of calling and resting males in *P. pustulosus* and *H. versicolor*, respectively. Pough and Gatten (1984), however, did show significantly higher lactate concentrations in calling male *H. crucifer*, although lactate may have been generated by movements associated with calling (Gatten, 1985). But even in the latter case, the actual contribution of anaerobically generated energy to support calling was minuscule (Gatten, 1985).

Given the high energetic cost of calling and the heavy reliance of males on aerobic metabolism, it is possible that the animal's metabolism might influence quantitative aspects of calling, such as the calling rate or the total number of calls produced during a night. At the species level, Bennett and Licht (1974) and Taigen et al. (1982) argue convincingly for a relationship between behavior and some measure of the animal's reliance on aerobically versus anaerobically generated energy used to support behavior. There are not enough data to allow a test of the hypothesis that physiology constrains calling behavior, although the prediction is clear. For closely related species with similar ecologies [especially modes of predator avoidance (Bennett and Licht, 1974) and foraging (Taigen et al., 1982)], species that devote more time to calling should have a greater ability to support behavior aerobically. This hypothesis was not supported at the populational level in *B. woodhousei*. In this species females prefer to mate with males that have high calling rates, for which there are consistent differences among males (Sullivan, 1983). Sullivan and Walsberg (1985) found no significant relationship between call rate and maximum aerobic capacity.

In many species of anurans laryngeal muscles exhibit sexual size dimorphism (Trewavas, 1933) suggesting a morphological adaptation for calling. Laryngeal muscles also appear to exhibit biochemical adaptations for maintenance of calling. In *H. arborea* they contain large mitochondria, and are rich in glycogen and lipids—all suggesting evolution in response to selection for increased performance of sustained behaviors (Eichelberg and Schneider, 1973, 1974). Taigen et al. (1985) examined trunk muscles involved in sound production in *H. crucifer*. They demonstrated biochemical differences between the sexes, and between trunk and limb muscles in males. Trunk muscles are larger in males than in females, who call infrequently; and, compared to limb muscles, trunk muscles exhibit a greater oxidative capacity and ability to oxidize fat.

Calling is perhaps the most important behavior in which a male frog engages. Given the high energetic costs associated with this behavior, the significant variation among species in their ability to support behavior aerobically (Bennett and Licht, 1974; Bucher et al., 1982; Taigen et al., 1982; Ryan, 1985a), and the ability to measure energetic costs of calling, it seems that this area offers promise for studies attempting to integrate behavior, physiology, and evolution.

VII. SENSORY CONSTRAINTS

Acoustic communication involves both a sender and a receiver. Evolutionary changes in the sender will only be incorporated into the population's genome if these changes can be perceived by the receiver. Thus the auditory system clearly can constrain the evolution of the advertisement call. There are very few data suggesting that this is actually so. Below I review some suggestions as to how the sensory system might constrain call evolu-

tion. Although most of these suggestions, in theory, can be tested, the data to do so are not as yet available.

A. Sensory Constraints on Call Structure

The frequencies to which the amphibian papilla (AP) are most sensitive (the best excitatory frequency; BEF) are lower than those frequencies for the basilar papilla (BP) (reviewed by Zakon and Wilczynski, this volume). Not only are the frequencies lower, but at least in small species, the neural thresholds also are often lower for the BEF of the AP than for the BP. Gerhardt (this volume) indicates that behavioral experiments also reflect this difference in absolute sensitivity between the AP and BP. Combined with the fact that low frequencies attenuate less in the environment, this might suggest reliance on the AP for more efficient communication over long distances.

The AP and BP are functionally quite distinct organs. The former has a membrane that supports a traveling wave and is tonotopically organized (reviewed by Lewis, this volume). Although it has not yet been demonstrated, this organ might endow frogs with pitch discrimination. The BP is a resonator whose hair cells are innervated by fibers that appear to be tuned to a single BEF. Frogs probably can discriminate frequencies in the range to which the BP is most sensitive only based on perceived loudness. Zakon and Wilczynski (this volume) have considered how the different mechanics of these two organs can influence call structure. Due to a lack of pitch discrimination by the BP information from frequency modulations (FM) can not be decoded, thus FM calls should be limited to lower frequencies. For species in which the frequencies of the advertisement call fall within the BEF range of the BP, temporal cues should be most important in mate recognition. Information coding in the BP should rely extensively on amplitude modulation (AM).

Temporal properties of the call are often critical for mate recognition, thus it is necessary to consider the ability of the auditory system to decode temporal cues, especially AM rates. There is much less understanding of temporal processing compared to spectral processing, and much of the current information is reviewed by Capranica et al. (1985). Eighth nerve fibers, regardless of their BEF, appear to be able to synchronize their firing AM rates from about 10–200 Hz. This encompasses most if not all of the variability of pulse repetition rates in anuran calls. These units in the periphery are not selective. However, there are a group of units in the torus semicircularis that are tuned to the AM rate that characterizes the species' advertisement call (Rose and Capranica, 1983, 1984). Relative to the topic of constraints, it would seem that the ability of the vocal system to modulate the amplitude of the advertisement call, either passively through the action of the arytenoid valves, or actively, through the control of the rate of lung contraction (see Schneider, this volume), could be more likely to limit the

available rates of AM rather than the ability of the auditory system to perceive those rates.

One must be cautious in attempts to evaluate sensory constraints on the evolution of call structures. Clearly, there are many more data documenting call variation than there are data documenting variation in the auditory system. This tempts one to evaluate call variability, and then to conclude how patterns of call variability might arise from constraints of the auditory system. This might be a successful endeavor if done cautiously; cautiously, because as Gerhardt (reviewed in this volume) has demonstrated extensively, not all of the measurable variation in calls is meaningful to females. As far as the auditory system is concerned some of it is noise, and our deciphering of the signal from the noise can be accomplished only with behavioral or physiological experimentation. I think broad interspecific comparisons will be very helpful in elucidating much about call evolution, but clearly these comparisons will send us back to the field and the laboratory to garner additional data.

B. Can Variation in Sensory Systems Influence Speciation Rates?

There is some suggestion that variation in the structure of the AP has limited the opportunity for call divergence and consequently the opportunity for speciation in different lineages of frogs.

Lewis (reviewed in this volume) showed significant variation in the morphology of the AP. This variation can be classified into four types, differing in the degree of caudal extension (or complexity, longer being more complex) of the papilla. This morphological variation has a functional counterpart—the degree of caudal extension of the papilla seems to influence the frequency range to which the animal is most sensitive. I suggested that this morphological and functional variation should influence the probability of a random mutation in a call's frequency falling within the range to which a female is sensitive (Ryan, 1986b). If this is so, then divergence of advertisement calls should be more likely in those frogs with a greater range of frequency sensitivity. Since divergence of advertisement calls is a crucial component of the speciation process, the opportunity for speciation should increase with the extension of the AP. I tested this hypothesis by comparing the number of species in each group of frogs characterized by different types of AP. As predicted, the number of species increases with the complexity of the AP. This prediction holds when an estimate of extinctions, as well as number of species, is analyzed (Table 1).

The extension of the amphibian papilla might have additional influences on call evolution. The species characterized by the most simple AP might not be able to efficiently produce frequencies low enough to stimulate this organ. These animals should confine the frequencies of their calls to that range to which the BP is most sensitive.

Acoustic communication is a two-component process involving a signal-

TABLE 1. The Call Character, the Number Representing That Call Character on the Cladogram in Figure 9, the Means by Which Evolutionary Change in the Character is Regulated, and the Unit Character Consistency (UCC) for Each Call Character for Species in the Genus *Kassina*

Character	No.	Regulator	UCC
Call complexity	1	Behavioral physiological	0.40
Amplitude modulation	2	Behavioral physiological	0.60
Dominant Hz	3	Morphological	1.00

ler and a receiver. Understanding the evolution of anuran advertisement calls is perplexing enough when addressing those factors that might directly affect the call: mate recognition, sexual selection, predation, habitat, and morphology. However, because the advertisement call is crucial in assuring a male's reproductive success, it is influenced by social interactions: male competition and, especially, female choice. Because the call must be perceived, call evolution is also influenced by the auditory system. For those interested in behavioral evolution, it is naive to suppose that we can understand how calls might evolve without considerable knowledge of the interaction of the sensory system and the behavior. This observation should not be daunting; the sensory and behavioral interactions enrich studies of behavioral evolution in the anuran acoustic system significantly beyond that available in many other systems of communication (see also Wilczynski and Ryan, this volume).

VIII. COEVOLUTION

Signalers and receivers comprise acoustic communication systems. These components exhibit congruence within a species; congruence that is maintained throughout evolutionary time by coevolution. How these two systems coevolve is sometimes simple, but in many cases hardly understood. I will review suggestions of how communication systems coevolve.

A. Specific Models for Generation of Genetic Covariance

1. Pleiotropy

a. Allometry. An understanding of the coevolution of communication systems requires elucidation of mechanisms responsible for genetic correlations between signal production and perception. Pleiotropy, multiple phenotypic effects of one gene, could simplify coevolution of communication systems (Alexander, 1962). One possibility is pleiotropic effects of genes that influence body size. Phenotypic correlations are common among traits that show allometric relationships to body size (Huxley,

1932). Such allometries appear to explain coevolution of some communication systems in anurans.

The BEF of the BP appears to be determined by its size; the larger the BP the lower its BEF (Zakon and Wilczynski, this volume). As discussed above (Section IV.A), the dominant frequency of the advertisement call also correlates negatively with body size. If the dominant frequency of the advertisement call contributes significantly to mate recognition, and this frequency is best perceived by the BP, then a change in the species' body size will simultaneously change both the call and the BEF of the BP; in spite of evolutionary change the system will tend to maintain congruence.

This scenario probably applies to Blair's (1955) suggestion that divergence in body size has led to divergence in the dominant frequency of the advertisement calls in *Microhyla carolinensis* and *M. olivacea*. He suggested that these call differences are responsible, in part, for speciation. However, not only must the calls diverge for speciation, this evolutionary change must be perceived by the females' auditory system. Because the dominant frequency of the calls falls into that range best detected by the BP, body size divergence between the two species (in both sexes) probably also results in divergence of auditory systems. The simultaneous changes in these two separately evolving systems, call and BP, are not random with respect to one another; they remain congruent due to their similar relationships to body size. This phenomenon probably also explains auditory coding for populational call differences in *Acris crepitans* (Capranica et al., 1973; Nevo and Capranica, 1985) and *B. viridis* (Nevo and Schneider, 1976; Walkowiak et al., 1981).

The potential role of allometry in the evolution of communication systems is also highlighted by the study of Wilczynski et al. of *H. crucifer* (1984; see also Brenowitz et al., 1984); their data suggest that these effects may, in some sense, actually disrupt this communication system. *H. crucifer* produces a narrowly tuned call (dominant frequency of ca. 2.9 kHz) that falls within the frequency range best detected by the BP. This species exhibits sexual size dimorphism; females are larger. If the BEF of the BP is determined by the size of the BP, which itself is correlated with body size, then the frequency of the call can not coincide with the BEF of both sexes; one will be somewhat mismatched. Although sexual dimorphism in the BEF–body size allometry could result in the BEF of both sexes matching the call's dominant frequency (i.e., males have relatively larger, or females relatively smaller BPs), this appears not to be the case. Males and females fall along the same line when BEF is plotted against body size (Wilczynski, personal communication).

Calls match the BEF of females, males are mismatched. There are evolutionary hypotheses that predict this outcome, but a more interesting question addresses the dynamics of coevolution. For example, consider a species initially monomorphic in size which then evolves sexual size dimorphism. The relationship between call and tuning in *H. crucifer* (i.e., that

the call only matches females' BEF) could have evolved by one or both of the following: (1) the call frequency–body size allometry could remain stable, and a change in the BEF–body size allometry could change, bringing the female "into tune" with the call but resulting in a mismatch between the male's call and his BEF; (2) the BEF–size relationship could remain stable and the call–size allometry change. This question is important because, if answered conclusively, it would suggest if one component of the auditory system is a constraining or a driving feature in the coevolutionary process.

b. Central Pattern Generator. Coevolutionary changes in many communication systems, such as those involving temporal cues, are not as simple to explain as the apparently similar pleiotropic effects, due to body size allometry, on call frequency and frequency tuning of the auditory system. Another possible role of pleiotropy is Hoy's (1978) hypothesis of a central pattern generator. Briefly, he suggested that there are neurons or neural elements that determine both the generation of temporal patterns of the signals and the recognition of these temporal patterns (the latter through a corollary discharge that would act as a temporal filter or a template). Doherty and Gerhardt (1983, 1984) suggested evidence for this phenomenon in treefrogs.

In a review of this topic, Doherty and Hoy (1985) suggested that there are two competing hypotheses: genetic correlation and "coevolution" (two separately evolving systems), and that they make different predictions. The former predicts hybrid preference for hybrid signals, while the "coevolution" hypothesis makes no such prediction. The authors suggest that the central pattern generator hypothesis is supported by results showing that hybrids of two treefrogs, *Hyla chrysoscelis* and *H. femoralis*, preferred the hybrid call to the call of *H. chrysoscelis*. However, the problem in accepting these results as demonstrative of genetic coupling is emphasized by Doherty and Hoy (1985; see also Doherty and Gerhardt, 1983, 1984). If call traits and recognition traits are determined by a locus or loci with additive gene action then hybrids would be expected to show traits intermediate in both respects, predicting exactly the results obtained with the treefrogs and also with crickets (Hoy et al., 1977). These results seem to have little bearing on the role of pleiotropy, in general, and the central pattern generator, in particular, in the coevolution of communication systems.

Other evidence suggested in support of the central pattern generator theory is temperature coupling of the signal and receiver systems (see Section III.C). Certainly, if there were the same neural elements controlling generation and recognition of temporal patterns, temperature coupling would be expected. However, again as the researchers themselves indicate (e.g., Doherty and Hoy, 1985), many physiological systems could exhibit the same response to temperature. These data too do not offer strong

support for the central pattern generator theory. As Doherty and Hoy (1985) emphasize, this theory can only be evaluated critically with detailed analyses of the genetic bases of signals and receivers. This is not an easy task, and perhaps this is one area in which the anuran auditory system does not offer promise for major contributions to our understanding of the evolution of acoustic communication systems.

2. Linkage Disequilibrium

Phenotypic correlations can result from pleiotropic effects, as discussed above, or they can result from linkage disequilibrium between two systems under different genetic control. For example, suppose that both sexes possess genes for signal production and recognition (the appropriate genes are expressed only in the appropriate sex) and there is genetic variation in both systems. Matings will result in offspring that have a combination of alleles for both the recognition and the generation of the same pattern. The degree to which this association, or covariance, of these pairs of alleles depart from random is the linkage disequilibrium. Fisher (1958) used this phenomenon to explain the evolution of female choice under runaway sexual selection. Once there is genetic covariance between trait and preference, then the female preference will evolve as a correlated response to selection on the male trait—selection in this case is exerted by the females themselves (appropriately termed "self-reinforcing choice" by Maynard Smith, 1978). Lande (1981) and Kirkpatrick (1982) have formalized Fisher's theory in mathematical models offering strong theoretical support for Fisher's intuition.

These models of coevolution of male traits and female preference under sexual selection are basically special cases of coevolution of communication, and might offer a framework for general models in this area. Especially interesting is Lande's (1982) model of how divergence of courtship signals and courtship preferences can lead to the rapid origin of reproductive isolation in a species with a continuous geographic range.

The possible role of linkage disequilibrium, to my knowledge, has not been applied explicitly to the problem of coevolution of communication systems outside of the context of sexual selection. If linkage disequilibrium was responsible for generating genetic covariance in communication systems, not only would female preferences (receptors) exhibit a correlated response to male signals, but the converse also would be true. Although the models might be straightforward, their validity ultimately would need to be evaluated by data on phenotypic variance in the trait and the preference. Although there is a plethora of data for the former, data are almost totally lacking for the latter. The problem of eventually demonstrating heritable variation for the phenotypic variation could be a daunting task.

Each topic I reviewed up to this point suggests that anurans are an ideal system for integrative studies of the evolution of acoustic communication

systems (see also Wilczynski and Ryan, this volume). However, an actual understanding of how these systems might coevolve, except in the most simple cases (allometric responses to change in body size), is almost nonexistent. Unfortunately, an understanding of the genetic mechanisms giving rise to variation in call production and recognition is the key to answering this problem. Due to problems imposed by generation times and raising frogs to sexual maturity, we can expect few contributions in this area of the genetic basis of signals and receivers, and these will lag behind those data already available from organisms better suited for such studies, such as *Drosophila* (e.g., MacDonald and Crossley, 1982) and ladybirds (O'Donald and Majerus, 1985).

B. Is a Special Explanation Needed?

There is one additional caveat. The coevolution of communication systems is only a special case of coevolution in general. Usually coevolution refers not only to separately evolving systems, but to genetic systems present in different species, such as in plant–pollinator, predator–prey, and host–parasite systems. Obviously, pleiotropy and linkage disequilibrium can not be responsible for coevolution in these systems. Special explanations have been sought for the coevolution of communication systems because these systems only function if they maintain congruence during evolution. But perhaps the coevolution of communication systems is not a special problem requiring special explanations. It might be helpful to ask to what extent communication systems might evolve in concert if the signal and receiver were not influenced by pleiotropy or linkage disequilibrium. One only needs to reflect on "the various contrivances by which orchids are fertilised by insects" (Darwin, 1877) to realize the power of selection in maintaining congruence between separately evolving systems.

IX. INVESTIGATING PATTERNS OF CALL EVOLUTION

A. The Problem

A problem in studying evolution, as opposed to functional morphology, physiology, or behavior, is that usually the researcher is not able to witness the process. It is a fact that evolution occurs; the process by which it occurs is the subject concerning evolutionary biologists.

Although we can not witness the process, we do have a record, albeit incomplete, of the outcome of the process of evolution—the current distribution of closely related species together with the characters that define those species. The task of systematists is to unravel the sequence by which related species evolve, and to propose of phylogeny. These phylogenies—hypotheses of species origination—often are graphically depicted as a dendogram or a cladogram.

Most behaviorists and physiologists have little interest in systematics outside of having a name to call the species they study and, sometimes, knowing a closely related species to which to compare results. Part of this aversion is because of the interminable jargon that must first be mastered to understand the various schools of phylogenetics, especially in cladistics; and because phylogenetics is one of the most controversial fields in evolutionary biology, often, if not usually, characterized by vitriolic debate. Most nonsystematists prefer to avoid these controversies.

Nevertheless, the need for applying phylogenetics to any field concerned with evolutionary biology has been argued strenuously by a number of authors, and those arguments need not be detailed here (e.g., Clutton-Brock and Harvey, 1977; Vrba, 1980, 1983; Ridley, 1983; Wanntorp, 1983; Northcutt, 1984; Felsenstein, 1985). A general problem is the identification of evolutionarily independent events in testing theories of adaptation. For example, in asking if a morphological trait has evolved due to selection exerted by a certain habitat, one will attempt to correlate the presence of that trait with habitat. But what taxonomic level should be used for analysis—species, genera, or families? Species are the usual currency, but if all species of a genus share a trait because it is inherited from a common ancestor, these species can not be considered independent samples in testing this hypothesis of adaptation. A phylogeny is needed to distinguish between the hypothesis that a trait is exhibited by different taxa due to multiple, independent evolution of the trait as opposed to inheritance of the trait from a common ancestor.

Although it has been less appreciated (but see Ryan, 1986b), there is another important application of phylogenetics. A "true" phylogeny of a group of species might lend important insights into patterns of evolution of traits. In some cases it might even allow us to elucidate why those patterns arose. But clearly, a description of the patterns is the initial step. I suggest a method for attempting to understand patterns of evolution of characters that comprise frog calls. I then illustrate one approach for two groups of frogs with admittedly very small sets of data. However, even such a limited analysis reveals some interesting suggestions.

B. A Method and Example

There are several schools of thought in the field of phylogenetics. I apply the cladistic approach as advocated by Hennig (1966). I am not suggesting that this approach is superior in all instances to all other approaches, but a starting point.

A cladogram is a hypothesis of patterns of divergence. Briefly, this method consists of using shared, derived characters to construct a network depicting phylogenetic relationships among taxa. Cladistics employs the method of parsimony; that is, the preferred network minimizes the number of evolutionary changes of homologous characters needed to describe

the pattern of divergence (see Wiley, 1981, for perhaps the most coherent description of this controversial field). It must be emphasized that a cladogram is not offered as a true phylogeny, but instead it is a hypothesis that should be continually tested with new data as they become available. Nevertheless, for investigating patterns of evolution, a cladogram can be accepted as the best representation of the phylogeny with the caveat that it is a hypothesis and that any conclusions about patterns of character evolution would need to be reevaluated as hypotheses of phylogenetic relationships are modified.

Fortunately for those interested in the evolution of anuran advertisement calls, call characters rarely are used to delimit relationships among species. Their main use in frog systematics is to identify frogs as conspecific or heterospecific. Therefore, the cladograms and the patterns of species divergence they represent are not constructed with the traits of interest.

Given certain assumptions, patterns of species divergence represented by cladograms, we can deduce something about how calls evolve. For example, suppose a cladogram suggests that species A and B are more closely related to one another than to other species (i.e., they are sister species). If A has a call repetition rate of 10/s and B a rate of 100/s, then there must have been considerable evolution of the call rate from the time they diverged from a common ancestor. If they both have the same dominant frequency, then there is likely to have been no evolution of call frequency. If this pattern were repeated frequently it would suggest mosaic evolution of frog calls, and that call rate is a less conservative trait than is frequency. It might then lead us to ask why this is so.

The degree of conservation of a trait can be quantified for a larger number of species. First, the variation in the trait is classified into different character states. These character states are then superimposed on a cladogram that depicts the hypothesized relationships of the species studied. This is referred to as the character state distribution. The minimum number of evolutionary changes needed to explain that particular character state distribution is determined, and this is compared to the theoretical minimum for that set of characters. The theoretical minimum number of evolutionary changes needed is one less than the number of character states. For example, if there are two character states there had to be at least one evolutionary change. The number of hypothesized evolutionary changes will depend on the character state distribution. If this distribution of characters on the cladogram is explained with the theoretical minimum number of changes, then the character state distribution and the cladogram are perfectly consistent. A measure of this consistency is called the unit character consistency (UCC) and is simply the range of the character (the number of character states minus 1) divided by the number of evolutionary changes needed to describe that particular character state distribution. Perfect consistency of a character with a cladogram yields a UCC of 1. A

comparison of the UCCs for various call characters allows an evaluation of how evolutionarily conservative a trait might be, and comparisons across various groups of anurans allow an evaluation of the generality versus the taxon-specificity of such trends.

I analyzed patterns of frog call evolution for two genera of frogs: *Smilisca* (family Hylidae) and *Kassina* (family Hyperoliidae). The cladogram and descriptions of the calls for *Smilisca* are from Duellman and Trueb (1966), the cladogram for *Kassina* is from Drewes (1985), and call data are from Tandy and Drewes (1985). Because the call analysis is drawn from the literature, the characters available for each group are not identical. For each genus the character, its code (e.g., 1 refers to call complexity in *Kassina*, and 1, 1', and 1'' represent different states of character 1), and its UCC are listed in Tables 1 and 2. The cladogram with the superimposed call characters are represented in Figures 9 and 10, and the characters states for each species are denoted in parentheses next to the species. Also shown on the cladogram are the positions of the hypothesized evolutionary changes for each character state. The hypothesized changes are parsimonious; that is, they invoke the fewest number of changes in the character needed to explain the character state distribution. There are other hypotheses of where the changes occurred on the cladogram which are equally as parsimonious. For this approach, this is not important since we are interested in the number of evolutionary changes per character rather than precisely where they occur on the cladogram.

There are some interesting findings. First, some call characters exhibit very high consistencies with the cladogram, while other characters are poor predictors of hypothesized species relationships. Thus if anuran systematists relied extensively on frog calls to test their hypotheses of phylogenetic relationships, my analysis suggests they might get mixed results: some supportive, some contradictory. Mosaic evolution characterizes calls in these two genera; some characters remain stable over evolutionary time while others change. Also, there is some pattern as to which characters are more likely to evolve. All of the characters analyzed are under either active or passive control. Evolutionary changes in those characters under active

TABLE 2. The Call Character, the Number Representing That Call Character on the Cladogram in Figure 10, the Means by Which Evolutionary Change in the Character is Regulated, and the Unit Character Consistency (UCC) for Each Call Character for Species in the Genus *Smilisca*

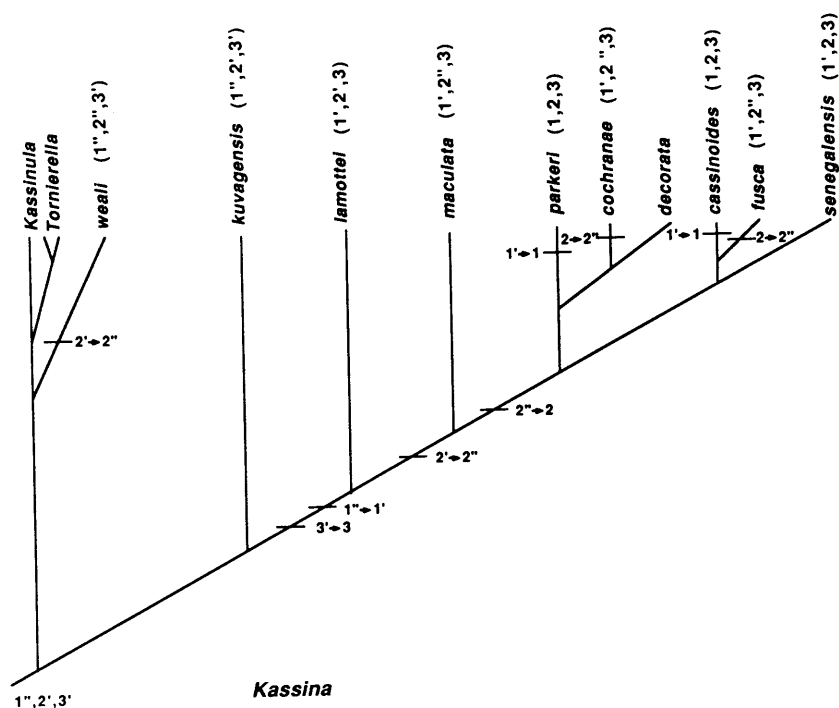| Character	No.	Regulator	UCC
Pulses/s	1	Behavioral physiological	0.50
Call duration	2	Behavioral physiological	0.33
Notes/call	3	Behavioral physiological	1.00
Dominant Hz/body size	4	Morphological	1.00
Dominant Hz	5	Morphological	0.50

FIGURE 9. A cladogram depicting hypothesized relationships among species in the genus *Kassina*. The numbers in parentheses adjacent to each species represents the characters defining that species, the characters defined by each number are given in Table 1. The horizontal lines represent proposed character state changes.

control, usually temporal characters, result from changes at the level of behavior and physiology—such characters as call rate, the number of notes in the call, and the presence or absence of amplitude modulation (see Schneider, this volume). Spectral characters, on the other hand, usually are determined by vocal morphology. Interestingly, in this limited data set those characters regulated by behavior and physiology are much less conservative than are those characters that would require morphological modification for evolutionary change. This seems to support a general, although not universally shared (e.g., see Geist, 1986) impression that behavior is much more evolutionarily flexible than is morphology.

It is not clear why behaviorally and physiologically regulated characters are more likely to evolve than morphologically regulated characters. It might indicate something about the likelihood of an evolutionary change in behavior and physiology compared to that in morphology. However, it also could indicate something about the likelihood of congruent changes in the auditory system which would track changes in the call, because, as discussed in Section VIII, modifications in the signal will only persist in evolutionary time if they are matched by modification in the receiver. For
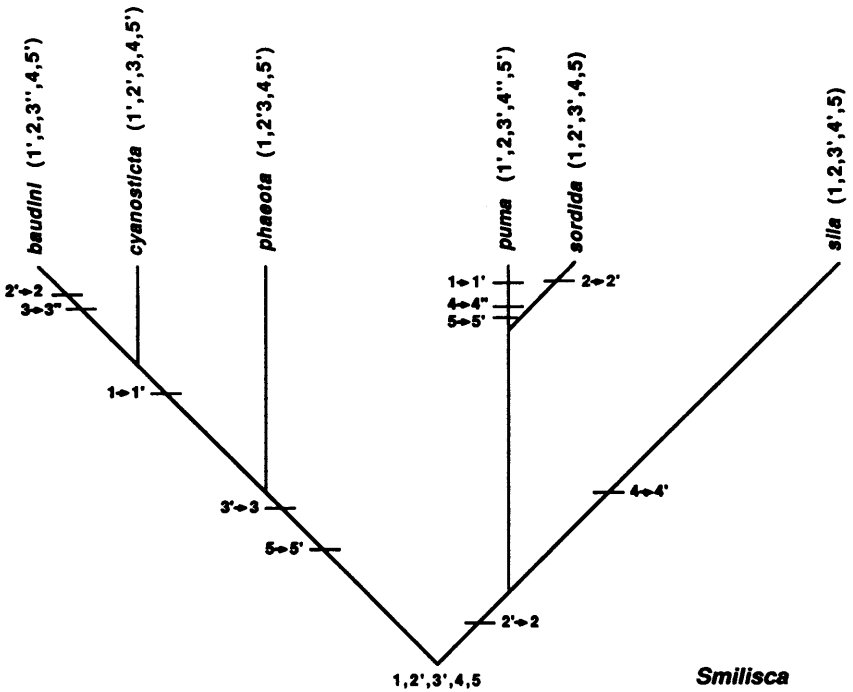
FIGURE 10. A cladogram depicting hypothesized relationships among species in the genus *Smilisca*. The numbers in parentheses adjacent to each species represents the characters defining that species, the characters defined by each number are given in Table 2. The horizontal lines represent proposed character state changes.

example, species in the genus *Kassina* have FM calls with dominant frequencies that probably are concentrated either in the BEF range of both the AP and BP (character state 3) or restricted to the AP only (character state 3'). Thus the change in character states of the call could involve a major alteration in how the female perceives the call—using one inner ear organ or two.

As I indicated earlier, few generalizations can be drawn from such a limited data set. However, it seems that even the tentative results from this analysis are tantalizing enough to suggest further examination of phylogenetic patterns of frog call evolution.

X. SUMMARY

The auditory system of anurans is intricately involved in acoustic communication, and thus to understand its evolution it is necessary to understand the evolution of the communication system as a whole. The adver-

tisement call is the most conspicuous and the most significant signal in the communication system, as it serves to identify conspecific males to females and to regulate social interactions among males. Thus species recognition and sexual selection are important selective forces in the evolution of the call.

The advertisement call is under a variety of constraints and counter-selective forces that can prohibit the call from evolving to an optimum dictated only by species recognition and sexual selection. A variety of studies show that sexual selection favors those males that produce signals that are more intense when they reach the female. Low frequencies transmit through the environment with less attenuation than high frequencies, thus calls concentrating energy in these frequencies should be more intense when they reach the female. The frequency of the call can be decreased either by increasing body size, and thus the mass of the vocal cords, or by independently loading the vocal cords with fibrous masses. However, the animal's morphology sets a lower limit to the frequencies that can be effectively coupled to the environment due to the inverse relationship between long wavelengths (low frequencies) and coupling efficiencies imposed by small (relative to the wavelength) radiating structures, such as those possessed by frogs. A further consequence of small radiating structures is that the energetic efficiency of calling is very low in the one species of frog in which it has been measured.

Male frogs do not communicate their presence to females in a private communication channel, and the presence of acoustically foraging predators can also influence the evolution of the advertisement call. In *P. pustulosus*, males can actively add chucks to the introductory whine component of the advertisement call. Females prefer whines with chucks to whines without chucks. The fringe-lipped bat, *T. cirrhosus*, eats frogs and uses the frog's call for localization cues. Like the female frogs, the bats also are attracted preferentially to calls with chucks. This suggests that the variable complexity of the *P. pustulosus* call evolved as a compromise to sexual selection and natural selection exerted by females and bats, respectively.

For a call to evolve it must be perceived by the female. It is possible that the auditory system limits those call mutations that can be incorporated into the genome. The frequency range to which the AP is sensitive varies among families, and it is suggested that this variation influences the degree to which call frequencies can evolve; because the call is an important species-isolating mechanism, it also influences the opportunity for speciation. The available data support this hypothesis.

The communication system consists of two components—the signaler and the receiver. These systems must change in concert to remain effective. These systems exhibit phenotypic covariance, and there have been several suggestions as to how the underlying genetic covariance responsible for coevolution is generated. In some species this is due to similar

allometric relationships between body size and vocal production and perception. As body size increases the dominant frequency of the call and the BEF of the BP decrease. Another model of pleiotropy, the central pattern generator, suggests that common neural elements control the signal and perception of the signal. However, data supporting this hypothesis can not distinguish between the central pattern generator model and the alternative hypothesis of separate systems involving loci with additive effects. Two other hypotheses are discussed. Linkage disequilibrium, as put forth by Fisher, is thought to explain the phenomenon of runaway sexual selection. In essence, this phenomenon is only a special case of the coevolution of communication, and I suggest that the more general case be modeled. I also suggest that special explanations might not be needed, and that communication systems do not offer special problems relative to other coevolving systems, such as host-parasite or plant–pollinator systems.

Although the evolution of anuran advertisement calls has received considerable attention over the last three decades, scant attention has been given to the patterns by which these calls evolve. I discussed why this should be a significant problem in evolutionary biology, and proposes a method and an example of the method for examining this problem. The tentative results suggest that calls evolve in a mosaic fashion, and that call components under behavioral physiological control are less evolutionarily conservative than are those components under morphological control.

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