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## The Behavioral Ecology of Anuran Communication

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### 1. Introduction

As the last rays of sunlight disappear from the evening sky, a shallow marsh in Panama begins to come alive with the calls of frogs and toads. Among these is a small yellow and brown hourglass treefrog, *Hyla ebraccata* (Fig. 3.1C). First, a single male begins giving a tentative series of single-note, buzzlike advertisement calls. Soon other males join the first one, and a chorus begins to develop. The first male responds to the calls of his neighbors by placing his own calls immediately after their calls, and he soon increases his calling rate and begins to add clicklike secondary notes to his calls in an attempt to outsignal his rivals. Suddenly another male calls only a few centimeters away, and the first male responds by modifying the introductory notes of his calls, producing aggressive notes with a pulse repetition rate about three times that of his advertisement calls. As the two males approach each other, they gradually increase the duration of their aggressive calls and eventually stop giving secondary click notes as a short wrestling bout ensues. After a few seconds, the intruding male withdraws, and the first male returns to advertisement calling.

Having sorted out spacing within the chorus, most of the males soon settle into a regular rhythm of advertisement calling, punctuated by occasional aggressive calls. Periodically they stop calling as their calls are overpowered by bursts of calling from groups of males of another frog, the small-headed treefrog (*Hyla microcephala*) (Fig. 3.1D). The males of *H. ebraccata* have difficulty making their calls audible when surrounded by the other species, and they attempt to place their calls in the silent periods between bursts of *H. microcephala* calling activity. After two hours of calling, the first male detects the movement of a noncalling frog nearby. Sensing that a female may be approaching, he immediately switches to a rapid series of repeated introductory advertisement call notes. The female turns toward the male, and with a few zigzag hops, approaches his calling site and allows him to clasp her in amplexus. The pair then moves off to find a suitable leaf on which to lay their eggs, positioned a half meter or so above the shallow water where the tadpoles will complete their development. After mating,

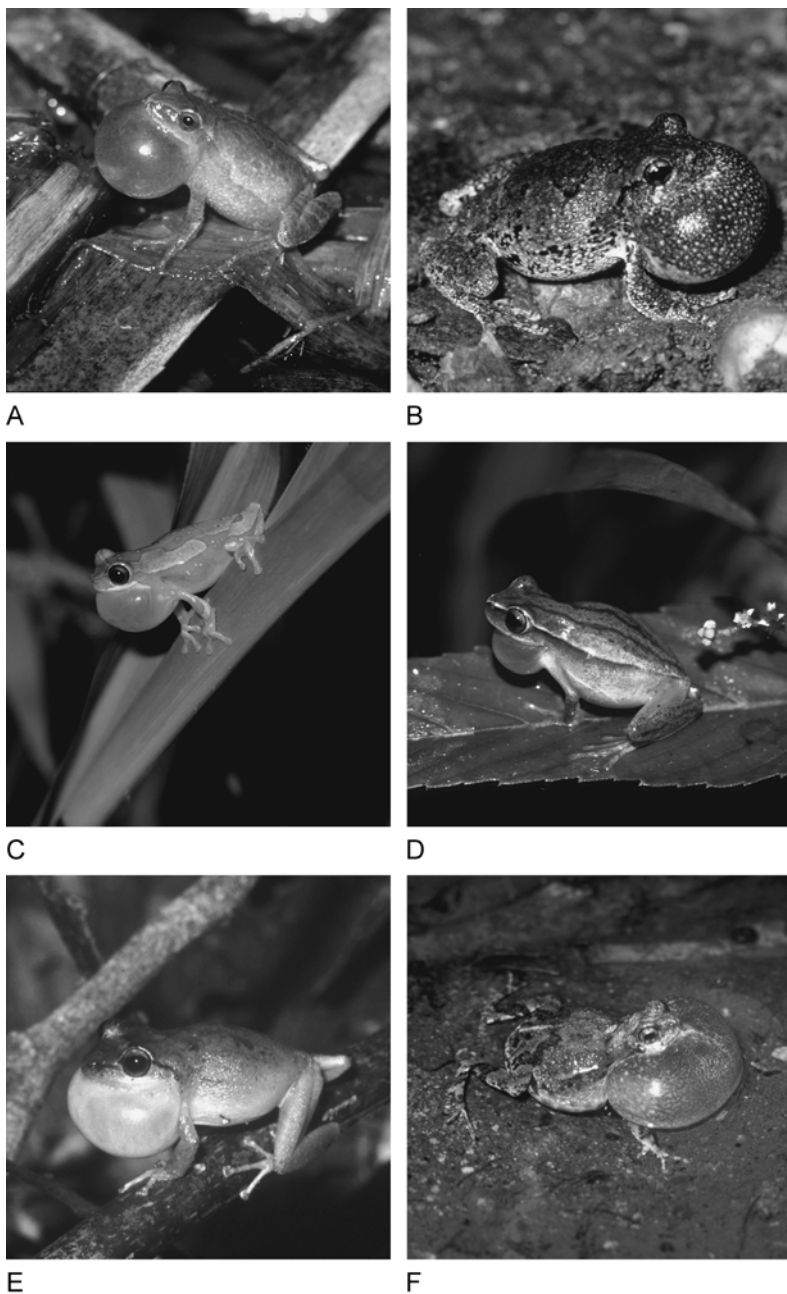


FIGURE 3.1. Calling males of some anurans in which vocal communication has been studied in detail. (A) *Pseudacris crucifer* (Hylidae). (B) *Hyla versicolor* (Hylidae). (C) *Hyla ebraccata* (Hylidae). (D) *Hyla microcephala* (Leptodactylidae). (E) *Eleutherodactylus coqui* (Leptodactylidae). (F) *Physalaemus pustulosus* (Leptodactylidae). Photos by Kentwood D. Wells.

the male takes no further interest in his offspring, but moves to a nearby calling perch and resumes calling.

These scenes, which can be repeated dozens of times each night in a single breeding assemblage in Panama (Schwartz and Wells 1984a; Wells and Schwartz 1984a,b), illustrate the complexity of vocal interactions that can occur in a chorus of frogs. Many anurans have repertoires consisting of several distinct types of calls, and they often exhibit considerable plasticity in their use of different call elements, responding to changes in local chorus density, the presence of nearby conspecific and heterospecific callers, and to approaching females by modifying their vocal signals (Wells 1988; Gerhardt and Huber 2002). All male frogs have the same ultimate goal: to outsignal their competitors and attract females, eventually fertilizing their eggs to contribute their genes to the next generation of frogs. The ways in which they accomplish this goal vary among species, however. Some anurans have relatively simple calls, whereas others have exceedingly complex calls. Males of some species are very aggressive toward other males in a chorus, whereas males of other species seldom react to their neighbors.

This chapter reviews the behavioral ecology of anuran vocal communication. First, the influence of sexual selection on the production and energetic cost of calls is briefly reviewed. Next, the major types of calls produced by male anurans, as well as the less common vocal signals of females are discussed. The interactions among males in choruses and the ways in which these interactions affect the ability of males to attract mates are covered in some detail, followed by a brief discussion of ways in which features of the anuran auditory system contribute to communication within a chorus setting.

## 2. Sexual Selection, Energetic Constraints, and Signaling System Evolution

When Charles Darwin originally outlined his theory of sexual selection in his book, he had relatively little to say about sexual selection in amphibians. He did suggest that the calls of frogs are analogous to the songs of birds and probably were shaped by sexual selection. Indeed, subsequent research has shown that sexual selection is the main driving force in the evolution of anuran acoustic communication (Gerhardt and Huber 2002). Many features of anuran calls can be shaped by sexual selection, including call intensity, calling rate, call duration, call pitch, and the temporal pattern of interaction among competing males. In addition, all of the morphological, physiological, and biochemical machinery involved in call production is molded by sexual selection. Because the energetic cost of calling in many species is quite high, selection should favor mechanisms to increase the efficiency of sound production and transmission, thereby enabling a calling male to conserve energy reserves while maximizing the transmission of signals to receivers, especially females.

## 2.1 Morphology and Physiology of Call-Producing Muscles

The basic mechanisms of sound production during calling are discussed in the next chapter (see Walkowiak, Chapter 4). The power for sound production is provided mainly by the sexually dimorphic trunk muscles, and sexual selection has produced a number of morphological and biochemical adaptations for call production by males, including highly aerobic muscle fibers, high concentrations of mitochondria, high activities of aerobic enzymes, heavy vascularization, and ample supplies of lipid and carbohydrates to fuel call production. There is a strong interspecific correlation between muscle structure and biochemistry and typical calling rates, with the most aerobic muscles being characteristic of species with high calling rates (Wells 2001).

The repeated contraction of the trunk muscles to produce calls can be energetically expensive in species with high calling rates (Wells 2001). The North American spring peeper (*Pseudacris crucifer*; Fig. 3.1A) produces single-note calls (Fig. 3.2A), each representing one contraction of the trunk muscles, and can produce up to 100 call notes per minute. Similarly, the tiny Neotropical small-headed treefrog (*Hyla microcephala*) (Fig. 3.1D) produces long trains of notes grouped into multinote calls (Fig. 3.2E) and also can produce up to 100 notes per minute (Wells and Taigen 1989). Males can call at these levels for several hours each night. Sustaining such high calling effort requires a high aerobic capacity, because anaerobic metabolism plays little role in call production. For these small treefrogs, rates of oxygen consumption during calling can be up to 25 times resting rates. This results in a significant drain on stored energy reserves. Short-term performance probably is limited mainly by carbohydrate reserves in the form of glycogen stored in the muscle tissue (Bevier 1997b), whereas lipid reserves are depleted over longer time intervals (Ressel 2001). The high energetic cost of calling probably explains the relatively short average chorus tenure of many male frogs (Murphy 1994), which exerts strong selective pressures on males to outsignal their competitors and attract females as rapidly as possible. Some frogs, however, invest much less effort in calling each night, but can remain in a chorus for several months (Bevier 1997a; Wells 2001). For these species, the ability to remain active for long periods of time probably is a more important determinant of mating success than nightly calling performance.

## 2.2 Vocal Sacs as Sound Radiators and Visual Signals

Because the metabolic cost of calling is high for many anurans, any adaptation to increase the efficiency of sound transmission will be favored by selection. Most anurans that call in air have inflatable vocal sacs that radiate sound to the external environment, providing greater energetic efficiency than would be possible with the larynx alone, because the vocal cords are much smaller than the wavelength of the call. Even so, the efficiency with which frogs convert metabolic energy into radiated sound energy is quite low (Prestwich 1994; McLister 2001). This problem is most acute for species with very low-pitched calls,

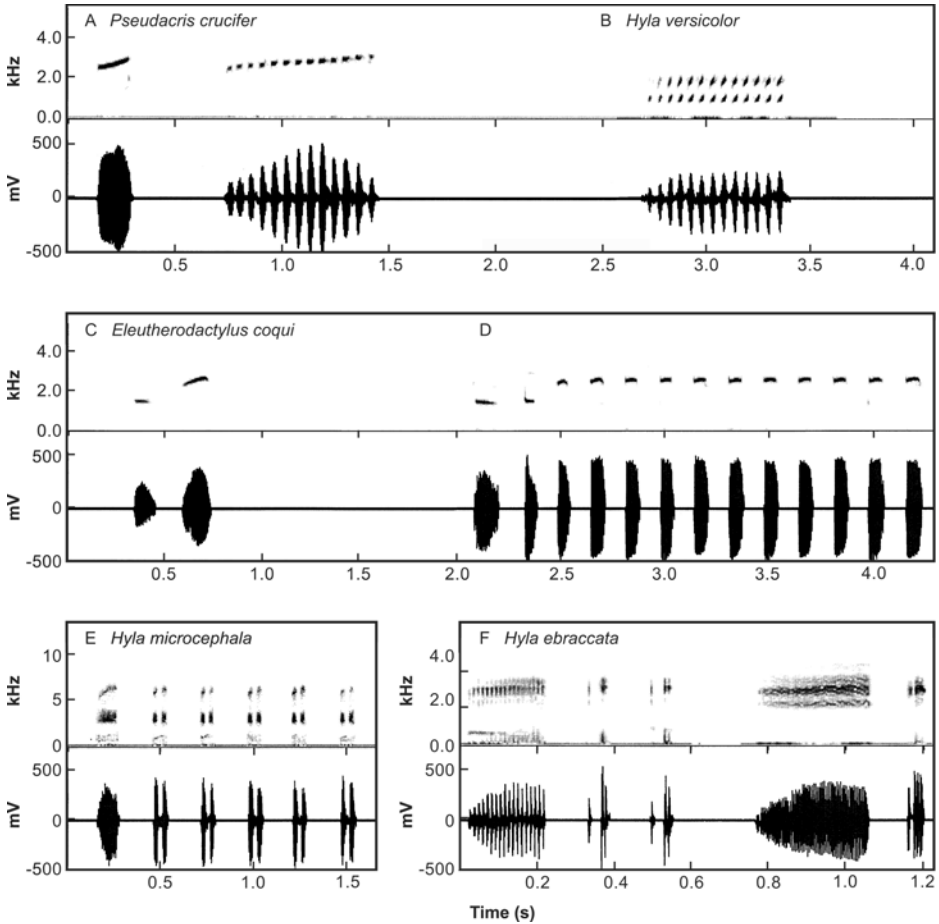


FIGURE 3.2. Representative anuran calls. The sound spectrograms at the top of each part show changes in frequency (kHz) over time. The oscillograms at the bottom of each part show changes in amplitude (mV), over time. (A) Tonelike peep of *Pseudacris crucifer*. (B) Amplitude-modulated aggressive call of *P. crucifer*. (C) Amplitude-modulated advertisement call of *Hyla versicolor*. (D) Multinote aggressive call of *E. coqui*. (E) Multinote advertisement call of *Hyla microcephala*, composed of an introductory note followed by several biphasic secondary click notes. (F) Three-note advertisement call of *Hyla ebraccata* (left) and two-note aggressive call of *H. ebraccata* (right), with much higher pulse rate in the introductory note. Recordings by Kentwood D. Wells and Joshua J. Schwartz.

because low-pitched sounds have long wavelengths. Small species with high-pitched calls and large vocal sacs relative to the size of the head (and larynx) can be expected to be more efficient sound radiators and have unusually loud calls for their body size. For example, both *Pseudacris crucifer* and *Hyla micro-*

*cephala*, which have proportionately large vocal sacs, weigh only about 1 g, but can produce calls as loud as those of songbirds that are 10 to 100 times heavier (Pough et al., 1992).

In addition to radiating sound, vocal sacs also can serve as visual signals, which can increase the effectiveness of acoustic signals by making them more detectable by receivers, especially in noisy environments. In many frogs, the throat region and vocal sac are conspicuously colored. Usually these are highly reflective colors such as white or yellow, but some frogs have black vocal sacs that also make the males conspicuous (see Hödl and Amezcuita 2001 for a review of visual signaling in frogs). Experimental studies using a mechanical frog model showed that a combination of an acoustic signal and a visual signal of a moving vocal sac was most effective in eliciting aggressive responses from males of a South American dendrobatid frog, the brilliant-thighed poison frog (*Allobates [Epipedobates] femoralis*; Narins et al. 2003). In another dendrobatid frog, the palm rocket frog (*Colostethus palmatus*) from Colombia, females were attracted to the moving vocal sac of a model male frog, but not to a model with a deflated vocal sac (Lüddecke 1999). Males of a leptodactylid frog, the Túngara frog (*Physalaemus pustulosus*), have unusually large and conspicuous vocal sacs (Fig. 3.1F). Video playback of a calling male with a moving vocal sac enhanced the attractiveness of an acoustic stimulus to females (Rosenthal et al. 2004).

### 2.3 Other Sound Radiators

Although vocal sacs probably are the main sound-radiating organs in most frogs, they are not the only ones. For example, much of the sound energy produced by a calling male North American bullfrog (*Rana catesbeiana*) is radiated not from the vocal sacs, which sit in the water, but from the very large tympanic membranes (Purgue 1997). Male bullfrogs, and males of a number of other ranid frogs, have tympana up to 50% larger than those of females. These enlarged tympana have a thickened central patch that increases the mass of the eardrum and apparently serves to decouple the auditory and sound-broadcasting functions of the eardrum. Males of a West African frog, Parker's water frog (*Petropedetes parkeri*), have a conspicuous spongy papilla projecting from the tympanum, offset from the center of the membrane. There is some evidence that the ears of these frogs are used for both sound reception and sound transmission, as in North American bullfrogs (Narins et al. 2001).

## 3. The Vocal Repertoires of Frogs and Toads

Some anurans have relatively limited repertoires of call types, whereas others have a diverse array of calls used in different social contexts. Most anurans have advertisement calls that are given by males to advertise their positions to females and to other males, although some species have secondarily lost the advertisement call (Wells 1977a). Many species also have release calls, produced by both

males and females, which are given when an unreceptive individual is clasped by a male. Some species also have distinct courtship calls, given by males when they detect females nearby. Less common are courtship calls given by females, often in response to the calls of males. Aggressive calls, used during agonistic interactions among males, are common, although anurans in some clades typically lack distinct aggressive calls (e.g., many toads in the genus *Bufo*). Some anurans also produce distress calls when seized by predators, although there is little evidence to suggest that these function in intraspecific communication. We focus our discussion on the three categories of calls used most commonly in social interactions in choruses: advertisement calls, courtship calls, and aggressive calls.

### 3.1 Advertisement Calls

The advertisement calls of anurans convey the same sorts of messages as do advertising signals of many other animals: they signal the species identity, sexual receptivity, position, size, and in some cases, the individual identity of males in a chorus. Hundreds of playback experiments with scores of species have shown that female frogs will approach conspecific calls presented alone or in choice tests with heterospecific calls (Gerhardt and Huber 2002). In species in which males call over long periods of time and females are in the same habitat, advertisement calls could stimulate hormone production in females and maintain reproductive condition in females, although this has rarely been demonstrated experimentally (Lea et al. 2001). Advertisement calls also advertise a male's position to other males and help to maintain spacing between calling individuals, with perceived call intensity providing information about the spatial proximity of competing males (Brenowitz et al. 1984; Wilczynski and Brenowitz 1988; Brenowitz, 1989; Gerhardt et al. 1989).

Males of some species can use the pitch of other males' advertisement calls to assess the body size of competitors (Davies and Halliday 1978; Arak, 1983b; Robertson 1984; Given 1987; Wagner 1989c). Males are more likely to approach or attack speakers playing high-pitched calls of small males, but retreat from the low-pitched calls of large males. Males of some species alter the pitch of their calls in response to those of neighboring males (e.g., *Rana catesbeiana*; Bee and Bowling 2002), but it is not always clear that this provides more accurate information about male body size to opponents (Bee et al. 2000; Bee 2002; see further discussion of aggressive interactions below).

Although the advertisement calls of most anurans consist of a single note, a series of identical repeated notes, or a long trill, some have complex advertisement calls with more than one kind of note (Wells 1988). Most frogs have only a few kinds of notes in their calls, but some rhacophorid and mantellid treefrogs have extraordinarily complex calls, with a dozen or more distinct kinds of notes. The functions of these very complex calls are not fully understood, but some call components appear to be used in aggressive interactions among males (Narins et al. 2000, Christensen-Dalsgaard et al. 2002; Feng et al. 2002).

In some species, different types of notes apparently convey separate messages to males and females. For example, in the Puerto Rican common coquí (*Eleutherodactylus coqui*) (Figs. 3.1E, 3.2C), the beginning “co” note elicits calling and aggressive responses from males, but they show little response to the secondary “qui” note (Narins and Capranica 1978). Females are attracted to the “qui” note, but show little response to the “co” note alone (Narins and Capranica 1976). In the Australian eastern smooth frog (*Geocrinia victoriana*), the long introductory note conveys an aggressive message to males, whereas the shorter secondary notes are attractive to females (Littlejohn and Harrison 1985). A somewhat similar system is found in the short-legged spiny reed frog (*Afrivalus brachynemis*) from southern Africa, which has a rapidly pulsed note that serves as an aggressive signal and a longer trill that is attractive to females (Backwell 1988). In Fornasini’s spiny reed frog (*Afrivalus fornasinii*), males give long trains of very short pulses (trills) that often grade into a series of repeated pulsed notes that are given mainly in response to other males (Schneichel and Schneider 1988). Some frogs add secondary notes to their calls during chorusing interactions (Figs. 3.2E,F), including *Hyla ebraccata* (Fig. 3.1C) and *Hyla microcephala* (Fig. 3.1D) from Panama; these are discussed in a later section.

### 3.2 Male Courtship Calls

Male frogs often alter their vocal behavior when females are nearby, producing calls that are likely to increase the signal-to-noise ratio of the male’s calls or provide directional cues to females (Wells 1977b, 1988). Male spring peepers (*Pseudacris crucifer*) give longer peeps when females are nearby (Rosen and Lemon 1974). Male gray treefrogs (*Hyla versicolor*) respond to approaching females by giving trills that can be several times the length of normal advertisement calls (Wells and Taigen 1986; Klump and Gerhardt 1987). Similar behavior is seen in the Trinidad poison frog (*Mannophryne trinitatis*; Wells 1980b). Males normally give two-note advertisement calls, but combine these into a continuous trill when females are approaching, producing a call with 50% more notes than the normal advertisement call (Fig. 3.3).

Often males simply increase calling rates in response to approaching females (reviewed by Wells 1988 and Gerhardt and Huber 2002). Others produce distinctive courtship calls, especially species in which the male leads the female to a concealed oviposition site during courtship (Wells 1977b, 1988; Townsend and Stewart 1986; Hoskin 2004). Distinctive courtship calls also occur in some species in which the male calls from a fixed location to attract the female (Greer and Wells 1980; Kluge, 1981; Robertson 1986). In midwife toads (*Alytes obstetricans*), males give courtship calls while moving toward females and females sometimes respond with calls of their own (Bush 1997). Courtship calls sometimes are given at lower intensity than advertisement calls, perhaps to avoid alerting other males to the presence of a female (see discussion of “eavesdropping” below). Ovaska and Caldbeck (1997b) showed that males of the Antilles robber frog (*Eleutherodactylus antillensis*) respond to playbacks of courtship calls by



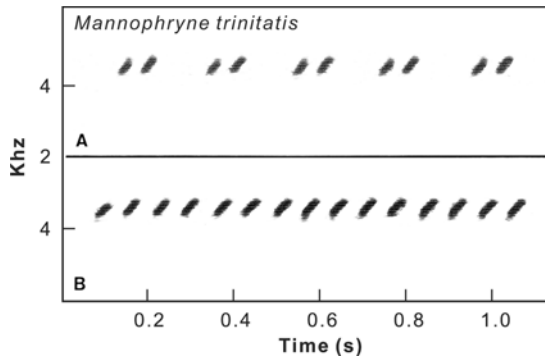


FIGURE 3.3. Sound spectrograms of (A) the advertisement call and (B) a courtship trill of *Mannophryne trinitatis*. Recordings by Kentwood D. Wells.

approaching the speaker playing the call, a behavior not seen during playbacks of advertisement or aggressive calls.

Some frogs have more than one type of courtship call. In Fleischmann's glass frog (*Hyalinobatrachium fleischmanni*) from Panama, a male gives long, frequency-modulated calls when a moving frog is first detected nearby. This appears to serve as an aggressive call when directed at males, but probably also provides direction cues to females. Once a female begins to approach the male, he switches to a series of short chirps (Greer and Wells 1980). In *Mannophryne trinitatis*, a male gives a long trill when courting a female at a distance, but switches to quiet chirps as he leads the female to a hidden oviposition site (Wells 1980b). Males of the Australian ornate frog (*Cophixalus ornatus*) give long courtship calls while leading females to nest sites, but give shorter calls when in a nest with a female (Hoskin 2004). Both types of calls are delivered at a high rate, but low intensity. Short-range courtship calls also have been reported in several dendrobatid frogs and some species of *Eleutherodactylus* with concealed oviposition sites (Ovaska and Hunte 1992; Bourne 1997; Ovaska and Caldbeck 1997a, 1999).

### 3.3 Female Courtship Calls

Some female frogs vocalize in response to the calls of males (Emerson and Boyd 1999), although all female frogs lack vocal sacs. The best-studied species are midwife toads in the genus *Alytes*. Female midwife toads call in response to male calls, and these calls elicit soft courtship calls from males (Bush 1997; Bosch and Márquez 2001). The calls given by females probably enhance the ability of males and females to find each other. Male midwife toads often call from hidden locations in rock crevices or burrows, but sometimes move toward females and engage in vocal duets with them (Bush et al. 1996; Bush 1997). Duetting between males and females also occurs in the African common platanna (*Xenopus laevis*), which often calls in muddy water where males may not be visible to females

(Tobias et al. 1998). Males of Serro Utyum robber frog (*Eleutherodactylus podiciferus*) from Costa Rica switch from the normal advertisement call trill to a series of squeak calls after hearing similar squeaks given by females (Schlaepfer and Figueroa-Sandí 1998). Low-intensity courtship calls have been reported in a number of ranid frogs, including the North American carpenter frog (*Rana virgatipes*) (Given 1987), bullfrog (*R. catesbeiana*; Judge et al. 2000), fanged frogs of the genus *Limnonectes* from Borneo and Southeast Asia (Emerson 1992; Orlov 1997), the Asian rice frog (*Limnonectes limnocharis*), water skipping frog (*Euphlyctis cyanophlyctis*), and red-eared frog (*Rana erythraea*), and the Levuka wrinkled ground frog (*Platymantis vitiensis*) from Fiji (Roy et al. 1995; Boistel and Sueur 1997). At least two nonexclusive functions of female courtship calling have been proposed: (1) facilitating mate location by eliciting more calling from nearby males, enabling females to distinguish territorial from satellite males, and (2) identifying of females as potential mates rather than territorial competitors (Emerson and Boyd 1999). To date, however, very few experimental studies of male responses to female calls have been done (Given 1993a; Bush et al. 1996; Bush 1997; Tobias et al. 1998; Bosch 2001, 2002), and both of these remain viable hypotheses.

### 3.4 Aggressive Calls

Many male frogs defend their calling sites against conspecifics and often have distinctive aggressive vocalizations. Aggressive and advertisement calls usually have similar dominant frequencies, but differ in temporal structure, but there is no unique temporal structure common to all aggressive calls. Certain constraints on call production probably limit divergence between aggressive calls and advertisement calls within species. Frogs that produce wideband calls typically produce relatively short pulses of sound and probably are incapable of producing notes of long duration, whereas frogs that produce narrowband calls typically have longer notes and probably cannot produce very short calls (Gerhardt and Huber, 2002). For example, in *Pseudacris crucifer*, the advertisement call is a tonelike peep, whereas the aggressive call is a long trill consisting of a series of slightly shorter pulses (Fig. 3.2A). In other chorus frogs in the genus *Pseudacris*, the advertisement call consists of trains of extremely short pulses, whereas aggressive calls are longer trains of the same type of pulses, sometimes delivered at faster rates (Owen 2003).

In a dendrobatid frog from Panama, *Colostethus panamensis*, the advertisement call is a short trill and the aggressive call is a long tonelike peep that resembles a trill with the notes merged together (Wells 1980a). These calls sometimes grade into each other as a male makes the transition from aggressive to advertisement calling (Fig. 3.4). Males of another species in the same genus, the Bogata rocket frog (*C. subpunctatus*), sometimes respond to calls of other males by grouping call notes into bouts of two or three notes. This does not appear to enhance the attractiveness of males to females, but does function as an aggressive signal (Lüddecke 2002). The Santo Andre snouted treefrog (*Scinax rizibilis*)

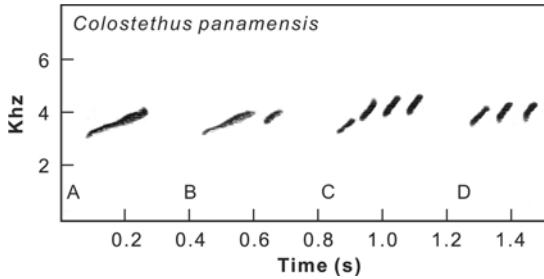


FIGURE 3.4. Sound spectrograms of the calls of *Colostethus panamensis*. (A) Single-note aggressive call. (B) Two-note aggressive call. (C) Transition from the aggressive call to an advertisement call. (D) Three-note advertisement call. Recordings by Kentwood D. Wells.

from Brazil has an advertisement call consisting of a series of repeated notes, whereas aggressive calls consist of irregular trains of short pulses. This species also has a close-range aggressive call consisting of short bursts of pulses (Bastos and Haddad 2002). In the Lesser Antilles robber frog (*Eleutherodactylus urichi*) from Trinidad, the advertisement call is a short, tonelike peep, the aggressive call an even shorter click (Wells 1981). In contrast, the aggressive call of *Eleutherodactylus coqui* is a long train of notes (Fig. 3.2D). The advertisement calls of the Angola forest treefrog (*Leptopelis viridis*) are short clicks, whereas the aggressive calls are about twice as long and have a slightly lower dominant frequency (Grafe et al. 2000).

A number of hylid treefrogs from South and Central America, including the hourglass treefrog (*Hyla ebraccata*), small-headed treefrog (*H. microcephala*), and veined treefrog (*H. phlebodes*) produce aggressive calls with a structure similar to that of advertisement calls (Fig. 3.2F), but with a much higher pulse repetition rate (Schwartz and Wells 1984a,b, 1985; Wells and Schwartz 1984b). Because aggressive calls do not function in species recognition, one might expect such calls to be less stereotyped than are advertisement calls. Indeed, in these and other anuran species, temporal features such as pulse repetition rate and number of pulses are much more variable in aggressive calls than in advertisement calls (Schwartz and Wells 1984a; Littlejohn 2001; Owen 2003).

Some frogs change the dominant frequency of their advertisement calls when responding to the calls of other males. This type of behavior has been reported in the white-lipped frog (*Leptodactylus albilabris*) from Puerto Rico (Lopez et al. 1988) and in several North American anurans, including Northern cricket frogs (*Acris crepitans*; Wagner 1989b, 1992), green frogs (*Rana clamitans*; Bee and Perrill 1996; Bee et al. 1999, 2000), carpenter frogs (*R. virgatipes*; Given 1999), bullfrogs (*R. catesbeiana*; Bee and Bowling 2002), and American toads (*Bufo americanus*; Howard and Young 1998). In all cases except *L. albilabris*, males lower the dominant frequency of their calls. This generally has been interpreted

as an aggressive response, perhaps a means of conveying information about the size of the caller, although in bullfrogs, such changes do not appear to be correlated with fighting ability (Bee 2002).

Many anurans have graded signaling systems in which long- and short-range aggressive calls represent two ends of a continuum. This has been studied in most detail in *Hyla ebraccata* from Panama (Wells and Schwartz 1984b; Wells and Bard 1987; Wells 1989). This species has advertisement calls consisting of an introductory note and a series of shorter secondary notes with the same dominant frequency and pulse repetition rate. Aggressive calls have introductory notes with much higher pulse rates and are more variable in duration. As males approach each other, they lengthen the introductory notes of their aggressive calls while gradually dropping secondary click notes (Fig. 3.5). The secondary notes make the calls more attractive to females, which are not strongly attracted to aggressive calls with high pulse repetition rate (Wells and Bard 1987). Hence, males gradually adjust the relative aggressiveness and attractiveness of their calls, depending on the proximity of their opponents. Similar behavior has been described in two other Panamanian treefrogs, *H. microcephala* (Schwartz and Wells 1985) and *H. phlebodes* (Schwartz and Wells 1984b). As in *H. ebraccata*, females of *H. microcephala* prefer the lower pulse rates of advertisement calls to the higher pulse rates of aggressive calls (Schwartz 1987a).

Some North American hyloid frogs also have graded aggressive calls. Male spring peepers (*Pseudacris crucifer*) increase the duration of their trilled aggressive calls in response to increases in the intensity and duration of an aggressive call stimulus (Schwartz 1989). Several other species in the genus *Pseudacris* also have trilled aggressive calls, and some of these show evidence of graded variation similar to that seen in spring peepers (Owen 2003). Northern cricket frogs (*Acris crepitans*) have a somewhat simpler system. Males produce calls with progressively more pulses as they approach each other, but they do not have structurally distinct aggressive calls (Wagner 1989a,c, 1992; Burmeister et al. 1999, 2002). In contrast to many other species, these changes in call structure actually make the calls more attractive to females, rather than less attractive (Kime et al. 2004). Hence, these calls may convey aggressive messages to males, or they may be a form of escalated competition among males for the attention of females, or both. Multinote aggressive calls are characteristic of several species of Caribbean robber frogs in the genus *Eleutherodactylus*, although the extent to which these calls are graded is not clear (Stewart and Rand 1991; Stewart and Bishop 1994; Michael 1997; Ovaska and Caldbeck 1997b; O'Brien 2002).

In the Old World, graded aggressive calls have been described in several clades of frogs, although most species have not been studied in as much detail as the New World species. Examples include Australian ground froglets (*Geocrinia*) and crowned toadlets (*Pseudophryne*; Pengilley 1971; Littlejohn and Harrison 1985), African reed frogs (*Hyperolius*) and spiny reed Frogs (*Afrixalus*; Backwell 1988; Grafe 1995), and Asian Bubble-nest Frogs (*Philautus*; Arak 1983a). Some frogs exhibit graded variation in both advertisement and aggressive calls. Males of the

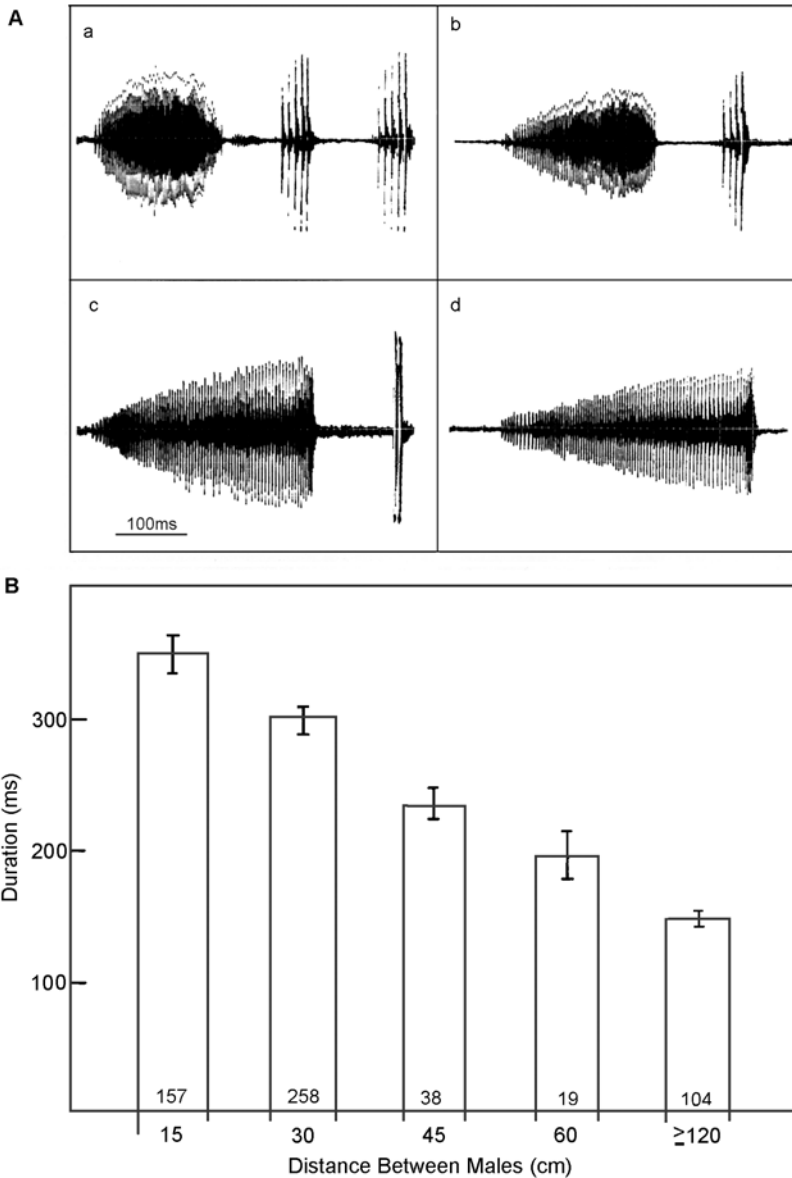


FIGURE 3.5. Graded aggressive calls of the Panamanian treefrog *Hyla ebraccata*. (A) Oscillograms of four aggressive calls recorded from the same male, showing a gradual increase in the duration of the introductory note and reduction in the duration and number of secondary click notes. Call (a) was given at the longest distance between males; call (d) was given at the shortest distance. (B) Duration of introductory notes of aggressive calls as a function of the distance between interacting males. Numbers at the bottom of each column are sample sizes. Recordings by Kentwood D. Wells. Data from Wells and Schwartz 1984b.

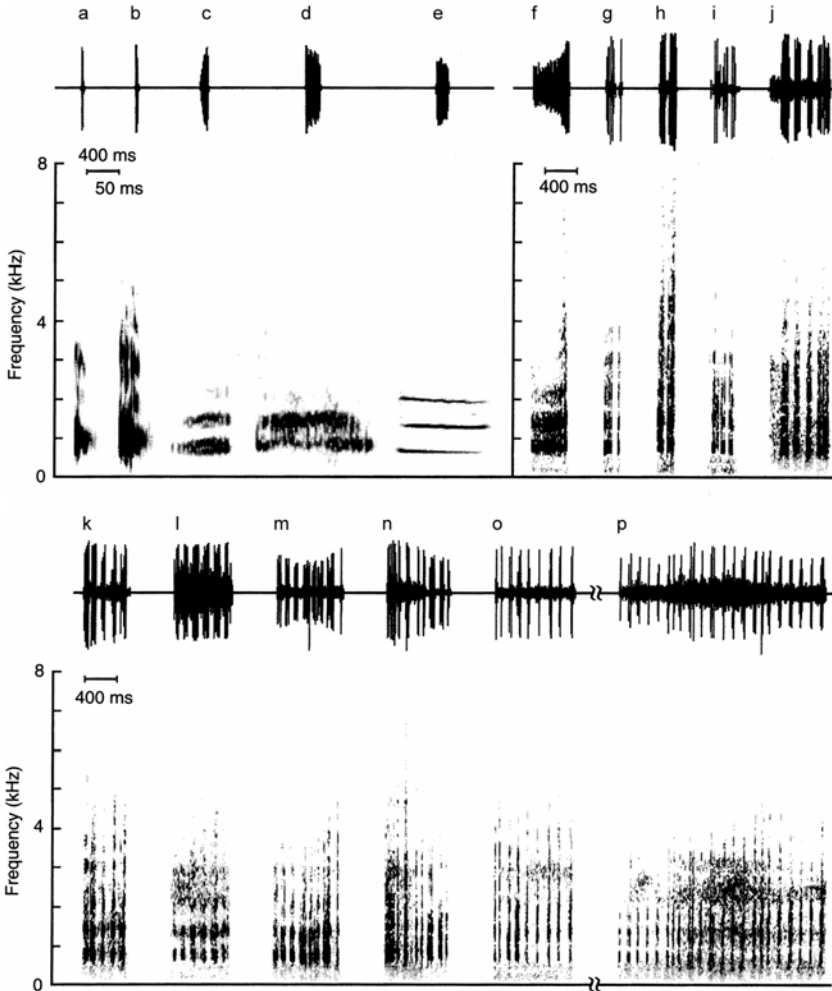


FIGURE 3.6. Complex vocal repertoire of *Boophis madagascariensis*. Oscillograms are shown on top of each part, sound spectrograms on the bottom. For the first set of calls (a)–(e), the time scale on the sound spectrograms has been magnified to show details of call structure. Time scales are the same for oscillograms and sound spectrograms for all other calls: (a) toc note; (b) short click note; (c) short rip note; (d) loud click note; (e) tonelike note; (f) long rip note; (g) creak note; (h)–(p) iambic notes with increasing number of pulses. Males give iambic notes more frequently in response to playbacks of conspecific calls, and these may represent a graded aggressive call system. Reprinted from Narins et al. (2000), Fig. 3, p. 287 with the permission of Cambridge University Press.

Nicobar frog (*Fejervarya nicobariensis*) from Malaysia produce multinote advertisement calls with 1 to 6 click notes, but when males are calling in close proximity, they produce up to 25 notes (Jehle and Arak 1998). Males in dense choruses give distinctly different squawkl-like aggressive calls, and these sometimes are followed by a series of clicklike notes similar to those in the advertisement calls. These compound calls apparently represent transition calls that convey an aggressive message to other males while retaining notes attractive to females. A rha-cophorid treefrog from Thailand, the Javan whipping frog (*Polypedates leucomystax*), has a repertoire of at least 12 distinct call types, many consisting of trains of pulses or clicks that appear to function as aggressive signals (Christensen-Dalsgaard et al. 2002). The Madagascar bright-eyed frog (*Boophis madagascariensis*) has an even more variable vocal repertoire of at least 28 different types of calls, although most of these appear to be variants of a single call type that differ in the number of notes and pulses produced (Narins et al. 2000). The most variable call types often were given in response to playbacks of similar notes at high intensities and have many of the characteristics of the graded aggressive calls seen in other species (Fig. 3.6).

#### 4. Chorusing Behavior

Many frogs and toads form aggregations in which males call to attract mates (Zelick et al. 1999; Gerhardt and Huber 2002). The term “chorus” is used here to describe any group of signaling animals (Gerhardt and Huber 2002), without specifying the spatial distribution or call timing relationships among individual males (Brush and Narins 1989). Choruses can both facilitate and impede communication between males and females. The acoustic environment of a chorus can be complex because of the spatial distribution of males, intense competition for mates, high levels of background noise, and temporal overlap among calls of neighboring males. The close proximity of calling males allows females to quickly assess multiple mates and may promote vocal competition among males (Wiley and Poston 1996). Males can acquire information about the capabilities of rivals that can be used when adopting perch sites, mating tactics (Humfeld 2003), or calling tactics (Wells 1988). However, a loud chorus also can make signal detection, localization, discrimination, and interpretation difficult (Wollerman and Wiley 2002a,b). For example, the call preferences of females in the field or in experiments using multispeaker designs that mimic the sonic complexity of natural choruses often differ from those in simple two-choice laboratory experiments (Gerhardt 1982; Telford et al. 1989; Márquez and Bosch 1997; Schwartz et al. 2001). Within a chorus, however, some females may be better able than others to discriminate among males because of differences in the local acoustic environment (Gerhardt and Klump 1988; Schwartz and Gerhardt 1989). The presence of calling heterospecific anurans may also create opportunities for mismatings and wasted reproductive effort (Gerhardt 1994; Pfennig et al. 2000; Gerhardt and Schwartz 2001).

#### 4.1 Choruses as Venues for Communication Networks and Competition

Anuran choruses allow for the exchange of information between numerous signalers and receivers, and choruses can be considered “communication networks” (McGregor and Peake 2000; Grafe 2005), rich in “public information” (Valone and Templeton 2002; Danchin et al. 2004). A network of signalers can affect the temporal dynamics of male calling behavior and the elaboration of male vocalizations. For example, playbacks of calls typically increase the calling effort of male receivers (see Table 9.1 in Gerhardt and Huber 2002), as manifested in increased calling rate, call complexity, or call duration. The sounds produced by a chorus can stimulate males to call (Schwartz 1991), with some minimum number of males being necessary to initiate and maintain chorusing activity (Brooke et al. 2000). Where many males can hear one another, calling efforts of individual males may rapidly escalate as a chain reaction occurs among signalers. This rapid escalation in male calling effort should facilitate comparison of potential mates by females (Wiley and Poston 1996), possibly outweighing any disadvantages imposed by masking and degradation of signals in the chorus.

Eavesdropping refers to “extracting information from signaling interactions between others” (McGregor and Peake 2000), and the network environment clearly makes possible eavesdropping by both males and females (Grafe 2005). Eavesdropping has not been studied experimentally in anurans, so we can only speculate on how it might affect their behavior. Males can acquire information on the capabilities of their competitors (Johnstone 2001), and they may detect nearby females as a result of a change in the calling behavior of a neighbor. For example, in *Hyla versicolor*, a male dramatically increases both call duration and calling effort when it detects a female. This change sometimes triggers similar changes in the calling behavior of neighbors (Schwartz et al. unpubl. data). Controlled experiments are needed to exclude the possibility that such neighbors are responding to the calls of their neighbors and not to cues produced by the female. Female-induced elevation in calling also may be exploited by satellite males, who may move towards females or even to begin to call (Grafe 2005). Nonsatellites also could take advantage of acoustic cues by moving towards individuals about to mate. Therefore, the low amplitude of courtship calls of some species could reduce the likelihood that satellite males will intercept females (Given 1993a). Satellites or less capable calling males may move to sites where more vigorous callers are likely to attract females (Pfennig et al. 2000, Gerhardt and Huber 2002, Humfeld 2003), as proposed in “hot-shot” models of lek evolution (Höglund and Alatalo 1995).

Females that eavesdrop on aggressive exchanges between males could utilize public information to select winners (McGregor and Peake 2000; Danchin et al. 2004) and so augment information supplied in advertisement calls with that transmitted in signals that are generally unattractive to females (the aggressive call).



## 4.2 *Agonistic Interactions and Male Spacing*

The use of aggressive vocalizations, including graded aggressive calls, was discussed in an earlier section. In most frogs, males seek to maintain some minimum distance between themselves and their nearest neighbors. Competition for calling sites can be mediated by both aggressive calling and actual fighting (Wells 1988; Gerhardt and Huber 2002). Male frogs apparently assess the proximity of competitors by the intensity of their calls (Wilczynski and Brenowitz 1988; Brenowitz 1989; Gerhardt et al. 1989; Marshall et al. 2003). Murphy and Floyd (2005) found that male barking treefrogs (*Hyla gratiosa*) entering low-density choruses spaced themselves farther from the louder of two speakers broadcasting advertisement calls than they did in high chorus densities. This difference could be because males have more difficulty gauging relative call intensities in high-density situations (perhaps due to noise-induced masking and threshold shifts; Schwartz and Gerhardt 1998). The increased proximity of calling males also could have made it hard for males to distance themselves from a speaker (Murphy and Floyd, 2005).

In many species, aggressive interactions tend to occur early in the evening as males sort out spatial relationships in the chorus (e.g., Wells and Bard 1987; Backwell 1988). Aggressive interactions probably are less costly at this time because females typically arrive later at night (Backwell 1988; Murphy 1999; Gerhardt and Huber 2002). This is important, because aggressive calls often are less attractive to females than are advertisement calls (Oldham and Gerhardt 1975; Schwartz and Wells 1985; Wells and Bard 1987; Backwell 1988; Grafe 1995; Brenowitz and Rose 1999; Marshall et al. 2003).

During the course of an evening, males may habituate to the calls of near neighbors, making them less likely to engage in costly aggressive interactions (Brenowitz and Rose 1999). Marshall et al. (2003) found that after just 10 min of advertisement call broadcasts (at 4 and 8 dB above the prestimulus aggressive threshold) to male spring peepers (*Pseudacris crucifer*), aggressive call thresholds were elevated nearly 10 dB. Qualitatively similar data were obtained for the Pacific treefrog (*P. regilla*; Brenowitz and Rose 1994; Rose and Brenowitz 1997). One important consequence of such plasticity is that on nights when large numbers of males enter the chorus, the percapita frequency of agonistic interactions and intermale distances may be relatively low. Thus, there is not only a synergistic relationship but also a dynamic interaction between spacing and aggression that largely explains the shifting spatial distribution of males in choruses over time. Stable choruses may develop not only when male attendance at a breeding site is low but also when it is high (Rose and Brenowitz 2002). At a proximate level, it appears that short-term habituation to specific callers, rather than adaptation of the auditory system, is sufficient to explain the experimental results with *P. crucifer* and *P. regilla*, as males responded with aggressive calls when the advertisement call stimulus was changed to aggressive calls. However, it seems reasonable that neural threshold shifts (Narins and Zelick 1988; Schwartz and Gerhardt 1998) also contribute to lower aggressive thresholds when background noise levels in the chorus are high.

Discrimination between the calls of familiar neighbors and unfamiliar “strangers” has been demonstrated in the green frog (*Rana clamitans*) (Owen and Perrill 1998), bullfrog (*R. catesbeiana*) (Davis 1987), and Beebe’s rocket frog (*Colostethus beebei*) (Bourne et al. 2001). Bullfrogs habituate to the calls originating from a particular location, as reflected by a reduced tendency to give aggressive calls or approach the caller. Habituation also could explain why bullfrogs are more likely to answer calls of distant males than those of near neighbors (Boatright-Horowitz et al. 2000). Nevertheless, males become disinhibited if the spectral characteristics of the vocalization are altered by 10% during playback tests, or if the source of the calls is moved (Bee and Gerhardt 2001). Potential recognition cues also include fine temporal call features and even the pattern of variation of call features within males (Bee 2004).

### 4.3 Advertisement Call Plasticity

Competition among males for the attention of females often results in considerable plasticity in advertisement calling, with males modifying their calls in ways that increase the signal-to-noise ratio of their vocalizations or make their calls more attractive to females. For example, males often respond to the calls of others by increasing the energy content of their signals by elevating calling rate, call duration, or call complexity (Wells 1988, 2001; see Table 9.1 in Gerhardt and Huber 2002 for examples and exceptions). Males of some species alter call dominant frequency or the distribution of spectral energy (Lopez et al. 1988; Wagner 1989a, 1992; Bee and Perrill 1996; Howard and Young 1998; Given 1999) and adjust call amplitude (Lopez et al. 1988). Many of these changes are presumed to increase a male’s relative attractiveness to females (Ryan and Keddy-Hector 1992; Andersson 1994; Halliday and Tejedo 1995; Sullivan et al. 1995). This hypothesis has been supported by phonotaxis experiments in which gravid females were presented with acoustic alternatives broadcast from speakers in a laboratory arena (e.g., Ryan 1980) or in the field (e.g., Schwartz et al. 2001). Additional support comes from observations of mate choice in nature (e.g., Passmore et al. 1992; Schwartz et al. 1995; Grafe 1997) or artificial choruses with real males (Schwartz et al. 2001). For example, computer-based monitoring of choruses of male *Hyla microcephala* confirmed that males with the highest rates of note production were the first to attract females (Schwartz et al. 1995). Males of this species tend to match the number of notes in their calls during pairwise interactions (Schwartz 1986).

Approximate note matching has been reported in other species as well (Arak 1983a; Pallett and Passmore 1988; Jehle and Arak 1998; Gerhardt et al. 2000a) and may be a way for males to fine-tune calling effort to match that of their closest competitors. Males are expected to expend only the minimum energy necessary to nullify another caller’s advantage (Arak 1983a; Jehle and Arak 1998; Benedix and Narins 1999). Such behavior also could reduce a male’s risk of predation (Tuttle and Ryan 1981; Zuk and Kolluro 1998; Gerhardt and Huber 2002, page 2004). In the Australian red-legged froglet (*Crinia georgiana*), males responded

to playbacks of calls from two speakers as if they were summing the notes from these different sources (Gerhardt et al. 2000a). Therefore males appeared to expend more energy than was necessary to surpass the calling performance of individual rivals. This behavior probably reflects erroneous auditory grouping (see Farris et al. 2002) and thus a failure of test males to take thorough advantage of available spatial information. In *C. georgiana*, males that produce more notes per call do not necessarily gain a mating advantage (Smith and Roberts 2003). There also are different signaling routes to mating success in this species: large males did best when they produced more pulses in the first notes of their calls, whereas smaller males did best when they called at high rates.

Broadcasts of low-frequency calls that resemble those produced by large males can induce males to move away from a speaker (e.g., Arak 1983b), and the frequency shifts observed in the calls of some species may be an attempt by males to dupe rivals into misjudging their size. For example, the playback tests of Bee et al. (2000) indicate that such a bluffing strategy is conditional in green frogs, *Rana clamitans*, depending on the relative size of the interactants. Alternatively, spectral changes may honestly communicate size or size-independent fighting ability (Wagner 1992).

In some species, a subset of males may reduce or stop calling when exposed to the calls of another male (Gerhardt and Huber 2002; Humfeld 2003; Tobias et al. 2004). Males also may adopt satellite tactics and attempt to parasitize the calling efforts of other males (Halliday and Tejedo 1995). Such behavior probably represents an attempt by individuals to minimize energy expenditure for either mate attraction or aggression in the face of superior competition. In explosive breeders, very high chorus densities may cause males to cease vocal activity altogether and actively search for females (Wells 1977a; Halliday and Tejedo 1995).

Socially mediated changes in calls or calling behavior may render signals inherently more attractive to females (Wells 1988; Ryan and Keddy-Hector 1992; Sullivan et al. 1995; Schwartz 2001; Gerhardt and Huber 2002), but could these alterations improve a male's odds of mating in other ways? One possibility is that such changes modify the redundancy of signals and so improve signal detection and localizability, and reduce recognition errors by receivers under noisy conditions (Wiley 1983; Bradbury and Verhencamp 1998; Ronacher 2000; Narins et al. 2000). Kime (2001) tested and rejected the hypothesis that call complexity reduces masking vulnerability in the northern cricket frog (*Acris crepitans*), and the Túngara frog (*Physalaemus pustulosus*). Males of the former species cluster their calls within "call groups" and typically add calls to these groups, as well as the number of pulses per call, in response to the calls of other males (Wagner 1989b; Burmeister et al. 1999). Male *P. pustulosus* produce FM "whines" to which they append a variable number of chuck notes following acoustic stimulation by neighbors (Ryan 1980). Although females of both species find calls with greater complexity more attractive (Ryan 1980; Wagner 1991), these changes did not enhance signal efficacy in noise (Kime 2001).

Schwartz et al. (2001, 2002) hypothesized that call-induced increases in call duration and accompanying reductions in calling rate in *Hyla versicolor* are

related to the increased threat of acoustic interference in larger choruses. In this species, pulse shape and the duration of pulses and interpulse intervals have a strong impact on the relative attractiveness of calls (Gerhardt 2001; Schul and Bush 2002) and can easily be obscured during call overlap. Females also exhibit strong discrimination against very short calls (Gerhardt et al. 2000b; Schwartz et al. 2001), and they prefer long calls delivered at a low rate to short calls delivered at a high rate. Therefore, by giving long calls, even at a low rate, in an acoustically cluttered environment a male may increase the chances that there will be a sufficient number of call pulses and interpulse intervals clear of call overlap to attract a female. Preliminary data on male call overlap (Schwartz et al. 2001, 2002) were consistent with the hypothesis, and more focused experiments to test the idea are in progress. In addition, experiments to test whether longer calls are more easily detected in chorus noise are underway. The threat of call overlap also could explain why males of *E. coqui* increase call duration (albeit to a much smaller degree than *H. versicolor*) in response to the vocalizations of conspecifics. Benedix and Narins (1999) suggested that by shifting to longer calls, a male compensates for constraints on calling rate imposed in choruses by the reduced number of available quiet intervals into which a male could insert his calls without interference. Male frogs also could increase the detectability and attractiveness of vocalizations under noisy conditions by increasing signal amplitude. This has been reported for Puerto Rican white-lipped frogs (*Leptodactylus albilabris*) (Lopez et al. 1988), but whether this is a general response to background noise is not known.

#### 4.4 Patterns of Call Timing

Call interaction between males is a dynamic process and the timing relationships between males typically are fluid and change in response to the ambient acoustics or the level of male–male competition. Accordingly, leader–follower relationships may shift during chorusing (Moore et al. 1989; Bosch and Marquez 2001; Gerhardt and Huber 2002; Grafe 2003), yielding timing patterns that temporarily are perceived as alternating, synchronized, or partially overlapping (Fig. 3.7). Nevertheless, at particular spatial and temporal scales (Schwartz and Wells 1985; Given 1993b; Boatright-Horowitz et al. 2000), certain call timing patterns may dominate and a variety of hypotheses is available to explain such behavior at both proximate and ultimate levels (Greenfield 2002; Gerhardt and Huber 2002).

At a coarse temporal scale, call-timing shifts may occur in response to the calls of other species of frogs. For example, Littlejohn and Martin (1969) reported that males of one species of myobatrachid frog with especially long calls inhibited calling by another species with shorter calls. Schwartz and Wells (1983a,b) reported similar behavior in Panamanian tree frogs. Calling by males of *Hyla ebraccata* was inhibited by chorusing of groups of nearby *H. microcephala* or *H. phlebodes*. For *H. ebraccata*, these two species are especially potent sources of interference. *Hyla microcephala* calls in dense aggregations and employs calls with many notes. Even pairs of *H. phlebodes* can produce rapid-fire sequences

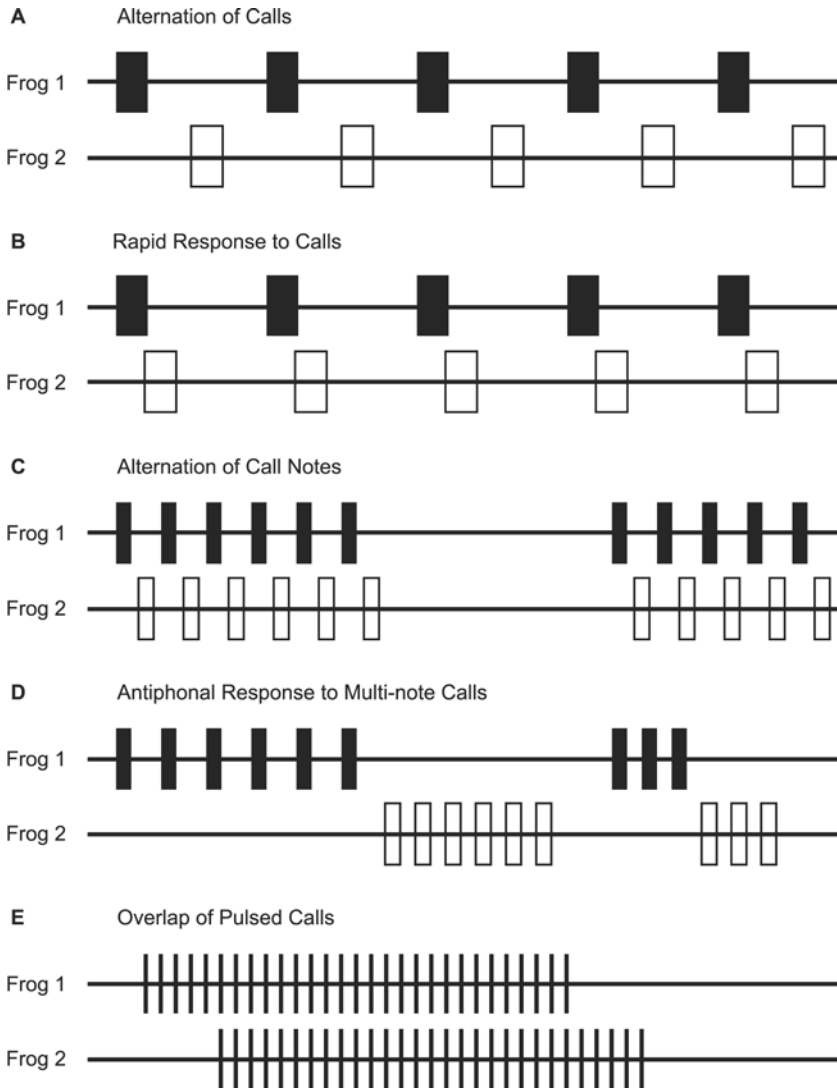


FIGURE 3.7. Diagram of several possible types of vocal interaction between neighboring males in a frog chorus. (A) Calls consist of relatively long notes given at regular intervals, with the calls of the second male precisely alternated with those of the first. (B) Calls consist of relatively long notes given at regular intervals, with the calls of the second male starting immediately after the end of the first male's calls. (C) Calls consist of a variable number of closely spaced short notes, with individual notes of the second male's calls alternating with those of the first male. The result is minimal acoustic interference and relatively precise matching of the number of call notes. (D) Calls consist of a variable number of short notes. Calls of the second male are given immediately after the entire sequence of notes of the first male has ended, with fairly precise matching of the number of call notes. (E) Calls are trills made up of a rapid series of short pulses. Calls are overlapped with no attempt to avoid acoustic interference.

of alternating multinote calls that briefly monopolize the “air-time” for vocal advertisement. Males of *H. ebraccata* exploit silent periods when calling by these species subsides. This is most obvious during interactions with *H. microcephala*, because males of this species chorus in a roughly cyclical pattern in which bouts of vocal activity lasting about 5 to 25 seconds alternate with periods of inactivity of comparable duration.

The roughly on–off or cyclical pattern of chorusing observed in *H. microcephala*, sometimes referred to as unison bout singing (Greenfield and Shaw 1983; Schwartz 1991), also has been reported in other species (Duellman and Trueb 1966; Rosen and Lemon 1974; Whitney and Krebs 1975; Schneider 1977; Zimmerman and Bogart 1984; Ibañez 1991). The cycles last from several seconds to a few minutes, and calling bouts are initiated when the calls of one male stimulate others to join the chorus. Although males of some species of anurans appear oblivious to the calls of others (e.g., the American toad, *Bufo americanus*, and the southern toad, *B. terrestris*; Gerhardt and Huber 2002), male frogs of many species adjust the timing of their calls or call elements relative to the individual calls of conspecifics and heterospecifics. Thus these changes can occur extremely rapidly (e.g., Narins 1982b; Schwartz and Wells 1985; Narins and Zelick 1988; Grafe, 2003) and typically involve either abbreviating or elongating the call period in response to specific calls or call elements of neighbors (Klump and Gerhardt 1992). The outcome of the behavior is often called alternation and males of some species may even interleave notes of multipart calls (or calls of call groups) with those of other males (Schwartz and Wells 1984a; Schwartz and Wells 1985; Grafe 2003; Fig. 3.8). However, alternation between pairs of males may be inconsistent and so result in some acoustic interference (e.g., Schwartz et al. 2002; Gerhardt and Huber 2002). Moreover, in vocal dyads among heterospecifics, there may be species asymmetries in responsiveness (e.g., between the two species of gray treefrogs, *H. versicolor* and *H. chrysoscelis*, Marshall 2004).

*Hyla microcephala* males provide an excellent example of how selection has acted at different levels to shape call timing in a noisy assemblage of calling males. Males produce multinote calls and are stimulated to call and add notes to their calls in response to vocalizations. Chorusing by even a small number of males can be quite noisy, and the calls of males frequently overlap, but when overlap occurs, the constituent notes of neighboring males usually do not. Rather, notes of each interacting male are timed so as to fall within the internote intervals of the other male (Schwartz and Wells 1985; Schwartz 1993). The resulting pattern of note alternation is facilitated by mutual inhibition of note production by each note of the neighbor (Fig. 3.8B). Accordingly, during call overlap between two males, each male will lengthen an inter-note interval when the note of the other male falls within the interval. Conversely, during call overlap, the drop in sound intensity accompanying the end of each interrupting note triggers a male to produce his next note. The ability to rapidly interleave notes is also present in *Hyla phlebodes*, although this occurs without concomitant changes in internote intervals (Schwartz and Wells 1984b; Fig. 3.8A). Precise note alternation may be

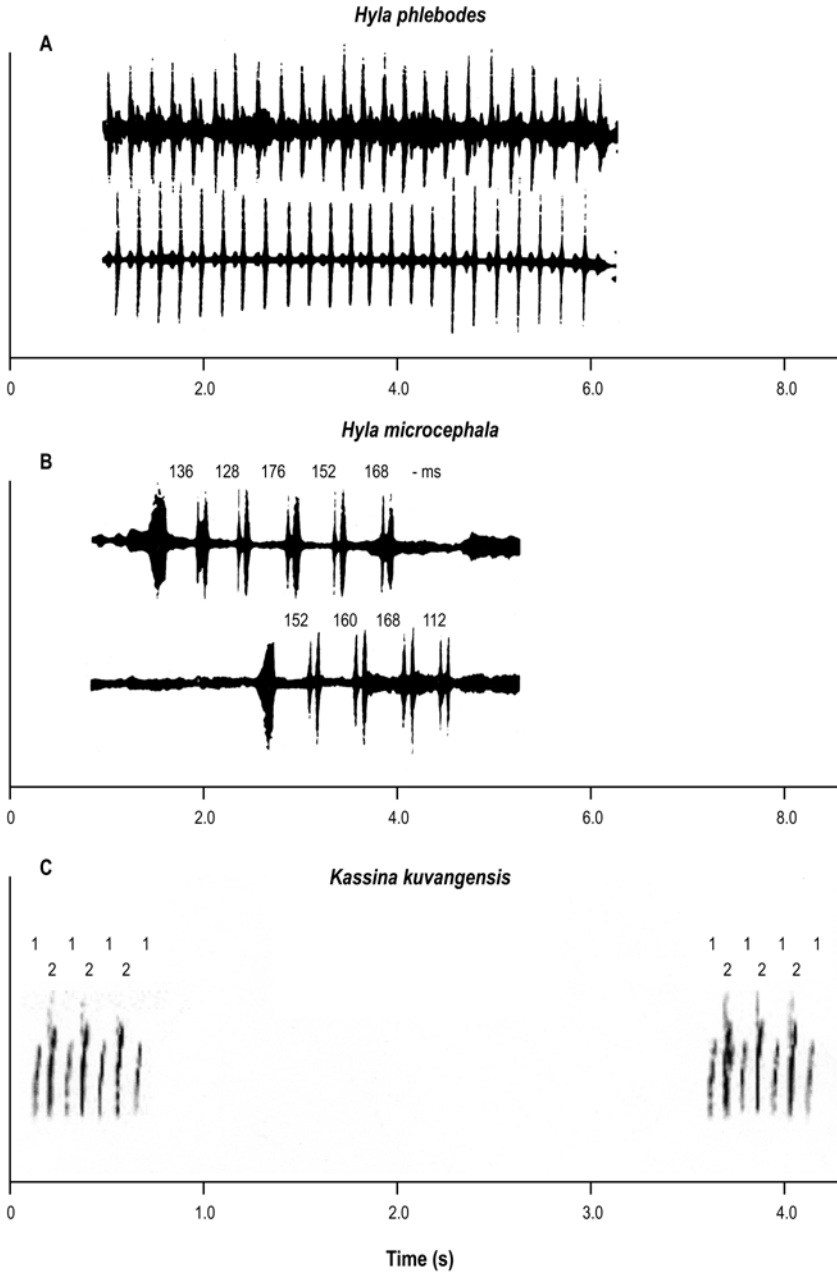


FIGURE 3.8. Two males of (a) *Hyla phlebodes* alternating notes within multinote calls (recordings by Kentwood D. Wells and Joshua J. Schwartz). (b) Same for *Hyla microcephala*, showing an increase in internote intervals (in ms) in overlapped portions of the calls (modified from Schwartz and Wells 1985; reproduced by permission of the American Society of Ichthyologists and Herpetologists). (c) Pair of *Kassina kuvangensis* males alternating calls within “call groups” (modified from Grafe 2005, Fig. 13.1, p. 281; reprinted with the permission of Cambridge University Press). Males of *H. microcephala* and *K. kuvangensis* also alter the spacing between their notes or calls, respectively, in response to the signal elements of alternating competitors.

difficult to achieve, as there are males of other species that produce multinote calls that fail to exhibit note alternation (reviewed in Grafe 2003).

Obviously, in a chorus with many males, pairwise note-by-note timing would not be an effective means to reduce acoustic interference. The solution adopted by *H. microcephala* is to adjust note timing with respect to only a male's loudest (and nearest) one or two neighbors in the chorus while ignoring (for note-timing purposes) the notes of more distant individuals (Schwartz 1993). This behavior has been referred to as "selective attention" and was first reported in frogs by Brush and Narins (1989) in their study of *Eleutherodactylus coqui*. Greenfield and Rand (2000) described similar behavior in *Physalaemus pustulosus* and further demonstrated that the "rules" frogs use to delimit their zone of selective attention are flexible enough to accommodate the dynamic nature of frog choruses. A combination of chorus monitoring and playback tests with interrupting stimuli indicated that such flexibility also characterizes selective attention in *Hyla microcephala*. Nevertheless, additional work on the relative importance of spatial and intensity cues are clearly needed.

The gray treefrog (*H. versicolor*) does not exhibit a comparable pattern of selective attention. In pairwise interactions, males significantly reduced call overlap, but this was not so in groups of three to eight males (Schwartz et al. 2001). Moreover, adjacent males overlapped calls more than did more widely separated individuals. It is possible that these findings were an artifact of the testing environment: an artificial pond with males equally spaced around the pond perimeter. With the additional spatial cues and more pronounced intensity differences present in a natural chorus, male behavior might be similar to that of the aforementioned species. Another possible explanation is that males of *H. versicolor* are not as severely penalized when calls overlap as are some other species. Schwartz and Gerhardt (1995) found that spatial separation of interfering call sources mitigated the effects of acoustic interference. This was not the case with the smaller species *H. microcephala* (Schwartz 1993), however. As discussed above, an intriguing possibility is that males rely on changes in call duration and rate, rather than selective attention, to compensate for the increased risk of call overlap in dense choruses.

Some species of frogs appear to time their calls so that they are more likely to overlap than to alternate (e.g., Ryan 1986; Ibañez 1993; Grafe 1999). At a proximate level, such (approximate) synchrony on a fine-scale may occur via call-period changes induced by a neighbor's call that falls in a certain time-window after the subject's call (Gerhardt and Huber 2002; Greenfield 2002). Alternatively, signal detection may trigger a short-latency vocal response that may or may not occur before the stimulating call has ended (Fig. 3.9A). For example, calling by males of the brown running frog (*Kassina fusca*) from West Africa is triggered by the onset of conspecific calls, leading to overlap (Fig. 3.9B), and the offset of some heterospecific calls, leading to alternation (Grafe 1999). In *Hyla ebraccata*, signals with a rapid rise time are especially effective in eliciting short-latency vocal responses (Schwartz and Wells 1984a). In *H. microcephala*, such sound-induced stimulation evidently occurs in conjunction with sound-induced



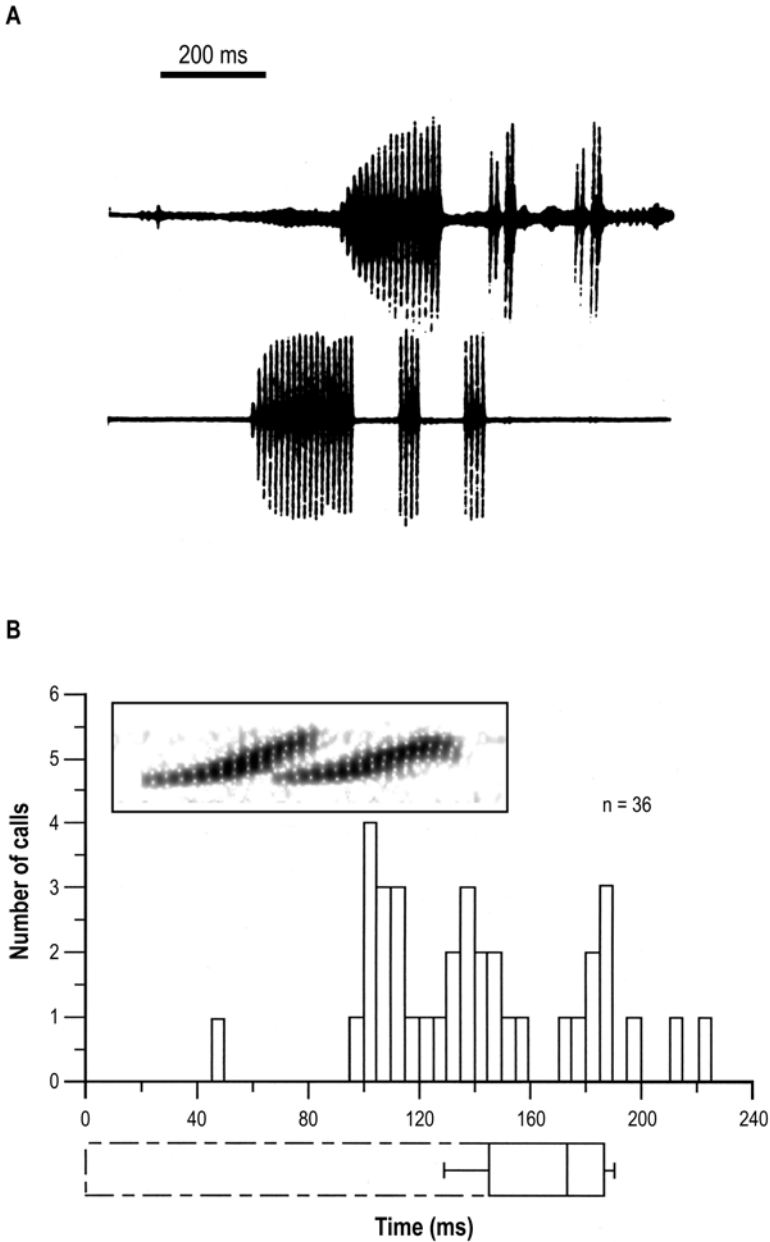


FIGURE 3.9. (A) Call timing between two males of *Hyla ebraccata*, resulting in the primary note of the following male overlapping a secondary note of the leading male. Recordings by Kentwood D. Wells and Joshua J. Schwartz. (B) Call overlap between two males of *Kassina fusca*. The histogram shows the distribution of call latencies of one male to the calls of the other male. The dashed box gives the duration of male calls and encloses a box plot giving the median, interquartile range, and 10th and 90th percentiles of response call latencies. Modified from Grafe 1999, Fig. 1, p. 2333; reprinted with the permission of the Royal Society of London.

inhibition. As mentioned previously, note production also is stimulated by a drop in sound intensity following the end of a neighbor's note (Schwartz 1993; also see Zelick and Narins 1983 for another report of this phenomenon). Thus interacting males overlap calls but rapidly alternate the notes within their calls. Elucidating the neural mechanisms controlling this behavior will be both challenging and fascinating.

#### 4.5 *Ultimate Explanations for Call-Timing Adjustments*

The relationships between the timing of male vocalizations within anuran choruses can have a profound impact on mating success that is comparable to those associated with call structure and rate (Schwartz 1987b; Klump and Gerhardt 1992; Grafe 1999; Schwartz et al. 2001). Background noise levels within choruses often can be very high, and the problem of call overlap and masking interference can be ameliorated if males adjust the timing of their calls relative to those of other individuals. As described above, the time scale of these adjustments may be flexible and relate to the nature of the source of acoustic interference. For example, males of *Hyla ebraccata* may adjust the fine-scale timing of their calls in a way that reduces overlap with the individual calls of males of *H. microcephala* or alternate with groups of chorusing *H. microcephala* on a coarse scale. Phonotaxis experiments showed that males of *H. ebraccata* improved their chances of attracting females by avoiding call overlap with neighboring males (Schwartz and Wells 1984a) and by concentrating calling during quiet periods (Schwartz and Wells 1983b).

Broadcasts of chorus noise did not support the hypothesis that males of *H. microcephala* periodically quiet down during unison bout singing because of an increased threat of masking and acoustic interference (Schwartz 1991). Analysis of muscle glycogen reserves and calling rates suggested that males periodically stop calling to save energy and increase total calling time (Schwartz et al. 1995). Additional factors also may be relevant. For example, cyclical patterns of activity may emerge as a result of the intrinsic auditory sensitivities and response properties of individuals when grouped, but have no functional basis per se (Schwartz 2001). An intriguing possibility is that cyclical calling reduces individual risk of predation, but this hypothesis has yet to be tested.

Both competition and cooperation can occur simultaneously in choruses, and these interactions have been invoked to explain both call synchrony and call alternation (Greenfield 2002; Gerhardt and Huber 2002; Grafe 2005). Males reduce the chances that their signals overlap by alternating calls, part of a general strategy to exploit brief periods of relative quiet (Grafe 2003). On the other hand, males may synchronize calls because the resulting overlap amplifies their signals. This form of cooperation could be advantageous for individuals that call in areas with chronic high background noise, such as streams (Marshall and Gerhardt, unpublished data on canyon treefrogs, *H. arenicolor*). Whether males of some anuran species gain a per capita mating advantage by elevating the signal amplitude in this manner, or by concentrating calls in time, is unknown, but deserves

further study. However, the risk of degrading important fine-temporal information (Schwartz 1987b) within the calls might outweigh any advantages of improved detectability. Reduced risk of predation, perhaps when coupled with cyclical or unpredictable bouts of chorusing, may benefit synchronizing callers. Tuttle and Ryan (1982) presented evidence consistent with this hypothesis in their study of the Panama cross-banded treefrog (*Smilisca sila*) and the frog-eating bat *Trachops cirrhosus*.

Rather than being a manifestation of male–male cooperation, synchrony sometimes may result from male–male competition for females (Greenfield 2002). In *Hyla ebraccata*, rapid male vocal responses result in masking of shorter secondary notes of a leading conspecific male with the longer primary note of a following male (Fig. 3.9A). Tests with females demonstrated that following males are favored under such circumstances (Wells and Schwartz 1984a). In *Kassina fusca*, females also discriminate in favor of overlapping follower calls under some relative call timing arrangements but leader calls under others (Fig. 3.9B), a result that may be due to backward masking or a precedence effect, respectively (Grafe 1999). During interactions and playback tests, Grafe found that responding males timed their overlapping calls to fall in a time window preferred by females.

Greenfield (2002, 2005) proposed that both alternation and synchrony result from a neural process that resets a male's call-timing following perception of another male's call. This call-timing change can increase the likelihood that a male's calls will occupy a leading position relative to those of his neighbor's. Males that are successful in this regard may gain a mating advantage because of an inherent response property of the auditory system of many species known as the precedence effect (for reviews see Zurek 1987, Litovskya and Colburn 1999). In fact, computer modeling has demonstrated that "inhibitory-resetting" of call-timing and also selective attention may be favored by selection when female mate choice is biased by a precedence effect (Greenfield, 2005). Although the term "precedence effect" has been applied when there is a preference for a leading call, in auditory psychophysics the application of the term is more restricted. Under appropriate conditions of signal duration and timing, lagging sounds will be localized at the source of a leading sound. If this phenomenon occurs in female frogs, the advantage to a leading male is obvious. Unfortunately, data are not yet available to conclusively demonstrate a precedence effect in the restrictive sense in anurans. Whatever the mechanistic explanation (e.g., precedence effect, forward masking; Grafe 1996; Gerhardt and Huber 2002), there is growing evidence for preferences by females for leading calls (Dyson and Passmore 1988a,b; Klump and Gerhardt 1992; Grafe 1996; Greenfield et al. 1997; Bosch and Marquez 2002; Marshall 2004; Schwartz unpublished data), although species are known in which females show a follower or no order preference (Wells and Schwartz 1984a; Ibañez 1993; Bosch and Marquez 2001; Gerhardt and Huber 2002; Grafe 2003). In fact, in some cases, leader preferences may be sufficiently strong to counteract or reverse other preferences. For example, in the spring peeper (*Pseudacris crucifer*) females show a leader preference that can tolerate

a 6 to 9 dB relative intensity disadvantage (Schwartz unpublished). If calls do not overlap, a preference is absent. Thus, the call-timing relationships that might confer an advantage to a male are quite circumscribed in this species. Moreover, whether some males are sufficiently consistent as leaders to achieve an advantage and how putative female call-timing preferences respond to increasing levels of acoustic complexity within natural choruses are currently unknown. In the gray treefrog, *Hyla versicolor*, Marshall (2004) demonstrated that females prefer leading calls only when calls, and their component pulses, overlap. Under these circumstances, the preference is so strong that it can reverse the female aversion to calls of *H. chrysoscelis* (Marshall et al., in press). Thus in mixed-species choruses of gray treefrogs, call overlap and a leader preference could result in mismatings and loss of fitness. In Fischer's dwarf frog (*Physalaemus fischeri* [eneseftae]), call order can reverse the bias of females favoring calls with lower dominant frequencies (Tárano and Herrera 2003).

Schwartz (1987b) and Schwartz and Rand (1991) tested three hypotheses, using four species, for why males alternate calls. Hypothesis 1 proposed that alternation allows interacting males to more easily hear one another. This could be advantageous because (a) call intensity cues are used to mediate intermale spacing and/or (b) call detection enables males to adjust their signal attractiveness to match or exceed that of competitors. Interactive playback experiments (Schwartz 2001) supported Hypothesis 1. Hypothesis 2 proposed that alternation helps preserve the fine temporal structure within calls that might otherwise be obscured or degraded by call overlap among males. This hypothesis also was supported. Females of *Hyla versicolor* and *H. microcephala*, species with pulsatile calls or call notes, respectively, discriminated in favor of alternating relative to out-of-phase overlapping calls in four-speaker choice tests. *Pseudacris crucifer* and *Physalaemus pustulosus* females failed to discriminate between calls in the same circumstances. Both of these species lack calls consisting of pulses. *Physalaemus pustulosus* has a frequency-modulated introductory "whine" in its call that contributes to call recognition by females (Rose et al. 1988; Wilczynski et al. 1995). Schwartz and Rand (1991) speculated that the spectral filtering characteristics of the auditory system enable females to sufficiently discern the downward frequency sweep of the whine, even when calls partially overlap. Hypothesis 3 proposed that alternation facilitates the localization of call sources. If this were the case, females of all species should have discriminated against overlapped calls when these were presented precisely in phase. This did not occur. Results from some other studies are also inconsistent with Hypothesis 3 (Passmore and Telford 1981; Backwell and Passmore 1991; Grafe 1996; Marquez and Bosch 2001). Nevertheless, certain call-timing relationships (e.g., overlapped calls with leading versus following pulses, Marshall 2004) may have an impact on localization in a way that was not detected using the stimulus arrangements in the aforementioned experiments.

In addition to the advantages described above for Hypothesis 1, call-timing shifts may have an additional role during male–male interactions. Based on field

observations and results of playbacks to calling *Polypedates leucomystax*, Christensen-Dalsgaard et al. (2002) recently proposed that short-latency responses are a way for males to direct their calls to a particular individual.

## 5. Auditory System Features: Contributions to Communication in Choruses

Features of the auditory system of anurans may facilitate the task of detecting, discriminating, and localizing relevant communication signals within the often noisy and spatially complex “real-world” acoustic environment within choruses (Feng and Ratnam 2000). Most of these characteristics are not qualitatively unique to members of this taxon, although evolution may have fine-tuned the relevant attributes in ways that improve their effectiveness under biologically relevant circumstances.

### 5.1 *Signal Detection and Discrimination*

The tuning of the peripheral auditory system of frogs tends to be well (but not perfectly) matched to the dominant frequency of the species-specific advertisement call and often more complex spectral patterns of call energy distribution (Gerhardt and Schwartz 2001). In fact, the role of the anuran auditory system as a matched filter that can improve the detection of biologically relevant signals in the presence of background noise has long been appreciated (Capranica and Rose 1983). This filtering potential is reflected not only in audiograms (obtained at threshold) but also in critical ratios (e.g., Narins 1982a; Moss and Simmons 1986; Simmons 1988). Certain characteristics of the acoustic milieu of choruses may also be exploited by central neuronal processes and so facilitate call detection. For example, the amplitude envelope of natural background noise can be dramatically modulated with this temporal structure correlated across sound frequencies (Nelkan et al. 1999). In some taxa (e.g., Klump and Langemann 1995), tone detection thresholds are reduced when embedded in noise with such structure as compared to detection thresholds in noise lacking modulations. The actual contribution of this “comodulation masking release (CMR)” to communication of frogs is currently poorly understood (Goense and Feng 2003), but could be significant in situations with considerable abiotic noise or in multispecies assemblages. However, for most chorusing species the most potent source of background noise is that produced by conspecifics rather than heterospecifics with call spectra different from their own. Thus solutions other than matched filtering or CMR must play a part in reducing the potentially serious problems for males and female anurans imposed by masking and call overlap. If males cannot detect the individual calls of neighboring males they may not be able to accurately assess the nature and intensity of competition in their vicinity and may fail to adjust their spacing appropriately. Masking of conspecific calls may impede a female’s

ability to not only find a mate, but assess relative performance within a group of males and so possibly more effectively improve her fitness (e.g., Welch et al. 1998).

In spite of their relatively small interaural distances (e.g., <2.5 cm, Gerhardt and Huber 2002, p. 230), available data indicate that some anurans are able to exploit directional cues to extract signals from the background din of a chorus or calls of overlapping males. In *Hyla cinerea*, separation of speakers broadcasting calls from those broadcasting noise facilitated both detection of advertisement calls and discrimination of advertisement calls from aggressive calls by females during phonotaxis experiments (Schwartz and Gerhardt 1989). Schwartz and Gerhardt (1995) also found that separation of speakers (by 120 degrees) broadcasting overlapping calls of *Hyla versicolor* elicited discrimination in their favor relative to speakers that were not separated. The timing of the overlapped calls was such that call interference rendered the resulting pulse pattern unattractive (Schwartz 1987b). At each ear, separation of call sources may reduce the strength of the auditory input contributed by one of the overlapping calls and so facilitate encoding of an effective pulse pattern (Schwartz and Gerhardt 1995). Interestingly, an earlier experiment with *H. microcephala* failed to reveal such discrimination when speakers were separated by 120 degrees, perhaps because the interaural separation of females in this species is less than half that of *H. versicolor* (Schwartz 1993). Discrepancies between the note-timing behavior of males during natural interactions as compared to those in response to overlapping notes broadcast from a single speaker suggest that angular separation of callers may contribute to the ability of *H. microcephala* males to selectively time their call notes with respect to a subset of chorus members (Schwartz 1993).

The data of Schwartz and Gerhardt (1989) on green treefrogs (*Hyla cinerea*) are consistent with the notion that signal discrimination is a more difficult task than signal detection. However, under some circumstances low to moderate noise levels within choruses may actually enhance the ability of females to discriminate among males. Schwartz and Gerhardt (1998) found that females of *Pseudacris crucifer* preferred synthetic advertisement calls of 3500 Hz to those of 2600 Hz only in the presence of background noise (filtered to resemble that produced by a natural chorus). Multiunit recordings from the auditory midbrain of females suggested a likely explanation. The noise induced a desensitization of the auditory system (this phenomenon is quite familiar to anyone who has been to a loud rock concert) that, in turn, increased the stimulus level at which auditory neurons would reach saturation in their firing rate. This threshold shift was reflected not only in right-shifts in plots of neural activity versus stimulus amplitude but also in plots of neural activity versus stimulus frequency. Relatively flat iso-intensity response plots obtained at high call intensities became peaked after exposure to noise and so resembled those obtained at low to moderate call intensities. Perhaps most significantly, only in the presence of noise was there a significant relationship between the frequency eliciting the maximum multiunit neural activity and the frequency preference of individual females.

Schwartz and Gerhardt (1998) speculated that noise-induced threshold shifts may have their greatest impact on discrimination not for females within aggregations of conspecifics but for females attempting to discriminate males of their own species within mixed-species assemblages (where spectral differences would be more profound than between conspecifics). The peripheral auditory system of anurans is particularly adept at detecting the amplitude–time envelope of sounds and thus, through phase-locking, neurons of the eighth nerve encode modulations in amplitude (e.g., waveform periodicity, pulses) present in the calls of many species (Feng and Shellart 1999; Gerhardt and Huber 2002). High levels of background noise impair this process (Simmons et al. 1992). In mammals low-intensity noise may improve phase-locking (Rhode et al. 1978; Lewis and Henry 1995), but whether noise might augment signal detection or discrimination in anurans through such a mechanism is largely unknown (but see Narins et al. 1997).

## 5.2 *Signal Restoration*

In humans (Warren 1970; Samuel 1981) and starlings (Braaten and Leary 1999), the brain can fill in signal elements that are missing or inaudible due to the presence of masking noise. This process, known as phonemic restoration or temporal induction, provides an illusion of signal continuity and could potentially be useful to anurans within loud choruses. For example, a female *Hyla versicolor* might more rapidly and effectively compare the call duration of adjacent males if she could interpolate between inaudible or obscured sections of calls that might be overlapped by the calls of other males or the background noise of the assemblage. This hypothesis was recently tested using phonotaxis tests using calls containing silent gaps, portions masked by filtered noise, or interrupted by overlapping calls (Schwartz et al. 2004). Results failed to support the presence of a significant restorative process. Females did not “fill in” missing information when large gaps were present, although obscuring pulses within a call with other signals appeared less detrimental than removing pulses.

## 6. Summary

Anuran amphibians are unique among ectothermic tetrapods in the degree to which they depend on acoustic communication to attract mates, advertise territory ownership, or otherwise communicate with conspecifics. The sound production mechanism of most frogs also is unique in that the trunk muscles involved in forcing air out of the lungs and through the vocal chords are not used for normal respiration. Hence, the hypertrophied muscles of male frogs can be considered a sexually selected trait, driven by competition among males for access to females. Anurans with very high calling rates have highly aerobic muscles with high mitochondrial and capillary densities and often large reserves of lipids that are not

present in leg muscles. These morphological and physiological traits support the high metabolic demands of calling. Our knowledge of the physiological, biochemical, and morphological basis of call production is limited, however, to a relatively small sample of anuran species and is not necessarily representative of all anurans. There also has been relatively little research on the structure and function of vocal sacs and how variation in vocal sac structure relates to differences in calling behavior, or the use of vocal sacs as visual signals that complement or amplify acoustic signals.

Many anurans produce several types of calls with different functions, although some have relatively simply vocal repertoires. Most anurans have advertisement calls given spontaneously by males to advertise their species identity, sexual receptivity, and spatial location to females and to other males. Males of many species also have distinctive aggressive calls, which sometimes are graded in a way that allows males to modify the intensity of their aggressive message or trade off female-attracting and male-repelling functions of their calls. Males of some species modify advertisement calls during close-range courtship interactions with females, and in some species, females respond with calls of their own. Both male and female courtship calls are poorly studied and probably are much more common than currently recognized.

Although a frog chorus often seems to be a disorganized cacophony, closer examination often reveals complex networks of interactions among males in a chorus. Males of many species probably attend to the calls of only a few near neighbors, with the remaining males simply contributing to background noise. Males respond to calls of near neighbors in ways that enable them to minimize acoustic interference and maximize the signal-to-noise ratio of their calls. Male frogs become habituated to particular levels of calling activity, so the acoustic threshold for responding to other calling males changes with chorus density. Males of some species that maintain long-term territories are able to recognize neighbors individually and respond more aggressively toward intruding strangers than toward familiar neighbors. Many of the acoustic interactions in choruses can be seen as products of intense sexual selection, with males competing to outsignal their competitors for the attention of females, often increasing rates of signaling as chorus density increases.

Characteristics of the anuran auditory system facilitate the detection and discrimination of biologically relevant signals. The peripheral auditory system of both males and females is selectively tuned to the frequencies of conspecific calls, allowing the frogs to filter out heterospecific calls broadcast on other frequency bands. Upward shifts in auditory response thresholds and directional cues aid communication by some species within noisy chorus environments. Although background noise can interfere with call discrimination, males of some species exhibit enhanced signal discrimination in the presence of low to moderate levels of background noise. This may be particularly important in mixed-species choruses in which heterospecific calls elevate levels of background noise, but are mostly broadcast on different frequency bands from conspecific calls.



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