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Call Monitoring and Interactive Playback Systems in the Study of Acoustic Interactions among Male Anurans

Introduction

Communication is a dynamic process in which a signal given by one individual can influence the behavior of another (Wiley 1994). Often communicative interactions involve the reciprocal exchange of signals as well as changes in the character of signals (Bradbury and Vehrencamp 1998). If many individuals are signaling within a shared active space, the details of the interactions may be quite complex. Additional complexities are imposed by changing social conditions, the presence of background noise, interference of signals, and the fact that the same signal may transmit different messages and have different meanings to different receivers. The acoustic environment in a chorus of frogs is characterized by just such complexities (Littlejohn 1977; Narins and Zelick 1988; Wells 1988; Gerhardt and Schwartz 1995). Nevertheless males successfully advertise information on their location, species identity, and perhaps even condition, not only to other males but also to gravid females that they are attempting to attract (Gerhardt 1994). How males communicate such information may involve the use of adjustments in call timing, elaboration of calls, exchange of graded signals, and selective attention to a subset of chorus members. Moreover vocal competition among males in choruses can be intense, and males need to use flexible calling strategies and favorably distinguish themselves from competitors while also maintaining sufficient reserves of energy to fuel signaling for those periods of time in which females are available (Schwartz et al. 1995).

Although courtship calls may be directed at an adjacent member of the opposite sex before pairing in some species (e.g., Given 1993; Bush 1997; Ovaska and Caldbeck 1997), advertisement calls are the principal signal type used by males to attract females in choruses of anurans (Wells 1977a, 1977b; Gerhardt 1994). In fact selection of a mate by females from among those conspecific males available on a given night is based largely on features of the advertisement call or the manner in which it is given. These features may be spectral (e.g., dominant frequency), temporal (e.g., call duration), or females may even evaluate such calling attributes as call rate and call complexity (Gerhardt 1994; Sullivan et al. 1995). If a male is to be reproductively successful, he must effectively transmit those attributes of his signals or signaling behavior relevant to decision-making by females, often in a noisy environment. He must also be aware of the calling behavior of his neighbors and respond rapidly to changes in their vocal performances to maintain his relative attractiveness. In addition males may not tolerate the loud calls of nearby individuals and respond to these with aggressive calls (Brenowitz and Rose 1994). Aggressive calls also may be exchanged during physical interactions (Wagner 1989a). Both advertisement calls and aggressive calls may be simple, consisting of a single note or notes of one type or complex, formed from notes of different form and even function (Narins and Capranica 1978; Littlejohn and Harrison 1985; Wells and Bard 1987; Backwell 1988; Jehle and Arak 1998). During vocal exchanges male frogs may alter call rate, complexity, duration, and intensity (Lopez et al. 1988; Wells 1988). There is evidence that males of a few species change their call frequency during interactions (Lopez et al. 1988; Wagner 1989a, 1989b; Grafe 1995; Bee and Perrill 1996; Howard and Young 1998; Bee et al. 1999; Given 1999), perhaps to deceive opponents during assessment of size or to increase their relative attractiveness to females.

How male anurans communicate in a chorus environment has been the focus of much research (Narins and Zelick 1988; Wells 1988) and is one focus of this chapter. I concentrate on recent studies of how males shift the timing of calls or call elements, adjust qualities of their advertisement calls, and use aggressive calls. I use primarily examples from those species that I have studied extensively: *Pseudacris crucifer, Hyla microcephala,* and *H. versicolor.* Interspecific interactions receive little attention in this chapter, and interested readers are referred to the review of Gerhardt and Schwartz (1995). A challenge for students of animal communication has been to develop effective techniques for data acquisition from interacting individuals and the presentation of signals in a way that elucidates how and why they are used. Accordingly a second focus of this chapter is how computer hardware has been and can be used to answer questions about communication in the complex acoustic environment of anuran choruses. I focus on systems that allow researchers to simultaneously monitor the vocal activity of more than two members of a chorus and interactive playback methods that facilitate subject-driven presentation of acoustic stimuli. I discuss how multichannel systems can reveal call-timing interactions that reduce acoustic interference with just a subset of chorus members, help us identify acoustic criteria used by females during mate choice, and illustrate how energetic constraints and male vocal competition may shape chorusing dynamics. I also describe how interactive playback can be used to dissect the details of call-timing behaviors in a way that may illuminate their underlying mechanisms and functions and enable researchers to set up vocal contests between a male and a simulated competitor in investigations of aggressive calling.

Computer-Based Monitoring and Playback Techniques

When I began research on anuran communication in 1980 I studied male–male acoustic interactions with playback experiments and by making stereo tape recordings of male–male vocal exchanges. In the playback tests males were presented with prerecorded calls of one type and their responses, along with the stimulus calls, were tape-recorded on a second machine. Analysis of the recordings was extremely tedious and involved listing each subject's call types and measuring the timing of notes on a storage oscilloscope. Since the late 1980s I have employed a computer-based system to conduct interactive playback experiments and monitor the vocal interactions among male frogs. With a computerized record of experiments, the analysis of data is relatively expeditious. Therefore within a field season I can design additional experiments or modify my testing protocol based on my results. Another important advantage of a computer-based approach is that one is not constrained by the unnatural form of a fixed sequence of tape-recorded playback stimuli. Rather, with computer-controlled playback, one has considerable flexibility in both the timing and the type of stimuli that are broadcast to the subjects. Furthermore, with computer-based monitoring, it is relatively easy to obtain a record of the calls given by many more males than just the two individuals that are possible with a stereo tape recorder. Because males within choruses often call relatively near one another, a multichannel system allows one to determine who is and who is not interacting vocally. The spatial structure of vocal interactions will shape the pattern of vocal competition among males and also has important consequences for acoustic interference within the aggregation.

Call-Monitoring Systems

Two general approaches have been used recently to monitor the vocal activity of more than two males in what McGregor and Dabelsteen (1996) have called a "communication network." In the first of these, individual microphones are placed near each male and an electronic interface transforms their analog signals before they are either tape-recorded or sampled by a computer. For example, in the system used by Brush and Narins (1989) to study the chorusing dynamics of *Eleutherodactylus coqui,* above-threshold sound production by each of up to eight subjects triggered a tone pulse at a unique frequency by a multichannel encoder. Recordings of these tones were decoded using bandpass filters and additional circuitry that produced a voltage change

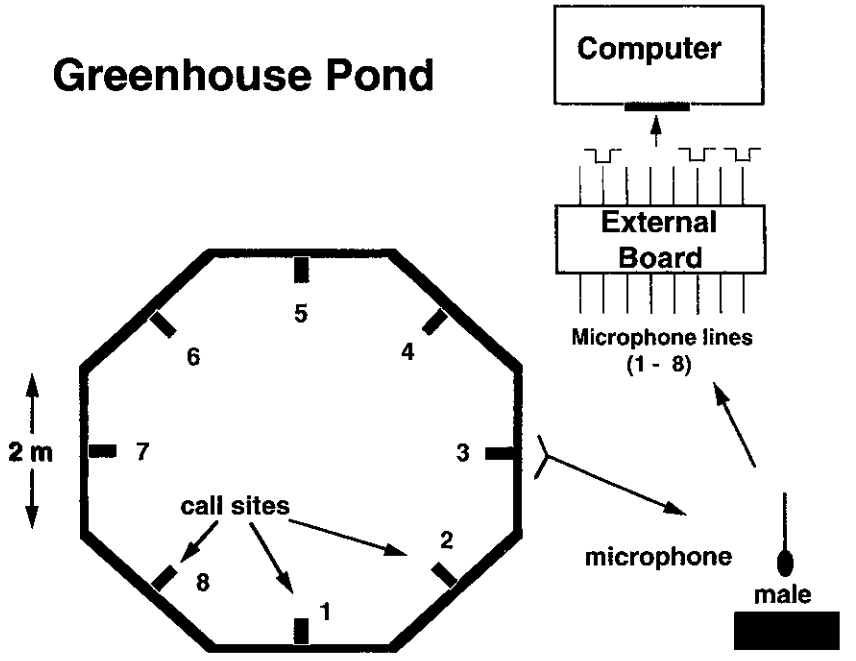

Figure 14.1. Schematic diagram of the artificial pond in the greenhouse as seen from above. The calls of up to eight males are monitored with a computer and an eight-channel custom-built interface board. A unidirectional microphone is suspended above each perch and a cable is run to the computer interface box outside the enclosure. If frogs call at positions 2, 6, and 8 in the pond, high to low voltage transitions, as shown, will be detected on the corresponding data lines of the computer's parallel port. The call monitoring system has also been used to monitor males in the field.

in response to an above-threshold signal at a particular frequency. These voltage changes were detected by a computer sampling the eight data lines of its parallel port and were stored as either zero or one. Therefore each of the eight-bit values in every byte of data indicated whether a male was calling at a particular location for any time sample.

The approach I have used with *Hyla microcephala* in the field (see Schwartz 1993 for additional details) and *H. versicolor* in an artificial pond is similar but avoids the frequency encoding and decoding steps used by Brush and Narins. With my system, up to eight microphones are connected to a battery-powered interface board that sends its output to a computer via the parallel port (Figure 14.1). The output for each of eight parallel channels of the board undergoes a voltage transition, of preset duration, in response to above-threshold input from a microphone. By adjusting the duration of the output pulse from the board and the sampling rate of the computer, it is possible to change the temporal resolution of the system. Thus calls, notes, or even individual pulses within calls may be discerned, and the specific frogs that are calling, or not calling, at a particular time are indicated in the pattern of zeros and ones in each byte of data. Because the interface board does not encode the spectral information in calls, the high sampling rate that would be needed to store such data is unnecessary. I have found that a sampling rate of 100 or 200 Hz is adequate to answer questions about call duration or note timing, and so it is possible to record many hours of data with relatively small amounts of computer memory.

Conceptually similar systems have been used in other studies of either anurans (Passmore et al. 1992) or chorusing insects (Bertram and Johnson 1998; Michael Greenfield, personal communication). A difference between these systems and my own is that the analog signals from each microphone are sampled sequentially rather than simultaneously and the data multiplexed in the computer record. Although the hardware used by the first two research groups cited limited their observations to a maximum of eight males, in principle an unlimited number of individuals could be monitored. Maintaining temporal resolution requires an increase in sampling rate with an increase in the number of data channels multiplexed. Moreover this method requires that each time sample be correctly identified as coming from a particular channel. If any glitches in computer timing occur they can cause a serious problem during analysis.

While working on the African painted reed frog (*Hyperolius marmoratus broadleyi*), Grafe (1997) used a second general approach originally developed to monitor the songs of cetaceans in the open sea (Clark 1989; Spiesberger and Fristrup 1990). He was able to use differences in the time of arrival of male calls at three microphones at the edge of a chorus to calculate both the location of each individual and its calling rate. McGregor and Dabelsteen (1996) and McGregor et al. (1997) discuss in more detail advantages and limitations of acoustic localization systems (ALS) as applied in studies of avian acoustics.

Interactive Playback

During interactive playback the broadcast of an experimental stimulus is triggered, after a preset delay, by the calls of the subject (Pina and Channing 1981). If an analog synthesizer is used the kinds of sounds produced can be seriously constrained by the electronics of the device, although careful design can allow for the creation of a variety of stimuli that can be used with different species (Narins and Capranica 1978; Narins 1982a; Schwartz 1987a, 1989). Moore et al. (1989) used a custom digital recording and playback device that allowed call-triggered playback of calls previously digitized and stored in RAM. Under circumstances requiring a clone of a natural stimulus call, this kind of system has some advantages over an analog synthesizer, but for greatest flexibility a PC-based approach should be used. The use of a computer (with sound hardware built in or added as a peripheral) essentially frees the researcher from the limitations on signal form imposed by an analog synthesizer, while allowing playback of digitized natural or synthetic calls if they are required.

Use of a computer also provides the researcher with many options for the delivery of stored sounds to the subject (Table 14.1). These sounds might be broadcast after a key is pressed or delivered automatically. Interactive playback experiments with birds have until now relied on the first form of delivery (reviewed in Dabelsteen and McGregor 1996). For example the "SingIt" program written by Bradbury and Vehrencamp (1994) responds to strikes of the keyboard or clicks of the mouse and can be run on a Macintosh PowerBook in the field. A system in which the computer responds automatically should be used for experiments in which very rapid or low-variability stimulus-response times are required. In a simple scheme for automatic stimulus delivery, one could have the computer respond after a fixed time delay following the detection of sound produced by the subject above a preset intensity. Following a programmed "dead" time, the computer could be triggered again. The interactive playback "effect module" (for SoundMaker software running on Apple computers) written by Alberto Riccio in collaboration with Rafael Márquez (Márquez et al. 1998) permits such tests. In a more complicated experiment the computer could identify different call or note types produced by a subject and then respond to each with a different kind of stimulus (e.g., Schwartz 1994). One could even have the computer digitize a subject's calls and echo these calls back to him. Unfortunately it would be difficult to design a software package that could accommodate the range of experiments that many different users might desire. Learning how to program the hardware of the computer used in the field will often be a necessary chore for those requiring a complex or idiosyncratic algorithm. This is the approach I have taken for interactive playback using Commodore Amiga computers.

Types of Vocal Interactions

Fine-Scale Call Timing Adjustments by Males

For communication to occur, information must be transmitted from a signaler in a form recognizable to a receiver. If abiotic noise or the signals of other organisms attempting to use the same communication channel obscure important elements of a call, information transfer will be impaired. One possible solution to this problem of interference is to move away from the noise source. Another is to call loudly. A caller may also make his signals redundant—that is, call a lot or use a call with copies of important elements. However anuran amphibians often call in choruses, and in dense aggregations of conspecifics this response may be inadequate. Not only are different males calling at similar frequencies, but also they typically elevate their rate of signal production (but see Sullivan and Leek 1986) because females may approach the most vigorous callers. In multispecies assemblages, heterospecific males may also pose a serious noise problem if the frequencies of their calls fall within the critical bands surrounding the frequencies of the conspecific call (Scharf 1970; Schwartz and Wells 1983a, 1983b).

Males of diverse taxa of chorusing organisms adjust the timing of calls or notes to those of other individuals (Klump and Gerhardt 1992; Greenfield 1997), and this behavior often mitigates the problems of masking and other forms of

Table 14.1 Some options for interactive playback

Trigger Reference	Response Delay	Response Type	
Call start	Fixed	Matching	Different
Call end	Variable	Single	Multiple
Specific call	Random	Discrete	Graded
Call element		Interrupting	Alternating
Alternate calls		Stored	Echo of subject
		Constant amplitude	Variable amplitude

acoustic interference (e.g., Schwartz 1987a). Nevertheless there are different adaptive explanations for certain temporal adjustments (see below). Call-timing interactions in anurans have been studied extensively using descriptive and empirical approaches (for review see Klump and Gerhardt 1992). Although the calling of some species may have little or no effect on the calling of others (e.g., calls of *Rana catesbeiana* on *Hyla versicolor,* Schwartz et al., unpublished data), careful analysis of recordings can reveal nonrandom patterns of call or note timing among conspecific or heterospecific males. Moreover the temporal relationships can be influenced profoundly by the spatial relationships among callers (Schwartz 1993).

Male anurans may answer the individual vocalizations of conspecific or heterospecific males with short-latency responses or react with small shifts in the timing of their calls. Although this behavior can produce overlapping calls or notes as in *Hyla ebraccata* (Wells and Schwartz 1984a), *Smilisca sila* (Ryan 1986), or *Centrolenella granulosa* (Ibáñez 1993), the resulting "entrained" calls often fall in the intercall (or internote) intervals of the stimulating male and may produce a pattern of alternation. For example, Schwartz and Wells (1984a, 1984b, 1985) demonstrated, using playbacks of recorded vocalizations, that males of *H. ebraccata, H. phlebodes,* and *H. microcephala* made similar adjustments in the timing of their calls to calls of conspecifics and congeners. Males often answered stimulus calls within a few hundred milliseconds, producing a loose pattern of alternation. A particularly impressive study is that of Zelick and Narins (1985) on the Puerto-Rican species *Eleutherodactylus coqui* and it demonstrates the importance that gap detection may have on the relative call timing of interacting males. Zelick and Narins presented males with long and short tone-bursts in which they had placed 750 ms gaps in a pattern that should have been unpredictable to their subjects. These gaps were just long enough for a male to place a Co and a Qui note. Nevertheless male "coquis" had little difficulty with a task that proved beyond the abilities of human subjects: two-note calls were placed in the intervals without overlapping the tones. An additional experiment demonstrated that males could detect and respond to reductions in tone intensity at least as small as 4 dB SPL (Narins and Zelick 1988). Grafe (1996) has demonstrated that *Hyperolius marmoratus broadleyi* males are also quite adept at placing their calls within brief gaps during tone broadcasts.

My studies of *Hyla microcephala* demonstrated that detection of brief drops in background noise intensity may contribute to the ability of males to avoid acoustic interference (Schwartz 1993). Males of this species produce calls that may contain over 15 notes, and because males answer their neighbors with short-latency responses, calls of vocally interacting individuals often overlap. Inspection of stereo recordings from pairs of males revealed that in such instances acoustic interference rarely occurred because the notes of each male's calls alternated with those of the other (Schwartz and Wells 1985). Recordings also indicated that this note alternation is facilitated by an increase in internote spacing during interruptions. Similar behavior has been reported in *Smilisca sila* (Ibáñez 1991), although in this species males are not as effective in avoiding note interference as in *H. microcephala.*

I used an interactive playback experiment to investigate the phenomenon in *Hyla microcephala* in more detail. I programmed my computer to answer a male's introductory note with a synthetic note ranging from 20 to 1000 ms in duration (Schwartz 1991). During the experiment, the computer stored a record of the timing of the subject's notes. I found that males increased the spacing between their notes during interruptions of all durations. If the interruption was 400 ms or longer, however, this increase was often insufficient to prevent overlap with the stimulus (Figure 14.2). In interactions with conspecific males, the majority of interruptions (by the introductory and secondary notes of advertisement calls) would be less than 100 ms in duration. Therefore acoustic interference with close neighbors can often be avoided.

The increase in internote spacing during an interruption probably results from a temporary inhibition of note production whose strength decays with time. For two males to effectively alternate notes in overlapping multinote calls, they need also to respond rapidly following the termination of each interrupting note. A second experiment using interactive playback of interrupting 200 ms notes with centrally placed gaps of 10, 20, 30, or 40 ms indicated that gaps greater than 10 ms resulted in a disinhibition of note production (Schwartz 1993). Thus males often overlapped the second half of the split stimulus note with the second note of their own call.

Work on call timing in *Hyla microcephala* could benefit from additional research using interactive playback or randomly timed stimuli (Klump and Gerhardt 1992). For example, interrupting stimuli with varying time delays could be used to test elements of the model of call timing put forth by Moore et al. (1989) based on their study of *Leptodactylus albilabris.* The model is an elaboration of an earlier formulation of Narins (1982a) and posits that there are periods in a male's intercall interval during which acoustic stimulation may inhibit calling, stimulate calling to different degrees, or have no effect.

The problems of acoustic interference and call leadership are more difficult in a large chorus than when only one competing male is nearby. How do male frogs adjust the timing

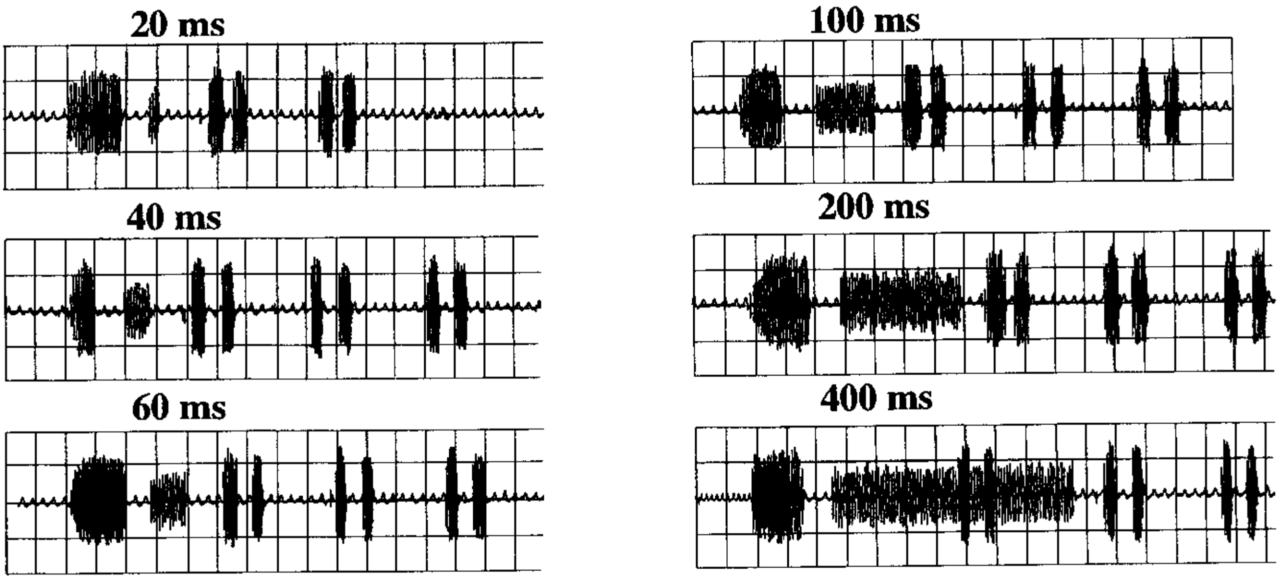

Figure 14.2. Oscillograms of the calls of a male *Hyla microcephala* in response to interruptions with computer-generated synthetic notes of 20–400 ms. The changes in note timing by the male accommodated interruptions below 400 ms in duration. Modified from Schwartz (1991).

of their calls in situations in which many other males are signaling? For example, do males exhibit selective attention by responding to just a subset of chorus members (Table 14.2)? Moreover, under conditions of increased acoustic complexity would these adjustments in timing result in enhanced attractiveness to females? I attempted to answer these questions using call monitoring, interactive playback, and female choice tests with *H. microcephala* (Schwartz 1993).

In four groups of 6, 5, 4, and 4 males, I found that males were most responsive to other chorus members whose calls were loudest at their position. These were typically, but not always, their nearest neighbors in the group. That is, males increased the spacing between their notes in response to interruptions by those individuals whose calls might be expected to pose the most serious interference problem. However males often failed to respond in this way to interrupting notes of certain males that should have been audible to them (Figure 14.3). For example, in Figure 14.3 one can see that male 4 responded when interrupted by male 3 but not by male 5—although the estimated intensity of the calls of male 5 was just 1 dB below those of male 3 (96 vs. 97 dB SPL at the position of male 4). The data suggested that males near the edge of a chorus were more likely to ignore the calls of other males than were more centrally located individuals.

When I used interactive playbacks to interrupt males with the simultaneous broadcast of a lower intensity long (200 ms) note and a higher intensity short (60 ms) note, I predicted that the longer note would be overlapped because of selective attention to the shorter note. This expectation was only partially met. In the experiment I varied the relative intensity of the two interrupting notes (from 0 to –15 dB). As the relative intensity of the longer note increased to approach that of the shorter note, there was a gradual increase in the spacing between the notes of the interrupted males. Therefore, the all-or-nothing character of responses that was observed in the natural chorus was not evident. One possible explanation for this difference is that directional cues were available to test subjects in the natural chorus that may have enabled them to identify neighboring callers as discrete sound sources at different positions. Because a single speaker was used to broadcast both interrupting notes in the playback experiment, only information on the intensities of notes was available to the test subjects. The data suggest that information on proximity of calling males augments information on intensity during calling in *H. microcephala*. This hypothesis could be tested in playback tests using two speakers at different distances from the test subjects.

Four-speaker choice tests with females of *H. microcephala* demonstrated that males who allow their notes to be overlapped by members of the chorus close to themselves might jeopardize their opportunities to attract a female. However there may not be much of a penalty for acoustic interference among most males whose calls differ by at least 6 dB at the position of a female (Schwartz 1993). Because calling males are usually ignorant of the position of females in or near the chorus, the best realizable strategy may be for males to time-shift notes in response to their loudest neighbors.

Selective attention by chorusing males of other taxa has also been reported. Individuals of the tarbush grasshopper,

Table 14.2 Hypotheses that address the form, proximate causes, or functional significance of aspects of anuran vocal behavior discussed in this chapter; the explanations are not necessarily mutually exclusive

Selective Attention

1. **Call Interference.** Call interference with a male's nearest or loudest neighbors jeopardizes that male's chances of attracting a mate more than interference with other males in the chorus. Therefore males selectively adjust the timing of their calls with respect to only the most potent sources of acoustic interference (Brush and Narins 1989; Schwartz, 1993).
2. **Threshold Shift.** A noise-induced change in auditory sensitivity reduces the number of callers a male can hear (Narins 1987; Schwartz and Gerhardt 1998).
3. **Call Leadership.** Selective attention facilitates adjustments in call-timing during contests among males for call leadership position that attracts females (Greenfield et al. 1997).
4. **Proximity-Based Call Elaboration.** Males selectively elaborate their calls with respect to their nearest neighbors in the chorus. This may be because males do not detect the calls of other males or because a female only evaluates a subset of chorus members in her immediate vicinity (this chapter).
5. **Attractiveness-Based Call Elaboration.** Males selectively elaborate their calls with respect to their most attractive audible neighbor in the chorus (this chapter).
6. **Context-Dependent Attention.** Males respond to different subsets of chorus members with respect to the timing and elaboration of their calls (this chapter).

Call Alternation

1. **Call Detection.** Alternation helps a male to either detect a neighbor's calls or assess their intensity (Lemon 1971; Passmore and Telford 1981; Schwartz 1987; Schwartz and Rand 1991; Narins 1992).
2. **Signal Degradation.** Males alternate because overlap can degrade fine temporal information within advertisement calls critical to call recognition or species discrimination by females (Littlejohn 1977; Wells and Schwartz 1984a; Schwartz 1987; Schwartz and Rand 1991).
3. **Localization.** Alternating calls are easier for females to localize than overlapped calls (Passmore and Telford 1981; Zelick and Narins 1985; Wells and Schwartz 1984a; Schwartz 1987a; Schwartz and Rand 1991; Grafe 1996).
4. **Epiphenomena of Signaling Interactions.** Alternation is an epiphenomenon of call-timing mechanisms that evolved in response to selection favoring males whose calls lead those of other males (Greenfield and Roizen 1993; Greenfield et al. 1997).

Cyclical Calling

1. **Fatigue.** Males must periodically cease calling because lactate accumulates in their calling muscles (Whitney and Krebs 1975; Pough et al. 1992).
2. **Female Preference.** Females discriminate in favor of males that call in bouts (Schwartz 1991).
3. **Noise.** Calls stimulate calling at low noise levels, but at high noise levels calling is inhibited (Schwartz 1991).
4. **Energetic Constraint.** Periodic pauses in calling conserve long-term energy reserves. This allows males to call for many hours each night at high short-term rates (Schwartz 1991; Schwartz et al. 1995).
5. **Predation Risk.** Periodic pauses in calling of the group make it more difficult for predators to find males within the group (Tuttle and Ryan 1982).
6. **Emergent Property.** Cyclical calling emerges as a mathematically predictable byproduct of mutual acoustic stimulation of chorus members (Cole and Cheshire 1996; Goodwin 1998).

Elaboration of Calls

1. **Female Attraction.** Males attempt to exceed the acoustic energy content of the advertisement calls of their competitors (via elevation of call rate, call intensity, call duration, or number of notes) because females are preferentially attracted to calls of relatively higher perceived energy (Ryan 1988; Ryan and Keddy-Hector 1992; Schwartz et al. 1995; Sullivan et al. 1995).
2. **Energy Conservation.** To avoid wasting energy males should modulate calling behavior in ways that reflect the level of competition in the chorus (Wells and Taigen 1986, 1989; Ryan 1988; Pough et al. 1992; Schwartz et al. 1995).
3. **Noise Level-Based Response.** Males gauge the intensity of competition for females indirectly and so elaborate their calls with respect to the overall background noise level of the chorus (this chapter).
4. **Focally Directed Responses.** Males elaborate their calls with respect to particular (one or more) chorus members (see "Selective Attention," this chapter).

Graded Aggressive Calls

1. **Bifunctionality.** Graded calls allow males to simultaneously vary the aggressive content of the call as well as its attractiveness to females (Wells and Schwartz 1984b; Wells and Bard 1987; Wagner 1989a; Grafe 1995).
2. **Motivation.** Longer calls signal an increased likelihood that the signaler will vigorously defend his calling site and even attack an opponent (Schwartz 1989, 1994; Wagner 1989a; Grafe 1995).
3. **Assessment.** Longer calls signal greater resource-holding potential (e.g., size, strength, energetic reserves) (Schwartz 1989, 1994; Wagner 1989a; Grafe 1995).
4. **Call Disruption.** Longer calls more effectively disrupt a rival's calling and so impair his ability to attract a female (this chapter).
5. **Behavioral Efference.** Aggressive calling increases the level of aggression in the caller. Therefore call duration of males escalates during an encounter through a process of positive feedback (Bond 1989a, 1989b).

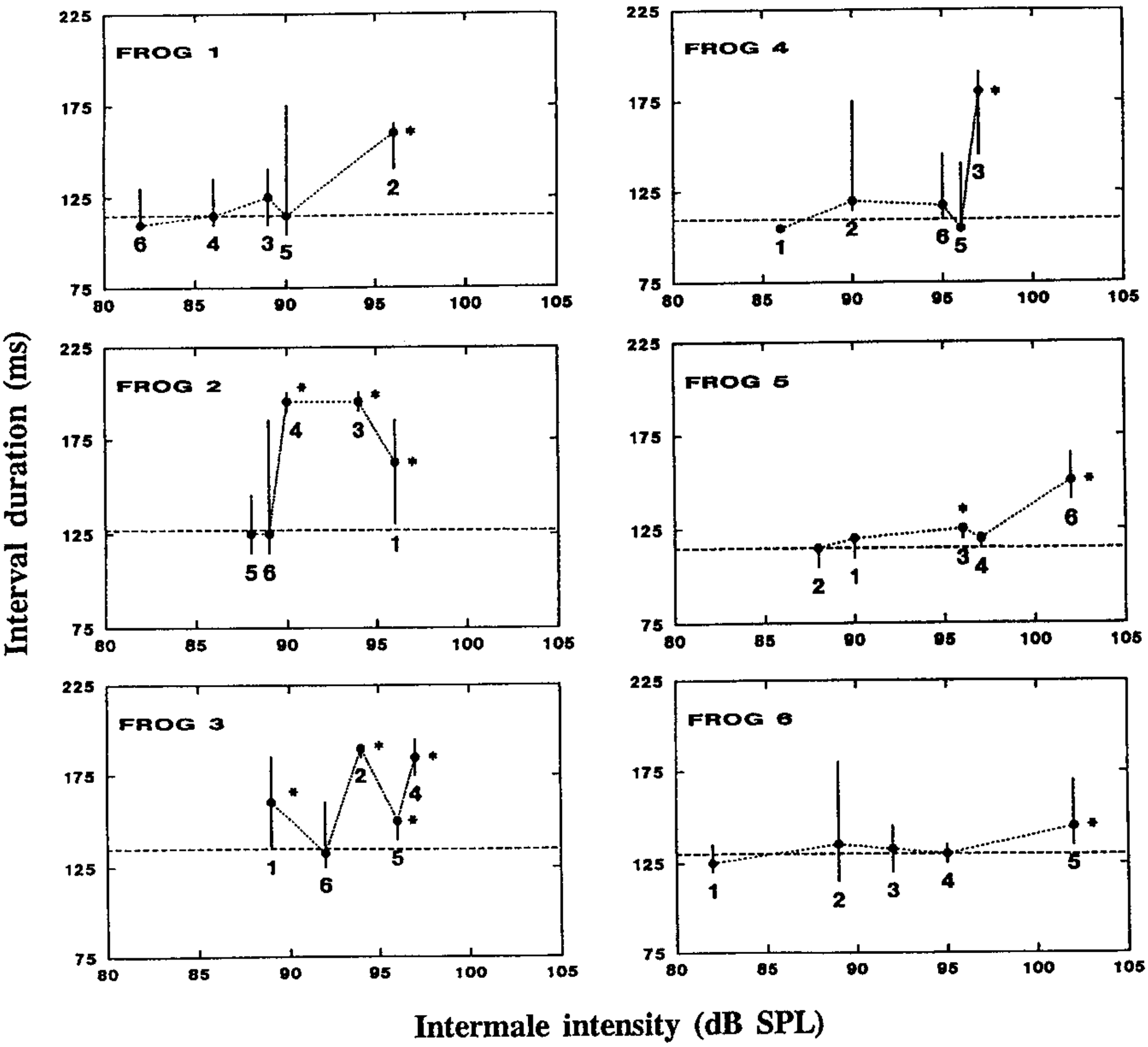

Figure 14.3. Durations (median values, approximate 95% confidence intervals) of the interrupted internote intervals of each of six males in a group of *Hyla microcephala* when interrupted by one other frog in this group. The number below each data point indicates the interrupting male. The estimated sound intensity (peak, dB SPL) of the notes for each interrupting male at the position of the interrupted male is shown along the abscissa. An asterisk indicates that the durations of interrupted internote intervals were significantly greater ($p < 0.05$, Wilcoxon two-sample test) than those internote intervals that were not interrupted (median duration indicated by the horizontal dashed line). The 95% confidence interval around the median duration of uninterrupted intervals (not shown) was 5 ms or less for all frogs except male 1 (10 ms). From Schwartz (1993).

Ligurotettix planum, attempt to shift their calls to a leading position with respect to their nearest neighbors, but not with respect to more distant members of the chorus (Minckley et al. 1995). Moreover this is a dynamic process whereby the sphere of acoustic interaction can change depending on the spacing and relative intensities of males in the chorus (Snedden et al. 1998). Especially interesting is the finding that the inhibitory-resetting of call timing modeled by Greenfield et al. (1997) is evolutionarily stable in choruses only if males exhibit selective attention. Brush and Narins (1989) used their eight-channel call-monitoring system to study call-timing interactions within groups of four and five males of *E. coqui*. Randomization of the call durations and intercall intervals enabled them to test whether patterns of acoustic interference among pairs of males differed significantly from those expected by chance. The analysis revealed that males typically avoided overlap with just two of their neighbors. Recently, Snedden and Rand (unpublished data) have discovered that males of the túngara frog, *Physalaemus pustulosus*, reset the timing of their "whines" with respect to only their nearest and loudest neighbors in the chorus.

With Bryant Buchanan and Carl Gerhardt, I have investigated call timing of *Hyla versicolor* following manipulations of chorus size. Up to eight males were allowed to call from equally spaced perches around the edge of an octagonal artificial pond in a greenhouse (Figure 14.1). As in *H. microcephala*, the percentage of a male's calling that was free from acoustic interference decreased as a function of chorus size (Figure 14.4A; Kruskal-Wallis test, $\chi^2 = 106.3$, $p < 0.0001$). However selective avoidance of interference with nearest neighbors appeared to be absent; rather, individuals were more likely to overlap an adjacent male in the pond than males separated by two or more positions (Figure 14.4B; Kruskal-Wallis test, $\chi^2 = 47.7$, $p < 0.0001$).

It is possible to test statistically for nonrandom calling interactions between pairs of male frogs in various ways. For example, Klump and Gerhardt (1992) describe approaches using distributions and plots of among- and within-male intercall intervals, distributions of relative phase angles, cross-interval histograms, and cross-correlation. Using an approach initially outlined by Popp (1989) and also used by Brush and Narins (1989) in which observed call durations and intercall intervals are randomized, we found that the males in choruses of eight frogs were more likely to overlap their closest neighbors than was expected by chance (Figure 14.4C). In fact just 11.25% of such pair-wise interactions showed significantly less than expected interference. Active avoidance of overlap occurred only when chorus size was reduced to two males and was significant in 70% of interactions. Therefore if large groups ($n \geq 8$) of *H. versicolor* call in close proximity (as in the artificial pond), on average more than half of the pulse trains produced by a male will be overlapped by the calling of other individuals. In a natural setting, males have considerable freedom to adjust their spacing and thus more easily avoid acoustic interference with callers they perceive as loud. Nevertheless it is obvious to anyone who has listened to males in a dense aggregation that overlap of calls occurs.

Given that call interference can impair a male's ability to attract a female, why do males of *H. versicolor* not exhibit selective attention to timing of calls? One explanation may be that the expectation for call overlap between any particular pair of males is already quite low. Even for adjacent males in our eight-male choruses, such overlap represented only about 11% of calling time (Figure 14.4B). Another factor is that females may not discriminate against males with overlapping calls if these males are well separated. This failure to discriminate against them may occur because directional cues provided by the female's auditory system reduce degradation of the inherent pulse structure within overlapping calls of the interacting males (Schwartz and Gerhardt 1995). Interestingly, in *H. microcephala*, a smaller species than *H. versicolor* that shows selective attention, I found angular separation of speakers did not change female discrimination against overlapping calls (Schwartz 1993).

Perhaps what we observe as "selective attention" may be a by-product of the masking of the calls of all but a male's closest neighbors by the background din of the chorus. Although masking certainly circumscribes the range of male vocal interactions within aggregations of frogs (Narins 1982b), it seems inadequate to explain the difference in responses of males of *H. microcephala* to call intensities that were nearly equal. Another possibility is that high levels of background noise cause a shift in auditory threshold in chorus members (Table 14.2). Thus calls of distant males that would be audible on a quiet night fall below the threshold for hearing after a male has been in a chorus for some period of time. In fact neurophysiological experiments have revealed such threshold shifts in frogs (Narins 1987; Schwartz and Gerhardt 1998). Although this may be part of the answer, this phenomenon probably cannot explain the extremely small differences in intensity between interruptions that were ignored and those that were not by males of *H. microcephala*. Neurophysiological data obtained from crickets (Pollack 1988) and bushcrickets (Römer 1993) indicate that the auditory system may itself augment differences in the intensity of sounds from different individuals in a way that could promote selective attention. Similar data are not yet available for anurans.

The Role of Fine-Scale Call Timing in Attracting Females

How might alternation of calls or notes help a male attract a female? I tested three hypotheses (Table 14.2) with *Hyla microcephala, H. versicolor, Pseudacris crucifer*, and *Physalaemus pustulosus* using interactive playback and female choice tests (Schwartz 1987a; Schwartz and Rand 1991). The first hypothesis posits that a male attempts to avoid interference because this would impair his ability to detect the calls of other males. Hearing competing males is potentially important because it (1) enables a male to adjust his calling effort in a way that maintains his relative attractiveness, and (2) helps maintain intermale spacing in the chorus. The second hypothesis is that acoustic interference can degrade or obliterate temporal features in calls critical for species discrimination by females. The third hypothesis proposes that it is difficult for females to localize the source of calls that are overlapped. I chose *H. microcephala* and *H. versicolor* because the fine pulse structure of the advertisement calls of these

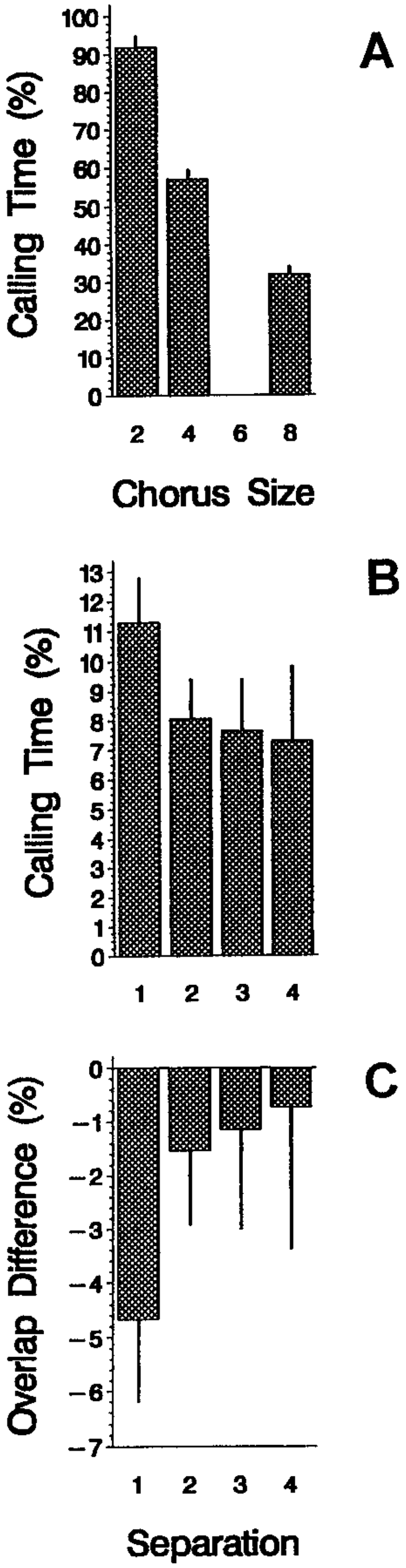

Figure 14.4. (A) Calling time (mean percentage of total time producing sound, n = 10 choruses) of males of *H. versicolor* that was not obstructed by the calls of any other male in the chorus for choruses of different sizes in the Greenhouse pond. (B) Calling time of males that was overlapped by the calls of other males as a function of separation (in terms of calling site positions in the artificial pond; n = 10 choruses of 8 frogs). (C) The difference between expected and observed call overlap among pairs of males as a function of separation. An expected level of acoustic interference was obtained by randomizing listings of the call durations and intercall intervals of each male and then recalculating call overlap. If the observed level of interference was less than that expected for at least 95 of 100 such randomized data sets, I characterized the interaction between a pair of males as showing significant avoidance of interference. The size of the difference between the expected and observed overlap was calculated as: 100 × (Expected overlap[i][j] – Observed overlap[i][j]) ÷ Calling time[i]. Male [i] is the "interfering" male whose calls follow and overlap those of the "leading" male [j].

species is important in species discrimination (Gerhardt 1978; Schwartz 1987b). *Pseudacris crucifer* has a tonal and only weakly frequency-modulated advertisement call that lacks temporal information of this kind, and so it served as an important control. Finally Rand and I tested *Physalaemus pustulosus* because the whine note of the advertisement call is strongly frequency modulated. This frequency modulation can be important in call recognition (Rose et al. 1988; Wilczynski et al. 1995).

I tested the first hypothesis by presenting males with call-triggered synthetic advertisement calls that either alternated with or overlapped their own calls. For all three hylids I found that males were more likely to give aggressive calls to alternating than overlapping stimuli. For *Physalaemus pustulosus,* males were more likely to add chuck notes to their whines if the stimulus was nonoverlapping than overlapping. Both sets of results suggest that males have a more difficult time detecting or gauging the intensity of calls that overlap their own. This may occur because the sound of a male's own call jams the calls of other males coincident with his own or because the increase in buccal pressure accompanying calling stiffens the tympanic membranes (Narins 1992).

I tested the second and third hypotheses with four-speaker choice tests in which females were exposed to simulated pairs of males that either alternated or overlapped one another. When the overlapped calls of *Hyla microcephala* and *H. versicolor* were 180 degrees out of phase so that the pulse rate of the calls seemed to have doubled, females discriminated in favor of the alternating calls. If the overlapped calls were precisely in phase, no discrimination occurred. There was also no discrimination when *Pseudacris crucifer* or *Physalaemus pustulosus* females were tested with either phase relationship. These data support the second hypothesis for species with amplitude-modulated calls while suggesting that frequency-modulated calls are less vulnerable to degradation caused by acoustic interference. The absence of discrimination when overlapping calls were in phase is inconsistent with the prediction of the third (localization) hypothesis. The time of approach to simultaneous versus alternating calls during two-speaker choice tests with *Hyperolius marmoratus* (Passmore and Telford 1981; Grafe 1996) also failed to support this hypothesis.

Perhaps alternation has no function per se but, as argued by Greenfield and his collaborators, is merely an epiphenomenon of signaling interactions that evolved for reasons unrelated to the problem of acoustic interference. In particular it is proposed that a preference by females for leading calls has influenced the evolution of call timing mechanisms that result in the patterns of alternation or even synchrony that are observed among acoustically signaling insects and anurans (Greenfield and Roizen 1993; Greenfield 1997; Greenfield et al. 1997). In this scenario competing males that do not adjust call timing suffer reduced mating success because they have fewer calls in a leading position than males that do adjust call timing. The most recent modeling efforts, incorporating time lags due to the velocity of sound and interactions in simulated choruses of up to 10 males, support this explanation (Greenfield et al. 1997).

The leader preference of females may be a consequence of an innate feature of the auditory system and has been termed the *precedence effect.* In the psychoacoustic literature this terminology has been used when a subject perceives the source of two sounds in a partially overlapping or a close leader-follower timing arrangement to be the location of the leading sound (Zurek 1980; Moore 1982). However in the animal communication literature, the terminology has often been applied when an animal orients towards the leading sound (e.g., Greenfield et al. 1997). The proximate cause of leader preferences in anurans is not known (Grafe 1996). The preference may be mediated in the peripheral or central auditory system and be due to a temporary reduction in sensitivity to following sounds (Yin 1994; Römer et al. 1997). Alternatively both leading and following calls may be equally audible to females, yet processing of the sounds by the brain results in erroneous localization of the calls of followers at the position of the leader.

The call-timing mechanism advocated by Greenfield (1994a, 1994b) relies on an "inhibitory-resetting" of an underlying free-running neuronal oscillator that controls the rhythmic production of calls by a male. Moreover Greenfield's basic model can be elaborated to be consistent with other models based on data from experiments with anurans (e.g., Loftus-Hills 1974; Lemon and Struger 1980; Narins 1982a; Moore et al. 1989). It is likely that an inhibitory-resetting process can explain patterns of fine-scale call timing during interactions between males for species of frogs with fairly simple advertisement calls or patterns of calling (Greenfield 1994a, 1994b; Greenfield et al. 1997). This explanation may also hold for *Physalaemus pustulosus* (Snedden et al., unpublished data). However experiments to elucidate the processes involved in call-timing shifts have been undertaken for only few anuran species, and more are needed. In particular modification of the model may be needed to explain some of the more complex patterns of calling and flexibility found in the vocal behavior of males of certain species.

In *Hyla microcephala,* for example, the inhibition in the production of a secondary note following an interrupting stimulus wanes after about 200 ms of interruption. Perhaps some neural mechanism integrates the output of an oscillator during inhibition and initiates calling following the crossing of a threshold level (Schwartz 1991). Another observation that needs explanation is that the presence of a brief gap in the middle of the interruption results in a strong rebound from vocal inhibition, such that a dilatory effect on vocalization of the second half of a split interrupting note is absent. Furthermore, although the calls of neighbors have an excitatory effect on male calling, chorusing individuals periodically cease vocal activity (see below). Thus there is no stable "free-running" call rhythm. It is likely that in this species different neural circuits may govern elements of the timing of calls and the timing of notes within calls. Finally the production and timing of advertisement and aggressive calls may be under the control of different circuits. In *H. microcephala* aggressive call responses to broadcast calls came significantly later (mode, 1200 ms; median, 2400 ms, $n = 812$) than did advertisement call responses (mode, 400 ms; median, 960 ms, $n = 3511$; Schwartz and Wells 1985). This may reflect the need for more sophisticated processing of a signal used in male–male assessment, additional delays in "choosing" a response, and physiological constraints on aggressive call production.

The distribution and causes of leader preferences in anurans needs further investigations using a comparative phylogenetic analysis (Jennions 1994). Studies of such preferences would also benefit from a systematic analysis of the influence of signal form, timing, and amplitude. In some species, such as *Hyla regilla* (Whitney and Krebs 1975), *Hyla cinerea* (Klump and Gerhardt 1992), *Hyperolius marmoratus* (Dyson and Passmore 1988a, 1988b), and *Bufo americanus* (Howard and Palmer 1995), females clearly show leader preferences. In other species, such preferences are absent (e.g., *Hyla versicolor,* Klump and Gerhardt 1987; *Centrolenella granulosa,* Ibáñez 1993) or the data are equivocal (*Pseudacris crucifer,* Forester and Harrison 1987; Schwartz and Gerhardt, unpublished data). In tests with *Hyla ebraccata,* Wells and Schwartz (1984a) found that females approached a speaker broadcasting a two-note call that followed and overlapped the secondary note of a leading two-note call. This pattern of calling was frequently observed in pair-wise vocal interactions among males. In *Physalaemus pustulosus,* Schwartz and Rand (1991) failed to detect a preference for the leading of the partially overlapped calls used in the four-speaker choice tests, although the statistical power was low. However Snedden et al. (unpublished data) observed strong leader preferences in a series of two-choice tests with females of this species. Schwartz and Gerhardt (unpublished data) have found that females of *Pseudacris crucifer* preferred the leading of two partially overlapped calls (by 20 ms of their 150 ms duration; 18:3, $p < 0.002$, two-tailed binomial test) even if the leading call was attenuated by 6 dB (11:1; $p < 0.006$). In *Hyla microcephala,* females did not prefer the leading call when offered two single-note calls separated by 200 ms (Schwartz 1986).

Coarse-Scale Patterns of Call Timing

Shifts in call timing among chorusing males may also occur on a gross scale. For example, Littlejohn and Martin (1969) demonstrated temporal partitioning of calling bouts whereby the Australian frog, *Pseudophryne semimarmorata,* is inhibited from calling in response to the vocal activity of *Geocrinia victoriana.* Schwartz and Wells (1983a, 1983b) also observed such a coarse shift in call timing by males of *Hyla ebraccata* in response to the vocalizations of groups of *H. microcephala* or *H. phlebodes.* The calling of *H. microcephala* was found to reduce both the ability of a male *H. ebraccata* to detect the calls of other males (as evidenced by a reduction in aggressive calling) and his ability to attract a mate. Calling relationships between pairs of species may be asymmetric. For example species that produce the longer calls or longer bouts of calling (and thus the most potent sources of masking interference) may inhibit species producing shorter calls or shorter bouts (Littlejohn and Martin 1969; MacNally 1982; Schwartz and Wells 1983a; Littlejohn et al. 1985).

The choruses of males of some species are active cyclically on a time scale of seconds to minutes such that, on a gross time scale, vocalizations are periodically synchronized before the entire chorus periodically goes silent. The calling part of the cycle is repeated after a male begins to call and so stimulates other members of the chorus to vocalize. In some of the literature on insects, such behavior has been called unison bout singing (e.g., Greenfield and Shaw 1983). Rosen and Lemon (1974) and Whitney and Krebs (1975) have described this behavior in the North American treefrogs, *Pseudacris crucifer* and *Hyla regilla,* respectively. Fellers (1979) indicated that these two species as well as *Hyla cinerea* call in bouts. Similar patterns of simultaneous chorusing have also been reported in the neotropical hylids *Osteocephalus taurinus* (Zimmerman and Bogart 1984), *Phyllomedusa tomoptera* (Zimmerman and Bogart 1984), *Smilisca baudina* (Duellman and Trueb 1966), *Smilisca sordida* (Duellman and Trueb 1966), and *S. sila* (Ibáñez 1991), and the European treefrog *Hyla arborea* (Schneider 1977). I have conducted a series of experiments investigating unison bout singing in *Hyla microcephala* (Schwartz 1991; Schwartz et al. 1995). In this species, bouts of calling typically last less than 30 seconds and intervening quiet periods last approximately the same length of time.

Why do males periodically stop calling (Table 14.2)? Whitney and Krebs (1975) tested the hypothesis that males of *Hyla regilla* stop to repay an oxygen debt incurred during vocalization. However their data were inconsistent with this explanation. Moreover data from subsequent research implicated aerobic pathways in the support of vocal activity in anurans (for review see Pough et al. 1992). Another possibility is that a pattern of group calling followed by cessation of vocal activity makes it more difficult for predators to capture chorus members than would otherwise be the case. Tuttle and Ryan (1982) found that frog-eating bats (*Trachops cirrhosus*) were less likely to approach a speaker broadcasting synchronized than asynchronous calls of *Smilisca sila*. These treefrogs call at low rates ($\bar{x} = 1.7$ calls/minute; Ryan 1986) in rough synchrony (often with partially overlapping calls; also see Ibáñez 1991) for brief periods ($\bar{x} = 488$ ms) followed by longer periods of quiet ($\bar{x} = 15$ seconds; Ibáñez 1991). The predation hypothesis may be less relevant for those species of frogs (e.g., *Hyla microcephala*) or insects that use longer chorusing bouts with less synchronized calls than *Smilisca sila* or are attacked by predators that rely less on auditory cues than frog-eating bats. Nevertheless the hypothesis requires further testing. A third possibility is that the cyclical pattern of chorusing is an emergent property of calling by individuals that can be stimulated to call by other males in the chorus. Such rhythmic patterns of activity appear in groups of ants as density increases and emerges in computer models of their behavior (Cole and Cheshire 1996; Goodwin 1998). This hypothesis does not posit that cyclical calling has a functional basis, but it does not preclude this possibility. Therefore factors such as sensitivity of males to acoustic stimulation might be shaped by selection in part because they could influence features of cyclical calling that affect male mating success.

I have tested three additional hypotheses using *Hyla microcephala*. One hypothesis proposes that females actively discriminate in favor of males that call in discrete bouts relative to males that do not. An arena-based female-choice experiment was conducted using two stimuli with equal long-term note rates. The temporal structure of one stimulus resembled that of a natural chorus with a 15-second bout of high note-rate calling (2 two-note calls per second) alternating with a 15-second block of silence. The second stimulus was a recording of calls with a note rate half that given during bouts in the first stimulus. Females failed to show a preference, and so the hypothesis was rejected.

The "noise hypothesis" proposes that as males join a chorusing bout and add notes to their calls during its progress the benefit of advertisement drops below its cost. This could be because calls are too degraded by interference to attract a female or because males can no longer accurately judge the calling behavior (e.g., the number of notes per call) of their neighbors. Therefore males stop calling briefly. The cycle starts again when a male in the group calls. I tested for an inhibitory role of chorus noise in two ways. First I broadcast a simulated chorus composed of digitized calls at 90, 95, and 100 dB SPL (re 20 μPa) in random order. By using the computer system for playback, it was possible to broadcast simulated bouts of calling and silent periods that were each of random duration within a 5- to 25-second range. If loud chorus noise inhibited calling, I predicted that males would reduce their calling during simulated bouts and increase their calling during quiet intervals as stimulus intensity increased. This did not happen. Second, with the computer in interactive mode, I tested whether the calling of subjects would be inhibited when more males call. The computer was programmed to broadcast calls only when the subject called and simulated the calling of one neighbor, two neighbors, and a large group of up to 12 males. Thus the cyclical calling of the subject controlled the cyclical activity of the simulated chorus, an essential ingredient of the experiment. As chorus size was artificially increased the noise hypothesis predicted that subjects would abbreviate their calling bouts. Again, the results were inconsistent with those predicted.

The work of Wells and Taigen (1989) demonstrated that males of *Hyla microcephala* often have very high rates of energy expenditure during calling. Perhaps fuel reserves were insufficient to meet the metabolic demands of calling at high rates during the entire time period females might arrive to breed during an evening. Therefore by pausing between bouts of vigorous calling a male could extend his period of advertisement over this 4- to 5-hour block of time. To test this "energetic constraint hypothesis," Stephen Ressel, Catherine Robb Bevier, and I used the computer-based call-monitoring device and biochemical analysis of tissue samples (Schwartz et al. 1995). Assays of glycogen levels in the trunk muscles of males gathered at the start of chorusing and of monitored males collected near the end of chorusing enabled us to estimate a cost in muscle carbohydrate of producing a note. With this estimate (0.98 μg glycogen per note) we calculated the length of time each of our monitored males could have called, without pausing, until exhausting his supply of trunk muscle glycogen. We found that with an average starting level of glycogen, over 80% of the males would have exhausted this fuel reserve in less than 3 hours. Since males often call for 4 to 5 hours a night, our results were consistent with the energetic constraint hypothesis.

Because cyclical calling is not especially common among species of frogs, it seems likely that continuous calling was the ancestral pattern of chorusing for *Hyla microcephala*. For cyclical calling to evolve, spread, and be maintained in this species, cyclical callers should have a greater mating success than that of continuous callers. That is, we would expect that a "mutant" male who structured his calling behavior into bouts in order to conserve energy reserves would be more likely to attract a mate than other males who called steadily but were forced by an energetic constraint to stop calling earlier in the evening. In 1996 I initiated a field-based experiment on female choice to test whether this was so.

During July and August ($n = 14$ nights) I assembled an artificial chorus consisting of eight 360-degree speakers (Radio Shack #40–1352) driven by an Amiga 600 computer. Each speaker was suspended inside a 90-cm-tall wire frame tomato stand and a screened enclosure with openings designed to capture approaching females. The chorus simulated four pairs of interacting neighbors giving calls of one to five notes. Each night, one speaker, selected randomly from the array, simulated a male with the "mutant" strategy of cyclical calling. This speaker would broadcast calls for 5 hours; however calls were not broadcast during alternate bouts. The remaining seven speakers mimicked steady callers and would broadcast calls for only 3 hours. The starting and ending times of calling for each of the seven "steady" speakers were staggered over a period of 30 minutes each night. This temporal arrangement approximated the typical pattern of males in a chorus. The "cyclical" speaker began broadcast 15 minutes into the experiment.

I checked the traps at approximately 15-minute intervals and turned off a speaker if I found a female on or inside its screening. Unfortunately the abundance of *Hyla microcephala* in my study site during midsummer 1996 was low: I caught a total of only eight females during the course of the experiment. Six were captured at the speaker broadcasting with the cyclical pattern, whereas just two were captured at speakers broadcasting steadily. All but one of the females at the cyclical speakers "paired" after all the steady speakers went silent. Because the odds favored the "population" strategy by 7:1, this result was statistically significant ($p < 0.0001$, binomial test) and suggests that the mutant strategy could successfully invade. Nevertheless I plan to increase my sample size and also rerun the experiment using the steady calling pattern as the "mutant" strategy.

Elaboration of Calls during Vocal Competition for Mates

Female anurans often discriminate in favor of real or simulated males producing sound at higher amplitudes, greater delivery rates, and for longer time periods than other call sources (Wells 1988; Forester et al. 1989; Ryan and Keddy-Hector 1992; Passmore et al. 1992; Gerhardt 1994; Schwartz et al. 1995; Sullivan et al. 1995; Wagner and Sullivan 1995; Grafe 1997). For example the now classic work of Rand and Ryan (1981) on *Physalaemus pustulosus* demonstrated that females prefer "complex" calls formed from a whine plus chuck notes to those without chucks. Such preferences may be manifest in dense choruses as demonstrated with multichannel call-monitoring systems for call rate in *Hyperolius marmoratus* (Passmore et al. 1992) and for note rate in *Hyla microcephala*. In choruses of *H. microcephala* mean note rates were higher for mated than unmated males when rates were calculated over time intervals ranging from 5 to 60 minutes before pairing (Schwartz 1994). Moreover on a night when all monitored males paired, the order of pairing was inversely related to the males' note rates (Schwartz et al. 1995).

Data from playback experiments indicate that males of chorusing species may increase call rates (e.g., Rosen and Lemon 1974; Ayre et al. 1984; Wells and Schwartz 1984a), notes per call (e.g., Arak 1983; Wells and Schwartz 1984a; Ryan 1985; Jehle and Arak 1998), call note duration (e.g., Wells and Taigen 1986), and even call intensity (Lopez et al. 1988) in response to simulated competitors. Therefore preferences of females may select for males with superior anatomical and physiological attributes related to call production (Table 14.2). Nevertheless because calling may incur significant energetic costs (Pough et al. 1992; Prestwich 1994; Bevier 1997; Wells, this volume), males should modulate calling behavior in ways that reflect the level of competition in the chorus. Here I describe some recent results with *H. versicolor* that demonstrate such behavior.

The grey treefrog, *Hyla versicolor*, is a common species throughout much of the eastern half of North America. The number of pulses in its advertisement call may vary both within and among males in the chorus. In two-stimulus choice tests in the laboratory, females discriminate in favor of higher call rates. They also discriminate among calls that differ by as little as 10% in pulse number (i.e., two pulses for calls about 20 pulses long; Gerhardt et al., unpublished data), preferring those of longer duration. This preference for longer calls is maintained even when longer calls and shorter calls are delivered at equivalent calling efforts (number of pulses per call × call rate; Klump and Gerhardt 1987; Gerhardt et al. 1996). Consistent with data on other species of frogs (Wells 1988; Schwartz 1994), Wells and Taigen (1986) demonstrated that males of *H. versicolor* alter their vocal behavior in response to changes in their competitive environment. In the field and during playback tests males tended to increase call duration with increasing levels of acoustic stimulation while reducing call rate. Accordingly there were usually only small changes in calling effort. Wells and Taigen suggested that the tradeoff between call duration and call rate is a reflection of a physiological limit that males cannot surpass on a long-term basis.

During the night the size and local density of choruses of frogs such as *H. versicolor* change as males pair with females or stop calling for other reasons. How do the remaining callers react to such shifts in the composition of their neighborhood? Bryant Buchanan, Carl Gerhardt, and I recently performed manipulations of chorus size in our greenhouse pond that demonstrated the sensitivity of males of *H. versicolor* to acoustic conditions. In one set of manipulations ($n =$ 12 nights) we modified chorus sizes in steps of 50% (from 8 to 4 to 2, on two of the nights, initial chorus size was 7 males). We acquired data on vocal behavior using the call monitoring system for 10-minute periods at each chorus size before attempting to reverse the pattern of density change. The increasing series of chorus sizes was used to control for any effect of time of night on the calling behavior of our subjects. Some males did not call in the increasing density series, perhaps due to effects of removal and handling. In a second set of density manipulations ($n = 4$ nights) we used step sizes of one male and initial choruses of 6 to 8 males. In these tests we acquired data for 5 rather than 10 minutes and only reduced densities. The order in which we removed males was randomized.

When we changed chorus size in steps of 50%, "focal" males present for all treatments reduced the number of pulses in their calls during the reductions and raised them with increases in chorus size (Kruskal-Wallis test, $\chi^2 =$ 1432.0, $p < 0.0001$, $n = 10$ males from 5 choruses). Males also decreased pulse number in response to removals of one male at a time. For three of the four focal males in the four choruses, a drop in the average pulses per call accompanied each reduction by one male. Although all males altered the duration of their calls during these manipulations, their ranking relative to other chorus males with respect to call duration changed little (50% reductions, mean change in rank between sequential chorus sizes = 0.203; 1 male reductions, $\bar{x} = 0.359$). For example the male that gave the longest calls at the start of the experiment typically continued to give the longest calls at the chorus sizes he experienced.

Our results raise many interesting questions. First, do some males (e.g., those with the longest calls or highest calling effort) exert a disproportionate influence on the vocal behavior of other chorus members? Second, why do lower ranking males maintain their relative rank at lower chorus sizes although they are capable of giving longer calls (as evidenced by their behavior at higher chorus sizes)? Are males reacting primarily to changes in the background noise level or does the spatial distribution of competitors exert a significant effect on vocal performance (Table 14.2)? How does the auditory system integrate and process the complex acoustic environment of the chorus in both spatial and temporal dimensions? Additional analyses and experiments that use interactive playback, multispeaker simulations of a chorus, and neurophysiology should help us find answers.

Aggressive Interactions

Adjacent males may exchange aggressive vocalizations with one another and use these calls almost exclusively if the vocal encounter escalates to a physical conflict. Male frogs often respond to loud broadcasts of conspecific calls by increasing their proportion of aggressive calls and may also respond differentially to advertisement and aggressive calls. For example aggressive calls may elicit a higher level of aggressive calling or even a cessation of calling, and their broadcast may also result in a withdrawal from the experimenter's speaker (see review of Wells 1988). Aggressive calls of many species exhibit a temporal structure that distinguishes them from advertisement calls. For example, in *Hyla ebraccata* (Wells and Schwartz 1984b) and *H. microcephala* (Schwartz 1986), the difference is quantitative: introductory notes of aggressive calls have a higher rate of amplitude modulation than those of advertisement calls. In *Pseudacris crucifer* (Schwartz 1989) and *H. cinerea* (Gerhardt 1978), the difference is qualitative: aggressive calls are amplitude modulated, whereas advertisement calls are not, although occasionally calls intermediate in form occur. In other species, males may simply increase the rate of delivery of advertisement-like calls or notes during agonistic interactions (Lopez et al. 1988; Stewart and Rand 1991). Some species of frogs incorporate an added degree of flexibility in their communication systems by using graded aggressive signals (Arak 1983; Wells and Schwartz 1984b; Schwartz and Wells 1984a; Littlejohn and Harrison 1985; Schwartz 1989; Wagner 1989a; Stewart and Rand 1991; Grafe 1995). In such systems males gradually change the temporal structure of aggressive calls as intermale distance decreases or the sound level of broadcast calls increases. Call duration appears to be a feature commonly altered, with calls or call elements increasing in length in response to the actual or simulated approach of an intruding male. Other call features may change in a correlated fashion with duration (e.g., Wells and Schwartz 1984b). This degree of flexibility may be useful to a male not only in the context of male–male interactions (Wells 1989), but may also allow him to vary those elements of his call that are attractive to females as warranted during a developing agonistic interaction (Wells and Schwartz 1984b; Wells and Bard 1987; Wagner 1989a; Grafe 1995).

A critical question concerns the functional significance of graded aggressive calls in anurans (Schwartz 1989; Wagner 1989a; Wells 1989; Table 14.2) as well as in other taxa that employ similar agonistic displays (Clutton-Brock and Albon 1979; Becker 1982; Bond 1989a, 1989b, 1992; Lambrechts 1992; McGregor and Horn 1992; Bradbury and Vehrencamp 1998; Payne and Pagel 1997). I have followed up earlier investigations of aggressive calling in both *Hyla*

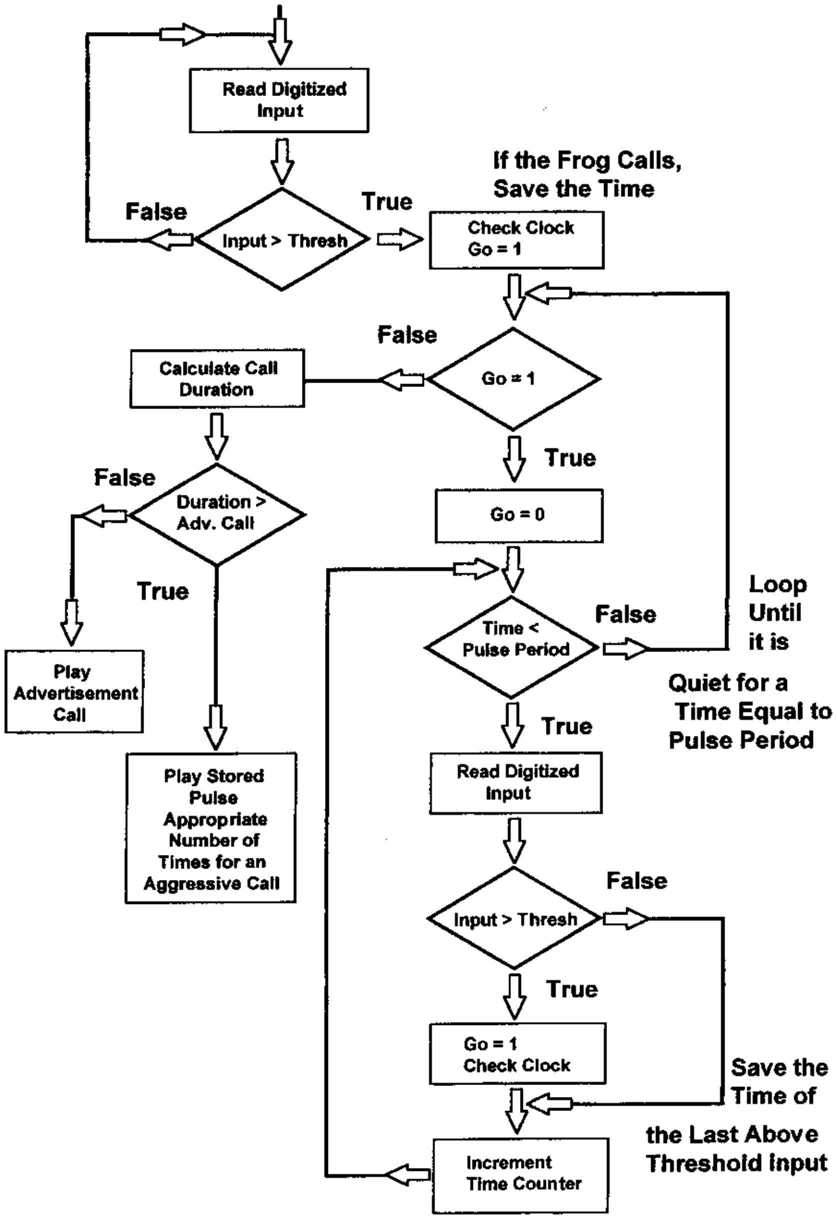

Figure 14.5. Flow chart of an algorithm for interactive playback tests using pulsed calls. In response to above-threshold input, the system time is requested. Data are read until digitized input is below threshold for a period of time equal to the pulse period of the call, at which time the call has ended. The call duration is calculated from the call start time and the time of the last above-threshold input. If the call is longer than some minimum duration, the call is an aggressive call. The call duration is used to calculate the number of pulses in the subject's aggressive call. Response calls of desired duration (e.g., shorter, equal, or longer than the subject's) are created by instructing the computer to play a stored pulse and an interpulse interval the appropriate number of times. A second version of this program, which counts pulses directly, is available. The system has been used successfully with *Hyla microcephala* and *Pseudacris crucifer* to play pulsed aggressive calls and with *H. versicolor* to play pulsed advertisement calls.

microcephala (Schwartz and Wells 1985) and *Pseudacris crucifer* (Schwartz 1989) with experiments using computer-based interactive playbacks. The research, not yet completed, is designed to improve our understanding of the functional significance of graded signals.

In my experiments I stage vocal contests between my subject and a simulated competitor (Figure 14.5). In some tests, after a no-stimulus period, males are presented with four stimulus treatments chosen randomly and with intervening recovery periods. In the control treatment the computer is programmed to respond with advertisement calls to all calls given by the subject. In the remaining treatments the computer responds to the subject's advertisement calls as before, but it answers each aggressive call with an aggressive call with an introductory note of duration (1) equal to, (2) twice as long as, or (3) half as long as those of the subject. The program uses note duration to distinguish the subject's advertisement from his aggressive calls. In tests with *Hyla microcephala* the computer distinguishes between introductory notes and secondary notes using note timing information.

If call duration facilitates assessment of an opponent's strength, a male should reduce the intensity of his aggressive response to a stronger individual. Moreover interactions should escalate and assessment of strength should take longer if two opponents have similar vocal behavior. Data currently available on *H. microcephala* are consistent with these predictions. Males gave shorter aggressive calls and had shorter bouts of aggressive calling in response to aggressive

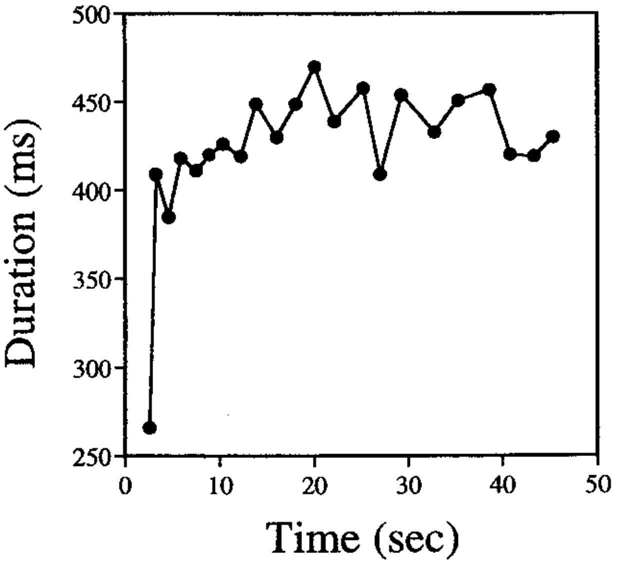

Figure 14.6. Durations of the calls of a male *Pseudacris crucifer* during a bout of aggressive calling. The sequence of calls was recorded during a no-stimulus period in an interactive playback test.

calls that were twice as long as their own aggressive calls as they did to stimulus calls that were equivalent in duration (Friedman test, $p < 0.01$, $n = 15$ males). Stimulus calls that were half as long as the subject's calls also elicited briefer bouts of shorter response calls than equivalent duration stimuli. The changes in call duration during bouts of aggressive calling also support the idea that producing a series of long aggressive calls is physically taxing. Individuals tended to start bouts with a short call, give a series of longer calls, and finally give a short call before ending the bout and returning to advertisement calling (Friedman test, $p < 0.005$).

Although aggressive calls given by males of *Pseudacris crucifer* to the longest stimulus aggressive calls were not significantly shorter than those given to aggressive calls equivalent in duration to their own, males did give longer bouts when presented with stimuli of equivalent duration. This finding and an earlier result suggesting an energetic constraint on aggressive calling (see Figure 14.5 in Schwartz 1989) are also consistent with the strength assessment hypothesis. Intriguingly field data from some individuals were supportive of Bond's (1989a, 1989b; 1992) behavioral efference hypothesis that posits that the primary function of graded aggressive display is modulation of the level of aggressive arousal of the signaler. Not only those males challenged with responses from the computer but also those that initiated aggressive calling during a no-stimulus period tended to increase their call duration (Figure 14.6). Observations that male frogs often continue to give aggressive calls when physically fighting are also consistent with both Bond's behavioral efference model and the strength-assessment hypothesis. Perhaps aggressive calling gradually primes a male for fighting through positive feedback and also advertises to an opponent that he can afford to pay the cost of producing expensive calls even while fighting.

Conclusions

The sound environment in which frogs communicate can often be characterized by considerable heterogeneity along spatial and temporal dimensions. Males of many species respond to acoustic flux in the chorus with rapid adjustments in their vocal behavior. Such responses can be important in maintaining the relative attractiveness of males to gravid females and in allocating energy reserves efficiently. Interactive playback and multichannel call-monitoring systems provide researchers with powerful techniques for generating and testing hypotheses about communication in anurans. Use of a computer obviously provides for greater realism and flexibility in the form of sound delivery than does the use of prerecorded playback stimuli. In particular, interactive playback is a necessity in experiments requiring precise control of stimulus timing relative to the vocalizations of the subject and in tests in which stimuli must change in specific ways in response to changes in the subject's calls. For example I learned from recordings of pair-wise natural interactions and tape-based playbacks that males of *Hyla microcephala* respond to interrupting sounds by increasing the spacing between their notes. However it was only with interactive playback that I was able to efficiently explore details of this behavior. Similarly tests in which I simulated a subject-driven escalated aggressive exchange would not have been possible without computerized playback. This is not to say that playback tests using a pre-recorded sequence of sounds cannot be very informative. Such playback methods have the advantage over call-triggered playback in that all test subjects receive the same number of stimuli (although the relative timing of the subject's calls and stimuli may vary). Unfortunately it is not known how responses of male frogs might differ if presented with stimuli delivered in an interactive (e.g., call-triggered) and noninteractive fashion. Experiments specifically designed to make such a comparison would be very helpful to those planning a study of anuran communication involving sound playbacks to males.

Chorusing is one of the most noteworthy habits of many species of frogs. Indeed it would be incredible if the consequences of calling in aggregations had failed to exert profound effects on the evolution of male vocal behavior. Equipment and software that permit researchers to monitor calling males within a network of interacting individuals are indispensable if we are to elucidate the vocal dynamics within these assemblages. In particular, patterns of male–male vocal competition as well as the details of call-timing adjustments and selective attention are phenomena that require investigation in additional species using approaches outlined in this chapter. Testing the link between male mating success and vocal behavior under chorus conditions is a critically important but difficult exercise that also lends itself well to multichannel monitoring of calling males. Published studies that used this technique indicate that females of two species do well in the field at selecting males producing signals with relatively high energy content (Passmore et al 1992; Schwartz 1994; Schwartz et al. 1995). However work in progress with *H. versicolor* suggests that patterns of selectivity observed in the laboratory sometimes may be much weakened in the chorus (Schwartz, Buchanan and Gerhardt, unpublished data; also see Sullivan and Hinshaw 1992; Bertram et al. 1996).

Interactive playback used with multichannel monitoring could be particularly effective in investigations of communication (McGregor and Dabelsteen 1996). For example the vocal behavior of male frogs in aggressive encounters might be correlated with their relative ability to produce attractive advertisement calls—especially if physical condition or fuel reserves constrain both forms of signaling. To test this idea the attributes of advertisement calls could be ascertained by monitoring chorus members. Then these individuals could be challenged with interactive playbacks. In fact such an experiment is in progress using males of *Hyla versicolor* calling in the artificial pond. It is not certain whether patterns of selective attention as described for call-timing adjustments extend to the elaboration of advertisement calls of males for any species. Do males adjusting the attractiveness of their signals attend to the overall level of background noise in the chorus or fine-tune the energy content of their vocalizations to just their closest neighbors? It is also possible that males might preferentially attend and respond to only the "best" caller they can detect. Thus it is conceivable that there are different spatial arrays of vocal interaction for call timing and call elaboration (Table 14.2)! Call monitoring combined with simultaneous playbacks from one or more speakers should allow us to test these possibilities. Males of some species alter their calling behavior when they detect a female nearby (Wells 1988). This change may be detected by other males, who in turn increase the attractiveness of their calls (e.g., *H. versicolor;* Schwartz and Buchanan, unpublished data). Call monitoring of the chorus could reveal the dynamics and extent of this process, while interactive playback tests during female releases could explore the efficacy of such behavior.

Although only a handful of biologists have used the newer methods in studies of animal communication, I hope that these technologies will be effectively exploited by more scientists in the near future. This should enhance our ability to tackle interesting questions that once may have been considered too difficult to answer.

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