AMER. ZOOL., 34:616–624 (1994)

Male Advertisement and Female Choice in Frogs: Recent Findings and New Approaches to the Study of Communication in a Dynamic Acoustic Environment[1]

JOSHUA J. SCHWARTZ

Division of Biological Sciences, University of Missouri, Columbia, Missouri 65212

SYNOPSIS. Typically, anuran amphibians communicate in a complex acoustic environment to which the calls of many males contribute. Although research has demonstrated that male vocal behavior is responsive to changes in this environment, a more thorough understanding of male-male interactions should benefit from the use of computer based systems for data acquisition and interactive playback. I discuss how I have used such systems in studies of note timing behavior, unison bout singing, aggressive behavior and female choice. In addition, I indicate how energetic constraints may be involved in shaping the temporal dynamics of chorusing.

INTRODUCTION

The chorusing of male anurans is an impressive acoustic phenomenon. Collectively, the calls of both conspecific and heterospecific males can result in high levels of background noise in the chorus, posing a potential problem for effective intraspecific communication. Male frogs of a number of species are sensitive to changes in their acoustic milieu and modify their advertisement calls in ways that can both increase an individual's relative attractiveness to females and reduce acoustic interference in the chorus (Wells, 1988; Narins and Zelick, 1988; Klump and Gerhardt, 1992; Gerhardt and Schwartz, 1994). The flexibility of the vocal behavior of males may be manifest in additional ways. For example, the communication systems of a number of species may incorporate graded signals, and in particular graded aggressive calls (see Wells, 1989; Gerhardt and Schwartz, 1994 and references therein). However, we have only a rudimentary knowledge of the functional significance of changes males make in these signals. In this paper I describe some of my recent work that illustrates the dynamic nature of male vocal behavior in anurans and its functional significance. I also discuss some new methods for investigating communication of frogs and other acoustically signalling organisms.

TRADITIONAL METHODS

Traditionally, researchers interested in frog communication have relied on a few technically simple but dependable methods. First, one observes the behavior of males in the field and records on tape their vocalizations. Second, after the basic elements of the vocal repertoire have been identified, natural recordings of these can be used to create stimulus tapes. Stimulus calls are broadcast to males and both the stimuli and male's responses are recorded. These experiments reveal the types of calls males are most likely to give in response to different vocalizations and the temporal relationships between stimuli and responses. Finally, the preferences of females for particular calls or call characteristics can be determined using choice tests. Gravid females, captured in amplexus, are typically tested within a few hours in an arena in which speakers broadcast recorded natural or synthetic calls. In the usual design, two speakers are placed at opposite sides of the arena; a female displays a choice by moving to one of the speakers (Gerhardt, 1988).

---

[1] From the symposium *Acoustic Communication in Anurans and Insects: Common Mechanisms in Behavior, Neurophysiology and Evolution* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1993, at Los Angeles, California.

NEW METHODS

One obvious limitation imposed by the aforementioned approaches is that stimuli are temporally invariant during a given test. For example, in playbacks to males each stimulus tape usually is prepared with a fixed inter-call interval. However, the call rate of males is rarely static, either within a night (Passmore *et al.,* 1992) or among nights (Sullivan and Hinshaw, 1992), and we do not know how the presentation of calls with fixed inter-call intervals influences male vocal behavior during playback tests. A tape-based playback system also is incapable of responding rapidly to changes in the calling of the test subject, something a real neighboring male would often do. A more realistic approach is to use an interactive, or call-triggered, system to present stimuli. In these systems, a timing circuit allows the experimenter to vary the temporal relationship between the stimulus and the subject's vocalizations (Narins, 1982), a technique that is very useful for studying note or call timing by males (Narins and Capranica, 1978; Schwartz, 1987).

Although an analog synthesizer is certainly more versatile than a tape recorder, the hardware imposes limitations on the design of stimulus calls and the way they can be presented to the frogs. For this reason, I have developed a computer-based system whose capabilities are less constrained by hardware, but rather only limited by the skill and imagination of the programmer. I use a sound digitizer to input digitized frog calls to a Commodore Amiga computer, which has been programmed to present stimulus calls in a specific manner. Stimulus calls are either digitized from filtered recordings of males or synthesized using custom software (Schwartz, 1991). A computer-based playback system also provides the flexibility often required to more accurately simulate the acoustic complexity of a natural chorus during choice tests of females. For female choice experiments requiring four or more speakers, I use an Amiga computer and a custom-built switching circuit, controlled from the computer, that can direct calls to up to eight speakers.

I now describe the application of these systems to several problems I have addressed recently, including some which illustrate the utility of interactive playback in studies of animal communication.

Note-timing behavior

Males of many chorusing species make adjustments in timing of their calls or call notes in response to the calls of other males (Greenfield, 1994; Narins and Zelick, 1988). Such behavior may be related to the problem of background noise or to specific call-order preferences of females (*e.g.,* Greenfield and Roizen, 1993), among a variety of possible explanations (Greenfield, 1994).

Schwartz and Wells (1985) discovered that neighboring males of *Hyla microcephala* often give short-latency vocal responses to one another that result in partial overlap of multi-note calls. However, the individual notes of the overlapping calls of the two interacting males alternate so that there is rarely any acoustic interference. Also, males make very rapid adjustments in note timing, on a note-by-note basis, and can dramatically increase inter-note intervals in response to long interruptions (see Fig. 7 in Schwartz and Wells, 1985). This further reduces note interference.

To gain a more thorough understanding of this behavior, I programmed my computer to interrupt males, following their primary (*i.e.,* introductory) notes, with synthetic advertisement calls 20–1000 msec long (Schwartz, 1991). During testing, the computer used digitized input from a directional microphone to monitor the male's vocal activity and stored a record of note timing. Males significantly increased their inter-note intervals in response to interruptions of all durations. However, for synthetic notes longer than 200 msec, the adjustment of note-timing by males was often insufficient to prevent overlap with the interruptions. Because males are most commonly interrupted by the primary and secondary notes of conspecifics that are less than 100 msec in duration, the behavior of males prevents acoustic interference during most pair-wise vocal interactions.

A more recent experiment indicates that note alternation by males of *H. microcephala* may involve both inhibition and disinhibition of vocal activity (Schwartz, 1993).

I interrupted males with 200-msec notes containing centrally placed gaps of 10, 20, 30 or 40 msec. In response to all stimuli but the first, males failed to increase their internote spacing enough to accommodate the 200 msec interruption. In natural interactions, males delay giving secondary notes when interrupted while calling; however, in order to alternate notes effectively, males must be responsive to the brief decreases in sound intensity that occur following the note of another frog. Such decreases evidently disrupt any inhibition of vocalizing caused by the interrupting note.

The results of the studies I have described indicate how males adjust the relative timing of their notes during pair-wise interactions but do not address the question of how they do so under the acoustic conditions in a dense chorus. To answer this question, I built an interface board for my computer that allowed me to monitor simultaneously the vocal activity of up to eight males (see Schwartz [1993] for technical details and Brush and Narins [1989] and Passmore *et al.* (1992) for descriptions of similar systems). I found that males were most responsive to their closest and loudest neighbors in the chorus. In fact, many males responded with note-timing shifts to the interrupting calls of only the loudest neighbor in their group—even when the estimated call intensities of other males were nearly as great. Similar behavior has been reported in another frog (Brush and Narins, 1989) and insects (Greenfield, 1994). Moreover, data from neurophysiological recordings of both crickets and bushcrickets have demonstrated selective auditory coding to louder stimuli during presentation of multiple calls (Pollack, 1988; Römer, 1993). Studies are needed of the neural mechanisms responsible for selective vocal responses by frogs to more intense calls.

Cyclical chorusing

Males of *H. microcephala* alter their long-term call production as well (Schwartz, 1991). Choruses of males call in bouts (lasting usually less than 30 sec) and punctuate these with periods of relative quiet of about the same duration. This behavior, termed unison bout singing, has been reported in other species of frogs (Rosen and Lemon, 1974; Whitney and Krebs, 1975) and acoustic insects (Greenfield, 1994). Two fundamental questions about unison bout singing, which may be addressed at both the proximate and ultimate level, are (1) why do males call together and (2) why do males periodically stop calling. Whitney and Krebs (1975) suspected that male frogs may stop calling because of lactate buildup in their calling muscles; however, their data as well as results of more recent studies of anuran energetics (Pough *et al.,* 1992) do not support this hypothesis. I tested a number of additional hypotheses to learn why males periodically stop calling (Schwartz, 1991).

Males might call cyclically because females prefer males that do so. To test this hypothesis, I gave females a choice between stimuli that mimicked a cyclical (on/off) and a non-cyclical chorus. The periodic high note rate of the former stimulus was double the note rate of the non-cyclical stimulus so that the long-term average note rates of the two stimuli were equal. Females did not discriminate, and so the data failed to support the female preference hypothesis.

A second hypothesis is that noise levels, which often become quite high as a bout progresses, inhibit calling. I used my computer system to test this idea in two ways. First, I used the system in a non-interactive mode to expose individual males to simulated choruses at intensities of 90, 95, and 100 dB SPL (re 20 μPa). The computer broadcast bouts of calling followed by periods of silence that were both of random duration between 5 and 25 sec; this pattern mimics that of a natural chorus. If loud chorus noise causes males to stop calling, then test males should have shifted their calling into the quiet periods between stimulus broadcasts of high intensity. This did not happen.

Second, I designed an interactive experiment to test whether males are inhibited from calling when many other males call. For this test it was critical that the simulated chorus not drive the subject's cyclical calling pattern. Rather, I wanted the stimulus calling pattern to conform to that of the subject. To accomplish this, the stimulus was repeatedly triggered by the calls of the subject but ceased if the subject stopped calling. Using a digitized three-note call stored in the computer's memory and the four sound channels of the Amiga, I simulated one, two, or 12 calling males.

The noise hypothesis predicted that males would end their calling bouts sooner in response to broadcast of the large simulated chorus than when exposed to the one or two-male simulated choruses. Although calls were broadcast at 100 dB SPL, males actually lengthened rather than shortened their bouts during the large chorus stimulus. Thus, both playback tests failed to support the noise hypothesis.

With two colleagues, Stephen Ressel and Catherine Bevier, I recently tested an energy conservation hypothesis. It proposes that by periodically quieting males are able to extend the portion of the night or the number of nights in which they call, while maintaining the ability to call at high rates. This may improve a male's chances of mating. *H. microcephala* often call more than four hours each night and can produce over 6000 notes per hour (Wells and Taigen, 1989).

We tested the energy conservation hypothesis by estimating the amount of glycogen stored in trunk muscle that is used by *H. microcephala* males during calling. We did this by analyzing muscle tissue from males collected near the beginning and end of chorusing activity. For some of the males collected in late evening, we obtained a complete record of vocal activity by using the multi-channel computer system. Based on our estimate of the cost of producing notes, most males, starting with an average level of glycogen, would exhaust their reserves of trunk muscle glycogen in under 3 hr if they called continuously at the rate characteristic of chorusing bouts. Thus there is support for the hypothesis that males of *H. microcephala* cease calling in order to conserve energy, although the precise proximate cues that cause males to periodically cease calling are unknown.

Advantages of calling in a group

Why males gather in choruses to advertise for females has been the subject of debate for many years (Bradbury, 1981; Ryan, 1985; Arak *et al.*, 1990). Males may join groups for reasons unrelated to female behavior (*e.g.*, to reduce predation risk) or because females are more attracted to groups of males than to individual callers. In the second case, females may prefer males in groups because it facilitates a comparison of males. Alternatively, the pooling of the calls of many males may result in a more potent phonotactic stimulus.

One hypothesis is that females are disproportionately attracted to assemblages, and so males that join groups have a greater mating success than those that do not. This possibility has been tested with insects using playbacks or advertising males, with mixed results (Morris *et al.*, 1978; Cade, 1981; Doolan, 1981; Walker, 1983; Greenfield and Shelly, 1985; Arak *et al.*, 1990; Shelly and Greenfield, 1991). Moreover, some of the methods used make it difficult to interpret findings. For example, in the study of Morris *et al.* (1978), choice stimuli simulating calling by a single *versus* two male katydids were broadcast to females from two rather than three speakers. Therefore, discrimination by females in favor of the multi-male stimulus may have resulted from a preference for a male with a higher call rate rather than a preference for a group of males. In Cade's (1981) study, although individual speakers were used to mimic individual calling crickets, calls directed to different speakers were broadcast simultaneously from the same tape recording; this synchronous temporal pattern is certainly unnatural.

Playback tests on frogs similar to those conducted with insects have not been reported, but some field data address the relationship between female attraction and the size of male aggregations. Ryan (1985) found that larger choruses attracted more females per male in *Physalaemus pustulosus*, but these data were gathered at the same spot over different nights rather than at different spots on the same night. Similar data are available from the study of Wagner and Sullivan (1992) on *Bufo valliceps* at two ponds. In *Bufo calamita*, the per-capita attraction of females to males in groups of different size did not vary significantly within nights (Tejedo, 1993).

Using a multi-speaker design, I recently

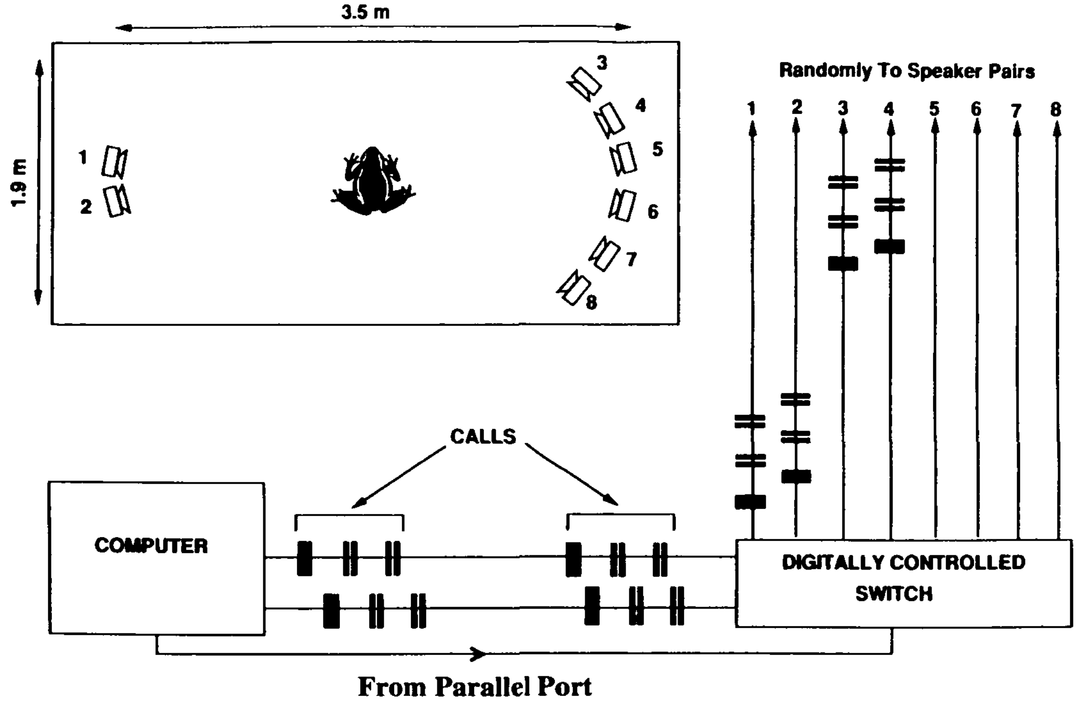

FIG. 1. Diagram of the choice arena and equipment used in tests of female discrimination of chorus sizes. Illustrated is a choice between two and six sound sources during the broadcast of 3-note calls. Calls of 1–5 notes were directed to randomly chosen pairs of adjacent speakers until broadcasts of each call type had been completed to all speakers. As shown, calls are being first directed to speakers 3 and 4 and next to speakers 1 and 2. The four stereo amplifiers (Realistic SA-10) interposed between the switch and the speakers are not illustrated.

tested the responses of female *H. microcephala* to different numbers of calling males. I avoided some of the problems of certain insect studies by using an Amiga computer and a custom-built circuit incorporating digitally controlled analog switches. This system enabled me to broadcast non-interfering calls from up to eight speakers (Realistic Minimus 0.3) and also to simulate much of the temporal dynamics of a natural chorus (see Shelly and Greenfield, 1991, for another example of a "computerized chorus"). The basic methods were identical to those I have used previously with this species (Schwartz, 1993) except that the arena was larger (Fig. 1).

During testing, the computer stored in memory two copies of a digitized, natural, five-note call. The second call was delayed by 122 msec so that the calls, when output in stereo using the left and right channel of the computer, did not interfere (intensity = 90 dB Peak SPL at central female release point). Calls from each channel could be directed to any of 4 speakers by sending the appropriate bit pattern to the switching circuit via the parallel port. Because males of *H. microcephala* typically commence chorusing bouts with calls of few notes and progressively add notes to their calls before pausing (Wells and Taigen, 1989), I had the simulated males in my artificial chorus behave the same way. Bouts began with 1-note calls and progressed through 2, 3, 4, and finally, 5-note calls. For 5-note calls the computer was programmed to broadcast the stored stimulus calls in their entirety. Each bout was followed by 10 sec of silence. Calls were output from the left and right sound channels of the computer and directed to speaker pairs (chosen randomly without replacement) until all speakers had broadcast a call. Then calls with the next highest number of notes were played. Thus, each speaker pair mimicked a pair of neighboring males in a chorus, which often overlap calls

TABLE 1. *Chorus sizes female choice tests.*

Females choosing		Females tested	Chi-Sq	P*	P†
1 spkr	7 spkrs				
6	50	64	0.163	0.686	<0.001
1 spkr	2 spkrs				
13	20	37	0.545	0.460	0.134
2 spkrs	6 spkrs				
5	35	47	3.333	0.068	<0.001

Chi-square statistic tests for deviation from expectation that equal numbers of females chose each speaker.

* P-value associated with the Chi-square statistic.

† Two-tailed binomial probabilities under the null hypothesis that females chose chorus sizes equally.

TABLE 2. *Note rates of mated and unmated males.*

Interval	Mated†	Unmated	Z	P
1 min	2.82 (14)	3.29 (53)	−1.43	0.152
5 min	1.89 (14)	3.60 (56)	−2.42	0.016*
10 min	1.71 (14)	3.66 (58)	−2.67	0.008*
15 min	1.64 (14)	3.68 (59)	−2.79	0.005*
30 min	1.71 (14)	3.68 (62)	−2.79	0.005*
60 min	2.04 (14)	3.63 (63)	−2.67	0.008*

† Values are mean ranks of notes given in different time intervals prior to amplexus for nine nights. Numbers in parentheses give the number of males in each catagory. For example, in the 15 min prior to pairing, 14 males ranked, on average, between first and second in note production relative to the males which did not pair in their choruses. Z and P-values are for a Wilcoxon Signed Ranks test performed on the mean notes given by mated and unmated males calculated for each of the 14 instances of amplexus.

* Significant using the Sequential Bonferroni Test (Rice, 1989).

but alternate notes within calls (Schwartz, 1993).

I simulated three different chorus choices for the females: 1 *vs.* 7 males, 2 *vs.* 6 males, and 1 *vs.* 2 males. In two of the three tests, the side of the arena with more speakers attracted significantly more females; however, there was no difference in the per capita attractiveness between large and small "choruses" (Table 1). Although these results suggest that males of *H. microcephala* do not increase their chances of mating by aggregating, this conclusion should be considered tentative for several reasons. First, even though I used a large testing arena, females may have interpreted their choice as one among different males in a single chorus rather than among different numbers of males. Second, because males of *H. microcephala* in groups may increase their note rates in response to the calls of competing males, females may be more attracted to natural groups than to my artificial groups, in which average note rates per speaker were the same. Because of these possibilities my experimental data should be supplemented with field observations of the number of females visiting choruses of different sizes on the same nights.

Mate choice in the field

Although female-choice tests allow the researcher to determine female preferences in a well-controlled acoustic environment, female selectivity may be reduced when acoustic complexity is increased (Gerhardt, 1988; Telford *et al.*, 1989). To learn how male vocal behavior influences mating success in nature, workers have recorded the calls of focal males in the chorus periodically, over short intervals during the night, and observed which males obtained matings (*e.g.*, Sullivan, 1983; Lopez and Narins, 1991; Sullivan and Hinshaw, 1992). In general, data from such studies support the hypothesis that females prefer males that produce more sound. However, sampling during brief periods provides only an estimate of a male's overall calling performance and may miss potentially important data on variation in calling (but see Runkle *et al.*, 1994).

Females of *H. microcephala* discriminate in favor of call sources with higher note rates relative to those with lower note rates in two-choice tests (Schwartz, 1986). I have used my multi-channel computer system for monitoring male calling to determine how well female behavior in a natural chorus setting resembles what I have observed in the well-controlled acoustic environment of a choice arena. I also gathered data on variation within and among males in note production. With such a device one can acquire an unbroken record of calling for many males over a number of hours, eliminating problems associated with the traditional sampling schemes.

I monitored choruses of 2–7 males on 12 nights in 1991 and 1993. On nine of these nights one or more males went into amplexus. Females of *H. microcephala* preferred males with high note rates relative to those of their neighbors in the chorus, and most often selected the caller with the highest note rate. This preference was significant when note rates were calculated over the 5, 10, 15, 30, and 60 min prior to amplexus, but not the minute just before pairing (Table 2). Males also were consistent in their rates of note production relative to other males on a minute to minute basis during the entire time period prior to amplexus (Kendall's Coefficient of Concordance, $P < 0.01$ for each of 11 nights). Passmore *et al.* (1992) reported similar results for *Hyperolius marmoratus.*

The function of graded aggressive calls

Male frogs may exchange aggressive calls with other calling males and their propensity to give these vocalizations is influenced by proximity (Wells, 1988). Use of aggressive calls may escalate to and accompany fighting, and in some species males change these vocalizations in a graded fashion during agonistic interactions. For example, males of *P. crucifer* (Schwartz, 1989) and *H. microcephala* (Schwartz and Wells, 1985) give aggressive calls of longer duration to louder calls than to calls of lower intensity. Males of *Pseudacris crucifer* and *H. ebraccata* respond to increases in the duration of aggressive call stimuli with increases in the duration of their aggressive call responses (Schwartz, 1989; Wells, 1989). Therefore, if two males approach one another during an aggressive encounter, they increase the duration of their calls. Similar data, from natural interactions and playback tests, are available for other hylids (see Wells, 1989); however, aspects of agonistic behavior important to a more thorough understanding of the function of graded aggressive calls may be missing in such data. One reason is that it is difficult to observe aggressive encounters among male frogs from their onset. Usually, I have become aware of such interactions only by hearing distant males trade aggressive calls. Another reason is that individual playback tests have typically used stimuli which incorporate calls of fixed duration and rate.

Because of the dynamic nature of aggressive interactions among male anurans, and the potential role of graded signals in male-male assessment, playback experiments using an interactive system are very useful in testing hypotheses about graded signal function. Indeed, McGregor *et al.* (1992) have used an interactive approach in their studies of the function of strophe length in birds. I conclude by briefly describing work in progress on the function of graded aggressive calls in anurans which further illustrates the usefulness of a computer-based, interactive playback-system.

One hypothesis (strength assessment) proposes that long aggressive calls are energetically expensive, and thus their production is an honest indicator of a male's resource holding potential (Clutton-Brock *et al.,* 1979). Under this hypothesis, males should increase the duration of their aggressive calls during agonistic interactions in order to assess asymmetries in strength or condition. Assessment of relative strength should be difficult for males when call differences are small. Therefore, individuals would be more likely to engage in protracted aggressive displays with males that are close to their own strength than with those that are either much weaker or stronger than themselves (Enquist *et al.,* 1990). In interactions with individuals of similar strength, males should give more aggressive calls and escalate vocal encounters to a stage where longer calls are exchanged.

As one test of the strength assessment hypothesis, I simulated the calling behavior of males that are weaker (give shorter calls), stronger (give longer calls), or of the same strength as the subject. A computer program determined call duration of the subject in real time and used this information to distinguish between his advertisement and aggressive calls. Aggressive call stimuli were generated only in response to the aggressive calls. The primary and secondary notes of *H. microcephala* were distinguished using inter-note timing information, and the computer responded with a stimulus broadcast only to the primary note. Aggressive calls of the desired durations for the different experimental treatments (0.5, 2.0, 1.0 times the duration of the subject's note) were created by repeating a stored digitized pulse and inter-pulse interval the appropriate number of times. Thus each test subject was exposed to a simulated rival that he may have regarded as weaker, stronger or equivalent in strength. Preliminary results for *H. microcephala* are consistent with a prediction of the strength assessment hypothesis: males gave more and longer aggressive calls when confronted with aggressive calls of similar duration than when exposed to broadcasts of shorter or longer aggressive calls (Friedman Test, $P < 0.01$, $n = 15$ males). However, although I expected bouts of aggressive calling given in response to longer stimulus calls to be the shortest, bouts were similar in numbers of calls to bouts during broadcasts of shorter calls. I plan additional measures of males' physical condition (*e.g.*, size, V_{O_2}-max, endurance during exercise) and their relationship to calling behavior.

In work with other species where an interactive playback approach is desirable, more sophisticated algorithms may prove useful in discriminating different vocalizations of test subjects as well as in simulating various calling strategies. For example, a neural network program could be trained to perform the call discriminations. With such software tools and electronic hardware of ever increasing speed and sophistication, biologists interested in the dynamic aspects of animal signalling can look forward to increased opportunities to understand complex communicative processes.

ACKNOWLEDGMENTS

I thank Carl Gerhardt, Kit Murphy, Steve Tanner, Mac Given, and Michael Greenfield for comments on the manuscript. I am especially grateful to Stan Rand for many stimulating discussions over the years and his generosity with equipment and facilities in Panama. I also thank my collaborators, particularly Kentwood Wells. Financial support was provided by Smithsonian Short Term Visitor Awards.

REFERENCES

Arak, A., T. Eriksson, and T. Radesater. 1990. The adaptive significance of acoustic spacing in male bushcrickets *Tettigonia viridissima*: A perturbation experiment. Behav. Ecol. Sociobiol. 26:1–7.

Bradbury, J. W. 1981. The evolution of leks. *In* R. D. Alexander and D. W. Tinkle (eds.), *Natural selection and social behavior*, pp. 138–169. New York, Plenum Press.

Brush, J. S. and P. M. Narins. 1989. Chorus dynamics of a neotropical amphibian assemblage: Comparison of computer simulation and natural behaviour. Anim. Behav. 37:33–44.

Cade, W. H. 1981. Field cricket spacing, and the phonotaxis of crickets and parasitoid flies to clumped and isolated cricket songs. Z. Tierpsychol. 55:365–375.

Clutton-Brock, T. H., S. D. Albon, R. M. Gibson, and F. E. Guiness. 1979. The logical stag: Adaptive strategies of fighting in red deer *Cervus elaphus*. Anim. Behav. 27:211–225.

Doolan, J. M. 1981. Male spacing and the influence of female courtship behaviour in the bladder cicada, *Cyclostoma saundersii* Westwood. Behav. Ecol. Sociobiol. 9:269–276.

Enquist, M., O. Leimar, T. Ljungberg, Y. Mallner, and N. Segerdahl. 1990. A test of the sequential assessment game: Fighting in the cichlid fish *Nannacara anomala*. Anim. Behav. 40:1–14.

Gerhardt, H. C. 1988. Acoustic properties used in call recognition by frogs and toads. *In* B. Fritszch, W. Wilczynski, M. J. Ryan, T. Hetherington, and W. Walkowiak (eds.), *The evolution of the amphibian auditory system*, pp. 455–483. John Wiley, New York.

Gerhardt, H. C. and J. J. Schwartz. 1994. Interspecific interactions in anuran courtship. *In* H. Heatwole and B. K. Sullivan (eds.), *Amphibian biology*, Vol. 3. *Social behaviour*. (In press)

Greenfield, M. D. 1994. Synchronous and alternating choruses in insects and anurans: Common mechanisms and diverse functions. Amer. Zool. 34:605–615.

Greenfield, M. D. and T. E. Shelly. 1985. Alternative mating strategies in a desert grasshopper: Evidence for density dependence. Anim. Behav. 33:1192–1210.

Greenfield, M. D. and I. Roizen. 1993. Katydid synchronous chorusing is an evolutionarily stable outcome of female choice. Nature 364:618–620.

Klump, G. M. and H. C. Gerhardt. 1992. Mechanisms and function of call-timing in male-male interactions in frogs. *In* P. McGregor (ed.), *Playback and studies of animal communication: Problems and prospects*, pp. 153–174. Plenum Press, New York and London.

Lopez, P. T. and P. M. Narins. 1991. Mate choice in the neotropical treefrog, *Eleutherodactylus coqui*. Anim. Behav. 41:757–772.

McGregor, P. K., T. Dabelsteen, M. Shepherd, and S. B. Pedersen. 1992. The signal value of matched singing in great tits: Evidence from interactive playback experiments. Anim. Behav. 43:987–998.

Morris, G. K., G. E. Kerr, and J. H. Fullard. 1978. Phonotactic preferences of female meadow katydids (Orthoptera: Tettigoniidae: *Conocephalus nigropleurum*). Can. J. Zool. 56:1479–1487.

Narins, P. M. 1982. Behavioral refractory period in

Neotropical treefrogs. J. Comp. Physiol. A 148: 337–344.

Narins, P. M. and R. R. Capranica. 1978. Communicative significance of the two-note call of the treefrog *Eleutherodactylus coqui.* J. Comp. Physiol. 127:1–9.

Narins, P. M. and R. Zelick. 1988. The effects of noise on auditory processing and behavior in amphibians. *In* B. Fritszch, W. Wilczynski, M. J. Ryan, R. Hetherington, and W. Walkowiak (eds.), *The evolution of the amphibian auditory system,* pp. 511–536. John Wiley, New York.

Passmore, N. I., P. J. Bishop, and N. Caithness. 1992. Calling behavior influences mating success in male painted reed frogs, *Hyperolius marmoratus.* Ethology 92:227–241.

Pollack, G. S. 1988. Selective attention in an insect auditory neuron. J. Neurosci. 8:2635–2639.

Pough, F. W., W. E. Magnusson, M. J. Ryan, K. D. Wells, and T. L. Taigen. 1992. Behavioral energetics. *In* M. E. Feder and W. W. Burggren (eds.), *Environmental physiology of the amphibians,* pp. 395–436. University of Chicago Press, Chicago.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

Römer, H. 1993. Environmental and biological constraints for the evolution of long-range signalling and hearing in acoustic insects. Philos. Trans. R. Soc. Lond. 340:179–185.

Rosen, M. and R. E. Lemon. 1974. The vocal behavior of spring peepers, *Hyla crucifer.* Copeia 1974: 940–950.

Runkle, L. S., K. D. Wells, C. C. Robb, and S. L. Lance. 1994. Individual, nightly, and seasonal variation in calling behavior of the gray treefrog, *Hyla versicolor*: Implications for energy expenditure. Behav. Ecol. 5:318–325.

Ryan, M. J. 1985. *The tungara frog.* University of Chicago Press, Chicago.

Schwartz, J. J. 1986. Male calling behavior and female choice in the neotropical treefrog *Hyla microcephala.* Ethology 73:116–127.

Schwartz, J. J. 1987. The function of call alternation in anuran amphibians: A test of three hypotheses. Evolution 41:461–471.

Schwartz, J. J. 1989. Graded aggressive calls of the spring peeper, *Pseudacris crucifer.* Herpetologica 45: 172–181.

Schwartz, J. J. 1991. Why stop calling? A study of unison bout singing in a neotropical treefrog. Anim. Behav. 42:565–577.

Schwartz, J. J. 1993. Male calling behavior, female discrimination and acoustic interference in the Neotropical treefrog *Hyla microcephala* under realistic acoustic conditions. Behav. Ecol. Sociobiol. 32:401–414.

Schwartz, J. J. and K. D. Wells. 1985. Intra- and interspecific vocal behavior of the neotropical treefrog *Hyla microcephala.* Copeia 1985:27–38.

Shelly, T. E. and M. D. Greenfield. 1991. Dominions and desert clickers (Orthoptera: Acrididae): Influences of resources and male signaling on female settlement patterns. Behav. Ecol. Sociobiol. 28: 133–140.

Sullivan, B. K. 1983. Sexual selection in woodhouse's toad (*Bufo woodhousei*). II. Female choice. Anim. Behav. 31:1011–1017.

Sullivan, B. K. and S. H. Hinshaw. 1992. Female choice and selection of male calling behaviour in the grey treefrog, *Hyla versicolor.* Anim. Behav. 44:733–744.

Tejedo, M. 1993. Do male natterjack toads join larger breeding choruses to increase mating success? Copeia 1993:75–80.

Telford, S. R., M. L. Dyson, and N. I. Passmore. 1989. Mate choice occurs only in small choruses of painted reed frogs *Hyperolius marmoratus.* Bioacoustics 2:47–53.

Wagner, W. E. and B. K. Sullivan. 1992. Chorus organization in the Gulf Coast toad (*Bufo valliceps*): Male and female behavior and the opportunity for sexual selection. Copeia 1992:647–658.

Walker, T. J. 1983. Mating modes and female choice in short-tailed crickets (*Anurogryllus arboratus*). *In* G. K. Morris and D. T. Gwynne (eds.), *Orthopteran mating systems: Sexual competition in a diverse group of insects,* pp. 240–267. Westview Press, Boulder, Colorado.

Wells, K. D. 1988. The effects of social interactions on anuran vocal behavior. *In* B. Fritszch, W. Wilczynski, M. J. Ryan, T. Hetherington, and W. Walkowiak (eds.), *The evolution of the amphibian auditory system,* pp. 433–454. John Wiley, New York.

Wells, K. D. 1989. Vocal communication in a neotropical treefrog, *Hyla ebraccata*: Responses of males to graded aggressive calls. Copeia 1989:461–466.

Wells, K. D. and T. L. Taigen. 1989. Calling energetics of the Neotropical treefrog, *Hyla microcephala.* Behav. Ecol. Sociobiol. 25:13–22.

Whitney, C. L. and J. R. Krebs. 1975. Mate selection in Pacific tree frogs. Nature 255:325–326.