University of Texas at Austin, Austin, Texas

Changes in the Frequency Structure of a Mating Call Decrease Its Attractiveness to Females in the Cricket Frog *Acris crepitans blanchardi*

Klaudia Witte, Michael J. Ryan & Walter Wilczynski

Abstract

In many species, females often prefer male signals that are more complex than in nature or beyond the range of calls naturally produced by conspecific males in spectral, temporal and amplitude features. In this study we examined both the ability of females to recognize signals outside the normal range of spectral frequency variation seen in male advertisement calls, and the influence of increasing call complexity by adding spectral components to enhance the attractiveness of a male advertisement call in the cricket frog *Acris crepitans blanchardi*, while keeping its amplitude constant. We used two different natural male call groups and created the following synthetic call groups: with a dominant frequency at 3500 Hz, i.e. at the normal dominant frequency with a frequency band within the sensitivity range of the inner ear basilar papilla; with a dominant frequency at 700 Hz, i.e. outside the normal range of variation and with a frequency band outside the sensitivity range of the basilar papilla but within the range of the amphibian papilla; with two dominant frequencies, one at 700 Hz and another at 3500 Hz, stimulating the basilar and amphibian papilla simultaneously. In double choice experiments we tested all combinations of the three call groups, and we tested the 3500 Hz call groups against the same natural call groups. Additionally, we tested the 700 Hz call groups against white noise to see whether these signals are meaningful in mate choice. Females preferred 3500 Hz call groups over all other call groups. The synthetic call group was as attractive to females as the same natural call group. The 700 Hz call group was not meaningful in mate choice. The combined (700 Hz + 3500 Hz) call group was significantly less attractive to females than the 3500 Hz call group. Thus, making a call more spectrally complex without increasing its overall amplitude decreases its attractiveness to cricket frog females.

Corresponding author: Klaudia Witte, Lehrstuhl für Verhaltensforschung, Universität Bielefeld, Postfach 100131, 33501 Bielefeld, Germany. E-mail: Klaudia.Witte@Biologie.Uni-Bielefeld.de

Introduction

In many cases of communication between the sexes males display signals to females and females base their mate-choice decision on those signals. Vocal signals such as the male advertisement calls produced by many species of insects, frogs, and birds, vary between species in spectral, temporal and amplitude features. Even within a species there is variation in calls along all three of those dimensions (Wilczynski & Ryan 1999).

Many studies have examined how the natural variation in signal and receiver characteristics influences mate choice (Ryan 1983; Gerhardt 1988; Wagner 1989; Ryan & Wilczynski 1991; Rand et al. 1992; Kime et al. 1998; Wollerman 1998). There are also many examples in which female receivers respond to, and may actually prefer, signals that males never produce. In some cases, these are signals that fall well outside the range of variation seen naturally (Ryan & Keddy-Hector 1992; Ryan et al. 1992; Searcy 1992; Wilczynski et al. 1999). Other cases in several species show that females respond to novel stimuli and that females may even prefer males as mates when those males bear a novel trait. Females of four different bird species prefer males with an artificial feather crest on the forehead even though males in these species lack crests (Jones & Hunter 1998; Tyler Burley & Symanski 1998; Witte & Curio 1999). In swordtail fish, Basolo (1990, 1995a, b) showed that females prefer males with an artificial sword even in species in which conspecific males lack swords. Túngara frog females *Physalaemus pustulosus* prefer advertisement calls, or 'whines' containing any number of artificial acoustic signals as well as the 'chuck' normally produced by males (Ryan 1985, 1991; Wilczynski et al. 1995), while females of a related species *Physalaemus colorado-rum* prefer male advertisement calls with a digitally added 'chuck' to the normal conspecific whine even though males of that species produce no 'chucks' (Ryan 1990; Ryan & Rand 1993).

In all of these cases, the signals that yielded enhanced female preference were either additions to an existing signal (artificial feather crests, adding additional syllables to a call), or extensions of a signal along some dimension to a point beyond which males normally signal. Left unexplored are those types of signal manipulations that could test limits of the power of unusual signals to enhance female responses. One relates to complexity. Adding components to a signal, such as additional visual or acoustic adornments, is one way to make a signal more complex, and such additions do tend to make signals more attractive. Ryan & Keddy-Hector (1992) suggested that the mechanism for doing this is increased signal energy, which makes the signal more stimulatory to the female. But another way to make a signal more complex is to distribute spectral components over more frequency channels keeping overall signal amplitude constant. Such a manipulation would increase signal complexity but would do so without

increasing overall signal energy. A second type of manipulation involves extending a signal along a dimension to the point where it enters the domain of a sensory structure not normally used in the organism's communication system. Such a manipulation is difficult to achieve in most communication systems. However, the acoustic communication system of frogs allows such a test because of the unusual organization of the amphibian auditory system. The amphibian inner ear contains two separate auditory sensory papillae, each tuned to a different frequency range (Capranica 1976; Wilczynski & Capranica 1984; Lewis & Lombard 1988; Zakon & Wilczynski 1988), the basilar papilla and the amphibian papilla. The amphibian papilla contains an array of tonotopically organized hair cells, each most sensitive to a different frequency. The basilar papilla contains many fewer hair cells all tuned to similar frequencies. The amphibian papilla is most sensitive to stimuli of low and mid range frequencies (< 1200 Hz); the basilar papilla is most sensitive to stimuli of high frequencies (> 2000 Hz in most small anurans). By selecting a species that uses only one papilla for detecting its communication signal, we can ask what happens if the spectral properties of the signal are shifted into the sensitivity range of the other auditory end-organ. To test both types of signal variation on female mate choice, we investigated the influence of variation in one key component of the male advertisement call, its spectral frequency composition, on female preferences in the cricket frog, *Acris crepitans blanchardi*.

In most anuran species, males produce calls and females recognize their own species and choose between conspecific males on the basis of these advertisement calls (Wells 1977; Gerhardt 1988; Rand 1988). In some species, such as the túngara frog *Physalaemus pustulosus* (Ryan et al. 1990) or the green treefrog *Hyla cinerea* (Gerhardt 1988), females use both papillae for detecting male calls. In these species, females may respond to stimulation of only one auditory organ, but signals that stimulate both are more attractive. In contrast to *P. pustulosus* and *H. cinerea,* in cricket frogs, *Acris crepitans*, the energy in advertisement call falls only in the sensitivity range of the basilar papilla (Capranica et al. 1973; Ryan & Wilczynski 1988; Keddy-Hector et al. 1992; Wilczynski et al. 1992). Therefore, the natural situation in this species is to use only the basilar papilla for intraspecific communication even though it, like all other frogs, has an amphibian papilla as well. Male cricket frogs *Acris crepitans* produce a broad-band, high-frequency advertisement call with a single, high-frequency, spectral peak, the dominant frequency. The call is a series of click-like pulses. Calls are combined to form call groups, in which calls tend to increase in both the number of pulses and call duration from beginning to end (Ryan & Wilczynski 1991; Ryan et al. 1992). The call varies in dominant frequency among populations and among individuals within a population from about 2.7–4.0 kHz (Ryan & Wilczynski 1991; Wilczynski et al. 1992; Wilczynski & Ryan 1999), and contains numerous sidebands that probably result from low-frequency amplitude modulation of the carrier frequency. Female cricket frogs can distinguish among calls that differ only in dominant frequency within the natural range of variation, and most often prefer calls with lower dominant frequencies (Ryan et al. 1992; Wilczynski & Ryan 1999).

A similar preference for low-frequency calls has been reported in other frogs and toads (Ryan 1985; Wollerman 1998). As in other frog species, bigger males produces lower-frequency calls (Keddy-Hector et al. 1992), and thus females prefer to mate with bigger males. Both females (Wagner 1989; Kime et al. 1998) and males (Venator & Wilczynski 1998; Burmeister et al. 1999) also recognize variation in temporal call characters when spectral features are held constant. Thus both spectral and temporal call features are significant in call recognition.

We investigated the effects of two types of frequency manipulations on female mate choice in this study. With one set of tests, we investigated how cricket frog females would respond to a male advertisement call with its spectral energy shifted much lower than the lowest call frequencies in their population range while keeping amplitude and temporal pattern information constant and equal to the normal values. We altered the call frequency from its normal range stimulating the basilar papilla to the lower frequency range of the amphibian papilla. Cricket frogs are quite sensitive to sound in the amphibian papilla's frequency range; in fact, thresholds are lower for amphibian papilla fibers than for basilar papilla fibers (Venator 1999; Wilczynski & Ryan 1999). This experiment was designed to determine if temporal information was sufficient to support female mate choice even when the spectral information was radically shifted and to determine if amphibian papilla stimulation was an adequate, or even enhanced, route to eliciting female mate choice even though only basilar papilla stimulation occurs with the actual conspecific call. With a second set of tests, we investigated if increasing the complexity of a call without increasing its overall energy by distributing call energy over two, rather than one, frequency band would make a cricket frog call more attractive to females. This was accomplished by having a low-frequency component centered at 700 Hz, that is, in the amphibian papilla frequency range, combined with one at the normal dominant frequency at 3500 Hz, that is, in the basilar papilla sensitivity range. This experiment parallels earlier studies in a variety of taxa examining the effect of increasing signal complexity on mate choice, but does so keeping signal amplitude constant. Furthermore, the added spectral component stimulates the amphibian papilla in a species that normally only uses the basilar papilla for call recognition, thus adding complexity with a signal that is detected in part by a portion of the auditory system not normally used in call recognition.

Methods

Study Species

We collected cricket frog females (n = 111) at a semipermanent pond in open grassland on Gill Ranch, Travis County, Texas, at night between 12 March and 9 July 1997. All females were in amplexus with a male when captured. We kept females for 2 d in the lab, toe-clipped them, and returned them, following behavioral testing, to the pond on the third night after catching.

Stimuli

The dominant frequency of males of the population we studied in 1997 at Gill Ranch, Travis Co., Texas was 3382 Hz ± 153 (x ± SD) with a range between 3014 Hz and 3713 Hz (n = 38 males, measurements were adjusted to a surface temperature of 20°C; Kime, pers. comm.). We digitized two natural male call groups of the Gill Ranch population, termed here the Gill 4 and the Gill 5 call group. We used two call groups so that our results did not depend on an effect peculiar to one call group. The call group Gill 4 lasted 3474 ms, and contained 25 calls at a call rate of 6.45 calls/s. The call group Gill 5 lasted 5739 ms (milliseconds), and contained 24 calls at a call rate of 4.16 calls/s. We produced three synthetic call groups from the natural Gill Ranch call groups. One synthetic call group had a dominant frequency at 700 Hz; one had a dominant frequency at 3500 Hz; and a third synthetic call group with two dominant frequencies was composed of a combination of the 700 Hz and the 3500 Hz synthetic call groups. We chose 700 Hz as the dominant frequency of the low frequency call group, because this would place the peak energy of the call within the most sensitive region of the cricket frog amphibian papilla while keeping major secondary peaks of this relatively broad band signal within the sensitivity range of the amphibian papilla. We produced the synthetic call groups with the software program SIGNAL Version 2.2 (© Engineering Design, Belmont, MA) by taking the envelope of a digitized natural call group and multiplying the envelope with a sine wave at 700 Hz or 3500 Hz. All stimuli had a sample rate of 15625 Hz. We filtered the 700 Hz call group with a low pass filter at 1500 Hz and the 3500 Hz call group with a band pass filter between 1500 Hz and 4500 Hz. After filtering we added the 700 Hz synthetic call group to the 3500 Hz synthetic call group to create the third synthetic call group with two dominant frequencies (3500 + 700 Hz). Fig. 1(a) shows the time wave form of the natural Gill 4 call group and Gill 5 call group. Fig. 1(b) and 1(c) show the power spectra of the two natural call groups and the three synthetic call groups of Gill 5 and Gill 4. Each stimulus had an equal total energy.

Phonotaxis Experiments

We performed all phonotaxis experiments in a sound attenuating chamber (Acoustic Systems) (1.80 m × 2.7 m × 1.8 m) under dim red light. The temperature in the chamber was 24°C. The stimuli were broadcast from a computer (DELL 486/66), each through a separate channel via an amplifier, to two wide-frequency range speakers (Cambridge SoundWorks, Cambridge, MA) placed directly opposite one another on the floor positioned in the middle of the side walls, 2.7 m apart. The stimuli lasted 8 s and were presented alternately at an intensity of 80 dB SPL (peak RMS, re: 20 μPa) measured in the center of the chamber. Before testing we placed the female under a cone in the middle of the chamber and played the stimuli during a 2-min acclimation period. We then lifted the cone using a remote device. We observed the female's movements and determined if she approached one of the speakers within 15 min. A positive
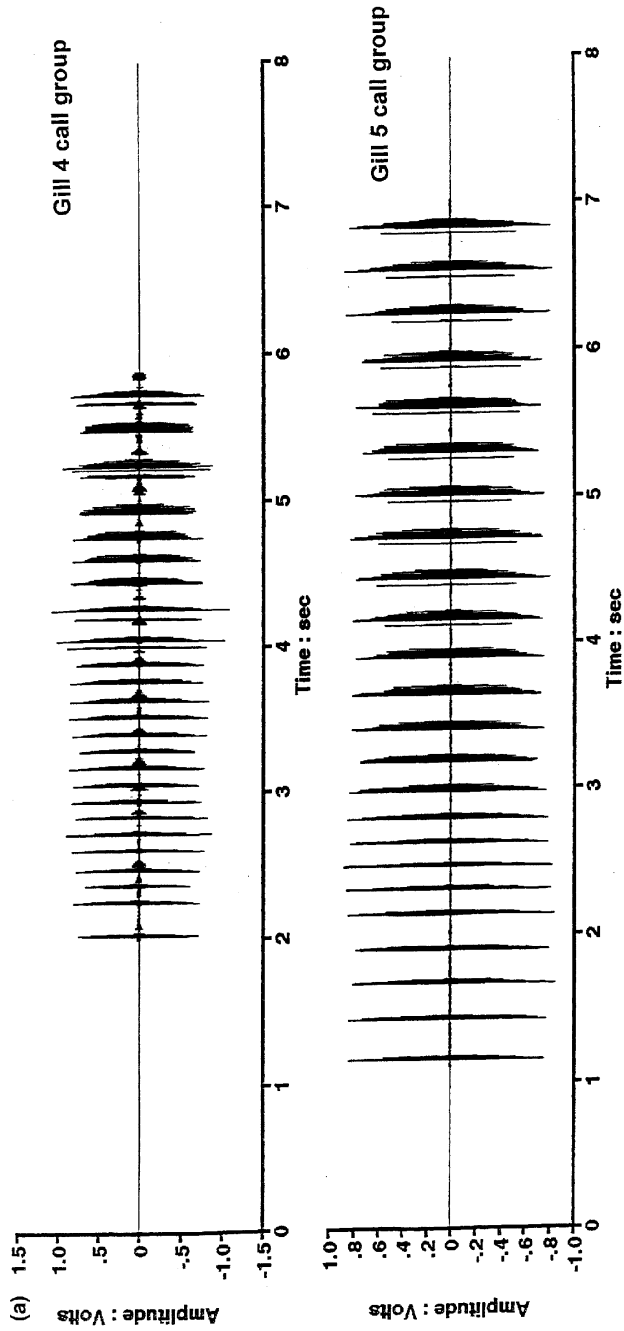
K. Witte, M. J. Ryan & W. Wilczynski

Fig. 1(a): Time wave form of the natural Gill 4 and Gill 5 call groups
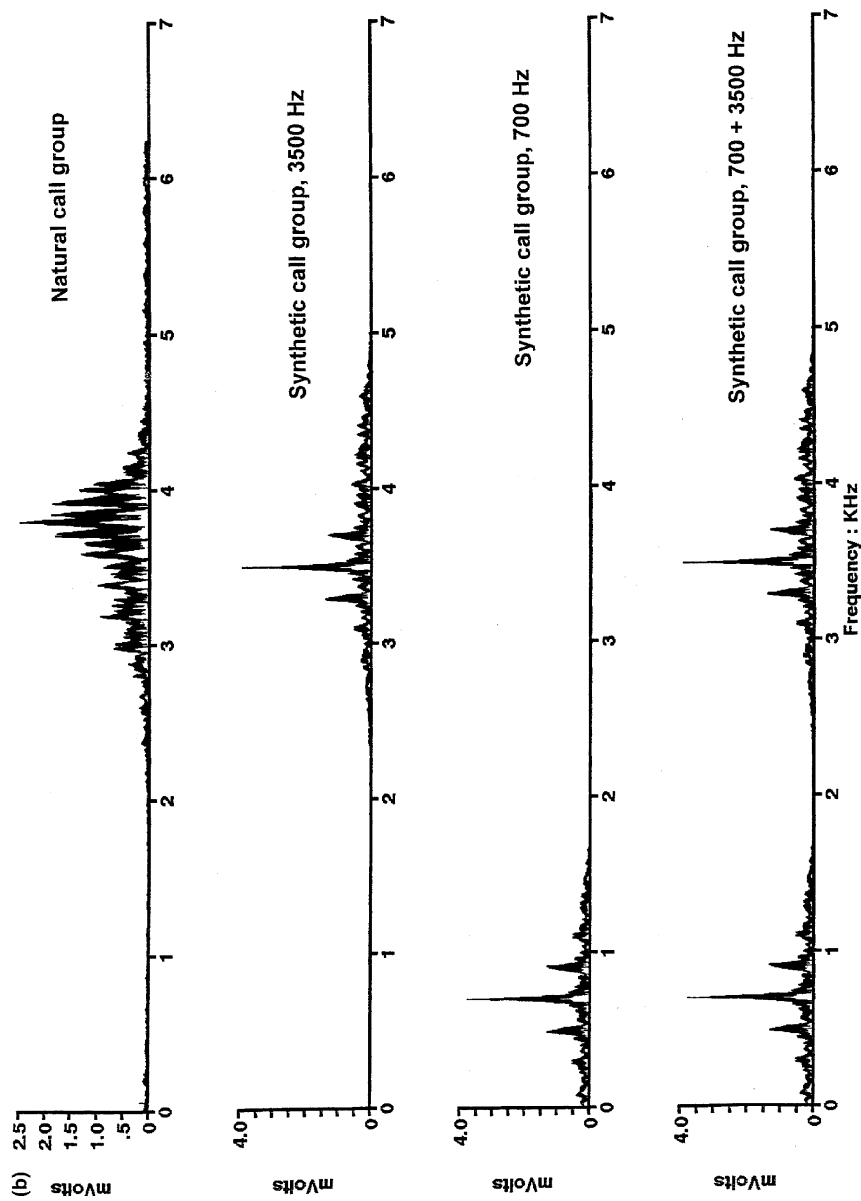
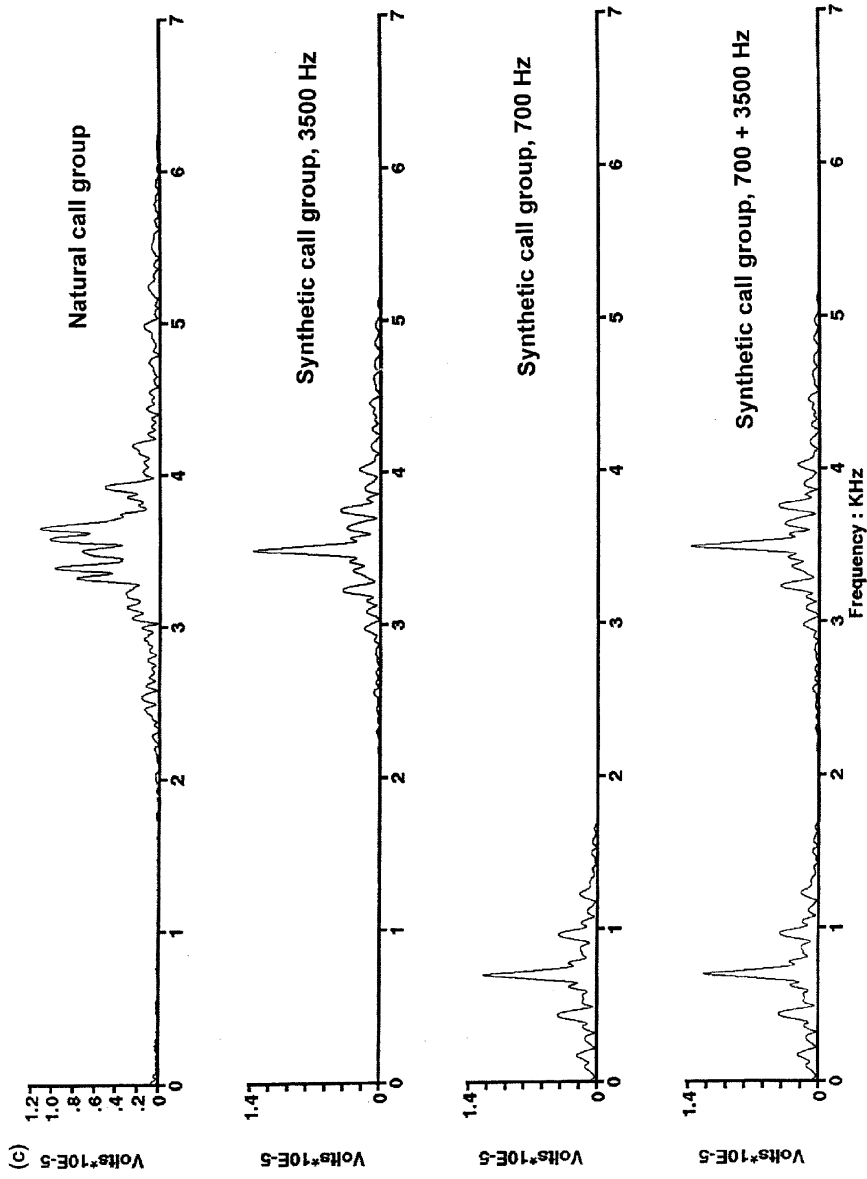*Fig. 1 (b):* Power spectra of the natural Gill 5 call group and the three created synthetic call groups

Fig. 1(c): Power spectra of the natural Gill 4 call group and the three created synthetic call groups

response to a stimulus was recorded when she approached within 20 cm of a speaker within that time. Females that did not approach a loudspeaker within this time were considered nonresponsive. Each female was tested once with each stimulus pair, but was used in other experiments as well. The order of stimulus presentation was randomized.

We played the stimuli antiphonally in double choice experiments: for both call groups we tested 3500 Hz against 700 Hz, 3500 Hz against 3500 + 700 Hz, and 700 Hz against 3500 + 700 Hz. We also tested the 700 Hz Gill 4 call group against equal amplitude, equal duration white noise created by SIGNAL to test if the low-frequency call group is a meaningful stimulus in terms of female mate choice. We also tested a natural Gill 4 and Gill 5 call group against the synthetic 3500 Hz Gill 4 and Gill 5 call group.

Within each experiment we switched the stimuli to the opposite speaker after each test to control for side biases. If a female was not responsive in one test we tested her again on the following night. For each stimulus pair we tested 20 females.

Before and after each test we tested females with other stimuli known to be attractive to females to assess female motivation. Females that were not responsive in these probe tests (i.e. did not approach the speaker within 15 min) were excluded from the analysis. To detect female preferences within a stimulus pair we used the binomial test. We used Fisher's Exact test to compare preferences between the Gill 4 and the Gill 5 call groups.

Results

In the experiments with the Gill 5 call group, females clearly preferred the 3500 Hz call group over the 700 Hz call group (binomial test, p < 0.001, Fig. 2).
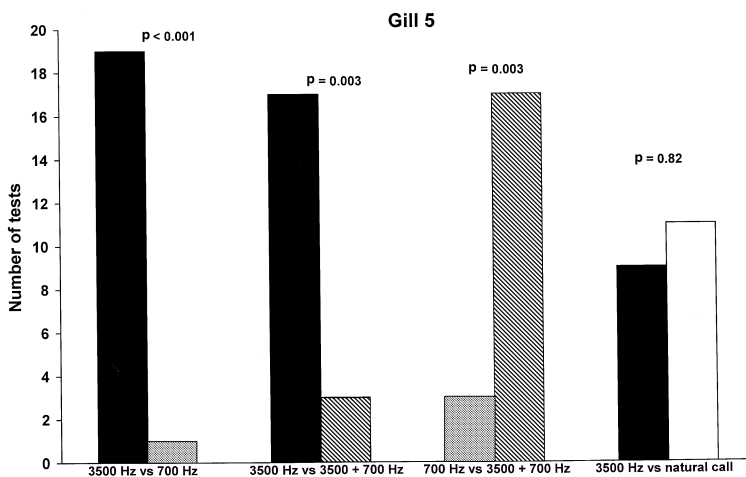

Fig. 2: Number of tests in which females chose one of two broadcast stimuli of the Gill 5 call group

A significantly higher number of females exhibited a preference for the 3500 Hz call group over the combined call group with two dominant frequencies at 3500 Hz and 700 Hz (binomial test, $p = 0.003$, Fig. 2). When we tested this combined call group alternately against the 700 Hz call group, however, females showed significantly more phonotactic responses to the combined call group (binomial test, $p = 0.003$, Fig. 2). Thus, the combined call group was still meaningful in terms of female mate choice, but distributing signal energy over both the basilar and amphibian papilla decreased the attractiveness of male advertisement calls to females relative to a natural call. In tests pairing the natural call group and the synthetic call group at 3500 Hz, females did not discriminate between the stimuli (binomial test, $p = 0.82$, Fig. 2). Thus the synthetic call group is similarly attractive to females as a natural call group, although the synthetic call group contains fewer frequency components than the natural call group.

In tests with the synthetic Gill 4 call groups we found similar results. Females significantly preferred the 3500 Hz call group over the 700 Hz call group (binomial test, $p = 0.001$, Fig. 3). Females also preferred the 3500 Hz call group over the combined call group which contained dominant frequencies at 3500 Hz and at 700 Hz (binomial test, $p < 0.001$, Fig. 3). When females could choose between the 700 Hz call group and the combined call group, they preferred the combined call group over the 700 Hz call group (binomial test, $p < 0.001$, Fig. 3). Females did not discriminate between a natural Gill 4 call group and the synthetic call group with a dominant frequency at 3500 Hz (binomial test, $p = 1.0$, Fig. 3), as was the case in tests with the Gill 5 call group.

When we compared the results of phonotactic responses in females to the Gill 4 and Gill 5 call groups, females showed similar responses in all three combinations of the three synthetic call groups (Fisher's Exact tests: 3500 Hz vs. 700 Hz, $p = 1.0$; 3500 Hz vs. 3500 + 700 Hz, $p = 1.0$; 700 Hz vs. 3500 Hz +
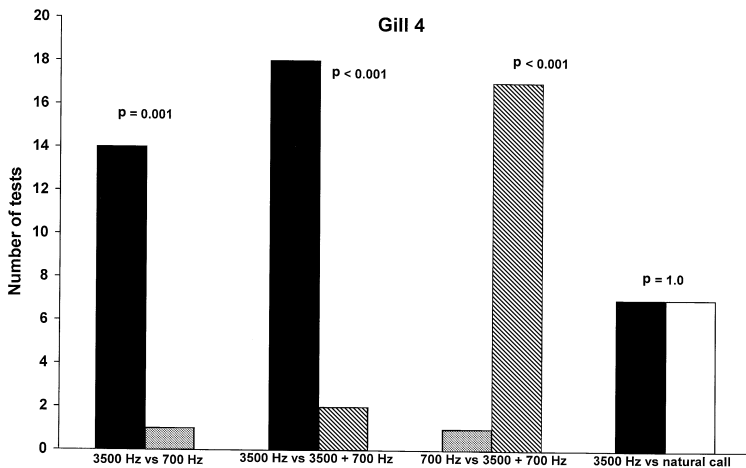

Fig. 3: Number of tests in which females chose one of two broadcast stimuli of the Gill 4 call group

700 Hz, p = 0.61). Thus females responded consistently to the different synthetic stimuli constructed from both call groups.

Additionally, we tested females (n = 10) in a situation where they could choose between white noise and the 700 Hz Gill 4 call group. None of the 10 females chose the call group. This shows that a 700 Hz call group is not meaningful in mate choice.

Discussion

Cricket frog females significantly preferred a synthetic call group with a dominant frequency at 3500 Hz over the same call group with a dominant frequency at 700 Hz. Females also significantly preferred a call group with two dominant frequencies at 3500 Hz and 700 Hz over the same call group at 700 Hz. When we paired the 700 Hz call group against white noise, females did not respond to the call group. These same females responded to normal calls before and after this test, and therefore the failure to respond was not due to a general lack of motivation. These results show that the female cricket frog's preferences for low frequency calls within the natural call range (Ryan & Wilczynski 1988; Ryan et al. 1992) does not extend to the amphibian papilla range of frequency sensitivity, as the abnormally low frequency call was not more attractive than a normal, much higher frequency call, and did not even seem to be recognized as a conspecific advertisement call. These results also show that normal temporal information and amplitude patterns are not sufficient to support female mate choice when the spectral information was radically shifted to a frequency outside the sensitivity range of the basilar papilla and into the range of the other inner ear auditory organ.

When females could choose between the call group at 3500 Hz and the same call group with equal energy divided between two dominant frequencies they significantly preferred the call group with the single dominant frequency at 3500 Hz. These results were true for the two different call groups, which we used for creating the synthetic call groups. Thus, distributing frequency components so that both papilla are stimulated significantly decreases the attractiveness of the call group. We note that the overall signal level was equal for all stimuli. This would have had the effect of spreading the sound energy across more frequency channels in the combined 700 + 3500 Hz call group, making the 3500 Hz peak lower than the 3500 Hz peak in the 3500 Hz call group. If the females were simply ignoring any sound stimulating the amphibian papilla, as the tests of the 700 Hz call group suggests, they may have made their choice because their basilar papilla was more stimulated by the 3500 Hz signal than the combined signal. Although we have not tested amplitude sensitivity in *Acris crepitans*, *Hyla cinerea* females will choose signals that differ by as little as 3 dB (Gerhardt 1987). The results indicate that making the call more spectrally complex does not necessarily make it more attractive, all other factors being equal. Support for this also comes from our experiments showing that females did not distinguish between synthetic call groups with a dominant frequency at 3500 Hz and the natural call groups with

a dominant frequency at 3500 Hz that included numerous frequency sidebands within the basilar papilla range. Thus, the synthetic call groups were as attractive to females as the natural call groups despite the natural calls being spectrally more complex. As both the synthetic and natural call groups were presented at the same amplitude, and both would stimulate only basilar papilla fibers, we would expect both would stimulate this auditory organ about equally. Ryan & Keddy-Hector (1992) suggested that, as a general rule, 'attractive' male signals might be those that better stimulate female sensory systems. For this species, the general rule seems to hold, if one qualifies the rule to say 'better stimulates the female sensory structure normally used for detecting the male signal'. For *Acris crepitans*, that is the basilar papilla specifically, not the auditory system in general.

The cricket frog results are in contrast to what Wilczynski et al. (1995) found in the túngara frog *Physalaemus pustulosus* and what several authors have found in other acoustic communication systems (Catchpole 1986; Ryan & Keddy-Hector 1992; Searcy 1992). In general, more complex signals are more attractive. For example, in the túngara frog *Physalaemus pustulosus*, a minimally effective male call can be made more attractive by adding additional frequency components (Wilczynski et al. 1995) in either the amphibian or basilar papilla range. Furthermore, male túngara frogs can add up to three 'chucks', vocal signals that mainly stimulate the basilar papilla, to the first part of their call, the 'whine', which stimulates the amphibian papilla. This addition increases the whine's attractiveness to females (Ryan 1985, 1988). Wilczynski et al. (1999) showed that even adding the chuck to the whine in almost any position makes the whine more attractive to females, and no position made it less attractive. This includes positions that overlapped the whine in time, analogous to this experiment's two-peak artificial signal. Adding additional components to increase signal complexity will make a mate attractant signal more complex even when those signals do not occur in nature, as has been demonstrated in both acoustic (Ryan & Rand 1990; Searcy 1992; Wilczynski et al. 1995) and visual (Basolo 1990; Jones & Hunter 1998; Tyler Burley & Symanski 1998; Witte & Curio 1999) communication systems.

One difference between the cricket frog signal and others tested in this way is the simplicity of the cricket frog call's spectral characteristics. Previous studies investigating extreme signal variation or the capacity of artificial acoustic adornments to make calls more attractive have focused on species with more spectrally complex calls that stimulate multiple frequency regions within the amphibian papilla or both inner ear papillae. For example, in the túngara frog and other *Physalaemus* species, the species-specific 'whine' sweeps through a large portion of the amphibian papilla frequency range, and the 'chuck' of *P. pustulosus* or the various secondary vocal signals of other *Physalaemus* species stimulate the basilar papilla (Keddy-Hector et al. 1992; Wilczynski et al. 1992). Either the use of multiple frequency channels during normal communication, or the use of the amphibian papilla for species recognition, predisposes anurans to accept added spectral complexity as more attractive. We note that such a communication system does not necessarily mandate such a process, as one *Physalaemus* species

(*P. enesefae*) does not find the addition of heterospecfic chucks attractive (Tarano & Ryan submitted). Nevertheless, it may be that only in those anurans, such as *Physalaemus* species, that use the amphibian papilla is the female auditory system potentially open to additional stimuli, and only there can it drive the evolution of more complex male advertisement calls. In anurans using the basilar papilla, such as the cricket frog, females may be more restricted in their preferences to the normal range of the male call. This could be tested in the many other anuran species that use only one papilla for their advertisement call. It would also be interesting to determine if only anurans using the amphibian papilla for mate recognition use additional vocal signals to make their call more attractive.

Much of the recent work on female responses to extreme or unusual male signals has been guided by ideas that have come out of the 'sensory exploitation' hypothesis (Ryan 1990, 1998; Ryan et al. 1990; Ryan & Keddy-Hector 1992). Although this idea is fundamentally a phylogenetic hypothesis concerning the evolutionary antecedents in receivers of successful signals in senders, experimental evidence from current species has taken the form of demonstrations that unusual signals can be attractive to females if they stimulate their sensory system, often including unused sensory channels (Ryan & Keddy-Hector 1992; see also the 'sensory drive' idea of Endler 1992). Indeed, as reviewed above, there are many examples of this now in the literature. What has to date largely been missing from such studies are carefully controlled experiments that try to define what type of 'extra' stimulation would be effective, and thus place limits on the sensory exploitation process. The present study does that, and, combined with other mate-choice studies in this species (Ryan & Wilczynski 1988; Ryan et al. 1992) shows that, for cricket frogs, signals that provide enhanced stimulation to the female's basilar papilla are more attractive, but signals that stimulate the more sensitive amphibian papilla are not (and are not even recognized) even when all other call features are present. Furthermore, the present study shows that stimulating more frequency channels in the absence of an overall increase in stimulus energy actually decreases the attractiveness of the signal. That is, one cannot exploit the other sensory channels by trading off spectral complexity for focused stimulation. How the results of the present experiment relate to more general rules concerning the evolution of animal communication systems is a question that cannot readily be answered, given that we do not know how broadly, or under what circumstances, the results from this one species can be applied across taxa. Nevertheless, this study does show that there are limits to the ability of extreme or unusual signals to elicit female mate choice, and we suggest that a careful examination of those limits may be important.

In summary, our experiments showed that a low-frequency signal outside the natural frequency range of a cricket frog call, but within its range of hearing, would not solicit mate attraction despite normal temporal and amplitude patterns. Furthermore, adding low-frequency components to a male call to make it more complex may not make it more attractive; on the contrary, in this study it decreased the attractiveness of the cricket frog call. It remains to be determined if

changes in the complexity of the temporal or amplitude pattern of the call lead to the same result, and whether signals that precede or follow the call will alter its attractiveness.

Acknowledgements

Literature Cited

Basolo, A. 1990: Female preference predates the evolution of the sword in swordtails. Science **250,** 808—810.

Basolo, A. 1995a: A further examination of a pre-existing bias favouring a sword in the genus *Xiphophorus*. Anim. Behav. **50,** 365—375.

Basolo, A. 1995b: Phylogenetic evidence for the role of a pre-existing bias in sexual selection. Proc. R. Soc. Lond. B. **259,** 307—311.

Burmeister, S., Wilczynski, W. & Ryan, M. J. 1999: Temporal call changes and prior experience affect graded signaling in the cricket frog. Anim. Behav. **57,** 611—618.

Capranica, R. R. 1976: Morphology and physiology of the auditory system. In: Frog Neurobiology (Llinas, R. & Precht, W., eds). Springer, New York, pp. 551—575.

Capranica, R. R., Frischkopf, L. S. & Nevo, E. 1973: Encoding of geographic dialects in the auditory system of the cricket frog. Science **182,** 1272—1275.

Catchpole, C. K. 1986: Song repertoires and reproductive success in the great reed warbler (*Acrocephalus arundinaceus*). Behav. Ecol. Sociobiol. **19,** 439—445.

Endler, J. 1992: Signals, signal conditions, and the direction of evolution. Am. Nat. **139,** S125–S153.

Gerhardt, H. C. 1987: Evolutionary and neurobiological implications of selective phonotaxis in the green treefrog (*Hyla cinerea*). Anim. Behav. **35,** 1479—1589.

Gerhardt, H. C. 1988: Acoustic properties used in call recognition by frogs and toads. In: The Evolution of the Amphibian Auditory System (Fritzsch, B. Ryan, M. J. Wilczynski, W. Hetherington, T. E. & Walkowiak, W., eds). John Wiley, New York, pp. 455—483.

Jones, I. L. & Hunter, F. 1998: Heterospecific mating preferences for a feather ornament in least auklets. Behav. Ecol. **9,** 187—192.

Keddy-Hector, A. C., Wilczynski, W. & Ryan, M. J. 1992: Call patterns and basilar papilla tuning in cricket frogs. II. Intrapopulation variation and allometry. Brain Behav. Evol. **39,** 238—246.

Kime, N. M., Rand, A. S., Kapfer, M. & Ryan, M. J. 1998: Consistency of female mate choice in the túngara frog: a permissive preference for complex characters. Anim. Behav. **55,** 641—649.

Lewis, E. R. & Lombard, R. E. 1988: The amphibian inner ear. In: The Evolution of the Amphibian Auditory System (Fritzsch, B. Ryan, M. J. Wilczynski, W. Hetherington, T. E. & Walkowiak, W., eds). John Wiley, New York, pp. 93—124.

Rand, S. 1988: An overview of anuran acoustic communication. In: The Evolution of the Amphibian Auditory System (Fritzsch, B. Ryan, M. J. Wilczynski, W. Hetherington, T. E. & Walkowiak, W., eds). John Wiley, New York, pp. 415—431.

Rand, S., Ryan, M. J. & Wilczynski, W. 1992: Signal redundancy and receiver permissiveness in acoustic mate recognition by the túngara frog, *Physalaemus pustulosus*. Am. Zool. **32,** 81—90.

Ryan, M. J. 1983: Sexual selection and communication in a neotropical frog, *Physalaemus pustulosus*. Evolution **37,** 261—272.

Ryan, M. J. 1985: The Túngara Frog. A Study in Sexual Selection and Communication. Univ. of Chicago Press, Chicago, Illinois.

Ryan, M. J. 1988: Constraints and Patterns in the Evolution of Anuran Acoustic Communication. In: The Evolution of the Amphibian Auditory System (Fritzsch, B., Ryan, M. J., Wilczynski, W., Hetherington, T. E. & Walkowiak, W., eds). John Wiley, New York, pp. 637—677.

Ryan, M. J. 1990: Sexual selection, sensory systems and sensory exploitation. Oxford. Surv. Evol. Biol. **7,** 157—195.

Ryan, M. J. 1991: Sexual selection and communication in frogs. Trends Ecol. Evol. **6,** 351—354.

Ryan, M. J. 1998: Sexual selection, receiver biases, and the evolution of sex differences. Science **281,** 1999—2003.

Ryan, M. J., Fox, J. H., Wilczynski, W. & Rand, A. S. 1990: Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus.* Nature **343,** 66—67.

Ryan, M. J. & Keddy-Hector, A. 1992: Directional pattern of female mate choice and the role of sensory biases. Am. Nat. **139,** S4—S35.

Ryan, M. J., Perrill, S. A. & Wilczynski, W. 1992: Auditory tuning and call frequency predict population-based mating preferences in the cricket frog *Acris crepitans.* Am. Nat. **139,** 1370—1383.

Ryan, M. J. & Rand, S. 1990: The sensory basis of sexual selection for complex calls in the túngara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). Evolution **44,** 305—314.

Ryan, M. J. & Rand, S. 1993: Sexual selection and signal evolution: the ghost of bias past. Phil. Trans. R. Soc. Lond. B. **340,** 187—195.

Ryan, M. J. & Wilczynski, W. 1988: Coevolution of sender and receiver: Effect on local mate preferences in cricket frogs. Science **240,** 1786—1788.

Ryan, M. J. & Wilczynski, W. 1991: Evolution of intraspecific variation in the advertisement call of a cricket frog (*Acris crepitans, Hylidae*). Biol. J. Linn. Soc. **44,** 249—271.

Searcy, W. A. 1992: Song repertoire and mate choice in birds. Amer. Zool. **32,** 71—80.

Tyler Burley, N. & Symanski, R. 1998: 'A taste for the beautiful': latent aesthetic mate preferences for white crests in two Australian grassfinches. Am. Nat. **152,** 792—802.

Venator, K. R. 1999: The influence of signal attenuation and degradation on behavior and midbrain auditory thresholds in the cricket frog, *Acris crepitans blanchardi.* PhD Thesis, Univ. of Texas at Austin.

Venator, K. R. & Wilczynski, W. 1998: Behavioral response of male cricket frogs to attenuated and degraded mating calls. Am. Zool. **38,** 170A.

Wagner, W. E. 1989: Social correlates of variation in male calling behavior in Blanchard's cricket frog, *Acris crepitans blanchardi.* Ethology **82,** 27—45.

Wells, K. D. 1977: The social behavior of anuran amphibian. Anim. Behav. **25,** 666—693.

Wilczynski, W. & Capranica, R. R. 1984: The auditory system of anuran amphibians. Prog. Neurobiol. **22,** 1—38.

Wilczynski, W., Keddy-Hector, A. C. & Ryan, M. J. 1992: Call patterns and basilar papilla tuning in cricket frogs. I. Differences among populations and between sexes. Brain Behav. Evol. **39,** 229—237.

Wilczynski, W., Rand, A. S. & Ryan, M. J. 1995: The processing of spectral cues by the call analysis system of the túngara frog, *Physalaemus pustulosus.* Anim. Behav. **49,** 911—929.

Wilczynski, W., Rand, A. S. & Ryan, M. J. 1999: Female preferences for temporal order of call components in the túngara frog: a Bayesian analysis. Anim. Behav. **58,** 841—851.

Wilczynski, W. & Ryan, M. J. 1999: Geographic variation in animal communication systems. In: Geographic Variation in Behavior (Foster, S. A. & Endler, J. A., eds). Oxford Univ. Press, Oxford, pp. 234—261.

Witte, K. & Curio, E. 1999: Sexes of a monomorphic species differ in preference for mates with a novel trait. Behav. Ecol. **10,** 15—21.

Wollerman, L. 1998: Stabilizing and directional preferences of female *Hyla ebraccata* for calls differing in static properties. Anim. Behav. **55,** 1619—1630.

Zakon, H. H. & Wilczynski, W. 1988: The physiology of the anuran eight nerve. In: The Evolution of the Amphibian Auditory System (Fritzsch, B. Ryan, M. J. Wilczynski, W. Hetherington, T. E. & Walkowiak, W., eds). John Wiley, New York, pp. 125—155.