Female preferences for socially variable call characters in the cricket frog, *Acris crepitans*

NICOLE M. KIME*, SABRINA S. BURMEISTER† & MICHAEL J. RYAN*†

*Section of Integrative Biology, University of Texas at Austin
†Institute for Neuroscience, University of Texas at Austin

Male cricket frogs produce only one type of call, the advertisement call, which both attracts females and repels rival males. The temporal and spectral structure of this call varies in a graded fashion with social context: males increase the temporal complexity and decrease the dominant frequency of their advertisement calls when interacting with neighbouring males. Previous studies of male behaviour suggested that vocal escalation signals fighting ability or aggressive intent. In this study, we examined an alternative hypothesis for the function of vocal escalation, that it increases a male's relative attractiveness to females when other males are nearby. We tested female cricket frogs for phonotactic preferences with respect to spectral and temporal call characters. Females did not show preferences for call dominant frequency, although they tended to choose calls with dominant frequencies near the population mean over calls with high or low dominant frequencies. Females preferred temporal call characters representative of interacting males to the temporal characters of undisturbed males. Males may use changes in temporal call characters to facultatively increase their relative attractiveness to females in the presence of other males.

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In most species, males compete for mating opportunities, and communication plays a central role in this competition. Males compete directly (often agonistically) with each other for access to females or resources, and they also compete indirectly for female mate choice (Darwin 1871). In some species, males use separate aggressive and attractive communication signals in these two contexts. In other species, males use a single dual-function communication signal that both repels rival males and attracts females (reviewed in Berglund et al. 1996).

The intensity of both direct and indirect competition varies with the number and density of males in an area. Accordingly, males often escalate signalling behaviour when other males are nearby (reviewed in Wells 1988; Andersson 1994). For dual-function signals, escalation may increase a male's dominance status in direct male–male competition, increase his relative attractiveness to females, or both. Discriminating between these possible functions of socially mediated escalation in dual-function signals has been a persistent problem in studies of sexual selection and communication (e.g. Searcy & Yasukawa 1990; Grafe 1995; Morris et al. 1995; Kodric-Brown 1996; Howard & Young 1998; Candolin 2000).

In Blanchard's cricket frog, *Acris crepitans blanchardi*, males produce a dual-function advertisement call that is used both to attract females and to mediate territorial interactions between males in a chorus (Nevo & Capranica 1985; Perrill & Shepherd 1989; Wagner 1989c). The temporal and spectral structure of this call varies in a graded fashion with social context; males increase the temporal complexity and decrease the dominant frequency of their advertisement calls when interacting with neighbouring males. Previous studies of male behaviour suggested that this vocal escalation is aggressive in nature and signals fighting ability or aggressive intent (Wagner 1989a, b, c, 1991, 1992; Burmeister et al. 1999a, b, 2002). It was also suggested that escalation might decrease a male's attractiveness to females, and that socially mediated signal variation thus reflects a trade-off between the advertisement call's functions in aggression and mate attraction (Wagner 1989c).

An alternative (but not necessarily exclusive) hypothesis for the function of vocal escalation in cricket frogs is that males change their spectral and temporal call characters in

Correspondence and present address: N. M. Kime, Department of Natural Science, Edgewood College, 1000 Edgewood College Drive, Madison, WI 53711, U.S.A. (email: nkime@edgewood.edu). S. Burmeister is now at the Department of Biology, University of North Carolina, Chapel Hill, NC 27599, U.S.A. M. J. Ryan is at the section of Integrative Biology C0930, University of Texas, Austin, TX 78712, U.S.A.
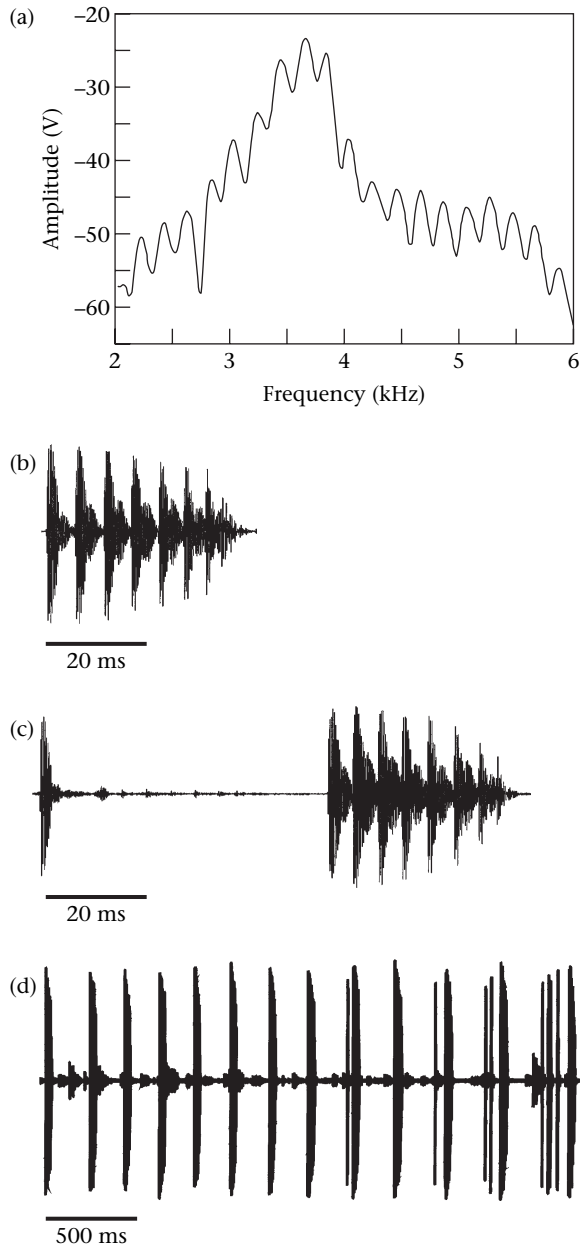
Figure 1. *Acris crepitans* call structure. (a) Power spectrum of one advertisement call from an Austin, Texas (Gill Ranch) male (24.4-Hz frequency resolution, smoothed to 50 Hz). Side bands are not harmonics, but are the result of amplitude modulation within the call. (b) Oscillogram of one advertisement call with seven pulses. (c) One advertisement call with eight pulses in two pulse groups. (d) Call group of 13 calls. Note the different timescale on this oscillogram. Also note the variation across the call group in the number of pulses and pulse groups in individual calls.

temporal call characters that males change in interactions with other males. We test the hypothesis that vocal escalation increases a male's relative attractiveness to females.
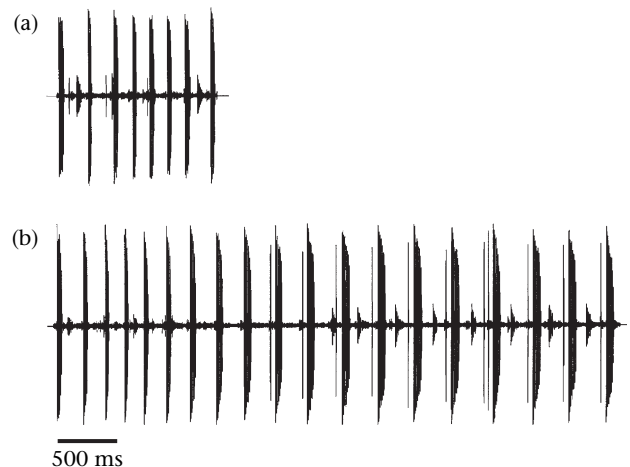
METHODS

Cricket Frog Calls

Cricket frog males produce advertisement calls that consist of a single amplitude-modulated carrier frequency (Fig. 1a). Each call contains a variable number of pulses. Most of the pulses within a call are produced continuously (Fig. 1b), but sometimes pulses are partitioned into two or more distinct clusters, or pulse groups (Fig. 1c). Individual advertisement calls are produced in bouts, or call groups (Fig. 1d). In general, the calls near the end of a call group contain more pulses and more pulse groups than calls near the beginning.

A male's spectral and temporal call characteristics vary with his immediate social environment. Males decrease the dominant frequency of their calls when confronted with a real or simulated intruder (Wagner 1989a, b, 1992; Burmeister et al. 1999b, 2002). The extent of this frequency change varies between males and with the call characteristics of the intruder, but in one study, males lowered their frequency by an average of 132 Hz in response to a stimulus broadcast at 100 dB (range 69–363 Hz) (Wagner 1989a; see also Burmeister et al. 1999b, 2002). Males also increase the temporal complexity of their advertisement signal when they have nearby neighbours or are interacting with intruders (Wagner 1989c; Fig. 2). They increase the number of pulses per call, the number of pulse groups per call, and the number of calls per call group. Changes in pulse and pulse group number occur primarily among calls near the end of the call group (Wagner 1989b, c, 1992; Burmeister et al. 1999b, 2002).

We refer to the decrease in dominant frequency and the increase in temporal complexity as vocal escalation. This

order to increase their relative attractiveness to females when other males are nearby (Wagner 1991). Although other studies have tested female preferences in this species (Ryan & Wilczynski 1988; Wagner 1991; Ryan et al. 1992; Perrill & Lower 1994), the question of how vocal escalation influences female mate choice has not been resolved. In this study, we used phonotaxis experiments to test for female preferences with respect to the spectral and

Figure 2. Temporal vocal escalation. (a) Call group representative of males calling undisturbed within a chorus. (b) Escalated call group representative of interacting males.

terminology is not meant to imply function, but simply to reflect the complexity of the signals and the social circumstances under which males change their calls. In cricket frogs, escalation of both frequency and temporal call characters occurs in a graded fashion, meaning that a male's calls and the extent of his call changes vary systematically with the proximity of his neighbours, as well as with the amplitude, frequency and temporal characteristics of his rival's calls (Wagner 1989a, b, c, 1992; Burmeister et al. 1999b).

Phonotaxis Experiments

We collected female cricket frogs from two populations near Austin, Texas, U.S.A. At Gill Ranch (30°18′N, 97°59′W), males call at a semipermanent pond on private property. At McKinney Falls State Park (30°11′N, 97°44′W), males call in an area surrounding a spring-fed stream. Both of these populations have been used extensively in studies of male–male interactions (Wagner 1989a, b, c, 1991, 1992; Burmeister et al. 1999a, b, 2002).

We collected 64 females from Gill Ranch between 3 April and 9 July 1997, and between 18 March and 21 April 1998. We collected 41 females from McKinney Falls between 2 March and 9 August 1999, and between 14 April and 29 June 2000. At both sites, we collected females between 2100 and 2400 hours. All females were in amplexus with a male when captured. Immediately after capture, we brought the females to our laboratory at the University of Texas, where they were maintained at 4–6°C in order to delay oviposition.

We tested females in a two-choice phonotaxis paradigm. We began experiments either on the night of capture (1997 and 1998) or on the morning following collection (1999 and 2000). After allowing each female at least 30 min to acclimate to room temperature (21–24°C), we placed her under a cone in the centre of an insulated test chamber (Acoustic Systems, Austin, Texas; 1.8 × 2.7 × 1.8 m) that was illuminated by dim red light. We then presented her with two synthetic advertisement calls from speakers placed equidistant from the female at opposite ends of the chamber (2.7 m apart). Stimuli were presented antiphonally, each at a rate of one per 2 s. Before each testing session, we used a single reference stimulus to calibrate the peak output intensity of each speaker to a sound pressure level, SPL, of 78 dB (re 20 µPa, measured at the centre of the chamber where the female was to be released, 1.35 m from the speaker).

We observed the female via closed circuit camera. After a 2-min stimulus acclimation period, we remotely lifted the cone. If the female approached to within 10 cm of one of the two speakers, we scored a positive response to that stimulus and immediately tested her with a different stimulus pair. If the female failed to make a choice within 15 min, or if she climbed the walls of the chamber, a no response was scored and she was not tested further in that session. Females who failed to respond in one session were often tested again within 24 h, after a resting period of at least 1 h during which they were maintained at 4–6°C. After all testing was complete, females were measured,

marked with a unique toe-clip combination (see Ethical Note, below), and returned to the site of capture. Most females were returned to the field site prior to oviposition. Recaptured females were not retested with the same stimulus pairs.

To control for potential side biases, we randomized the speaker assignments for each stimulus pair. Overall, there appeared to be no side bias with respect to our testing arena; during the time-course of these experiments females chose 388 times from the left and 373 times from the right speaker (two-tailed exact binomial probability: $P = 0.612$; these data include experiments not reported here). As noted above, we often tested females with more than one pair of stimuli during a testing session (up to 11 tests per session). To control for potential order effects, we randomized the presentation order of stimulus pairs within a testing session. The number of preceding tests and time since capture did not appear to influence female responses (N. M. Kime, unpublished data). Seven of the 41 females from the McKinney Falls population chose repeatedly from the same speaker (six of seven choices from the same speaker, the preferred side varied between females), suggesting a possible side bias in these individuals. Removing these females did not change the interpretation of our results, so these seven females were retained in the analysis of the data.
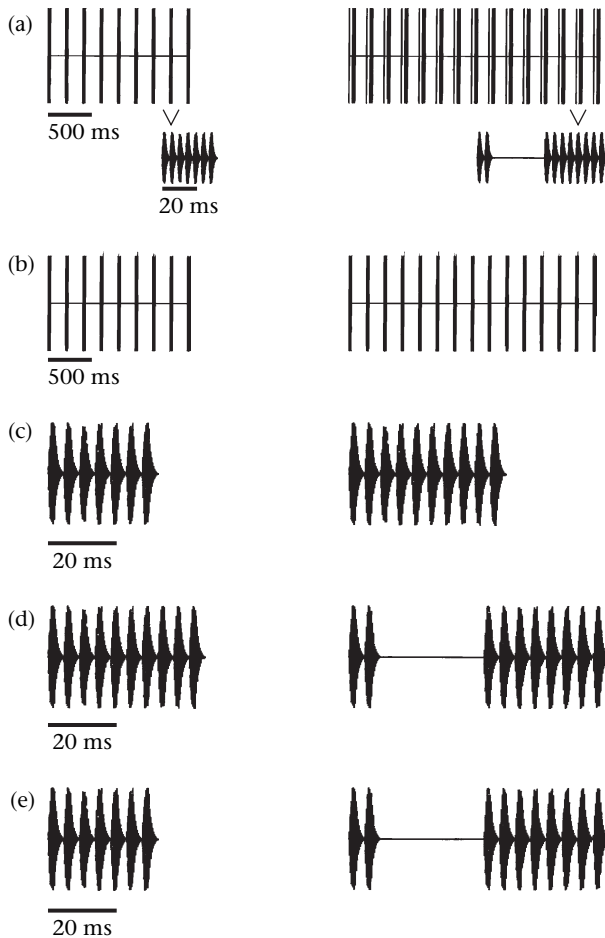
Experimental Stimuli

All preference experiments were conducted using synthetic advertisement call stimuli. To create stimuli, we used the software program SIGNAL (Beeman 1996) to amplitude-modulate a single carrier frequency to the temporal pattern of a cricket frog advertisement call. Calls were concatenated into synthetic call groups. The sampling rate for all stimuli was 25 kHz.

Temporal call characters

We tested females from McKinney Falls for phonotactic preferences with respect to temporal call characters. The dominant frequency for all stimuli was 3670 Hz, near the mean for this population. Stimuli varied in the number of pulses per call, the number of pulse groups per call, and the number of calls per call group. Stimulus parameters were based on data from a McKinney Falls study of male vocal responses to simulated intruders (J. Chu, unpublished data) and are comparable to those used in a recent male playback study at this site (Burmeister et al. 1999b).

We conducted five preference experiments. First, we tested females for preferences with respect to a suite of temporal call changes that males make in vocal escalation (Fig. 3a). The baseline (undisturbed) stimulus had nine calls per call group, with each call having seven pulses in one pulse group. The alternative escalated stimulus had 15 calls per call group, with each call having 10 pulses in two pulse groups. Calls with two pulse groups had a 30-ms interval between the second and third pulse of the call. The call rate within each stimulus was maintained at five calls per s; because calls differed in length it was necessary that the baseline and escalated stimuli differed in intercall

Figure 3. Stimuli for temporal call character phonotaxis experiments. (a) Baseline versus escalated stimuli. The baseline stimulus had nine calls per group (top left), with each call having seven pulses in one pulse group (bottom left). The escalated stimulus had 15 calls per group, with each call having 10 pulses in two pulse groups. (b) Nine calls per group versus 15 calls per group. (c) Seven pulses versus 10 pulses per call (one call is shown from each stimulus group of nine calls). (d) One pulse group versus two pulse groups per call. (e) Seven pulses in one pulse group versus 10 pulses in two pulse groups.

interval (168 and 125 ms, respectively). To reduce the number of tested variables, we did not vary the number of pulses and pulse groups across each call group. Instead, each stimulus contained a group of identical calls that represented the temporal characters of calls near the end of call groups (J. Chu, unpublished data).

We also tested females for preferences with respect to each of the individual call characters noted above. We tested females for preferences with respect to stimuli that differed only in the number of calls per call group (9 versus 15 calls per group; Fig. 3b), the number of pulses per call (7 versus 10 pulses per call; Fig. 3c), or the number of pulse groups per call (one versus two pulse groups per call; Fig. 3d). In these experiments, all untested variables were held constant at the baseline level. In one additional experiment, we held the number of calls per call group constant at nine and varied both the number of pulses and the number of pulse groups per call (seven pulses in one group versus 10 pulses in two groups; Fig. 3e).

Dominant frequency

We tested females from Gill Ranch for phonotactic preferences with respect to call dominant frequency. All stimuli were identical in temporal structure and consisted of call groups of 15 calls. Calls varied across the call group. The beginning five calls of each group had six pulses in one pulse group. The centre five calls of each group had seven pulses in one pulse group. The remaining five calls had eight pulses in one pulse group. These temporal call characters were determined from analysis of recordings from this population (N. M. Kime, unpublished data).

Test stimuli varied only in carrier frequency. The dominant frequency of cricket frog calls varies with a male's body size, and there is also a large amount of variation between males in frequency escalation (Wagner 1989a, b, 1992; Burmeister et al. 1999b, 2002). Males are more likely to lower their call dominant frequency if their baseline frequency is higher than that of an intruder (Wagner 1989a). Moreover, the magnitude of a male's frequency change depends on the relative frequency difference between his calls and those of an intruder; males rarely lower their call dominant frequency below that of an intruder (Wagner 1989a). Given this size-related variation in frequency and frequency escalation, dominant frequencies are not easily characterized as one mean value produced before and after escalation.

We conducted a suite of phonotaxis experiments in which we varied stimulus frequency relative to the population mean. In four experiments, we paired a stimulus frequency near the Gill Ranch population's pre-escalation mean (3370 Hz) with a stimulus frequency lower than the population mean (3172, 3073, 2974, or 2875 Hz). These four experiments tested the effects of frequency escalation for a cricket frog male with an average dominant frequency. In an additional four experiments, we paired a stimulus frequency higher than the population mean (3865, 3766, 3667, or 3568 Hz) with a stimulus frequency near the population mean (3370 Hz). These experiments tested the effect of frequency escalation for males with high pre-escalation frequencies (those males who are most likely to change the frequency of their calls).

Previous studies of dominant frequency preferences in female cricket frogs did not vary temporal call structure across the call group (Ryan & Wilczynski 1988; Ryan et al. 1992). In a ninth experiment, we tested females with a pair of stimuli previously reported to produce a preference (Ryan & Wilczynski 1988). In this experiment, the synthetic call group consisted of 10 calls. Each call within the group had six pulses and one pulse group.

Statistical Analyses

Our target sample size was 20 females per experiment, but female availability did not always permit this. We tested at least nine females with each stimulus pair. We used Bayesian analysis to evaluate population-level phonotactic preferences (following Gerhardt 1992; see also Gelman et al. 1995). We assumed a continuous range of possible population-level preference strengths for one of
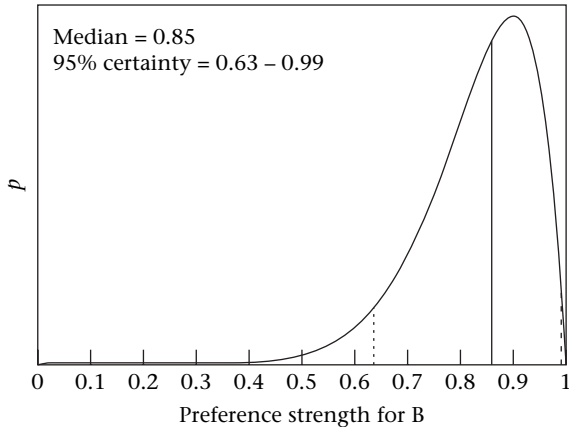
Figure 4. Posterior probability density for a female choice experiment in which one female chose stimulus A, and nine females chose stimulus B. Solid vertical line = median strength of preference for stimulus B. Dashed vertical lines = 95% certainty interval.

the two stimuli (range 0–1, expressed as the proportion of females in a population that would choose that stimulus over the alternative) and a uniform prior probability density. We calculated preferences for escalated call characters in the temporal character experiments and for the lower-frequency stimulus in dominant frequency experiments.

We used the Beta distribution as a continuous conjugate for binomial probability. We report the median of the posterior probability distribution as an approximation of the population-level strength of preference for this stimulus. We also report the lower and upper bounds of the posterior's 95% certainty interval. Certainty intervals were calculated as high-density regions, the narrowest range that includes 95% of the posterior probability density. We rejected a hypothesis of no preference when a preference strength of 0.5 fell outside of the 95% certainty interval. An example is shown in Fig. 4.

Ethical Note

We toe-clipped the females used in these phonotaxis experiments to avoid retesting recaptured females with the same stimuli. Given the duration of this study and our long-term use of these field sites, we required a permanent marking technique. Cricket frogs are too small to tag and they lack natural markings that reliably distinguish between individuals. We therefore chose to follow the toe-clipping recommendations put forward in the Guidelines for Use of Live Amphibians and Reptiles in Field Research (compiled by the American Society of Ichthyologists and Herpetologists (ASIH), The Herpetologists' League (HL), and the Society for the Study of Amphibians and Reptiles (SSAR), available online at http://www.asih.org/pubs/herpcoll.html). Toe clipping did not demonstrably interfere with the animal's survival or behaviour.

RESULTS

Temporal Call Characters

The results of experiments assessing female preferences for temporal call characters are summarized in Table 1. When the tested stimuli differed simultaneously in multiple temporal characters, female cricket frogs preferred the escalated stimulus (15 calls, each with 10 pulses in two pulse groups) to the baseline stimulus (nine calls, each with seven pulses in one group). When stimuli differed only in the number of calls per group, females preferred more calls per group (15 to 9 calls). Holding the number of calls per group constant at nine, females showed a preference for escalated calls (10 pulses in two groups to seven pulses in one group). This preference was mediated by a preference for multiple pulse groups. We could not reject a hypothesis of no preference with respect to pulse number, but females preferred calls with two pulse groups to calls with one pulse group.

Dominant Frequency

We could not reject a hypothesis of no preference in any of the four experiments testing the effects of frequency escalation for males with average dominant frequencies (population mean versus lower frequencies). The majority of females chose the higher, mean frequency, however, and in one experiment, females appeared to have a weak

Table 1. Temporal call character phonotaxis data

Stimuli		Choices		Posterior probability distribution			
A	B	A	B	95% CI	Median	Preference	*P**
Baseline	Escalated	1	9	0.63–0.99	0.85	Escalated	0.021
Nine calls	15 calls	1	9	0.63–0.99	0.85	15 calls	0.021
Seven pulses in one group	10 pulses in two groups	1	9	0.63–0.99	0.85	10 pulses in two groups	0.021
Seven pulses	10 pulses	8	8	0.28–0.72	0.50		1.000
One pulse group	Two pulse groups	3	13	0.59–0.95	0.79	Two pulse groups	0.021

Certainty intervals (CI) and median preference strengths are expressed in terms of the proportion of females in the population that would choose stimulus B (the stimulus with escalated call characters). A hypothesis of no preference was rejected when a preference strength of 0.5 did not fall within the 95% certainty interval.
*Two-tailed binomial probabilities are reported for reference only.

Table 2. Dominant frequency phonotaxis data

| Stimuli (Hz)		Choices		Posterior probability distribution			
A	B	A	B	95% CI	Median	Preference	*P**
3370	3172	10	9	0.27–0.68	0.48		1.000
3370	3073	9	7	0.23–0.67	0.44		0.804
3370	2974	14	6	0.14–0.51	0.31		0.115
3370	2875	8	6	0.21–0.67	0.43		0.791
3865	3370	9	9	0.29–0.71	0.50		1.000
3766	3370	5	4	0.18–0.73	0.45		1.000
3667	3370	6	14	0.49–0.86	0.69		0.115
3568	3370	9	11	0.34–0.75	0.55		0.824
3800†	3500†	2	8	0.52–0.96	0.76	3500†	0.109

Certainty intervals (CI) and median preference strengths are expressed in terms of the proportion of females in the population that would choose stimulus B (the lower-frequency stimulus). A hypothesis of no preference was rejected when a preference strength of 0.5 did not fall within the 95% certainty interval.
*Two-tailed binomial probabilities are reported for reference only.
†Replicated experiment (after Ryan & Wilczynski 1988). Stimuli did not have temporal call character variation across the call group.

preference for the mean over a lower frequency (Table 2, Fig. 5). We also could not reject a hypothesis of no preference in the four experiments testing the effects of frequency escalation for males with high pre-escalation frequencies (higher versus mean frequencies). Again, females appeared to have a weak preference for the mean in one experiment.

In the replicated experiment (no temporal variation across the call group, 3800 versus 3500 Hz, after Ryan & Wilczynski 1988), females tended to prefer a lower-frequency call to a higher-frequency call (Table 2).
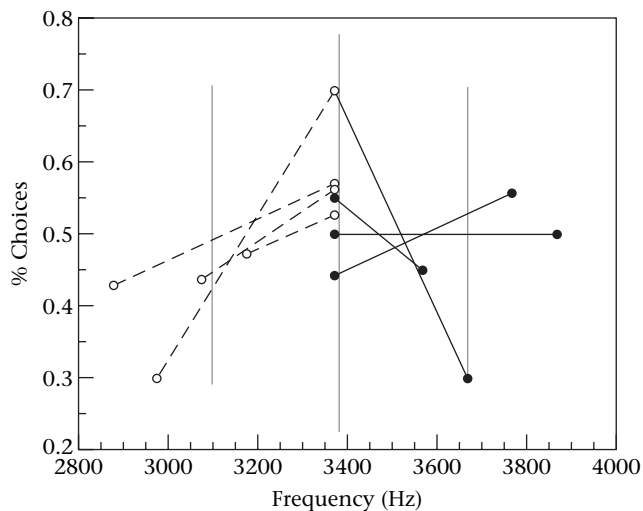
Figure 5. Proportion of female choices for stimuli differing in dominant frequency. Dashed lines connect stimulus pairs testing the effect of dominant frequency escalation for cricket frog males with an average pre-escalation frequency. Solid lines connect stimulus pairs testing the effect of dominant frequency escalation for males with relatively high pre-escalation dominant frequencies. Grey vertical lines show the range of variation in a sample of males recorded at the same study site ($=\overline{X}\pm2$SD).

DISCUSSION

Male cricket frogs increase the temporal complexity and lower the dominant frequency of their advertisement calls when interacting with other males. Earlier male playback studies suggested that this vocal escalation is aggressive in nature and functions in direct male–male aggression. In this study, we tested the hypothesis that escalation increases a male's relative attractiveness to females. We found that females prefer temporally complex stimuli that are similar to the signals that males produce during vocal escalation. This suggests that males facultatively increase their relative attractiveness to females as local competition increases, and that vocal escalation of temporal call characters functions (at least in part) in indirect competition for female mate choice. Females did not show strong preferences for dominant frequency; thus our results do not suggest that frequency escalation plays a role in competition for female mate choice.

Temporal Call Characters

In the current study, female cricket frogs preferred more calls per call group and more pulse groups per call. These results are consistent with some, but not all, previous female preference experiments in this species. Wagner (1991) reported that female cricket frogs from the Gill Ranch population preferred calls with more pulse groups and fewer pulses, and that the preference for multiple pulse groups was relatively more important than the preference for fewer pulses. Later experiments with females from the same population, however, failed to demonstrate a significant preference for fewer pulses (W. E. Wagner, Jr, personal communication). Studies of cricket frog populations in Indiana and Bastrop, Texas, U.S.A. did not demonstrate preferences with respect to either pulse number or pulse group number (Perrill & Lower 1994). The reason for the differences between studies is unknown.

It is usually assumed that socially mediated variation in agonistic or mate-attraction signals occurs because there are large costs associated with the production of escalated signals. Escalated signals may, for example, be energetically expensive to produce or increase predation risk. These costs may limit the production of escalated calls to those times when competition between males is strongest (e.g. Ryan 1985). Socially mediated signal variation may also reflect a conflict between the different functions of a display. In many frogs, for example, males produce calls that vary continuously between attractive and aggressive, and produce their most aggressive calls when other males are nearby (reviewed in Wells 1988; see also Grafe 1995). Females usually fail to recognize aggressive calls as salient mate-attraction signals (e.g. Backwell 1988) or discriminate against them in favour of attractive calls (e.g. Oldham & Gerhardt 1975; Wells & Bard 1987; Grafe 1995; Brenowitz & Rose 1999). In these systems, graded-aggressive signalling presumably reflects a trade-off between the benefits of escalation in aggression and its costs with respect to female mate choice.

Wagner (1989c) suggested that, in cricket frogs, vocal escalation of temporal call characters may reflect a conflict between the signal's function in mate attraction and aggression. Female cricket frogs might disfavour temporally escalated advertisement calls, and males may produce attractive calls until they are threatened by an intruder, at which point they begin to produce unattractive, aggressive calls. In the current study, however, females either preferred escalated stimuli or showed no preference (see also Wagner 1991). They did not discriminate against any escalated temporal call character. There is therefore no present evidence for a conflict between the two functions of the advertisement call. Instead, as has been suggested for several other frogs (e.g. Rand & Ryan 1981; Pallett & Passmore 1988; Howard & Young 1998; Jehle & Arak 1998; Benedix & Narins 1999), male cricket frogs increase the attractiveness of their advertisement signals with increasing social competition.

In cricket frogs, as in many other frogs, energetics may limit a male's production of temporally escalated calls (reviewed in Ryan & Kime 2002). Most aspects of temporal vocal escalation increase the total energy in each call group, and presumably the energetic cost of call group production. Many male cricket frogs decrease call rate during escalation, however, suggesting that males use call rate to compensate for the energy expenditure of escalation (Wagner 1989b). This strategy is similar to the calling behaviour of grey treefrogs, *Hyla versicolor*, in which males increase call duration but decrease call rate in male–male interactions. Male grey treefrogs probably call at their energetic maximum, resulting in a necessary trade-off between call duration and call rate (Wells & Taigen 1986). Female grey treefrogs prefer longer calls when they are produced at lower rates but equal energy per unit time (Klump & Gerhardt 1987), so the pair of socially mediated call changes results in an increase in overall attractiveness. In cricket frogs, like grey treefrogs, the fact that males lower call rate when increasing signal complexity may reflect an energetic constraint on signal production. The relative influence of call rate on the preferences of female cricket frogs is unknown.

Females did not show a preference with respect to pulse number, indicating that escalation of this call character does not influence competition for female mate choice. Socially mediated variation with respect to pulse number may function in direct male–male competition, although previous studies report inconsistent results about the role of pulse number in male–male agonistic interactions (Wagner 1989c, 1991; Ophir et al. 1997; Burmeister et al. 1999b, 2002). One alternative to a functional explanation for pulse number escalation is that males increase the number of pulses in their calls in order to produce attractive, multiple pulse group calls. In other words, it may be that the physiological mechanisms of call production in cricket frogs necessitate that males who produce calls with more pulse groups also produce calls with more pulses.

Dominant Frequency

In the current study, we did not find strong preferences for lower-frequency calls, although it is possible that there is a weak preference for the population mean that we were unable to uncover due to small sample sizes (Fig. 5). Given the current data, we must conclude that our phonotaxis tests offer no support for a function of frequency escalation in indirect competition for female mate choice, but additional studies more directly addressing this hypothesis are needed.

Previous studies have suggested that female cricket frogs prefer lower-frequency calls (Ryan & Wilczynski 1988; Ryan et al. 1992). Although our replicated experiment produced results consistent with previous studies, the group of dominant frequency experiments suggest no preferences or weak preferences for the mean. There are several possible explanations for the discrepancy between our data and other studies. Female tuning or preferences may have changed over time. Alternatively, the temporal complexity of the stimuli in our study may have influenced the females' ability to attend to or discriminate frequency differences. A recent study in cricket frogs tested two natural, temporally complex call groups (with dominant frequencies of 3633 and 3770 Hz) against calls with the same temporal envelope but a lower, synthetically generated carrier frequency (3500 Hz) (Witte et al. 2001). Females showed no preference in either experiment. Although the stimuli tested in these experiments differed in characters other than frequency and temporal complexity (e.g. the natural calls were more broadband than the synthetic calls), these data are consistent with the possibility that frequency discrimination is influenced by call complexity.

If females do not show strong preferences for dominant frequency, what are the costs that limit escalation of this call character? When male cricket frogs decrease dominant frequency, they also decrease call amplitude and thus the active space over which the call can reach receivers (Wagner 1991). Wagner (1991) used a model that combined information about covariation in amplitude and frequency with data on female auditory tuning to demonstrate that undisturbed males maximize the active space

of their calls to female receivers, and that facultative decreases in dominant frequency result in a reduction of active space. The production of low-frequency calls could therefore compromise the detection of advertisement calls by distant females.

Conclusions

The cricket frog has served as a model for understanding social flexibility in a dual-function signal. Most previous studies concentrated on the benefits of signal escalation in direct male–male interactions (but see Wagner 1991). The addition of female choice data clearly lends a different perspective, and suggests that at least some aspects of socially mediated signal escalation (also) benefit indirect competition for female mate choice.

Communication systems are often a delicate balance of the costs and benefits associated with signal production (Ryan 1985; Endler 1993). One way of achieving such a balance is through social flexibility in signal properties. Studies of many other species demonstrate that signal changes are correlated with changes in the social environment and concomitant shifts in the relative costs and benefits of signal production. In cricket frogs, more work is clearly needed to understand the changing relationship between the costs and benefits of signal production in different social circumstances.

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