RESPONSE TO VARIATION IN CHUCK FREQUENCY BY MALE AND FEMALE TÚNGARA FROGS

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ABSTRACT: We examined how male and female túngara frogs, *Physalaemus pustulosus*, respond to variation in the frequency spectrum of the chuck component of the advertisement call. We varied chuck frequency in two different ways. In the fixed frequency series, the sequence of calls within each series had chucks of the same dominant frequency. Different fixed-frequency series had chucks of different dominant frequencies designated as high, high–medium, medium, medium–low, or low frequency relative to variation in the test population. In the second varying frequency series, the sequence of calls varied in the chuck's dominant frequency such that the individual series had the same average frequencies as the high, high–medium, medium, medium–low, and low fixed-frequency experiments. Both males and females tended to respond more to lower-frequency chucks. The responses of both sexes to the same mean chuck frequency was similar to the fixed- and varying-frequency series of chucks.

Key words: Communication; *Physalaemus pustulosus*; Sexual selection; Túngara frogs

IN most animal mating systems, males increase their reproductive success by maximizing the quantity of mates fertilized, whereas females do so by maximizing mate quality (e.g., Bateman, 1948; Trivers, 1972). The resulting prediction, that males tend to be more promiscuous and females more coy, has been borne out by studies of most mating systems (reviewed in Andersson, 1994). Because mating behavior is regulated by communication signals, the divergent interests of males and females might result in divergence of perceptual and behavioral mechanisms that underlie responses to sexual signals (e.g., Jacobs, 1996). There have been few studies, however, that allow us to evaluate the hypothesis that the sexes perceive and react to sexual signals differently (but see Jones and Hunter, 1993; Morris and Ryan, 1996; Qvarnström, 1997; Searcy and Brenowitz, 1988; Vehrencamp, 2000). We address this issue by comparing responses of male and female túngara frogs (*Physalaemus pustulosus*) to the same variation in male advertisement calls.

The advertisement call of the túngara frog has two components: a whine and a chuck (Fig. 1). The whine initiates the call, is always present, may be followed by one or several chucks, or can be produced alone. Thus the call can vary in complexity from simple (whine-only) to complex (whine with chucks). The whine has several harmonics although most of the whine's energy is in the fundamental (Rand and Ryan, 1981; Ryan, 1985), and only the fundamental influences female phonotaxis (Wilczynski et al., 1995). Females have a weak preference for lower frequency whines but only when the difference is substantial (Bosch et al., 2000*b*). The chuck has a much different acoustic structure. It typically has a fundamental frequency of 250 Hz and is characterized by 14 harmonics, thus having a frequency range from 250–3500 Hz. More than 90% of the chuck's energy is within the higher-half harmonics, and the dominant frequency averages 2500 Hz (Ryan, 1985; Ryan et al., 1990). When chucks are added to the whine, they are appended near the end of the whine. Up to six chucks can be added, although one, two, or sometimes three chucks are more common.

Females and males respond to variation in call complexity. In nature, males call from stationary sites competing for the attention of females, and females are free to move unimpeded throughout the chorus to choose a mate (Ryan, 1985). As for most frogs, the call appears to be the primary
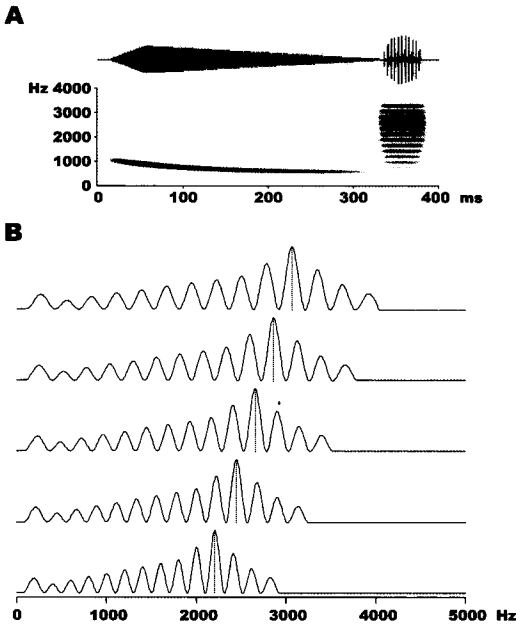
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B

FIG. 1. (A) Synthetic call used in the playback experiments: a whine followed by one chuck. (B) Spectrum of the five chucks used in the playback experiments (the dominant frequency is shown in dashed line).

cue used by females in mate assessment and choice. Phonotaxis experiments have shown that a whine is both necessary and sufficient to elicit female phonotaxis (Ryan, 1980, 1985). When females are given a choice between a whine-only and a whine with chucks, females prefer the latter (Rand and Ryan, 1981; Ryan, 1985). The addition of chucks enhances call attraction but the relationship is barely detectable beyond two chucks (Rand and Ryan, 1981; Rand et al., 1992; Wilczynski et al., 1995). Males respond to call complexity similarly: a whine will evoke calling from males, but whines with chucks evoke calls with more chucks (Rand and Ryan, 1981, 1998). The chuck's dominant frequency is weakly, but significantly, negatively correlated with male body size. Females show a weak, but repeatable, preference for lower frequency chucks (Ryan, 1980, 1983, 1985; Wilczynski et al., 1995) that coincides with a large male mating advantage in nature (Ryan, 1980, 1983, 1985). The response of males to variation

in chuck frequency has not been evaluated, although we have shown that males respond with more calls and more complex calls to whines of relatively higher frequencies (Bosch et al., 2000a).

In a previous study (Ryan and Rand, 1998), we showed that both males and females respond more strongly (calling by males and phonotactic preferences of females) to a whine plus a novel stimulus substituted for a chuck versus a whine alone. Males and females share similar response biases that could have promoted the evolution of the chuck. In this study, we compare the responses of males and females to variation in chuck frequency and determine to what degree the response of each sex differs when chuck frequency is stable or varies within a call series. We also determine if this response depends on call repetition rate.

MATERIALS AND METHODS

Male Evoked Calling Experiments

We collected calling male and amplectant female túngara frogs near the facilities of the Smithsonian Tropical Research Institute in Gamboa, Panama throughout May and June 1998. We maintained males under a natural light-dark cycle and temperature regime by keeping them in clear plastic bags with water in an un-airconditioned, but well ventilated, room: thus males were tested at typical nocturnal temperatures. When a male concluded the tests, or after 3–4 days, we gave him a unique toe-clip and returned him to his capture site. Prior to testing, each male was placed in a plastic bag inside a testing chamber. These chambers (30.5 × 46 × 30.5 cm) were lined with sound absorbent material both for sound-proofing and to reduce reverberation. Each chamber contained a small, wide-frequency range speaker and a Radio Shack miniature microphone. The plastic bags containing the males were acoustically transparent, and there was minimal reverberation within the bag (Ryan and Rand, 1998). Prior to each experiment, we stimulated the males with a continuous tape of a small chorus; when a male called, we initiated the play-

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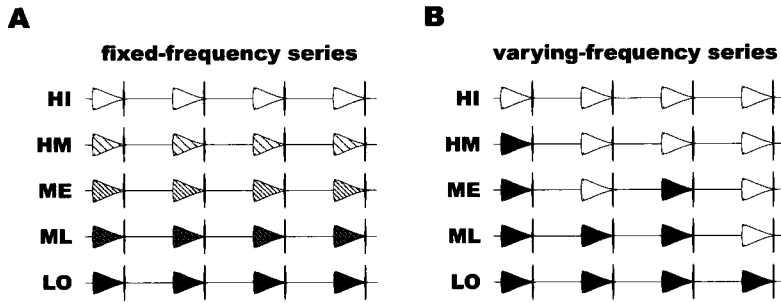**fixed-frequency series**

B

varying-frequency series

FIG. 2.　Synthetic stimuli used in the playback test. (A) Fixed-frequency series obtained by adding different calls with identical chuck frequency calls. (B) Varying-frequency series obtained by adding two different chuck frequency calls: high frequency chuck calls (white) and/or low frequency chuck calls (black). HI: high frequency series, HM: high–medium frequency series, ME: medium frequency series, ML: medium–low frequency series, LO: low frequency series.

back experiments. Males were tested between 1900 h and 0500 h.

Variables for constructing the synthetic stimuli were based on the statistical distribution of calls in this population (M. J. Ryan and A. S. Rand, unpublished data). Stimuli consisted of a whine plus one chuck that we synthesized with Sound-Maker 1.0.3 software (sampling rate: 44.1 kHz,16 bit; Fig. 1A). The whines had a duration (326 ms) and frequency (initial frequency 1000 Hz, final frequency 560 Hz) equal to the average for this population. Changes in amplitude during rise (42 ms) and fall (282 ms) were linear. We synthesized only the fundamental frequency sweep of the whine because playback experiments show that upper harmonics do not influence female phonotaxis (Wilczynski et al., 1995). We synthesized five different chucks of average duration (50 ms) with 14 harmonics. Chucks were synthesized by addition of 14 sine waves with different frequencies and amplitudes, whose relationships were similar to a natural standard call. We synthesized chucks with five different dominant frequencies (Fig. 1B): 3064 Hz (high frequency, HI), 2859 Hz (high–medium frequency, HM), 2654 Hz (medium frequency, ME), 2449 Hz (medium–low frequency, ML) and 2244 Hz (low frequency, LO).

We used a whine plus high frequency chuck (3064 Hz) as the stimulus in the control presentation (see below). In each experiment, the control was presented once before and once after each presentation of the test/control stimulus. The average response to the control stimulus in the two presentations was compared to the response to the treatment stimulus. This was done in order to control for any changes in male motivation during the experiment. Each presentation (control and test stimulus) was separated by 1 min of silence. Thus each experiment consisted of Control-1 (1 min), Silence-1 (1 min), Experiment (1 min), Silence-2 (1 min), and Control-2 (1 min) (see also Ryan and Rand, 1998). We broadcast these stimuli directly from the audio output of an Apple PowerBook 1400cs computer. Stimuli were broadcast in random order at an amplitude of 90 dB SPL (re. 20 μPa) at 0.5 m, measured by a GenRad model 1982 sound pressure level meter. The response of the male and the stimuli were recorded with a Sony WM D6 cassette recorder.

In fixed frequency playbacks, the treatments were five different call series. In each series, the chuck's dominant frequency was the same, but the series differed in the chuck's dominant frequency: high frequency (HI-fixed), high–medium frequency (HM-fixed), medium frequency (ME-fixed), medium–low frequency (ML-fixed), and low frequency (LO-fixed; Fig. 2A). In the varying frequency playbacks, there were also five different call series but chuck frequency varied within the series. Specifically, we varied the sequence of high frequency chucks and low frequency

chucks in a manner that resulted in each series having an average frequency that corresponded to the chuck frequencies of the fixed-frequency series just described: 100% high frequency chucks (HI-vary), 75% high frequency and 25% low frequency chucks (HM-vary), 50% high frequency and 50% low frequency (ME-vary), 25% high and 75% low frequency (ML-vary), and 100% low frequency chucks (LO-vary).

Each series of the fixed- and varying frequency experiments was tested at two call repetition rates. In the low-rate experiments, we used an intercall interval of 1.87 s, which is the population average. In the fast-rate experiments, we used an intercall interval of 0.48 s, which mimics the repetition rate of four males calling in alternation (although we cannot assume that the frogs perceived it as such). Varying call rate allows us to determine if chuck frequency preferences might be influenced by more complex calling patterns in a natural chorus.

The sample size was 12 for the low-call rate experiments and 11 for the fast-call rate experiments. During each period of an experiment (Control-1, Silence, Experiment, Silence, Control-2), the number of chucks produced by the male was counted. Responses to the two controls were averaged, and the ratio of experiment/(average control + 1) was calculated (1 was added to deal with periods in which males had no response (0)). We transformed the data by log (x + 1) to meet parametric assumptions of a normal distribution.

Female Phonotaxis Experiments

We followed the general methodology for the female phonotaxis tests employed by Wilczynski et al. (1995). When a female concluded the tests, we gave her a unique toe-clip and returned her to the capture site. The stimuli used in the phonotaxis experiments were the same as those used for the males, but we used only the low call repetition rate, which is the average for the population. We determined female phonotaxis preference for the HI chuck versus each of the following: HM-fixed, HM-vary, ME-fixed, ME-vary, ML-fixed,

ML-vary, and LO (LO-fixed and LO-vary are the same, see above). We tested 20 females in each experiment.

Calls were broadcast directly from the stereo audio output of an Apple Power-Book 1400cs computer and were amplified through a stereo amplifier. Synthetic calls were broadcast antiphonally from two speakers (ADS L2000) in a dark acoustic chamber (Acoustic Systems Inc., Austin, Texas; 1.82 × 2.74 m) illuminated with an infrared light. Females' movements were monitored remotely with a Fuhrman infrared video camera and video monitor system. Temperature in the arena was maintained between 26 C and 28 C. The amplitude of the synthetic whines was adjusted at the release point (center of the arena) to 82 dB SPL (re. 20 μPa) with a GenRad model 1982 sound pressure level meter (flat weighting, peak response). Females were tested the morning immediately following their capture, between 0300 h and 0800 h, and thus usually within 12 h of their capture. We placed each female with random orientation under a cone in the center of the arena. We raised the cone remotely after broadcasting the stimuli for 3 min. We scored a positive phonotaxis response if the female approached within 10 cm of a speaker and ceased movement. No response was scored if a female remained motionless for 5 min after the trial began, stopped without moving again for 2 min during any part of the trial, passed a speaker while travelling along the perimeter of the chamber, or did not show a phonotactic response within 15 min after initiating the trial.

Statistical Analyses

We used a three way-ANOVA test of repeated measures with planned comparisons to test if male response differed between stimulus rates (low and fast rate), series of frequency variation (fixed and varying series), and variation in chuck frequency (HI, HM, ME, ML, and LO frequency). We removed from the analysis males tested to both fast and slow stimulus rates. Responses to HI and LO frequencies do not figure in comparing responses between fixed and varying frequency series
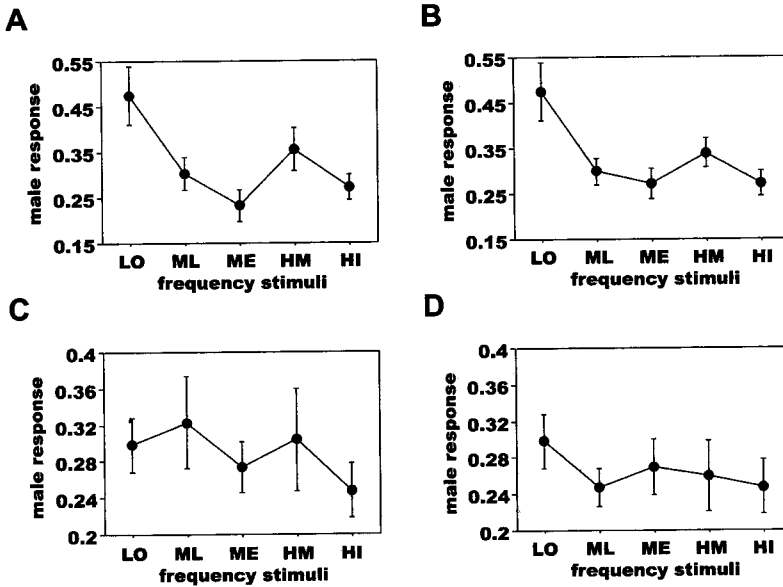
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FIG. 3. Magnitude of the male response to playback experiments (calculated as log of 1 + number of chucks in Experiment divided by the average number of chucks in Controls +1; mean ± SE). (A) Low rate, fixed-frequency series. (B) Low rate, varying-frequency series. (C) Fast rate, fixed-frequency series. (D) Fast rate, varying-frequency series. LO: low frequency chucks, ML: medium–low frequency chucks, ME: medium frequency chucks, HM: high–medium frequency chucks, and HI: high frequency chucks.

because these stimuli are the same in both series (i.e., HI-fixed = HI-vary, LO-fixed = LO-vary).

We used an exact binomial to test the hypothesis of no female preference in the phonotaxis experiments. We used a one-tailed test because there was an a priori expectation of the response direction. We conducted a power analysis to determine our ability to detect significant preferences ($P < 0.05$) given the observed female responses and our sample size, as well as the sample size needed for the observed effect to be detected with a power of 0.80.

We also compared male and female responses to the same sets of stimuli. We considered only the low stimulus repetition rates because females were only tested with this rate. Because the sexes were tested in experiments with different bioassays (evoked calling versus phonotaxis), we standardized the responses of each sex by dividing the response (either number of evoked calls or number of females phonotaxis responses) to every chuck frequency series by the corresponding response to the high frequency chuck. We then com-

pared the responses with a Kendall rank correlation.

RESULTS

Male Evoked Calling Experiments

Males exhibited a strong change in their vocal response to variation in mean chuck frequency ($F_{4,84} = 3.80$, $P = 0.007$) and a weaker but still significant response to variation in stimulus repetition rates ($F_{1,21} = 5.13$, $P = 0.034$). Their response was not significantly influenced by differences in the series of frequency variation (i.e., fixed versus varying series of chuck frequency; $F_{1,21} = 0.53$, $P = 0.473$). The interaction of the series of frequency variation with mean chuck frequency was significant ($F_{4,84} = 3.15$, $P = 0.011$) while the other interactions were not (rate-by-frequency variation source: $F_{1,21} = 1.05$, $P = 0.317$; rate-by-chuck frequency: $F_{4,84} = 2.17$, $P = 0.079$; rate-by-frequency variation source-by-chuck frequency: $F_{4,84} = 1.95$, $P = 0.110$). Inspection of Fig. 3 makes it clear that the significant effect due to variation in mean chuck frequency is due primarily

TABLE 1.—Results of phonotaxis tests for both sources of frequency variation (fixed-frequency and varying-frequency series). Number of females attracted to low/high frequency alternative, the probability of rejecting the null hypothesis (one-tailed exact binomial test), the power of the test, and the sample size needed given the observed effect to achieve statistical power of 0.80.

Test	Choices	P	Power	n (Power = 0.80)
Fixed frequency				
HM vs. HI	12/8	0.252	0.126	158
ME vs. HI	11/9	0.412	0.055	618
ML vs. HI	12/8	0.252	0.252	158
Lo vs. Hi	14/16	0.058	0.412	37
Varing frequency				
HM vs. HI	10/10	0.500	NA	NA
ME vs. HI	12/8	0.252	0.126	158
ML vs. HI	10/10	0.500	NA	NA

to the males' responses to the lowest frequency.

Female Phonotaxis Experiments

Females exhibited a tendency to prefer low-frequency over high-frequency chucks. In five of the seven separate experiments, a majority of females were attracted to the lower frequency call while in two experiments, equal numbers of females were attracted to each stimulus (Table 1). Thus treating each experiment as a datum shows an overall preference for lower frequency chucks across experiments (Wilcoxon signed rank test, $z = -2.1$, $P < 0.05$).

The differences in response to lower versus higher frequency were not statistically significant for any of the tests, although there was a near significant preference for the LO versus HI frequency chuck ($P = 0.058$; Table 1, Fig. 4). The power analysis shows that given the females' responses in this experiment (14 versus 6) we would need a sample size of 37, rather than our sample size of 20, to uncover significant differences 80% of the time. Thus it would be unwise to suggest that these results reflect a lack of preference. In the other phonotaxis experiments, in which all $P > 0.50$, we would need much larger sample sizes (either 158 or 618, Table 1) to have equivalent statistical power.
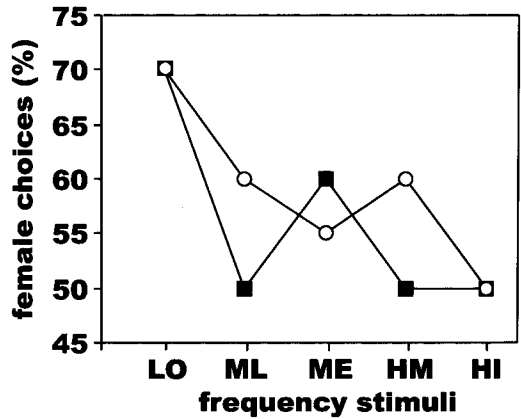

FIG. 4. Results of female phonotaxis experiments for fixed-frequency (open circles) and varying-frequency (closed squares) series (proportion of females attracted by the lower frequency alternative). LO: low frequency chucks, ML: medium–low frequency chucks, ME: medium frequency chucks, HM: high–medium frequency chucks, and HI: high frequency chucks.

Male and Female Responses

A Kendall rank correlation did not show a significant relationship between the responses of males and females across frequencies (Fig. 5; $\tau = 0.32$, $P = 0.439$). Inspection of Fig. 5, however, shows that both sexes exhibit greater response to the lowest frequency chuck versus the others, and little if any discrimination of higher frequency chucks.

DISCUSSION

Previous studies have shown that the complex call of the túngara frog, *Physalaemus pustulosus*, is biologically salient to both sexes. Males and females show enhanced responses to a complex advertisement call, a whine plus one chuck, relative to a simple call, a whine only. The female's enhanced response is evident in phonotaxis and the male's response in more evoked calls or more complex calls (i.e., more chucks: Rand and Ryan, 1981; Ryan, 1985; Ryan and Rand, 1998). In this study, we asked if both sexes also respond similarly to variation in chuck frequency.

Both sexes respond weakly and similarly to differences in mean chuck frequency; low frequency chucks tended to elicit greater response relative to high frequency
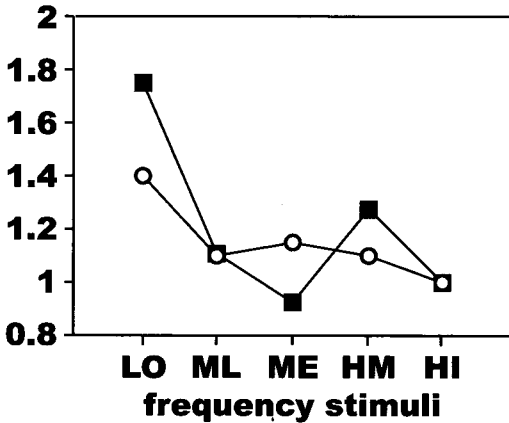
FIG. 5. Magnitude response for males (closed squares) and females (open circles) to the playback tests. Male and female responses were each standardized by dividing the values of every chuck frequency series by the corresponded value obtained in the high frequency chucks series. HI: high frequency chucks, HM: high–medium frequency chucks, ME: medium frequency chucks, ML: medium–low frequency chucks, LO: low frequency chucks.

chucks. The strength of the female's low-frequency preferences in these tests are weaker than in those shown by Ryan (1980, 1985) but are similar to more recent experiments with better control of the spectral properties of the stimuli (M. J. Ryan and A. S. Rand, unpublished data). In these more recent experiments, female preference for low versus high frequency chucks all had probability values in the vicinity of 0.05 (all $n = 20$, P values $= 0.13$, 0.05, 0.05, 0.02). Combining the results of these independent tests shows an overall preference for low frequency chucks (Fisher combined probability analysis, $P < 0.005$).

Ryan et al. (1990) suggested that the preference for low frequency chucks is influenced, in part, by the tuning of the peripheral auditory system. In túngara frogs, most of the sound energy is in the range of frequencies to which one inner ear organ used for sensing air born sound, the amphibian papilla (AP), is most sensitive, while most of the energy in the chuck is within the hearing range of the other inner ear organ, the basilar papilla (BP). Ryan et al. (1990) suggested that the preference for low frequency chucks results from the

BP's higher sensitivity to frequencies below the average dominant frequency of the chuck. Because males and females respond similarly to variation in chuck frequency, this suggests the hypothesis that males and females are similarly tuned. Although female túngara frogs are larger than males, and variation in tuning of the BP is often correlated with variation in body size (e.g., Zakon and Wilczynski, 1988), the average difference between male and female size is only a few millimeters (see Fig 6.6 in Ryan, 1985). More neurophysiological data are needed to explore any potential differences in BP tuning between the sexes.

The response of males and females to variation in mean chuck frequency of a call series did not depend on whether the sequence of chucks had the same or varying frequencies. If females perceive such series as equivalent in the chuck's mean dominant frequency, it might suggest rather long temporal integration of signals. The literature suggests, however, much faster integration times, on the order of 200 ms rather than 2 s (Dunia and Narins, 1989). If females do perceive the differences in the sequence of chuck frequencies within a varying series, we would find it surprising that a female would respond equivalently to one sound source mimicking an average sized male (i.e., a medium frequency chuck) and another mimicking a small (high frequency chuck) and large (low frequency chuck) male calling in alteration. On the other hand, in this study we were only able to compare differences in response to fixed and varying sequences over the range of variation in mean chuck frequencies in which males and females show little or no discrimination. Thus, we feel that these results cannot be interpreted in any meaningful way. To further elucidate the role of temporal variation in chuck frequency among calls, it would be best to compare calls of the same mean chuck frequency in fixed and varying sequences in the same phonotaxis test.

Speculations on the Evolution of Biased Response to Chuck Frequency

The tuning of the BP is not significantly different among the eight species of *Phys-*

alaemus that we have examined (five in the *Physalaemus pustulosus* species group, three outgroup species; Wilczynski, et al., 2001). There is a significant correlation between tuning and body size among species, as is expected (Zakon and Wilczynski, 1988). We note, however, that the body size differences among species is much greater than the body size difference between male and female túngara frogs. Because most of these species do not produce chucks, we cannot argue that the tuning of the BP originally evolved within túngara frogs to respond more to lower frequency chucks because of an advantage to show such behavioral discrimination. The tuning of the BP seems to be a property of these kinds of frogs rather than this particular species.

The behavioral discrimination of chuck frequency, and thus the underlying neural mechanism of it, does appear to be maintained by selection in females. The females' preference for lower-frequency calls leads them to mate with larger males. Females are larger than males, and the number of eggs fertilized increases as the amplectant male and female are closer in body size (Ryan, 1983, 1985). Thus female preference for lower-frequency chucks and larger males increases her immediate reproductive success and thus should be maintained by selection. Similar results have been reported in other frogs (*Bufo bufo*: Davies and Halliday, 1977; *Uperolia laevigata*: Robertson, 1990; *Scinax rubra*: Bourne, 1993). We do not know if the biased response of males to chuck frequency is advantageous; it might be they compete more with males that are more attractive to females. In other species, males similarly alter their vocalizations in response to size-based vocal cues of other males (Bee et al., 1999; Bosch and Márquez, 1996; Given, 1999; Wagner, 1989), thus túngara frog males might also need to assess size of vocal competitors.

Another adaptive hypothesis for bias to low-frequency chucks is that the difference between BP tuning and chuck dominant frequency is much less at far distances than close distances because the chuck's higher frequencies attenuate more

rapidly than lower frequencies (Ryan, 1986). Thus, the enhanced response to lower frequencies at close distance might be an incidental consequence of having the BP tuning and the chuck frequency spectrum better matched at long distance where there might be more of a detection problem. A computational model by Sun et al. (2000) supports this hypothesis.

SUMMARY

Chuck frequency has a weak but predictable influence on responses of male and female túngara frogs. In both sexes there is a tendency for lower-frequency chucks to elicit greater, sex-appropriate responses. The tuning of the peripheral auditory system relative to the chuck might be responsible for this preference. These tuning properties, however, are also characteristic of closely related species without chucks and thus are not evolved adaptations for increasing responsiveness to lower frequencies and the correlated larger size of the caller. It is possible that such responses, and thus the underlying sensory mechanisms, are maintained by selection for the increased fecundity advantage to females of mating with larger males (Ryan, 1983, 1985), for males being able to assess competitor size in behavioral interactions (although there are no data to test this hypothesis), or as an incidental consequence of needing to detect chucks over varying distances (Sun et al., 2000).

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