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CHORUS SIZE AND CALL INTENSITY: FEMALE CHOICE IN THE PAINTED REED FROG, HYPEROLIUS MARMORATUS

by

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Summary

1. In two-choice phonotaxis experiments female painted reed frogs (*Hyperolius marmoratus*) preferentially chose the stimulus with the greater sound pressure level (SPL) at source when all other call parameters were identical.
2. However, this preference was not apparent when we increased the distance of the louder stimulus from the female such that the SPL of the two stimuli at the release point was equivalent. This suggests that females simply move up sound gradients ('passive attraction').
3. Female choice of the loudest stimulus was also affected by the number of speakers.
4. There were significantly fewer responses to the loudest speaker in some four-choice compared to matched two-choice phonotaxis experiments.
5. Together these experimental results may partially account for the absence of a large male mating advantage in the field.

Introduction

Female frogs tested in two-choice phonotaxis experiments consistently show a preference for louder advertisement calls (RYAN, 1985; SCHWARTZ, 1986; GERHARDT, 1987; ARAK, 1988; HÖGLUND & ROBERTSON, 1988). In several species there is also evidence that call intensity is positively correlated with body size (*e.g.* GERHARDT, 1975; PASSMORE & TELFORD, 1983). Researchers have often assumed that larger males are of better

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'quality' than smaller males (but see SEMLITSCH, 1994). It has therefore been suggested that a female preference for louder calls could be an adaptive trait allowing them to mate with larger males (reviewed in ARAK, 1988). There are, however, two problems with this interpretation.

First, females may not be actively seeking out the loudest males in the population, but simply moving up a sound gradient (ARAK, 1988). Although there is debate on the usefulness of the concept of 'passive attraction' (*e.g.* SULLIVAN, 1989; MAYNARD SMITH, 1991), in this case it has an unambiguous meaning. 'Passive attraction' occurs if females do not take into account the distance between themselves and potential mates, but simply approach the male whose signal is loudest at the point where they are (PARKER, 1983). In *Bufo calamita*, for example, females in phonotaxis experiments preferentially chose the louder of two stimuli when speakers were equidistant from the female release point. No preference was exhibited, however, when the position of the loudspeakers was manipulated so that the calls had the same intensity at the release point (ARAK, 1988). A potential mechanism females could use to determine their distance from males is to calculate the relative intensity of different frequencies in the call. Higher frequencies attenuate more rapidly than lower frequencies, so the ratio of the amplitude of high to low frequencies will decrease as distance increases (GERHARDT, 1976).

Second, the ability of females to discriminate between calls differing in intensity may only be possible in the comparatively simple situation of a two-choice phonotaxis arena. Increasing the complexity of the choice by increasing the number of speakers (GERHARDT, 1987), or by adding background noise (SCHWARTZ & GERHARDT, 1989) may reduce the ability of females to choose louder calls. Whether this occurs or not will depend on the ability of the species in question to separate out conspecific calls from background noise. For example, in *B. calamita* there is a large male mating advantage which appears to be related to the greater intensity of larger males' advertisement calls (ARAK, 1983, 1988).

Here we investigate female preferences based on call intensity in the painted reed frog, *Hyperolius marmoratus*. We show that female choice in two-choice and four-choice experiments differs significantly, but depends on the variation in call intensities offered in the four-choice experiments.

Methods

General.

Phonotaxis experiments were conducted during December-January in Mtunzini, South Africa (28°51′ S, 31°46′ E). Amplexing females were captured at two nearby ponds and transported to the testing site (less than 5 km away). Females were separated from males immediately prior to testing. All females were tested on the night of capture, and released the following night at the ponds. They were tested in an outdoor arena with a canvas floor of 2.5 m × 2.5 m, and 0.4 m high walls. The arena was illuminated by a dimmed 60 W red bulb suspended 1 m above the arena. The release container was a perforated plastic box. Ambient temperature ranged from 18.3 to 26.3°C.

The acoustic stimulus was a synthetic *Hyperolius marmoratus* call broadcast at a repetition rate of 60 calls/min. It had a frequency excursion of 2850 to 3350 Hz and was 80 ms in duration, with a rise time of 10 ms and a fall time of 25 ms. These values approximate the means of these variables in the study population (JENNIONS *et al.*, 1995; POLAKOW *et al.*, in press). The stimulus was relayed from a Nagra III tape recorder to a custom-built, four channel analogue sequence controller (J. NEL, C.E.S., University of the Witwatersrand). Use of the sequence controller ensured that the inter-call interval between successive stimuli was identical. If calls overlap or abutt, females prefer the leading call (DYSON & PASSMORE, 1988). The loudspeaker broadcasting the first call in each successive trial was randomised.

Sound measurements were made using a Bruel and Kjaer 2230 sound level meter with a Bruel and Kjaer type 4165 microphone. The sound pressure level (SPL) of the 'standard intensity' stimulus was set at 104 dB (peak) at 50 cm, which is the mean intensity of a natural call at this distance. The speaker broadcasting this stimulus is referred to as the 'Standard speaker', speakers broadcasting other stimuli are referred to as 'Experimental speakers'.

As in almost all frog phonotaxis work, we tested individual females for several different stimulus pairs/sets of four stimuli, presented as sequential tests on the night they were collected (*e.g.* WILCZYNSKI *et al.*, 1995). However, no female was tested more than once with any one stimulus pair/set of four stimuli. The maximum number of tests performed by females was seven. Three types of experiments were performed: two-choice intensity discrimination; four-choice intensity discrimination; and distance *versus* intensity discrimination. We wanted to make statistical comparisons between the results from certain two-choice and four choice tests. We therefore ensured that no females were used in more than one experiment type so that the data was statistically independent for these comparisons.

Within an experiment type, the test order of the different stimuli combinations was randomised, as was the speaker broadcasting the standard intensity stimulus. Females were left in the release container for two minutes prior to the first test, and for a minimum of two minutes between subsequent tests. We scored a positive response if the female touched the speaker or approached to within 5 cm of the speaker. Females were discarded if they remained immobile for more than 10 minutes, or attempted to escape from the arena. In each of the three types of experiments we also performed a test in which all speakers broadcast the standard intensity stimulus. These results were examined to check whether there was any side-bias in the arena. There was no bias in any of the three types of experiments. In total we performed 417 individual female-choice tests using 100 females (N = 21, 37 and 42 females for two-choice, four choice and distance *versus* intensity experiments respectively).

Two-choice intensity discrimination experiments.

In each of three tests females were offered a choice between the standard intensity stimulus and an alternative stimulus (Table 1). The experimental speakers broadcast stimuli with peak SPL at 50 cm of 101 dB, 98 dB and 92 dB. Loudspeakers were placed 2 m apart, facing each other and equidistant from the release container.

Four-choice intensity discrimination experiments.

Speakers were placed at the ends of a symmetric cross such that the release point was equidistant (1 m) from all four speakers. In all seven tests at least one of the loudspeakers broadcast the standard intensity stimulus. The experimental choices are summarised in Table 2. There were three categories:

A. 2:2 Type with two standard speakers and two experimental speakers broadcasting identical intensity stimuli
B. 3:1 Type with one standard speaker and three experimental speakers broadcasting identical intensity stimuli.
C. 1:1:1:1 Type with each speaker broadcasting different intensity stimuli.

Distance versus intensity discrimination experiments.

Six tests were performed. In each test one loudspeaker was 1 m from the release point and broadcast the standard intensity call. Experimental speakers broadcast stimuli with peak SPL (at 50 cm) greater than or equal to the standard speaker. The distance of the experimental speakers from the release point was manipulated to vary peak SPL at the release point (see Table 3).

Statistical analysis.

In two-choice tests the number of responses to each speaker was analysed using exact binomial probabilities. In the four-choice tests we used chi-square tests to compare the number of responses to each stimulus type to an even distribution based on an equal number of responses to each speaker. (Analysis based on the number of responses to each speaker produced qualitatively similar results. That is, the significance of results did not change; alpha significance set at 2%.) Binomial tests were one-tailed because we expected females to prefer the stimuli with the greater SPL at the release point.

To test for an effect of a greater number of speakers, we compared the proportion of responses to the standard stimulus in four-choice tests where there was only one experimental stimulus to the proportion of responses in two-choice tests involving the same stimulus. In these four-choice tests, more than one speaker broadcasts the same stimulus, so we calculated the average number of responses per speaker for a given stimulus. We then compared the proportion of responses to the standard and experimental stimuli in two-choice and four choice tests using Fisher's exact tests. One-tailed tests were used because we expected greater chorus complexity to reduce female ability to localise speakers broadcasting the loudest calls. We believe that pooling responses from different speakers broadcasting the same stimuli is justified for two reasons. First, we confirmed that the number of responses to each speaker broadcasting the same stimulus did not differ (Chi square or binomial tests, all $p > 0.05$). Second, the control test showed that there was no speaker bias, hence speakers broadcasting the same stimulus are equivalent.

Results

Two-choice experiments: intensity at source.

We carried out 55 individual choice tests using 21 females. Results are presented in Table 1. Females showed a significant preference for the

louder stimulus in all three tests (all $p \ll 0.01$). The smallest difference between peak SPL at the release point was 5 dB.

Four-choice intensity discrimination experiments.

We carried out 213 individual choice tests using 37 females. Results are presented in Table 2. In the 3:1 type tests females did not show a preference for the louder standard speaker when the difference between the peak SPL at the release point was 5 dB (93 dB *versus* 98 dB) or 8 dB (90 dB *versus* 98 dB). However, they did show a preference when the difference was 13 dB (85 dB *versus* 98 dB). There was a significant decrease in the proportion of responses to the louder standard speaker compared to those in the equivalent two-choice tests for peak SPL differences at the release point of 8 dB (Fisher's exact, $p = 0.038$); and a marginally significant decrease for peak SPL differences at the release point of 5 dB (Fisher's exact, $p = 0.058$). There was no significant change in the preference for the louder standard speaker when the difference in peak SPL at the release point was 13 dB (Fisher's exact, $p = 0.31$). In the 2:2 type tests there was a significant preference for the louder standard speakers when the difference in peak SPL at the release point was 5 dB (93 dB *versus* 98 dB) or 8 dB (90 dB *versus* 98 dB). In the 1:1:1:1 type tests the distribution of responses was non-random in both experiments. There were also significantly more responses to the standard speaker than to the next loudest experimental speaker (17 *versus* 5, $p = 0.009$; 22 *versus* 6, $p = 0.019$, both one-tailed binomial probabilities).

TABLE 1. Results of two-choice intensity discrimination experiments

Standard = 101 dB (98 dB) *versus* Experimental	Number of responses: Standard	Number of responses: Experimental	Probability
101 dB (93 dB)	17	2	0.011
98 dB (90 dB)	11	1	0.003
92 dB (85 dB)	10	0	<0.001
104 dB (98 dB)	9	11	0.82 *

Speaker SPL at 50 cm is given. The SPL in parenthesis is that measured at the female release point. Probabilities are from one-tailed binomial tests.
* Control [illegible]

TABLE 2. Results of four-choice intensity discrimination experiments

	Speaker number 1	2	3	4	Experimental probability[1]	Comparison probability[2]
SPL	101 (93)	101 (93)	101 (93)	104 (98)	1.00 (df = 1)	0.058
Number of responses	6	11	7	8		
SPL	98 (90)	98 (90)	98 (90)	104 (98)	0.76 (df = 1)	0.038
Number of responses	7	6	8	8		
SPL	92 (85)	92 (85)	92 (85)	104 (98)	<0.001 (df = 1)	0.31
Number of responses	7	1	1	19		
SPL	101 (93)	101 (93)	104 (98)	104 (98)	0.007 (df = 1)	0.37
Number of responses	6	2	9	14		
SPL	98 (90)	98 (90)	104 (98)	104 (98)	0.002 (df = 1)	0.27
Number of responses	4	3	10	14		
SPL	95 (87)	98 (90)	101 (93)	104 (98)	0.0006 (df = 3)	
Number of responses	6	2	5	17		
SPL	86 (78)	92 (85)	98 (90)	104 (98)	<0.0001 (df = 3)	
Number of responses	0	3	6	22		
SPL	104 (98)	104 (98)	104 (98)	104 (98)	0.95 (df = 3) *	
Number of responses	7	7	9	8		

Speaker SPL at 50 cm is given. The SPL in parenthesis is that measured at the female release point.
[1] Chi-square tests for even distributions. When speakers broadcast the same stimulus the number of responses to each speaker was pooled and the degrees of freedom adjusted accordingly.
[2] Fisher's exact tests (one-tailed) based on a comparison of the mean number of responses to each stimulus with those from the two-choice experiment (see text).
* Control test.

TABLE 3. Results of distance *versus* intensity discrimination two-choice phonotaxis experiments

Standard = 104 dB (98 dB) *versus* Experimental	Distance	Number of responses: Standard	Experimental	Probability
109 (98)	2.0 m	10	11	1.00
110 (99)	2.0 m	7	10	0.32
115 (102)	2.0 m	5	13	0.048
104 (95)	1.16 m	9	8	1.00
104 (93)	1.4 m	9	1	0.01
104 (90)	2.07 m	13	3	0.01
104 (98)	1.0 m	9	11	0.82 *

Speaker SPL at 50 cm is given. The SPL in parenthesis is that measured at the female release point. Probabilities are from one-tailed binomial tests. Distance measured from the experimental speaker to female release point.

Distance *versus* intensity discrimination experiments.

We carried out 119 individual choice tests using 42 females. The results are summarised in Table 3. When the difference in peak SPL at the release point was 3 dB or less there was no significant preference for either speaker. When the difference was 4 dB there was a preference for the call with the louder peak SPL at the release point, even though it was twice as far from the female. When the SPL at the source was the same for both speakers (104 dB at 50 cm), females preferentially chose the call with the louder peak SPL at the release point when the difference was 5 dB or greater, but not when the difference was 3 dB. Females chose the call with the louder peak SPL at the release point, irrespective of the intensity of the call at the source.

Discussion

The results of the two-choice experiments showed that females are capable of discriminating a difference of 5 dB or more between calls, and prefer louder calls. The distance-intensity experiments suggest, however, that females do not distinguish between louder calls produced at a greater distance and softer calls produced at a shorter distance. Rather, the difference in SPL at the female's point of release predicted which speaker she approached. A similar finding was recorded by ARAK (1988) for *Bufo calamita*.

There was no evidence that females used variation in the attenuation of different frequency components of the call to 'correct' for distance to ensure that they approached the speaker with the greatest SPL at source. However, the distance over which the speakers were moved (maximum of 2.07 m) may have been insufficient to lead to differential attenuation of frequency components. The possibility therefore remains that this cue might be used when calls are emitted at greater distances from the female. There is another possible explanation why females do not preferentially approach the call with the greatest SPL at source. Females may indeed obtain information about the relative distance of calls, but a preference for absolutely louder calls could be countered by the costs of travelling a greater distance to reach the speaker broadcasting them (anonymous reviewer, personal communication). This appears unlikely, however, as the increased travel distance was a maximum of 1.07 metres

Passive attraction of females to those calls perceived as loudest will reduce selection on male call intensity when compared to a situation where females take into account their distance from males. In spite of this, there will still be selection on males to produce louder calls than their counterparts. Even if females simply move up sound gradients when approaching potential mates, a male producing a louder call increases the relative area over which he is more attractive than his neighbour, hence his chances of attracting a mate (ARAK, 1988).

In *Hyperolius marmoratus* there is a positive correlation between male size (snout-vent length) and peak SPL ($r = 0.43$: PASSMORE & TELFORD, 1983). Based on the two-choice experiments we would thus predict a large male mating advantage to occur. However, two large studies of mating success in the field (one involved the systematic marking of over 1000 males), both failed to find a relationship between male size and mating success (PASSMORE & TELFORD, 1983; DYSON *et al.*, 1992). The absence of a relationship between size and mating success is unlikely to be explained by a trade-off with other attractive call traits. Larger males produce lower frequency calls ($r = -0.63$: PASSMORE & TELFORD, 1983), and two-choice phonotaxis indicates a female preference for lower frequency calls (JENNIONS *et al.*, 1995). Call rate, which is the only trait that predicts mating success in the field, is unrelated to male size ($r = 0.003$: PASSMORE *et al.*, 1992).

The results of the four-speaker experiments provide a possible explanation for the field data on mating success. They suggest that the increased chorus size in the field may reduce the likelihood that females will mate with larger males with louder calls. However, the experimental results need to be placed in context. There was a strong preference for the loudest calls when all four stimuli differed. There was also a preference for the loudest calls when two speakers broadcast identical softer calls, and two identical louder calls. It was only when three speakers broadcast identical softer calls that females failed to show a preference for the loudest calls. We interpret this as follows. When there are four speakers it is probably more difficult to estimate call intensity, and females may be more likely to initially move in a random direction. Once a female has moved, her subsequent choice is likely to be between the two nearest speakers as these will now tend to be the loudest. The probability of moving towards two speakers differing in intensity is 75% when there are two speakers per stimulus (2:2 type). In contrast, when there are three 'quiet' speakers and one 'loud' speaker (3:1 type), the probability is only 50%. This may partially explain the difference between the 3:1 and 2:2 speaker results, as well as the difference between the two-choice results and those for 3:1 type four-speaker experiments.

When all four speakers broadcast calls differing in intensity (1:1:1:1 type), regardless of the initial direction in which they move, females always move towards two speakers differing in SPL. Perhaps more importantly, the intensities of the quietest and second quietest calls were respectively 20 dB or 11 dB and 13 or 8 dB less than the loudest call (depending on the experiment). Given these very large differences in SPL, females may find it comparatively easy to identify the louder calls, so that the situation reduces to a simple two-choice scenario. Certainly the preferences seen in 1:1:1:1 type four-speaker experiments are almost as strong as those from the two-choice tests.

In natural populations of *H. marmoratus* inter-individual variation in the SPL of advertisement calls is only 5-6 dB (PASSMORE & TELFORD, 1983). Females are thus likely to be confronted with a choice between several males calling at similar intensities. The results of the 3:1 type four-speaker experiments suggest that under these circumstances females are unable to locate the loudest male. In the four-speaker experiments this was true even when the difference in SPL between stimuli was 8 dB which is 2-3 dB greater than the natural range. Consequently our results may provide a partial explanation for the absence of a large-male mating advantage in the field. In a study of captive males TELFORD *et al.* (1988) found a large-male mating advantage in small choruses, but not in larger choruses. Our results suggest that female choice in small choruses was not based on call intensity, but rather call frequency which is also correlated with body size. The absence of a large male mating advantage in bigger captive choruses was therefore probably due to a decreased ability of females to discriminate between different frequency calls.

Although generally accepted that two-choice phonotaxis may be too simple a set-up to reveal patterns of female choice in the more complex field situation, explicit tests of this using multi-speaker phonotaxis are few. GERHARDT (1987) and KLUMP & GERHARDT (1987) have also investigated the effect of increased chorus complexity and background noise for female choice based on call frequency: and in *Hyla cinerea* a female frequency preference seen in two-choice phonotaxis was not apparent in four-choice phonotaxis (GERHARDT, 1987). However, more studies of the role of chorus complexity are needed. It would be particularly interesting to perform multi-speaker phonotaxis in species such as *Physalaemus pustulosus* where strong evidence for female choice based on call frequency and call components comes from two-choice phonotaxis and correlations between male call parameters and mating success in the field (RYAN, 1985). If female choice is responsible for the male trait/mating success correlations, females should still be capable of discriminating between calls in phonotaxis experiments in the presence of background noise, or when there are more speakers.

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