Analysis and significance of female reciprocal call in frogs

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Female vocalization in frogs, feeble as it is, has often escaped the attention of researchers. Most of the work has focused on male vocalization and female phonotaxis experiments. The present study has for the first time compared in detail the temporal and spectral properties of the male advertisement and conspecific female reciprocal calls and focused on the role of female vocalization in the breeding biology of amphibians.

While studying anuran acoustic communication in the frogs of northeast India, female reciprocal calls given in response to the male advertisement call were recorded from Rana erythraea, Rana limnocharis and Rana cyanophlyctis. Once the female responds to the advertising males, more activity is observed in the breeding colony, involving mostly jumping around and across the responding female. The advertisement calls made by the male after the reciprocal call of the female have a higher intensity.

Comparative Fourier analysis of the female reciprocal call and the conspecific male advertisement call showed that the frequency domain of the male call is almost double that of the female call and accordingly there is a shift in the dominant frequency, whereas the spectral pattern consisting of a single or bimodal frequency distribution is common to both.

Animals often produce vocal signals for communication14. In amphibians vocal signals have proved invaluable in studying systematic relationships5-7, and the process of sexual selection8-10. Males of many amphibian anuran species produce species-specific complex sounds composed of numerous, closely spaced, often harmonically related components with predominant amplitudes that fall into distinct frequency bands, the locations of which are characteristic for each species. Male calls help to advertise their position, to defend their territories and to attract conspecific females to the breeding site, thus acting as an important determinant of mate choice11-13. Females recognize the calls of conspecific males, locate them within a chorus of the calling conspecific and heterospecific males and find a mate. Playback experiments have verified the importance of both the gross and fine temporal characters, as well as the spectral domain and spectral pattern of the call in a noisy acoustic environment14. Thus, the use of species-specific temporal and spectral character is one strategy for reducing heterospecific interference and maintenance of reproductive isolation14-16.

Acoustic communication plays a significant role in the reproductive behaviour and breeding biology of amphibians. Anuran vocalization has been classified according to the behavioral context in which the calls are elicited18-20. Most of the literature pertaining to anuran acoustic communication deals specifically with species-specific temporal and spectral characters of the male calls21,22,23. Although female vocalization had been reported as early as 1929, these reports were restricted only to the alarm, release and aggressive calls in Rana silvatica24, R. pipiens25, R. esculenta26, Colostethus inguinalis27 and Eleutherodactylus coqui28.

Reciprocal call given in response to the male advertisement call was reported in the genus Tomodactylus based only on behavioural observations, with, no call recordings29. Heinzmann30 working on Atyes sp., recorded two types of male calls—mating call and distress call. This work gives a brief description of the oscillogram for the reciprocal calls of the females, with no details of temporal and spectral characteristics. Female calling has also been reported in R. ridibunda31 and R. virgatipes32. It is noteworthy to mention here that, though sketchy reports on female reciprocal calls existed32 since 1957, in-depth study to look into the role of female reciprocal call in the breeding biology of amphibians has started only recently. A reason for this could be that the sensation of hearing for humans is most acute in the 2000-5000 Hz frequency range and the female calls occur much below this. Indeed, it is difficult to distinguish and record a female call, which is usually masked by the loud advertisement calls of the conspecific and heterospecific males in the vicinity.

While studying acoustic communication and related behavioural displays in the courting frogs of northeast India, we observed that females of R. erythraea, R. limnocharis and R. cyanophlyctis emitted reciprocal calls in response to male advertisement calls. Due to their feebleness and short call duration, these reciprocal calls would not have been noticed had they not been given in rapid succession, producing at times chirp-like calls, which attracted our attention. We then recorded and analysed the female reciprocal calls.

The calls were recorded during the active breeding period (May to August 1993 and 1994). In 1993 only behavioural observations were made and in 1994 the calls along with behavioural observations were recorded and analysed. The calls were recorded with a unidirectional AKG C451EB shotgun condenser microphone held approximately 40-60 cm away from the calling female. The calls were recorded with a professional SONY WM-DD6C cassette recorder and stored on Maxell XLII cassette tapes. Sound pressure level was measured by playing back the isolated female calls on a Philips double cassette player DR920 with playback volume level fixed at 4 and the CYGNET 2021 sound pressure...
level meter held approximately 60 cm away from the sound source.

Recorded acoustic stimuli were digitized via a Microsoft analogue-to-digital interface board on to an IBM PC and stored on diskettes. Oscillograms, sonograms and mean spectra were prepared with a computerized Fourier analysis system (FFT) after passing through bandpass filters and printed with a laser printer.

*R. erythraea* are mostly arboreal in nature and hence their calls and reproductive behaviour were easier to observe and record in comparison to the calls of *R. limnocharis* and *R. cyanophylctis*. The latter two species called mostly sitting on land on the edge of a swamp and while hovering on water surface, respectively. Besides, these two species were more easily disturbed, and swam deep into the water at the slightest disturbance. Calls of *R. erythraea* were recorded at Guwahati, Assam (200 m ASL; 91.5°E; 26.1°N). *R. limnocharis* and *R. cyanophylctis* calls were recorded from colonies being maintained under near-natural condition in the froggyery adjacent to the Institute at Shillong, Meghalaya (1515 m ASL; 90.7°E; 24.0°N).

The females of *R. erythraea* (Figure 1A) are usually seen emerging and approaching the calling males after about 30 min of vocal advertisement by the male. When the distance between the calling male and the approaching female reduces to about 10 cm, the male which had been calling till then stops advertising. The female makes feeble reciprocal calls in response to the male advertisement call. This feeble call of the female at times continues up to 1 h, with several bouts of call. The interval between each bout varies from 2 to 5 min, short intervals at the beginning and long intervals towards the end of the call. Only after the female responds to the male advertisement call, the male which had stopped calling on the appearance of the female restarts calling with a higher intensity. Concomitantly, all the other neighbouring calling males also start calling at a higher intensity. More activity is seen amongst the calling males—mostly jumping from one place to another, but all jumps are confined around and across that female, which responded by giving the reciprocal call.

*R. limnocharis* and *R. cyanophylctis* (Figure 1B, C) females called while submerged in water, making the feeble reciprocal calls very difficult to hear and record and the behavioural displays difficult to observe. In both the species the females responded to the male advertisement calls. Once the reciprocal calls were emitted, the male calls were louder and more activity was seen amongst the males which were nearer to the responding female.

The reciprocal call of *R. erythraea* is low-pitched, lasting approximately 32 ms. The call sometimes has 3 to 4 subunits, each subunit not lasting more than 10 ms. The call is composed of about 22 pulses. The dominant frequency is at about 1048 Hz, with no harmonics, and the frequency domain extends from about 746 to 1229 Hz, the SPL being 77 dB (Table 1; Figure 1a).

In *R. limnocharis* the calls lasted approximately 61 ms, with 45 pulses. The call had a single dominant frequency at about 1531 Hz, lacking harmonics. The frequency domain is comparatively small, extending from about 1300 to 1767 Hz, the SPL being 70 dB (Table 1; Figure 1b).

In *R. cyanophylctis* the call duration was approximately 20 ms, composed of 20 pulses, having constant interpulse interval. The frequency distribution was bimodal, with dominant frequency at about 740 Hz and its second harmonic at about 1433 Hz. The frequency domain extends from about 496 to 1746 Hz, the SPL being 65 dB (Table 1; Figure 1c).

Comparative spectral analysis of the female reciprocal calls with male advertisement calls of *R. erythraea* (Roy, unpublished), *R. limnocharis* and *R. cyanophylctis* shows that female calls are much shorter in duration, with comparatively more pulses, resulting in reduced interpulse interval and pulse overlap. There is a shift in the frequency domain towards the lower range (almost half) in all the three female reciprocal calls, resulting in a shift of dominant frequency as well. Interestingly, in spite of the spectral frequency shift to the lower range, the spectral pattern along with the envelope curve remains unchanged. Like their male counterparts, there is only a single dominant frequency in *R. erythraea* and *R. limnocharis* and bimodal frequency distribution in *R. cyanophylctis*.

Female vocalization due to its feebleness and the secretive nature of the females has often escaped the attention of researchers. Most works done till now have been on male vocalization and female phonotaxis experiments. This study has for the first time focused on the role of female vocalization in the breeding biology of the amphibians and demonstrated that the female reciprocal calls seem to act as a 'catalyst' for the enhancement of the reproductive activity of the breeding colony.

The feebleness of the call may be due to various reasons: (a) The bigger size of the females compared to the males. (b) The absence of vocal sacs in the females; the expandable pouch-like vocal sac present only in the males acts as a sound resonator and radiator. However, little evidence exists to support this hypothesis and it is now being contemplated that the vocal sacs in the males may have a 'variety of mutually nonexclusive functions'; this is still being worked upon. (c) The differences in the structural morphology and tension of the musculature of the vocal cords and larynx and also the tension of the trunk muscles. A comparative study on the morphology
Figure 1. A, Female *R. erythraea*; a, mean spectrum of female reciprocal call of *R. erythraea*; on the right: the corresponding sonagram (FFT length: 256, overlap: 50%, window: Hamming). B, Female *R. limnocharis*; b, mean spectrum of female reciprocal call of *R. limnocharis*; on the right: the corresponding sonagram (FFT length: 256, overlap: 50%, window: Hamming). C, Female *R. cyanophlyctis*; c, mean spectrum of female reciprocal call of *R. cyanophlyctis*; on the right: the corresponding sonagram (FFT length: 256, overlap: 50%, window: Hamming).
Figure 2. Top. Male (left) and female (right) *R. erythroa.* Bottom. Mean spectrum and sonagram of the male advertisement call of *R. erythroa* (left) and mean spectrum and sonagram of the female reciprocal call of *R. erythroa* (right) (FFT length: 256; overlap: 50%; window: Hamming).
Table 1. Comparative analysis of female reciprocal calls and male advertisement calls of
R. erythraea, R. limnocharis and R. cyanocephalus

<table>
<thead>
<tr>
<th>Species</th>
<th>No. of calls per species</th>
<th>Call duration (ms)</th>
<th>Pulse number</th>
<th>Frequency (Hz)</th>
<th>Dominant frequency</th>
<th>Lower limit</th>
<th>Upper limit</th>
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<tr>
<td>R. erythraea</td>
<td>Female</td>
<td>14</td>
<td>32 ± 9</td>
<td>22 ± 9</td>
<td>1048 ± 105</td>
<td>746 ± 126</td>
<td>1229 ± 114</td>
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<tr>
<td></td>
<td>Male</td>
<td>15</td>
<td>224 ± 4</td>
<td>25 ± 1</td>
<td>2459 ± 42</td>
<td>1495 ± 23</td>
<td>3724 ± 31</td>
</tr>
<tr>
<td>R. limnocharis</td>
<td>Female</td>
<td>14</td>
<td>61 ± 27</td>
<td>45 ± 7</td>
<td>1531 ± 204</td>
<td>1300 ± 224</td>
<td>1767 ± 213</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>40</td>
<td>503 ± 101</td>
<td>80 ± 13</td>
<td>2144 ± 1254</td>
<td>1576 ± 87</td>
<td>2685 ± 115</td>
</tr>
<tr>
<td>R. cyanocephalus</td>
<td>Female</td>
<td>12</td>
<td>20 ± 4</td>
<td>20 ± 6</td>
<td>740 ± 36</td>
<td>496 ± 57</td>
<td>1746 ± 4</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>34</td>
<td>615 ± 155</td>
<td>7 ± 1</td>
<td>1651 ± 43</td>
<td>1163 ± 124</td>
<td>3907 ± 42</td>
</tr>
</tbody>
</table>

Spectral data on the male advertisement call of R. erythraea (Roy, unpublished); spectral data on R. limnocharis and R. cyanocephalus from ref. 7.

Values are mean ± SD

as well as the kinematics of the vocal sacs of the conspecific male and female vocal apparatus is necessary to come to a definite conclusion in this matter.

Bioacoustic analysis of amphibian vocalization has emphasized the species-specific temporal and spectral characteristics of the calls. Shift in the temporal pattern occurs which helps avoid acoustic interference and increase the attractiveness of the call is well known\(^1\),\(^2\), but shift in the spectral frequency domain has not been reported. The present study in the three ranid species shows that the frequency domain of the male call is almost double that of the female call and accordingly there is a shift in the dominant frequency, whereas the species-specific spectral pattern of having a single or bimodal frequency distribution remains unaltered (Figure 2). The result of this comparative analysis raises an important question — should the spectral pattern, due to its unaltered species-specific nature, be considered more important than the spectral domain for species identification on the basis of bioacoustic analysis of frog calls?

Yttrium-, niobium- and zirconium-rich rhyolite dykes of Dhorio Nes area, district Jamnagar, Gujarat, India

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Anomalous high contents of Nb (818 ppm), La (173 ppm), Y (305 ppm) and Zr (> 1000 ppm) are reported for the first time in the rhyolite dykes/veins spatially associated with the Deccan basalt in Alech hills around Dhorio Nes, district Jamnagar, Gujarat. The enrichment of these elements is due to influx of alkalies and volatiles in rhyolites emplaced along the western continuity of E–W trending Son–Narmada rift.

The Deccan Traps, covering about one-sixth of India’s total land surface, comprise mostly of tholeiitic basalt. Acidic, alkalic and mafic alkaline rocks are found in the western part of the basalt plateau in western India in parts of Kutch, Saurashtra, Lower Narmada Valley and Bombay coast.

The Saurashtra region of Gujarat is known for a number of acid igneous rock complexes along the western extension of the Son–Narmada lineament. These include the Alech–Barda hills, Osham hills, Girnar hills and Chogat–Chamardi hills. These acidic rocks developed as an independent magma suite with rhyolite as a predominant rock type within the complex, or as an end product of differentiation.

In Alech–Barda hills, the acid igneous rocks comprise pitchstone, rhyolite, granophyre and diorite. The rhyolites occur as dykes and veins within the basalt, and also as flows of rhyolitic crystal tuffs. Two prominent pink- to buff-coloured, highly fractured E–W-trending rhyolite dykes were noticed in the south and southwest of Dhorio Nes (69°59′44″: 21°48′27″, Toposheet no. 41 G/13) in the Alech hill area, showing higher than background radioactivity (Figure 1). They extend over a length of 500 m with width varying from 10 to 30 m. They consist mainly of quartz, sanidine and glass along with some opaques and exhibit vitrophyric texture. The groundmass in the rhyolites is essentially composed of a glassy material along with crystallites of feldspars. The chemical data of these rocks along with the data of Pavagarh and Amreli rhyolites and the general abundance in rhyolites is given in Table 1. The samples show normative corundum, peraluminous (ACNK = 1.52), miaskitic (Al = 0.64) nature and enrichment of potash over soda.

Figure 1. Geological map showing rare-earth-, niobium- and zirconium-rich rhyolites of Dhorio Nes area, district Jamnagar, Gujarat