Communication signals and sexual selection in amphibians

Debjani Roy

Institute of Self Organising System and Biophysics, North Eastern Hill University, Shillong 793 022, India

Female mate choice is an important determinant for male reproductive success in anurans. The advertisement call of the males contains information for species recognition. These calls are used by the females to distinguish between heterospecifics and conspecifics and further to discriminate among conspecifics to choose the fittest male for the purpose of mating. In *Polypedates leucomystax*, the female responds by its feeble reciprocal call to the first calling male of the colony, which also is the largest and heaviest male amongst all other calling males. This male calls persistently throughout the night, or till amplexus is reached, without changing its call pattern. It increases the intensity of its call after the response of the female. The increase in the intensity, increase in the length of the individual call and persistent calling throughout the night make the call of this first calling male conspicuous. The call contains more acoustical energy which is indicative of good physical condition and the responding female chooses this male. Thus mating in *P. leucomystax* is non-random and influenced by female mate choice.

*Females* of various groups of vertebrates use communication signals produced by the males to choose the fittest male for the purpose of mating. It was this selection pressure which resulted in sexual signals of males to contain information far in excess than that was needed for species recognition. Male sexual displays allowed females to pick more vigorous males and this female choice thus caused further elaboration of male sexual displays. The idea was further extended by Fisher's theory of Runaway Selection. Thus there exists an important relation between communication signals and sexual selection.

Female mate choice has been demonstrated as an important determinant of male reproductive success in anurans. The advertisement calls produced by the males, contain information encoded spectrally and/or temporally important for species recognition. These calls potentially provide a receptive female with information pertaining to species identity, sex and reproductive fitness of the advertising male. These signals are used by the females to distinguish between heterospecifics and conspecifics, and further, to discriminate among conspecifics. Based on these informations, the female decides to accept or not to accept the calling male as a potential mate.

Till recently it was believed that it was for the male frogs to produce advertisement calls and act as senders, while the females act as receivers of the acoustic signals to choose the fittest male. As a result, most works were focused on male vocalization and female phonotaxis experiments. Female vocalization due to its feebleness and the secretive nature of the female, had mostly escaped the attention of researchers.

**Female reciprocal call**

The significance of female reciprocal call in the breeding biology of amphibians was highlighted by Roy et al. They demonstrated the 'catalytic' role of the female reciprocal call for the enhancement of the reproductive activity of the breeding colony. While studying anuran acoustic communication in northeast India and comparing male advertisement call with female reciprocal call in *Limnonectes limnocharis, Euphyllyctis cyanophlyctis and Polypedates leucomystax* (Figures 1, 2 and 3), many interesting observations were made. Out of the 3 species, *P. leucomystax* due to its perching habit and its responsive, active and alert nature, was chosen for in detail study of its communication signals and breeding behaviour.

**Reciprocal call and courtship display in Polypedates leucomystax**

The role of female reciprocal call has been studied in detail in *P. leucomystax* for 3 consecutive years (1994–1996) both in the field and laboratory. These frogs are mostly found perched on creepers which entwine bamboo fencing or on tall grass in the vicinity of water. Their perching habit makes them easier to observe than terrestrial or aquatic species and to follow their elaborate breeding behaviour (Figure 4a, b).

Weather condition seems to play an important role on the timing of beginning of the first male advertisement call. On dry hot days with temperature ranging between 26 and 37°C, the first male call is heard around 1800 h. On
cloudy or rainy days, with temperature ranging between 23 and 33°C, the call is heard much earlier in comparison to dry hot days around 1630 h. Similarly on cloudy or rainy days, the second male call is heard only 5–10 min after the first male call, whereas on dry hot days the second male begins to call 20–30 min after the first male call.

After the males have advertised for about 30 min, the receptive and responding females which are at times more than one, emerge mostly from under leaf litter. But only one female is seen to climb up and position herself near the first calling male of the evening in the colony. This first calling male occupies the highest perch, positioning itself at least 80 cm to 1 m above all other calling males of the colony.

This first calling male has a distinct call which sounds like P-A-K and therefore has been termed as the PAK call. It does not change its PAK call pattern even when other calling males approach. It continues to call PAK throughout the evening or till amplexus is reached, while other calling males of the colony produce graded calls depending upon the context which the calls subserve – territorial, aggressive or encounter.

When the distance between the first PAK calling male and the approaching female reduces to about 10 cm, the males which had been calling till then stop advertising. The female then makes a feeble reciprocal call in response to the male PAK call. This feeble call of the female continues at times up to 1 h with several bouts of call. The interval between each bout varies between 2–5 min, with short interval at the beginning and long intervals towards the end of the calling sequence. Only after the female responds to the male advertisement call, the male which had stopped calling on the appearance of the female frog restarts its PAK call but with a higher intensity. The mean intensity before the reciprocal call was 47.62, ± 0.865 dB, while after the reciprocal call it was significantly higher, 58.82, ± 1.459 dB, n = 93; p < 0.05; t-test. In each of the 93 cases without
exception, the intensity of the PAK call was greater than the intensity before. This clearly indicates that the 2 PAK calls are different both statistically as well as functionally. Thus, the advertisement call having higher intensity given after the female call can be classified as 'courtship call'. Concomitantly, all other neighboring males also start calling at a higher intensity but not as much as the first PAK calling male. More activity is seen amongst the calling males - mostly jumping from one place to another, but all jumps are confined around and across the female which has responded by producing the reciprocal call (Figure 5).

The low pitched feeble reciprocal calls of the females lead to two very significant findings: (1) The female reciprocal call seems to act as a 'catalytic' for the reproductive activity of the breeding colony; (2) Till now the general opinion was that females typically initiate sexual

Figure 3. Top, Male advertisement call and female reciprocal call of *Polypedates leucomystax*; Middle, An enlarged portion of male advertisement call (left) and an enlarged portion of the female reciprocal call (right); Bottom, Corresponding mean spectra and sonogram of male advertisement call (left) and female reciprocal call (left) (FFT length: 256; Overlap: 50%; Windows: Hamming)

Figure 4 a, b. Perching and climbing habit of *Polypedates leucomystax*.

Figure 5. Calling sequence and behavioural displays of the advertising male and responding female of *Polypedates leucomystax*.
contact by moving close to or touching a calling male and the males indiscriminately try to mate with frogs that move near or touch them. The present findings clearly indicate that prior to sexual contact the following should happen sequentially: (i) Distance between the advertising male and the responding female has to be 10 cm or less; (ii) The advertising male which had been calling till then should stop advertising; (iii) The responding female has to respond by producing reciprocal calls; (iv) Males which had stopped calling should restart calling but with a higher intensity – only then sexual contact is established. The establishment of sexual contact in terms of amplexus results after the change from the advertising call to courtship call and definite moves by both the advertising male and responding female which appear to be distance dependent.

**Female mate choice in P. leucomystax**

During the 3-year study, there were 358 days of field observations which started each day around 1600 h. Out of these 358 observational days, male advertisement calls were heard on 211 days of which the females appeared on 93 days. These data were recorded from 4 different colonies where all the individuals were tagged. The preference of the responding female on all 93 days was always for the first calling male of the colony. This first calling male always occupied the highest perch. At higher perch sites, sound gets less attenuated which is likely to attract more females. In male *Centrolenella fleischmanni*, calling from elevated sites acquired more mates and suggested this might be due to better sound transmission from elevated as compared to lower call sites.

The first calling male is found to be the largest and heaviest amongst all other calling males of the colony. Females are predicted to prefer older males of the colony not only because they may control resources of higher quality, but also because they possess phenotypes that have demonstrated their ability to survive numerous environmental conditions. Benefits obtained by females from their mates can be of two sorts: those affecting the genetic quality of their offspring and those affecting immediate reproductive output. Trivers suggested that all things being equal, females should select older males because they have demonstrated their ability to survive. He also suggested females should select males with faster growth rate because they have demonstrated their resource accrual ability. Larger males are either older or have faster growth rate. To the extent there is a heritable genetic component to growth and survival, these benefits will be passed on to the offspring of both the sexes. The daughters will benefit because of the correlation between female size and the number of eggs per clutch. Sons will have a higher probability of attracting mates if larger. Larger males have been reported to have larger acoustic territory than smaller males. This was probably due to their higher success in fights for calling sites and greater ability to inhibit other males from calling close by.

The first calling male continues to call PAK persistently, does not seem to be disturbed or threatened by the approach of other calling males. It calls at louder intensity after the female reciprocal calls are heard. It is reasonable to assume that males which outsignal competitors enhance the probability of their being noticed by sexually active females. This might be accomplished by employing any of the following strategies: (a) Increase in the intensity of the call; (b) Increase in the length of the individual call; (c) Persistent calling throughout the night. The males by employing any of these strategies, regardless of their size, increase the chance of being selected by the sexually active females. In case of *P. leucomystax* the first calling male does not change its call pattern throughout the evening. It continues to call PAK and continues persistently. It calls at a higher intensity after the female reciprocal call. This male seems to employ all 3 strategies. This call is therefore conspicuous, contains more acoustical energy and is indicative of good physical condition. Females which respond to such a male should benefit more. Females of several different anurans prefer calls which are louder, more rapidly repeated, longer and more complex. Males that produce more expensive calls may be fitter than other males in terms of their survival ability and such fitness may be heritable, which is still to be tested.

The females do not appear until the males start advertising and are seen only when they come out and perch themselves next to the first PAK calling male, the distance between the advertising male and the responding female being 10 cm or less. Similar reproductive behavioural results were reported by Ryan in *Physalaemus pustulosus*. Moreover, the conspicuous signaler may be advantageous because such a male may be easier to locate, closer to the female and thus costs of movement incurred by females tend to be minimized.

**Conclusion**

Mating in *P. leucomystax* is non-random like in other anurans and is influenced by female mate choice. I chooses males which are larger, heavier, produce louder and lower frequency calls. Sexual selection theory predicts that females may maximize the genetic contribution to future generation through selective mating. This means by which the female anurans differentially recognize fitter males is problematic but at least in some species, including *P. leucomystax*, fitness is thought to be positively correlated with body size and bod.
size may be predicted by parameters of the advertisement calls.


ACKNOWLEDGEMENTS. I thank the Department of Science and Technology, New Delhi for financial support, S. K. Dutta and I. Das for identification of P. leucosyra, the Indian Academy of Sciences, Bangalore for selecting the work for presentation at the Annual Meeting of the Academy held at Jodhpur, 1996.