Courtship in Frogs

Role of Acoustic Communication in Amphibian Courtship Behaviour

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Vertebrate vocalization came into existence for the first time in frogs. Acoustic signals produced by the frogs have well-defined physical characteristics and a clear biological meaning. The signals are meant to attract and assess the sex, species identity and genetic quality of potential mates. Acoustic communication plays a central role in the courtship behaviour of frogs.

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The chordates originated in the sea as jawless fishes. The bony fishes, which evolved from them are the most plentiful vertebrates today. The first vertebrate land dwellers were the amphibians, but they are not truly terrestrial because they still require frequent access to water. The first true terrestrial vertebrates were the reptiles, which independently gave rise to the birds and to the mammals, including humans (*Figure 1*).

The amphibians – descendants of the crossopterygian fishes were the first land dwellers. Their transition from fresh water to land was a momentous step in vertebrate evolution. The word amphibia is derived from the Greek word *amphibious* meaning *double life* because of their two phase life style: a free living larval aquatic stage and a terrestrial juvenile and adult stage. Contemporary amphibians include caecilians (Order *Gymnophiona*), salamanders (Order *Urodela*) and frogs and toads (Order *Anura*).

Amphibians were the first vertebrates to have evolved a partially terrestrial way of life. This became possible due to a series of anatomical and physiological adaptations to the new environment. One feature of this new environment was the acoustic world – the sounds that were abiotically caused. The amphibians that

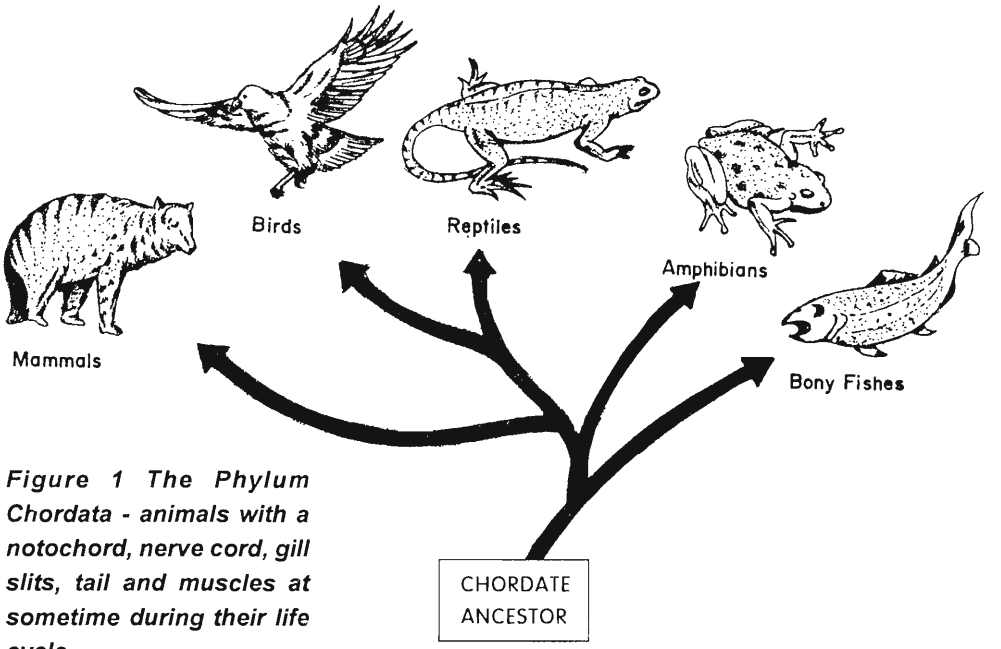


Figure 1 The Phylum Chordata - animals with a notochord, nerve cord, gill slits, tail and muscles at sometime during their life cycle.

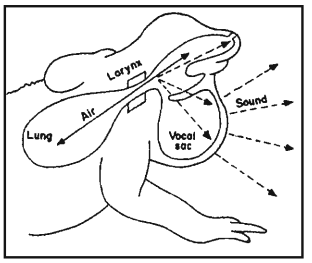


Figure 5a Sound production in frogs. Sound production uses the respiratory ventilation cycle without releasing air to the outside. Before calling the, bucopharyngeal force-pump inflates the lungs and vocal sacs. With the nostrils closed, the body muscles contract, pushing a pulse of air through the larynx, virbating the vocal cords. Sound radiates outwards and the vocal sacs resonate it.

adapted to the changed acoustic conditions of their environment most successfully were the frogs and toads (hereafter referred to collectively as frogs). They adapted so well that acoustic communication came to play a central role in their reproduction. Vertebrate vocalization came into existence for the first time in frogs.

The sound production apparatus of the frogs consists of the larynx and its vocal cords. The laryngeal apparatus is well developed in the males, who also possess a vocal sac. Air from the lungs is forced over the vocal cords and cartilages of the larynx, causing them to vibrate and regulate the frequency of sound. Muscles control the tension of the vocal cords. Vocal sacs act as resonating structures and increase the volume of the sound (*Figure 5a & b*).

The emitted sound consists of regularly alternating compressions and rarefactions of the air, basically increased and decreased air

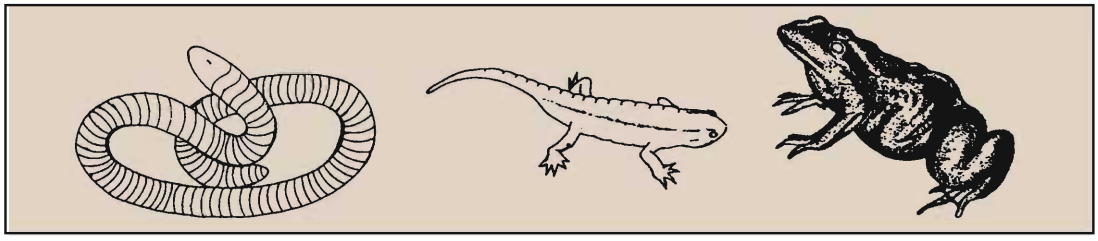


Figure 2 (top left) Gymnophis – Order Gymnophiona.
Figure 3 (top center) Hydromantoides – Order Urodela.
Figure 4 (top right) Rana Species – Order Anura.

pressure respectively forming a simple harmonic or sinusoidal motion. The resulting displacement of the air molecules form a sine wave. Like all sine waves it can be described fully by stating its *amplitude* or height and its *period*, which is the time required to go through one complete cycle. The period is inversely related to the *frequency*, which is the number of cycles per unit time.

Thus,

Period (Seconds) = 1/Frequency (Seconds^{-1}).

Sounds are usually designated by their frequency in cycles per second or hertz (Hz). A thousand hertz is called a kilohertz (kHz) (*Figure 6*).

The *amplitude* of the wave is correlated with its perceived loudness, and a special scale, the Decibel Scale, is used to measure the amplitude of pressure waves.

Sound Pressure Level (SPL) in decibels = 20 $\log_{10} Pt/Pr$ where, Pt is the test pressure and Pr is the reference pressure (2×10^{-4} dynes/cm^2). The background noise in a quiet room is generally about 30 dB SPL; a typical human voice heard at close range is about 60–80 dB SPL; and rock music as commonly played reaches 120–150 dB or higher. Some species of frogs can produce ear splitting sounds of 114 to 120 dB.

Figure 5b A calling toad – Bufo melanostictus with its vocal sac inflated.

Box 1 Amphibian Orders

Order *Gymnophiona*: Limbless, pelvic and pectoral girdles absent; body elongated and cylindrical, regularly encircled by grooves forming segments; head blunt and cone shaped with an overhung lower jaw and nearly invisible, degenerate eyes; tail if present short and blunt. They are usually in shades of pinkish brown and grey. They are fossorial, living by burrowing in soil, a few are aquatic (*Figure 2*).

Order *Urodela*: Lizard like, having low slung bodies with moderate length limbs and long tail; head broad with distinct eyes, separated from the body by neck. The aquatic forms have reduced limbs and appear eel like. They are coloured animals, sometimes with bold patterns. They are found in both cool mountaineous regions as well as hot lowlands, inhabiting slow moving or still water (*Figure 3*).

Order *Anura*: Body dominated by long powerful hindlimbs, an adaptation for their jumping locomotion. The entire body is adapted for such adaptation, with shortened body with broad head, no neck, no tail, with well developed forelimbs propelling synchronously with the hindlimbs. They have a wide range of colourations. A few species being entirely aquatic, most are semiterrestrial to terrestrial and arboreal (*Figure 4*).

For precise evaluation of frog calls for the message and meaning they emit, the sounds are recorded with the help of a professional walkman and unidirectional condenser mircophone and stored on audiocassettes. The sounds stored as waveforms on audiocassettes are next digitized by an analogue to digital converter to get oscillograms, sonagrams and mean spectra by using computerised Fast Fourier Transformations (FFT). The

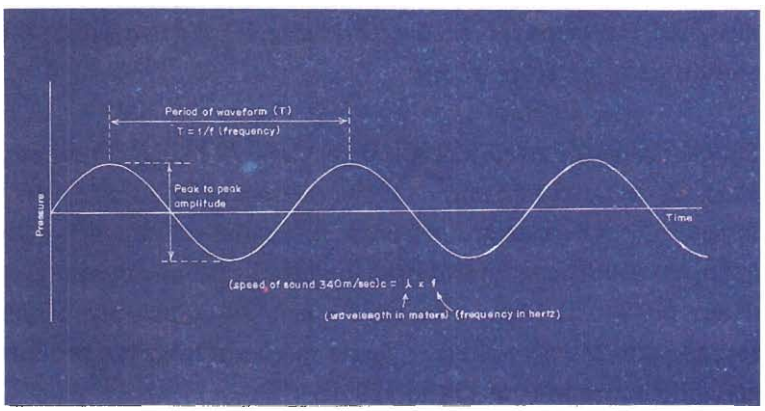


***Figure 6** A sinusoidal wave or sine wave propagates through space, the ambient pressure in the air is measured with a microphone probe at a fixed point. The speed of sound is constant in air (approximately 340m/sec) and is related to both the wavelength (l) and frequency (f) of the wave shown in the equation in the figure. The tympanic membrane of the ear moves in response to alternating condensation (peaks) and rarefaction (troughs) of the sound wave.*

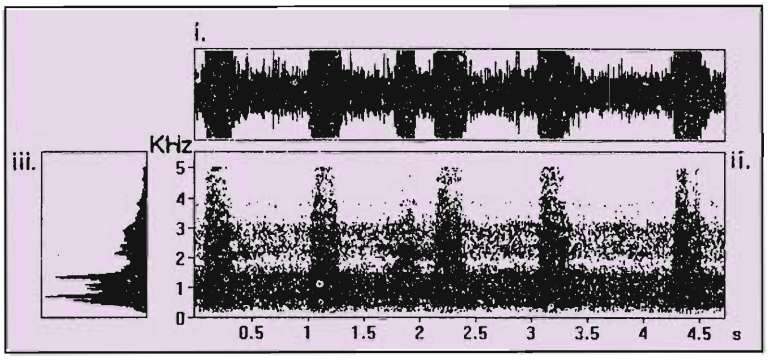


Figure 7a Bull frog – Rana tigerina.

Figure 7b (i) Oscillogram or waveform representation of the advertisement call of bull frog with amplitude in the abscissa and time in the ordinate. (ii) & (iii) Corresponding sonagram and mean spectrum with frequency in the abscissa and time trace in the ordinate with amplitude in shades of grey. The mean spectrum showing frequency spread from 0.13 to 4.91 kHz. The frequency distribution is bimodal with dominant frequency at about 0.69 and 1.34 kHz.

FFT allows one to obtain a frequency-domain representation of a time domain wave form. Its popularity derives from the availability of fast algorithms of its calculations and also from the ubiquity of its use in the analysis of acoustic signals in animal communications (*Figure 7a & bi, ii,iii*).

Most calls last about 2 secs. which may be repeated rapidly in sets. Calls generally lie between 200–500 Hz which is a good broadcast spectrum for these animals, since they can avoid interference from other sounds. Most frog calls span a broad frequency spectrum of 1–2 kHz, whose energy is concentrated in narrow frequency bands either with a single dominant fundamental frequency or first harmonic of the sound or in harmonics. Twice the fundamental frequency is called second harmonic, three times the third harmonics and so on. The sounds produced are not mere sounds or croaks of frogs but have definite physical, physiological and biological meaning. The sound production is a primary reproductive function of the frogs. Male frogs produce species specific complex sounds composed of numerous, closely spaced, often harmonically related components with predominant amplitudes that fall into distinct frequency bands, the location of

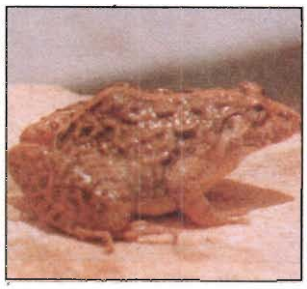


Figure 8a Cricket frog – Rana limnocharis.

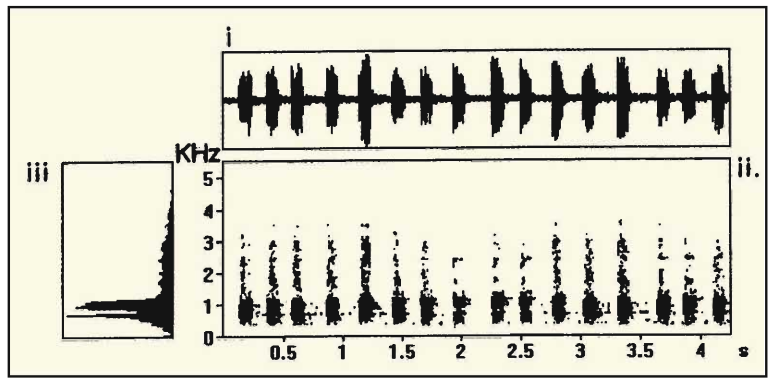


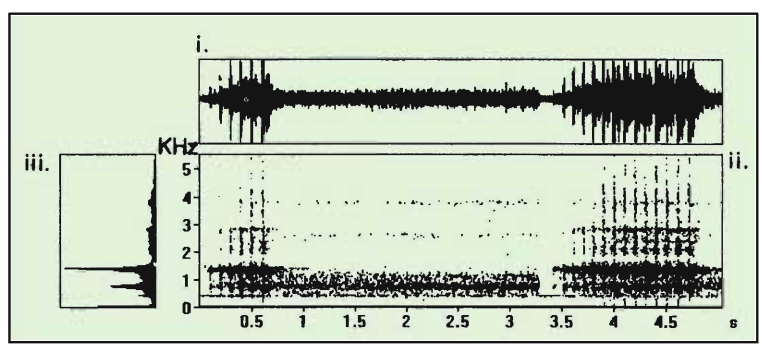
Figure 8b (i) Oscillogram or waveform representation of the advertisement call of cricket frog with amplitude in the abscissa and time in the ordinate. (ii) & (iii) Corresponding sonagram and mean spectrum with frequency in the abscissa and time trace in the ordinate with amplitude in shades of grey. The mean spectrum showing frequency spread from 0.35 to 4.40 kHz. The dominant frequency at 1.08 kHz.

which are characteristic for each species (*Figure 8a & bi, ii, iii; 9a & bi, ii, iii*).

The calls have species specific temporal and spectral characteristics. Notable features of the temporal structure are call duration (sec.), intercall interval (sec.), pulse number, interpulse interval (sec.), call intensity (dB); the spectral part consists of frequency

Figure 9b (i) Oscillogram or waveform representation of the advertisement call of skipper frog with amplitude in the abscissa and time in the ordinate. (ii) & (iii) Corresponding sonagram and mean spectrum with frequency in the abscissa and time trace in the ordinate with amplitude in shades of grey. Mean spectrum showing the frequency spread from 0.33 to 4.36 kHz. The frequency distribution is bimodal with dominant frequency at 0.78 and 1.42 kHz.

Figure 9a Skipper frog – Rana cyanophlyctis.



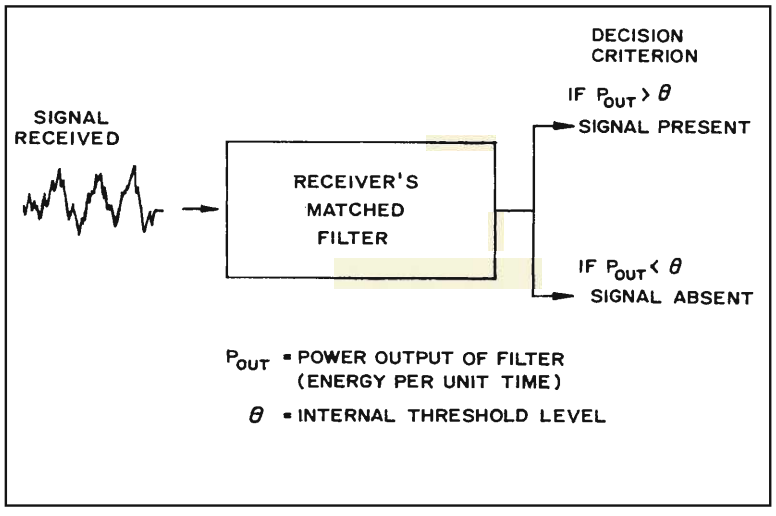


Figure 10 Decision criteria of a matched filter detector. The received signals pass through the receiver's matched filter. Whenever the power output of the filter exceeds a certain threshold, the receiver decides that the sender's signal is present. As long as the power output remains below threshold, the receiver concludes that no signal has been sent. By adjusting the internal threshold, the reliability of the receiver's decision can be altered.

domain (Hz), presence and absence of harmonics, dominant frequency (Hz). Shift in the temporal pattern occurs to avoid acoustic interferences and increase the attractiveness of the call. The spectral pattern of the conspecific calls remain unaltered. The sounds or calls of frogs can be classified according to the context in which they are produced.

The broadcasted sounds closely match the receptor sensitivities of both the males and the females of the same species. The sound characteristics provide the frogs with an effective signalling device, one that is finely tuned to the sensor capabilities of the intended receiver, yet can be adjusted to transmission of messages (*Figure 10*). Two such adjustments are changed intensity and modulation. A slight elevation of call rate towards a full aggressive call, alerts the intruding male of his presence and if the intruder does not depart, the call is further adjusted (*Figure 11*). Similarly in dense choruses males shift the timing of their call to avoid overlap with their nearest neighbours and increase the call rate and the number of call notes to improve attractiveness. Call frequency is also size dependent, with larger individuals producing lower call frequency. In most instances, females are attracted to the lower frequency calls. In others males calling on the greatest number of nights have higher success rates. Thus

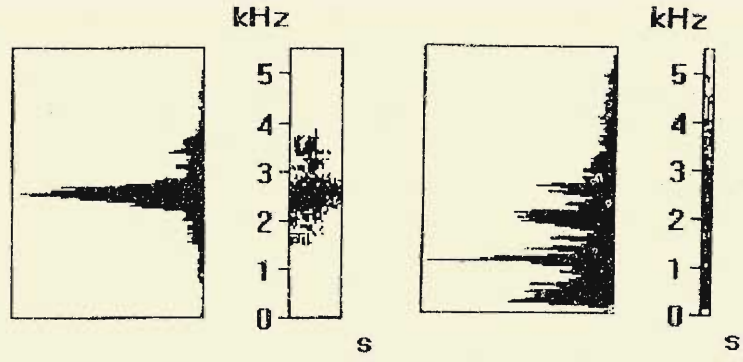


Figure 11 Male (left) and female (right) Rana erythraea [to the left]. *Mean spectrum and sonagram of the male advertisement call of R.erythraea (left) and mean spectrum and sonagram of the female reciprocal call of R.erythraea (right)* [above].

males which are larger, stronger and more durable in their nocturnal calls are favoured by the females for courtship followed by mating.

Courtship encompasses all reproductive activities prior to mating. Communication plays a key role in courtship behaviour. In the case of frogs, vocal communication plays a significant role in attracting and assessing mates. Signals help in the assessment of sex, species identity and genetic quality of the potential mate. If the potential mate passes the review, signals may increase the partner's reproductive readiness leading to the act of mating and transfer of gametes. Competition to access the female is intense, the intensity is compounded by the females selectively which compels the males to have bright colour, ornate structures and courtship behaviour to attract and retain the females. The males must therefore demonstrate their relative superiority over other males by having a stronger voice, a high quality territory or more aggressive display. Of course the qualities sought by the female frogs are not always evident to the human eye.

In 1995 it was shown that the feeble female reciprocal call given in response to the male advertisement call plays a significant role in the courtship and breeding biology of frogs.

Frog courtship is dominated by auditory signals which were thought to be the male vocalization – the advertisement call given by the males. But in 1995 it was shown that the feeble

Box 2

1. *Mating or advertisement call*: These calls attract females to the breeding sites and announce to other males that a given territory is occupied. Advertisement calls are species specific and any one species has a limited repertoire. They may also help induce psychological and physiological readiness to breed. The intensity of the call varies from species to species. The intensity of the advertisement call increases by almost 10 dB after the appearance of the female. Mating calls are emitted by male frogs.
2. *Territorial call*: These calls by male frogs may be of long or short range. They serve to demarcate and defend the territory and are emitted either sporadically or at faster call repetition rates. They may be of functional significance in the maintenance of territories or the regulation of population densities.
3. *Release call*: These are short explosive sounds repeated at irregular intervals. They often resemble an accelerated or imperfect mating call interspersed by sounds or short durations in some instances. These calls inform the partner that a frog is incapable of reproducing. They are given by unreceptive females during attempts at amplexus by a male or by males that have been mistakenly identified as females by another male.
4. *Reciprocal call*: These low pitched feeble calls are produced by females in response to the male advertisement call. Due to the feebleness of the call, it had till now escaped the attention of researchers. Recently it has been shown that only after the female produces the reciprocal call, are the final mating and egg laying activities initiated.
5. *Distress call*: These are low pitched, to shrill cries or screams. They are not associated with reproduction but are produced by either sex in response to pain or while being seized by a predator. They may be loud enough to cause a predator to release the frog.

female reciprocal call given in response to the male advertisement call plays a significant role in the courtship and breeding biology of frogs. The female reciprocal calls seem to act as a *catalyst* for the enhancement of the reproductive activity of the breeding colony. 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.

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,

Although auditory signals dominate frog courtship, the tactile and visual signals serve in the final approach and amplexus.

whereas the spectral pattern is common to both (*Figure 11*).

Although auditory signals dominate frog courtship, the tactile and visual signals serve in the final approach and amplexus. For most frogs, the tactile role in amplexus must be emphasized as it stimulates ovulation in some frogs and oviposition in all. Migration is a common feature in the life cycle of terrestrial amphibians, due to the requirement of water for their eggs and larvae. This migration occurs just before or during courtship. Pond breeding amphibians move from their terrestrial or arboreal homes to temporary or permanent ponds. Usually the males precede the females and arrive hours or days before the females. Male frog calls or chorus guide the females to the breeding areas. They partition their breeding sites, each species having a calling microhabitat. Each male defends its own territory mostly by vocalization and when that fails, they defend by head butting, wrestling or biting.

Most frogs are twilight or nocturnal creatures. They leave their hidden recesses at dusk, based on a specific brightness level. During the day they sleep directly in the sunlight above the water. Bright daylight has a striking effect on mating behaviour in species which leave their homes only at night. Bright light and water acting together release the spawns, which are then fertilized by the amplexing male.

Suggested Reading

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