The Mechanism and Importance of Acoustic Communication, used by Anurans During Breeding.

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November 2007

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"A call is defined as a complete sequence of pulses separated from the next call by an inter-call interval" (Prohl, 2003)

Acoustic signalling has considerable significance in the life of frogs and toads, one of which is the advertisement calls used by the males to attract females during the breeding season in spring. They begin around April once they have emerged from hibernation, and will continue for afew weeks at most. The calls of each individual species have evolved through female preference so no two species calls are the same, making it an important behavioural isolating mechanism. The physiology of the hearing apparatus has co-evolved with these differing calls to respond to the correct frequency and temporal qualities for species recognition. Males can project these calls both above and below water, to which the females will respond phonotactically by approaching the male, assessing him further and initiate mating by touching the male on the back. This is obviously an adaptation to the lifestyle of anurans, being semi or totally aquatic.

Not only is the call thought to attract females to the breeding site, but it is also a signal to surrounding males, making them aware that breeding has started and where the site is. This could be especially important for species that breed in temporary pools instead of having a fixed site to return to each year. Males may also respond to other males' calls with territorial behaviour, switching to aggressive calling when competitors appear in their territory. This breeding mechanism evokes sexual selection, as the calls of individual males vary and so does female preference, inferring within-population fitness variation. Calling is an extremely costly activity for males, probably representing the most energetically expensive activity a frog or toad can perform. The theory behind sexual selection is that a males display – in this instance an advertisement call – is representative of their ability to bear such costs, and therefore their overall fitness. Therefore females should base their mating choice on energy-consuming traits because they are potential indicators of an individuals genetic quality, leading us to theorise females would prefer more intense calls, more complicated calls, or calls produced at a greater repetition rate. Added to this, previous female sensory bias may have been exploited my males, selecting for specific hereditary call qualities. Experiments on Dendrobates pumilio (Strawberry Poison Frog) have shown that "male calling activity is the most variable trait among males and the most important trait influencing their mating success" (Prohl, 2003). The other risk advertisement calls pose is the increase of potential predation, as the individual is not only advertising himself to females, but also to any predators within earshot.

A population genetics model can theoretically assess the pay offs of displaying to a breeding male, comparing fecundity advantage (+) with viability cost (-), e.g. higher calling males may attract more females, but they may also experience higher predation or a slower growth rate due to reduced energy reserves.

Each species has its own characteristic 'voice', but generally smaller anurans have shriller tones. Call similarities in genetically close species have also been observed across anurans. Generally four call types are used; aggressive calls, release calls, courtship calls, and advertisement calls. Some species have been noted to use more than one advertisement call, for example Hyla regilla (Pacific Treefrog), however most use just one species-specific call, ranging from 'melodious drones' to 'metallic clang' to 'birdlike notes' (Kingsley Noble,

1931). Researchers have used a range of synthetic sounds containing certain sets of acoustical properties similar to those of their species to determine the properties that initiate response. The females were played these synthetic calls and their responses recorded, and changes were made in the number, frequency and amplitude of the 'calls'. They seemed to show that most females show a significant preference for lower frequency calls, although the reason for which is still under discussion. Logically, it was thought that high frequency calls would be selected for more often as this would prove the male easier to locate by the female. One anomaly also to be addressed is the fact that there seems to be no correlation between body size and call frequency, disproving the theory that lower frequency calls are preferred because they usually advertise for larger males. This was tested on *Dendrobates pumilio* (Strawberry Poison Frogs) (Prohl, 2003). It is possible that the females are simply attracted to calls containing higher energy levels, in regard to both frequency and calls produced per unit time (Ryan, 1988).

Call Duration x Calling Rate = Total Time Spent Calling (Sullivan, Kwiatkowski, 2007), therefore when an upper energetic limit it reached, an increase in call duration must be accompanied by a decrease in call rate, and vice versa. This ties in with males using energetically-expensive displays to communicate their overall fitness to females. One theory put forward is that the lower frequency preference is due to male-male interactions, frequency being an assessment of fighting ability – the lower frequency the higher the ability. This would prove the male more able to hold territory, and have a higher overall fitness. However, more research is needed on female mate-search patterns to better understand the mechanism at work here.

One uncontrollable environmental factor that may contribute to the steady intra-population variability is the constant background noise level in the forest, or natural habitat of the anuran. This will vary over time and space, therefore certain frequencies of calls will be optimum at certain times, allowing males with a range of call frequencies to mate successfully.

Hormones regulate many aspects of vocal behaviours in anurans, ranging from the development of physiological structures and neuronal circuitry to the development of species-specific modulations. There are 3 important areas in the brain with regard to vocalizations; the preoptic area, the medulla-midbrain junction, and the medulla-spinal cord junction (Schmidt, 1973). The preoptic nucleus in the Thalamus is thought to be functionally divided into units, each activating a different aspect of mating behaviour. These areas are thought to contain important hormone receptors which project to and activate other vocal mechanisms in the brain. These hormones may play a part in the seasonal changes that occur in vocalizations, particularly by fluctuating levels of androgens in males as shown in Rana pipiens (Northern Leopard Frog) Auditory midbrain (Goense, Feng, 2005). Testicular androgens trigger a masculinising of the physiological structures that produce calls in males, such as the larynx. Levels of this hormone are also controlled environmentally, as it has been shown in Rana catesbeiana (Bull Frog) that levels in males that have been exposed to other vocal mature males is higher than that of males kept in auditory isolation (Moore, Boyd, Kelley, 2005). The number of responsive neurones also fluctuates seasonally; possibly a reaction to hormonal control, as does individual neural thresholds. The number of recruited neurones seems to be lower in the winter months, corresponding to hibernation and lack of output or stimulus. Neuronal stimulation parameters are also shifted seasonally – the number of neurones sensitive to lower frequency sounds was at its lowest during the winter months and rose progressively from summer to autumn, and the number of neurones sensitive to medium frequencies fell over the summer breeding season. This ties in with female preference for lower calls discussed earlier, but still does not explain the primary reason.

Certain processing areas work in harmony to assess calls and recognise species:

- It has been found in R. pipiens that calling can be induced by administering hormones to the anterior

preoptic nucleus, demonstrating that this area in the auditory midbrain is heavily involved in triggering call production (Goense, Feng, 2005).

- The torus semicirculus has also been shown to be essential for call assessment and selection in reproductively active Hyla versicolour (Grey Treefrogs) (Endepols et al, 2003).
- The Central Thalamic nucleus is sensitive to temporal features of calls in H. versicolour, e.g. repetition rate.
- The Posterior Thalamic nucleus is sensitive to a calls specific frequency, or sound spectrum.

It has been suggested that the thalamic nuclei are more involved with motivation and receptiveness to calls rather than overall recognition. This is thought to possibly involve the endocrine system, which triggers female ovulation and raises neural activity in the midbrain, heightening thalamic sensitivity to certain call properties. Once into breeding season, receiving appropriate advertisement calls strengthens the neural pathways, increasing each individuals territorial and species recognition abilities

Experiments with Metaphrynella sundana (Tree-Hole Frog) have shown individual males varied their calls over a general range of frequencies of 250kHz, with the most extreme individuals ranging over 383kHz (Lardner, Lakim, 2004). The experiment also showed a within-population variation of 1200kHz, which obviously, considering the previous data, cannot be attributed solely to individual variation. Could this range be a result of differences in the morphology of anuran vocal apparatus, rather than a difference in body size? If this is so, there must be an optimal frequency for which calling energy output by each individual male is minimized. As it has been shown that females show a preference for males with higher call energy outputs, lower frequencies, and higher number of calls produced per unit time, this must restrict the range at which an individual is at his most attractive, and therefore contribute to intra-population variation.

The underlying mechanism may also lie with the female and her inner-ear. All anurans use 2 separate structures for auditory reception; the basilar papilla, which detects high-frequency waves, and the amphibian papilla, which detects low-frequency waves. It has been shown with Rana catesbeiana (Bull Frogs) that females will only recognise a mating call if both of these receptors are stimulated, but to a different degree in each individual. Therefore a variation in frequency combination preference remains within the female population, which keeps the call variation within the male population. This morphological variation is also more pronounced between species, maintaining reproductive isolation among genetically or spacially close groups, and may have even contributed to speeding up the process of speciation, as “factors that have influenced the evolutionary divergence of courtship signals should also influence the rate at which new species have arisen” (Ryan, 1986). This can be shown in Scaphiopus couchi (Spadefoot Toad), which lacks a group of the VIIIth cranial nerve fibers that innervate the basilar papilla, meaning the neural pathway to allow the animal to perceive middle-frequency sounds is absent. This has resulted in a restriction of the accepted frequency range within calls in this species, significantly reducing the amount of individual range and within-species variation (Ryan, 1986).

During the end of Autumn, the inducing of mating calls is partly prompted by the ripening of the gonads. This shifts the hormonal balance, causing some species to begin calling persistently. However, not all individuals will go through this process at the same rate, being the reason why the reinforcing influence of sound was greatest during the breeding season, with the initial calls stimulating the whole chorus and colony.

The condition of the male at the end of the breeding season can depend on energy reserves used throughout the season, which is associated with advertisement calls as metabolic energy is coupled to acoustic energy inefficiently. This effect was also observed in R.catesbeiana and Bufo rangeri, as male mass actually declined throughout the breeding season. This limiting factor for a male’s calling ability and therefore fitness, called Endurance Rivalry, can produce sexual dimorphism as seen in Eleutherodactylus coqui (Caribbean Tree Frog).

However, we must remember that any physiological characteristic evolves under a variety of selective forces, and selection for increased energy input into calling could be opposed by any number of other pressures. The fact that female preference has induced such an energetically expensive trait to become so important has, in itself, decreased the male's ability to survive. The question is, why would certain traits become so popular if they have such a detrimental affect? Two theories are in circulation; the good genes theory, and the runaway sexual selection hypothesis. The good genes theory speculates that the calling trait has co-evolved with other 'good genes', such as increased foraging ability, competitive ability, or any factor that leads to increased survivorship, which are passed onto the offspring. The runaway sexual selection theory states that the trait has simply evolved through linkage of female preference to selection of male trait without any genetic selection advantage to the offspring. It may have been possible for this to happen if the female inner ear was tuned to certain frequencies for reasons other than for mating calls, e.g. the more complex the inner ear and a greater range of frequency sensitivity might allow the individual to perceive more of its environment, including potential predators and prey. Also, it is crucial in species that breed collectively or in leks for males to give females directional information through other complex habitat sounds. This is because males do not recognise females, females approach the males and initiate mating. The runaway sexual selection theory seems to be the favoured hypothesis presently, as discussed earlier call frequency showed no correlation to male body size, and the female preference actually decreases survivorship of males.

Future work to expand our understanding on this topic should include forming definitions of cost in relation to male mating displays, and researching theories that female choice may be based on or influenced by multiple male characteristics.

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