Sexual Selection and Communication in Frogs

Michael J. Ryan

Anuran communication has been a useful model for understanding behavioral and neural aspects of species recognition. By extending this paradigm to intraspecific mate choice, and by supplementing it with studies of phylogenetics, some new advances have been made in understanding sexual selection.

> . . . to speak of music, when applied to the discordant and overwhelming sounds emitted by male bull-frogs and some other species, seems, according to our taste, a singularly inappropriate expression.

Darwin[1], it seems, had little appreciation for frog calls. However, the devotion with which male frogs pursue their incessant, nocturnal serenade betrays a singularly important motivation – whether through attracting females or dominating other males, in most cases calling frogs are attempting to mate. This communication system has recently become a focus of studies investigating Darwin's notion that sexual selection can be an important factor in evolution even when it opposes natural selection. Here, I summarize some recent advances made during the last few years in studies of anuran sexual selection and communication.

Mating in frogs

By virtue of their amphibious nature, most frogs are at least partially terrestrial but are obliged to return to the water for reproduction. At the breeding site, males can maintain territories or interindividual distances, which commonly are mediated by vocalizations. But above all, males used sound to attract females. Not any sound will suffice. Most frogs produce a species-specific advertisement call, and females prefer conspecific to heterospecific calls. The ability to elicit female phonotaxis with artificial stimuli has allowed a detailed analysis of the acoustic properties involved in call recognition[2], and studies of advertisement calls as species-isolating mechanisms, initiated by Blair[3], have made important contributions to concepts of speciation and reproductive character displacement.

There have been intensive investigations of the receiver as well as the signal. Capranica[4] and his colleagues initiated a series of studies demonstrating how the auditory system decodes species-specific information in the male's advertisement call. Thus, the function of the anuran communication system in conspecific mate recognition is well documented, and has been addressed at levels of evolution, behavioral function and neural mechanisms. By extending studies of the anuran communication system to intraspecific mate choice[5], new advances are also being made in understanding sexual selection.

Issues in sexual selection

Although throughout its history sexual selection has been controversial[6–8], its basic tenet is clear. Sexual selection can favor traits that enhance an individual's ability to acquire mates even if these traits decrease survivorship. This hypothesis has given rise to three basic questions: Why are females attracted to some mates rather than others? How do males increase their attractiveness to females? How do males compete directly with other males for access to females? These basic questions have engendered more complex and subtle issues[6–8]; nevertheless, we can use them as guideposts for reviewing recent advances in anuran sexual selection and communication.

Mechanisms of female mating preferences

Some insights into the mechanisms of female preferences involved in sexual selection have come from identifying specific acoustic properties that elicit phonotaxis and characterizing the neural properties underlying call preferences.

In a recent summary of much of his own data on mating preferences in treefrogs, Gerhardt[9] compared the extent of intraspecific variation in call properties to the magnitude and direction of female preferences. In general, properties with extensive variation among and within individuals elicited strong directional and sometimes open-ended preferences. For example, in the gray treefrog (*Hyla versicolor*), call duration was very variable and females preferred calls of greater duration, even those that surpassed the range exhibited by the species. Also, females always preferred the variant of greater magnitude. On the other hand, relatively invariable call properties were correlated with female preferences for values near the mean, or if there was directional selection its magnitude was much less than for variable properties (Fig. 1). These results give some important insights: first, directional selection might be more extreme on variable call properties, which often do not encode species identity; second, females often prefer traits of greater magnitude; and third, despite strong directional selection, some traits maintain considerable variation.

Another approach that has contributed to understanding mechanisms of female preference comes from combining phonotaxis experiments with investigations of auditory neurophysiology. Capranica[4] showed that spectral properties of the advertisement call are matched to the tuning properties of one or both of the two peripheral auditory end organs, the amphibian (AP) and basilar papillae (BP), which are most sensitive to lower and higher frequencies, respectively. This congruence occurs between the two advertisement-call components and the two inner-ear organs of the túngara frog (*Physalaemus pustulosus*). The dominant frequency of the whine, which is necessary and sufficient for species recognition, is fairly well matched to the most sensitive frequency of the AP, while the dominant frequency of the chuck is close to the most sensitive frequency of the BP[10]. However, there

Michael Ryan is at the Dept of Zoology, University of Texas, Austin, TX 78712, USA, and the Smithsonian Tropical Research Institute, Balboa, Panama.

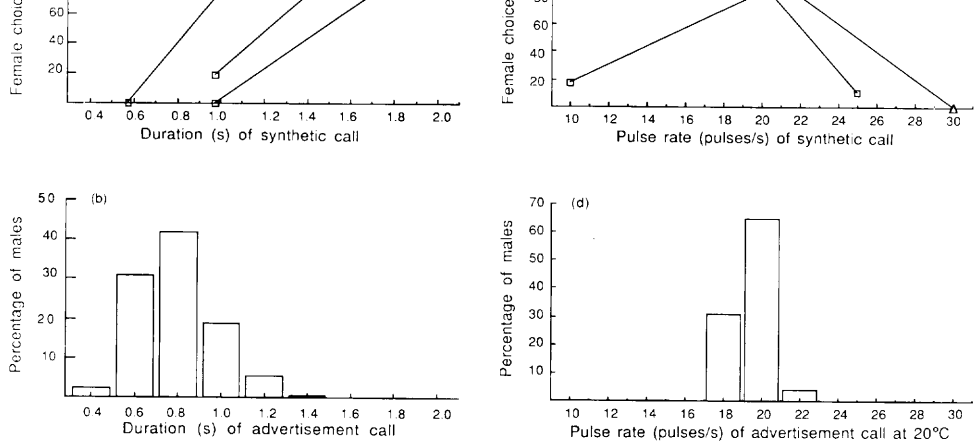

Fig. 1. Female preference for call duration (a) and pulse rate (c) and the distribution of each trait (b and d respectively) in a population (n = 168) of gray treefrogs (*Hyla versicolor*) in central Missouri. Females were given a choice between the standard (near the population mean) call versus an alternative call. Stimuli are represented by a box and each stimulus pair is connected by a line. The proportion of females preferring each stimulus is shown. The standard call had a pulse rate of 20 pulses per second and a duration of 0.84 s. For pulse rate, the triangles represent an experiment in which the standard call was 6 dB less than the alternative. *From Ref. 9.*

is a slight mismatch between the average chuck (2500 Hz) and BP (2100 Hz) frequencies; this mismatch could be responsible for the female preference for lower-frequency chucks[11] (Fig. 2).

A similar phenomenon is apparent in two other frogs. Gerhardt and Doherty[12] have shown that in *H. versicolor* the most preferred call is slightly below the average call and this preference also coincides with the tuning properties of the auditory periphery. In cricket frogs (*Acris crepitans*), populations differ in both the tuning of the BP and the dominant frequency of the advertisement call independent of body size. Within each population studied, females are tuned lower than the average call's dominant frequency. In examining preferences between populations, Ryan *et al.*[13] demonstrated that females sometimes preferred the local call and sometimes the foreign call, but if there was a preference it was always for the lower-frequency call.

These studies show that in frogs the neural basis of preferences can be elucidated, permitting a detailed understanding of how preferences work. Of course, these studies by themselves do not explain why females have certain preferences or certain tuning properties. But, as I next discuss, studies of frogs have made worthwhile contributions to this aspect of sexual selection as well.

Evolution of female mating preferences

Selection should favor mating preferences that have an immediate effect on the female's reproductive success, as might be the case when males provide oviposition sites[14] or paternal care[15]. Frog studies have revealed another form of direct selection – fertilization success. In *Bufo bufo*[16], *P. pustulosus*[11], *Rana temporaria*[17] and *Uperoleia laevigata* (= *rugosa*)[18], the relationship between the size of mated individuals influences fertilization success. Some of these studies are restricted to the laboratory, however, and it cannot be assumed that similar effects always occur in nature.

The question of why female preferences should evolve when there is no direct selection on mating preferences has been controversial[6–8]. One class of hypotheses, good genes, suggests that females should select traits that are indicative of heritable variation in viability. Investigations of parasites, larval survivorship and kin relationships suggest that testing good-genes hypotheses might be tractable in anurans.

One good-genes model, the parasite model of Hamilton and Zuk[19], suggests that male traits will be favored by females if they are indicative of heritable parasite resistance. Recent tests of some predictions of the parasite model with *H. versicolor*[20] and *Scaphiopus couchii*[21] showed no consistent relationship between male mating success and parasite load. Other tests of good genes focus on larval performance. In *Bufo woodhousii*, offspring of large males exhibited a larger size at metamorphosis; studies in the same population over five years show that larger males mate more often but it is not known if female mate choice operates[22]. Also in *Scaphiopus multiplicatus*[23], *S. couchii*[24] and *Hyla crucifer*[25], sire size can be related to larval characteristics that might indicate viability advantages. As these authors indicate, however, the support these data lend the good-genes hypothesis is tempered by uncertainty about whether these larval traits reflect greater viability over the lifetime, especially since some traits favoured by viability selection, such as shorter developmental time and larger size, are probably negatively correlated.

A less-discussed good-genes hypothesis is preference for genetic compatibility. Preference for conspecifics over heterospecifics results in adaptive assortative mating by genotype, but some researchers have suggested that intraspecific mate choice might also be mediated by genetic relatedness. Waldman[26] has documented 'incest avoidance' in mating patterns of *Bufo americanus*, when relatedness is estimated by the overall similarity of mitochondrial DNA haplotypes. Intriguingly, using DNA fingerprints he also reported that variation in several call properties is significantly correlated with genetic relatedness, as estimated by the number of shared fingerprint bands. This suggests the hypothesis that female mate choice might be mediated by call properties that indicate genealogy.

Good-genes models, as well as models of fisherian runaway sexual selection, require that male traits and female preferences coevolve[6–8]. An alternative is that males evolve traits that exploit pre-existing female preferences. This hypothesis, sensory exploitation, can be discriminated from those requiring coevolution because it predicts a specific phylogenetic sequence of preference/trait evolution. Some data supporting this model come from studies of frogs.

As mentioned above, *P. pustulosus* can add chucks to the end of its whine-like call. This is also true of its sister species, *P. petersi*, but not so of the other two species in the *P. pustulosus* species group or in the other 40 or so species in the genus

(Fig. 3). It appears that the chuck evolved once in the common ancestor of *P. pustulosus* and *P. petersi* after this species pair diverged from the other species pair in the group, which consists of *P. coloradorum* and *P. pustulatus* (Fig. 3). We determined whether female *P. coloradorum* would prefer chucks if they were to evolve by adding chucks from the call of *P. pustulosus* to the normal call of *P. coloradorum*. They did. Since *P. coloradorum* and *P. pustulosus* share the preference for chucks, it seems that this trait evolved before these species diverged from one another (Ryan and Rand, unpublished data). If so, this suggests that the preference evolved before the chucks, and that chucks evolved in males to exploit this pre-existing bias. Also, because the tuning of the BP in *P. pustulosus* is the same in *P. coloradorum*, it seems that this trait also existed prior to the evolution of chucks[10]. Therefore, these female characteristics did not coevolve with the chuck; this rejects the role of good-genes and fisherian runaway selection as explanations for the joint expression of preference and trait in *P. pustulosus*.

It is somewhat odd that females would evolve a preference for an acoustic structure as specific as a chuck before that structure has evolved. It only appears odd, however, because we often tend to define a female preference by the extant stimulus that will elicit it. Rand and I[27,28] manipulated the chuck and showed that as long as the total energy remained the same, females were equally attracted to several, but not all, variants; in fact, when the chuck was replaced by a burst of white noise this stimulus was equally attractive. So the pre-existing preference for chucks is a more widely defined preference, and the males happened upon one stimulus that could elicit it.

Sensory exploitation does not eliminate other forces, such as good genes and fisherian runaway, from influencing the evolution of preference. Certain scenarios might still implicate these or other forces in the establishment of the pre-existing bias or in the later maintenance and elaboration of the preferences. However, these studies have provided some insights into the complicated processes by which female preferences might evolve.

Energy costs of male calling

Calling is of paramount importance in acquiring mates, so we would expect sexual selection to influence the evolution not only of the call itself but also of any underlying physiological properties that influence the male's ability to call. Studies of frogs are beginning to provide some tantalizing insights into how sexual selection might influence or be constrained by physiology.

Calling uses a surprising amount of energy, and it also shunts energy from other important biological functions such as growth. This effect has been demonstrated quite clearly in the carpenter frog (*Rana virgatipes*), in which there is a trade-off between growth rate and calling effort for small frogs[29]. This would also suggest that the amount of energy available constrains the amount of calling by males. In an Australian frog, *Uperoleia laevigata*, Robertson[30] showed that calling males lost mass during the breeding season, while noncalling satellite males gained mass. However, the cause and effect relationship between cost of calling and male behavior is not clear.

In *P. pustulosus*, male mating success is strongly influenced by the number of nights calling[11]. Green[31] showed no effect of feeding regime on the amount of calling. But recently in a more detailed study, Marler (unpublished data) showed that males of this species did reduce calling when food availability was reduced. Calling males had higher lipid levels than noncalling males. Using implants, Marler showed that corticosterone inhibits calling and reduces testosterone levels independent of feeding regime. Thus, it is possible that the decreasing food levels induced a stress response, i.e. an increase in corticosterone, which either directly or through its mitigating effects on testosterone levels reduced calling.

In several taxa, sexual selection favors males that call more, and this might have resulted in adaptations at the biochemical and cellular level. Citrate synthase (CS) activity is correlated with the tissue's capacity for aerobic respiration. Trunk muscles are responsible for expelling air in the lungs, and thus generating power for calling. In *Rana virgatipes*, mass-specific CS levels are higher in trunk muscles of males than in hind-limb muscles, and higher than in trunk muscles of females. There is no difference in CS levels between the trunk and hind-limb muscles of females, and between hind-limb muscles in males and females. Also, the calling effort of *R. virgatipes* is lower than that of two hylid species that have been studied (*H. crucifer* and *H. versicolor*) and so is the CS level[32]. These studies support the interpretation of biochemical adaptations as being a response to sexual selection.

Costs of male calling behavior can be accessed easily through studies of behavioral performance, endocrine control mechanisms and cellular and biochemical physiology. Two approaches would be promising: first, more detailed investigations of intraspecific differences in the ability of males to support calling energetically and the behavioral consequences of such differences; and second, rigorous cross-species comparisons documenting inde-

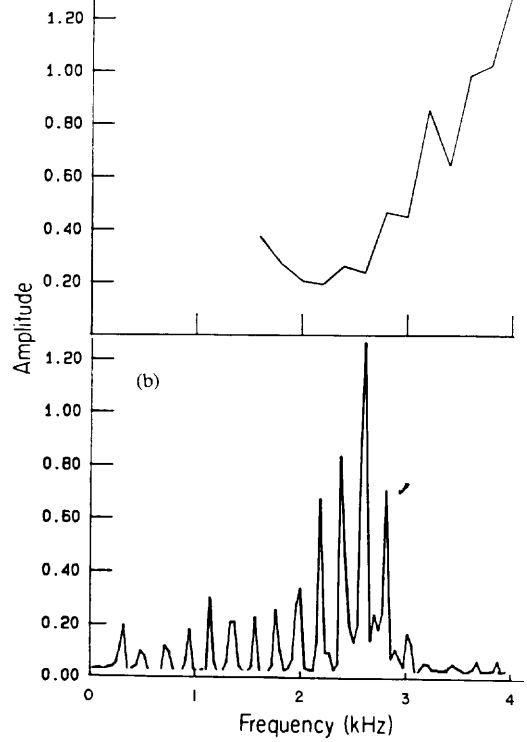

Fig. 2. (a) The mean audiogram of the basilar papilla of *Physalaemus pustulosus* derived from five individuals. Audiograms show the threshold of perception of each frequency. The truncation of the audiogram below 1.5 kHz is to eliminate influences of the amphibian papilla neurons. (b) Representative spectrum of a chuck. *From Ref. 10.*

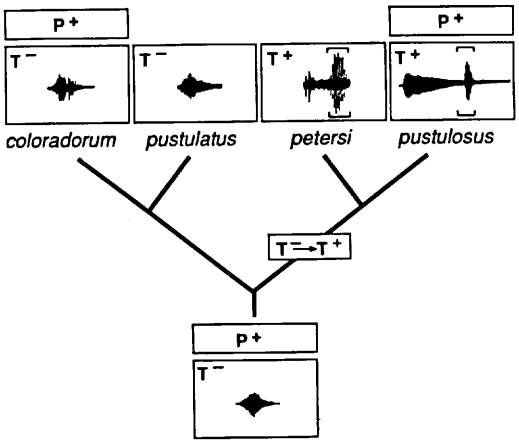

Fig. 3. Male advertisement calls and female preferences in frogs of the *Physalaemus pustulosus* species group. Only the sister species *P. pustulosus* and *P. petersi* add chucks to their calls (square brackets), and so this trait is assumed to have evolved in their immediate common ancestor. Females of both *P. pustulosus* and *P. coloradorum* prefer calls with chucks, from which it is inferred that the common ancestor of all four species had the preference (bottom). The preference for the chuck thus appears to have evolved before the chuck. (T^-, no chuck; T^+, chuck; P^+, female preference for chuck. The oscillogram at the bottom is representative of other species in the genus thought to be closely related to this species group.) *From Ref. 8.*

pendent evolution of physiological adaptations that are correlated with changes in calling behavior.

Male interactions

Vocalizations are also important in mediating male interactions at the breeding site. Recent studies have shown that calls used in male encounters are much less stereotyped than expected, and vary according to social situation.

The dominant frequency of a male's call is determined primarily by the mass of its vocal cords (and tension, in frogs that modulate the carrier frequency); thus, this call parameter was thought to be relatively stable within a male over short periods, and resistant to social influences. It was therefore somewhat unexpected when Lopez *et al.*[33] showed that the white-lipped frog (*Leptodactylus albilabris*) changes its dominant frequency to better match the call frequency of nearby males. A similar phenomenon has been demonstrated in *A. crepitans*. Wagner[34,35] showed that dominant frequency is negatively correlated with male size and that larger males win fights. Males use the opponent's call frequency to assess size and adjust their behavior accordingly. The real surprise is that when confronted with the lower frequency call of a larger opponent, males sometimes lower the dominant frequency of their own call.

Studies of male interactions suggest that frogs might also serve as valuable model systems for other questions besides those relating to sexual selection. For example: Does a graded signal suggest a graded rather than a categorical system of perception? Is variation in the signal indicative of a male's resource-holding potential, fighting ability, motivation or hormonal state? When males vary their signals are they bluffing or giving an honest account of themselves and their intentions?

Prospectus

Studies of sexual selection in anurans continue to contribute to our understanding of how sexual selection influences the evolution of communication systems. The more interesting advances come from addressing this phenomenon at multiple levels of investigation, especially by combining physiology and phylogenetics with studies of behavioral ecology. It is this integration that offers advantages to using frogs as model systems, while other aspects of sexual selection, such as heritability of and genetic correlations between traits and preferences, might be best pursued in other systems such as insects.

Acknowledgements

I thank R. Cocroft, J. Ellingson, C. Gerhardt, C. Marler, W. Wagner, K. Wells and W. Wilczynski for comments on the manuscript.

References

1 Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex*, Random House
2 Gerhardt, H.C. (1988) in *The Evolution of the Amphibian Auditory System* (Fritzsch, B. *et al.*, eds), pp. 455–483, John Wiley & Sons
3 Blair, W.F. (1958) *Am. Nat.* 90, 27–51
4 Capranica, R.R. (1976) in *Frog Neurobiology* (Llinas, R. and Precht, W., eds), pp. 525–575, Springer-Verlag
5 Fritzsch, B., Ryan, M., Wilczynski, W., Hetherington, T. and Walkowiak, W., eds (1988) *The Evolution of the Amphibian Auditory System*, John Wiley & Sons
6 Maynard Smith, J. (1991) *Trends Ecol. Evol.* 6, 146–151
7 Bradbury, J. and Andersson, M.A. (1987) *Sexual Selection: Testing the Alternatives*, Spring-Verlag
8 Kirkpatrick, M. and Ryan, M.J. (1991) *Nature* 350, 33–38
9 Gerhardt, H.C. *Anim. Behav.* (in press)
10 Ryan, M.J., Fox, J.H., Wilczynski, W. and Rand, A.S. (1990) *Nature* 343, 66–67
11 Ryan, M.J. (1985) *The Túngara Frog: A Study in Sexual Selection and Communication*, University of Chicago Press
12 Gerhardt, H.C. and Doherty, J.A. (1988) *J. Comp. Physiol.* 162, 261–278
13 Ryan, M.J., Perrill, S.A. and Wilczynski, W. *Am. Nat.* (in press)
14 Howard, R.D. (1978) *Ecology* 59, 789–798
15 Summers, K. (1989) *Anim. Behav.* 37, 797–805
16 Davies, N.B. and Halliday, T.R. (1977) *Nature* 289, 56–58
17 Gibbons, M.M. and McCarthy, T.K. (1986) *J. Zool.* 209, 579–593
18 Robertson, J.G.M. (1989) *Anim. Behav.* 39, 639–645
19 Hamilton, W.D. and Zuk, M.Z. (1982) *Science* 218, 384–387
20 Hausfater, G., Gerhardt, H.C. and Klump, G. (1990) *Am. Zool.* 30, 299–311
21 Tinsley, R.C. (1990) *Am. Zool.* 30, 313–324
22 Mitchell, S.L. (1990) *Evolution* 44, 502–519
23 Woodward, B.D. (1987) *Oecologia* 73, 626–629
24 Woodward, B.D. (1986) *Am. Nat.* 128, 58–65
25 Woodward, B.D., Travis, J. and Mitchell, S. (1988) *Evolution* 42, 784–794
26 Waldman, B. *Am. Zool.* (in press)
27 Ryan, M.J. and Rand, A.S. (1990) *Evolution* 44, 305–314
28 Rand, A.S., Ryan, M.J. and Wilczynski, W. *Am. Zool.* (in press)
29 Given, M.F. (1988) *Behav. Ecol. Sociobiol.* 22, 153–162
30 Robertson, J.G.M. (1986) *Anim. Behav.* 34, 773–784
31 Green, A.J. (1990) *Anim. Behav.* 39, 620–638
32 Given, M.F. (1990) *Copeia 1990*, 863–867
33 Lopez, P., Narins, P.M., Lewis, E.R. and Moore, J.W. (1988) *Anim. Behav.* 36, 1295–1308
34 Wagner, W.E., Jr (1989) *Behav. Ecol. Sociobiol.* 25, 429–436
35 Wagner, W.E., Jr (1989) *Anim. Behav.* 38, 1025–1038