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FROG VOCALIZATIONS AND SEXUAL SELECTION

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The calls of male frogs and toads given during the breeding season are the principal signals used in courtship by these animals. Early work has clearly shown that frog calls are species-specific, and in experimental tests using natural calls, females can discriminate between species on the basis of differences in fine structural properties of male calls (Bogert, 1960; Blair, 1964). Choice experiments using synthetic (that is, electronically generated) calls have identified exactly what parameters are important for coding species-specificity in certain species (e.g. Gerhardt, 1974).

More recently, attention has turned to the natural variation in call structure which occurs between members of the same species, and it is becoming apparent that the vocalisations of these animals are not as stereotyped as was once thought (Arak, 1983a). Subtle variation in calls encode information about the male signaller which is important in sexual selection (competition between males and mate choice by females). In the neotropical treefrog Hyla ebraccata, pulse rate and rise time of the buzz-like calls provides information about a male's aggressive motivation. Playbacks of synthetic calls in which both pulse rate and rise time were varied indicate that high pulse rate alone is sufficient to elicit aggressive call responses from other males, but calls with both high pulse rates and slow rise times elicit the most aggressive responses (Wells, in preparation). In a Sri Lankan treefrog, Philautus leucorhinus, males defend space in choruses by complex vocal interactions and ultimately by fighting off rival males. The aggressive motivation of a male is signalled by the number of notes in his calls and the total duration of the vocal interaction with a rival male. It is suggested that the level of 'escalation' in a vocal interaction is a graded threat signal, indicating the probability of attack (Arak, 1983b).

In many species, the frequency or pitch of calls is inversely correlated with male body size: larger males have deeper pitch croaks. There is some evidence that this information is used for mate choice by females (Ryan, 1980) and in sexual competition between males (Davies and Halliday, 1978). My work on the natterjack toad (Bufo calamita) has shown that call pitch is an important determinant of male mating success (Arak, 1983c). Natterjack toads breed for several months in spring and during this time males potentially can mate with several females as they arrive at the pond to choose a mate and lay their eggs. In a small population of toads studied in 1980, the most successful male mated with seven different females, whereas two males failed to mate at all. Partial regression analysis showed that, when other variables were controlled for, it was the males with the lowest frequency calls who were most successful.

One interpretation of this result is that female natterjack toads may prefer to mate with large males who produce deeper pitch calls (it is they who make the initial approach to a calling male). However, two-choice playback experiments using synthetic calls of different pitch, failed to show that females have any call pitch preferences.

In contrast, observations and experiments showed that the pitch of a male's call influences the behaviour of other males. Male natterjacks frequently fight for calling sites at the pond's edge and it is the larger males who tend to win these fights. In 56 out of 92 fights the attacking male was larger than the defender ($p < 0.05$, two-tailed binomial test), suggesting that males may use call pitch to assess the size of their calling rivals before attacking them. To test this hypothesis, I played back synthetic calls to males through a small loudspeaker. One low-pitch call (1200 Hz) and one high-pitch call (1800 Hz) were used, representing the largest and smallest males found at the study site, and the calls were broadcast for 5 min at uniform intensity approx. 1 m from each calling male. The proportion of males swimming away from the loudspeaker was significantly greater during playback of low pitch call, whereas the proportion of males attacking (jumping on the loudspeaker) was greater for the high pitch call. This result is consistent with the notion that call pitch is a signal of body size used by males to assess the fighting ability of other callers. Because larger males are better able to defend their calling sites and resist displacement by other males, ultimately they achieve more matings than small males.

The conclusion of this work is that call pitch influences a male's mating success via male-male competition rather than female choice. As evidence accumulates from work on other species, it is becoming clear that active female choice occurs in only a minority of cases and that, in most, observed differences in male vocalizations are likely to have more important consequences on interactions between males (Halliday, 1983).

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