

## Mate choice in the Neotropical frog, *Hyla ebraccata*: sexual selection, mate recognition and signal selection

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It is a truism that animals usually mate with conspecifics. Paterson (1985) has suggested that a specific-mate recognition system ensures this event. This system is described as a set of adaptive signals given between the sexes which ensure recognition (suitable response) of appropriate partners. An analogy Paterson used is the recognition of a specific antigen by a specific antibody. He dismissed any role of mate selection in signal evolution. In contrast, authors who support the concept of sexual selection by mate choice have attempted to distinguish between components of mating signals used in specific-mate recognition (often called 'species recognition') and those involved in mate choice (Verrell 1988; Ryan 1991). This dichotomy is only valid, however, if these components are distinguishable. In this work, we test whether components of a conspecific signal encode species identity, using data from the Neotropical frog, *Hyla ebraccata*.

Three species of hylid frogs, *Hyla ebraccata*, *H. phlebodes* and *H. microcephala* are sympatric in our study area (Gamboa, Republic of Panama). They can commonly be found calling and breeding within centimetres of each other, but neither hybridization nor interspecific clasping has been observed (Fouquette 1960; J. Schwartz, personal communication). Male advertisement calls are apparently sufficient to ensure that mating occurs only between conspecifics.

We recorded advertisement calls of the three species at natural breeding areas near Gamboa using a Sony TCD-5M tape recorder and a Sony ECM-16T microphone (air temperature: 25–26°C). All three species were present at the sites of recording. A typical introductory note for each species

was then digitized on an Amiga 2000 computer (see Fouquette 1960 and Schwartz & Wells 1984 for sonagrams and descriptions of call structure). A noise stimulus was synthesized using white noise with the duration and amplitude envelope of a *H. ebraccata* introductory note (J. Schwartz, sound synthesis program).

Phonotaxis experiments were conducted on 18 gravid female *H. ebraccata* during September and October 1991. Tests were conducted in a 3-m indoor sound arena with an ADS L200C speaker in the centre at each end of the arena. Stimuli were broadcast using an Amiga 2000 computer. The peak sound pressure levels of the stimuli were set at 100 dB at 50 cm (natural *H. ebraccata* call intensity) using a General Radio 1982 sound level meter. Stimuli were broadcast at a rate of 10 calls/min (natural *H. ebraccata* call rate). Arena temperature was between 25 and 26°C. Testing occurred on the night of capture. The female was placed at the centre of the arena under an opaque cone and allowed 2 min to acclimate before the cone was lifted. Females were tested, once each, in up to seven different trials (Table I). The order of the middle five trials was randomized, but the first and last trial were always a choice between a conspecific and heterospecific call (i.e. *H. ebraccata* versus *H. microcephala* or *H. phlebodes*). A positive response was scored if the female approached to within 10 cm of the loudspeaker and turned to face it, or made physical contact with it. Females were allowed 10 min to display a positive response. A 'no response' was scored if the female failed to display a positive response within the allotted time, but responded positively in both her first and last trial.

Female *H. ebraccata* preferentially approached conspecific calls (Table I). If the specific-mate recognition system view is correct, when offered a choice between two heterospecific calls, neither

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**Table 1.** Phonotactic responses of 18 *H. ebraccata* females to conspecific, heterospecific and noise stimuli

Stimulus 1	Number of responses	Stimulus 2	Number of responses	Binomial probability	Number of non-responses
<i>H. ebraccata</i>	14	<i>H. phlebodes</i>	4	*	0
<i>H. ebraccata</i>	10	<i>H. microcephala</i>	0	**	0
<i>H. phlebodes</i>	8	<i>H. microcephala</i>	1	*	9
<i>H. ebraccata</i>	9	Silence	1	*	1
<i>H. phlebodes</i>	8	Silence	1	*	7
<i>H. microcephala</i>	1	Silence	1	—	10
Noise	2	Silence	0	—	10

The binomial probability (two-tailed) refers to female response to the two stimuli.

\* $P < 0.05$ ; \*\* $P < 0.01$ .

call should be recognized, and there should be no preference. In fact, the females showed a significant preference for the call of *H. phlebodes*, indicating that females can discriminate between heterospecifics. Females also responded to the call of *H. phlebodes* when no alternative was available.

In other frogs, females given a conspecific–heterospecific choice also preferentially approach conspecifics. Females will also approach heterospecific calls if conspecific calls are absent (Gerhardt 1988). Our study is the first to show that females can also discriminate between heterospecific calls of sympatric species (but see Gerhardt 1970). Heterospecific calls cannot be uncritically regarded as meaningless noise. Male *H. phlebodes* are included in the pool of potential mates a female *H. ebraccata* recognizes. In *H. ebraccata*, specific-mate recognition probably does not involve an all-or-none response to species-specific signals. Rather, conspecific mating appears to be a consequence of mate choice involving discrimination between conspecifics and heterospecifics.

There is good evidence that female frogs' auditory systems are not only biased towards reception of conspecific signals, but also towards some call variants within the species (Gerhardt 1991). This aspect of female responsiveness is described as a force leading to sexual selection by mate choice. At the mechanistic level, however, there is no distinction between mate (species) recognition and mate selection. They both involve discrimination between potential mates, cause variation in mating success and arise through differential stimulation of the female's sensory system.

Female preferences for intraspecific call variants in frogs have often been documented in laboratory

studies, although preferences are seldom expressed under natural conditions. Random mating in relation to intraspecific call variants is documented in many field studies (Gerhardt 1988). It has been suggested that the complexity of the natural environment constrains the ability of females to act on preferences recorded in phonotaxis experiments (Gerhardt 1991). The commonly observed mating pattern of conspecific mating and random mating within species therefore appears to require only quantum recognition (Paterson 1985). The data, however, do not support this analysis. Our results suggest that females recognize a range of signals extending beyond those of conspecifics. It is only the relative attractiveness of conspecific calls that maintains the pattern of conspecific mating.

Within the range of call variants, there may be a gradient of signals providing increasing levels of stimulation. Along this continuum there is a 'jump' in the level of stimulation provided by heterospecific and conspecific calls, which is effectively responsible for the 'interspecific gap'. There is, however, no difference between mate (species) recognition and mate selection. The process of mate choice is based on a continuous gradient of female responsiveness, while the pattern of reproductive discontinuity between species forms the basis of the operational criteria used to delimit species' boundaries. This should not blind us to the fact that the underlying process of mate choice need not involve species-specific signals.

Despite evidence that mate choice alone can ensure conspecific mating, researchers continue to look for unique signal components involved in species recognition (e.g. Date et al. 1991). These call components are described as products of natural selection, in that their absence results in an inability

to attract mates. Additional components that cause variation in mating success are then viewed as products of sexual selection. The mating signal is therefore seen to consist of some parts that evolved under natural selection (essential components) and others that evolved under sexual selection by female choice (non-essential components). We believe that this distinction is usually untenable. We know of no studies in which the 'essential' components are not manipulable so as to cause variation in mating success, hence sexual selection.

At present, any mating call or behaviour that causes variation in mating success is viewed as a product of sexual selection. This occurs because there is no obvious way to partition a signal into sexually and naturally selected components (Grafen 1987). For example, Butlin et al. (1985) showed that in a grasshopper, *Chorthippus brunneus*, females prefer syllables of the same length as the population mean and described this in terms of stabilizing selection. However, they also suggested that syllable length functions in species recognition. This view effectively leaves no role for natural selection in the evolution of mating signals.

If no meaningful distinction can be made between call components functioning in species recognition and those involved in mate choice, then the only real process is one of mate choice arising from assessment of signals. Sexual selection (historically an explicitly intraspecific process) is an inappropriate description of this force, because mate choice may involve discrimination between males of several species. Zahavi (1991) has recently proposed that a single selection pressure has shaped exaggerated signals, and has labelled it signal selection. We suggest that this view will result in greater clarity. As Zahavi (1991) has noted, the real issue of interest is the evolution of extravagance. Focusing on what a mating call really indicates to the receiver, in terms of the sender's genetic compatibility and phenotype viability, will provide clearer terminology and more appropriate experiments.

Mating with conspecifics does not logically require recognition of species-specific call features.

All it requires is a strong preference for conspecifics. Searching for signal components that function solely in species recognition may often prove a futile task.

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## REFERENCES

- Butlin, R. K., Hewitt, G. M. & Webb, S. F. 1985. Sexual selection for intermediate optimum in *Chorthippus brunneus*. *Anim. Behav.*, **33**, 1281–1292.
- Date, E. M., Lemon, R. E., Weary, D. M. & Richter, A. K. 1991. Species identity by birdsong: discrete and additive information? *Anim. Behav.*, **41**, 111–120.
- Fouquette, M. J. 1960. Isolation mechanisms in three sympatric treefrogs in the canal zone. *Evolution*, **14**, 484–497.
- Gerhardt, H. C. 1970. Selected aspects of the reproductive biology of some Southeastern United States frogs and toads. Ph.D. thesis, University of Texas.
- Gerhardt, H. C. 1988. Acoustic properties used in call recognition by frogs and toads. In: *The Evolution of the Amphibian Auditory System* (Ed. by B. Fritzsche, T. Hethington, M. J. Ryan, W. J. Ryan, W. Wilczynski & W. Walkowiak), pp. 455–483. New York: John Wiley.
- Gerhardt, H. C. 1991. Female mate choice in treefrogs: static and dynamic acoustic criteria. *Anim. Behav.*, **42**, 615–635.
- Grafen, A. 1987. Measuring sexual selection: why bother? In: *Sexual Selection: Testing the Alternatives* (Ed. by J. W. Bradbury & M. B. Andersson), pp. 221–233. Chichester: John Wiley.
- Paterson, H. E. H. 1985. The recognition concept of species. In: *Species and Speciation* (Ed. by E. S. Vrba), pp. 21–29. Pretoria: Transvaal Museum.
- Ryan, M. J. 1991. Sexual selection and communication in frogs. *Trends Ecol. Evol.*, **6**, 351–355.
- Schwartz, J. J. & Wells, K. D. 1984. Interspecific acoustic interactions of the neotropical treefrog, *Hyla ebraccata*. *Behav. Ecol. Sociobiol.*, **14**, 211–224.
- Verrell, P. A. 1988. Stabilizing selection, sexual selection and speciation: a view of specific-mate recognition systems. *Syst. Zool.*, **37**, 209–215.
- Zahavi, A. 1991. On the definition of sexual selection, Fisher's model, and the evolution of waste and of signals in general. *Anim. Behav.*, **42**, 501–503.