



## Interaction between signal timing and signal feature preferences: causes and implications for sexual selection

Gerlinde Höbel\*

Department of Biological Sciences, University of Wisconsin – Milwaukee

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Females often choose their mates based on features of the male's advertisement signal, often preferring louder, deeper, longer, or faster signals. Females of chorusing animals also frequently have preferences for signal timing positions, generally preferring the leading signal. Under natural chorus conditions, females must choose among signals that vary in features as well as relative timing. I conducted playback experiments with female *Hyla cinerea* treefrogs to evaluate whether one type of preference (for attractive signal feature or attractive timing) dominates the overall attractiveness of a signal, or whether different types of preferences can interact. I found that the overall attractiveness of a signal was determined by a combination of timing and feature preferences. The specific signal feature (amplitude, frequency, duration, or rate) was important for the outcome of this interaction effect; signal frequency preferences were very strong and dominated overall signal attractiveness, while signal amplitude, duration or rate preferences were weaker and overall signal attractiveness was largely determined by signal timing preferences. I suggest that preference interactions can result in changes in the dynamics of sexual selection and in the maintenance of variation in signal traits, because males with unattractive signals could gain higher mating success by producing these signals in a leading position, thus weakening or even disrupting feature-based signal selection.

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In many species males aggregate during the breeding season and form choruses or leks (Höglund & Alatalo 1995; Gerhardt & Huber 2002; Greenfield 2002). In such cases, mate-searching females are faced with signalling environments characterized by some level of overlap between the displays of different males. Under these conditions, two types of mate preference come into play: preferences for signal features and preferences for the relative timing of signals. Signal feature preferences are those based on particular parameters of the advertisement signal, for example, preferences for signal duration, rate, frequency, colour or amplitude (reviewed in Gerhardt & Huber 2002; Searcy & Nowicki 2005). Signal timing preferences are those based on the relative timing of the signals of different males (Gerhardt & Huber 2002; Greenfield 2002). Signal timing preferences occur in a wide range of taxa and signal modalities (reviewed in: Gerhardt & Huber 2002; Greenfield 2002; Reaney et al. 2008). It is generally the leading of two signals in close succession that is preferred (Whitney & Krebs 1975; Dyson & Passmore 1988a; Klump & Gerhardt 1992; Grafe

1996; Greenfield et al. 1997; Bosch & Márquez 2002; but see Grafe 1999).

Little is known about the potential interaction between signal feature and signal timing preferences. This is a problem because mate choice often takes place under conditions in which females have to choose between signals that vary in acoustic features as well as in relative timing. A female may encounter situations in which a signal with unattractive features appears in an attractive temporal position, and vice versa. In such cases, there may be interactions between preferences of different types, such that the signal that is most attractive may not necessarily be predictable on the basis of a single type of preference. For example, signal feature preferences may be moderated or even dominated by signal timing preferences, such that males with otherwise unattractive signals may gain higher mating success by producing signals in a leading position. Such interactions have therefore the potential to change the dynamics of sexual selection.

Studies looking for an interaction between signal feature and signal timing preferences have been conducted with few species, but include examples from insects and anurans. This suggests that preference interactions are taxonomically widespread, and thus of potentially great importance for signal selection in group-displaying species in general. So far, interactions between signal

\* Correspondence: G. Höbel, Department of Biological Sciences, University of Wisconsin – Milwaukee, 3209 N. Maryland Ave., Milwaukee, WI 53201, U.S.A.  
 E-mail address: [hoebel@uwm.edu](mailto:hoebel@uwm.edu)

timing preferences and preference for the features amplitude and frequency have been described. The general pattern in anurans and katydid, two groups that have been the focus for studies of sexual selection and communication, seems to be that preferences based on signal amplitude are dominated by signal timing preferences. An amplitude difference of more than 6 dB (that is, twice the signal energy) in favour of the lagging signal is necessary to recapture the feature preference (Dyson & Passmore 1988b; Klump & Gerhardt 1992; Grafe 1996; Snedden & Greenfield 1998; Römer et al. 2002; Fertschai et al. 2007). Signal timing preferences also dominate or at least equalize preferences based on signal frequency in the few anurans tested so far (Dyson & Passmore 1988a; Howard & Palmer 1995; Grafe 1996). Little is known about the effect of signal timing preferences on signal rate preferences (but see Berg & Greenfield 2005), and signal duration preferences have to my knowledge never been examined in this respect. Signal duration preferences are especially problematic because examples of preferences for longer or more frequently repeated signals are particularly prevalent in nature (Ryan & Keddy-Hector 1992; Greenfield 2002), and finding that these feature preferences are affected by signal timing effects and preference interactions could change the expectations for the direction and strength of selection on signals.

The green treefrog, *Hyla cinerea*, presents an ideal opportunity to study the challenges faced by organisms that display and choose mates in dense choruses, where they are confronted with multiple, overlapping signals varying in signal features (e.g. frequency, intensity, duration and repetition rate). I evaluated whether signal timing and signal feature preferences interact with each other, and, if so, what determines overall signal attractiveness. To do this I conducted playback trials with *H. cinerea* females in which I simultaneously varied both signal timing as well as signal features.

First, I evaluated whether different types of preference (feature or timing) interact with each other. If signal feature preferences are key for overall signal attractiveness, then a signal with attractive features should always be preferred, independent of its relative timing. If, on the other hand, signal timing preferences are key for overall attractiveness, then a leading signal should always be preferred, independent of its signal features. If preferences interact, then the attractiveness of a signal feature should vary as a function of the relative timing in which it is presented. For example, a signal that is preferred during alternating signal presentation may become unattractive if it is presented in a lagging position.

If preferences interact, there may be different causes for the interaction. For example, a usually attractive signal with preferred features might lose its attractiveness when it is presented in a lagging position because the signal timing preference (favouring leading signals) dominates the interaction. In this scenario overall signal attractiveness would be determined by the stronger preference (preference strength hypothesis). A signal with normally preferred features might also lose its attractiveness if females become unable to exert signal feature preferences when signals overlap (preference impairment hypothesis). In this scenario, signal overlap, particularly high degrees of signal overlap, impairs a female's ability to perform phonotaxis to the source of a preferred signal. If females have difficulty performing phonotaxis, this should be reflected in the amount of time they take to reach the speaker broadcasting a preferred signal, and the effect should increase as the degree of signal overlap increases. Likewise, difficulties in performing phonotaxis should also be reflected in the frequency at which females reverse course during phonotaxis (i.e. start to walk towards one speaker, then turn around and ultimately approach the other speaker), and the effect should increase as the degree of signal overlap increases.

## METHODS

### *Study Species*

The green treefrog is a common inhabitant of lakes, ponds and swamps in the southeastern United States (Conant & Collins 1998). During spring and summer, males aggregate to advertise for females. Size and density of choruses can vary widely, from a few males spaced far apart to large, dense choruses with hundreds of calling males. Males start calling activity shortly after dark, and continue to signal for 2–4 h each night. The advertisement signal consists of a single pulse, lasting on average 163 ms, which is repeated every 738 ms, and there is considerable geographical variation in these temporal signal parameters (Asquith et al. 1988). The communication system of *H. cinerea* is well studied. Females show preferences for a range of signal features; they prefer average frequency over high-frequency signals (Gerhardt 1974; Höbel & Gerhardt 2003), louder signals, longer signals, and signals produced at higher rates (Gerhardt 1987). Females also show signal timing preferences. If two signals overlap, they prefer the leading of the two signals (Klump & Gerhardt 1992; Höbel & Gerhardt 2007). But as soon as there is a short silent interval between consecutive signals, relative signal timing no longer influences female choice (Höbel & Gerhardt 2007).

### *Study Site*

I conducted trials at Private John Allen National Fish Hatchery, Lee Co., Mississippi, U.S.A., during the field seasons (May–July) of 2001, 2003 and 2005. The average  $\pm$ SD temperature on nights that testing took place was  $20.5 \pm 2.4$  °C. Temperature did not vary significantly between years ( $F_{2,23} = 2.19$ ,  $P = 0.14$ ). I collected pairs in amplexus to ensure that all tested females would be sexually responsive. All females were tested only once with a given signal pair, and there was a time-out period of at least 5 min between different tests. Within tests of a series of females with the same pair of stimuli, I alternated the stimuli between loudspeakers to guard against side biases. I made all behavioural observations under dim red light and released all females at the site of capture within 1 day of being tested. Experimental procedures adhered to the ASAB/ABS Guidelines for the Use of Animals in Research, and were approved by the Animal Care and Use Committee of the University of Missouri (ACUC protocol no. 1910).

### *Playback System*

I tested all females in a two-choice playback design in a portable playback arena set up in the field. The playback arena was 2 m long and 1 m wide. The floor of the arena was a plywood board, the sides 50 cm high wood frames screened with lightweight black cloth. The speakers (RadioShack Optimus XTS-40) were placed 2 m apart, facing each other along the central long axis and just outside the arena. Sound files were broadcast from a laptop computer at a sampling rate of 44.1 kHz, using CoolEdit96 software (Syntrillium Software, Scottsdale, AZ, U.S.A.). The frequency response of the system was flat within  $\pm 2$  dB from 0.4 to 4 kHz. Unless otherwise indicated, the sound pressure level (SPL in dB re. 20  $\mu$ Pa, fast root-mean-square, RMS) of each signal was equalized to 85 dB using a Lutron SL-4001 sound level meter prior to each test.

For testing, I placed females individually in a small round wire cage (10 cm diameter) midway between the loudspeakers. Once the alternative stimuli had been played back for at least five repetitions, I remotely removed the lid of the release box by pulling a string, so that the female could move freely. I scored a positive response once a female touched the cloth in front of the speaker.

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