



# Females prefer leading males: relative call timing and sexual selection in katydid choruses

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## ABSTRACT

Females of several acoustic insects and anurans have recently been shown to orient preferentially to the leading of two identical male calls presented in close succession. We studied this phenomenon via two-choice phonotaxis trials in the neotropical katydid *Neoconocephalus spiza* and found that females avoided male calls occurring during an interval beginning immediately after the onset of a leading call. This avoidance occurred whether or not the following call was overlapped by the leader, indicating that the mechanism of preference for leading calls may represent a psychoacoustic precedence effect rather than simple call masking. We also found that females preferred leading calls as long as the amplitude of the following call was not more than 2 dB higher than the leader. Under certain circumstances, preferences for leading calls remained when females were presented with a sequence of four calls. Thus, preferences for leading calls probably influence a male's attractiveness and mating success in complex natural choruses: females are expected to orient towards males producing leading calls regardless of call length (and the probability of overlapping a following call), when the leading call is up to 1.5 times as distant as a follower, and when succeeded by multiple followers. We suggest that female preferences for leading male calls represent sensory biases that originated in contexts unrelated to sexual selection. None the less they currently play an important role in sexual selection and influence individual male signalling behaviour, and thus chorus structure.

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Males in many species produce conspicuous acoustic signals that function in territorial and sexual advertisement. Because females may discriminate between potential mates based on their sexual advertisement signals, many studies have investigated the potential information content of these signals and their role in intersexual selection (see Searcy & Andersson 1986). This research has concentrated on various aspects of spectral, temporal and energy characters of the signal: variation in these signal characters among males, influences of signal characters on female mate preferences and phenotypic and genotypic correlations between signal characters and other male attributes (see Ryan & Keddy-Hector 1992; Ryan & Rand 1993; Andersson 1994).

In nature, signalling males are often located in close proximity to one another. When close spacing occurs, temporally structured choruses in which neighbouring individuals either alternate or synchronize their calls may result (Greenfield 1994a, b). In these choruses the timing

of a male's calls relative to those of his neighbour(s) may represent an additional signal character critical for female attraction. For example, females in various acoustic insects (e.g. Stiedl 1991; Greenfield & Roizen 1993; Minckley et al 1995; Galliard & Shaw 1996) and anurans (e.g. Dyson & Passmore 1988a; Howard & Palmer 1995; Grafe 1996) prefer leading male calls: given two identical calls presented in close succession, a female usually orients towards the first call. Greenfield & Roizen (1993) and Greenfield et al. (1997) suggest that such preferences are largely responsible for chorus structure: female preference for leading calls selects for males that time their calls such that they most often produce attractive leading signals, and rarely ineffective following calls. The synchronous and alternating choruses observed in nature may emerge as incidental by-products of neighbouring males collectively using these timing mechanisms (Greenfield et al. 1997).

Several mechanisms might be responsible for a female preference for leading calls. For example, the transition from silence to sound at a call's onset may be a critical feature of the call's attractiveness and/or aid localization of its source, and the onset of a following call may simply

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be physically 'masked' by a leading call that overlaps it. Thus, the wavefront of a following call would not reach the (female) receiver in a clear form due to physical interference. Alternatively, a preference for leading calls may represent a 'precedence effect' (sensu Wallach et al. 1949; Zurek 1980; Wyttenbach & Hoy 1993) in which the first of two temporally separated signals to reach an animal suppresses the animal's peripheral or central auditory responses to the second call. Römer et al. (1997) have suggested that precedence effects operate via desensitization of the contralateral receptor during a given interval beginning shortly after the receptor ipsilateral to the leading acoustic stimulus has been activated.

While it is clear that preferences for leading calls may strongly influence how females choose synthetic stimuli and males in controlled two-stimulus experiments, the importance of such preferences in natural field populations is less certain. The extent to which preferences for leading calls override differential call amplitude (but see Dyson & Passmore 1988b) or whether leaders remain preferred when multiple (more than two) males are present are not generally known. These issues are expected to be significant in natural choruses wherein a female may hear several males located at varying distances; that is, a leading call may be succeeded by more than one following call, which may be perceived by a female as louder because the follower(s) are closer to the female. Additionally, we do not generally know whether preferences for leading calls can result from a precedence effect or whether call overlap, resulting in simple, simultaneous masking, is required for this preference to be expressed. In the former case, the leader's relative attractiveness would depend on distances of calling males from the female: owing to differential transmission times of sounds arriving from calling males, the female may not perceive call onsets of a more distant follower as overlapped by a nearby leader. Moreover, a leading male would only enjoy an advantage if it produces relatively long calls, likely to overlap a follower.

Here, we present a study of female preference for leading calls in the neotropical katydid *Neoconocephalus spiza* (Orthoptera: Tettigoniidae). Previous investigation (Greenfield & Roizen 1993) showed that female *N. spiza* prefer the first of two identical calls and that this preference persists when leading calls precede following calls by as little as 12 ms. In the present study we extend this investigation, using two-stimulus playback bioassays, to determine (1) whether the preference for leading calls can reflect a precedence effect rather than simple simultaneous masking and (2) whether the preference for leading calls persists as following calls increase in relative amplitude. We then examine female preference for leading calls in a multistimulus paradigm. Most often studies of female preference for various signal characteristics, including relative call timing, present females with a choice paradigm where females are asked to discriminate between two alternative song models. Here, in an attempt to represent a natural chorus of signalling males better, we examine the more realistic situation where females are faced with a choice between multiple stimuli (males). We examine the strength of female preference for leading

calls when females are presented with multiple signals representing males at varying distances (relative amplitudes) such as they would encounter in natural choruses. *Neoconocephalus spiza* males modify their call rhythm with an inhibitory-resetting mechanism, whereby they refrain from calling immediately after a neighbour to increase their chance of producing a leading call during the next cycle (Greenfield & Roizen 1993). This study examines whether these inhibitory-resetters continue to increase attractiveness to females when their calls are produced in complex natural choruses.

## METHODS

*Neoconocephalus spiza* are coneheaded katydids common in savannas and disturbed habitats throughout lowland Central America (Walker & Greenfield 1983). Males produce rhythmic advertisement calls during both day and night, with peak activity usually occurring from dusk until midnight (Greenfield 1988). The calls consist of chirps 20–70 ms in length, delivered at 1.8–3.6 chirps/s. *Neoconocephalus spiza* chirps are loud, with sound pressure levels (SPLs) of  $\approx 80$  dB at 1 m (0 dB = 20  $\mu$ Pa) and frequencies ranging from 9 to 13 kHz.

We conducted our study at the Smithsonian Tropical Research Institute facility in Gamboa, Panama from December 1995 to January 1996 and December 1996 to January 1997. Late-instar female nymphs were collected in the vicinity of Gamboa from October to December 1995 and November to December 1996. The nymphs were housed in mesh cages 40  $\times$  40  $\times$  40 cm, maintained at ambient photoperiod and temperature (23–28°C). We provided food, grass with seeds and rodent or cat chow ad libitum. The cages housing females were kept isolated from males and male songs at all times. After moulting to the adult, we marked each female with a number on the pronotum. We did not begin testing females in phonotaxis trials until at least 20 days following their adult moult, at which time they become fully sexually mature and phonotactic.

### Phonotaxis Testing

We conducted a series of phonotaxis experiments in a sound-attenuating room, 3  $\times$  3  $\times$  2.5 m, to test various aspects of female preference for leading male calls. All testing was done between 2000 and 0230 hours. The sound room was illuminated with dim red light to facilitate observation while minimizing interference with the insects' orientation, and temperature was maintained at 26°C. Prior to each phonotaxis trial, test females were held in individual cups in a light-proof box acoustically isolated from the sound room. At the beginning of each trial, we placed the test female beneath an inverted funnel on the floor at the centre of the sound room and allowed her to acclimate for several minutes. We then raised the funnel and began playback of stimuli from two or four surrounding loudspeakers. We considered that positive orientation (phonotaxis) towards a loudspeaker occurred if the test female moved to within 10 cm of it

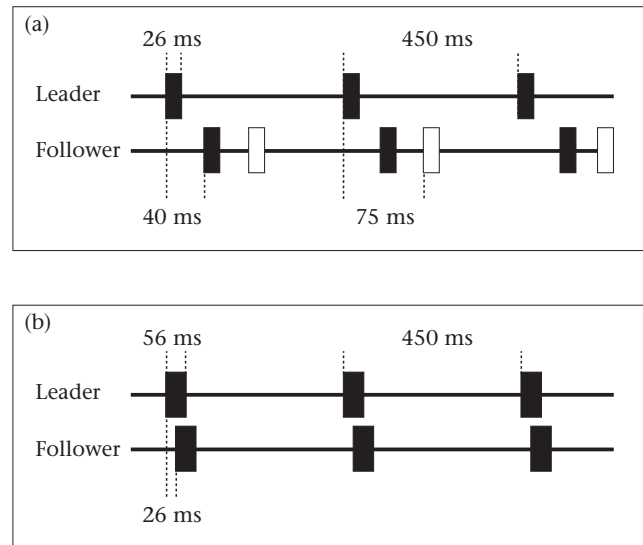
and remained there for at least 30 s. In most cases, females either flew or walked towards a loudspeaker within 1.5 min. Trials were discontinued when the female showed a response or after 5 min. Females were tested up to five times per night (see below), but a minimum of 30 min always elapsed between successive trials of a given individual. Only trials in which the female showed a response are used in the analysis.

All playback stimuli were derived from field tape recordings (Casio model DA-7 stereo digital cassette recorder, sampling frequency 48 kHz; Shure model BG 4.0 condenser microphone, flat response from 40 to 18 000 Hz) of *N. spiza* chirps (recorded when temperature was 26°C). These tape recordings were transferred to a computer via a two channel, 8-bit analog: digital (A:D) input board, digitized at a sampling frequency of 60 kHz, and saved to files. We selected a representative chirp from a file, filtered (high-pass digital filter; cutoff frequency = 7 kHz) a 450-ms block containing that chirp to remove background noise, and then copied the filtered block to a second channel. Using an editing program, we delayed the signal on the second channel by a specific time interval. We then continuously looped this edited two-channel block and, via the computer's D:A output board operating at a sampling frequency of 60 kHz (per channel), transferred 5 min of its repetition back to a tape segment on the digital tape recorder. Thus, we prepared playback stimuli in which identical chirps were repeated every 450 ms on two channels, with a specific delay separating chirps on the left and right channels.

We broadcast playback stimuli to the test female from loudspeakers (RadioShack tweeters) positioned on the sound-room floor and oriented vertically. Thus, stimulus SPL was relatively constant at a given radius from a loudspeaker in all horizontal directions. An amplifier and potentiometer were incorporated in the circuitry of each loudspeaker to allow precise calibration of the broadcast SPL. Using a sound pressure level meter (General Radio model 1982), we measured peak SPLs of the loudspeaker broadcasts of playback chirps each night when phonotaxis trials were conducted. The one-octave bandwidth filter on the SPL meter was centred at 8 kHz, and SPLs were measured at the test female's release point. We then adjusted ( $\pm 0.5$  dB) the loudspeakers to the required levels.

For experiments (1 and 2) in which only two loudspeakers were used, signals were played back from the outputs of the left and right channels of the stereo digital cassette recorder. For experiments (3a, b, and c) in which four loudspeakers were used, the digital cassette recorder and tape were replaced by the computer and 450-ms multichannel files were prepared via custom software (see Minckley et al. 1995). These files were continuously looped, and the signals were transferred directly to the loudspeakers via the eight-channel D:A output board installed in the computer. As above, a sampling frequency of 60 kHz (per channel) was used.

To determine whether a precedence mechanism might operate in this species (experiment 1; see below), we used short nonoverlapping 26-ms chirps, as previous evidence (M. D. Greenfield, unpublished data) suggested that the



**Figure 1.** Schematic representation of the leader–follower signal off-set used in (a) experiment 1a (■) and 1b (□); (b) experiments 2–3c. Signals are identical in spectral, temporal and amplitude envelope characteristics.

interval between calls, referred to as the ‘forbidden interval’ following a call during which females discriminate against following signals, extends to about 70–80 ms. Hence, we used short calls to provide the longest possible call delay without exceeding the forbidden interval. In experiments 2 and 3, designed to examine the strength of the preference for leading calls, we used normal 56-ms chirps, where the leading chirp overlapped the onset of the following chirp, so that the onset of following stimuli (up to three speakers; see below) would not occur outside the forbidden interval.

## Experiment 1

### *Can preference for leading calls reflect a precedence effect rather than masking? Two-speaker playback*

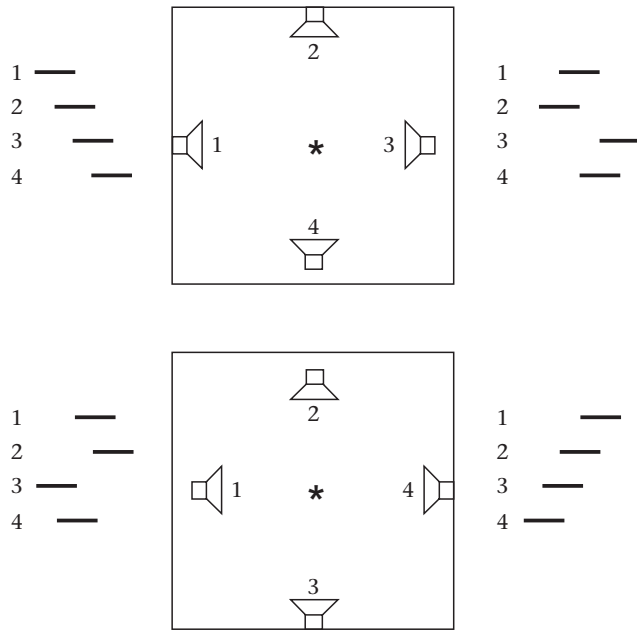
(a) We tested 20 females with playback of short (26-ms) chirps wherein the onset of the following chirp began 40 ms (absolute time) after the onset of the leader (Fig. 1a). We placed the loudspeakers 1.5 m away on opposite sides of the test female's release point. We set the SPLs of chirps from both loudspeakers to 80 dB at 1 m and switched positions of the loudspeakers broadcasting leading and following chirps between successive trials. Because leading chirps did not overlap following ones, female preference for the leading chirps could be construed as evidence of a precedence-effect mechanism.

(b) We tested 17 females as above except that the following chirps were delayed by 75 ms.

## Experiment 2

### *Can preference for leading calls override differential call amplitude? Two-speaker playback*

We tested 27 females with playback of normal (56-ms) chirps, wherein the onset of the following chirp began



**Figure 2.** Schematic representation of the loudspeaker arrangement and call order used in experiment 3a. Signals and off-sets are as in Fig. 1b. Call sequences were presented randomly, and speaker orientation was alternated between successive trials.

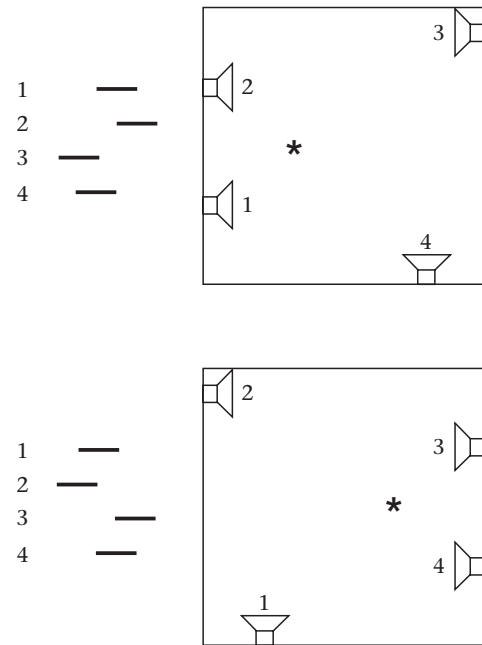
26 ms after the onset of the leader (Fig. 1b). Loudspeakers were situated as in experiment 1. We adjusted the amplitude of the loudspeakers such that there was an SPL differential (leader–follower) between chirps broadcast by the two loudspeakers. We set the SPLs of following chirps to 80 dB at 1 m in all five trials, and the SPL of the leading loudspeaker to +1.5, 0, –2, –4 and –6 dB, relative to the follower, respectively. We employed a randomized block design and tested each female once at each SPL differential.

### Experiment 3

#### *Does preference for leading calls remain when four calls are presented in close succession? Four-speaker playback*

Here we used four loudspeakers presenting calls in a leader–followers relationship at differing amplitude differentials to examine the strength of the preference for leading calls in a simulated chorus of males.

(a) We tested 18 females with playback of 56-ms chirps delivered in a regular sequence from four loudspeakers. The onset of each successive follower occurred 26 ms after the preceding chirp. Thus, the last following chirp began 78 ms after the leader (Fig. 2). We arranged the four loudspeakers such that azimuth angles separating adjacent ones were 90°. We situated the loudspeakers broadcasting the leading and first following chirps 2.0 m from the test female's release point, and those broadcasting the last two chirps 1.0 m from the test female; thus chirps broadcast at 1.0 m would be perceived as 3 dB louder (80 versus 77 dB SPL; Fig. 2). We tested each female four times, switching the directions (but not distances from the female) at which specific loudspeakers were placed between successive trials.



**Figure 3.** Schematic representation of the loudspeaker arrangement and call order used in experiments 3b and 3c. Signals and off-sets are as in Fig. 1b. Call sequence and speaker orientation was alternated between successive trials.

(b) We tested 24 females as in experiment 3a above except that we adjusted the loudspeakers and situated them such that the test female perceived the last two chirps as 4 dB louder than the leader and 2 dB louder than the first follower (76.5 versus 74.5 versus 72.5 dB SPL; Fig. 3).

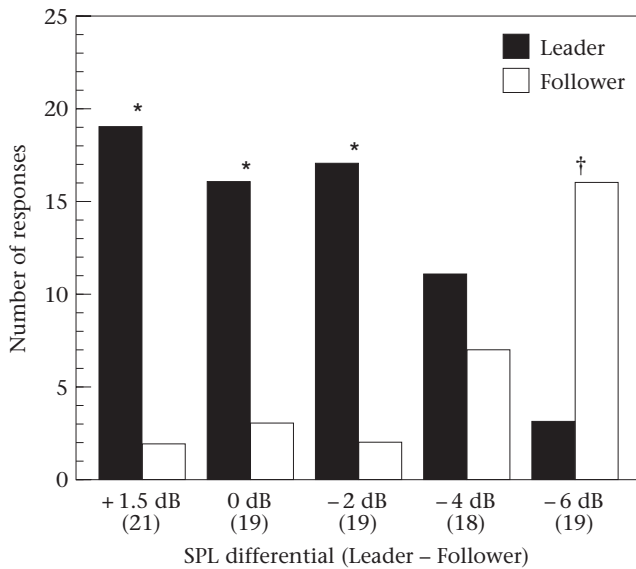
(c) We tested 16 females as in experiment 3b above except that we reduced the broadcast amplitudes of all loudspeakers by 3 dB. Thus, the test female would perceive the chirps as 73.5, 71.5 and 69.5 dB SPL.

In experiment 3, we tested females up to four times each at each stimulus. We calculated the binomial probability of responses to the leading stimulus for each female and then calculated an overall probability following the method of Fisher for combining probabilities (Sokal & Rohlf 1981). Thus, each female contributed only one independent data point to the overall analysis.

## RESULTS

### Experiment 1

In this experiment we asked whether the preference for leading males can result from a precedence effect. Eighteen of 20 females that displayed phonotaxis in trials where the following chirp was delayed by 40 ms, oriented towards the leader (experiment 1a; binomial test:  $P < 0.001$ ). In experiment 1b, however, where the following chirp was delayed by 75 ms, 49 ms after the end of the leading chirp, the preference for the leading calls disappeared: only 9 of 17 females that displayed phonotaxis oriented towards the leader (binomial test: NS).



**Figure 4.** Female orientation to the leading and following loudspeakers in experiment 2. Sound pressure differential is the difference (in dB) between the leading and following loudspeakers. Number of responses denoted by \* and † were significantly different ( $P < 0.01$ ). Numbers in parentheses indicate the number of trials conducted in which a response was observed.

**Experiment 2**

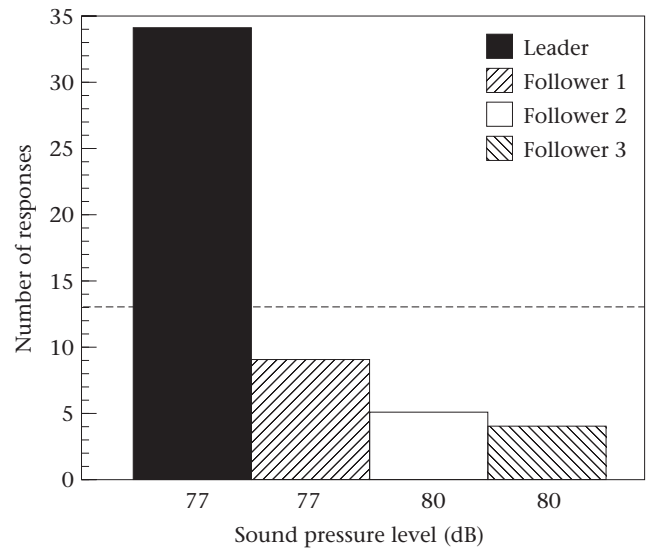
In experiment 2, we examined the strength of the female preference for leading calls versus call amplitude. Test females strongly preferred leading chirps as long as they were not more than 2 dB lower in SPL than following chirps (binomial test: all  $P < 0.01$ ; Fig. 4). When following chirps were 4 dB higher in SPL, females oriented equally towards leading and following chirps (binomial test: NS). When following chirps were presented at 6 dB SPL above leading chirps, females strongly preferred following chirps (binomial test:  $P < 0.05$ ).

**Experiment 3**

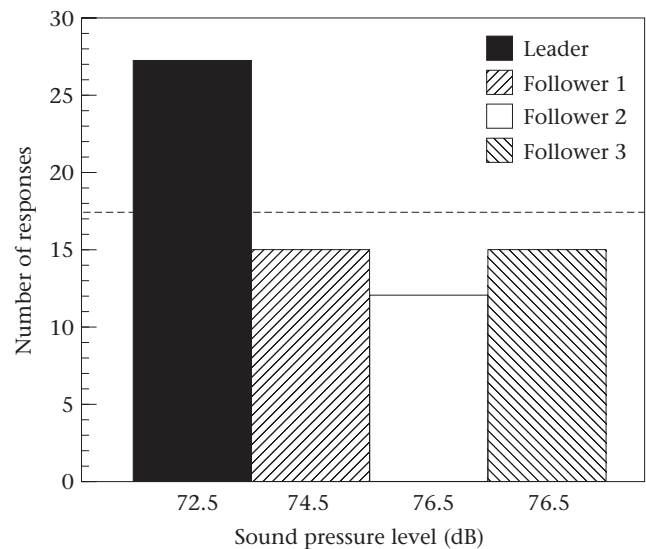
In experiment 3, we examined the strength of the preference for leading calls in a simulated chorus of males. When presented with four chirps, where the leader was broadcast at the same amplitude as the first follower but 3 dB lower in SPL than the second and third followers, females strongly preferred the leading chirp (chi-square test:  $\chi^2_{36} = 80.95$ ,  $P < 0.01$ ; Fig. 5). When relative amplitudes were adjusted such that the SPL of the leader was 2 dB lower than the first follower and 4 dB lower than the second and third followers, females oriented more often to the leader, but this difference was not significant ( $\chi^2_{48} = 52.82$ , NS; Fig. 6). When we reduced the absolute amplitudes of all speakers by 3 dB but used the same relative differentials, females oriented equally towards all of the chirps ( $\chi^2_{32} = 26.14$ , NS; Fig. 7).

**DISCUSSION**

Results from experiment 1a indicate that female preferences for leading calls in *N. spiza* can result from a

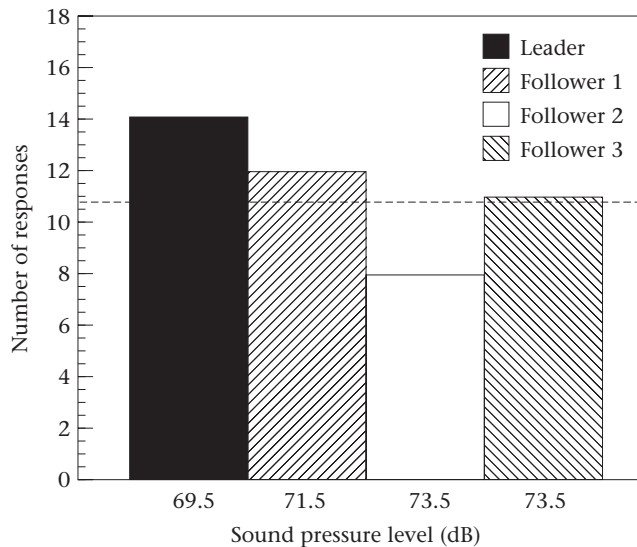


**Figure 5.** Orientation of females to each of the four loudspeakers in experiment 3a. The dashed line indicates the expected responses to each loudspeaker if females orient without regard to call order. Females oriented to the leading call significantly more ( $P < 0.001$ ) than expected if call order was disregarded. Sound pressure levels (dB) for each loudspeaker varied relative to the release point of the females (see Fig. 2). Data are from the 45 trials in which a response was observed.



**Figure 6.** Orientation of females to each of the four loudspeakers in experiment 3b. The dashed line indicates the expected responses to each speaker if females oriented without regard to call order. Orientation towards the loudspeaker broadcasting the leading call was greater than that towards any other loudspeaker, but this difference was not significant ( $P > 0.05$ ). Sound pressure levels (dB) for each loudspeaker varied relative to the release point of the females (see Fig. 3). Data are from the 75 trials in which a response was observed.

precedence effect rather than, or in addition to, simple masking of the onsets of following calls. Because following chirps did not begin until 14 ms after the end of the leading chirps, female preference for leading calls in



**Figure 7.** Orientation of females to each of the four loudspeakers in experiment 3c. The dashed line indicates the expected responses to each loudspeaker if females orient without regard to call order. Females oriented without regard for call order ( $P > 0.05$ ). Sound pressure levels (dB) for each loudspeaker varied relative to the release point of the females (see Fig. 3). Data are from the 58 trials in which a response was observed.

*N. spiza* does not necessarily depend on the masking of the onsets of following calls. Thus, any call occurring during a critical interval beginning shortly after the onset of the leading call is discriminated against whether or not it is overlapped. Both masking and precedence may occur in this species, depending on the degree of call overlap, and both mechanisms may be responsible for the observed preference for leading calls.

Results from experiment 1b indicate that the critical interval is shorter than 75 ms, whereas those from the four-loudspeaker playback in experiment 3a suggest that the critical interval extends for at least 80 ms, nearly 20% of an average call period. Consequently, males that produce leading calls should remain attractive even when their calls are relatively short and unlikely to overlap a follower (see also Greenfield & Roizen 1993).

Results from experiment 2 indicate that when perceived SPLs are 75–80 dB, females do not orient towards following calls whose perceived SPLs are 2–4 dB greater than leading calls: female preferences for leading calls in *N. spiza* can override this amplitude differential. This assumes that females are able to resolve a 2-dB SPL differential between equivalent signals: our results clearly show they can discriminate a differential of at least 4 dB. Thus, assuming equivalent absolute SPLs among males, females would be expected to orient towards males producing leading calls even when such males are located 1.5 times as distant as a follower (given the attenuation of the call with distance, assuming only spreading loss). In a naturally occurring chorus, females may therefore actively select males producing leading calls, rather than simply approaching those males that happen to be closest and encountered first by chance alone.

Results from experiments 3a and 3b indicate that female preference for leading calls in *N. spiza* persists when more than one call follows during the critical interval and certain amplitude differentials are not exceeded. This and the above findings suggest that the female preference for leading signals may represent a significant factor in complex natural choruses. Male *N. spiza* in natural populations should benefit from inhibitory-resetting, which increases the incidence of their leading calls, just as a loudspeaker producing leading calls attracts more females in a controlled, two-choice laboratory experiment.

The results of our multiloudspeaker trials suggest that the female preference for the leader in a sequence of multiple calls depends on absolute as well as relative SPLs of the calls (experiment 3c): the preference appears to diminish at lower SPLs, possibly owing to a decreased ability of the (weakened) leading call to suppress or inhibit the contralateral receptor (Römer et al. 1997). Thus, in a natural chorus females may orient towards the leader of several males only when males are aggregated within an area defined by a certain SPL above the female auditory threshold. The female preference for leading calls would then have a reduced selective impact on male signalling behaviour if males were widely dispersed in space. Field data on the distribution of male *N. spiza* suggest that signalling males are often aggregated such that their calls would be perceived by females within the area at higher SPLs than those used in our trials (unpublished data).

By selecting a leader, a female might orient more than 1.5 times as far as she would if she selected the loudest (nearest) male. This excess orientation distance may not be crucial over short distances, but it may represent a significant increase in risk (see Forsgren 1992; Hedrick & Dill 1993; Grafe 1997) when the males are further away and perceived at lower SPLs. Consequently, we may ask whether the observed reduction in preference for leading calls at lower SPLs is adaptive.

Why do females prefer leading calls at all? Females in many acoustic insects and anurans discriminate between potential mates on the basis of their calls (e.g. Ryan 1985; Hedrick 1986; Zuk 1987; Sullivan & Hinshaw 1992; Ritchie et al. 1995; Brown et al. 1996), and they may benefit 'directly' or 'indirectly' (sensu Kirkpatrick & Ryan 1991) from such discrimination. However, leading calls do not differ from following ones in any intrinsic physical character, and it is difficult to attribute any benefit(s) accruing from a preference for leading males. We suggest that the observed preference for leading calls is unlikely to have evolved to allow females to discern leading males per se, rather it may simply represent conservative elements in sensory design that evolved in (adaptive) contexts unrelated to intersexual selection. For example, receivers might locate sound sources such as predators or prey more easily or suppress responses to echoes by avoiding following stimuli (see Wyttenbach & Hoy 1993). Natural selection should then favour such a mechanism especially if females using such a mechanism reduce search costs associated with localizing a mate. Given that females do prefer leading calls, males should be selected

to avoid placing their calls shortly after those of their competitors, and chorusing males appear to have evolved specialized inhibitory-resetting mechanisms in response to these receiver biases (Greenfield et al. 1997). Once these mechanisms arise, precedence effects in female choice might be selectively maintained by a feedback loop: males that call at faster rates, a signal character often favoured by females (see Ryan & Keddy-Hector 1992; Johnstone 1995), and possibly correlated with direct or indirect benefits, are also those expected to produce more leading calls as a result of inhibition of slower signallers. Precedence effects, in conjunction with inhibitory-resetting, might be a means by which females reliably discriminate rapid callers in complex natural choruses. However, males of a grasshopper (Snedden et al.), a katydid (W. A. Snedden & M. G. Ritchie, unpublished data), and a frog (W. A. Snedden & A. S. Rand, unpublished data) show selective attention: males interact only with one or two of the competitors within their acoustic range. Thus, if precedence effects function (in part) to allow females to pick faster males out of a group, it could only be effective at low density. Irrespective of the evolved function, female precedence effects will result in sexual selection pressure on males, and hence influence their signal interactions and resultant chorus structure.

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### References

- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Brown, W. D., Wideman, J., Andrade, M. C. B., Mason, A. C. & Gwynne, D. T. 1996. Female choice for an indicator of male size in the song of the black-horned tree cricket, *Oecanthus nigricornis* (Orthoptera: Gryllidae: Oecanthinae). *Evolution*, **50**, 2400–2411.
- Dyson, M. L. & Passmore, N. I. 1988a. The combined effect of intensity and the temporal relationship of stimuli on phonotaxis in female painted reed frogs *Hyperolius marmoratus*. *Animal Behaviour*, **36**, 1555–1556.
- Dyson, M. L. & Passmore, N. I. 1988b. Two-choice phonotaxis in *Hyperolius marmoratus* (Anura: Hyperoliidae): the effect of temporal variation in presented stimuli. *Animal Behaviour*, **36**, 648–652.
- Forsgren, E. 1992. Predation risk affects mate choice in a gobiid fish. *American Naturalist*, **140**, 1041–1049.
- Galliard, P. L. & Shaw, K. C. 1996. The effects of variation in parameters of the male calling song of the katydid, *Amblycorpha parvipennis* (Orthoptera: Tettigoniidae), on female phonotaxis and phonoresponse. *Journal of Insect Behavior*, **9**, 841–856.
- Grafe, T. U. 1996. The function of call alternation in the African reed frog *Hyperolius marmoratus*: precise call alternation prevents auditory masking. *Behavioral Ecology and Sociobiology*, **38**, 149–158.
- Grafe, T. U. 1997. Costs and benefits of mate choice in the lek-breeding reed frog, *Hyperolius marmoratus*. *Animal Behaviour*, **53**, 1103–1117.
- Greenfield, M. D. 1988. Interspecific acoustic interactions among katydids *Neoconocephalus*: inhibition-induced shifts in diel periodicity. *Animal Behaviour*, **36**, 684–695.
- Greenfield, M. D. 1994a. Cooperation and conflict in the evolution of signal interactions. *Annual Review of Ecology and Systematics*, **25**, 97–126.
- Greenfield, M. D. 1994b. Synchronous and alternating choruses in insects and anurans: common mechanisms and diverse functions. *American Zoologist*, **34**, 605–615.
- Greenfield, M. D. & Roizen, I. 1993. Katydid synchronous chorusing is an evolutionary stable outcome of female choice. *Nature*, **364**, 618–620.
- Greenfield, M. D., Tourtellot, M. K. & Snedden, W. A. 1997. Precedence effects and the evolution of chorusing. *Proceedings of the Royal Society of London, Series B*, **264**, 1355–1361.
- Hedrick, A. V. 1986. Female preferences for male calling bout duration in a field cricket. *Behavioral Ecology and Sociobiology*, **19**, 73–77.
- Hedrick, A. V. & Dill, L. 1993. Mate choice by female crickets is influenced by predation risk. *Animal Behaviour*, **46**, 193–196.
- Howard, R. D. & Palmer, J. G. 1995. Female choice in *Bufo americanus*: effects of dominant frequency and call order. *Copeia*, **1995**, 212–217.
- Johnstone, R. A. 1995. Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biological Reviews*, **70**, 1–65.
- Kirkpatrick, M. & Ryan, M. J. 1991. The evolution of mating preferences and the paradox of the lek. *Nature*, **350**, 33–38.
- Minckley, R. L., Greenfield, M. D. & Tourtellot, M. K. 1995. Chorus structure in tarbush grasshoppers: inhibition, selective phonoresponse, and signal competition. *Animal Behaviour*, **50**, 579–594.
- Ritchie, M. G., Couzin, I. D. & Snedden, W. A. 1995. What's in a song? Female bushcrickets discriminate against the song of older males. *Proceedings of the Royal Society of London, Series B*, **262**, 21–27.
- Römer, H., Hedwig, B. & Ott, S. 1997. Proximate mechanism of female preference for the leader male in synchronizing bushcrickets (*Mecopoda elongata*). In: *Proceedings of the 25th Goettingen Neurobiology Conference*, vol. II (Ed. by N. Elsner & H. Waessle), p. 322.
- Ryan, M. J. 1985. *The Túngara Frog: a Study in Sexual Selection and Communication*. Chicago: University of Chicago Press.
- Ryan, M. J. & Keddy-Hector, A. 1992. Directional patterns in female mate choice and the role of sensory biases. *American Naturalist Supplement*, **139**, 5–35.
- Ryan, M. J. & Rand, A. S. 1993. Species recognition and sexual selection as a unitary problem in animal communication. *Evolution*, **47**, 647–657.
- Searcy, W. A. & Andersson, M. 1986. Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics*, **17**, 507–533.

- Snedden, W. A., Greenfield, M. D. & Jang, Y. 1998. Mechanisms of selective attention in grasshopper choruses: who listens to whom? *Behavioral Ecology & Sociobiology*, **43**, 59–66.
- Sokal, R. R. & Rohlf, F. J. 1981. *Biometry*. San Francisco: W. H. Freeman.
- Stiedl, O. 1991. Akusto-vibratorische Verhaltensuntersuchungen an Ehippigerinen im Labor und im Biotop. Ph.D. thesis, University of Marburg.
- Sullivan, B. K. & Hinshaw, S. H. 1992. Female choice and selection on male calling behaviour in the grey treefrog, *Hyla versicolor*. *Animal Behaviour*, **44**, 733–744.
- Walker, T. J. & Greenfield, M. D. 1983. Songs and systematics of Caribbean *Neoconocephalus* (Orthoptera: Tettigoniidea). *Transactions of the American Entomological Society*, **109**, 357–389.
- Wallach, H., Newman, E. B. & Rosenzweig, M. R. 1949. The precedence effect in sound localization. *American Journal of Psychology*, **62**, 315–336.
- Wytenbach, R. A. & Hoy, R. R. 1993. Demonstration of the precedence effect in an insect. *Journal of the Acoustical Society of America*, **94**, 777–784.
- Zuk, M. 1987. Variability in attractiveness of male field crickets (Orthoptera: Gryllidae) to females. *Animal Behaviour*, **35**, 1240–1248.
- Zurek, P. M. 1980. The precedence effect and its possible role in the avoidance of iteraural ambiguities. *Journal of the Acoustical Society of America*, **67**, 952–964.