

Variation and Repeatability of Female Choice in a Chorusing Katydid, *Ephippiger ephippiger*: an Experimental Exploration of the Precedence Effect

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Abstract

Female choice in various species of acoustic insects and anurans entails a psychoacoustic preference for male calls that lead their neighbors by a brief time interval. This discrimination, which can be termed a precedence effect, may select for various mechanisms with which males adjust call rhythm and thus reduce their incidence of ineffective following calls. At a collective level, alternating and synchronous choruses may emerge from these call timing mechanisms. Using playback experiments, we characterized the precedence effect in females of the katydid *Ephippiger ephippiger*, an alternating choruser in which males use a rhythm adjustment mechanism that prevents calling during brief intervals following their neighbors' calls. *E. ephippiger* females oriented toward leading male calls in >75% of trials when relatively young (<40 d old) and when playbacks were timed so that following calls began within 100–250 ms of the leading ones. However, this preference declined to below 60% as females aged and the interval separating leading and following call onsets increased. The strength of this precedence effect varied greatly between females, but within broad age classes the effect in a given female was statistically repeatable. Such repeatability indicates the possibility that additive genetic variance could be a significant component of variation in the precedence effect. We discuss the implications of our findings and inference on genetic variance for evolution of the precedence effect and for chorusing.

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Introduction

In many species of anurans and acoustic insects, males typically call within dense aggregations and collectively produce a temporally structured chorus (Greenfield 1994a; Gerhardt & Huber 2002). Where males call rhythmically, the temporal structure within a chorus often assumes an alternation or synchrony between neighbors' calls (Greenfield 1994b). While an alternating or synchronous chorus may appear to a human observer to be a complex, collective event with specialized adaptive function, playback experiments in various species have shown that chorusing can result from simple, pairwise interactions between neighboring males (Greenfield et al. 1997). An 'inhibitory-resetting' mechanism (Greenfield & Roizen 1993) is a common way in which male-male interactions among rhythmic singers yield alternating or synchronous phenomena: upon hearing a neighbor's call, a focal male inhibits its central rhythm generator and retains this state until the end of the neighbor's call, at which point it resets its rhythm and rebounds from inhibition. This delay of rhythm phase has both local and global effects: inhibition reduces the focal male's production of calls that immediately follow its neighbor's calls, and rebound from inhibition may increase the production of calls that immediately precede its neighbors'. On a global level, if all males within an aggregation sustain comparable calling rhythms and adhere to inhibitory-resetting, neighbors affect each other mutually: alternation emerges when rebound is shorter than the free-running call period; synchrony tends to emerge when rebound is comparable with the call period (Greenfield 1994b).

Investigations of female orientation and preference in various anuran and acoustic insect choruses indicate the adaptiveness of such inhibitory-resetting: females often prefer leading calls and ignore males whose calls immediately follow their neighbors' (Dyson & Passmore 1988; Minckley & Greenfield 1995; Snedden & Greenfield 1998). A recent study suggests that these female preferences, which may result from psychoacoustic 'precedence effects' (sensu Zurek 1987), can represent a sensory bias associated with auditory localization (Römer et al. 2002), but it is also possible that some leading preferences and precedence effects have co-evolved with a male signal trait; i.e. males which produce a high number of leading calls (by virtue of inhibitory-resetting and a fast calling rhythm) and are chosen as mates might be distinguished by features that are esthetically appealing (Fisherian selection) or by superior viability (good-genes selection). Here, precedence may be an effective means by which females can identify those males which sing with the fastest free-running calling rhythm (Greenfield 1997). This identification – generally a difficult task for non-human animals confronted with a dense chorus (Farris et al. 2002; also see Pollock 1998; Römer & Krusch 2000 on limitations of selective attention in acoustic insects) – could be far easier when a precedence effect and inhibitory-resetting operate: males which cannot sustain a fast calling rhythm are either repeatedly inhibited by their neighbors and seldom call, or they produce a high incidence of (non-attractive) following calls. Thus, a precedence effect might be selected for

because, ultimately, it magnifies small differences between potential mates that may be generally masked and undetectable in typical situations in natural populations (Greenfield 2002).

The alternatives presented above make it clear that an expanded knowledge of the parameters of female preference and precedence effects will be needed if we are to understand the evolution of male–male signal interactions and chorusing. Variation and repeatability are arguably the most important parameters to investigate first, as we may infer ‘evolvability’ (sensu Houle 1992) of the female preference trait from these measures. In order for a trait to evolve in response to selection, it must bear some heritable variation, the upper bound for which is set by its repeatability (Boake 1989). Thus, a female-preference trait that has little or no variation between individuals, and hence no meaningful repeatability, is unlikely to co-evolve with a male-signal trait. Here, the male-signal trait either evolved in direct response to an ancestral sensory bias operating outside the context of sexual activity (see Ryan et al. 1990), or the female preference and male-signal traits co-evolved in the past but the preference, and possibly the signal, have become fixed. However, where a female-preference trait does bear substantial variation between individuals but repeatability within individuals, it is potentially co-evolving with the male signal (see Andersson 1994; Houde 1997; Jennions & Petrie 2000). Presently, we have only meager information on the nature of variance in female-preference traits, and these data are available in only a small number of species (Bakker & Pomiankowski 1995; Jennions & Petrie 1997; for examples from acoustic species, see Ritchie 1996; Shaw & Herlihy 2000). For chorusing species and female preferences and preference functions relevant to male–male signal interactions, the data are limited yet further.

In this paper we present a study of female preference for leading male calls in the Mediterranean katydid *Ephippiger ephippiger* (Tettigoniidae: Bradyporinae). Previous work on this species has shown that females presented with two identical calls separated in space and by a brief time interval typically orient toward the leading call (Greenfield et al. 1997; Greenfield & Snedden 2003). Male *E. ephippiger* adjust their central rhythms with an inhibitory-resetting mechanism and are thereby afforded a reduced incidence of (relatively ineffective) following calls. The mechanism also generates chorusing in which bouts of call alternation emerge within pairs of neighboring males (Greenfield & Snedden 2003). Our current study determined (i) the temporal characteristics of interactive male calling for which females prefer the leader, (ii) changes in this female preference, or precedence effect, over age, and (iii) variation between and repeatability within individual females. We found that the strength and extent of female preference for leading calls declined with age in some individuals, that these preference features varied considerably between individual females, and that these were repeatable within individuals, at least within a given age class. The variation observed in female preference was considerably greater than that known within the associated male-signal interaction trait.

Natural History and Acoustic Communication in *E. ephippiger*

Ephippiger ephippiger is a flightless species found throughout the Mediterranean region of southern Europe, where various geographic populations are distinguished by the number of 'syllables' in the male advertisement calls (Heller 1988; Duijm 1990). We studied acoustic communication and female preference in a monosyllabic population from St Jean de Buèges, Dept. Hérault, France. The advertisement calls, which males produce by stridulating their vestigial forewings, average 130 ms in length (range = 110–140 ms) and are delivered rhythmically at approx. 1/s (range = 0.6–1.9/s at 25°C). Dominant frequency of the calls is 14 kHz (spectrum = 9–40 kHz; –6 dB cut-off values below and above dominant frequency = 12 and 16 kHz, respectively), and broadcast amplitude averages 90 dB peSPL at 1 m (0 dB = 20 µPa; (peSPL) peak equivalent sound pressure level). Males call during morning and mid-day hours from elevated perches in agricultural fields or garigue (chaparral), with distances between nearest calling neighbors averaging 4.8 m (range 0.2–12.7 m) (Greenfield & Snedden 2003).

Female *E. ephippiger* preferentially orient toward leading male calls when tested in laboratory choice trials (Greenfield & Snedden 2003). When presented with identical calls, each broadcast at 1/s from two loudspeakers situated at the arms of a y-maze, responding females in approx. 70% of trials walked toward the loudspeaker whose phase was advanced (see Fig. 1). This preference was observed if the time interval between onsets of the leading and following calls was 100–375 ms in length (phase angle between call rhythms 36°–135°), but it disappeared at shorter or longer intervals.

Additional playback tests conducted in the laboratory demonstrated that male *E. ephippiger* adjust their call timing with a relatively strong inhibitory-resetting mechanism. The adjustment was found in all individuals tested, and it effectively constrained males from initiating a call between 100–400 ms following a neighbor's call onset; it is assumed that calls initiated by a male between 0–100 ms following its neighbor had already been triggered by its central rhythm generator (Greenfield et al. 1997). Thus, two neighboring males possessing similar call rhythms may mutually inhibit one another every call cycle, and an alternation of calls within the pair is thereby established.

Materials and Methods

We conducted playback trials with *E. ephippiger* females to discern the parameters and prevalence of the precedence effect, i.e. their preference for and orientation toward leading male calls. In all trials, we used laboratory-reared insects derived from eggs collected at our field site near St Jean de Buèges, Dept. Hérault, France. The insects were reared in growth chambers at the University of Kansas, Lawrence, maintained at 24–27°C and under a 16.00:8.00 L:D photoperiod; photophase illumination was from overhead fluorescent bulbs. Females were held individually in small cylindrical containers (12 cm height; 8 cm diam.) throughout development and provided with a diet of cabbage, pollen, and fish

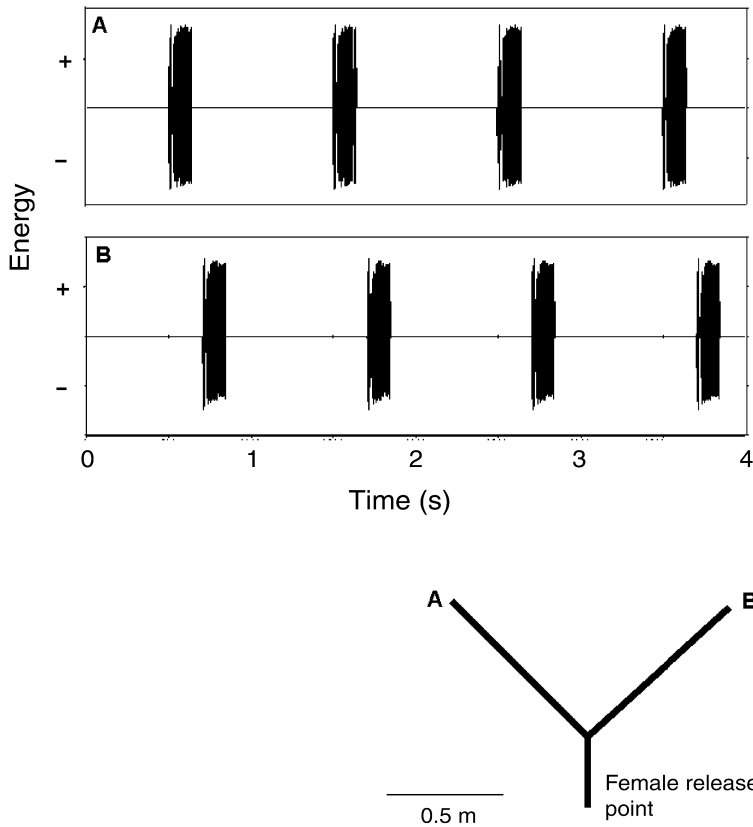


Fig. 1: Representative timing and spatial arrangement of the paired broadcasts of *E. ehippiger* male songs presented in playback experiments. Oscillogram traces show the broadcasts of loudspeakers A and B, each delivering calls at 1/s and situated at the respective locations indicated in the lower diagram illustrating the y-maze. The phase of the rhythm of A, the leading calls, is advanced by 72° (stimulus advance interval 200 ms) relative to B, the following calls, each call period

flakes ad libitum. The containers and insects were uniquely numbered so that we could track each individual's behavior in successive trials over its adult lifetime. To ensure the likelihood of sexual receptivity in females, all insects were ≥ 10 d old (post-adult molt) at the time of testing. Separation of males and females in different growth chambers also contributed to female receptivity, as habituation to male song was avoided.

Acoustic Playback

Playback trials were run in a semi-anechoic chamber ($3.5 \times 3.5 \times 2.5$ m) kept under the same conditions as the growth chambers. All trials took place during the first 6 h of the photophase, the time of sexual activity in natural populations

of *E. ephippiger*. To test for the presence and extent of the precedence effect, we played two identical, standard calls (a digitized natural recording of a call bearing spectral and temporal features average for the population) from two spatially separated loudspeakers (model 40-1377, Radio Shack Corp., Fort Worth, Texas, USA; ± 2 dB response from 4–50 kHz). The call rhythm of each loudspeaker's broadcast was held at 1/s in all trials, with the phase of one loudspeaker advanced by a constant angle (see Fig. 1). To prevent female directional biases from confounding our results, we switched the loudspeaker broadcasting the leading call in successive trials. We tested females individually on a y-maze whose two arms diverged 90° and projected upward at 10° directly toward the two loudspeakers (Fig. 1). The insects were monitored as they moved from the base of the 'y' to one of its arms during playback trials 2 min in length.

We created a stereo stimulus call by recording a male at our field site, amplifying the microphone (model-X M51; Linear X Systems Inc., Oregon, USA flat response from 10 to 40 000 Hz) output, and sending the output to two channels of a multi-channel analog-digital converter (model Power 1401, Cambridge Electronic Design Ltd.; Cambridge, UK; overall sampling rate set at 250 000 Hz) and then to a notebook computer, in which a 1-s segment that included a single standard call was saved, via Spike 2 software (Cambridge Electronic Design Ltd., Cambridge, UK), to a stereo file. Using additional digital signal processing software (SoundFX; SiliconSoft, San Jose, CA, USA), we advanced one channel of the stereo file by a prescribed time interval. To explore the extent of the precedence effect in *E. ephippiger*, we created six different stereo files for advance intervals of 100, 150, 200, 250, 300, and 350 ms, respectively (phase angles of 36, 54, 72, 90, 108, and 126° between call rhythms of the two channels, respectively). During playback trials in the semi-anechoic chamber, we looped the edited stereo file continuously on a desktop computer that drove the two (leading and following) amplified loudspeakers at the arms of the y-maze. Digital-analog conversion (SoundFX Engineering Version, SiliconSoft) of the computer output was performed at a sampling rate of 100 kHz to ensure that all frequencies in the *E. ephippiger* call were correctly reproduced in the broadcasts. Using a sound level meter (model 1982; General Radio Company, West Concord, MA, USA – set on peak response and 16 kHz band pass filter) and the method of peak equivalents (see Jang & Greenfield 1996 for general method), we adjusted the amplitude of loudspeaker broadcasts to 90 dB peSPL as measured at the female release point on the y-maze, 1 m distant (Fig. 1). This level was comparable with that observed in male *E. ephippiger* calls.

For each trial, we released the test female at the base of the y-maze and immediately began the playback. The female was allowed 2 min to walk toward one of the loudspeakers. We stopped the playback as soon as the female started to walk up one of the two arms of the y-maze, or at 2 min if it never left the base of the 'y'. We then began another trial of the same advance interval within 30 s. This procedure was repeated until a set of four consecutive trials using a given advance interval was completed. For the entire set, we tallied the numbers of trials in which the female oriented toward the leading speaker, toward the following

speaker, or failed to respond to either (did not leave the base of the 'y'). We used these tallies to calculate the proportion of responses within a set that were directed toward the leader. At the end of a set the female was replaced in its container and returned to the growth chamber.

On a given day, we tested from three to 15 females, each in two to six different sets of trials representing different advance intervals. We allowed a minimum of 30 min to elapse between the successive sets of trials in which a female was tested, and we arranged the different sets among the test females in a randomized-block design. For the majority of the 72 females used in the experiment, we began testing at the expected onset of sexual receptivity (10–20 d post-adult molt) and continued testing until morbidity, indicated by consistent failure to walk up the y-maze when presented with the playback of male song. A given female was tested every 3–5 d on average; if a female was tested on consecutive days, sets of different stimulus advance intervals were used. Females were tested with a given advance interval at least once every 10 d. We focused on the influence of age because it was deemed critical for a full understanding of variation and repeatability of female preference.

Data Analysis

We analyzed the playback trials first with all sets included regardless of the number of trials in which the female responded. A second analysis was performed including only those sets in which the female responded in all four trials, a restriction that eliminated approx. 10% of the sets. The latter method allowed us to focus on those females that exhibited consistent responses to male song. For both methods, we assigned females to 10-d age classes according to their age on the day of a trial. This age categorization was used because every female was tested with any given stimulus advance interval at least once every 10 d. Using ANOVA (general linear model), we determined the separate influences of age and of advance interval (phase angle) on the precedence effect in female orientation, and of the interaction between these two factors on precedence. For cases in which a female was tested with a given advance interval on more than one day during a given 10-d age class, we used only the set of trials from the first day in order to equalize the contributions of each female to the analyzed data. We then divided the data into approximately equal halves, separating data from trials on females < 50 d old from trials on females ≥ 50 d of age, and measured the repeatability of precedence in individual females within these two expanded age categories. Here, data from sets of trials run on all testing days within an age class were used to yield the large samples needed for determination of repeatability. We followed the method of Becker (1984) to compute repeatability measures [$\delta_{\text{individual}}^2 / (\delta^2 + \delta_{\text{individual}}^2)$] for the shorter (100–200 ms) and longer (250–350 ms) advance intervals. While categorization of data was necessary for repeatability analysis because female responses did change with age and stimulus advance interval, the expanded age and stimulus advance interval categories noted above yielded sufficient samples in each category. We used 50 d and 200 ms as the boundaries between age and

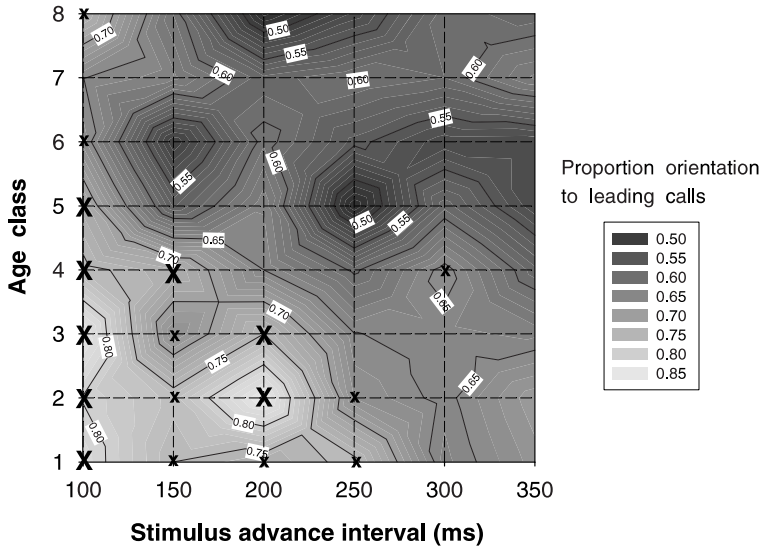


Fig. 2: Strength of the precedence effect in female *E. ephippiger* determined at various age classes and for the different stimulus advance intervals broadcast in two-loudspeaker playback trials (see Fig. 1). Precedence effect strength is indicated by shading in the filled contour plot and represents the proportion of orientations by responding females to the loudspeaker broadcasting leading calls, averaged across all tested females. Age classes are 10-d categories, with age class 1 = 10–19 d; age class 2 = 20–29 d, etc., and stimulus advance interval is length of time between onsets of the leading and following calls (A and B, respectively, in Fig. 1) broadcast in the playback trial; data were measured at grid intersections and interpolated between. Data were obtained from all sets regardless of the number of trials in which the female responded. Boldface 'X' at grid intersections indicate that precedence effect strength is significantly > 0.50 (Dunnett comparison test for two-way ANOVA, general linear model; upper case bold 'X' indicates $\alpha = 0.01$; lower case bold 'x' indicates $\alpha = 0.05$)

stimulus advance interval categories, respectively, because the strength of the female precedence effect started to decline markedly at these junctures (see 'Results' and Fig. 2).

Results

In any of the following analyses, the proportions of responses in a set in which females oriented toward the leading stimulus did not differ significantly from the normal distribution ($p > 0.10$; Ryan-Joiner test), and we therefore used untransformed data throughout. For both the complete data, wherein all sets were included regardless of the number of trials in which the female responded, or the restricted data, which included only those sets in which the female responded in all four trials, both female age and the length of the stimulus advance interval influenced the strength of the precedence effect significantly ($p < 0.01$; ANOVA, general linear model). Younger (< 40 d old) responding females oriented toward the leading stimulus call in 75–85% of trials when the advance interval was < 250 ms, but this percentage declined to 70 for older females (> 70 d old) tested

with an advance interval of 100 ms and for younger females tested with an advance interval > 250 ms (Fig. 2). For females > 40 d old tested with a stimulus advance interval > 200 ms, the percentage declined yet further to 55–60; however ANOVA (general linear model) did not reveal a significant interaction effect ($p > 0.50$) between the two factors, female age and stimulus advance interval. ANCOVA (general linear model) revealed significant effects ($p < 0.01$) of either female age or length of the stimulus advance interval, treated as covariates, on the strength of the precedence effect.

Our analyses found significant differences in response between individual females. For both complete and restricted data (see above), female identity was a significant factor contributing to variance in the proportion of orientations toward the leading stimulus ($p < 0.01$; ANOVA, general linear model). To analyze individual variation in the precedence effect further, for each of the 59 females tested in 10 or more sets of playback trials we regressed the proportion of leading stimulus orientations within a set versus stimulus advance interval and versus age class. In approx. 25% of females, preference for the leading stimulus declined significantly with increasing stimulus advance or with increasing age ($p < 0.05$; t-test for slope of least-squares linear regression). In the remaining females, these relationships did not differ significantly from the horizontal. Overall proportions of orientation toward the leading stimulus ranged from 0.95 to 0.35 among the females tested in 10 or more sets of trials ($\bar{x} \pm SD = 0.65 \pm 0.13$). Figure 3 shows the breakdown of this distribution among age- and stimulus-advance categories. All 12 females whose overall proportions exceeded 0.75 were characterized by consistent preference for the leading stimulus across stimulus advance intervals and age classes (regression slope not distinguished from horizontal). Some females with lower overall proportions were likewise consistent in remaining indifferent to the temporal relationship between stimuli, but others exhibited a significant decline in preference for leading calls as the stimulus advance interval or age increased.

The strength of the precedence effect was found to be modestly repeatable within the individual females in our sampled population. In young (< 50 d old) as well as old (≥ 50 d old) females, we found statistically significant repeatabilities for the proportion of orientations toward leading calls for both short- and long-stimulus-advance interval categories (Table 1).

Discussion

The overall level of the precedence effect in our *E. ephippiger* population was a 75% preference for leading male calls in females < 50 d old presented with stimulus advance intervals < 250 ms. From this finding we infer that the precedence effect would impose considerable selection pressure on male signal timing, which may have led to the inhibitory-resetting signal interaction mechanism observed, i.e. males not adhering to the mechanism may be expected to broadcast a high incidence of (ineffective) calls that follow their near neighbors.

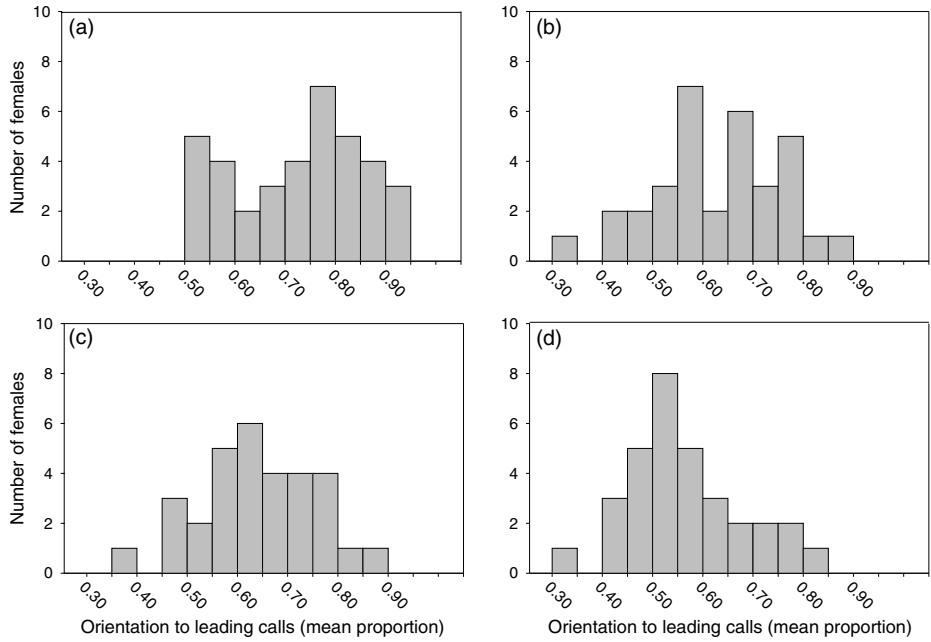


Fig. 3: Variation among individual *E. ephippiger* females in strength of the precedence effect. Histograms show frequency distributions of mean proportions of orientations toward leading calls among tested females. Data were categorized by female age and length of the stimulus advance interval (time between onsets of the leading and following calls broadcast in a playback trial; see Fig. 1); within each of the four similarly sized categories, data were restricted to females tested in 10 or more sets of trials; (a) age < 50 d, stimulus advance interval 100–200 ms; (b) age ≥ 50 d, stimulus advance interval 100–200 ms; (c) age < 50 d, stimulus advance interval 250–350 ms; (d) age ≥ 50 d, stimulus advance interval 250–350 ms

Table 1: Repeatability (R) of proportion of responses toward leading calls, categorized by female age and length of the stimulus advance interval (time between onsets of leading and following calls)

	Stimulus advance (ms)			
	100–200		250–350	
	Age < 50 d	Age ≥ 50 d	Age < 50 d	Age ≥ 50 d
Data obtained from females tested in ≥ 5 sets in given category	0.21 ± 0.05*	0.10 ± 0.04*	0.12 ± 0.05*	0.15 ± 0.05*
Data restricted to females tested in ≥ 10 sets in given category	0.07 ± 0.05	0.12 ± 0.06	0.13 ± 0.06*	0.21 ± 0.08*

*R > 2 SE.

R ± SE values calculated by the method of Becker (1984).

Our study revealed that in general *E. ephippiger* females retained a preference for leading male calls throughout their lives but that in many individuals the extent and strength of this preference declined with age, sometimes sharply. For those females attaining an age of 50 d or older, a marked preference for leading calls was primarily found when a stimulus advance interval of 100 ms was presented. Because the length of the stimulus in our trials was 130 ms, this specific preference may simply reflect direct masking of the onset of the following call by the end of the leading one, rather than more complex processes such as contralateral inhibition and forward masking (see Römer et al. 2002). The reason(s) for this change in preference with age, but prior to the decrease in level of responsiveness, is not clear. While sexual selection theory predicts that the level of mate discrimination may decline as females age (Andersson 1994), our observed decline would include a change in neural processing possibly associated with diminished ability to localize sound sources; i.e. the processes of contralateral inhibition and forward masking that likely generate the precedence effect may also, and primarily, magnify inter-aural intensity differences which enhance opportunities for sound localization (see Römer et al. 2002). Here, further neuroethological testing will be necessary to resolve the dilemma.

The most salient feature of female preference in *E. ephippiger* observed in our study was the variation in strength of the precedence effect between individuals. While acknowledging the limitations arising from small sample sizes in our study, we found that some females retained a strong preference for leading calls as they aged and regardless of the length of stimulus advance interval (100–350 ms), whereas other females were consistently equivocal in their orientation toward leading vs. following calls. A third group showed a decline in strength of the precedence effect at older age classes or greater lengths of the stimulus advance interval. Moreover, these characterizations were modestly repeatable within individual females. The repeatability values for *E. ephippiger* listed in Table 1 fall within the range of repeatability, and heritability, values reported by other quantitative studies of female preferences and preference functions (see Gray & Cade 1999; Jang & Greenfield 2000; Brooks & Endler 2001; Brooks 2002; Reinhold et al. 2002; Rodriguez & Greenfield 2003). While low in comparison with values generally reported for morphological and life history traits (cf. Weigensberg & Roff 1996), most of our *E. ephippiger* repeatabilities are statistically significant, indicating the possibility that additive genetic variance is an important component of the variation in precedence, and, in turn, that this female preference trait might be coevolving with the male signal interaction trait, inhibitory-resetting. Potentially, this co-evolutionary process could be driven by a heightened ability of females showing the preference trait to choose males bearing critical signal characters that would otherwise be difficult to discern (Greenfield 2002).

While there exists considerable variation in the extent of the female preference for leading calls, earlier experiments on this *E. ephippiger* population did not reveal comparable variation in the male signal interaction trait: all males tested exhibited inhibitory-resetting, with every individual refraining from calling during a 'critical interval' extending from 100–400 ms following the onset of a

neighbor's call or a playback stimulus (Greenfield & Snedden 2003). Does this sexual discrepancy mean that selection has been much stronger on the male response than on the female orientation and preference? Possibly, as all males should gain from inhibitory resetting even when only a proportion of females prefer leading calls. But it is also likely that some countervailing pressure has selected against or otherwise prevented a strong precedence effect in female orientation, thereby maintaining a considerable proportion of the female population that is equivocal in preference for leading vs. following calls. Importantly, this equivocation remains despite the potential that it is associated with reduced ability to localize sound sources as well as to detect singers maintaining a rapid free-running rhythm. Again, further behavioral experiments, neurophysiological investigation, and quantitative genetic analyses are called for.

Acknowledgements

We thank Alvaro Berg and Amelia Hund (Univ. of Kansas) for assistance with insect rearing; Simon Gray (Cambridge Electronic Design) and Kenneth Ratzlaff (Univ. of Kansas Instrumentation Development Laboratory) for technical advice and instrumentation development; and Anne Danielson-François, Gerlinde Hoebel, Rafael Rodriguez S. and two anonymous referees for critical reading of earlier versions of this manuscript. The work was supported financially by U.S. National Science Foundation grant IBN 98-16708 and conducted with permission of the U.S. Department of Agriculture.

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Received: September 30, 2003

Initial acceptance: December 8, 2003

Final acceptance: February 4, 2004 (S. A. Foster)