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Psychoacoustics of female phonotaxis and the evolution of male signal interactions in Orthoptera

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A series of playback experiments conducted in a field arena showed that female tarbush grasshoppers, *Ligurotettix planum* (Orthoptera Acrididae), were attracted to male calls and that when given the choice of calls that differed only in relative timing, females oriented toward the leading calls. This psychoacoustic feature, known as a "precedence effect," occurred when a 0.2 or 1.0-sec silent interval separated the leading and following calls. Preference for leading calls disappeared at separations longer than 2 sec and when calls overlapped; in the latter situation, females even failed to exhibit phonotaxis. Previous work demonstrated that neighboring *L. planum* males time their calls in an alternating fashion and that they achieve this chorusing format with an "inhibitory resetting" mechanism that averts calling during the 2-sec interval following onset of a neighbor's call. We propose that time constants in this inhibitory resetting mechanism evolved under selection pressure from the female precedence effect. Intermale signal interactions occur in many acoustic orthopterans and anurans, and we predict that female precedence effects, presently known in only a few species, will be revealed as responsible for various of these interactions. As in *L. planum* and another orthopteran species (*Neoconocephalus spiza*) in which both male signal interactions and female psychoacoustic preferences have been studied, inhibitory intervals in male interactive calling are expected to be congruent with or to exceed the lengths of precedence effects.

KEY WORDS: acoustic communication, chorusing, grasshopper, *Ligurotettix planum*, Orthoptera, sexual selection, signal competition.

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INTRODUCTION

Pair-forming systems characterized by long-range male signaling and female orientation toward these signals are favored by investigators of sexual selection. This attention is partly due to the potential opportunities that such systems afford for examining female choice in isolation from inter-male competition. Perhaps owing to advances in digital technology that allow sounds to be physically described, simulated, and played back with precision, a great share of these studies are conducted on acoustic signaling systems. In anurans and orthopterans the ability to test the phonotactic responses of females in many species may be added to the above features which render acoustic signaling a focus for empirical work on sexual selection (see SEARCY & ANDERSSON 1986, HARVEY & BRADBURY 1991).

Various studies on anurans and orthopterans have shown that females evaluate and select among males based on differences in calling rate, call duration, call frequency, or call loudness (RYAN & KEDDY-HECTOR 1992). In addition to assessing these physical signal parameters which may reflect available or allocated energy, several recent studies reveal that females may also be influenced psychoacoustically by the relative timing of calls (WHITNEY & KREBS 1975; DYSON & PASSMORE 1988a, 1988b; STIEDL 1991; KLUMP & GERHARDT 1992; GREENFIELD & ROIZEN 1993). That is, "precedence effects" (sensu WYTTENBACH & HOY 1993) may occur in which the second of two closely timed, identical calls is largely ignored during phonotaxis. If precedence is a sufficiently potent effect, a (focal) male would be subject to strong selection pressure to avoid calling shortly after a neighbor and, possibly, to relegate the neighbor to the disadvantageous (from the focal male's perspective) time interval as well.

When aggregated anuran and orthopteran males call, they commonly exhibit various forms of temporal signal interactions in which neighbors maintain specific phase relationships between their calls and collectively generate alternating (phase ≈ 180°) or synchronous (phase ≈ 0°) choruses (ALEXANDER 1975; GREENFIELD 1994a, 1994b). Traditionally, alternating and synchronous chorusing has been explained as a cooperative adaptation by which species specific information in signals is preserved (WALKER 1969; see also LLOYD 1973), natural enemies are avoided (OTTE 1977, TUTTLE & RYAN 1982), or peak signal amplitude of a group is maximized (WELLS 1977; see also BUCK & BUCK 1978). As implied above, however, some of these timing mechanisms and resulting chorusing patterns may also represent competitive interactions (see ALEXANDER 1975, OTTE & LOFTUS-HILLS 1979) between individual males vying to attract females influenced by precedence or other psychoacoustic effects. Consequently, female choice and inter-male competition may be more confounded in long-range signaling systems than generally believed.

While the timing mechanisms responsible for temporal signal interactions have been elucidated rather thoroughly in various anurans and orthopterans, these male behaviors have seldom been connected with or studied in association with female phonotaxis and choice (but see SCHWARTZ 1987, GREENFIELD & ROIZEN 1993, SCHWARTZ 1994). Unfortunately, our understanding of chorusing is therefore far greater from a neuroethological perspective than from an evolutionary one.

In a recent study on alternating chorusing in the tarbush grasshopper, *Ligurotettix planum* (Acrididae Gomphocerinae), we found that the collective pattern was generated by an "inhibitory resetting" mechanism wherein males did not call during a 1.8-sec interval beginning 0.2 sec following the onset of a neighbor's call (MINCKLEY et al. 1995). Moreover, males selectively phonoresponded to (were inhibited by) only their nearest one or two neighbors, and they timed their calls such that neighbors were more likely to call during the time interval following the focal male. Despite this extensive investigation of timing mechanisms in males, the function of relative call timing among adjacent males was left unanswered.

The present study examines whether *L. planum* females preferentially orient toward calls that differ only in their relative timing. We then interpret our results in light of the timing mechanisms used by calling *L. planum* males and evaluate the hypothesis that alternating chorusing is an evolutionary response to psychoacoustic features of female phonotaxis. Finally, we extend our interpretations to other acoustic species and show that a basic call timing mechanism, present in males of diverse taxa, is modified in accordance with the psychoacoustic preferences of conspecific females.

MATERIALS AND METHODS

Natural history and acoustic communication of L. planum

L. planum are endemic to the Chihuahuan Desert of southwestern North America, where they are found almost exclusively on a single host plant, *Flourensia cernua* (Asteraceae) (Otte & Joern 1975). Males commonly defend individual host plant bushes as mating territories (Shelly & Greenfield 1989). They accomplish this defense passively via stridulatory calls and actively via aggression if another male intrudes. Calling also influences females to orient toward a male's territory during inter-bush movements. The final stages of pair formation within bushes are undertaken entirely by the male, however. Female site fidelity is relatively low, and males have numerous opportunities to attract females when the latter make the 2-10-m movements between neighboring host plants.

Males produce two different hindleg/forewing stridulations which are distinguished by their onomatopoeic designations (Greenfield & Minckley 1993, Minckley et al. 1995). A "rasp" call is delivered at 4-15 min^{-1} during midday and serves as both a keep-out signal directed toward other males and a sexual advertisement to females. Rasps average 350 msec in length, 60-65 dB SPL in amplitude (measured ipsilateral to a stridulating hindleg and 1 m distant; 0 dB = 20 μPa), and 3-9 kHz in frequency (peak = 4.5-5 kHz). Males normally alternate rasp calls with their nearest calling neighbors. The distances separating nearest calling neighbors are typically 2-4 m. During aggressive encounters with intruders, males escalate to a more complex call in which 1-60 "shucks" precede the terminal rasp. More thorough treatments of the natural history and acoustic signaling of *L. planum* are provided in Shelly & Greenfield (1989), Greenfield & Minckley (1993), and Minckley et al. (1995).

Rearing of test animals

To obtain *L. planum* females for playback experiments, we collected nymphs at field sites 12 km north of Rodeo, New Mexico (see Shelly & Greenfield 1989 for a complete description of this area) during June 1993. We transported the nymphs to a screened rearing room at the Southwestern Research Station in Portal, Arizona where they were exposed to the local photoperiod. The nymphs were kept in groups of 15-20 within 30 × 30 × 30-cm screen cages and provided with fresh *Flourensia* foliage ad libitum; 60-w incandescent bulbs positioned over each cage provided supplementary warmth and light intensity during daylight hours. We checked the cages daily and noted all newly molted adults. Females were uniquely marked with enamel spots on the pronotum 2 days after the adult molt and returned to their cages. The delay in marking prevented handling damage to teneral individuals. Any males that were collected as nymphs were removed immediately after the adult molt. These measures insured that all tested females were unmated and had not even been exposed to courtship, adult males, or male calls. Preliminary experiments (during 1992) using field-collected adult females showed that such insects were unreceptive to playback of male calls, presumably because of prior mating or exposure to courtship, males, or calls.

Playback experiments

Test arena. Phonotaxis experiments on *L. planum* females were conducted during July 1993 in an outdoor arena at the Southwestern Research Station. The arena was circular, 9 m in diameter, and surrounded by a 1.5-m polyurethane foam wall that provided acoustic insulation and a homogeneous visual background. We arranged 16 *Flourensia* bushes, each supported in a 19-l bucket of moist sand, 1.8 m distant from each other and along a circle 1.5 m from the inside of the arena wall. Thus, neighboring bushes had azimuthal separations of 22.5° as viewed from the arena center. The bushes were roughly equivalent in height and stem and foliage density. We replaced all bushes with new ones every 2 days, the minimum retesting interval of females, to avert potential effects on phonotaxis caused by the learning of visual landmarks (see GREENFIELD et al. 1989). A 10-cm high bunch of grass located at the arena center served as a release point for the test animals.

Acoustic stimuli. Acoustic stimuli were broadcast from loudspeakers (Realistic model 40-1377; flat response from 4-50 kHz) positioned at the base of every 4th bush. Earlier work showed that females were more likely to orient toward calls broadcast from a host plant than from an open location. We oriented the loudspeakers upward to equalize their SPL as much as possible in all horizontal directions. Loudspeaker broadcasts were adjusted at the beginning and middle of each testing session (day) such that stimuli were ≈ 62 dB SPL at 1 m in a horizontal direction, the mean amplitude of natural rasp calls. Calibrations were made via a sound level meter (General Radio model 1982, with band-pass filter set at 4 kHz) and level controls in the circuits of each loudspeaker.

In all trials we used a genuine 400-msec rasp call as a stimulus. This call was recorded from a *L. planum* male via a Casio DA-7 stereo DAT recorder fitted with an AKG C451E directional microphone (both with flat responses to 20 kHz) and then digitized at a sampling frequency of 100 kHz via an 8-bit analog-digital converter in a “soundcard” (Supersound Engineering Model obtained from Silicon Shack, Ltd, San Jose, California). Using a signal editing program (SoundFX, Silicon Shack, Ltd), we copied the digitized call to a second channel and adjusted the onset times of the rasp calls on the two channels to a given phase relationship. We then used the program’s “looping” function and the soundcard’s digital-analog converter to transfer repetitions of the two-channel file back to a stereo DAT tape. Looping was set to generate 7-sec call periods on both channels, and we made five different 10-min stimulus tapes, each with a different phase relationship between the two channels. These five stimulus tapes included 0.03, 0.2, 0.6, 1.4, and 2.68-sec intervals between onsets of calls on the two channels, respectively. Thus, calls in the first two tapes were overlapping, whereas silent intervals of 0.2, 1.0, and 2.28 sec, respectively, occurred between the calls in the latter three tapes. We also made a 6th stimulus tape as above, save that calls were transferred to only a single channel of the DAT tape.

Experimental protocol. To determine the basic attractiveness of rasp calls to females, we played calls from the single channel stimulus tape on the Casio DA-7 stereo DAT recorder. One of the four loudspeakers in the arena was randomly selected for broadcasting in each trial. Test females were placed on the release point, and loudspeaker broadcasts were started after a 1-min “accustoming period.” Playback continued for the 10-min duration of the tape or until the female jumped or flew toward one of the *Flourensia* bushes in the arena, whichever juncture occurred first. With the direction from the release point toward the broadcasting loudspeaker normalized to a 0° azimuth angle, we measured to the nearest 11.25° the “departure azimuth” of each female by the point at which she initially intersected the circle of *Flourensia* bushes. Females were tested once in this experiment and then immediately returned to their rearing cage. Five subsequent experiments tested each of the five 2-channel stimulus tapes. The same basic protocol as above was used, save that we randomly selected a pair of loudspeakers on opposite sides of the arena for broadcasting in the initial trial of each experiment and chose which of the two loudspeakers would broadcast leading calls. In the next trial we used the same pair but switched the leading and following loudspeakers, and in the subsequent two trials we used the two permutations of the other pair of loudspeakers. This four-permutation sequence was repeated 7-8 times to complete all trials in an experiment. Two observers monitored the movement of the female during each trial and positioned themselves outside of the arena and on opposite sides to minimize the chance that their presence biased orientation toward one direction. For measuring departure azimuth, we normalized the direction from the release point toward the loudspeaker broadcasting leading calls to 0°.

Because of the unlikelihood of sexual receptivity in newly molted (reproductively immature) females (see UVAROV 1977), all insects were at least 8 days past adult molt at the time of testing. We tested females only once in each experiment, and if we retested them in successive experiments, a minimum of 2 days elapsed between tests. Ninety-three different females were used in the experiments, and they were tested 1-4 times ($\bar{x}$ = 1.90). Experiments were conducted between 09:30-16:00 (Mountain Standard Time) and only during full sunlight.

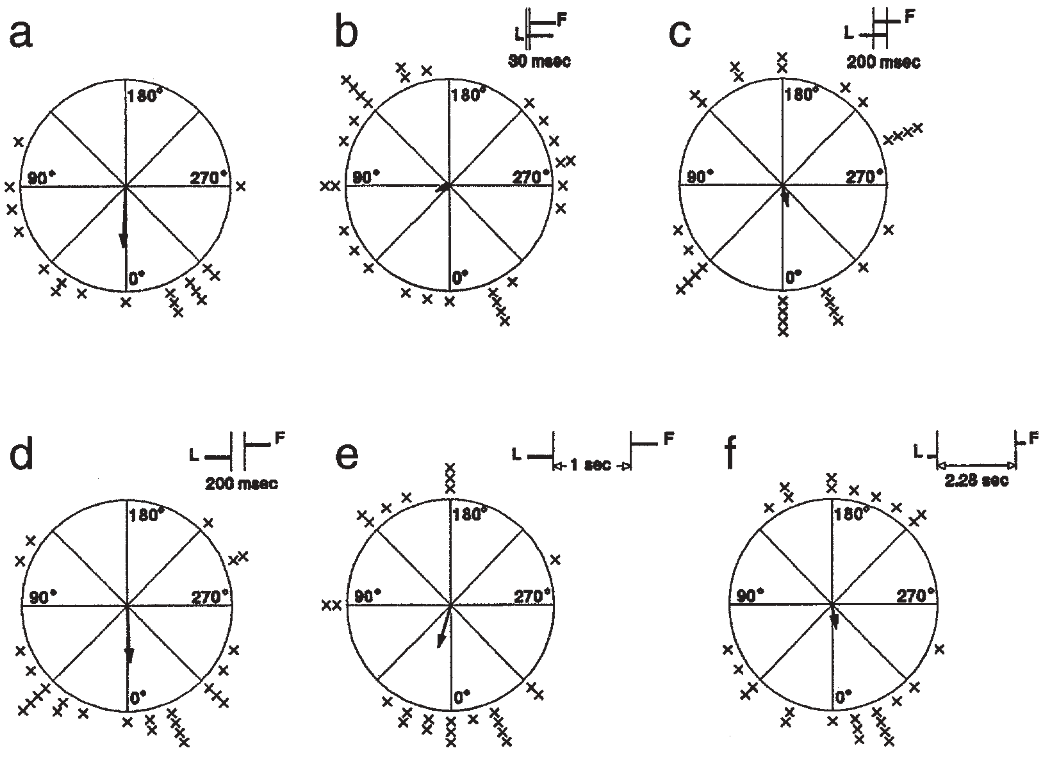

Fig. 1. — Departure azimuths of females (x) tested individually in arena phonotaxis experiments. The center of the circle represents the release point of each female. Arrows indicate the mean vectors (BATSCHELET 1981) of departure azimuths in each experiment; *a*, results of the single loudspeaker experiment, with the azimuth of the broadcasting loudspeaker normalized to 0°; *b-f*, results of the five 2-loudspeaker experiments, with the azimuths of the loudspeakers broadcasting leading (L, see insets in upper right) and following (F) calls normalized to 0° and 180°, respectively. Insets indicate the phase relationship between leading and following calls in each experiment.

RESULTS

When presented with calls from a single loudspeaker, females significantly clustered their departure azimuths around that loudspeaker ($P < 0.01$, V-test, Batschelet 1981). Fifteen of the 18 tested females that left the release point had departure azimuths between 270-90° (the same side of the arena as the broadcasting loudspeaker, Fig. 1a), two had azimuths equal to 270° and 90°, and only one had an azimuth between 90-270° (the opposite side of the arena).

In experiments in which calls were broadcast from two loudspeakers, females significantly clustered their departure azimuths around the leading loudspeaker when the silent interval between calls was 0.2 or 1.0 sec ($P < 0.01$ and < 0.05, V-tests; Fig. 1d-e). When adjusted for multiple tests (five 2-loudspeaker experiments were conducted), however, only results from the experiment with 0.2-sec silent intervals remained significant ($P < 0.05$, Holm multiple-test procedure, Krauth 1988). Females in the remaining three 2-loudspeaker experiments showed no significant clustering of departure azimuths around a single loudspeaker ($P > 0.05$, V-tests; Fig. 1b-c, f).

In the experiment with 2.28-sec silent intervals females significantly clustered their departure azimuths along the axis connecting the two loudspeakers ($P < 0.01$, V-test corrected for bimodal data and adjusted for multiple tests via the Holm procedure; Fig. 1f); i.e., they oriented toward the loudspeakers but did not prefer one over the other. Such axial orientation was not seen in the experiments where calls overlapped ($P > 0.05$, V-tests corrected for bimodal data; Fig. 1b-c). In both of these experiments the distribution of departure azimuths did not differ significantly from a uniform distribution ($P > 0.10$, Watson's U^2-test, Batschelet 1981; Fig. 1b-c).

DISCUSSION

Our single-stimulus phonotaxis trials showed that *L. planum* females were attracted to male calls 3 m distant. Based on the ability of males to phonorespond to calls 8 m distant (Minckley et al. 1995) and the assumption that male and female acoustic sensitivities are similar, females may detect and move toward calls (males) at much greater distances than those tested in the arena. When presented with a choice of two calls, broadcast from opposite sides and differing only in their relative timing, females clearly chose the leading call when a 0.2 or 1.0-sec silent interval separated the calls. The females showed strong phonotaxis but no preference for leading calls when the silent interval was lengthened to 2.28 sec. Preference for leading calls also failed to appear when the calls overlapped, but in this situation the level of phonotaxis toward either call was also insignificant. This latter effect may stem from an inability of acridids to separate centrally sounds emitted simultaneously from two different sources (cf. Helversen 1984), an ability that does occur in other orthopterans (Pollack 1988, Römer 1993).

The temporal parameters of the precedence effect in *L. planum* female phonotaxis are roughly congruent with those in the timing mechanism regulating male calling. That is, females ignore following calls when such calls begin 0.2-1.0 sec after the end of leading calls (the exact beginning and ending of this effect remain unknown), and males are inhibited from calling during a 1.8-sec interval beginning 0.2 sec after the call onset of a neighbor. The mechanism responsible for averting production of such following calls is resetting of the call timing oscillator to its "basal" level by onset of an acoustic stimulus (e.g. a neighbor's call) and inhibition at this level until termination of the stimulus (MINCKLEY et al. 1995). Rebound from inhibition to production of the next call then requires a minimum of 1.4 sec (longer if the inhibitory stimulus occurs early during the call period). Because *L. planum* regularly rebound from inhibition in less than 1.0 sec during inter-male "calling duels" (GREENFIELD & MINCKLEY 1993), albeit while producing shuck+rasp rather than rasp calls, we infer that the 1.4-sec minimum rebound interval during advertisement calling is not a physiological constraint. Rather, the length of this interval and its approximate congruence with the extent of the precedence effect in females probably reflect strong selection pressure on males to avoid calling when their calls would attract few local females.

Psychoacoustic influences on female phonotaxis and mechanisms regulating call timing in males have been studied jointly in few acoustic species. In the cone-headed katydid *Neoconocephalus spiza* (Orthoptera Tettigoniidae) the minimum rebound interval ($\approx$ 200 msec) in males greatly exceeds the duration (< 50 msec) of the female precedence effect (GREENFIELD & ROIZEN 1993). Unlike *L. planum*, the specific length of the rebound interval in *N. spiza* may be physiologically constrained (GREENFIELD 1994a, 1994b), because males who would rebound as soon as 50-200 msec after a neighbor would not be ignored by females. The basic (inhibitory resetting) mechanism yielding the rebound interval, though, most likely stems also from selection on males to circumvent the precedence effect in females (GREENFIELD 1993).

In *N. spiza* the minimum call period that males can sustain is only slightly longer than the minimum rebound interval. Consequently, males who are equally matched in their call rates would synchronize by default (GREENFIELD & ROIZEN 1993). Because even minimum call periods in *L. planum* are much longer than rebound intervals, regular alternation, rather than synchrony, would represent the default chorusing format among matched males in this species. Thus, various forms of collective chorusing may simply be incidental outcomes or epiphenomena that are generated by timing mechanisms operating on a call-by-call basis between competitive individuals "attempting" to avoid being jammed and, possibly, to jam one another as well. Accordingly, alternation should occur most frequently in species with relatively slow (< 1 sec^{-1}) calling rates, since call periods would more likely exceed rebound intervals — whether set by physiological constraints or precedence effects in females — in this situation. Surveys of acoustic insects and anurans seem to confirm this prediction (GREENFIELD & SHAW 1983, GREENFIELD 1994a).

Examination of various acoustic and bioluminescent animals demonstrates that periodically repeated signals are usually timed by central oscillators and that oscillator timing is often modified by an inhibitory resetting mechanism during interactive signaling (GREENFIELD 1994a, 1994b). Currently, the prevalence of precedence effects in female phonotaxis toward periodic signals is largely unknown. We anticipate that increased attention to potential psychoacoustic influences will reveal these effects in many acoustic species, including some without alternating or synchronous inter-male signal interactions (e.g., species with long, sustained "trills"). Moreover, we predict that wherever precedence and signal interactions co-occur, the mechanism that modifies oscillator timing will comply with the length of the effect. This prediction may account for the specific lengths of time constants (time window for inhibition, rebound interval following inhibition, see GREENFIELD 1994b) in interactive call mechanisms found in many insects and anurans. However, the prediction can not explain why psychoacoustic influences on female phonotaxis typically favor leading rather than following calls and why precedence effects occur in the first place. Evolution of these effects remains an enigma, and presently we hypothesize that they may result from "sensory biases" (sensu RYAN & KEDDY-HECTOR 1992), reflecting conservative elements of neural processing (see review in DUMONT & ROBERTSON 1986) such as "forward masking" (see SOBEL & TANK 1994), and/or from various aspects of Fisherian (arbitrary) or "good-genes" intersexual selection (see GREENFIELD 1994a).

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