

SELECTIVE ATTENTION AND THE SPATIO-TEMPORAL STRUCTURE OF ORTHOPTERAN CHORUSES

by

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Summary

Temporally structured choruses in which neighbouring males alternate or synchronize their calls are common among rhythmically singing Orthoptera. In many cases, chorusing appears to be driven ultimately by psychoacoustic precedence effects that influence females to orient toward leading male calls and to ignore males whose call onsets follow their neighbours' onsets by a critical interval, 0-70 msec in some species but as long as 0.2-2.0 sec in others. When such preferences occur, call timing mechanisms with which males reduce their production of following calls are favored by selection. These timing mechanisms are observed among rhythmically calling species, and they may generate the emergence of group synchrony or alternation as a byproduct of local pairwise signal interactions.

Where males are selected to adjust call timing and increase their incidence of leading calls, they confront a dilemma if density is high: Adjusting call rhythm in response to all singing neighbours may severely reduce the calling rate, whereas forgoing rhythm adjustment may lead to a preponderance of ineffective following calls. Simulations and laboratory experiments demonstrate that calling males may solve this problem by selectively attending to only a subset of neighbours.

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We studied three orthopteran species, *Ligurotettix planum*, *Ephippiger ephippiger* (both alternating chorusers), and *Neoconocephalus spiza* (synchronous choruser), in the field to determine the extent to which selective attention occurs in natural populations and structures chorusing. These three species were chosen because previous studies demonstrated moderate to strong precedence effects in females and timing adjustments in males with which they reduced production of following calls; moreover, controlled experiments indicated that selective attention influenced interactions among calling males in one of the species. As predicted, our studies of natural choruses showed that males in all three species maintained high call rates by attending to only some of their neighbours. Attended neighbours were generally the nearest, and loudest, ones, but other rules with which attention is applied may also occur. In *L. planum* and *E. ephippiger*, males generally attended to a single calling neighbour, but *N. spiza* males often attended to several. We propose that reduced selectivity in *N. spiza* reflects the synchronous nature of its chorusing, implying that a group effect emerging incidentally can influence via feedback the individual behaviour yielding that collective activity.

Introduction

When animals settle in dense aggregations, individuals may encounter special problems in communication that spatially dispersed signalers do not face. These problems involve competition with (West-Eberhard, 1984) and interference from (Römer *et al.*, 1989; Schwartz & Gerhardt, 1989) neighbours' signals, and they arise whether the aggregation is passively or actively driven. In the case of signals transmitted by sexually advertising males, aggregation may select for signal modifications wherein individuals match or exceed the energy, power, or complexity of their neighbours' advertisements (Jia *et al.*, 2001). A male failing to make these modifications would, in all likelihood, be relegated to inferior mating success should females choose mates on a simultaneous and/or relative basis. Female choice may also select males to modify their signal timing on several temporal scales (Greenfield, 1994a, b): On a broad scale, males may be pressured to initiate signalling whenever neighbours do, which can generate the collective calling bouts observed in many acoustic insects and anurans (Schwartz, 1991). At the opposite end of the temporal spectrum, (female) perception and orientation is often influenced by the relative timing of individual signals, with heightened receiver responses directed toward the first of two or more spatially separated signals (Snedden & Greenfield, 1998). This effect may operate when a leading signal precedes a following one by an interval ranging from mere milliseconds up to several seconds in length (Minckley & Greenfield, 1995),

and it can select for various adjustments with which males limit their broadcast of following signals (Greenfield, 1994a, b). In acoustic species that produce rhythmic calls, these adjustments may assume the form of 'inhibitory-resetting': Upon perceiving a neighbour's signal, a focal male is inhibited from initiating a call and resets the phase of his signal rhythm generator such that his next call is delayed (Greenfield & Roizen, 1993; *cf* Hanson, 1978; Buck *et al.*, 1981). Thus, he avoids producing a call shortly after his neighbour, which would be relatively unattractive to female receivers were it broadcast, and also increases his probability of being in the leading role during the next call cycle. Collectively, inhibitory-resetting can yield a temporally structured chorus in which neighbours' call rhythms are either synchronized (phase angle $\cong 0^\circ$) or alternate (phase angle $\cong 180^\circ$) with one another (Greenfield, 1994a). Studies of various acoustic insects suggest that these temporal structures often are simply emergent properties that arise as by-products of individual call rhythms and inhibitory-resetting adjustments. Little evidence indicates that female preferences or male rivalries select for synchrony or alternation *per se* (Greenfield, 1997).

While inhibitory-resetting can increase the relative attractiveness of a male's signals to local females, it also presents him with a troublesome dilemma, particularly when population density is high (Snedden *et al.*, 1998). Were a male to apply the inhibitory-resetting adjustment to all of his signalling neighbours, he would produce very few ineffective, following calls, but he might be repeatedly inhibited and seldom call. On the other hand, a male forgoing the adjustment would call regularly but would assume the following role during many call cycles. One solution to this problem would be selective attention directed toward only the subset of nearby neighbours (see Pollack, 1988; Römer & Krusch, 2000 on candidate neural mechanisms), as these individuals would probably represent the strongest competitors for females (Greenfield & Rand, 2000). Thus, a male might balance the conflicting demands of regular calling and avoiding the broadcast of ineffective, following calls. Selective attention is predicted by a Monte Carlo simulation developed to model chorusing interactions (Greenfield *et al.*, 1997), and playback experiments in several anurans and acoustic insects have demonstrated its occurrence (Snedden *et al.*, 1998; Greenfield & Rand, 2000). However, chorusing interactions in natural populations are far more complex than those in controlled experimental situations (Boatwright-Horowitz *et al.*, 2000), and it was not clear how selective attention might structure choruses in the field.

The research reported here was designed to examine the spatio-temporal organization of large chorusing aggregations in several species having different densities, movement patterns, and calling rhythms, and to determine whether males actually abide by the rules of selective attention as predicted.

We used multi-channel electronic devices to record choruses in three acoustic insect species, *Ligurotettix planum* (Acrididae), *Neoconocephalus spiza* (Tettigoniidae: Conocephalinae), and *Ephippiger ephippiger* (monosyllabic race; Tettigoniidae: Bradyporinae; see Duijm 1990 for treatment of song races in *E. ephippiger*). Previous studies demonstrated female preferences for leading signals — precedence effects — (see Methods and Discussion; see Greenfield & Roizen, 1993 for *N. spiza*; see Minckley & Greenfield, 1995 for *L. planum*; see Greenfield *et al.*, 1997 for *E. ephippiger*) and male inhibitory-resetting adjustments to signal rhythm in all three species (see Greenfield & Roizen, 1993 for *N. spiza*; see Minckley *et al.*, 1995 for *L. planum*; see Greenfield *et al.*, 1997 for *E. ephippiger*). Moreover, controlled experiments testing relatively simple male-male interactions in *L. planum* indicated selective attention for nearby neighbours in this species (Snedden *et al.*, 1998); the other two were previously unchecked.

Our current study shows that selective attention is a moderately strong organizer of natural choruses in *L. planum* and *E. ephippiger* but rather weak in *N. spiza*. The temporal structure of *L. planum* and *E. ephippiger* choruses is alternation whereas that of *N. spiza* is synchrony, and we propose that these different emergent properties may influence, via feedback, the degree of selective attention observed in the several species.

Methods and materials

Populations

We studied natural populations of *L. planum* and *N. spiza* at field sites near Portal, Arizona (July 1995, July-August 1997) and near Gamboa, Panama (July 1996), respectively. Descriptions of these sites and natural history of the insects are given elsewhere (Greenfield, 1988; Shelly & Greenfield, 1989). *E. ephippiger* was studied in garigue (chaparral) and vineyards near St. Jean de Buèges, Dept. Hérault, France during July 1999-2001; its general habitat and natural history are described in Hartley & Warne (1984).

General acoustic characteristics of the male calling songs are listed in Table 1, while male inhibitory-resetting and extent of the female precedence effect are depicted in Fig. 1. Both male and female characteristics were obtained in previous studies, except those reported for the *E. ephippiger* population whose choruses were recorded in the current study (see below).

TABLE 1. *Acoustic characters of male advertisement calls in three chorusing orthopteran species*

Species	Call length ^a	Call rate ^a	Carrier frequency ^b	Call amplitude (at 1 m)
<i>Ligurotettix planum</i> ^c (Acrididae)	400 msec; 310-440	5 min ⁻¹ ; 4-12	7 kHz; 3-9	65 dB peSPL
<i>Neonocephalus spiza</i> ^d (Tettigoniidae: Conocephalinae)	50 msec; 20-70	2 sec ⁻¹ ; 1.7-4.5	11 kHz; 9-13	85 dB peSPL
<i>Ephippiger ephippiger</i> ^e (Tettigoniidae: Bradyporinae)	120 msec; 100-130	1.0 sec ⁻¹ ; 0.6-1.9	14 kHz; 12-16	90 dB peSPL

^a Mean and range values shown.

^b Dominant frequency and range (lower and upper -6 dB cutoff values) are shown.

^c References: Shelly & Greenfield, 1989; Minckley *et al.*, 1995; Snedden *et al.*, 1998.

^d References: Greenfield, 1988; Greenfield & Roizen, 1993.

^e See Methods and materials, and Results.

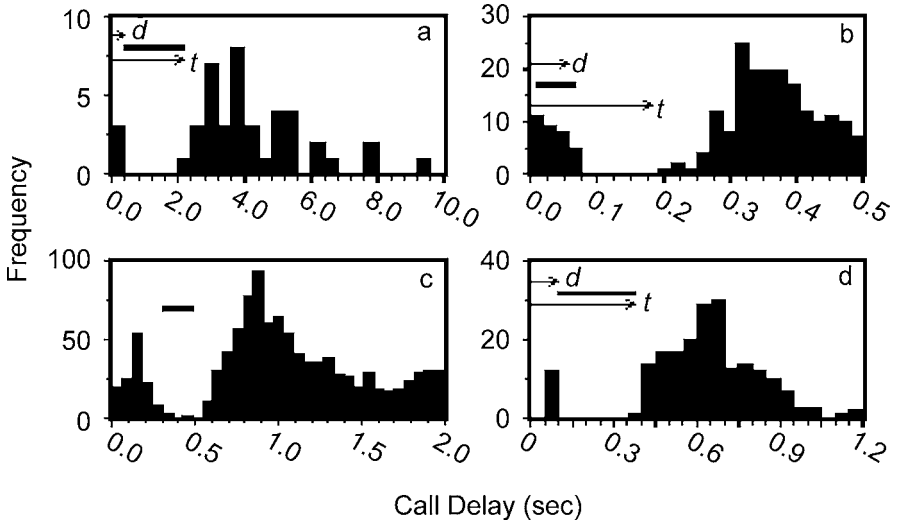


Fig. 1. Male call timing adjustment (inhibitory-resetting) and female preference for leading calls (precedence effect) in three species of chorusing Orthoptera. Male inhibitory-resetting mechanisms: histograms depict the incidence of calls following the broadcast of randomly timed playback stimuli (recordings of conspecific calls), the onsets of which are set equal to 0 sec. In each species, males do not call during an interval beginning 60-250 msec following playback onset and continuing for 150-2000 msec. Female precedence effects: horizontal bars indicate the interval following the onset of a (leading) male call during which females show reduced orientation toward another (following) call broadcast from a different direction; this phenomenon is known as the precedence effect when the following call begins after the end of the leading one. *d*: effector delay; *t*: maximum call delay for which precedence effect is observed or (b) delay to onset of post-stimulus calls, whichever is longer. (a) *Ligurotettix planum* (ref.: Minckley *et al.*, 1995); (b) *Neoconocephalus spiza* (ref.: Greenfield & Roizen, 1993); (c) *Ephippiger ephippiger*, two-syllable race (ref.: Greenfield *et al.* 1997); (d) *Ephippiger ephippiger*, monosyllabic race (current study; $N = 15$ males; see Fig. 4 for data pertaining to precedence effect in female orientation).

Chorus recording

For both *L. planum* and *N. spiza*, we recorded naturally occurring choruses by placing a tripod supporting a microphone adjacent to each male and sending the microphone outputs to a customized multi-channel recording device adapted to a portable computer. Digitized output from the recording device was saved to a file on the computer. In both species we either recorded chorusing aggregations whose nearest calling neighbours were at least 20 m distant or temporarily removed such neighbours if present. These measures ensured that all chorusing interactions were restricted to acoustic exchanges within the chorus. *L. planum* choruses were recorded between 1000-1300 MST, the period of peak daily calling and mating activity (Shelly & Greenfield, 1989), and only on days with hot, sunny weather. Most recordings were approximately 2 h in length and included a total of five to eight males, but one or more of the males present were normally silent at any given time (12-sec interval; see Fig. 2a). *L. planum*

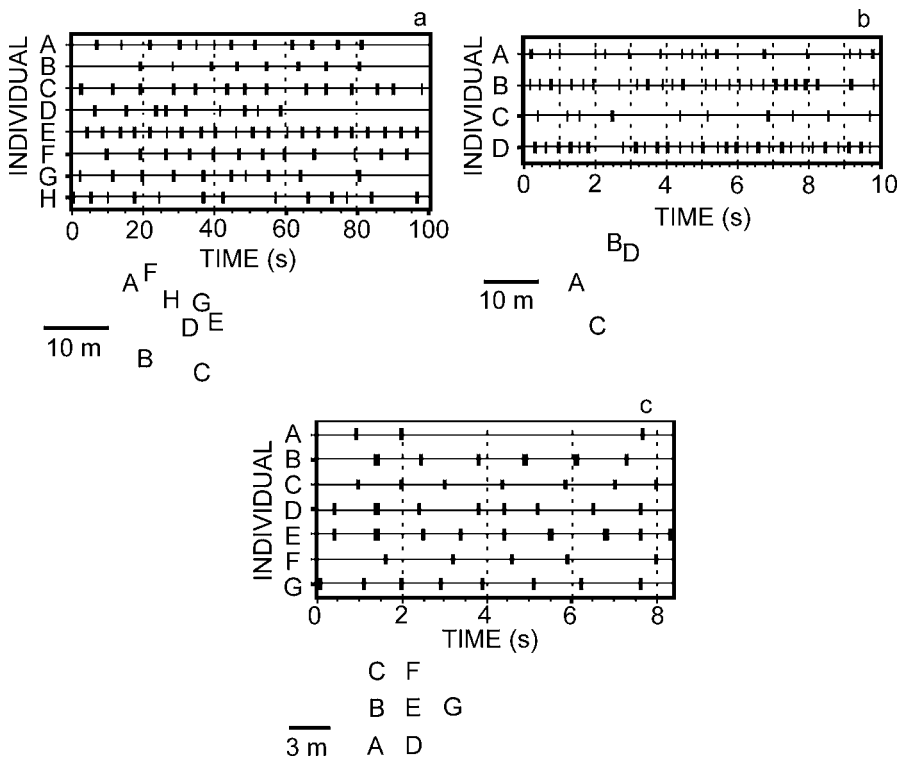


Fig. 2. Chorusing in three species of Orthoptera. Graphs show excerpts from lengthy chorus recordings of four-eight males (see Tables 2-4). Letters along y-axis designate individual males participating in the chorus, with vertical bars along each male's time line indicating its calls. Relative locations of the males are shown in the maps below the chorus graphs. (a) *Liguotettix planum* (Portal, Arizona; 1 August 1997); (b) *Neoconocephalus spiza* (Gamboa, Panama; 20 July 1996); (c) *Ephippiger ephippiger* monosyllabic race (St. Jean de Buèges, Dept. Hérault, France; 5 July 2000).

males seldom moved out of microphone recording range, and when they did move to different positions among their host plants, *Flourensia cernua* bushes, we were able to reposition the microphone without disturbing them or losing significant calling data. The latter advantage was possible owing to the relatively slow signal rate, $\approx 5\text{-}10$ calls $\cdot\text{min}^{-1}$. To keep track of the individuals being recorded and their positions, we applied unique enamel marks to the pronotum of each male in our field site, a $60 \times 130\text{-m}$ plot, and gridded the site with stake flags at 5-m intervals. We recorded *L. planum* choruses on six different days, one chorus being recorded per day. All recordings were made at the same site, and eight males (20% of the total) were re-recorded in two or three successive choruses.

N. spiza choruses were recorded between 1930-2230 EST, the period of peak activity (Greenfield, 1988), and only on evenings without rain. Because *N. spiza* move between calling locations more than *L. planum* do, and are also more easily disturbed, we made

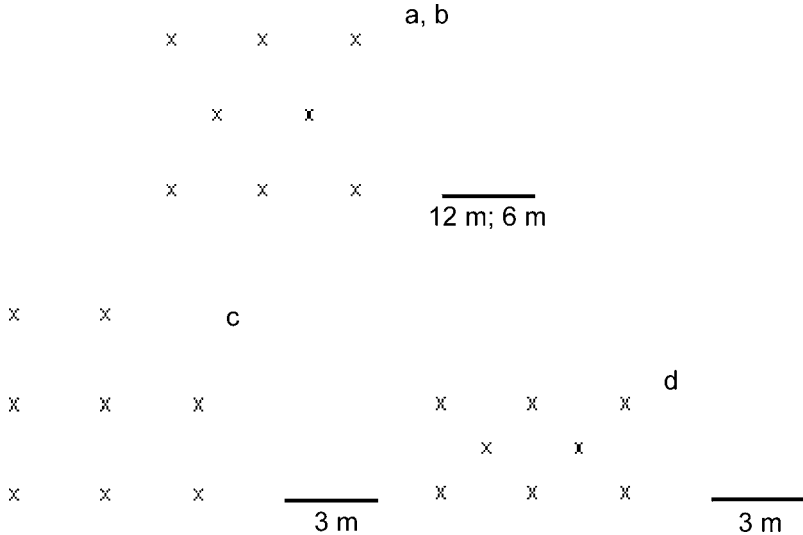


Fig. 3. Distributions of *Ehippiger ehippiger* (monosyllabic race) males in staged choruses established in the field during 1999 (a: nearest-neighbour distance = 12 m; b: nnd = 6 m) and 2000 (c: nnd = 3 m; d: nnd = 2.1 m). X denotes male location.

recordings averaging only 15 min in length. However, *N. spiza* signal at high rates, $\approx 2\text{--}4$ calls $\cdot\text{sec}^{-1}$, and we obtained sufficient data for meaningful analyses from these recordings. Our *N. spiza* choruses all included four males, but one or more of them often dropped out for several seconds to 1 min or longer and then reentered (Fig. 2b). We recorded six different choruses on as many evenings, and did not re-record any males. The location of each male within a chorus was mapped after the recording session. In the six recordings reported, all four males remained within microphone range throughout the session.

Unlike *L. planum* and *N. spiza*, most *E. ehippiger* males move slowly but constantly while calling, and we were forced to acquire much of our data on this species by using caged individuals with which we staged choruses. We obtained mature, calling *E. ehippiger* males from the field, uniquely marked them with enamel, and held them under ambient conditions within screen cages where they were provided food (cabbage, fish flakes, pollen) *ad libitum*. For staging choruses, we individually placed from six to eight males in 2-liter screen cages that we positioned in a large field > 100 m distant from naturally occurring *E. ehippiger* populations. We established these choruses during morning hours, the period of peak activity, and only on hot, sunny days. Cages were placed on gridlines such that all nearest-neighbour distances in a given chorus were equivalent: 2.1, 3, 6, or 12 m in the various choruses (see Fig. 3). These dispersions reflect the range of spacing found in naturally occurring choruses (see below). We recorded our *E. ehippiger* choruses for 1 to 2 h with microphones clipped on each cage and sent the microphone outputs through a multi-channel amplifier (Cambridge Electronic Design (CED) model 2806; Cambridge, U.K.) en route to a multi-channel recorder (CED model Power 1401). Using CED Spike 2 software, digitized output from the Power 1401 was transferred to a notebook computer and saved as a file. Our ability to stage *E. ehippiger* choruses relied on the propensity of males to call regularly while caged, behaviour

not observed in *L. planum* or *N. spiza*. Although we were able to record very little naturally occurring chrousing in *E. ephippiger* (see Results), we were afforded the opportunity to study chorus interactions under more controlled conditions in this species. Thus, we recorded seven and eight staged choruses on as many days during July 1999 and 2000, respectively (Fig. 2c). Several males were reused in successive choruses during 1999, but we did not reuse males during 2000.

We recorded chorusing males with either Shure BG-4.0 unidirectional cardioid microphones (flat response from 4 to 18,000 Hz; *L. planum*, *N. spiza*) or RadioShack 33-3003 omnidirectional microphones (± 2 dB response from 70 to 10,000 Hz; *E. ephippiger*). In *L. planum* and *E. ephippiger*, microphones were placed within 30 cm of calling males, and nearest-neighbour distances were relatively long. Consequently, call amplitudes recorded from the focal males adjacent to the microphones were always much higher than those of neighbours, and crosstalk between channels (recording the calls of non-focal males) was not a problem during analysis of chorus interactions. In *N. spiza*, however, microphones could not always be placed very close to the males, and nearest-neighbour distances were sometimes as short as 1 m. To reduce the crosstalk between microphones in our *N. spiza* recordings, we enhanced directionality of the microphones by placing them within conical metal shields.

Our multi-channel recording devices digitally sampled total microphone output at 20 kHz (custom device; *L. planum*, *N. spiza*) or 250 kHz (CED Power 1401; *E. ephippiger*). Because the effective digital sampling rate for each male (channel) equaled the total value divided by the number of males recorded, we did not obtain spectral information on the calls, all of which included frequencies above 10 kHz (see Table 1). However, the effective sampling rates were sufficiently high that we obtained precise information (± 1 msec) on call timing. This level of precision was enabled by digitally filtering (high-pass, set at 200 Hz) the computer files of our chorus recordings, which removed background noise and internal electrical spikes. We then applied a signal detection program (a modification of one available from CED) to the filtered files in order to identify call onset times and call lengths and saved these temporal values for the detected calls to an array in a data file.

Selective attention in Neoconocephalus spiza: Playback experiments

We supplemented our chorus recordings of *N. spiza* with a playback experiment investigating selective attention in this species. The basic method used in a previous study on *L. planum* (Snedden *et al.*, 1998) was applied: A focal calling male was selected, its conspecific calling neighbours were temporarily removed, and two loudspeakers (Radio Shack model 40-1377; ± 2 dB response from 4-50 kHz) were placed on opposite sides of the male, one relatively close (2 or 4 m distant) and the other farther away (4 or 8 m). Each loudspeaker broadcast a 'standard' *N. spiza* advertisement call, a natural recording 50 msec in length and delivered at $3.3 \text{ chirps} \cdot \text{sec}^{-1}$, driven by a stereo DAT recorder (Casio DA-7; sampling frequency = 48 kHz), the 'playback recorder.' Broadcasts of the two loudspeakers were maintained 180° out-of-phase, which caused the focal male to hear a chirp every 150 msec. Using a sound level meter (General Radio model 1982; set on peak response and 8 kHz band-pass filter), we adjusted the gain of both loudspeakers until the chirps broadcast by each were 80 dB peSPL (0 dB = $20 \mu\text{Pa}$) at 1 m, an amplitude comparable to that generated by males (*cf* Table 1). Thus, the focal male perceived broadcasts from loudspeakers positioned at 2, 4, and 8 m as *ca* 74, 68, and 62 dB, respectively. The loudspeaker configuration with close and distant positions at 2 and 8 m was tested in an additional series of trials wherein SPLs were adjusted

to 74 dB at 1 m; here, the focal male perceived broadcasts at *ca* 68 and 56 dB, respectively. This additional series of trials tested whether the SPL differential necessary for selective attention depended on absolute amplitude.

Each playback trial lasted for 1 min and consisted of three consecutive segments: (1) an initial 20 sec during which we only recorded the male's solo calling; (2) a 20-sec interval when we broadcast calls from both loudspeakers; (3) a final 20-sec interval when we broadcast calls from the distant loudspeaker only (see Snedden *et al.*, 1998). We recorded the focal male's calls during all three segments on a second stereo recorder (Marantz, model PMD-430) fitted with a directional microphone (AKG model C451E; flat response from 20-20,000 Hz); this recorder also received the loudspeaker stimuli via a patch cord from the playback recorder. To evaluate selective attention, we analyzed relative timing of the focal male's calls and the loudspeaker broadcasts; the latter was adjusted by the travel time of sound from the loudspeakers to the male. Males that were not strongly inhibited from calling shortly after broadcasts by the distant loudspeaker during playback segment 2 but who were so inhibited during segment 3 were considered to exhibit selective attention toward louder (nearby) calls: They could hear and respond to the more distant calls but ignored them when the nearer calls were broadcast.

For each of four loudspeaker configurations, we tested 9-20 individuals at our Gamboa, Panama site during July 1996. The four configurations included close and distant loudspeakers at 2 and 4 m, 2 and 8 m, and 4 and 8 m from the focal male, all with peSPL at 1 m adjusted to 80 dB, and close and distant loudspeakers at 2 and 8 m with peSPL at 1 m adjusted to 74 dB. Each individual was tested in one or two playback trials, a given trial using one of the four loudspeaker configurations; the successive trials with which an individual was tested were presented in random sequence. Results from these trials enhanced our interpretation of chorus recordings in *N. spiza*.

Precedence effect and Inhibitory-resetting in Ehippiger ehippiger: Playback experiments

We conducted two playback experiments with *E. ehippiger* to obtain baseline information on female preferences for leading calls and on male call rhythm adjustments in the specific population whose natural choruses were studied. In both experiments, we used laboratory-reared insects derived from eggs collected at our field site and tested them in a semi-anechoic chamber (3.5 × 3.5 × 2.5 m) at the University of Kansas, Lawrence, Kansas. The chamber was kept at 24-27°C and illuminated with overhead fluorescent bulbs. We restricted testing to the beginning 6 h of the photophase. To ensure that responses concomitant with reproductive maturity were observed, we only tested insects that were at least 20 days past their adult molt. Although the precedence effect and inhibitory-resetting were described previously for *E. ehippiger* (Greenfield *et al.*, 1997; see Fig. 1c), these earlier values were obtained from a different population, one in which calls included two, rather than one, syllables. Thus, results from the experiments described here were needed for accurate evaluation of our *E. ehippiger* chorus recordings.

We tested the extent of the precedence effect in *E. ehippiger* females by playback of two identical, standard calls (a digitized natural recording) from two spatially separated loudspeakers (Radio Shack model 40-1377; see Minckley & Greenfield, 1995 for basic method in *L. planum*; see Snedden & Greenfield, 1998 for *N. spiza*). The call rhythm delivered by each loudspeaker was held at 1-sec⁻¹ in all trials, with the phase of one loudspeaker delayed by a fixed time interval; the leading role was switched between the two loudspeakers in successive

trials to prevent female directional biases from confounding our results. Females were tested individually on a y-maze whose two arms diverged by 90° and projected upward at 10° directly toward the two loudspeakers. We monitored the insects as they moved from the base of the y to one of its arms during playback trials 2 min in length. Thus, we tested 36 females at each of 21 different phase-delay intervals (0-500 msec, in 25-msec increments). Each female was tested in 4-16 consecutive trials at a given phase-delay interval, with later sets of trials (at other intervals) on that day spaced every 20 min or longer. The selection of phase-delay intervals for successive sessions was randomized.

We created the call stimulus by recording a male at our field site, amplifying the microphone (Linear-XM51; flat response from 10-40,000 Hz) output, and sending the output to two channels of the CED Power 1401 recorder and then to the notebook computer, in which a 1-sec segment that included a single standard call was saved to a stereo file. Using digital signal processing software (SoundFX; SiliconSoft; San Jose, California), we delayed one channel of the stereo file by a prescribed time interval. For playback trials in the semi-anechoic chamber, we looped this edited file continuously on a desktop computer that drove the two (leading and following) loudspeakers. Digital:analog conversion (SoundFX Engineering Version, SiliconSoft) of the computer output was performed at a sampling rate of 100 kHz to ensure that all call frequencies were faithfully reproduced in the broadcasts. 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. This level was comparable to that which male *E. ephippiger* broadcast (cf Table 1).

Examination of inhibitory-resetting in male *E. ephippiger* was done similarly. Here, we used a single loudspeaker to present individual, caged males with call stimuli that were repeated at random intervals (1-10 sec) during 2-min playback trials (see Greenfield & Roizen, 1993 for basic method in *N. spiza*; see Minckley *et al.*, 1995 for *L. planum*). The random timing prevented males from entraining to a stimulus rhythm. We determined the relative timing of playback stimuli and the focal male's calls according to the protocol described above in *Selective Attention in N. spiza*. For each of the 15 males tested, we constructed a 'delay histogram' showing the frequency of calls that began within each of 24 consecutive 50-msec bins, bin 1 starting at the onset of the playback stimulus (cf Fig. 1). Males who reduced their incidence of calling during an interval beginning shortly after the stimulus onset were considered to be adjusting their call rhythm via inhibitory-resetting.

Natural choruses in Ephippiger ephippiger

We monitored the spacing of 62 males calling within naturally occurring *E. ephippiger* choruses to determine the range of inter-neighbour distances. This range was compared with the dispersions of caged males established in our staged choruses (see above). We also recorded two naturally occurring choruses of five to seven males to compare their calling with that of the caged males.

Data analysis

In all three species, we analyzed the data arrays derived from our multichannel chorus recordings to determine the number and identities of neighbours that a focal male attended to and the locations of those neighbours. Attention was defined as refraining from initiating calls

during a ‘critical interval’ following the onset of the neighbour’s call (see Fig. 1). We determined a species’ critical interval by inspecting its male call delay histogram and the extent of the precedence effect in female response. The delay histogram revealed that when males refrained from initiating calls following a stimulus onset, they did not cease immediately but only after a brief post-stimulus onset interval of length d (Fig. 1d; Greenfield & Roizen, 1993). This interval was interpreted as an effector delay, a latency between inhibition of the central rhythm generator by the stimulus and the peripheral manifestation of such inhibition, the cessation of song (Greenfield *et al.*, 1997). Thus, any call triggered by the central generator during a pre-stimulus interval of length d would still be produced during a post-stimulus onset interval of equivalent length. Data on the precedence effect indicated the longest time interval, t , between the onsets of two calls for which females exhibited a significantly higher response toward the leading one (Fig. 1d). Designating stimulus onset as time 0, we defined the critical interval as extending from d to t . In species where the maximum call delay at which females preferred the leading stimulus was much shorter than the delay between stimulus onset and a male’s first post-stimulus calls (*e.g.* Fig. 1b; here, inhibitory-resetting does not reduce the incidence of following calls during the call cycle concurrent with the stimulus; rather, it increases the incidence of leading calls during the next cycle(s)), however, we defined t as the onset of those first post-stimulus calls. By these criteria, calls broadcast during the critical interval (d to t) would be relatively ineffective sexual advertisements; potentially, they could be suppressed via inhibitory-resetting (see Appendix).

We began analysis of a chorus by considering only those call cycles during which all males sang: For each focal male in the chorus, we tallied the total number of calls for which, during the previous cycle, all other males called at least once (Appendix). Using this set of the focal male’s calls, we then tallied the number of times his call was broadcast during the critical interval of each neighbour and compared these observed values with the binomial expectation. For example, if the critical interval and call cycle were 275 and 1000 msec long, respectively, we expected 27.5% of the focal male’s calls to fall, by chance alone, during the critical interval of any given neighbour. Thus, for each focal male in a chorus, we determined the probability that he adjusted his rhythm such that calls did not follow a particular neighbour (Snedden *et al.*, 1998). Probability values were corrected for multiple tests with the Holm procedure (Krauth, 1988), and we calculated the power of each test (Zar, 1984). Because Euclidean distances between neighbours were noted, we also determined the spatial dispersion of those neighbours whom a focal male avoided following. In determining whether a focal male’s call fell during given neighbour’s critical interval, call onset times were adjusted by the travel time of sound from the neighbour to the focal male (Greenfield *et al.*, 1997). To boost sample sizes of calls in some of our *L. planum* and *E. ephippiger* choruses, we constructed and analyzed reduced matrixes that omitted one or more males who called infrequently.

Results

Baseline information: Precedence and inhibitory-resetting

Laboratory playback tests on our *E. ephippiger* population showed that the majority of females tended to orient toward leading male calls and that this

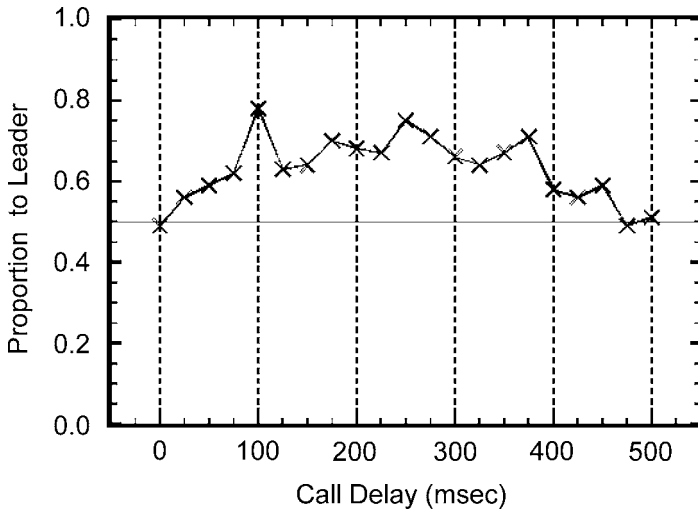


Fig. 4. Precedence effect in *Ehippiger ehippiger* (monosyllabic race). Graph shows proportion of orientation by females to the leading of two 110-msec calls broadcast from separate directions; call delay represents the interval separating the onsets of the two calls. At each call delay, 36 females were tested in 4-16 consecutive trials. For call delays ranging from 75 to 375 msec, a female was more likely to orient toward the leading call in > 50% of her trials ($p < 0.05$, sign test, corrected for multiple tests via the Holm procedure).

precedence effect continued until 375 msec after stimulus onset. That is, males whose calls followed a neighbour's by an interval from 75 to 375 msec would be relatively unattractive to females, who preferred leading calls approx. 70% of the time (Fig. 4). Playback tests also showed that males in our *E. ehippiger* population adjusted the phase of their call rhythm by an inhibitory-resetting mechanism. All 15 males tested refrained from initiating calls during a critical interval extending from 100 to 350 msec following stimulus onset (Fig. 1d). These characteristics are similar to, but do not match, those reported earlier for a different (two-syllable) *E. ehippiger* population (Greenfield, 1997; Fig. 1c).

Selective attention

Ligurotettix planum. Analyses of the six *L. planum* choruses in which four or more males regularly called showed that individuals who adjusted their call rhythms in response to their neighbours paid significant attention to only one or two of them (Table 2; Fig. 5). But, we also found that many individuals ignored all of their neighbours; *i.e.* they called during the critical intervals

TABLE 2. *Selective attention in *Ligurotettix planum* choruses recorded at Portal, Arizona*

Chorus date	N^a	Number neighbours attended to ^b				Mean number attended ^b	Proportion males attending to 1 st and 2 nd nearest neighbours ^b	Mean 1 st and 2 nd nearest neighbour distances (m)
		0	1	2	3			
17 July 1997	7 (5)	3 (2)	0 (1)	2 (2)	0.8 (1.0)	2/5, 2/5	5.15, 7.58	
19 July	5 (4)	0 (0)	4 (3)	0 (1)	1.0 (1.25)	4/4, 0/4	6.60, 10.36	
31 July	6 (5)	3 (3)	2 (2)		0.4 (0.4)	2/5, 0/5	9.76, 11.66	
1 August	8 (6)	5 (4)	1 (2)		0.17 (0.33)	0/6*, 1/6	5.66, 6.81	
2 August	6 (6)	5 (4)	1 (0)	0 (2)	0.17 (0.67)	1/6, 0/6	5.75, 7.91	
7 August	7 (4)	3 (1)	1 (2)	0 (1)	0.25 (1.0)	1/4, 0/4	4.71, 6.60	
grand mean ^c					0.43 (0.73), 0.34 (0.63)			

^a Total number of males in chorus, with number calling regularly (at least 30 calls produced during call cycles of other neighbours; see Appendix) shown in parentheses. Attention statistics are calculated from regularly calling males only.

^b Using a critical interval extending from 200-1800 msec following the onset of a neighbour's call (Fig. 1a) and a call cycle = 12 sec, attention is identified when a focal male produces significantly fewer calls ($p < 0.05$; 2-tailed binomial test corrected for multiple tests via Holm procedure) during a neighbour's critical intervals than predicted by uniform distribution; power of these tests ranged from 0.5-0.7. Parenthetical values indicate attention identified when focal male produces <50% of the number of calls during critical intervals than that predicted by a uniform distribution.

^c Values in second row are grand means determined after removing data from repeated recordings of given focal males on successive chorus dates.

* Number of asterisks indicates number of focal males not attending to nearest neighbour.

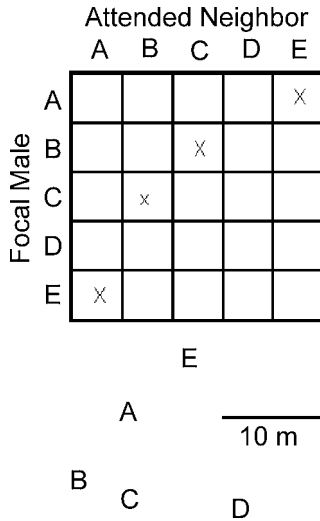


Fig. 5. Example of selective attention, as analyzed in a *Ligurotettix planum* chorus recorded at Portal, Arizona on 19 July 1997 (see Table 2). Relative locations of the five regularly calling males are shown in the map below. X indicates a focal male's attention to a neighbour, judged by refraining from calling during the critical interval following each of the neighbour's calls. X: $p < 0.05$; 2-tailed binomial test, corrected for multiple tests via Holm procedure. x: incidence of following calls $< 50\%$ that predicted by uniform distribution (see Appendix).

following every one. Because *L. planum* males are strongly inhibited by conspecific calls in controlled experiments (Fig. 1a), we judged that the low incidence of attention detected in natural choruses resulted from the small numbers of analyzable calls (see Appendix 1) produced by many males ($N < 40$ for 50% of males) combined with the low binomial expectation for a call to occur during a given neighbour's critical interval (0.133, calculated from a critical interval = 1.6 sec and a call cycle = 12 sec); moderate power (0.55-0.75; cf Tables 2-4) of our tests reflected this problem. But, long nearest-neighbour distances in some choruses (Table 2) may have also contributed to the low attention rate. In fact, the chorus in which males exhibited the second lowest overall incidence of attention (31 July) had the most dispersed distribution, with a mean nearest-neighbour distance = 9.76 m (Table 2).

The neighbours that a focal *L. planum* male attended to were generally the nearest or second nearest individuals within the chorus (Table 2). To examine the relationship between a neighbour's distance and his treatment by the focal male further, we relaxed our criterion for attention and considered any neighbour during whose critical intervals the focal male produced fewer

than 50% of the number of calls predicted by the binomial expectation. This relaxation yielded a larger sample of attended neighbours, and we again found that the majority were those nearest to the focal male (Table 2). We found that this generalization held in the reduced matrices that we analyzed and when repeated recordings of the same male in successive choruses (days) were removed from the data set.

Neoconocephalus spiza. Field playback tests on *N. spiza* revealed the existence of weak selective attention toward the nearer of two call stimuli. When presented with alternating calls broadcast 2 and 8 m distant (peSPL set at either 74 or 80 dB), most males (11 of 15 and 14 of 17, respectively) produced significantly more calling during the critical interval following the more distant stimulus than during the interval following the closer one ($p < 0.05$; 2-tailed binomial test, corrected for multiple tests by the Holm procedure). They also exhibited a small, yet significant ($p < 0.05$), reduction of calls following the distant stimulus when the closer one was turned off (Fig. 6). We did not observe significantly more calling following the more distant stimulus when the loudspeakers were placed 2 and 4 or 4 and 8 m distant (only 1 of 8 and 1 of 7 males, respectively, exhibited significant differences), implying that an SPL differential of 12 dB could elicit some selective attention toward the nearer call but a differential of 6 dB was insufficient.

Analyses of the six *N. spiza* choruses in which three or four males regularly called showed that 40% of individuals paid attention to all of their neighbours (Table 3). This high incidence of attention occurred regardless of the overall dispersion of the males. Unlike *L. planum*, the two *N. spiza* choruses in which the overall incidence of attention was lowest (15 July, 20 July), with most focal males attending to only one neighbour, did not have the most dispersed distributions (Table 3). Complicating the matter further, in these two choruses the particular neighbours whom the focal males attended were not the nearest ones.

Ephippiger ephippiger. Analyses of the 15 *E. ephippiger* choruses staged during 1999 and 2000 in which three to eight males regularly called showed that the majority of individuals adjusted their call rhythms in response to neighbours (Table 4). A focal male usually attended to one or two neighbours, but chorus dispersion influenced this number: In choruses with 6 or 12-m nearest-neighbour distances, many males did not attend to any neighbours, whereas in choruses with 2.1 or 3-m nearest-neighbour distances a

TABLE 3. *Selective attention in Neoconocephalus spiza choruses recorded at Gamboa, Panama*

Chorus date	N ^a	Number neighbours attended to ^b				Mean number attended ^b	Proportion males attending to 1 st and 2 nd nearest neighbours ^b	Mean 1 st and 2 nd nearest-neighbour distances (m)
		0	1	2	3			
15 July 1996	4 (3)	1	2			0.67	0/3**, 2/3	2.07, 3.53
16 July	4 (4)	0	0	1	3	2.75	4/4, 4/4	6.43, 8.95
19 July	4 (4)	0	4			1.0	3/4*, 0/4	2.55, 3.5
20 July	4 (4)	1	3			0.75	0/4***, 2/4	8.15, 10.8
28 July	4 (4)	0	0	1	3	2.75	4/4, 3/4	12.08, 14.93
29 July	4 (3)	0	1	2		1.67	2/3*, 3/3	9.93, 15.67
grand mean						1.64		

^a Total number of males in chorus, with number calling regularly (at least 30 calls produced during call cycles of other neighbours: see Appendix) shown in parentheses. Attention statistics are calculated from regularly calling males only.

^b Using a critical interval extending from 60-180 msec following the onset of a neighbour's call (Fig. 1b) and a call cycle = 480 sec, attention is identified when a focal male produces significantly fewer calls ($p < 0.05$; 2-tailed binomial test corrected for multiple tests via Holm procedure) during a neighbour's critical intervals than predicted by uniform distribution; power of these tests ranged from 0.58-0.75.

* Number of asterisks indicates number of focal males not attending to nearest neighbour.

TABLE 4. *Selective attention in Ephippiger ephippiger (monosyllabic race) choruses recorded at St. Jean de Buèges, Dept. Hérault, France*

Chorus date	N ^a	Number neighbours attended to ^b				Mean number attended ^b	Proportion males attending to 1 st and 2 nd nearest neighbours ^b	Mean 1 st and 2 nd nearest-neighbour distances (m)
		0	1	2	3			
18 July 1999	8 (8)	8				0		6, 6
19 July	8 (8)	8				0		6, 6
20 July	6 (6)	6				0		12, 12
21 July	8 (5)	5				0		12, 12
22 July	7 (5)	3	2			0.4	1/5*, 0/5	12, 12
23 July	6 (4)	1	2	1		1.0	2/4*, 1/4	12, 12
24 July	8 (5)	5				0		6, 6
5 July 2000	7 (5)	4	1			0.2	1/5, 0/5	3, 3
6 July	6 (4)	3	1			0.25	1/4, 0/4	3, 3
8 July	8 (6)	2	2	2		1.0	3/6*, 1/6	3, 3
13 July	6 (4)	0	2	2		1.5	2/4**, 1/4	3, 3
16 July	8 (4)	0	2	1	1	1.75	4/4, 1/4	3, 3
22 July	7 (5)	0	1	0	3	2.8	4/5*, 4/5	2.1, 2.1
23 July	5 (3)	1	0	2		1.33	2/3, 2/3	2.1, 2.1
25 July	6 (5)	1	1	1	1	2.0	3/5*, 2/5	2.1, 2.1
grand mean ^c						0.3, 0, 1.17, 2.15		

^a Total number of males in chorus, with number calling regularly (at least 30 calls produced during call cycles of other neighbours; see Appendix) shown in parentheses. Attention statistics are calculated from regularly calling males only.

^b Using a critical interval extending from 100-375 msec following the onset of a neighbour's call (Fig. 1d) and a call cycle = 1 sec, attention is identified when a focal male produces significantly fewer calls ($p < 0.05$; 2-tailed binomial test corrected for multiple tests via Holm procedure) during a neighbour's critical intervals than predicted by uniform distribution; power of these tests ranged from 0.6-0.8.

^c Four values indicate grand means determined in choruses with nearest neighbour distances = 12, 6, 3, and 2.1 m, respectively.

* Number of asterisks indicates number of focal males not attending to nearest neighbour.

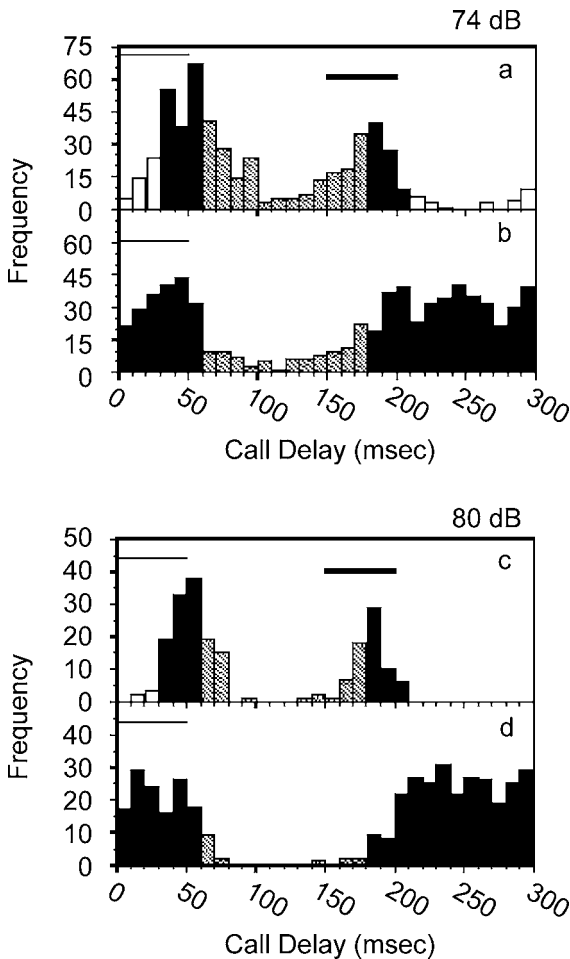


Fig. 6. Call delay histograms for playback experiment investigating selective attention in *Neoconocephalus spiza*. Open bars represent calls given during critical intervals (60-180 msec, measured from stimulus onset) following the stimulus broadcast from the closer loudspeaker (2 m); shaded bars represent calls given during critical intervals following the stimulus broadcast from the more distant loudspeaker (8 m); solid bars represent calls given outside critical intervals. Thick and thin horizontal bars indicate timing of close and distant stimuli, respectively, during each 300-msec cycle. Loudspeaker amplitudes were set to 74 dB SPL, at 1 m, in playback trials summarized in upper graph, which shows data pooled from the 17 males that called during trials; amplitudes were set to 80 dB SPL, at 1 m, in lower graph, which shows data pooled from 15 males. Both loudspeakers broadcast in (a) and (c); only the more distant loudspeaker broadcast in (b) and (d).

few males attended to three or four neighbours (Table 4). For all chorus dispersions, attended neighbours were generally the nearest ones.

Observations of 47 *E. ephippiger* monitored in vineyards and garigue near St. Jean de Buèges showed that calling males dispersed at distances (mean nearest-neighbour distance = 4.83 m, range = 0.20-12.75 m) comparable to those used in our staged choruses (Fig. 3). The two chorus recordings that we were able to obtain of free-ranging males indicated adjustment of call rhythm in response to a single nearest neighbour.

Discussion

Previous and current findings show that chorusing in all three orthopteran species studied may be driven ultimately by precedence effects (*sensu* Zurek 1987) in hearing. Females are more likely to orient toward the leading of two (or more) spatially separated male signals, and they exhibit this bias even when the following signal begins after a brief silent gap (see Fig. 1, Minckley & Greenfield, 1995, and Snedden & Greenfield, 1998 for previous studies on *L. planum* and *N. spiza*; see Fig. 4 for current findings on *E. ephippiger*). Thus, the responses cannot result only from simple masking of the onset of the following call by the leader. Males adjust their call rhythms by inhibitory-resetting mechanisms with which they reduce their production of following calls (see Fig. 1a, b, d, Greenfield & Roizen, 1993, Minckley *et al.*, 1995, and Greenfield *et al.*, 1997 for previous studies; see Fig. 1d for current findings on *E. ephippiger*). Collectively, such call adjustments yield clusters of local alternation within *L. planum* (Fig. 2a) and *E. ephippiger* choruses (Fig. 2c) and chorus-wide imperfect synchrony in *N. spiza* (Fig. 2b).

In effecting their call adjustments, *L. planum* and *E. ephippiger* males pay attention on average to a single calling neighbour (Tables 2, 4). When nearest-neighbour distances are 6 or 12 m, however, *E. ephippiger* males may call regardless of their neighbours, attending to none (Table 4). At these dispersions, the perceived amplitudes of neighbours' calls possibly fall below hearing thresholds or thresholds for selective attention. Conversely, when nearest-neighbour distances are 2.1 m, *E. ephippiger* males may attend to two or more calling neighbours. Our distribution maps show that mean nearest-neighbour distances in natural *E. ephippiger* choruses cover the full range from 2.1 to 12 m. Intra-chorus variation among focal males

may reflect their different calling rhythms, which could influence their signal interactions with neighbours, or variation in their neighbours' calling (see below). *N. spiza* males differ from the other two species by attending to an average of two calling neighbours (Table 3). Some *N. spiza* attend to at least three neighbours (the maximum present in our samples), and they may display this level of response even when nearest neighbours are dispersed by 10 m or more. While it is conceivable that attention to multiple neighbours resulted when a focal male periodically switched its attention among several individual neighbours, dissection of our *N. spiza* choruses into separate time blocks revealed that this artifact did not occur.

In *L. planum* and *E. ephippiger*, males generally attend to nearest neighbours, presumably because their calls are perceived as having the loudest amplitude. These neighbours may also be a focal male's strongest competitors for local females, and the conflict between regular calling and inhibitory-resetting for avoiding the production of following calls may be resolved best by attending only to them. At this time we cannot identify the specific algorithms by which males in the various species attend to some neighbours and ignore others. Previous studies on *L. planum* (Snedden *et al.*, 1998) and other chorusing species (*e.g.* túngara frogs; Greenfield & Rand, 2000) suggest that a combination of sliding-threshold and fixed-number rules may be used. That is, a focal male may attend to the loudest neighbour and any others whose call amplitudes as perceived are within X dB of the loudest individual yet above the hearing/behavioural threshold (sliding-threshold rule), but he may ignore some of these other neighbours if the number of them exceeds a critical value (fixed-number rule). Moreover, this value may not be fixed absolutely. Rather, it may be modified by amplitude, with higher values used when the nearest neighbour is close and perceived as loud (*cf* Table 4).

Our consideration of attention as based primarily on distance and the relative amplitude of neighbours' calls makes several assumptions. First, all males produce identical calls broadcast with the same absolute amplitude, as measured at a given distance and direction, and from similar elevations above the ground. Second, a neighbour's posture relative to the focal male's ears is either invariant or does not influence perceived amplitude of the neighbour's calls. Third, vegetation between neighbouring males does not attenuate call amplitude. Clearly, each of these assumptions will often be violated (*e.g.* Römer, 1993; Forrest, 1994; Greenfield, 2002), and these violations may account for some of the instances where focal males ignore their nearest neighbours but attend to more distant ones, who may be calling at higher absolute

amplitudes or beaming their calls toward the focal male. Such violations may also explain why a given neighbour is attended to while one or more equidistant ones are ignored. But, it is also possible that chorusing males use other rules, possibly arbitrary ones, with which they select the particular neighbours whom they attend. For example, a focal male may resolve ambiguities by spectral features of neighbours' calls or by attention to the call on his left (or right; *i.e.* a pattern of earedness might characterize orthopteran populations, Greenfield, 2002). These possibilities would represent a more sophisticated form of selectivity that does not simply depend on sensory adaptation to a specific background intensity and responses to stimuli exceeding that level. Our current field data cannot determine whether sophisticated rules as these do occur, however further playback experiments of appropriate design may.

The major difference in attention among the three species studied is that *L. planum* and *E. ephippiger* males are rather selective whereas *N. spiza* seemingly attend to all nearby neighbours. This variation could reflect differences in neural processing among Orthoptera (see Pollack, 1998), but the different acoustic environments that arise in the various choruses may also play a role. Both *L. planum* and *E. ephippiger* call at relatively slow rhythms (≤ 1 call \cdot sec $^{-1}$), and inhibitory-resetting interactions yield alternation between neighbours: A focal individual inhibited and reset by a neighbour's call can rebound from inhibition much faster than the free-running call rhythm and will thereby produce his next call midway through the neighbour's call cycle (Greenfield, 1994b). On the other hand, *N. spiza* rhythms are much faster (> 2 calls \cdot sec $^{-1}$), and here inhibitory-resetting yields synchrony. Whereas both forms of chorus structure are merely emergent outcomes from the call rhythms of individual signalers (Greenfield, 1994a, b), these outcomes represent very different acoustic — and social — environments within which the individual signalers must operate. In the case of alternation, a focal male will likely be exposed to a nearly continuous stream of calls broadcast by his several neighbours, with only a few brief inter-call intervals of silence punctuating the chorus (Figs. 2a, c). Thus, the pressure to adopt a means of selectively attending to only a subset of neighbours may be strong. In synchrony, however, most neighbours' calls occur nearly simultaneously, and a focal male will not hear any calling during a large proportion of time (Fig. 2b). Consequently, he may attend to most neighbours and still

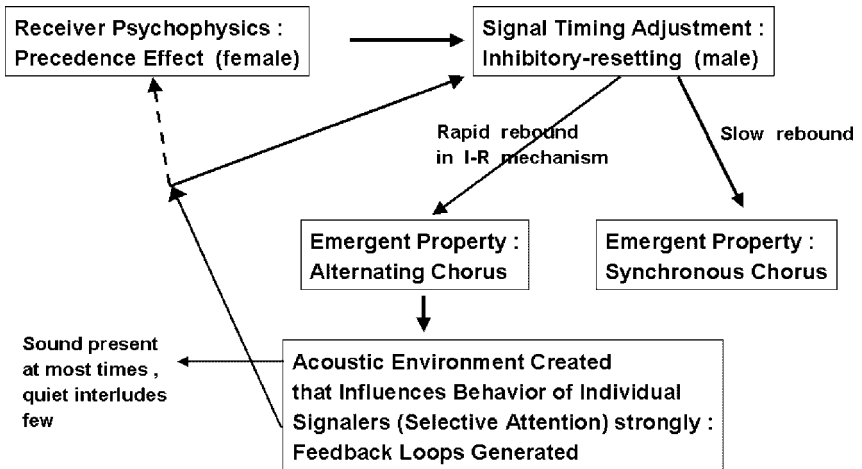


Fig. 7. Feedback loops that potentially influence the spatio-temporal structure of orthopteran choruses. When precedence effects influence receiver (female) perception, selection may favor timing adjustments — inhibitory-resetting (I-R) mechanisms — in signalers (males) that reduce the incidence of calls produced immediately after neighbours' calls. I-R mechanisms can generate alternating or synchronous choruses as emergent phenomena; alternation is generated when the rebound from inhibition in an I-R mechanism is rapid, whereas synchrony is generated when the rebound is relatively slower. An alternating chorus presents an acoustic environment in which sound is present at most times, silent interludes being rare: This environment may select strongly for selective attention in the I-R mechanism responsible for establishing the alternating chorus in the first place. Possibly, it influences the nature of receiver psychophysics (precedence effects) as well.

produce a relatively high number of calls. This expectation, observed in chorus recordings (Table 3), is consistent with the results from our playback experiment investigating selective attention in *N. spiza*; *i.e.* a 12-dB differential was necessary to elicit selective attention to a closer neighbour in *N. spiza* (Fig. 5), whereas 6 dB was sufficient in *L. planum* (Snedden *et al.*, 1998). These playback results confirm that the lack of selectivity detected in *N. spiza* recordings is real and not simply an artifact of the synchronous structure of chorusing, wherein a focal male's neighbours broadcast most of their calls during very narrow windows in time (Fig. 2b).

Selective attention to nearby neighbours is predicted by a Monte Carlo simulation of rhythmic chorusing (Greenfield *et al.*, 1997), and our observations of natural populations are roughly consistent with this prediction. However, our observations demonstrate that selectivity may be relaxed under certain conditions, indicating that the model needs refinement. Most im-

portantly, we raise the possibility that a group effect that arises simply as an emergent property may yet influence behaviour of the individuals contributing to that group effect (Fig. 7). Currently, our most critical need is field observation of additional species that may support or refute this general feedback mechanism and the proposed relationship between chorusing format and the degree of selectivity in attention.

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Appendix

We analyzed selective attention within choruses as follows: For each (focal) male in a recorded chorus, we identified all of its calls that were preceded, during an interval equal in length to a call cycle, by one or more calls broadcast by every other male in the chorus; the time length used for the call cycle was the upper limit for call period (=1/call rate) in the population. This set comprised those calls by the focal male that could have been influenced by any one of its neighbours. For a given focal male/ neighbour pair, we then distinguished

those calls, from the set identified above, that occurred during the critical interval of the neighbour; the critical interval was defined as lasting from d to t msec following onset of the neighbour's call that immediately preceded the focal male's call (see text and Fig. 1). Calls so distinguished may be relatively ineffective in attracting females to the focal male, but the focal male could inhibit them if he were attending to the given neighbour. We compared the proportion of calls made by the focal male during the neighbour's critical interval with the proportion expected during this interval were its calls distributed uniformly over time. If the focal male's proportion was significantly less than expected ($p < 0.05$; 2-tailed binomial test, corrected for multiple tests with the Holm procedure), we considered him to be paying attention to that neighbour.

When the focal male's set of calls that were immediately preceded by calls made by every other male in the chorus was small (<30), a common occurrence in *L. planum* choruses, we removed that focal male and created a reduced focal male/neighbour pairwise matrix (see Fig. 5) to analyze. For each chorus reported in Tables 2, 3, and 4, data on attention are taken from the largest matrix in which every focal male produced at least 30 calls that were immediately preceded by calls made by every other male listed. Thus, we restricted our analyses to those focal male/neighbour pairs in which calling was regular enough for us to detect attention if it were occurring. The computer program used to perform these analyses is available from the authors upon request.
