

Chorus structure in tarbush grasshoppers: inhibition, selective phonoresponse and signal competition

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Abstract. In species where sexually advertising males signal in groups, the timing of an individual's signals relative to those of neighbours may be a critical aspect of mating success. Temporal signal interactions and their relation to female attraction were examined in the tarbush grasshopper, *Ligurotettix planum*. The acoustic signals of neighbouring *L. planum* males form a crudely alternating chorus. Alternation within male pairs is effected by an (inhibitory resetting) mechanism that causes a male to refrain from calling for at least a 1.8-s interval beginning 0.2 s after the onset of a neighbour's call. This mechanism is not equally applied to all neighbours. Rather, males are selectively inhibited by only their nearest one or two neighbours, whereas more distant, but audible, callers are ignored. Males also time their calls to occur shortly before calls at the ends of predictably recurring silent intervals. Consequently, males do not decrease their calling rates in high population density, and they compete effectively for females. Phonotaxis in *L. planum* females is characterized by preference for leading calls, a psychoacoustic feature that would select for timing mechanisms that avert the production of following calls in males. The inhibitory resetting mechanism averts such calls. Moreover, because males are only inhibited by nearest neighbours, their strongest competitors, they can avoid producing unattractive following calls and still maintain normal calling rates. By calling at the ends of silent intervals, males may actively compete with neighbours via 'attempting' to relegate the neighbours' calls to ineffective, from the neighbour's perspective, time intervals following the focal male's call.

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Many animal species in which males produce long-range sexual advertisement signals typically occur in population densities sufficiently high that signallers can perceive one another. In such circumstances it is not unusual for neighbouring males to adjust their signal timing mutually and thereby collectively produce a non-random temporal pattern (Alexander 1975; Greenfield & Shaw 1983). Of the various non-random patterns of collective signalling reported, the extremes of synchrony and alternation are most fascinating because of the precise timing often evident. Synchrony may be defined as an incidence of overlap of rhythmic signals much greater than that expected by chance, whereas alternation is a

situation in which rhythmic signals overlap less often than the random expectation. These patterns are developed most fully in acoustic and bioluminescent animals and are best known in insects, anurans and birds (Greenfield 1994a).

Population density is expected to exert a strong influence on patterns of collective signalling, particularly in species that normally alternate. This has been appreciated only recently, because most studies of signal interactions have focused on the experimentally ideal situation of an isolated pair of individuals or a single individual interacting with a playback stimulus (but see Brush & Narins 1989; Schwartz 1993, 1994). Under natural conditions, however, a male is likely to be surrounded by numerous signalling neighbours. As the number of neighbours increases, the focal male's opportunity to avoid signal overlap decreases incrementally with each added individual. Therefore, a male must either reduce his signalling rate or commit overlap. Evaluating the consequences

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of either option would depend on understanding the function of alternation, and this is the eventual objective of the study reported here.

Signal alternation in acoustic species has been ascribed either an adaptive/cooperative (Greenfield & Shaw 1983) or an incidental/competitive (e.g. Greenfield & Minckley 1993) function. Cooperative explanations include contentions that alternation per se has been selected for because an absence of signal overlap in a male group (1) maximizes the group's duty cycle and attracts more females per male (Greenfield 1994a) or (2) ensures that signal features conveying species identity or signaller 'quality' are unambiguously broadcast (see Passmore & Telford 1981; Schwartz 1987, 1994; Ibáñez 1993). The first cooperative explanation assumes that males compete for females on an inter-group basis and that females integrate acoustic power over a relatively long time interval during assessment of group loudness. The second explanation assumes that individual males within groups avoid behaviour that is strongly spiteful.

Competitive explanations claim that alternation results from male-male signal interactions between individuals within groups (Alexander 1975; Otte & Loftus-Hills 1979). For example, if a male's signal is ineffective when broadcast at a particular time relative to that of a neighbour, a male would be expected to time his calls so that signalling during this interval does not occur. This adjustment may also relegate the neighbour's call to an ineffective (from the neighbour's perspective) time interval relative to the focal male's call. If two males that sustain equivalent signalling rates both adhere to such a mechanism, a striking collective pattern can result incidentally. Recent work on the chorusing katydid, *Neoconocephalus spiza*, showed that male calls produced shortly after those of neighbours were relatively ineffective, because a strong 'precedence effect' existed in which females oriented towards the first call heard (Greenfield & Roizen 1993). This precedence effect led males to avoid calling immediately following their neighbours, and they collectively generated a synchronous chorus. However, in species that time their calls with slightly different mechanisms, alternation may conceivably result (Greenfield 1994a, b).

In the present paper we describe a study of an orthopteran that alternates its calls with its nearest neighbours, the tarbush grasshopper, *Ligurotettix planum* (Orthoptera: Acrididae:

Gomphocerinae). This paper focuses on (1) the nature of signal interactions in groups found in the field and (2) the mechanisms that regulate these complex interactions with multiple neighbours. Although our ultimate goal is an understanding of the function of signal interactions, we recognized that elucidating the proximate mechanisms involved would be prerequisite to thorough testing of the various hypotheses listed above. In a separate paper, we combine the timing mechanisms revealed here with information on female choice to discern fully the function of alternation in this species and how female choice may influence signal interactions in general (Minckley & Greenfield, in press).

Natural History of *Ligurotettix planum*

Ligurotettix planum are territorial grasshoppers endemic to the Chihuahuan Desert of southwestern North America. In the northern part of their range they restrict their feeding to *Flourensia cernua* (Asteraceae) foliage (Otte & Joern 1975). Dominant males defend individual host-plant shrubs, or groups of contiguous shrubs, as mating territories (Shelly & Greenfield 1989). If population density is low, defence is passively accomplished via stridulatory calls that result in a regular spacing of males. At higher density, males often intrude on each other's territories, and owners actively defend their territories against intruders via overt aggression (Greenfield & Minckley 1993).

The insects produce two types of stridulatory calls. Males deliver a 250–450-ms 'rasp' call, which serves both as a sexual advertisement signal and a territorial indication to neighbouring males, at 4–12 calls/min throughout midday hours. During aggressive encounters, males switch to a more complex call in which a variable number of 15–35-ms 'shucks' precede, and at times follow, a terminal rasp (Greenfield & Minckley 1993). Both stridulations include principal frequencies from 3 to 9 kHz and are generated by the hind femora rubbing against the forewings at approximately 150 legstrokes per s (at 30°C). Rasps entail simultaneous movement of both hind legs, and consequently their sound fields are relatively omnidirectional (cf. Bailey et al. 1993). Sound pressure levels (SPLs) of rasps are 60–65 dB (re 20 µPa) at 1 m.

The settlement of *L. planum* females among *Flourensia* shrubs is influenced by rasp calls of the

males (Minckley & Greenfield, in press). Females show considerably less site fidelity than males, and during inter-shrub movements females may be attracted by rasp calls. After a female arrives at a given shrub, the male usually detects her visually and makes the final approach.

Male *L. planum* display a chorusing pattern that superficially appears to be a form of alternation. However, closer observation reveals that the alternation of rasp calls of neighbours, males situated on *Flourensia* shrubs 2–10 m apart, is occasionally punctuated by synchrony (for other examples, see Alexander 1956; Jones 1966; Shaw 1968). This synchrony, plus the complications yielded by multiple neighbours and variable call rates among males, indicate critical issues that must be addressed to understand the mechanisms controlling call timing in natural populations.

EXPERIMENT 1: SIGNAL INTERACTIONS IN CHORUSES

Methods

Study sites

Signal interactions among male *L. planum* were studied at field sites near K-Bar, Big Bend National Park, Texas (July–August 1992) and Rodeo, New Mexico (July 1993). Both locations are typical Chihuahuan Desert habitats and are described in detail elsewhere (Greenfield & Minckley 1993 and Shelly & Greenfield 1989, respectively). At K-Bar we used the previously described plots, situated within a large stand of *Flourensia* shrubs, and an additional site that included only 20 *Flourensia* shrubs. This latter plot, termed the 'Weather Station Site', was separated from all other *Flourensia* shrubs by 40 m and was therefore invaluable for studying isolated choruses that included only a limited number of males. All field plots were gridded with stake flags spaced at 5-m intervals to facilitate precise determination of the insects' positions.

Recording

During July 1992 we individually marked all seven *L. planum* males at the K-Bar Weather Station Site and monitored their positions and signalling activity daily (Greenfield & Minckley 1993). The advertisement calls of groups of males were recorded on metal tape using a Marantz PMD 430 stereo cassette-recorder fitted with an

AKG C451E directional microphone and a Schoeps CMC4 cardioid response microphone (both with flat responses to 20 kHz). Observers oriented the microphones towards different parts of the focal chorus and announced the identity of the male responsible for each rasp call. Thus, the call and information on the insect producing it were recorded on the same tape channel. As long as we did not make sudden movements or disturb the *Flourensia* shrubs, our presence among the insects did not interrupt their calling.

We made recordings on 20–22 July 1992 of two two-male choruses, two three-male choruses, and one four-male chorus. All chorus recordings lasted 280–300 s and were made during peak male activity (1130–1430 hours Central Daylight Savings Time). In the two two-male choruses, males were spaced 2.5 and 2 m apart, respectively, and in the three- and four-male choruses inter-male distances ranged from 2.1 to 10 m ($\bar{X} \pm \text{SD} = 5.6 \pm 1.9$ m, $N=12$). We regulated the specific numbers and identities of individuals in these recorded choruses by removing three to five individuals to vials in an insulated, shaded box during the recording. After the recording we returned the removed males to their original shrubs. Within 15 min after we returned males to their shrubs, they usually resumed calling at rates comparable to those exhibited before removal. None the less, we did not use these individuals in subsequent chorus recordings for at least 2 h. Removal of males reduced the number of individuals between which interactions might take place in the focal chorus and thereby revealed interactive timing mechanisms. We then applied these mechanisms to understand the temporal structure of larger, natural choruses.

To evaluate how males change their pattern of calling when in the presence of other calling males, we also made 10-min recordings of six of the above individuals while all neighbouring males were removed. These sequences of solo calling were used in statistical analyses of the calling patterns of chorusing individuals.

We made additional recordings of *L. planum* choruses at Rodeo on 25–26 July 1993. We chose the Rodeo site because we had obtained data on female phonotaxis and choice from insects in this population (Minckley & Greenfield, in press). Seven pairs of regularly calling males were recorded for 206–451 s using the Marantz cassette-recorder and two AKG C451E directional

microphones oriented towards each insect. Inter-male distances within pairs ranged from 3 to 5 m, and all pairs were naturally isolated from their nearest calling neighbours by at least 8 m. Thus, we used the Rodeo sample to supplement the small sample of two-male choruses induced via the removals at the K-Bar site, and were also able to compare calling by males in manipulated (K-Bar) choruses with those in natural (Rodeo) choruses including the same number of individuals.

We determined the timing of calls in each chorus by sampling the recordings digitally at 25 kHz with a computer (486 processor; 33 MHz clock speed) equipped with a two-channel 'soundcard' (an input/output board, including 8-bit analogue:digital and digital:analogue converters, obtained from Silicon Soft, San Jose, California). After transcribing caller identities announced on the tape, we digitally filtered (high-pass filter set at 2.7 kHz) the recording to remove the observer's commentary and environmental sounds. Filtered, digitized signals were then analysed in the time domain using appropriate software (obtained from Silicon Soft and the University of Kansas Instrumentation Design Laboratory) to the nearest 10 ms.

We examined signal interactions in all pair-wise combinations of males i, j in a chorus by calculating the interval between the onset of male i 's call and the onset of the preceding call of male j . We determined this interval, termed the 'call delay', for all calls produced by each focal male i relative to the preceding call of every other chorus participant j made during i 's last call period (interval between onsets of consecutive calls of a given male).

Analysis of call delays

For statistical analysis, we compared the observed distributions of call delays within every pair of males in a chorus with a random distribution of call delays. We generated the random distribution by using calls of three males randomly chosen from the six recorded in solo and combining these isolated individuals into a simulated chorus. We then began the call sequence of each male in the simulated chorus at a random time, tabulated all six distributions of call delays, and combined the six distributions into one. In each of the nine two-male and two three-male choruses recorded, we compared the observed distributions of call delays with the simulated

distribution. We also performed this analysis on the four-male chorus, except that we chose four solo males for the simulated chorus generating the random distribution. The calling of isolated males is not influenced by the calls of neighbours and therefore would be expected to generate a close approximation to a null distribution of call delays when combined. Consequently, we chose to create the simulated choruses with isolated males rather than with the actual chorusing males; call periods of the latter were probably influenced by their neighbours and would not be expected to generate a null distribution of call delays.

Our analyses only considered call delays less than 5 s in length. Longer delays would include some spurious data based on calls not affected by a neighbour's call. That is, males occasionally do not call until an interval of two normal periods has passed since their last call, a phenomenon seen in both solo and chorusing individuals. Presumably, harmonics occur because central rhythm is retained in the absence of effector output (Buck et al. 1981a). Consequently, lengthy call delays may reflect spontaneous skipping of calling for a cycle rather than a response to a neighbour's call.

Analysis of call overlap

We developed a software program (available from the authors) that simulates calling by neighbours that do not influence one another, to compare the observed levels of call overlap between neighbouring males with levels of call overlap expected under the assumption that a male's calls are unaffected by his neighbour(s). We first rearranged call periods exhibited by given chorusing males in random sequences. To preclude relationships between the initial calls of neighbours, we then started randomized sequences of call periods of both males in a pair to be simulated at random times during their first call periods. Based on observed call lengths ($\bar{X} \pm \text{SE} = 0.351 \pm 0.034$ s, $N = 5-20$ calls of five males), all calls in simulated pairs were set at 0.35 s. We chose to generate these simulations by using call periods from the actual chorusing males to test specifically whether the distribution of call overlaps was random. Thus, we could detect any specific tendency to avoid overlap contributing towards the general non-randomness expected in call periods and call delays among chorusing individuals.

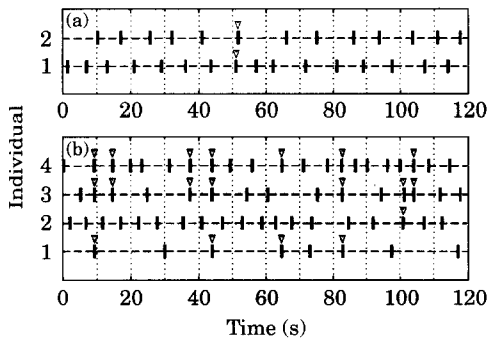


Figure 1. Examples of timing of calls (vertical lines) in groups of (a) two males and (b) four males. Arrows indicate calls that overlap calls of other males in the group.

We calculated the number of ‘call overlaps’, defined as occasions when the interval between the call onsets of two males was less than or equal to 0.35 s, for all pair-wise combinations within two-, three- and four-male choruses, and then compared these values with the number occurring in the corresponding simulation. Each simulation was run 1000 times, and we considered the observed number of call overlaps to be significantly less than the random expectation if this latter value exceeded the observed number in 95% of the simulation runs (Brush & Narins 1989).

Results and Discussion

Calling pattern in choruses

The majority of calls made by males in groups of two or more did not overlap calls of other males (Fig. 1), although some call overlap

occurred in groups of all sizes. Call overlap may be a consequence of inter- and intra-individual variation in call period. Males in the same group that were recorded at the same time exhibited approximately four-fold differences in mean calling periods (Table I). Within-individual variation in calling period was also high: the mean coefficient of variation for the chorusing males recorded at the Weather Station Site was 41% (range=29–56%). Because this intra-individual variation in call period was similar to the variation displayed by these males when all of their neighbours were removed (mean coefficient of variation 48%, range=38–60%, $N=6$), it is likely that some variation in call period was spontaneous and did not result from interactions with other calling males. This variation in calling period would prevent males from readily maintaining constant phase relationships with the calls of neighbours.

We expected the incidence of call overlap to increase as group size increased, and this hypothesis was generally supported. This incidence, computed as the number of overlapped calls divided by the total number of calls made by the group, increased from an average proportion of 0.04 in two-male choruses (range=0.00–0.09, $N=9$ pairs), to 0.13 in the three-male choruses, to 0.34 in the four-male chorus.

Because signal interactions may involve only a subset of neighbours, we examined the relationship between inter-male distance in male pairs and the incidence of call overlap within those pairs. In the three-male chorus where males were unequally spaced and in the four-male chorus, call overlap

Table I. Calling parameters of males in one four-male chorus and two three-male choruses recorded at Big Bend National Park during 1992

Date	Male identity	Call period (s) ($\bar{X} \pm \text{SD}$)	No. calls	Proportion of calls overlapped*
22 July	A	20.5 ± 8.9	14	0.53
	B	8.3 ± 4.6	34	0.24
	C	6.3 ± 2.0	47	0.43
	D	5.2 ± 1.8	56	0.32
22 July	B	7.9 ± 2.2	38	0.37
	C	7.0 ± 2.0	43	0.23
	D	5.9 ± 1.6	51	0.31
21 July	A	8.5 ± 2.9	49	0.16
	D	8.2 ± 2.8	51	0.29
	E	6.8 ± 2.4	61	0.21

*Proportion of calls that overlapped at least one other male’s call in the chorus.

Table II. Pair-wise comparisons among individuals in the four-male chorus and two three-male choruses treated in Table I

Male <i>i</i>	Male <i>j</i>				
	A	B	C	D	E
A	—	0.02** (10.1)	0.02** (5.4)	0.07* (5.0)	
B	0.02* (10.1)	—	0.05 (5.0)	0.04 (6.0)	
C	0.02*** (5.4)	0.05 (5.0)	—	0.06 (2.1)	
D	0.07 (5.0)	0.04 (6.0)	0.06 (2.1)	—	
B		—	0.05** (5.0)	0.07** (7.0)	
C		0.05** (5.0)	—	0.12 (4.0)	
D		0.07*** (7.0)	0.12 (4.0)	—	
A				0.04 (6.0)	0.09 (6.1)
D	0.04*** (6.0)			—	0.05* (6.0)
E	0.09* (6.1)			0.05* (6.0)	—

For each pair, proportional call overlap (proportion of all calls made by both males that overlap each other) and call delay skewedness (departure of a male's observed call delay distribution from the random, simulated distribution, as determined by Kolmogorov–Smirnov two-sample test) are shown. Nine cases of significant call delay skewedness remained significant ($P < 0.05$) when adjusted by the Holm multiple test procedure. Values in parentheses are inter-male distances (m) within pairs.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

level was generally higher in pairs separated by smaller distances (Table II). This result was contrary to our expectation that call adjustment would be greatest among nearest neighbours and would result in lower levels of overlap. In the three-male chorus where males were evenly spaced, the proportions of overlapping calls were similar in two of the male pairs, but higher in one pair. Selective response might result from other call features such as rate or length.

Call delays calculated for each pair-wise combination of males in all three- and four-male choruses showed that most males adjusted the timing of their calls in response to calls made by another individual. Of the 12 pairs of males in these three choruses, a non-random distribution of call delays occurred in both males in five pairs and in only one of the males in three pairs (Table II).

The non-random distribution of call delays by male *i* could be characterized by an absence of calls in the 1.8-s interval beginning 0.2 s after the onset of calls by male *j*. Examples (taken from an isolated pair) of this pattern of call delays are shown in Fig. 2. In all 24 males (*i*) in the 12 pairs, the number of calls produced in the 1.8-s intervals beginning 0.2 s after the onsets of the neighbour's (*j*) calls was less than the number of calls produced in the subsequent 1.8-s intervals beginning 2.0 s

after the onsets of the neighbour's calls (2.0–3.8 s; sign test, two-tailed: $P < 0.01$).

There was no obvious relationship between a male's incidence of call overlap and his calling rate in three- and four-male choruses (Table I). A male's incidence of call overlap was also not clearly related to his distribution of call delays (Table II). Some male pairs had a significantly non-random distribution of call delays yet exhibited relatively high levels of call overlap. Conversely, other male pairs did not mutually adjust the timing of their calls, but had low levels of overlap. Overall, the calling pattern of chorusing *L. planum* males is complex, and adjustments in call timing are only made between certain individuals. Signal interactions could be characterized as a general avoidance of call overlap, but a strict temporal relationship between the calls of the interacting individuals was not apparent.

Calling pattern in pairs

The distribution of call delays in pairs again showed that males adjusted the timing of their calls in response to calls of neighbours. Call delays of 13 of the 18 males in the nine pairs examined differed significantly (Kolmogorov–Smirnov two-sample test, adjusted by the Holm multiple test

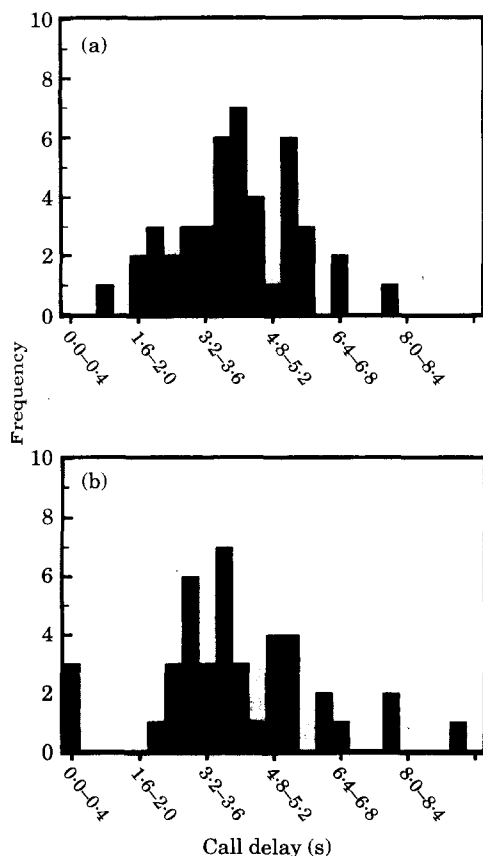


Figure 2. Distribution of time intervals (call delays) between the onsets of a focal male's (*i*) call and its neighbour's (*j*) preceding call, made since *i*'s last call, within an isolated pair, males 1 (a) and 2 (b). For statistical purposes, only call delays less than 5 s were considered (see experiment 1 for justification)

procedure: $P < 0.05$; bin width = 0.1 s) from the random (simulated) distribution of call delays. Adjustment was commonly bilateral: in five pairs the distributions of call delays of both males were non-random, but in three pairs only one male displayed a non-random distribution. The results are comparable to the incidence of non-random distributions of call delays observed in pair-wise combinations within larger chorusing groups (Table II).

As in choruses of three or more males, males rarely called during the 1.8-s interval beginning 0.2 s after the onset of a neighbour's call (Fig. 2).

In 17 of the 18 males (*i*) in the nine isolated pairs, the number of calls produced in the 1.8-s intervals beginning 0.2 s after the onset of the neighbour's (*j*) calls was less than the number of calls produced in the subsequent 1.8-s intervals (sign test, two-tailed: $P < 0.01$). This result suggested that the alternation observed in choruses occurred because males were inhibited from initiating calls shortly after their neighbours called. To test whether the level of call overlap between males was less than the level expected if males called regardless of when neighbours called, we compared the observed incidence of overlap in the nine pairs with the expected incidence of call overlap generated by the random simulations. Surprisingly, all males overlapped their calls as often as predicted by the random simulations.

The presence of call overlap was immediately referable to the specific timing of the 1.8-s silent interval in the observed distributions of call delays. Calling was not avoided until approximately 0.2 s following the onset of the neighbour's call. This behaviour would greatly reduce the incidence of males calling within 2 s of one another, but would not necessarily reduce the incidence of actual overlap. Assuming that calls are timed by a central rhythm oscillator and that effector output is triggered at a juncture slightly before call onset, males would be neurophysiologically incapable of an inhibitory response to a neighbour's call initiated after their own call is triggered (Buck et al. 1981b). Consequently, call overlap would not occur less frequently than randomly predicted.

EXPERIMENT 2: INHIBITORY RESETTING MECHANISM

Methods

Playback of single stimuli

Recordings of naturally occurring choruses, particularly those including two males only, confirmed our impression that *L. planum* adjusted their call timing in a predictable but complex manner that did not always avert overlap. To investigate these adjustments more accurately, we conducted playback experiments in which single rasp calls were broadcast to isolated males signaling at relatively constant rates. We used a genuine 0.35-s rasp call, representative of the K-Bar population, as the stimulus. This call was recorded and

digitized as in the recording of natural choruses, stored on a computer file, and then transferred to both channels of a digital-audio (DAT) tape. The tape was played back through a Casio DA-7 stereo DAT recorder, and the signal on one channel was broadcast through a Radio Shack 40-1377 loudspeaker (flat response from 4 to 50 kHz) oriented upward and placed approximately 3 m from a test male. Using a level control incorporated in the loudspeaker circuit and a sound level meter (General Radio model 1982), we adjusted the broadcasted rasps to 62–65 dB SPL as measured 1 m from the loudspeaker in any horizontal direction. The signal on the other channel of the playback stimulus tape was sent, by a patch cord, to a second 'recording' stereo cassette-recorder (Marantz PMD-430), which also recorded the response of the test insect via a directional microphone. Thus, the relative timing of the insect and stimulus was recorded on the same tape, which was then analysed in the same fashion as recordings of natural choruses. To determine the insect's initial calling rate, we began recording the insect at least 1 min prior to stimulus presentation.

We tested 26 males at the K-Bar plots during July 1992 with single playback rasps as above. An additional five males at Rodeo were tested on 27 July 1993. The stimulus rasp was presented to the test insect at a random time (call delay) during his call period. We calculated stimulus phase ($360^\circ \times$ call delay of the stimulus rasp, divided by length of the insect's previous call period, T_{n-1}) and response phase ($360^\circ \times$ lengthening or shortening of the call period ending immediately after the stimulus, $T_n - T_{n-1}$, divided by length of the immediately previous period, T_{n-1}) for each stimulus presentation. We then presented the regression of the response phase versus stimulus phase as a phase response curve (Walker 1969; Sismondo 1990).

As in the recording of natural choruses, we removed all calling *L. planum* males within 10 m of the focal male during playback tests. This simplifying measure reduced the number of acoustic stimuli in the focal insect's environment such that the playback rasp was at least 12 dB louder than the calls of any local males. As above, we returned removed males to their shrubs immediately after the playback, but did not subject them to playback tests until the following day.

Playback of lengthened stimuli

Recordings of natural choruses and playback of single stimulus rasps indicated that the mechanism regulating interactive signalling in *L. planum* was based on delaying the subsequent call upon perceiving a neighbour's rasp. To determine whether delaying was accompanied by inhibition throughout the duration of a call, we tested the responses of males to an abnormally long stimulus. This stimulus was made with a computer signal-editing program that lengthened the digitized 0.35-s stimulus rasp to a duration of 7 s without changing its principal frequencies (Greenfield 1993; Greenfield & Roizen 1993). Using the same playback protocol as above, we broadcast this 7-s stimulus twice to the five males tested at Rodeo on 27 July 1993.

Playback of serial stimuli

Besides adjusting the relative timing of their calls when in the presence of signalling neighbours, males may also modify their rate of calling. Because *L. planum* vary considerably in their solo calling rates, rate matching may allow males to maintain regular alternation. To determine whether this response occurred, we conducted playback tests in which we subjected focal males to 0.35-s, 62-dB stimulus rasps repeated at 6.2 calls/min for 2 min. Because the solo calling rates of the sampled males ranged from 4 to 9 calls/min, these playbacks included stimuli that were repeated slower than, equivalent to, or faster than the subject's calling rate.

We tested 44 males at the K-Bar plots during July 1992 in these 2-min playback tests broadcasting serial stimuli. Only males calling consistently were used. As before, we temporarily removed all neighbours within 10 m of the focal male. We created the 6.2-call/min serial stimulus from the single stimulus signal by using the 'looping' option in the computer signal-editing program. Unlike the tests using a single stimulus, loudspeaker broadcasts of the serial stimuli were driven directly from the output port of the computer's soundcard. To determine initial solo calling rates, we recorded males over a 4-min interval that began 2 min before the onset of the playback.

Results and Discussion

Responses to single stimuli

Males responded similarly to playback stimuli and to calls of other males, further confirming

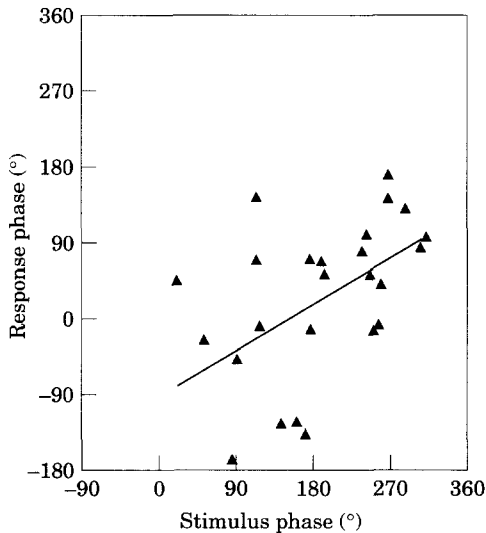


Figure 3. Phase response curve showing least-squares regression of response phase ($360^\circ \times$ lengthening or shortening of the call period ending immediately after a stimulus, divided by length of the immediately previous period) versus stimulus phase ($360^\circ \times$ call delay of the stimulus, divided by length of the insect's previous call period). Data represent single responses of 26 tested males that called regularly. $Y = -97.92 + 0.61X$; $r = 0.49$, $P < 0.01$; t (slope) = 2.78, $P < 0.01$.

that males were inhibited from calling after hearing a neighbour's call. When presented with a single stimulus rasp at a random time during their call period, males responded by lengthening their concurrent period by an amount commensurate with the delay of the stimulus. Response phase was approximately $0.6 \times$ stimulus phase, yielding a phase response curve with a slope approximately equal to 0.6 and passing below the origin (Fig. 3). This shallow phase response curve slope reflected an inhibitory response in which a male's central rhythm oscillator was reset to the basal level by a neighbour's call, but then rebounded to trigger the next call after an interval somewhat shorter than the normal (solo) call period (Greenfield 1994a).

Responses to lengthened stimuli

Males refrained from calling throughout the duration of the 7-s stimulus and lengthened their concurrent call period ($T_n > T_{n-1}$) in all but one of the 10 trials (binomial test, two-tailed: $P < 0.05$). Moreover, the call delay ($\bar{X} \pm \text{SD} = 1.7 \pm 1.5$ s)

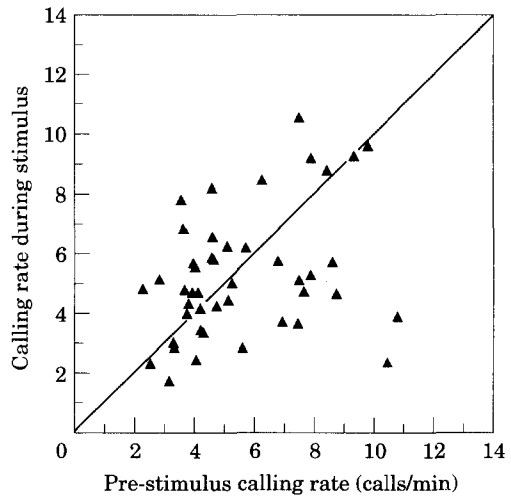


Figure 4. Calling rate during 2-min presentation of a 6.2-calls/min serial stimulus versus calling rate prior to stimulus presentation ($N = 44$). The diagonal line separates individuals that increased their calling rate during stimulus presentation from those that decreased it.

between the end of a 7-s stimulus and the onset of a male's subsequent call was similar to the call delay following a 0.35-s stimulus (cf. Fig. 2). These findings suggest that when the oscillator of an *L. planum* male is reset to its basal level at the onset of a stimulus call, it remains inhibited at that level, possibly until the termination of the stimulus. Playback of longer stimuli will be necessary to determine the full extent of this inhibition.

Responses to serial stimuli

We found no significant relationship between a male's solo calling rate and his propensity to increase or decrease calling rate during presentation of the 6.2-call/min serial stimuli (Fig. 4). We grouped the 44 test males into three categories according to whether their pre-stimulus calling rate was slower (less than 4.5 calls/min), comparable to (4.5–7 calls/min), or faster (greater than 7 calls/min) than the stimulus rate. After excluding the few males that did not change their calling rate during stimulus presentation, we found no consistent change in rate in any of the three groups (binomial test, two-tailed: $P > 0.05$). Therefore, it is unlikely that any observations of alternation were facilitated by males matching their calling rates.

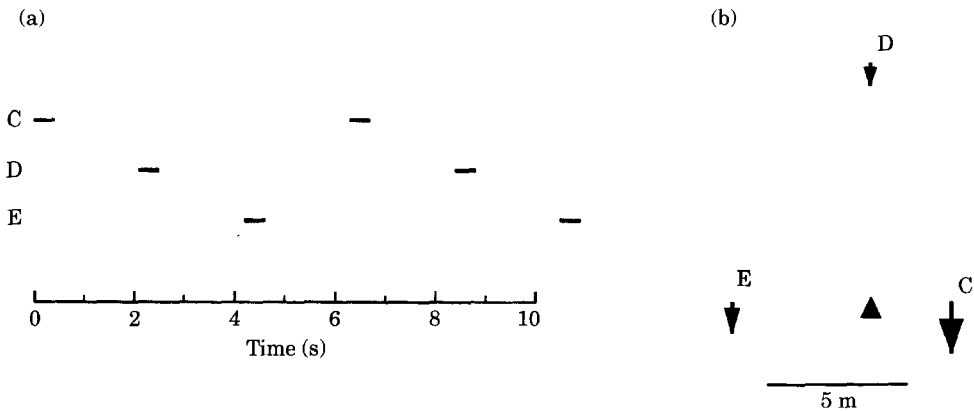


Figure 5. Experimental design testing selective phonoresponse to 0.35-s stimulus calls broadcast from loudspeakers C, D and E positioned 3, 5 and 8 m, respectively, from the focal male. (a) Timing of the calls (horizontal bars) presented sequentially from loudspeakers during 6.2-s stimulus periods. (b) Positions (\downarrow) of loudspeakers with respect to the focal male (\blacktriangle).

EXPERIMENT 3: SELECTIVE PHONORESPONSE

Methods

In choruses of three or more individuals we found that males responded most strongly to their nearest neighbours. To investigate this selectivity with greater accuracy, we conducted playback tests in which focal males were surrounded by three loudspeakers positioned 120° apart and 3, 5 and 8 m distant, respectively (Fig. 5). Each loudspeaker broadcast a rasp call every 6.2 s and 120° out of phase with the calls of the other two speakers. Thus, the focal male was subjected to rasps approximately every 2.1 s. We used a relatively fast (9.7 calls/min) stimulus rate in this and the following experiment so that all males, even those with fast solo rates, would call no more than once during a stimulus period. This feature greatly simplified data analysis.

We presented this multiple playback to nine males at the K-Bar plots in 8-min tests during August 1992. As before, we only used males that called consistently and removed all neighbours calling within 15 m during the tests. Each stimulus call was an identical 0.35-s, 62-dB (at 1 m from the loudspeaker) rasp, the same call used in single and serial stimulus playbacks, and the timing of the calls was controlled from the computer. Loudspeakers were driven directly from the port of an eight-channel output board in the computer. Six

males were subjected to a repeated sequence of broadcasts from the loudspeakers at 3, 5 and 8 m, and three males were subjected to a repeated sequence from the loudspeakers at 3, 8 and 5 m. We analysed the males' responses by measuring their call delays following broadcasts from each loudspeaker. Measurements made at the location of the focal male in every trial confirmed that the SPL of broadcasts always decreased as distance to the loudspeaker increased.

A potential difficulty with interpreting results from the preceding experiment was that males may not have perceived calls from the most distant loudspeaker (at 8 m). To determine whether this was a legitimate concern, we repositioned two loudspeakers at 8 m and adjusted their timing such that calls were broadcast at 0 and 2 s during each 6.2-s period. Thus, a 4.2-s silent interval occurred in every period. We subjected each of the nine males tested above to 2 min of this playback, during which all calling neighbours within 15 m were removed. Other playback experiments (see experiment 4) and observations of natural choruses indicated that males presented with regularly repeated silent intervals called mostly during the ends of the intervals. Therefore, we inferred that males that primarily called late in these 4.2-s silent intervals perceived signals at 8 m and that a strong response by these males to the nearest loudspeaker in the preceding experiment entailed facultative disregard for the distant broadcasts.

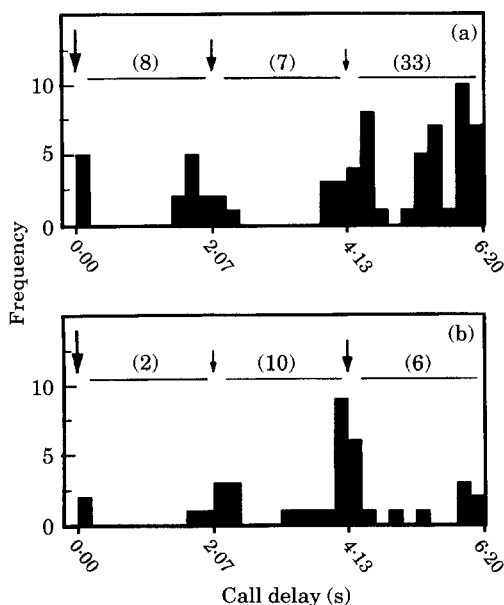


Figure 6. Examples of distributions of call delays (see Fig. 2) tabulated for two males, (a) and (b), presented for a period of 8 min with broadcasts from three loudspeakers 3, 5 and 8 m distant (see Fig. 5). Call delay is measured as the interval between the onset of a male's call and the onset of the preceding 3-m loudspeaker broadcast. The broadcast sequence repeatedly progressed from the 3-, 5- and 8-m loudspeakers (a) or from the 3-, 8- and 5-m broadcasts (b). Thick, medium and thin arrows indicate delays of the 3-, 5- and 8-m broadcasts, respectively, during each 6.2-s stimulus period; delay of the 3-m broadcast is 0 s by definition. Horizontal bars indicate 1.8-s intervals beginning 0.2 s after each loudspeaker broadcast, and values in parentheses are total numbers of calls given during these intervals, which span 8.5 bins.

Results and Discussion

Males did not respond equivalently to calls broadcast from loudspeakers at different distances (Fig. 6). In eight of the nine males tested, the number of calls produced in the 1.8-s intervals beginning 0.2 s following onsets of loudspeaker stimuli was highest for the (most distant) loudspeaker positioned 8 m away (binomial test, two-tailed: $P < 0.01$). We tabulated calls during these specific intervals, because results in experiment 1 showed that males seldom initiated calls 0.2–2.0 s following the call onsets of their neighbours.

Inability to hear broadcasts from loudspeakers 8 m distant cannot account for males calling

during the intervals 0.2–2.0 s following onsets of these broadcasts. When presented with stimulus calls broadcast from two loudspeakers each positioned at 8 m, males produced most of their calls during the ends of the 4.2-s silent intervals, a result also found with loudspeakers positioned at 3 m (see experiment 4). The distribution of call delays, pooled from 10.4 ± 5.6 calls ($\bar{X} \pm SD$) per male, differed from the random distribution of call delays generated from the simulated chorus (Kolmogorov–Smirnov two-sample test: $P < 0.05$; bin width = 0.1 s).

EXPERIMENT 4: SIGNAL COMPETITION

Methods

The tendency of male *L. planum* to call during the ends of regularly repeated silent intervals noted above could result from various timing adjustments. Males may (1) simply avoid calling shortly after any (nearby) neighbour, (2) entrain to the neighbour that regularly calls just before the interval and avoid calling after him, (3) entrain to the rhythm of the silent interval, or (4) entrain to the neighbour that regularly calls first after the interval and call shortly before him in an 'anticipatory' fashion. To discern which of these possible mechanisms regulated signal interactions, we conducted the following sequence reversal experiment. Three loudspeakers, C, D and E, were placed 3 m from a focal male at positions 120° apart (Fig. 7). As in the above experiment that tested perception of calls at 8 m, the loudspeakers broadcast identical 0.35-s 62-dB rasp calls at 0, 1 and 2 s, respectively, during a 6.2-s period, thereby leaving a 4.2-s interval. We programmed the computer to broadcast calls in this sequence for 2 min and then effect a reversal such that loudspeakers E, D and C broadcast calls at 0, 1 and 2 s, respectively, for an additional 2 min. With a tape-recorder receiving input from both the loudspeakers' broadcasts and the focal male's calls, we monitored the male's call timing throughout the 4-min playback test and detected any changes occurring after the reversal. We tested eight males, around which calling neighbours within 10 m were removed, with the above playback at the K-Bar plots during August 1992. Replacement and subsequent testing of replaced males in this and the above experiment followed the protocol outlined in experiment 1.

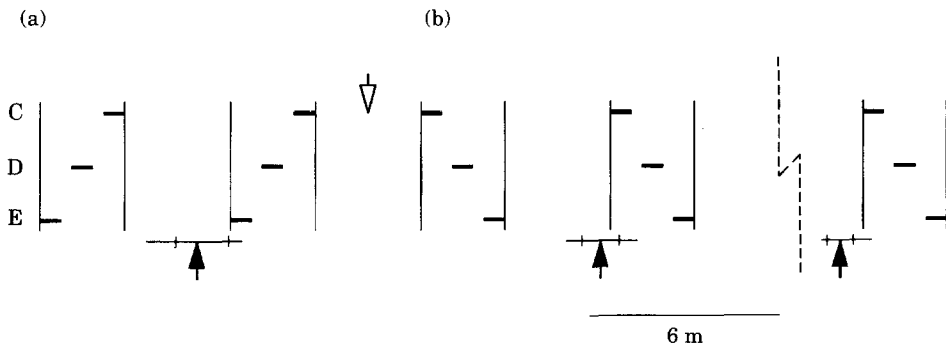


Figure 7. Experimental design testing phonoresponse to a reversal in the sequence (open arrow) or presentation of calls broadcast from three loudspeakers positioned 3 m from the focal male and separated by 120° azimuth angles. (a) Pre-reversal timing of calls (short horizontal bars) from loudspeakers C, D and E; solid vertical lines show the beginning and end of the 4.2-s silent interval present in each 6.2-s stimulus period. Mean (solid arrow), SD (vertical ticks) and range (horizontal bar) are indicated for the average times during stimulus periods that males called ($N=8$). (b) Post-reversal timing of calls. Mean, SD and range of the average times that tested males called are indicated for the first and fourth 30-s intervals following reversal.

If males simply avoided calling shortly after any neighbour (hypothesis 1) or entrained to the rhythm of the silent interval (hypothesis 3), we predicted that after the sequence reversal they would continue to call at the same relative time during the silent interval. We predicted that avoidance of calling shortly after the particular neighbour that regularly called just prior to the silent interval (hypothesis 2), however, would result in advanced calls: males may not readjust immediately to the new role assumed by that neighbour. Similarly, we predicted that 'anticipatory' calling prior to the neighbour that regularly called first after the silent interval (hypothesis 4) would result in delayed calls.

Results and Discussion

When we reversed the sequence of stimuli, seven of the eight males tested initially delayed their calls such that they occurred later in, or even following, the 4.2-s silent interval (Fig. 7). Perhaps because of the small sample size, this result was not significant (binomial test, two-tailed: $P=0.07$). None the less, the trend suggested that males timed their calls from the broadcasts of the loudspeaker that followed the silent interval during the pre-stimulus period (hypothesis 4). This purported response implies that males used information on distance (SPL), azimuth and sequential timing of neighbours (loudspeakers) to regulate their own

call timing and that they associated particular calls with broadcast locations.

GENERAL DISCUSSION

The pattern of advertisement calling among male *L. planum* is a crudely alternating one that persists despite the constraints imposed by a relatively complex acoustic environment. Sources of this complexity include within- and between-male variation in call period, irregular spacing of males, and the unique set of neighbours that each male hears and to which each male can potentially respond. This last point is largely due to territoriality in *L. planum*: calling males are usually separated by more than 2 m, and a given male is unlikely to hear all of the same males as a neighbour.

Our data strongly suggest that alternation arises because males rarely call during a 1.8-s interval beginning 0.2 s after the onset of a neighbour's call. However, alternation is occasionally interrupted by synchrony when fluctuations in call periods result in two (or more) males calling at the same time. Neighbouring males do not respond by matching their calling rates. They also do not decrease their calling rates as population density increases, which leads to an inevitable increase in the overall incidence of call overlap within a chorus.

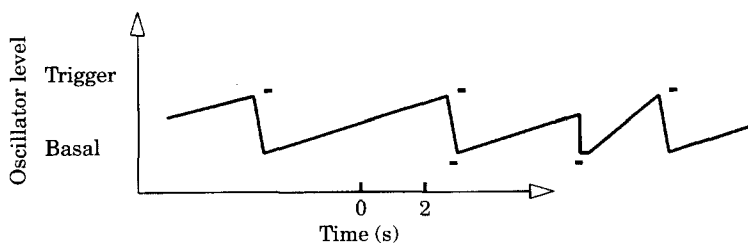


Figure 8. Hypothetical oscillator regulating call rhythm in *L. planum*. Oscillator level of the focal individual is indicated by the sawtooth function, and calls of the focal and a neighbouring male are represented by upper and lower dashes, respectively.

Inhibition

The inhibitory response to rasp calls of neighbours forms the basis of chorus structure in *L. planum*. Based on results from the single stimulus playbacks (Figs 2, 3), this response can be characterized most parsimoniously as 'inhibitory resetting' (Greenfield & Roizen 1993). Call production is assumed to be regulated by a central rhythm oscillator that triggers a call shortly before its onset (Fig. 8). The oscillator falls quickly to its basal level after triggering a call, and then rises slowly over 4–5 s (minimum call period) or longer until it again attains the trigger level. Lack of calling during the playback of lengthened stimuli indicates that when an insect hears an acoustic stimulus such as a neighbour's rasp, the oscillator is immediately reset to the basal level and remains inhibited at that level until the stimulus ends. However, calls may be produced during the initial 0.2 s following stimulus onset, implying that calls are triggered approximately 0.2 s prior to their onset and that resetting will not affect calls already triggered. Calling may resume again 2 s following the onsets of neighbours' calls, suggesting that after stimulus termination the oscillator can rebound from inhibition to the trigger level in as little as 1.45 s when stimuli occur late during the call period. This rebound is considerably faster than the normal rise time during solo calling.

In an ideal situation where an isolated pair of males call at identical, stable rates, the above mechanism would generate regular alternation via mutual inhibition except in rare events where both males happen by chance to initiate their first calls at the same time. Here, synchrony would result (Sismondo 1990). If mean call rates were identical but stochastic fluctuations occurred, alternation would occasionally be interrupted by synchrony

when the males' rates diverged and their calls would be triggered within 0.2 s of one another. Even if mean call rates differed, males adhering to the inhibitory resetting mechanism would be able to alternate crudely because (1) adjustments in call timing are made on a period-by-period basis and (2) the rebound following inhibition can be rapid. Period-by-period adjustment, characteristic of 'phase-delay' mechanisms of signal interaction (Buck 1988), would allow males to avoid call overlap regardless of when a neighbour's call occurs during the focal male's call period (e.g. Loftus-Hills 1974; Lemon & Struger 1980; Zelick & Narins 1985). Rapid rebound following inhibition, reported in several species of anurans (e.g. Zelick & Narins 1985; Moore et al. 1989), specifically averts synchrony and would allow a slower male to insert his calls into some inter-call intervals of a faster neighbour.

Selective Phonoresponse

Whereas the basic inhibitory resetting mechanism could yield some form of alternation within most pairs of males, it could not be solely responsible for the temporal structure of larger choruses. Males can probably hear neighbours at least 8 m distant, and several callers are found within this radius of most males. Inhibitory resetting is modified by selective responses to calls that allow males to interact with only one or two neighbours. Otherwise, males would be restricted to very reduced calling rates at high population density.

Chorus recordings and playback experiments indicate that males interact (via inhibitory resetting) with only their nearest one or two neighbours and facultatively ignore the others. This is not an unreasonable feat, because acoustic

interneurons capable of 'selective attention' to particular stimuli isolated from others by large angular separations are known in the Orthoptera (Pollack 1988). Selective response is probably based largely on call loudness, although other contributing factors cannot be excluded. For example, results from experiment 4 suggest that males may selectively interact with calls that repeatedly occur at particular times relative to other calls. This ability may be critical when population density is very high and one or two neighbours cannot be selected on the basis of loudness or distance.

Comparable selectivity towards the closest neighbour(s) has been found in chorusing anurans (Brush & Narins 1989; Narins 1992; Schwartz 1993), and it may be a common phenomenon in animal species that respond to conspecific acoustic signals. This selectivity may be particularly common in species that normally alternate, because selective attention is a simple means of expanding the allowable time during which calls can be produced. Alternatives would include calling very infrequently or following (or overlapping) the calls of one's nearest neighbours. The final section explains why the latter option may be disadvantageous.

Signal Competition

The adaptiveness of inhibitory resetting can only be appreciated in light of female choice. When *L. planum* females orient towards (spatially separated) male calls, they display a strong preference for the first of two otherwise identical calls (Minckley & Greenfield, in press). Such precedence effects influence phonotaxis in various acoustic insects (e.g. Greenfield & Roizen 1993; Wytenbach & Hoy 1993; Stiedl et al. 1994) and anurans (e.g. Dyson & Passmore 1988a, b; Klump & Gerhardt 1992). In *L. planum*, the precedence effect is strongest when call onsets are separated by intervals of 0.6–1.4 s; at smaller separations, phonotaxis towards both leading and following calls is greatly reduced. The delay following a neighbour's call when a focal male resumes calling (Fig. 2) corresponds to the maximum call separation interval at which the precedence effect is exhibited.

Because of the precedence effect in female choice, males that avoid calling shortly after neighbours possess a competitive advantage over males with comparable signalling prowess that call randomly in time relative to their neighbours.

Males that time their signals with the inhibitory resetting mechanism can avoid calling shortly after neighbours on most occasions. If two neighbouring males that call in solo with similar rates both adhere to inhibitory resetting, they will alternate calls on a one-for-one basis when chorusing (e.g. Fig. 1a). Regular alternation as such, however, merely represents an incidental by-product of neighbours happening to possess matched solo rates (Greenfield & Minckley 1993). Otherwise, a slower male (e.g. individual 1, Fig. 1b) calls only occasionally, because he is repeatedly inhibited by his faster neighbour. We have observed no indications that faster males reduce their signalling rates to 'accommodate' slower neighbours.

Liguotettix planum males generally rebound and call much sooner after inhibition by a neighbour's call than after being reset to the basal level during solo calling (Fig. 8). Such relatively short rebound intervals may be responsible for generating alternating, as opposed to synchronous, chorusing (Greenfield 1994a, b). That is, alternation may result incidentally from a neurophysiological ability to rebound from inhibition in an interval that happens to be considerably shorter than the call period; if call periods and rebound intervals were similar, synchrony would arise. Alternatively, the short rebound intervals and/or long call periods that generate alternation may have been specifically selected for, because females do not orient towards synchronized calls. Our finding that the incidence of call overlap is not less than the random expectation conflicts with this latter explanation.

Assuming that inhibitory resetting is essentially a means of signal competition, selective response may be a modification by which males direct that competition most effectively. That is, a focal male's strongest competitors for females are expected to be his nearest (and relatively loudest) neighbours. If sporadic calling resulting from responding to all audible neighbours attracts few females, the most viable alternative would be to call at a normal rate but adjust one's phase such that calls following the nearest neighbour(s) are not produced. In many vertebrates an analogous means of selectively limiting the number of individuals treated competitively is seen in the 'dear enemy' effect (see Temeles 1994) by which territory owners learn their neighbours' signals and only attack novel signallers.

Selective phonotaxis by females would constitute further support for the signal competition hypothesis. It is currently unknown whether *L. planum* females facultatively ignore distant callers when orienting towards leading calls; however, comparable selectivity has been observed in other acoustic insects and anurans during female evaluation of multiple callers (Gerhardt & Klump 1988; Römer 1993).

Our playback experiments suggest that males not only avoid calling immediately after neighbours but also 'anticipate' certain regularly repeated stimuli and call shortly before them. This interpretation is indicated by calls occurring just prior to the ends of predictably recurring 4.2-s intervals (Fig. 7). Thus, males may 'attempt' to relegate their competitor's calls to the very time intervals that they themselves avoid via inhibitory resetting. Of course, such 'attempts' would seldom be successful in situations involving two males rather than a male and a loudspeaker: both individuals would follow the same mechanism and occasionally synchronize, possibly accounting, in part, for the surprising incidence of call overlap between nearest neighbours observed in choruses.

Observational and experimental findings reveal that *L. planum* males employ a variety of sophisticated mechanisms for signal competition. Chorus structure represents the collective outcome of these mechanisms, which apparently were selected for by critical psychoacoustic features inherent in female choice.

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