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Abstract

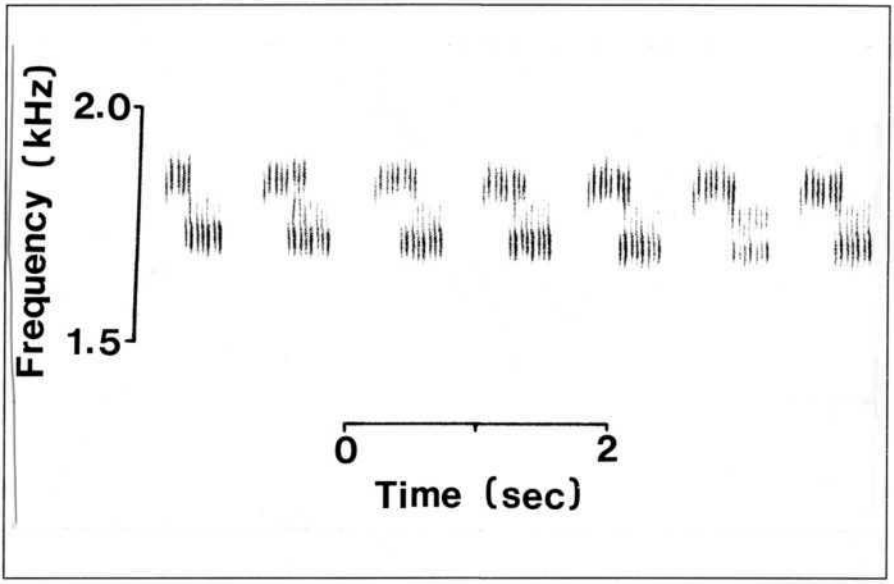
Call synchrony has been reported for the snowy tree cricket (*Oecanthus fultoni*), but the degree to which it occurs in natural interactions has not been previously investigated. I recorded acoustic interactions among ten pairs of male snowy tree crickets to determine the degree to which call synchrony occurs. High levels of call synchrony (percent of calls that temporally overlapped another call) were found in all pairs, but in only half of the pairs was synchrony greater than expected by chance. Males differed considerably in their tendency to temporally overlap the calls of their neighbors. There was minimal frequency overlap of calls in all pairs. Avoidance of frequency overlap may have allowed calls of individual males to be distinguished when there was temporal overlap.

Introduction

The temporal patterning of acoustic communication among the Orthoptera has received considerable attention. Alternation of calls between individuals, synchronization of calls, and unsynchronized chorusing have all been reported (Otte 1977; Greenfield and Shaw 1983). Call synchronization has received relatively little attention (Jones 1966; Walker 1969; Samways 1976; Otte 1977; Greenfield and Shaw 1983), but has been reported for the snowy tree cricket (*Oecanthus fultoni*) (Walker 1969). Walker (1969), however, concentrated on the responses of crickets to playbacks, so the extent of call synchrony in natural interactions is not known. In this study, I recorded natural calling interactions of snowy tree crickets to answer the following questions: 1) To what extent does call synchrony occur?; 2) Does call synchrony occur more than expected by chance?; 3) Does each individual contribute equally to maintaining call synchrony?

Methods

I recorded interactions between calling males on 15-17 September 1987, between 20:00 and 22:00 CST, at Elkhart Lake, Sheboygan County, Wisconsin. The tree crickets were calling from bushes along the edge of a semi–residential area and a hardwood forest. I recorded interactions with a Sony Professional Walkman Cassette-recorder and a Nakamichi CM-100 microphone. I began a recording session when two males in close proximity (within 5 m) began calling and continued until one or both males stopped calling. Only interactions in which each male gave at least 20 calls and in which only two males were calling in close proximity were included in the analysis. I analyzed calling interactions between males in ten pairs. Based on the spatial locations of the recorded pairs, the ten pairs under study involved 20 different individuals. The entire sequence of calls for each interaction was analyzed using a Kay 7800 Digital Sona-Graph. The frequency setting and the scale magnifier were set, so that the range used for all sonograms was between 1 and 2 kHz (Fig. 1). By using this



setting, I could readily distinguish the calls of each male and avoided problems with identifying calls of individual males (see Walker 1969). For each individual, I measured the inter-call interval, the duration of each call (in both seconds and number of pulses), and the number of times a call temporally overlapped the call of the other male. Two calls were considered synchronized if they showed any temporal overlap. Synchronization of a call occurred if either that call overlapped the call of a neighbor or if a neighbor's call overlapped that call. I could determine, therefore, the contribution each individual made to call synchronization by counting the number of times each individual overlapped its neighbor's calls. By simulating the calling patterns of each pair of crickets, I determined the degree of call synchrony expected if individuals were singing at random with respect to each other (Popp 1989). I simulated singing patterns by randomly choosing call durations and inter-call intervals from the observed distribution of lengths for each individual. The expected number of synchronized calls was the number that occurred during the simulated (random) calling bouts. I compared observed and expected numbers of synchronized calls, and observed and expected numbers of times each individual overlapped its neighbor's calls using the G-test for Goodness-of-fit (Sokal and Rohlf 1981). Results are presented as percentages only for the readers' convenience.

Results

Frequency separation

An unanticipated result was the minimal frequency overlap between calling males. In eight of the ten pairs, calls of the two crickets did not overlap in frequency. In the remaining two pairs, only minimal frequency overlap occurred (see Fig. 1). In all pairs, each individual maintained the same role (higher versus lower frequency) throughout the calling interaction. In each pair, the male with the higher frequency will be referred to as male A and the other as male B.

Call and inter-call interval durations

As reported by Walker (1969), most calls were composed of either five or eight pulses, although calls with four, six, or seven pulses were recorded. I grouped calls as either long calls (seven or eight pulses) or short calls (six or fewer pulses). Most individuals used long calls more than short calls (Table 1). Inter-call intervals were short and had low variance (Table 1).

Table 1. Inter-call intervals and percent of calls that were long calls for each male snowy tree cricket.

		Inter-call Interval (secs)		Percent
Pair	Individual	Mean	Standard Deviation	Long Calls
1	A	0.68	0.05	84.4
	B	0.70	0.06	84.4
2	A	0.73	0.20	79.4
	B	0.75	0.09	71.4
3	A	0.69	0.09	33.3
	B	0.73	0.23	66.7
4	A	0.72	0.21	70.4
	B	0.64	0.03	100.0
5	A	0.76	0.06	66.7
	B	0.76	0.25	74.0
6	A	0.75	0.14	37.8
	B	0.66	0.03	80.0
7	A	0.69	0.08	31.0
	B	0.68	0.10	79.5
8	A	0.65	0.12	86.1
	B	0.68	0.04	97.2
9	A	0.69	0.13	77.3
	B	0.65	0.07	93.2
10	A	0.66	0.08	90.6
	B	0.71	0.07	87.1

Degree of call synchrony

The percent of calls that were synchronized was high in most pairs (Table 2). The observed number of synchronized calls was, however, significantly higher than expected in only five pairs. Two of the remaining pairs had significantly fewer synchronized calls than expected by chance. Synchronized and unsynchronized calls were not distributed randomly during interactions. Calls occurred in bouts of either all synchronized or all unsynchronized calls. Runs tests showed these bouts to differ significantly from a random distribution in nine of the ten pairs. In the other pair (#8), the runs test could not be computed because there were too few unsynchronized calls.

Table 2. Observed and expected number of calls that were in synchrony for each pair.

	Percent of Calls				
Pair	Observed	Expected	G	P	N
1	87.5	46.9	46.4	<0.001	64
2	92.8	43.5	75.9	<0.001	69
3	53.3	48.9	0.4	n.s.	45
4	76.4	90.9	10.1	<0.01	55
5	73.1	53.8	16.2	<0.001	104
6	71.1	73.3	0.2	n.s.	90
7	71.6	74.1	0.3	n.s.	81
8	97.2	72.2	32.2	<0.001	72
9	36.4	22.7	8.3	<0.01	88
10	82.5	95.2	13.6	<0.001	63

n.s. = not significant

Maintenance of synchrony

Nine of the 20 individuals overlapped their neighbor's calls (and thus produced synchrony) more than expected by chance (overlappers) (Table 3). In four of the five pairs with significantly high levels of synchrony, one individual was an overlapper, while the other individual overlapped as frequently as expected by chance. In the remaining pair (#2), both males were overlappers. In contrast, two of the overlappers were from pairs with significantly low levels of synchrony. These last two individuals were both paired with neighbors who strongly avoided overlapping calls (Table 3).

Table 3. Observed and expected percent of calls for each individual that overlapped the call of its neighbor.

Pair	Individual	Percent of Calls Observed	Expected	G	P	N
1	A	56.3	25.0	13.9	<0.001	32
	B	31.3	21.9	1.5	n.s.	32
2	A	50.0	26.5	8.4	<0.001	34
	B	42.9	17.1	12.5	<0.001	35
3	A	25.0	37.5	1.7	n.s.	24
	B	28.6	9.5	6.0	<0.01	21
4	A	74.1	51.9	5.5	<0.01	27
	B	3.6	39.3	19.8	<0.001	28
5	A	27.8	35.2	1.3	n.s.	54
	B	46.0	18.0	20.4	<0.001	50
6	A	24.4	22.2	0.1	n.s.	45
	B	46.7	51.1	0.4	n.s.	45
7	A	52.4	40.5	2.4	n.s.	42
	B	17.9	33.3	4.6	<0.01	39
8	A	55.6	63.9	1.0	n.s.	36
	B	41.7	8.3	28.9	<0.001	36
9	A	9.1	18.2	2.9	n.s.	44
	B	27.3	4.5	25.3	<0.001	44
10	A	81.3	56.3	8.8	<0.001	32
	B	0	54.8	48.5	<0.001	31

n.s. = not significant

Whether an individual overlapped its neighbor's calls more than expected or not was not related to its call rate or call duration. Comparisons of mean inter-call intervals, inter-call interval variances and percent of long calls between overlappers and non-overlappers were not significant (T-test, $P > 0.05$).

In all pairs except four and ten, both males overlapped calls to some extent. In five of these eight pairs, the sequence of overlaps by each male was not randomly distributed over the course of the interaction. Overlaps produced by each individual tended to occur in bouts (runs test, $P < 0.05$). For example, in pair #9 all overlaps at the start of the interaction were by male A, this was then followed by an uninterrupted bout of overlaps by male B.

Discussion

Considerable variation occurred among pairs in the degree of call synchrony, and among individuals in their tendency to overlap their neighbor's calls. Although call synchrony was high in most pairs, it was significantly higher than expected by chance in only half of the pairs. The short and regular (low variance) inter-call intervals could produce frequent overlap of calls by chance alone, and, therefore, high expected rates of synchrony (Popp 1989). Synchronized calls occurred in bouts suggesting that the calls of the interacting males may shift in and out of phase with each other as noted for *Platycleis intermedia* (Samways 1976). Call synchrony in the snowy tree cricket can not be considered to be as absolute as has sometimes been reported (i.e. Otte 1977; Greenfield and Shaw 1983).

Individuals differed in their tendency to overlap calls, ranging from complete avoidance of call overlap to frequent call overlap. This variation occurred both within and between pairs. In six of the pairs, an overlapper was calling with an individual that overlapped as frequently or less frequently than expected. The reasons for this variation are not clear. Individual differences in temporal patterning during acoustic interactions have been reported for other Orthopterans that show call synchrony (Greenfield and Shaw 1983). Temporal patterning of calls may communicate information about the status of the caller. In *Neoconocephalus nebrascensis*, males adopt either a "leader" or "follower" role, and the nature of the role may be related to dominance (Meixner and Shaw 1979). Behavior similar to leader—follower behavior occurred in pairs four and ten of this study. In both of these pairs, male B tended to call first (leader) and then was overlapped by the call of male A (follower). Calling could be influenced by the distance between calling males or the proximity of receptive females to one of the males. Microhabitat differences in temperature could affect the relative calling rates of the males, and therefore, their tendency to overlap calls (Samways 1976).

Although calls temporally overlapped, they only minimally overlapped in frequency. During all interactions recorded, one male consistently called at a frequency slightly higher than its neighbor. Females might use the frequency difference to distinguish the calls of the two males when calls were temporally overlapped. This suggestion would be dependent on the hearing ability of the female being sufficient to differentiate the calls.

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