

THE ACOUSTIC BEHAVIOUR OF THE BUSH CRICKET *PHOLIDOPTERA GRISEOAPTERA*

1. ALTERNATION, SYNCHRONISM AND RIVALRY BETWEEN MALES

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INTRODUCTION

In a number of species of insects alternation or synchronism takes place between singing males; the subject has been reviewed by Dumortier (1964). Regen (1908, 1914, 1926) was the first to study this behaviour in detail when he worked on the alternation singing of *Pholidoptera (Thamnotrizon) aptera* (F.). He found that actively singing males alternated their chirps in a regular manner if they were within hearing range. Destruction of the tympanal organs abolished alternation and the males chirped independently. He was able to demonstrate, by suspending each male from a balloon, that transmission of the sound through the air was more important than transmission through the substratum.

Baier (1930) carried out similar work with *Pholidoptera griseoaptera* (DeGeer) and showed that singing males tended to alternate and 'avoid' clashes. If a group of males were singing together they did not sing in any particular order. Allard (1917, 1918) and Fulton (1934) drew attention to the occurrence of synchronism, or chirping in unison, in a number of Orthoptera, the best known being the snowy tree cricket, *Oecanthus niveus* (DeGeer); in addition Fulton (1934) reported alternation singing in *Orchelimum bradleyi* R. and H., and *Pterophylla camellifolia* (F.). In the latter species he noticed that occasionally one of the males would sing out of turn and this could result in both chirping together. If this happened they would chirp in synchrony for the next one to five chirps before one would 'pause' and bring about alternation again. Specialized chorusing of a number of insects, among them *Pterophylla*, has been discussed by Alexander (1960). In this insect collective alternation and synchronism of a population may result in a great pulsing sound which goes on for hours.

Weih (1951) studied alternation in a number of species of Orthoptera and found that in *Chorthippus brunneus* (Thunberg) (= *bicolor* (Charp.)) there is an acceleration of emission when a male starts to alternate its song with that of another male. When the distance between two males is short, the 'responding' song changes into the rivalry song and there is a further acceleration of the emission rate.

The work of Busnel, Busnel & Dumortier (1956*a*), and Busnel, Dumortier & Busnel (1956*b*) on intra- and interspecific alternation in a number of species of the genus *Ephippiger* is particularly relevant, and they have put forward a number of schemes to describe the various ways in which responses between two males may be exchanged.

The present paper describes alternation singing and rivalry behaviour in the bush

cricket *Pholidoptera griseoptera* (DeGeer) and gives the results of a detailed time-study on alternation singing and synchronism in this insect. A preliminary account of some of this work has been given by Jones (1964). There appears to be good evidence that mutual inhibition between singing males is the most important factor in determining the pattern of alternation. Mutual excitation may also play a part, particularly in the evocation of rivalry behaviour. The schemes put forward by Busnel *et al.* (1956*b*) and repeated by Dumortier (1964) give an approximate description of the interaction of *Ph. griseoptera* males, but are not satisfactory when the interaction is studied in more detail.

A second paper will give the results of experiments using artificial sound signals.

MATERIALS AND METHODS

Insects

Insects were collected either as late instar nymphs or adults. They were housed in large cages and supplied with fresh turf, lettuce, soaked wheat seeds and small caterpillars or aphids. They could be kept with little mortality for several months. When nymphs were collected, both males and females were collected and reared together and males were only removed from the females when recordings were to be made. When adults were collected, this was done by stalking a singing male and thus only males were collected. In this case recordings were made within a few days of capture in order that prolonged isolation from females should not affect the results. No difference in results was observed between males captured as mature adults and those captured as nymphs.

Once adult, all males were marked by painting dots on the pronotum with 'Humbrol' and each was identified by a letter of the alphabet.

Recording technique

Males which were to be recorded were placed in separate, cylindrical, wire-framed muslin cages, 6 in. high and 6 in. in diameter. They were placed in position in a darkened room several hours before the recordings were to be made. Pairs of males could be placed at any distance up to 20 ft. apart. Curtains and carpet helped to reduce echoes.

A crystal microphone was hung outside each cage by a wire hook. The microphone was connected by a short coaxial lead to a transistor preamplifier built to amplify frequencies above 1000 cyc./sec. The preamplifier was connected by a long lead to a tape recorder in another room. A Brenell Mk. 5 stereophonic tape recorder was used so that when two alternating insects were being recorded each insect could be recorded on a separate channel of the recorder.

Whenever a recording was made, the time, ambient temperature and relative humidity were noted.

Analysis of recordings

Tape recordings were analysed oscillographically or by making paper records with a Palmer 3-pen Chronograph. In the latter case the loudspeaker output of each channel of the tape recorder was rectified and used to operate one of the pens, and the third

pen was operated by a time marker. Paper records were usually made at the rate of 1 in. of paper per second of recording. This greatly facilitated the measurement of records.

Terminology

In the description of song types or units of song, the terminology of Broughton (1964) has been used wherever possible.

RESULTS

Vocabulary and song patterns

In this species only the males sing, since the females are apterous. A male can produce two types of chirp, a short chirp which lasts about 100 msec. (at 18° C.) and a long chirp which can last as long as 4 sec.

The short chirp is used in the proclamation song when a male is singing alone, or in the responding song, where he is alternating with other males. Sexually responsive females come to singing males and mate with them. The chirp consists of three or occasionally four syllables (wing movements). Fig. 1 A and B are oscillograms of trisyllabic chirps (at 20° C.) by two different males. Fig. 1 C is a trisyllabic chirp and D is a group of five syllables at the beginning of a long chirp, both recorded at 22.5° C.

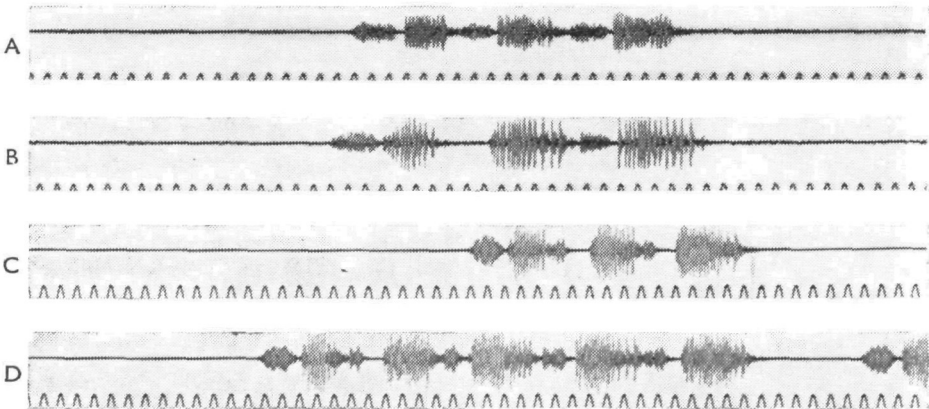
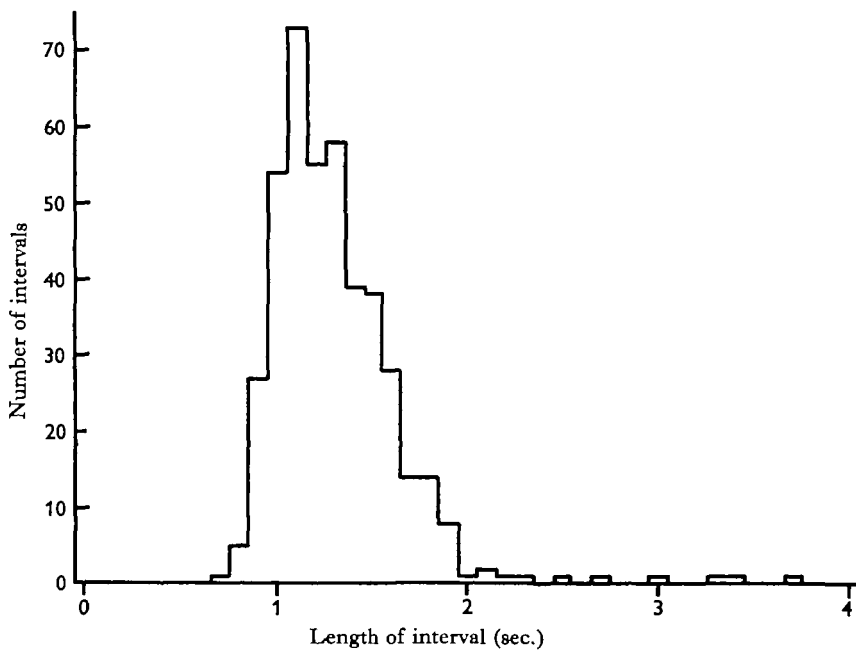


Fig. 1. A and B are trisyllabic chirps (at 20° C.) by two different males. C is a similar chirp and D is a group of five syllables at the beginning of a long chirp, both recorded at 22.5° C. Time marker 200 cyc./sec.

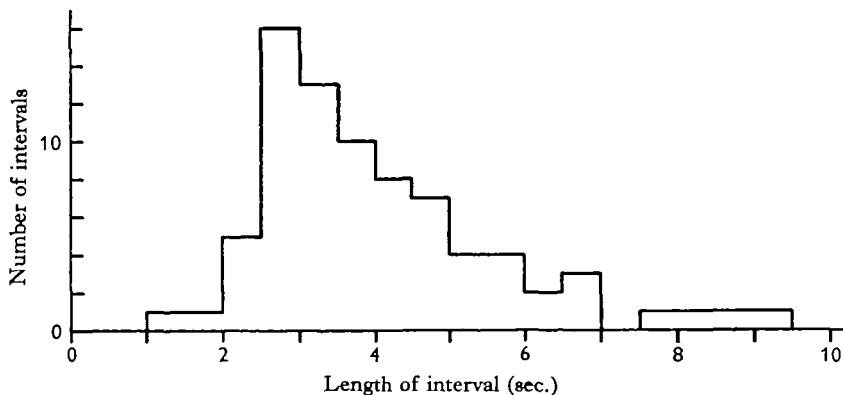
A, C and D are all by the same insect. It can be seen that each syllable consists of two parts probably corresponding to movement of the wings in each direction. There is a certain amount of variation between the chirps of different insects and often the second or third of the less intense half-syllables may be omitted (see Fig. 1 B). The syllable rate is approximately constant for any given temperature, but, at the end of a three- to four-syllable short chirp or of a group of syllables in a long chirp, the period of the syllables is increased. This is particularly noticeable where the group of syllables is four or more. This effect can be seen very easily in Fig. 1 D. This indicates that the rate of wing movement is decreasing at the end of the chirp or group of syllables. There

is an approximately linear relation between the length of a standard three-syllable chirp and the temperature. At 13°C . the length is 140–160 msec. and at 25°C . 50–60 msec.

The chirp rates, both of solitary males and of males singing with other males, are very variable. Individual chirp rates from 0 to 80 per min. have been recorded. The highest rates have been recorded when males were singing together. Chirp rates vary very much with the time of day, since these insects sing mostly in the late afternoon, evening and night. However, males under apparently identical conditions of time, temperature and humidity can still sing with very different chirp rates even when they



A



B

Fig. 2. A. Distribution of intervals between chirps of a single solitary male during a 10 min. recording at 18.5°C . when the mean chirp rate was 42.6 per min. B. Similar distribution when the mean rate was 14.6 per min.

are singing together. Chirping can be very irregular, especially when the rate is moderate or low. In this case the only regularity of the pattern is that the insect tends to produce approximately the same number of chirps in consecutive minutes. Baier (1930) has made similar observations. In addition it is noticeable that the higher the chirp rate, the more constant are the intervals between chirps.

Fig. 2A is a histogram of the distribution of intervals between chirps of a single male (R) during a 10 min. recording (at 18.5° C.). The mean chirp rate was 42.6 per min. with a range from 30 to 54 per min. Fig. 2B is a similar histogram from a 5½ min. recording (at 20.0 °C.) of the same insect when its mean chirp rate was 14.6 per min. with a range from 12 to 18 per min. It can be seen that in both cases there are relatively few intervals less than the mode.

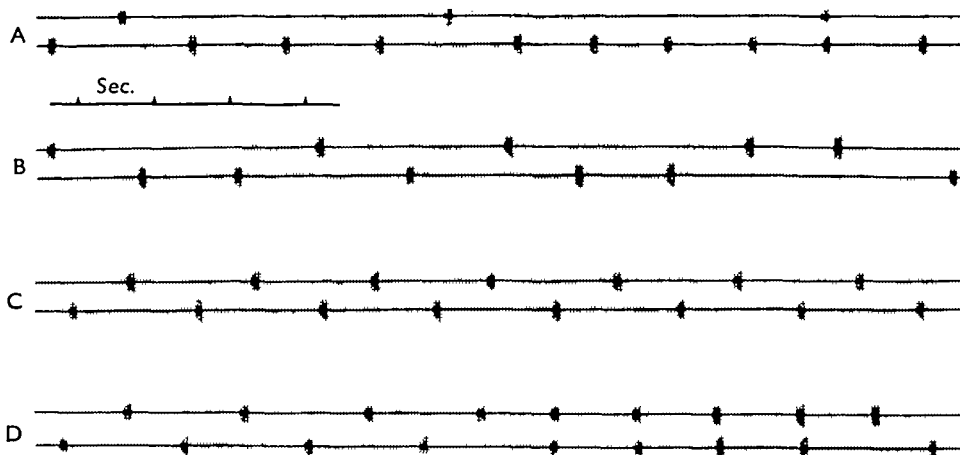


Fig. 3. Examples of the interaction of two singing males. In A, one is chirping at a higher rate than the other and is inhibited when the other chirps except when they chirp synchronously. In B the rates are more equal and this leads in C to perfect alternation. In D they go from equal alternation to synchrony for four consecutive chirps and then back to alternation.

When two or more males are singing within hearing range of each other they sing in alternation or occasionally synchronize their chirps. Fig. 3 shows examples of this interaction. In A one male has a higher chirp rate than the other and is temporarily inhibited when the other chirps except when they chirp synchronously. In B and C the chirp rates are fairly equal and in C this leads to perfect alternation. In D they go from equal alternation to synchrony and then chirp in synchrony for four consecutive chirps before going back to alternation. It is very noticeable that the change from alternation to synchrony and back is very sharp. The chirps are either clearly separated or in synchrony, and this is quite obviously not a case of interference between two individuals chirping at slightly different frequencies. These observations are very similar to those made by Fulton (1934) on *Pterophylla camellifolia*.

The long chirp consists of a machine-gun-like burst of syllables lasting usually about 1–2 sec. It may consist of a prolonged polysyllabic version of a short chirp with a few gaps or 'stutters' or a group of short chirps following very closely one after the other. Sometimes it is a mixture of the two, starting with one or several groups of six to ten

syllables and ending with a series of rapidly repeated groups of two to three syllables. Figs. 4 and 5 give examples of sequences in which long chirps occur. In Fig. 4, following consecutive chirps by one male (marked by arrows), the other male produces groups of two, three, four and then five short chirps. The short chirps in these groups do not fuse together, but follow each other with a short but distinct interval between them. In Fig. 5 there is more fusion to form polysyllabic long chirps but each of these can be seen to be breaking up into groups of two to three syllables towards the end.

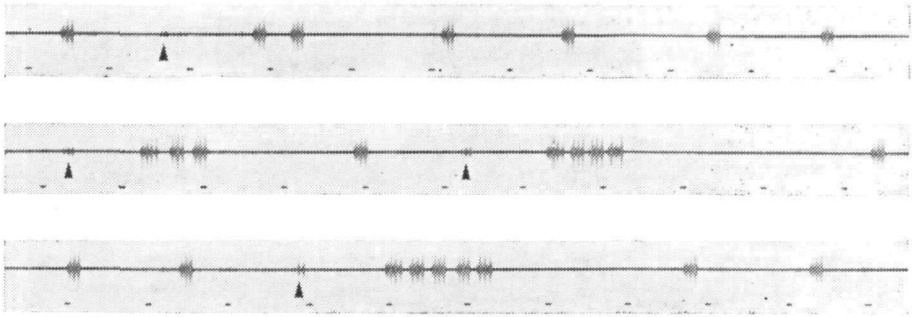


Fig. 4. In response to consecutive chirps by one male (marked by arrows) the other produces groups of two, three, four and five short chirps. Time marker 2 per sec.

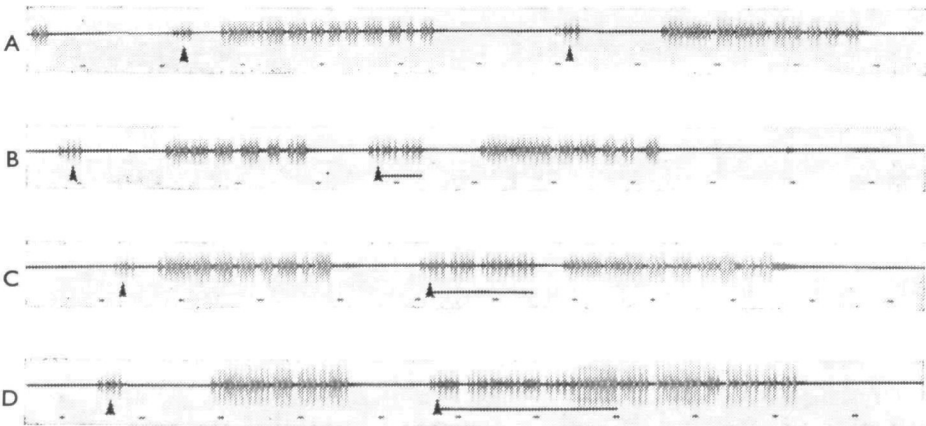


Fig. 5. A shows alternation between long chirps by one insect and short chirps by the other (marked by arrows). In B and C the second male also produces long chirps. In D a long chirp by one male is 'interrupted' by a long chirp by the other. Time marker 2 per sec.

Situations leading to the production of long chirps

The long chirp appears to be produced in situations of conflict between males and is probably what Broughton (1964) would call an intimidation call. It has been heard in the field when two or more males were very close together, and caged males have often been observed standing on the same twig facing each other, lashing antennae, and emitting long chirps. Usually one male drives the other away. A series of experiments was carried out using each time a pair of males in separate cages 5–15 ft. apart. When they were alternating vigorously, one was moved suddenly up to the other so

that the insects were about 2–3 in. apart. This was done on fourteen different occasions with eight different pairs of males. On two of these occasions the males resumed alternation. On another, the male which had been moved stopped chirping, and the other one went on chirping with short chirps. On eight occasions the undisturbed male started producing long chirps as soon as the other resumed chirping, and the long chirps of one alternated with the short chirps of the other. On two occasions, both males produced long chirps and they alternated with these but several times interrupted each other. On the remaining occasion the male which had been moved produced the long chirps.

Figs. 4 and 5 A give examples of alternation between short chirps by one insect and long chirps by the other. Fig. 5 B and C give examples of alternation between long chirps by both insects. In Fig. 5 D a short chirp by one insect is followed by a long chirp by the other. The first then produces a long chirp and this is interrupted by a long chirp by the second. In all these examples, chirps by one partner are marked with arrows and, in the case of a long chirp, a line. Usually after several minutes the two males went back to normal alternation. It was noticeable that males which had been giving long chirps chirped at a high rate when alternation was resumed. During several of these exchanges four-syllable chirps were more numerous than usual and also intermediate chirps were recorded. These included five-syllable chirps and groups of two or three short chirps very close together.

No significance is attached to the observation that the long chirps were produced mainly by the undisturbed male. The one that was moved usually stopped chirping and only resumed its chirping at a lower rate. When this type of behaviour was observed in the cages, the more vigorously chirping male was usually the one which was the more pugnacious.

Analysis of alternation and synchronism

Fig. 6 shows the distribution of the intervals during a 5 min recording (at 20° C.): (a) between successive chirps by insect O (O–O), (b) between chirps by this insect and those of its partner R (O–R), and (c) between chirps by R and chirps by O (R–O). During this period O chirped 221 times and R 131 times. It can be seen that the distribution of the intervals in (a) is distinctly bimodal. The shaded area indicates those intervals in which there was no chirp by R, and the unshaded areas where there were one, or occasionally more chirps by R. It can be seen from the O–R intervals that R tended to chirp just before a chirp from O was due. When this happened O's chirp was delayed. It appears that chirps by R had an inhibitory effect on O. The effect of O on R was similar. However, the higher chirp rate of O meant that there were more uninterrupted O–O intervals than R–R intervals. In the 5 min. there were only nine uninterrupted R–R intervals. It can be seen that R–O intervals tend to be shorter than O–R.

Eighteen recordings involving ten males paired in eleven different ways and adding up to a total time of nearly 2 hr. were analysed in detail. Table 1 gives details of the insects, the chirp rate, the time at which the recording began, the duration of the recording, the temperature and the occurrence of synchrony. Table 2 gives the lengths of the uninterrupted intervals between consecutive chirps by one insect (e.g. 1–1 and 2–2) and of the intervals between consecutive chirps by different insects (e.g. 1–2 and

2-1) in fourteen of these recordings. Mutual inhibition was most noticeable when the total chirp rate was high, because there was then the most interaction between the two partners. Bimodal distributions such as that in Fig. 6A were best obtained when one male was chirping at a higher rate than the other, and the chirp rate was high. If the rates were equal there were hardly any intervals without interruption by the other partner, due to the almost perfect alternation. The two types of interval given determine the pattern of interaction. The 'interrupted' interval between consecutive chirps by one insect, say insect 1, are made up of interval 1-2 plus the duration of one chirp by insect 2 plus interval 2-1.

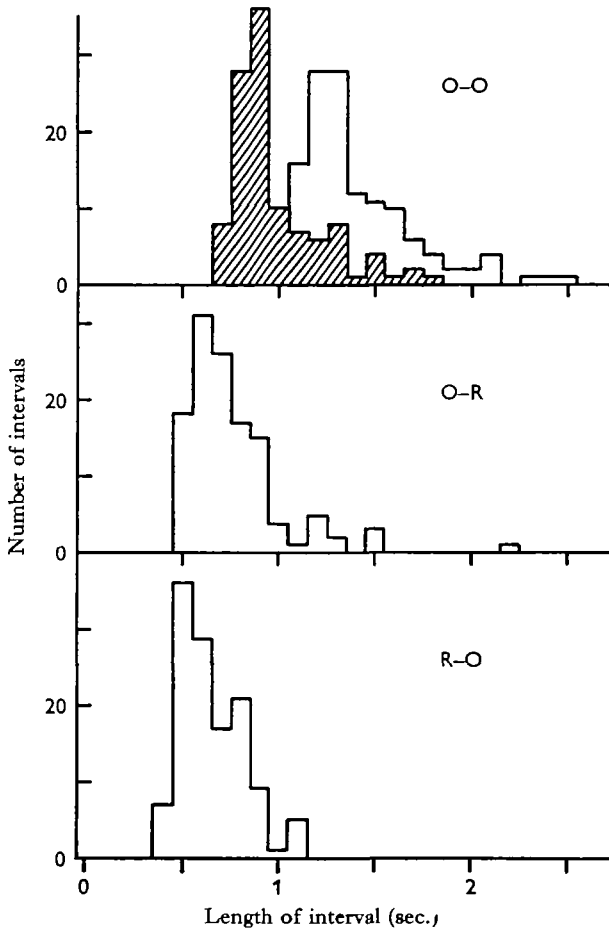


Fig. 6. Histogram showing the distribution of intervals between chirps in a 4 min. exchange between two males (O and R). In the top histogram the shaded area denotes uninterrupted intervals, and the unshaded area denotes interrupted intervals between consecutive chirps by male O.

In Table 3 the recordings analysed in Table 2 are broken down into separate minutes and the data are grouped according to the total chirp rate (of both insects) for each minute. This removes the effect (on the data in Table 2) of changes in total chirp rate during the recordings. It can be seen that the lengths of all the intervals decrease as the chirp rate increases, but that the relation between the various types of

Table 1

Ref. no.	Duration of record (min.)	Time of start B.S.T.	Temp. (°C.)	Insects		Chirps/min. mean (and range)		Total chirps/min. mean (and range)	Number of synchronies lasting the indicated number of chirps					
				I	2	Insect 1	Insect 2		1	2	3	4	5	6
1*	6	1930	16.5	G	I	16.0 (8-28)	6.5 (4-9)	22.5 (15-34)	—	—	—	—	—	—
2*	5	2110	17.0	I	H	7.2 (6-8)	3.0 (3)	10.2 (9-11)	—	—	—	—	—	—
3	7	2035	18.0	I	G	8.9 (7-10)	7.7 (5-11)	16.6 (12-21)	2	—	—	—	—	—
4*	4	0555	18.0	H	G	43.0 (36-46)	17.0 (13-20)	60.0 (55-65)	13	1	—	—	—	—
5*	4	0545	18.0	C	H	40.3 (38-42)	32.8 (29-36)	73.1 (67-78)	17	1	—	1	—	—
6	7	2227	18.5	C	A	8.0 (6-11)	2.6 (1-5)	10.6 (8-16)	—	—	—	—	—	—
7*	5	2120	20.0	O	N	26.6 (23-35)	8.0 (5-17)	34.6 (29-42)	4	—	—	—	—	—
8*	5	2130	20.0	O	R	31.2 (26-36)	8.2 (5-13)	39.4 (34-45)	6	—	—	—	—	—
9*	10	2300	20.0	O	R	26.2 (18-36)	20.4 (8-39)	46.6 (29-75)	17	—	—	—	—	—
10*	5	2340	20.0	R	N	34.8 (32-40)	13.8 (5-22)	48.6 (41-56)	11	1	—	—	—	—
11*	5.5	2320	20.0	R	O	28.5 (7-37)	28.5 (6-38)	57.0 (33-75)	7	—	—	—	—	—
12*	5	2135	20.0	O	R	44.2 (38-49)	26.2 (10-39)	70.4 (48-88)	18	1	—	—	—	—
13	7	2340	22.0	G	H	12.9 (5-24)	0.7 (0-2)	13.6 (5-26)	—	—	—	—	—	—
14*	4	2120	22.0	O	P	40.2 (36-43)	19.8 (18-21)	60.0 (56-62)	11	—	—	—	—	—
15	14	0830	22.0	Q	R	32.3 (22-41)	29.7 (13-45)	62.0 (37-82)	56	5	—	—	—	—
16*	10	2310	22.0	Q	P	55.4 (38-63)	51.2 (45-55)	106.6 (84-118)	37	9	8	1	1	—
17*	4	0010	22.0	Q	N	69.8 (67-75)	61.5 (61-62)	131.3 (128-136)	10	7	3	2	—	1
18*	10	2330	22.5	O	N	62.0 (52-75)	56.1 (36-81)	118.1 (92-156)	51	3	2	—	—	—

• Recordings in which the intervals were measured.

interval remains approximately the same. 1-1 type intervals and 2-2 type intervals are considered together, but there are relatively few of the latter when the chirp rates of the two insects are unequal. When one insect is chirping at a lower rate than the other, the natural 2-2 interval tends to be so long that there is usually an interruption by insect 1. Only the shortest 2-2 intervals are uninterrupted and these are comparable in length with the 1-1 intervals.

Table 2. *Intervals between chirps (sec.) (numbering as in Table 1)*
mode, mean and minimum

Ref. no.	1-1	2-2	2-1	1-2
1	1.5-1.9, 2.4, 1.1	—	—, 2.0, 1.1	—, 2.3, 0.9
2	7.5-8.5, 7.9, 2.3	—	—, 3.0, 1.3	—, 6.1, 2.8
4	1.0, 1.0, 0.6	(1.1, 1.4, 1.1)†	0.7, 0.8, 0.6	0.9, 0.9, 0.6
5	0.9, 0.9, 0.7	(1.0, 1.0, 0.8)†	0.7, 0.7, 0.5	0.7, 0.7, 0.5
7	1.1, 1.9, 0.9	—	0.9, 1.2, 0.6	0.9, 1.9, 0.7
8	1.3, 1.6, 0.9	—	0.8, 1.1, 0.6	1.0, 1.4, 0.8
9	1.4, 1.6, 1.0	—, 1.5, 0.8	0.8, 1.0, 0.5	0.9, 1.2, 0.5
10	1.1, 1.2, 0.8	—	1.2, 1.2, 0.6	0.9, 1.1, 0.6
11	1.0, 1.2, 0.8	1.1, 1.5, 0.9	0.7, 1.0, 0.5	0.6, 0.8, 0.4
12	0.9, 1.0, 0.7	(0.8, 0.8, 0.7)†	0.5, 0.7, 0.4	0.6, 0.8, 0.5
14	1.2, 1.1, 0.8	—	0.7, 0.8, 0.4	0.9, 0.9, 0.4
16	0.6, 0.7, 0.6	0.7, 0.8, 0.6	0.4, 0.5, 0.3	0.4, 0.5, 0.2
17	0.6, 0.6, 0.5	0.6, 0.6, 0.5	0.3, 0.3, 0.2	0.4, 0.4, 0.3
18*	0.4, 0.4, 0.4	—	0.3, 0.3, 0.2	0.3, 0.3, 0.2

* Intervals only measured during last 2 min. when total chirp rate was 143-156 per min.

† Intervals based on less than 25 measurements are bracketed.

Table 3

Total chirps/min.	Mean chirps/min. by each insect		Uninterrupted interval between consecutive chirps by same insect			Interval between alternating chirps						Min. analysed
	1	2	Mode	Mean	Min.	2-1			1-2			
						Mode	Mean	Min.	Mode	Mean	Min.	
9-11	7	3	(7.9)	7.9	2.3	—	3.0	1.3	—	6.1	2.8	5
15-25	14	7	(3.0)	3.0	1.5	(1.7)	2.2	1.3	(1.8)	2.6	0.9	5
30-39	25	9	1.3	1.9	1.1	0.8	1.4	0.6	1.3	1.9	0.7	11
40-49	30	12	1.3	1.5	0.9	0.8	1.2	0.5	0.9	1.4	0.5	11
50-59	35	20	1.0	1.1	0.8	0.8	1.0	0.5	0.9	1.0	0.5	7
60-69	39	23	1.0	1.1	0.6	0.7	0.8	0.4	0.8	0.9	0.4	11
70-79	40	34	0.9	1.0	0.7	0.7	0.7	0.4	0.7	0.7	0.4	6½
80-99	48	40	0.8	0.8	0.6	0.5	0.6	0.3	0.5	0.6	0.4	4
100-119	60	54	0.7	0.7	0.6	0.4	0.4	0.3	0.4	0.5	0.3	4
120-139	70	61	0.6	0.6	0.5	0.3	0.3	0.2	0.4	0.4	0.3	4
140-159	79	71	0.4	0.4	0.4	0.3	0.3	0.2	0.3	0.3	0.2	2

It can be seen that the 1-2 intervals are longer than the 2-1 intervals and that the 1-1 (or 2-2) intervals are longer than either, but only approach twice the shorter intervals when the chirp rate is very high.

Table 1 also gives the number of times synchrony occurred in each recording and the number of times synchrony lasted for from one to six consecutive chirps. It can be seen that synchrony occurs more often at high chirp rates and that the greatest number of consecutive synchronies occur when the chirp rates of the two partners are equal

or nearly equal. The intervals between consecutive synchronous chirps are the same as those between consecutive chirps by one male when it was not interrupted by the other.

In Table 4 the results from each minute of recording are grouped together according to the total chirp rate. It can be seen that the percentage of chirps involved in first synchronies increases with total chirp rate up to 60–79 chirps/min. and then remains fairly constant. A group of consecutive synchronies counted as one first synchrony.

The synchrony is hardly ever perfect. The period between sixty-eight pairs of synchronous chirps was measured. The maximum period was 45 msec. (at 20° C.) when allowance was made for the distance between the insects. This indicated that the reaction time for acoustic inhibition of chirping was in the region of 50 msec. at this temperature.

Table 4

Total chirps/min.	No. of min. observed	Number of first synchronies	% of chirps in first synchronies
0–19	22	2	1·0
20–39	17	8	2·8
40–59	25	48	8·1
60–79	22	86	11·2
80–99	10	48	11·1
100–119	10	63	11·2
120–159	8	52	9·8

Effect of acoustic interaction on the chirp rate

An attempt was made to test the effect, on the chirp rate of a male which had been isolated for several hours, of bringing a chirping male into its hearing range. In one of these experiments the chirp rate remained approximately the same. In another there was a decrease followed by a slight increase and in two more there was an increase (χ^2 test; $P < 0\cdot01$). However, it proved very difficult to introduce and remove another male without affecting the chirping of both males.

In one experiment, the chirping of one male was played over a loudspeaker to a previously isolated male in another room. In this case there was a significant increase in chirp rate while the loudspeaker was transmitting (χ^2 test; $P < 0\cdot01$). However, in view of the difficulty of controlling the output of the 'stimulator' this work was continued with artificial sound signals which could be more easily controlled; the results of this will be given in the second paper.

DISCUSSION

The basic unit of *Ph. griseoptera* song appears to be the three- to four-syllable short chirp. This appears to function as an 'all-or-nothing' phenomenon. A chirping male may be likened to a relaxation oscillator where there is a build-up of excitation to a threshold resulting in a chirp which decreases the excitation. The chirp rate would depend on the rate of build-up of excitation and the threshold. This 'pacemaker' system may be similar to that found in the decapod crustacean cardiac ganglion (Maynard, 1961). The variability of the intervals between chirps could be due to changes in excitation or threshold or both.

If another male chirps during this hypothetical 'build-up' phase, the chirp by the first male is delayed, apparently due to the inhibitory effect of the auditory input. A similar inhibitory effect has been observed when artificial sound signals are used (Jones, 1963, 1964).

Mutual inhibition appears to take place even at low chirp rates, but it is seen most clearly when the total chirp rate is high and chirps are coming as close together as possible. The pattern of interaction appears to be determined by (1) the interval at which a male follows its own chirp when the other male has not chirped, (2) the interval at which a male follows another male, and (3) the inhibitory reaction time. The second type of interval is shorter than the first, but is generally more than half its value. The actual values of the intervals appear to be adjusted to the total chirp rate of the two insects. It appears that when two males begin to interact the interaction tends at first to decrease their individual chirp rates, but that the two types of interval decrease until they can both produce their chirps at the required rate. There seems to be some evidence that interaction ultimately increases their individual chirp rates and Weih (1951) has observed a marked acceleration of emission in *Chorthippus brunneus* when two males start to interact.

The occurrence of synchronism in the midst of alternation and the sharp change from one to another is most interesting. The initial synchronization of chirps appears to be accidental. If one male is slightly late in following a chirp by the other, this one may chirp again as if it had not been interrupted. Synchronism occurs if the two chirps are so close together that one has not had time to inhibit the other. If the two males have substantially the same chirp rates the uninterrupted interval between chirps by each insect will be the same, and they will continue to sing in synchrony because each of them is singing as if it had not been interrupted. This will continue until the chirps become sufficiently out of phase for one to inhibit the other. They then go back to alternation.

The maximum number of consecutive synchronies observed was six. The probability of the chirps getting out of phase increases rapidly with the number of consecutive synchronies because of the variability in the length of the intervals. The higher the chirp rate, the more constant are the intervals and thus the greater the probability of continued synchrony.

The proportion of chirps involved in first synchronies increases with chirp-rate until a steady level is reached at about 11%. This may even decline slightly at very high chirp rates. When the chirp rate is low, the timing of chirps by one insect relative to those of another is relatively random. As the rate increases the probability of accidental synchrony also increases, but at high rates the intervals become so precise that changes from alternation to synchrony (or back) are less likely to occur.

The contribution of each of the partners to the total chirp rate obviously is important in determining the number of synchronies; in the extreme case, where one of the males is doing all the chirping, no synchronies will occur, no matter how high the chirp rate. The results obtained so far do not give a great deal of information on the effect of the difference between the chirp rate of the two partners in modifying the effect of the total chirp rate, since the recordings with the greatest percentage difference are also those where the total chirp rate was low.

Fulton (1934) and Alexander (1960) have both observed, in the field, similar

alternation and synchronism in *Pterophylla camellifolia*. Their observations indicate that the relation between the two types of interval is similar to that found in *Pholidoptera griseoptera*. Also Fulton's observations indicate the accidental nature of the synchronies which occur.

Busnel *et al.* (1956*a, b*) have studied intra- and inter-specific alternation in a number of species of *Ephippiger*. They came to the conclusion that responses between two males may be exchanged in three ways: (1) each insect keeps its own rate and the responses are regularly interspersed in such a way that the final rhythm is doubled; (2) the rate of each individual is halved and the two alternate so that they produce the same rhythm as one singing alone; (3) if one stops the other can respond in its place and so sing twice as much; this keeps the rate with or without alternation. This scheme gives an approximate description of the interaction in *Ph. griseoptera*, but breaks down when the intervals are measured more accurately. It also fails to take into account the occurrence of synchronism. It appears possible that a closer look at the interaction between *Ephippiger* males may reveal similarities with *Pholidoptera*. Busnel *et al.* used a single-channel recording apparatus which might well have obscured occasional synchronies, and the technique does not appear to have allowed such accurate measurement of intervals.

Huber (1964, 1965) has worked with gryllids and acridids on the role of the C.N.S. during stridulation. He has described three systems of controls, the mushroom bodies and central body of the brain, and the thoracic ganglia. The thoracic system controls the stridulatory muscles, but when isolated from the brain is able only to start a basic form of the stridulatory movement and to maintain it for a short time. Normally impulses from the brain modulate the thoracic system with the rhythm of chirp and sequence rate. The mushroom body appears to determine the song type and also may inhibit as well as excite the central body, which appears to translate these higher 'commands' into the actual pattern of excitation which determines the temporal pattern of stridulation.

It is probable that the controls in *Ph. griseoptera* are essentially similar. Simple excitation of the thoracic mechanism by a single nerve impulse or a short burst of impulses would excite the mechanism enough to produce a short chirp of three or four syllables. Longer groups of syllables would be produced if sufficient impulses or bursts of impulses arrived at the thoracic centre to maintain the excitation at a sufficiently high level. The breaks in the long chirp would occur if the impulses or bursts did not arrive sufficiently close together to maintain the excitation.

The syllable rate appears to be relatively constant for any given temperature except at the end of the chirp or group of syllables in a long chirp when the rate decreases. This decrease may be due to the waning of the excitation of the syllable-producing mechanism. It seems probable that as long as the excitation is sufficient the wings oscillate at a rate determined mainly by the temperature. Pringle (1957) has observed that a single stimulus to the sound-producing mechanism in cicadas results in a group of syllables which are produced at a declining rate, presumably as the excitation of the tymbal muscle is waning. It is not possible at this stage to suggest whether the syllable-producing mechanism in *Ph. griseoptera* is neurogenic or myogenic. The syllable rate is about 35-40 per sec. at 20° C.

It seems probable that the thoracic mechanism is controlled by a pacemaker system.

Huber's work makes it seem likely that the pacemaker is in the central body of the brain. The activity of this would be modified by excitation or inhibition, possibly from the mushroom bodies. Long chirps would result when the excitation of this pacemaker was particularly high. Proximity of another chirping male appears to be especially effective in producing this excitation. No work has been done to find whether this is due solely to acoustic stimulation or to a combination of visual, olfactory, acoustic and perhaps mechanical stimulation, but Alexander (1961) has shown that many factors are important in determining aggressiveness in crickets. Males which are already chirping at a high rate are more likely to produce long chirps when another male is put close to them. It appears that chirp rate and the production of long chirps are linked by the same system of excitation. Alexander (1962) has discussed the possibility that, in crickets, the aggressive song has evolved from the calling (proclamation) song, and Ewing & Hoyle (1965), working on the neuronal mechanisms underlying the control of sound production in the cricket *Acheta domesticus* (L.), have commented on the similarity between calling and aggression. They have proposed that the same central mechanism is concerned in both types of song and that it is switched on for longer to give more sound 'pulses' in aggression, probably due to stimulation by the presence of another male.

The acoustic reception of another chirp has a rapid (50 msec. at 20° C.) inhibitory effect on chirping and possibly a delayed excitatory effect. The speed of the reaction makes it probable that there are only a very small number of synapses involved. It is also possible that auditory feedback from the insect's own chirp may have a similar effect. Alexander (1960) has discussed the possible role of auditory feedback in stabilizing the chirp output of a singing male.

It is interesting to speculate on the significance, to the insect, of the acoustic interaction between males. The main function of the proclamation song appears to be that of guiding sexually responsive females to similar males. Alternation singing and the production of long chirps when another male is too near may have the function of spacing the males and thus increasing the probability of successful mating of all the females. Alexander (1960) has stated that in the Tettigoniidae the males are sometimes sedentary and territorial. Alternation may give each male the chance to assess the loudness of the other's song and therefore its proximity. Also, it may aid the female in locating an individual male by reducing the background noise of other males singing. Long chirps may be used if the mechanism breaks down and two males get too close together. It seems that long chirps are produced only when the other male sings; a silent male may well be confused with a female. Walker (1964) has pointed out that stridulation may have the disadvantage that it helps in the location of the insect by a predator. A short high-frequency chirp, produced at irregular intervals, may help to minimize this danger and group singing may make it more difficult for a predator to concentrate on one insect, as males cease singing at the slightest disturbance. When one male stops singing, the others sing in its place and could well distract a predator from the now silent insect. It is interesting that in this case the song is inhibited for minutes rather than fractions of a second.

To sum up, it appears that it is possible to explain the acoustic interaction between males in terms of excitation and inhibition of a pacemaker system. The pattern of alternation and synchronism is mainly determined by mutual inhibition between the

singing males, although it is probable that the interaction has a general excitatory effect. Mutual excitation appears to be important in rivalry behaviour.

SUMMARY

1. *Pholidoptera griseoptera* males singing alone or alternating with other males produce short chirps of three or occasionally four syllables (wing movements) lasting about 100 msec. (at 18° C.).

2. Close proximity of singing males may result in rivalry behaviour where chirps lasting up to about 4 sec. may be produced. The long chirp is not usually continuous but has a number of breaks or 'stutters'.

3. The syllables and syllable rates in the long chirp and short chirp are essentially similar.

4. At the end of a short chirp or of a group of syllables in the long chirp, the syllable rate is decreased, possibly indicating a waning of excitation of the syllable-producing mechanism.

5. Males within hearing range of each other alternate or occasionally synchronize their short chirps. The pattern of this interaction appears to be determined mainly by mutual inhibition between the singing males. Mutual excitation may cause an increase in chirp rate during the interaction.

6. Chirping may be controlled by a pacemaker system which can be inhibited or excited by its various inputs. A long chirp is possibly the result of a high level of excitation of this mechanism.

7. Alternation singing and rivalry behaviour between males may have a territorial significance.

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