PAIR-FORMING ACOUSTIC SYSTEMS OF PHANEROPTERINE KATYDIDS (ORTHOPTERA, TETTIGONIIDAE)

By JOHN D. SPOONER

Department of Biology, Augusta College, Augusta, Georgia 30904, *U.S.A.*

Progress in describing the sounds of North American Ensifera and in explaining the biological significance of their sounds has largely been limited to crickets (Gryllidae) (e.g. Alexander, 1957, 1960, 1961, 1962b; Walker, 1957, 1962a,b, 1963). Few Tettigoniidae have been investigated; they are generally more difficult to study in the laboratory than crickets. Evidence to date indicates that most tettigoniid males produce sound while alone and produce no sound while in intimate contact with females. A few kinds of male produce sound during close contact with other males (Alexander, 1960; Pierce, 1948). Males produce only one kind of sound, and most females are mute.

The acoustic behaviour of most North American Phaneropterinae differs from that of other Ensifera. Lone males (either out of all range or only in acoustic range of other individuals) produce more than one kind of sound, and the females of all species investigated produce short ticks that attract sexually responsive males. No other female Ensifera are known to stridulate during pair formation. Among the Conocephalinae (Tettigoniidae) and Nemobiinae (Gryllidae) lone males of certain species produce two kinds of sound, but the females of these species are mute. The general acoustic behaviour of these latter species conforms with non-phaneropterine behaviour. Another distinction in phaneropterine acoustic behaviour is that males may vary the intensity of their sounds; different intensities of the same sound may trigger different responses.

Subjective terms used to describe different phaneropterine sounds reflect differences in movements of the stridulatory apparatus as well as differences in the sound patterns. Ensiferan sounds are delivered in pulses which correspond either to single strokes of the tegmina moved at rates fast enough to engage many stridulatory file teeth in a fraction of a second, or to single toothstrikes when the tegmina are moved so slowly that each toothstrike can be detected by ear. In each case, what seems to the human ear to be a single sound unit (pulse) evidently functions as the smallest detectable unit (phoneme) for the katydid. Pulse rates differ among species. The pulse rate seems to be information-carrying parameter when the pulse rate is greater than three per second (Walker, 1957). When pulse rates are lower than two or three per second, individual pulses are the morphemes or information-carrying units (this paper). In the latter case pulses are of two kinds. One kind, a *tick*, involves striking only one or a few teeth of the stridulatory file (1 to 10, usually 1 to 3). The other kind of pulse, a *lisp*, contains a large number of toothstrikes, and has a consistent length that is species-typical. A third kind of sound not fitting into the above categories is called a *click*. Clicks contain two pulses (sometimes three or four) that differ from each other in intensity, duration or both. The meanings of other terms (*buzz*) should be self-explanatory.

Singing by lone phaneropterine males varies from relatively simple repertoires in certain species, i.e. groups of similar pulses are produced each time an individual sings, to complex repertoires involving strikingly different sounds. Some species with complex repertoires produce their different sounds in no predictable sequence (Spooner, 1964b); other species produce different sounds consecutively in stereotyped sequence (Alexander, 1960).

Little has been reported about the biological significance of any kind of phaneropterine singing. Some workers (Riley, 1874; Fulton, 1933; Grove, 1959; Alexander, 1960) have heard females of some species answering certain conspecific male sounds with a short tick. Spooner (1964b) described the behavioural significance of the sounds of *Scudderia texensis*.

This paper provides descriptions of the sounds of nine species, including some previously unreported sounds, and presents the results of numerous experiments investigating the behavioural significance of these sounds. Descriptions of the sounds of several other species and more complete tabular data for seven of the species discussed here can be found in Spooner (1964a).

Methods

Extensive tape recordings of field-collected katydids were made in the laboratory with an Ampex 351-P recorder or a Nagra III PH recorder; a few field recordings were made with the Nagra III or a Magnemite 610E recorder. In all cases a dynamic microphone (American Microphone Model D33A, or RCA Model MI-4048-E, Type 88A) and low-print tape at 15 in. per second were used. The recorded sounds were analysed with a sonograph, which allows accurate measurements of pulse rates and pulse durations. Sonograms often indicated considerable variation in dominant frequencies (pitch) of songs of different individuals of the same species and sometimes between phrases of single songs (Fig. 1, Plate III). No doubt some variation was inherent in the songs, though much was due to the methods of recording and analysis (Morris, 1965).

The functions of the sounds were ascertained by broadcasting recorded sounds to individually caged virgin females, and to males of differing age and experience. The experimental cage, or response arena, is illustrated by Spooner (1964b).

Complete details of the methods employed during this research are presented by Spooner (1964a).

Species Comparisons

Inscudderia strigata (Scudder)

Lone males of Inscudderia strigata produce three distinct sounds, none of which has been described. Two sounds commonly heard are lisps (Fig. 2a, Plate III) and ticks which are alternated in long series in each acoustic performance. Lisps, delivered 1·3 to 2·2 sec apart at 25°C are alternated with one to seven (usually five to six) ticks. The number of ticks is loosely correlated with the time interval between successive lisps. The intensity of the sounds and the lisp rate in each series increases slightly during the first two to three lisps. The number of ticks is usually one to two initially; one to two ticks are added each time until the singer produces the characteristic five to six. Often the ticks appear in pairs, but the tick rate is seldom constant. The series of lisps and ticks is usually terminated with about a dozen ticks.

Males of strigata are seldom completely isolated from other conspecific individuals. Their host plant, Hypericum fasciculatum, typically grows in isolated stands. If found in one of these stands, strigata is usually abundant, five individuals having been collected on a single bush 2 ft in diameter. I have observed the acoustic behaviour of natural congregations involving fifty or more individuals on more than 10 different nights and on 3 different days in midmorning. Sound production in congregations appears to be the same in daylight and darkness; it differs from solitary singing in that singing males interact. When one male starts a series of lisps and ticks, others for several feet around join his ticking with their own ticks, so that there is an almost regular alternation of lisps by one individual and ticks by many. When the lisper reaches the end of his series, another male usually begins lisping immediately. The result often is continuous lisping and ticking for long periods (not timed; I have been at locations for over an hour where large numbers sang with only occasional pauses of a few seconds). More continuous singing seems to occur when large numbers of individuals are congregated. Since the nymphal stages are as congregated as the adults, sound is probably not a congregating mechanism for strigata, except possibly when females are acoustically active (discussed later).

Ten lisps from each of three males laboratory-recorded at 25·8, 25·8, and 26·6°C, respectively, averaged 78 msec (range (R) = 73 to 84, standard deviation (SD) = 5). Average delay of the first tick after a lisp was 574 msec (R = 523 to 600). Six lisps of one individual averaged 48·5 teeth struck (R = 46 to 52). Eight ticks from the same male averaged 7·5 teeth struck (R = 4 to 10). The two other individuals struck 1 to 5 teeth per tick.

The least commonly produced sound of strigata, heard once in darkness, is a low-intensity, two-pulsed click (Fig. 3, Plate III), repeated in series and produced at times of low acoustical activity. In one laboratory tape-recorded series of thirteen clicks (25·5°C), the interval between clicks averaged 1·7 sec (R = 1·5 to 2·2). The intensity and tooth strike rate of the second pulse were greater than those of the first. Three teeth were struck in the second pulse, 3 to 5 in the first pulse. The pulse rate within clicks averaged 9·0 pulses per sec (SD = 0·2). In calculating pulse rate, time was measured from the beginnings of the pulses.

Laboratory behaviour of males was like field behaviour except when virgin females ticked immediately after each lisp. Ticking of the males then became erratic and more intense. Females answered lisps with or without the alternating male ticks.

Timings of the interval between a broadcast lisp and the female responding tick (37 timings involving three females recorded between 24·8 and 29·0°C) averaged 97 msec (R = 48 to 147, SD = 19). One female answered a singing male ten times at 80 msec (R = 61 to 116, SD = 18) (28·0°C). In no case was the female tick delayed until the shortest timing of a male tick.

In experiments the lisp stimulated the three test females to tick after the lisp in whatever arrangement or intensity it was broadcast. Each experimental female oriented towards the loudspeaker on one occasion, and two of them moved a short distance towards the loudspeaker. These movements suggest that females may move towards lisps in the field. However, the movements occurred at the beginnings of test series, the females having been in darkness for at least 10 min without having heard any male sounds. During subsequent tests the females either remained motionless or walked in a random pattern, always ticking after lisps.

Ticks and clicks had no visible effect on test females at any intensity; these sounds apparently function only in male interactions.

The only reaction given by five test males to lisps, or to combinations of lisps and ticks, was ticking at the time when they would have ticked in natural situations, i.e. in alternation with lisps from other males. Movement either did not occur or was random. Often, when the recorded sounds were turned off at the end of a test, the test male would produce a series of lisps and ticks. Low intensity lisps almost always caused the test males to produce lisps and ticks during the tests, whereas high intensity lisps elicited only ticks. Such contrasting behaviour suggested that high intensity lisps and ticks had an inhibitory effect upon male lisping. To test the idea, six individually caged males were observed as sounds were broadcast to them from 3 ft away. The males were allowed to start singing, and then the recorder was turned on. The result was inhibition of male lisp production by the recorded lisps or ticks when a pulse of high intensity sound preceded and overlapped the time the singer would have begun a lisp. This would be enough to inhibit lisping from all but one male in a congregation of singing individuals. In the groups studied there was a modal, and usually minimal, period of 1·5 sec at 25°C between successive lisps of a singer. All males observed the refractory periods between lisps while just one male lisped. To start lisping, another male would have had to abandon the

somewhat longer intervals between his initial lisps in order to intercede the already lisping male. The tick rate of the terminal ticks of the observed series always decreased; thus, there was greater opportunity for a new singer to start a lisp–tick series at the end of another male's series than at any other time.

Tests with the click were inconclusive but suggested that clicks function in male spacing. Not enough observations were made of the 24-hr cycle of acoustic activity to rule out the possibility of a particular time in which clicking is prominent. Spooner (1964b) found that, during the evening twilight, *Scudderia texensis* males produce a low intensity ticking which functions in male spacing.

Answering females attracted test males. To avoid the possibility of chemical or visual stimuli attracting test males, a female was placed out of sight but within hearing distance of the test males. Her answer, broadcast at the arena, attracted males to the loudspeaker.

In the field non-lisping males apparently go to females answering lisping males. Four unmutilated test males went to a female, answering a recorded lisp. A silenced male (stridulatory file removed) went all the way to the female on each of several tests when the female answered a recording. One night in the field I stood in the midst of a group of singing males and imitated a female tick by snapping the edges of my fingernails together after the lisps. Not only did the 'lispers' orient and move toward me, but a number of 'bystanders' did so as well.

Microcentrum rhombifolium (Saussure)

Lone males of *Microcentrum rhombifolium* produce two distinct sounds, lisps (Fig. 2d, Plate III) and ticks, both of which are made during the closing strokes of the tegmina (Allard, 1928a, b; Fulton 1932, 1933; Alexander, 1956, 1960; and others). Grove's (1959) account is the most descriptive.

Both lisps and ticks may be heard at any time of day or night, although more acoustic activity is apparent at night. In most instances lisps and ticks are isolated accomplishments, having no constant relation one to another, but sometimes a male may give a couple of lisps in rapid succession to follow with a series of ticks. Combined songs usually occur when a male becomes acoustically active after a period of silence.

M. rhombifolium is chiefly arboreal and thereby difficult to collect in numbers. I studied only

one female and two males in the laboratory. One male had a lisp rate (26·0°C) of one per 3·0 sec (n = 13, R = 2·0 to 4·1), a lisp duration of 25 msec (n = 10, R = 22 to 30, SD = 3) and 20 to 24 (n = 4) toothstrikes per lisp at about 880 toothstrikes per sec. A series of ticks (one phrase) in the ticking song of *rhombifolium* corresponds to individual toothstrikes of one closure of the tegmina. Three phrases from each male, averaged 8·5 (25°C) and 8·8 (25·5°C) ticks per sec, respectively, and contained 22 to 34 ticks per phrase. Other workers have noted phrases of 28 to 32 ticks (Grove, 1959) and 15 to 30 ticks (Alexander, 1956).

Allard (1928a) and Fulton (1933) noted that females produce a low intensity tick after a series of male ticks and that males go to females when such acoustic interaction takes place. I attracted several males to me in the field by imitating the female tick. Alexander (1960) described the acoustic interaction between a male and a female caged near each other but out of sight from each other. The female's response was so precisely timed that her tick seemed almost a part of the male series. Grove and Alexander both noted that after the female's answering tick, the answered male would often produce an irregular shuffling sound. Grove conjectured that this may serve to confuse the location of the female, for he noticed that 'listening' males sometimes produced the shuffling sound after having heard a male–female sequence and often moved towards the females. Some males reached females and copulated without having made a single sound. My female died before a male–female acoustic sequence was recorded, so it was impossible to test Grove's observation in the laboratory. However, I attracted non-singing males by 'answering' singing males.

The function of the lisps has been the subject of conjecture. Grove saw males in cages jump about when other males lisped; he postulated that lisps had a territorial function. Certainly, if males in the field were so irritable when lisps were produced, they would tend to move away from the sound. Grove also suggested that the lisps may keep responsive females in the vicinity of a lisping male, and Alexander (1960) seemed to favour this idea.

Three series of tests of the lisps were conducted at 55, 75 and 90 dB, with the single female. At 55 dB she went immediately to the loudspeaker in all tests. At 75 dB she usually turned towards the loudspeaker, but she went towards it in only two tests and then only part way. At 90 dB she did not move. The female never ticked after any lisp. Two weeks after the above tests I repeated the experiment with the same female and she gave a similar performance, i.e. no response to high intensity lisps, but immediate orientation and movement towards the loudspeaker at low intensity. Similar behaviour is exhibited by females of *Scudderia texensis* which move towards one conspecific male sound only at low intensities (Spooner, 1964b). This explains why Grove never saw this function of the lisps in his caged individuals; females near males receive the lisps at too high an intensity.

Montezumina modesta (Brunner)

Little is known about *Montezumina modesta*. I have collected it, equally abundant, in both a xeric, sand-hill community and in a hydric cypress head, but only in locations with some shrub or tree cover. Individuals are difficult to observe, due to their cryptic coloration and the way they perch underneath leaves and on inner branches of shrubs.

In terms of complexity of solitary singing, *M. modesta* is unique among the phanteropterines studied. The male sings primarily in late afternoon and early twilight but only occasionally in late twilight and darkness. I listened to a group of these katydids for a period of about 2 weeks. As the sun sank behind the trees, but not below the horizon, large numbers of lisps by males were answered by ticks from both males and females. Lisps, spaced 0·5 to 1·0 sec apart, were delivered in series of 10 to 35. Responsive ticks from answering males and females came an instant after each lisp. Lone males not only lisped but most often produced a low intensity tick immediately after each lisp so that lisp–tick was suggestive of the sound produced in one opening and closing of the tegmina. Responding males produced single ticks or 3 to 4 rapidly delivered ticks.

In the laboratory caged individuals sang rapidly when twilight conditions were simulated by leaving the door open for the only light source. Males had two characteristic lisps (Fig. 4, Plate III). In most lisp series the initial lisps were 'short', delivered about $\frac{2}{3}$ sec apart (stopwatch timings) at 25°C, the terminal lisps were 'long', and about 1 sec apart. Average lisp durations for short and long lisps were 19 msec (n = 40, R = 13 to 23, SD = 2) and 30 msec (n = 25, R = 23 to 39, SD = 3), respectively. The female tick response was the same, about
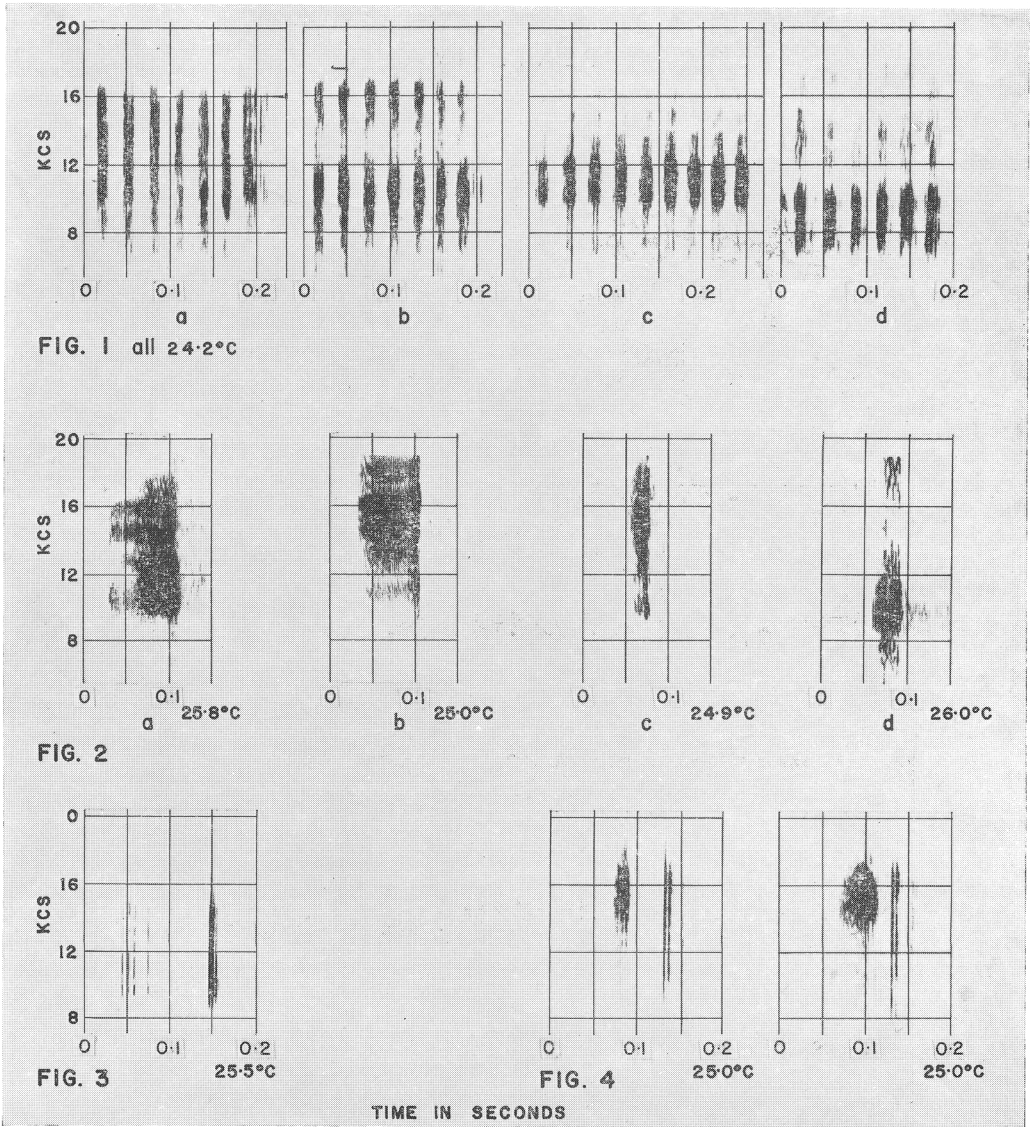
PLATE III

Fig. 1. *Amblycorypha floridana* buzzes showing variations in frequency spectrums. a and b—same individual; b and c—two other individuals.

Fig. 2. Single lisps of four species. a. *Inscudderia strigata*. b. *Scudderia furcata*. c. *Scudderia cuneata*. d. *Microcentrum rhombifolium*.

Fig. 3. Single click from *Inscudderia strigata*.

Fig. 4. Short and long lisps of *Montezumina modesta* with answering female ticks.
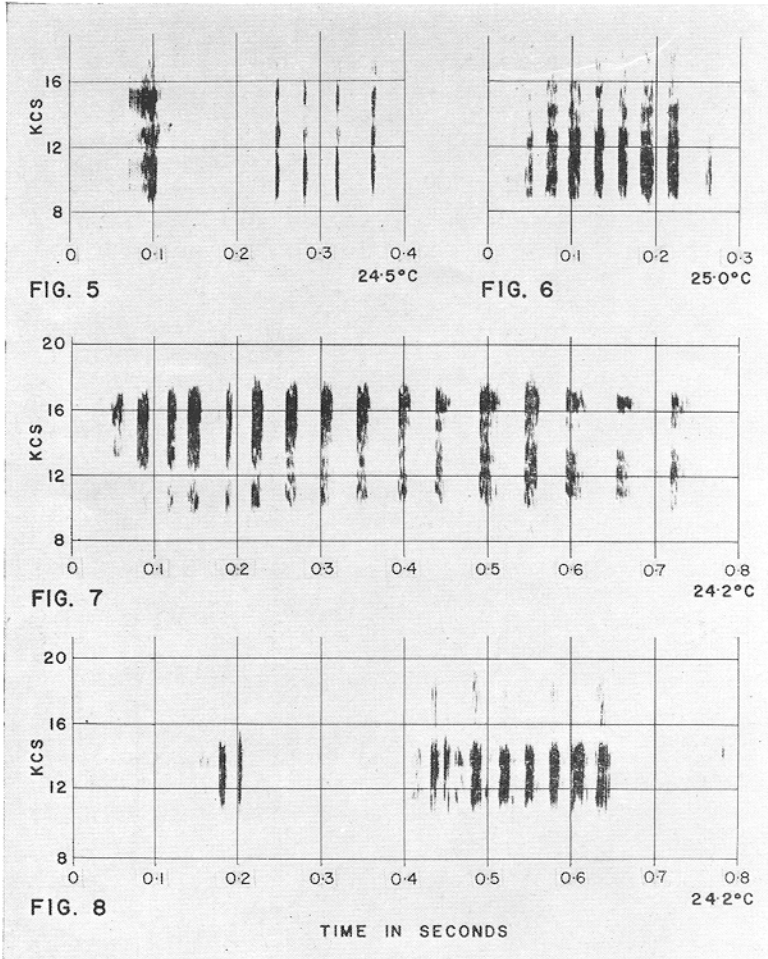
PLATE IV

Fig. 5. Lisp–tick sequence from *Turpilia rostrata*.
Fig. 6. Normal pulsed phrase from *Scudderia furcata*.
Fig. 7. Erratic, many-pulsed phrase from *Scudderia furcata*.
Fig. 8. Two clicks and a buzz from *Amblycorypha floridana*.

60 msec (R = 53 to 68), to both types of lisp when time was measured from the beginnings of the lisps. Responses timed from the ends of lisps were not the same. This suggested that the females only secondarily answered long lisps after having answered a series of short lisps. Indeed, female responses to long lisps were not nearly as vigorous as they were to short lisps (see discussion of intensity of response in a later section); often long lisps were not answered at all. Experiments indicated that female ticking after long lisps is not important.

Virgin females responded to recorded lisps only after all frequencies below 15,000 Hz were filtered out. Lisps were broadcast at 50, 55 (the maximum measured from a male), and 60 dB to two females. In these tests females answered the short lisps at all intensities, but moved very little towards the short lisps, though they often oriented towards the loudspeaker. Long lisps attracted females when broadcast at high intensities; low intensity long lisps elicited no response. These reactions differ from those of *Scudderia texensis* and *Microcentrum rhombifolium* in which females are attracted from a distance to the vicinity of a male. My experiments with a single male of *modesta* clearly indicate that *modesta* males move towards answering females, but only so long as they hear the answering females at low intensities. Females of *modesta* bridge the final gap between the sexes by moving towards high intensity long lisps.

Scudderia curvicauda Brunner

This katydid is found over the whole of eastern North America, inhabiting herbaceous and shrub strata. I have never seen *curvicauda* where its population density was more than about two males per acre, estimated by listening to singing individuals, and often the density appears less. Males fly about at night singing from each perch. They have only one kind of song, a series of phrases with each succeeding phrase containing one pulse more than the preceding phrase. The usual song contains 2, 3, 4, and 5 pulses per phrase, but seven-pulsed phrases are occasionally heard. Often a male will repeat phrases of a certain number of pulses, producing a sequence like 2, 3, 3, 4, 5, 5. Songs are produced several minutes apart. Pulse rates in my recordings varied from 4·5 to 5·8 pulses per sec at 25°C.

In the laboratory males occasionally synchronized with other males, but usually they responded with high intensity ticks immediately after each phrase. Perhaps intensity of sound determined the type of response.

One female answered each phrase of a male's song at an average timing of 835 msec (n = 9, R = 718 to 942, SD = 88) after the end of the phrase. In the presence of responsive females non-singing males ticked immediately after the singing male's phrases, were silent at the timing of the female tick and ticked subsequent to the female tick.

Evidently, females do not move towards singing males: movement of the latter would make it almost impossible. No experimental female moved towards male sounds. In the field I watched a male locate a female by flying a few feet at a time towards the female's answering tick from an initial separation of about 75 ft. By imitating the female tick, I have attracted males from 100 ft away. An important factor in attracting males was to maintain a constant (high intensity) simulated female tick. As males came closer to me they produced less intense sounds. If I decreased the intensity of the simulated answer, the males would increase the intensity of their phrases, as if signalling to a female farther away, and would fly past me, as if trying to locate the female from a greater distance than that separating the male and me. In the laboratory males usually lowered the intensity of their phrases once a female answered. This behaviour would lessen the likelihood of a non-singing male locating a responsive female. Experiments showed that males of this species go to females answering other males.

Scudderia cuneata Morse
and
Scudderia furcata Brunner

Scudderia cuneata and *Scudderia furcata* are discussed together because of their close relationship, overlapping geographical distributions, and similar sounds. Alexander (1960) pointed out the problem of understanding how heterospecific males and females of *cuneata*, *furcata*, and *S. fasciata*, a third species which overlaps geographically with *furcata* and possibly with *cuneata*, maintain reproductive isolation when the song patterns of the males of the three species are apparently identical. He suggested that the timing of female responses may differ.

Both *cuneata* and *furcata* are common in the southeastern coastal plain; mostly they occur in different habitats and adults are present at different times of the year. Both frequent shrubby woods more than completely open habitats; *cuneata* is generally present in hydric to mesic situations, and *furcata* usually frequents

xeric to mesic situations. *S. cuneata* has one generation a year, adults being found from the middle of July until early November; *furcata* has two generations a year, adults being found from early May until November, but with reduced numbers in August and September prior to the maturation of the second generation. Thus, only a relatively small number of individuals in the two species have the potentiality for confusion in pair formation. My data show that the sounds of *cuneata* and *furcata* are sufficiently different to cause reproductive isolation by specificity of response to conspecific sounds.

The acoustic behaviours of lone males of *cuneata* and *furcata* are so similar that only a trained ear can distinguish them in mixed populations. Both species produce single-pulsed lisps (Figs 2b and 2c, Plate III), which they reiterate a few seconds apart in series of three or four. Different series are spaced anywhere from 1 to 30 min apart. A second sound produced by both species, but much less often than lisps, is a short phrase (Fig. 6, Plate IV), which is repeated at rates of one every 4 to 5 sec to 1 min.

The only difference between day and night acoustic activity appears to be increased singing at night. Both lisps and pulsed phrases can be heard at any time of day, but I have no information on whether the pulsed phrases are more frequent than the lisps at some specific time of day. These descriptions agree in general with those of other authors who have described *furcata* sounds from aural impressions, except that Allard (1911) and Cantrall (1943) observed more singing from *furcata* in the afternoon than at night. Low night temperatures could account for their observations.

Lisp analysis at 25°C for the two species was as follows: *cuneata* one per 2·3 sec (R = 1·7 to 3·0) with 16 msec (n = 26, R = 12 to 25, SD = 3) duration, *furcata* one per 3·3 sec (R = 2·4 to 4·2) with 75 msec (n = 18, R = 55 to 90, SD = 9) duration. Lisp durations are distinct. Analysis of twenty-seven phrases involving four *cuneata* males and six phrases involving two *furcata* males revealed no marked difference in pulse rates between the two species. *Cuneata* averaged 35·0 pulses per sec between 25·2°C and 25·9°C; *furcata* averaged 35·6 pulses per sec at 25°C. One difference between the pulsed phrases of the two species may be the phrase duration, reflected by the number of pulses per phrase. *Cuneata* produced two to four pulses per phrase, almost always four. All of the six phrases of *furcata* contained more than four pulses. Experimental evidence from both species (discussed later) also suggests that phrase durations may be important in eliciting response.

I have heard only lisps and pulsed phrases from lone males of either *cuneata* or *furcata*. Yet Cantrall (1943), Fulton (1930) and Pierce (1948) have described a very low intensity ticking sound from *furcata*. Cantrall heard the ticks once and says they were barely audible 5 feet away; single 'tsips' were produced every 2·5 sec. Fulton observed ticking from males of *furcata* in late afternoon in Oregon, the ticks being emitted 2 to 3 sec apart 'to a rate too rapid to count'. He added that females occasionally produce a similar but somewhat fainter sound. Pierce's observation may have been made in either the laboratory or the field, but I suspect it was in the laboratory for he obtained 'several records' from *furcata*, and this could be done more easily in the laboratory. I have never heard ticking from lone males of *cuneata* or *furcata*, nor from congregated males of either species where no responsive females were present. However, in the laboratory where virgin females ticked in response to lisps, both *cuneata* and *furcata* males produced ticks irregularly in the manner described by Fulton for *furcata*. In the presence of responsive females, males ticked continuously except when a lisp was being made and during the period when a female tick would have been expected. Immediately after a lisp, males usually produced a few rapidly delivered ticks and stopped before the time of the female tick. After the time of the female tick, whether a female ticked or not, males ticked irregularly at slow rates. When responsive females were removed from the room, males continued to tick for a few minutes slowly by themselves or in response to lisps; after a few minutes with no responsive females around, male ticking always subsided. These situations were created a number of times with the same results: males ticked only in the presence of a responsive female. Near Statesboro, Georgia, I heard both *furcata* and *cuneata* males making loud ticks on several different nights in the field, but investigation always revealed the presence of a responsive female. Possibly responsive females precipitated the ticking that both Fulton and Cantrall reported. If Pierce actually did his recording in the laboratory, then he may possibly have had a responsive female present, thus simulating a situation like that in my laboratory. Of course, it is possible that *furcata* from other locations may produce a ticking sound in solitary

situations similar to that of *Scudderia texensis* (Spooner, 1964b). As mentioned, *cuneata* or *furcata* males were almost always silent at the expected time of a female-answering tick; this agrees with the behaviour of other *Scudderia*.

Occasionally a male of *cuneata* or *furcata* produces a single tick after his own lisp approximately when the female should tick. The mean delay of the tick after the lisp in this sequence is greater than the mean delay of a female tick, although the ranges of timings of male ticks and female ticks overlap for each species. Six lisp–tick sequences (three each from two males) of *cuneata* averaged 399 msec (R = 343 to 440, SD = 36) between lisp and tick; twenty-one sequences from one *furcata* male averaged 1366 msec (R = 1260 to 1644, SD = 58). The timing of response at 25°C for *cuneata* females was 353 msec (n = 36, R 270 to 409, SD = 24); for *furcata* 1118 msec (n = 23, R = 840 to 1384, SD = 120).

The foregoing shows species-specific lisp durations and species-specific timings of female response for the two species. In the laboratory young females answered only the lisps of conspecific males. After having been kept in the laboratory for a long period without being allowed to copulate, females would sometimes answer heterospecific lisps, but even then at species-specific timings.

The only consistent responses exhibited in experiments were female ticking following conspecific male lisps and male attraction to conspecific females. Other responses were so inconsistent between successive tests with single individuals and between individuals that no definite conclusions can be drawn from the data. *Cuneata* females usually answered *cuneata* four-pulsed phrases and sometimes answered *furcata* six-pulsed phrases, whereas *furcata* females seldom answered any phrase. In a few tests certain females of both species oriented and went towards intermediate intensity conspecific lisps and pulsed phrases of males of either *cuneata* or *furcata*. Non-singing test males of both species did not move to females answering recorded lisps.

Neither fast nor slow ticking had any apparent effect on test females of either species. However, test males of both species almost always turned and erratically moved away when ticking sounds were broadcast. Ticking sounds from males of either species are alike; both repel heterospecific and conspecific males.

Another sound, not yet mentioned and heard in both laboratory and field from *furcata* males

when females were answering and several males were ticking loudly, was a high intensity, many-pulsed phrase (Fig. 7, Plate IV) which decreased continually in intensity and pulse rate. This sound had no apparent effect on test individuals, probably because of inability to simulate the conditions in which the sound was produced.

Amblycorypha floridana Rehn and Hebard

Adults of *Amblycorypha floridana* are abundant throughout Florida from early June to July in almost any lushly vegetated area except dense forests. Lone males produce a sequence of several *clicks* followed by a *buzz* (Fig. 8, Plate IV), and the sequence is usually repeated several times (three to twenty-five repetitions heard). One sequence of clicks and a buzz can be termed a *sentence* (Broughton, 1964). When starting to sing after a period of non-singing, a male usually clicks at a slow rate initially and increases the click rate through about a dozen clicks before producing the buzz. In succeeding sentences only four or five clicks are usually made before the buzz. The time interval between sentences is usually decreased during the first three or four sequences and increased towards the end of the series. Usually a dozen or more clicks end a series.

In normal singing, the two clicks before the buzz are produced in more rapid succession than the preceding clicks, and the buzz follows the last click with almost no break, so that the sentence may be divided into parts—part I: the initial 3 to 4 clicks given at a rate of 2 to 3 per sec, part II: the two clicks just preceding the buzz, and part III: the buzz.

Most often *floridana* is found congregated in favourable habitats, and in such congregations the predominant sound is clicking. When several males are singing close together *only* one male makes both clicks and buzzes at any given time. Other males click loudly until the one male producing sentences stops buzzing. Then another male clicks and buzzes while his neighbours click. Buzzing evidently inhibits sound production from the males. A high intensity, high frequency buzz from a male of *Atlanticus glaber*, present in the laboratory at the same time, caused *floridana* males completely to cease sound production. A loud, orally produced hiss often caused the same effect. I also stopped single males from buzzing or clicking by broadcasting a recorded *floridana* buzz just ahead of and during the time when the singing males would have made a sound.

Completely solitary males of *floridana* sometimes produce only the initial one to two clicks, pause, and then buzz. In the abbreviated sentences the click just before the buzz is usually present, although certain individuals consistently omit even this click. Thus, instead of the usual click, click, click, click, click, click-buzz, the abbreviated sentence is click, ——, ——, ——, ——, click-buzz. Such singing occurs when a male is acoustically isolated from other singing males as may occur early in the season and in atypical habitats. Some of these solitary males fly about, singing a few sequences from each perch.

In the middle of a series the sentence is repeated about every 2 sec (R = 1·4 to 2·6), depending on the individual. In an experiment to determine the effects of temperature on orthopteran sounds, T. J. Walker (personal communication) found the pulse rate of the buzz of three males of *floridana* from Alachua County, Florida, averaged 45·2 pulses per sec at 25°C. I recorded at 24·2°C a series of sentences from each of seven males from different localities in Florida and made two sonograms (different samples) of each recording. Some of the results are shown in Table I.

Individuals from the Pensacola Bay area had slower pulse rates than central Florida individuals. The click pulse rate is faster than the buzz pulse rate. Tooth strike rate (not shown) in the click pulses is slower than the tooth-strike rate in the buzz pulses. Clicks apparently consist of two cycles of opening and closing the tegmina.

Females answer each sentence shortly after the buzz. The answering tick of three females from central Florida averaged 138 msec (n = 30, SD = 13) delay after the buzz of broadcast sentences. One female from southern Florida averaged 161 msec (n = 10, SD = 27) delay.

To determine what part of the sentence is important in evoking ticks from females, I broadcast parts of the sentence—I, II and III—singly and in different combinations, at 55 dB from a loudspeaker 1 ft away from individually caged females. Each part or combination of parts was broadcast fifty times. Three females were tested, one at a time. Each female was tested twice but not twice in succession. Thus two series of tests were made with each female. The first involved the same randomized sequence of successive tapes played to each female; the second involved a different randomized sequence each time a different female was tested. On tapes which had part of the sentence deleted a blank piece of tape was inserted to keep the remaining parts of the sentence normally spaced. The results of these tests are presented in Table II. In no case was the response to any part as great as to the whole sentence, and different combinations of clicks and buzzes evoked greater response than clicks or buzzes alone, suggesting that clicks and buzzes, combined in that order, are important in eliciting ticks from females. In the field females have been heard responding readily and consistently to the abbreviated sentence described earlier; more work is needed to clarify this problem.

Table I. Results of Analysis of Sonograms of Songs of *Amblycorypha floridana* Recorded at 24·2°C

Location of collection in Florida	Individual identification number	Pulses per buzz	Average no. pulses per sec	
			buzzes	clicks
Pensacola Bay	24	7–8	34·4	50·3
Pensacola Bay	25	7	35·9	56·8
Pensacola Bay	26	6	33·6	46·4
Pensacola Bay	27	9–10	33·9	55·1
Pensacola Bay	29	9	38·1	49·5
Salt Springs (Marion County)	30	9–11	49·0	63·7
Gainesville	31	10	42·8	57·7

Table II. Results of Experiments to Determine which Part of the Male Sound Sequence is Important in Evoking the Tick Response from Females of *Amblycorypha floridana*.

Test series	Individual females	Part of sentence broadcast						
		I	II	III	I–II	I–III	II–III	I–II–III
1	20	7	13	26	26	40	1	48
		10	17	19	24	33	44	45
1	21	0	3	9	11	31	8	36
		0	6	7	5	31	1	40
1	23	0	0	2	0	41	30	50
		7	5	35	1	50	48	49
2	20	5	0	7	8	19	23	38
		7	0	3	7	18	12	33
2	21	2	0	4	5	21	15	31
		4	0	6	7	19	13	34
2	23	7	0	9	7	22	15	47
		9	1	11	19	23	30	50

Numbers in the columns represent the number of different repetitions of the sound to which the female responded out of 50. The order of the column headings reflects in no way the order in which the different sounds in the experiment were played.

Response arena tests involved broadcasting sounds at 80 dB (the high-intensity measured from singing males), 55 dB and barely audible; sound was repeated every 2 sec.

Males changed only their acoustic behaviour during the acoustic parts of all tests regardless of the intensity of broadcast sound. Low intensity sentences stimulated males to sing, but they were inhibited from buzzing by high intensities.

To barely audible sentences three test females ticked consistently, but never oriented towards the sound. They answered most sentences at 55 dB and apparently were stimulated to move about, as evidenced by their starting to move or increasing their speed of movement when the broadcast began. However, they moved without orienting towards the loudspeaker. Sentences at 80 dB caused immediate orientation and movement to the loudspeaker; except in two tests each two females went only part-way towards the loudspeaker and simply remained oriented towards it for the rest of the test.

To get a better comparison of the responses at 55 and 80 dB, I conducted a 15-min test: five min of silence, five min at 55 dB, and five min at 80 dB. The females exhibited the same kinds of reaction in these tests as they had done to separate tests at 55 dB and 80 dB sentences. The three kinds of movement exhibited to the three parts of the tests were (1) no movement,

(2) random movement, and (3) oriented movement towards the speaker. Females ticked after sentences at barely audible and at 55 dB intensities, but at 80 dB they ticked only occasionally.

In determining which part of the sentence evoked such movements, any part or combination of parts that included clicks stimulated more movement. At 80 dB, clicks evoked strong orientation and movement towards the loudspeaker. Part III, the buzz, evoked no response from any females at any intensity. Since these were the same females listed in Table II, one would expect some ticking response to part III. These females were about 2 weeks older by the time the latter tests were conducted, so age may have been a factor in the difference in behaviour. Part III preceded by clicks evoked ticks from the test females in about the same proportions as shown in Table II.

These results indicate that *floridana* females move the final distance between the sexes. Unfortunately, the *floridana* males involved in the above experiments died before I realized that in some species males move towards females answering at long range and females make the final movements in forming sexual pairs. One observation is relevant here. Before conducting any of the foregoing experiments, I opened the cage of a *floridana* female and placed a single, caged *floridana* male in the same room 12 ft away on another table. The male sang many

sentences; the female answered almost every sentence, climbed onto the top of her cage, and oriented towards the male. After a few minutes she climbed down, walked rapidly across the table, and leaned over the table edge towards the singing male. Later I released the male 12 ft away from the caged female but on the same table. The male oriented immediately towards the answering female but did not move until after he had produced several sentences. En route towards the female he often stopped and stridulated loudly. The closer he came to the female, the greater number of clicks he produced between buzzes. When he finally reached the female's cage, he climbed over it producing nothing but clicks; the female ticked occasionally.

Subsequent experiments involving one male and one female substantiated previous results. This male always went to the answering female, but near the female he produced more clicks and moved forward more slowly. When the female was muffled (by covering her cage with cellu-cotton), the male always went rapidly the total distance to the female. Singing males stimulate other males to click; thus, the predominant sound from congregated individuals is clicking. Such sound production can operate like the 'calling' function of a cricket calling song (Alexander, 1960), a female moving towards clicks until she reaches a male. A sentence would release a tick from the female, which would reveal her presence and location to all males in the immediate vicinity. In contrast, a lone male could produce buzzes as well as clicks and move towards an answering female while she simultaneously moved toward him. The results of the following tests support these hypotheses.

Using the male and female of the latter experiment, I placed the female at an arena corner while the male was in the arena. When the female began answering his sentences, I broadcast clicks or sentences (different tests), and the male always produced many rapidly delivered, high intensity clicks. In other tests with the same pair, I broadcast sentences before the male began singing, the female answered, and the male's reaction was again to produce high intensity clicks.

Amblycorypha oblongifolia (De Geer)

Amblycorypha oblongifolia was not known from Florida before this study. T. J. Walker collected one female from Liberty County (western Florida) early in June, 1963, thus extending the limits of its known southern distribution. This particular female was very responsive to the song of a single *oblongifolia* male from Berkeley County, South Carolina.

Lone males of *oblongifolia* produce a short, loud, complex sound at varying intervals. Pierce (1948) made an electronic analysis and Alexander (1956, 1960) made an audiospectrographic analysis of the sound. My analysis generally agrees with that of Alexander (1956). Our male sang only in darkness and at sporadic intervals producing ten to twenty phrases each time. The phrases were usually spaced 4 to 7 sec apart.

Alexander (1956) says 'the chirp contains 2, 3, or 4 pulses. . . . The first pulse is longer and different from the others in the chirp, giving the impression of speeding up. My sonograms looked essentially like the one shown by Alexander; all were three-pulsed with the first pulse being longer than the others. The pulse rate for the last two pulses from six phrases averaged 20·0 pulses per sec (SD = 0·5) at 25°C. The average total duration of the phrases was 199 msec. The toothstrike rate during the first pulse was highly variable. The average number of toothstrikes in the three pulses of the phrase was 15, 10, and 9 respectively. The first pulse had greater duration due to the tegmina being closed more slowly (assuming the pulses are made on the closing strokes of the tegmina) and more teeth being struck.

The male went straight to the female in every test. The female ticked after most phrases at an average delay (25°C) of 208 msec (SD = 13). In tests she made no oriented movements to 95 to 100 dB phrases but she always oriented towards 70 to 80 dB phrases, and, in about one-half of the tests, moved a short distance towards the loudspeaker, remaining oriented and answering some of the phrases after stopping her movement. She answered few below 80 dB. The female died before tests could be conducted at lower intensities. These limited studies indicate that the female may have been attracted towards low intensity phrases and would not have ticked after them.

Turpilia rostrata (Rehn and Hebard)

This species has been found in the subtropical hammocks and mangrove swamps of southern Florida. Where found, it was abundant.

Males of *rostrata* produce different songs involving lisps and ticks: a lisping song, a lisp-tick song (Fig. 5, Plate IV), and ticking. No

Table III. Results of Analysis of Sonograms of Songs of *Turpilia rostrata*

Kind of song	Individual identification no.	°C	No. phrases analysed	Ticks/sec $\bar{x}$	Ticks/sec s_x	Lisps/sec $\bar{x}$	Lisps/sec s_x	Lisp duration (msec) $\bar{x}$	Lisp duration (msec) s_x
Ticking	2	26·0	10	26·0	2·1				
Lisping	2	26·0	1			2·5		30	2
Lisping	3	25·0	4			3·4	0·5	31	2
Lisp–tick	8	24·5	5	26·1	0·7	2·4	0·3	35	2
2 males (caged together)	11 & 12	25·0	5	26·2	2·5				

sound is made during the daytime. Ticking is produced during the evening twilight. As darkness sets in, ticking gives way to lisping songs, and still later lisp–tick songs. Late at night, lisping songs and lisp–tick songs are produced in about equal numbers. Certain individuals predominantly tick late at night. At times a singer may produce a lisp–tick song followed by a series of lisps.

Ticking is produced in a series of phrases irregularly spaced 0·3 to 4·0 sec apart, each phrase composed of one to five ticks (usually two to three). The tick rate is uniform within the tick phrases (see Table III), but the number of ticks per phrase is completely unpredictable. A series of phrases of a ticking song may contain 2, 3, 3, 3, 1, 4, 2, 2, 4, 1 etc. pulses per phrase. Duration of the ticking period is indefinite and proceeds more or less continuously until a lisping song is produced later in the twilight.

The lisping song consists of a series of five to eleven lisps produced at a regular rate until the last two to three lisps; then the lisp rate slows down. The lisp rates indicated in Table III are calculated from the first five to seven regularly delivered lisps of each song. Intervals between songs may vary from one to several minutes.

In the lisp–tick song of Table III the singer added a series of lisps to each of the five lisp–ticks so that the intervals (35 to 65 sec) between successive lisp–ticks were not typical. Another recording, made at 23·5°C in the field between 10 and 11 o'clock at night, had two series of five and seven lisp–ticks respectively which averaged 5·7 sec (R = 4·0 to 8·3) apart.

Inability to keep individuals of *rostrata* alive in the laboratory for more than a few days made experimentation difficult. Experiments with

males were totally unproductive. On the basis that ticking in certain other species results in male spacing, ticking in *rostrata* may function in the same manner. This idea is supported by the fact that the two males caged together in a four-in. cubical cage (see Table III) produced many erratic, intense ticking sounds. At times the tempo from the two males would lessen, and tick rates during these quieter periods were similar to those of individual 071-2 (field recording), assumed to be out of physical contact with other males. However test males never moved.

Only two females responded to male sounds. These two, reared from nymphs, were responsive when no males were alive in the laboratory. They ticked at an average timing of 76 msec (n = 36, R = 41 to 115, SD = 17) after low intensity lisps. These females made no ticks after louder lisps and never oriented towards recorded sounds.

Discussion

Kinds of response to sound stimuli. A katydid subjected to a sound may do any one of several things. Typically, its behaviour is not changed by sounds of other species. Sounds of conspecific individuals usually evoke kineses or taxes. Kinetic reactions are evidenced by a katydid's starting to move when it hears a sound, continued random movement—frequent turning—as long as the sound is repeated, and stopping soon after the sound ceases. Such kineses were the typical responses of males of certain species to ticking sounds. In natural populations such movement could result in the spacing of individuals. There may be inter-specific interaction in these respects, since many species with ticking sounds in their repertoire often occur together. Taxes occur when individuals are attracted to a sound. Such re-

actions may be more strictly called telotaxes, for the orientations are directed towards single sources of sound when many sounds are present.

Intensity of response to sound stimuli. Different intensities of response have been noticed from different individuals to the same sound and by a single individual to the same sound at different times. A katydid may simply walk towards an attracting sound or produce one tick after a tick-eliciting sound. At other times the same individual responding to an attracting sound may alternately lean towards one side and then the other, holding up the front leg on the high side as if to expose more fully the auditory tympanum on that leg to the sound. Between successive alternations of 'leaning and listening' the katydid may run a few steps towards the sound. In the same context, females often produce, in response to tick-eliciting sounds, not one, but two, three, or more ticks in rapid succession.

Sexual maturation of adults. Every species studied showed a surprisingly long delay between the time of moulting to the adult stage and the time of attaining sexual maturity, as evidenced by the beginning of sound production by males and responsiveness to conspecific male sounds by females. In almost every species, 5 to 7 days passed after the final molt before the insect became acoustically active.

During the first few days of the season in which a species attains adulthood, and occasionally all during the adult season, katydids may be heard far from their normal adult habitats, indicating that dispersal may occur prior to sexual maturity.

Stimulus situation for sound production. Little is known about the external stimuli important in inducing individuals to sing. In some species certain male sounds are necessary to evoke ticking responses from females or other males. The chief problem lies in determining the stimulus situation for different sounds in those species which produce more than one kind of sound in solitary situations. In many cases (e.g. most species of *Amblycorypha*), low light intensity is required for any sound production. In other cases (e.g. *Scudderia texensis* and *Turpilia rostrata*) certain sounds may be produced principally by day, other sounds principally in twilight, and still others at night. In a few cases (e.g. *S. furcata* and *S. cuneata*) the same sounds are produced day and night. But what causes a male to produce one kind of sound for a period and suddenly change to a

second kind of sound? The change must be within the singer, because no external cues seem to change at rates correlating with changes in the sounds.

Necessity of acoustic interactions in pair formation. An insect species with no intrinsic mechanism to aid in uniting sexually responsive males and females would seem to have slim chances when populations are sparse. In other words, males and females are not likely to meet accidentally unless the population density is high and the individuals of the species concerned are active. Populations with low densities, as is the case with several Phaneropterinae, can breed effectively only if some special mechanism aids in pair formation. Several such mechanisms are known for different kinds of insects—for instance, attraction to specific host plants, and the pheromone systems of certain Lepidoptera and other insects. The acoustic systems of singing insects function in this fashion.

Acoustic interactions may also be necessary preludes to copulation in some species. One bit of evidence supports such an idea. On two occasions I placed an acoustically active male and a responsive female of *Scudderia texensis* in antennal contact on a table top in order to observe copulation close at hand. The only source of light was a nearby $7\frac{1}{2}$ W red light. On both occasions the male and female slowly circled, each feeling the other with its antennae, and, after 1 to 2 min of such behaviour, separated. A few minutes later the male produced his slow-pulsed song, and the female answered. In both instances the male turned immediately towards the female, lowered the intensity of his sounds, produced another slow-pulsed song, and moved rapidly towards the answering female. The sequence of low intensity, slow-pulsed song and the female tick was repeated a few times; the male went straight to the female, moving the last 7 to 8 in. without singing. On both occasions a brief play of antennae was followed by the male's turning round, raising his wings somewhat, and the female mounting him from the rear. Copulation resulted in the first case, but in the second I accidentally disturbed the pair and the male flew to the other side of the darkened room. Almost immediately he sang again and flew towards the answering female. When he finally came in antennal contact with the female, they antennated briefly, the male turned round and raised his wings and the female mounted. These observations suggest that, in *S. texensis*

at least, mating may be the consummatory event in a sequence of acoustic interactions.

Specificity of acoustical communication systems. Songs described here are clearly species-specific, particularly those involved in male–female interactions. This is predictable since orientation and movement towards sound is the primary mechanism bringing males and females together. Not only are male songs species-specific, but the timing of the female response is characteristically specific among species in which heterospecific male songs are sufficiently similar to cause confusion. Thus, preventing contacts between heterospecific pairs is as significant a function of the acoustic systems as their role in pair formation. Alexander (1962a) advises that 'it is an expensive procedure to bring together sexually responsive, compatible males and females, and the mechanisms involved should be highly specific and efficient'.

Among species in which the males produce lisps, similarities between heterospecific lisps may sometimes confuse females. Three species-pairs are discussed.

Lisps of males of *Inscudderia strigata* and *Scudderia furcata* are 77 msec and 75 msec long (average values), respectively. The frequency spectrum of both species are practically the same and females answer the lisps. Adults of *I. strigata*, which has only one generation a year, occur mostly from mid-July through August. *S. furcata* has two generations a year; the break between adult populations occurs during the peak adult population of *I. strigata*. Nevertheless adults of both species are sometimes present at the same time. I have collected adults of *S. furcata* within a few feet of *Hypericum fasciculatum* bushes containing *I. strigata* adults. No doubt, females in these situations sometimes answer heterospecific male lisps. Yet, no deleterious movements should result, for the timing of the female tick in each species is specific. A tick with the wrong timing evokes no response from males.

The second species-pair with similar lisps is *Montezumina modesta* and *Microcentrum rhombifolium*. The long lisp of *modesta* (31 msec average duration) overlaps the lisp of *rhombifolium* (25 msec average duration) at 28 to 29 msec. Females of *modesta* are attracted to low intensity conspecific lisps. However, the highest intensity lisps of *modesta* are in reality low in intensity for *rhombifolium*. Differences in spacing of males and females may result in females moving towards the wrong sound at times,

possibly sometimes even resulting in contact between heterospecific males and females. Two striking differences may prevent wasteful expenditure of time and energy. Lisps of *modesta* generally have much higher frequencies (dominant frequencies 12 to 18 kHz) than *rhombifolium* lisps (8 to 12 kHz). This difference may allow discriminatory responses by females, as evidenced by females of *modesta* not responding to broadcast lisps until after I had filtered out sounds below 15,000 Hz to emphasize higher frequencies. Lisps of these two species also differ in rate of production: *modesta* long lisps about one sec apart, *rhombifolium* lisps 2 to 3 sec. Females of *rhombifolium* may not respond to lisps produced faster than about two per sec.

The third species-pair with similar lisps is *Scudderia cuneata* and *Montezumina modesta*. Lisps of *cuneata* average 16 msec in duration, *modesta* short lisps 19 msec; the ranges are broadly overlapping, as are the dominant frequencies. However, specific differences in lisp rates and female timings may allow discriminatory responses.

The importance of lisp rate has been noted. In the laboratory a male could seemingly lisp too rapidly to evoke responses from listening conspecific individuals. I have mentioned that by rubbing my thumb across the edge of a piece of paper I have elicited ticks from females of several different species, depending on the duration of the 'lisps' I produced. With increases in lisp rate, the females stopped answering but often resumed answering when I resumed the lisp rate characteristic for the species. An important defect in this evidence is not knowing the actual duration of the synthetic lisps.

Importance of toothstrike rate. In species which lisp, differences in toothstrike rate within lisps could be discriminatory cues. Analysis of several lisps from each species showed only small differences in toothstrike rate except between the lisps of *Inscudderia strigata* and *Scudderia furcata*, which have lisps with identical durations and frequency spectra. Lisps of *strigata* had a toothstrike rate of 630 per sec, those of *furcata* 806 per sec. Even with such distinct differences I doubt that toothstrike rates are important in discrimination; otherwise, I should have obtained no response from artificial lisps in which there was no toothstrike rate.

Intensity proportional to population density. A few cases support the idea that species with low intensity sounds have relatively greater

population densities than species with high intensity sounds. Sounds of most of the species reported here have about the same range of intensities. *Microcentrum rhombifolium* and *Scudderia curvicauda* produce sounds that can be heard for two to three hundred feet, and only once have I found more than two or three individuals per acre. On the other hand, *Montezumina modesta* produces low intensity sounds and often is found in high density groups, individuals separated by only a few feet.

Increase in intensity during songs. Some species increase the intensity of sound production toward the end of certain parts of songs, or song sequences. Known cases are *Scudderia texensis*, slow-pulsed song, gradual increase in successive pulses; *S. furcata*, increase in successive lisps and within single lisps; and *S. curvicauda*, increase in successive pulses. One obvious advantage of increasing the intensity between successive units, at least in those species which repeat the basic functional unit of sound successively, is to allow individuals successively farther from the singer to hear the sound. But why do intensities change within functional units? Scanty evidence indicates that increases towards the end may be communicative. A recording of one phrase of a *S. texensis* slow-pulsed song in our tape collection does not show any change in intensity from beginning to end. Females never answered this recording, although they consistently answered a recorded phrase with similar pulse rate but with increasing intensity towards the end. Similarly, *S. texensis* females would answer simulated slow-pulsed songs, produced by rubbing a finger back and forth across a piece of paper, only when the pulses gradually increased in intensity. Females of *S. furcata* seemed most readily to answer artificial lisps which terminally increased in intensity.

Complexity of acoustic repertoire. The acoustic repertoire of lone males of the species studied can be grouped into four classes of complexity. The first class has an increase in intensity of each successive pulse in a phrase, the pulses otherwise identical. Increases of intensity in successive pulses requires that the singer engage the stridulatory apparatus harder in each successive sound-producing stroke. Lone males of *Scudderia curvicauda* make only this kind of sound.

The second class of repertoire complexity involves strikingly different sounds produced

from time to time in no fixed sequence. Four species studied are grouped here. They are *Microcentrum rhombifolium*—ticks and lisps; *Scudderia cuneata*—lisps and pulsed phrases; *S. furcata*—lisps and pulsed phrases; and *S. texensis*—fast-pulsed song, slow-pulsed song, and ticks. The different sounds of each species have no constant relation and each functions independently. Tegminal movements are identical in producing each pulse of a given kind of sound (except for some differences in intensity), but are different from one kind of sound to the next.

The third class of complexity involves producing certain sounds independently, as in the second class, and other sounds (sometimes the same sounds that are at other times produced independently) in a stereotyped sequence. In this class are *Inscudderia strigata*—clicking and lisp–tick song; and *Turpilia rostrata*—ticking, lisping song, and lisp–tick song. Lisps and ticks of lisp–tick songs are identical with isolated lisps and ticks. This class of complexity no doubt represents an intermediate step in the evolution of more complicated singing.

The fourth class of complexity involves two or more different sounds produced in a stereotyped sequence. Three species discussed here are in this class: *Amblycorypha floridana*—regularly repeated sequence of clicks and buzzes; *A. oblongifolia*—regular sequence of one long pulse plus two short pulses, and *Montezumina modesta*—regular sequence of a series of short lisps followed by a series of long lisps.

This classification may be modified as more types of complexity are discovered, and once the mechanisms of nervous controls of complex singing have been worked out.

Movements involved in pair formation. Pair formation among the species reported here does not always involve the same kinds of movement on the part of the two sexes. Relative kinds and amounts of movement by males and females are put into three categories. In one category the male produces the female tick-elicitor, the female ticks but does not move, and the male moves the entire distance to the female (*Scudderia furcata*, *S. curvicauda*, *S. cuneata*, and *Inscudderia strigata*). In the second category the male produces a sound which attracts the female toward, but not all the way, to the male. The male produces a second kind of sound which evokes ticks from the female. The female ticks attract the male, which moves the final distance

separating them (*Scudderia texensis* and *Microcentrum rhombifolium*). The third category includes species in which the male produces the female tick-elicitor, the female ticks, and the male moves part way to the female. The male produces a second sound which stimulates the female to move the final distance to the male (*Montezumina modesta* and *Amblycorypha floridana*). *Amblycorypha oblongifolia* and *Turpilia rostrata* may fit into either of the first two categories.

No phaneropterine species is known in which females are silent and move all the way to the males, the most common method of pair formation in other Ensifera. Apterous females of *Dichopetala* probably exhibit such behaviour. Another category one would expect is one in which males produce female tick-elicitor, females answer, and both the males and females move towards each other until contact is made. This may occur in *Amblycorypha floridana* at sparsely populated sites. The obvious disadvantage of such a system is the difficulty of homing on a moving source of sound. Since the Phanopterinae mostly inhabit coarse vegetation and fly towards conspecific sounds, it is not likely that many cases of this sort will be found. Such a system could function well only where males and females could move relatively slowly, walking or running, toward one another in a relatively straight line.

Summary

Acoustic signalling during pair formation is more complex in Phaneropterinae than in any other Ensifera. Lone males of most species produce more than one kind of sound, and females of all species studied produce sound during pair formation, a phenomenon with no known parallel in other Ensifera.

This report includes (1) an analysis of the singing behaviours and the descriptions of sounds of nine species of Phaneropterinae and (2) the results of numerous experiments with these species to determine the behavioural significance of their sounds. Three kinds of male–female acoustic systems occur in the species studied: (1) the male makes a particular sound, the female answers with a tick and the male goes all the way to the female, (2) the male makes one kind of sound which attracts females from a distance (but not at close-range), the male makes a second sound which the female answers with a tick and the male goes to the female from close-range, and (3) the male makes one kind of sound, the female answers with a tick, the male moves towards the female from a distance (but not all the way), and the male produces a second kind of sound which attracts the female the remaining distance. Some species produce stereotyped sequences of different kinds of sounds; different responses occur to different sounds in the sequences.

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