

COMPARATIVE STUDY OF THE ACOUSTICAL
BEHAVIOR OF PHANEROPTERINAE
(ORTHOPTERA, TETTIGONIIDAE)

By

JOHN D. SPOONER

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INTRODUCTION

Much progress has been made recently in describing Orthopteran sounds and in explaining their biological significance. However, some areas remain unexplored. Perhaps the most important of these is the nature and significance of the acoustical behavior of many species of Phaneropterinae. The acoustical behavior of most species in this subfamily differs from that of almost all crickets and other Tettigoniidae (except Conocephalinae) in that they produce more than one type of sound in solitary situations. A solitary situation exists when a singer is out of contact, except in some cases of acoustical contact, with other conspecific individuals. Also the females of several species of Phaneropterinae are known to produce sound which functions in intraspecific communication, a phenomenon with no known parallel in other Tettigoniidae. (See Alexander, 1960, for a comprehensive review of sound communication systems in Orthoptera.)

Gryllidae and Tettigoniidae make sound by rubbing together a file and a scraper at the tegminal bases. Complicatedness of solitary singing may be measured in terms of the tegminal movements involved. In simple singing the singer opens and closes his tegmina in the same manner each time he does so. The result is a series of similar pulses of sound, i. e. a phrase. The number of pulses in a phrase and the pulse repetition rate are usually characteristic of the species involved. Species which produce more than one kind of sound, involving more than one kind of tegminal movement, in solitary situations may be said to exhibit complicated singing behavior.

I have recordings, some of which were made by other workers, of all 20 species of Phaneropterinae known from Florida. I have made extensive observations of the solitary repertoire of 18 species. Four of these exhibit simple sound production and the remaining 14 species exhibit varying degrees of complicated singing.

Generally, complicated singing by solitary males is of two classes. In one class different kinds of sound are produced at different times and in no fixed sequence. For instance, males of Scudderia texensis produce three strikingly different sounds at different times and in no predictable sequence (Spooner, 1964). In the second class different kinds of sound are produced consecutively in stereotyped sequences. In this group is Amblycorypha uhleri, which produces the most involved sequence of sounds known for any insect (Alexander, 1966). The song of this species may last 40 seconds or longer and involves gradual and sudden changes in intensity, pulse rate and pulse duration. The fourteen species reported here with complicated singing generally fall into one or the other of these two groups. Two have acoustical behaviors somewhat intermediate between the two classes.

Very little is known about the biological significance of any kind of complicated singing. Some workers (Riley, 1874; Fulton, 1933; Grove, 1959; Alexander, 1960; Spooner, 1964) have observed females of certain species answering certain conspecific male sounds by producing a short hiss or tick. My work (Spooner, 1964) with Scudderia texensis is the only investigation reported which reveals the behavioral significance of sounds of a species with complicated singing. The objectives of this paper are 1) to describe the sounds of several

species whose sound production has been heretofore unreported, 2) to present the results of numerous experiments with seven species investigating the behavioral significance of their sounds, and 3) to suggest how complicated singing could have evolved.

METHODS AND MATERIALS

Observations were made in the field to determine the acoustical behavior of the different species in natural situations. These observations were compared with those made in the laboratory.

The individual katydids used in this investigation were collected in the field as late instar nymphs or as adults. The adults were caged individually in cubical, screened cages, four inches on a side and with metal bottoms. The nymphs were caged together by species in 12-inch x 12-inch x 16-inch screened cages and allowed to mature. When the nymphs transformed to adults, each individual was caged separately as noted above for collected adults. In all cases the katydids were fed dog biscuit (Purina Dog Chow, Ralston Purina Company, St. Louis, Missouri), water, and occasionally some lettuce. Since Inscudderia walkeri feeds almost exclusively on the foliage of pond cypress, Taxodium disticum nutans (Ait.) Sweet, a few sprigs of pond cypress were fed to this species daily in addition to dog biscuit and water. Likewise, Inscudderia strigata was fed sprigs of Hypericum fasciculatum Lam. With the exception of Turpilia rostrata and Arethaea phalangium all the other species of katydids studied are apparently general feeders and lived on the dog biscuit and water diet for long periods. T. rostrata apparently feeds on mangrove, which does not grow near Gainesville, Florida, the investigation site. T. rostrata always died after a few days in the

laboratory. Nothing is known about the food habits of A. phalangium. Individuals are not very common around Gainesville, and are collected only by accident when sweeping is done in relatively open, dry, weedy areas. Individuals of A. phalangium die within a few days in the laboratory.

All caged individuals were kept in an air-conditioned laboratory in which the temperature was maintained at about 25° C. On certain days the temperature fluctuated very slowly from about 24° C to about 27° C.

Lights were kept burning continuously so that individual katydids could be placed in darkness at any time to record their sounds. These katydids are mostly nocturnal singers and often they could be induced to sing by this maneuver. Continuous light did not seem to inhibit the acoustical behavior of any species for more than a couple of days. Light has no effect upon the nature of the sound produced, but may well determine which type of sound is produced or whether sound is produced at all (personal observation and Walker, 1962). For instance, the characteristics of the fast-pulsed song or slow-pulsed song of Scudderia texensis are not altered by either light or darkness, but light intensity does determine to some degree which song is produced in natural situations (Spooner, 1964).

Field recordings were made using either a Magnemite 610E (Amplifier Corporation of America, New York, New York) or a Nagra III PH (Kudelski, Paudex-Lausanne, Switzerland) portable tape recorder and a microphone centered in a 24-inch parabolic reflector. Laboratory recordings were made using the Nagra III PH recorder or an Ampex 351-P tape recorder (Ampex Corporation, Redwood City, California). In all cases a dynamic microphone (Model D33A, American Microphone Company, Buchanan, Michigan, or Model MI-4048-E,

Type 88A, Radio Corporation of America, Camden, New Jersey) and low-print tape (Scotch No. 131, Minnesota Mining and Manufacturing Company, St. Paul, Minnesota) at 15 inches per second were used. Tape speeds were checked periodically and varied less than 1 per cent throughout the investigation. In the field, temperature was measured immediately after each recording with a mercury thermometer held as near the singer as practical. In the case of Stilpnochlora coluniana which sings from treetops in hardwood forests, this was sometimes as much as 100 feet away. The actual temperature in which the insect sang could have been several degrees different from the measured temperature. In the laboratory, temperature was measured with a mercury thermometer immediately after each recording and usually within a few inches of the singer. A few temperature readings measured three to four feet away from the singer were taken as valid since the air was continuously circulated within the laboratory and thermometers in different positions in the laboratory showed insignificant variation after calibration and correction. Frings and Frings (1962), Walker (1962) and Spooner (1964) show the effect of temperature on the nature of the sounds produced. At higher temperatures, tegminal movements are faster.

The sounds of individual katydid were recorded in the laboratory whenever individuals sang. It was necessary to place some individuals in low intensity light and others in darkness to induce them to sing. Whatever the situation the microphone was held close to the singer's cage and the input level of the recorder was adjusted so that the VU meter read between -10 and -7. Acoustical interactions between individuals were recorded by placing their cages close

together in front of the microphone. Several recordings were made of females answering recorded male sounds.

The sounds of each species were analyzed by making audiospectrographs (sonagrams) with a Kay Sona-Graph (Kay Electric Company, Pine Brook, New Jersey). The Sona-Graph used will analyze frequencies from about 100 cps to 9500 cps. Because the sounds of Phaneropterinae contain frequencies greater than 9500 cps, recordings were played at one-half speed into the Sona-Graph, reducing the frequencies in the recordings of the natural sounds by one-half, i. e. to a range which could be graphed by the Sona-Graph. The structural unit of the sounds of these katydids, the pulse, graphs as a vertical bar, the width corresponding to the duration of the pulse and the height corresponding to the range of frequencies present in the sound (see sonagrams displayed in Figures 1-19).

At least one sonagram was made of each kind of sound recorded from each species. Certain species produce a single-pulsed lisp as a characteristic sound. Since the lisp duration is important in eliciting species-specific responses, ten sonagrams were made of the first ten lisps of each recording. All lisps were graphed if less than ten had been recorded. In cases in which two or more different recordings of the same individual were available more than ten sonagrams of the lisps of that individual were made. When possible, ten sonagrams of the male-female acoustical sequence were made for each female. In species which have characteristic pulse rates in certain sounds at least two sonagrams were made of each recording at timings of five seconds and ten seconds from the beginning of the recording.

The sonagrams were analyzed with respect to lisp durations, pulse rates, pulses per phrase, frequency spectrums, etc. Time was measured in inches with a Bruning No. 2148P scale (Charles Bruning Company, Inc., New York, New York) estimated to the nearest 0.01 inch and converted to seconds by multiplying by 0.0976 seconds per inch, the speed of the Sona-Graph drum surface. This is essentially the same as estimating to the nearest 0.001 second. Variations in methods of recording and analysis are presented under the discussions of individual species. The frequency spectrums were determined by comparing sonagrams of the sounds with sonagrams of pure frequencies from a Hewlett-Packard Model 201C (Hewlett-Packard Company, Palo Alto, California) audio oscillator. This method has certain limitations. For instance, the response of the microphones used to record the sounds decreased rapidly to frequencies above 15,000 cps (manufacturer's specifications and our own calibration). The sounds of many of the species discussed herein contain frequencies well above 15,000 cps so that the comparison of relative intensities of frequencies displayed by the sonagrams is not valid. No doubt much higher intensities of frequencies from 15,000 to 20,000 cps are present in most sounds than are indicated throughout the figures shown in this paper. Another limitation lies in the inability of the Sona-Graph to graph frequencies higher than 19,000 cps at its normal drum speeds while using convenient tape recorder speeds. Certain sounds undoubtedly have substantial intensities of sound at about 19,000 cps, as evidenced by the abrupt termination of any markings at 19,000 cps when graphing certain sounds. See, for example, the tick-lisp song of Arethaea phalangium (Fig. 14).

One gets a strongly biased idea of the frequency spectrum of a song when

one looks at a single sonagram of one phrase of a song. There are differences in dominant frequencies in the songs of different individuals of the same species. Sometimes within a single song there are changes in dominant frequencies from one phrase to the next in a sequence of closely spaced phrases and often even between successive pulses within one phrase. Figure 1 illustrates nicely such differences between individuals and differences between successive phrases within a single song.

A study of sonagrams pictured by Alexander (1960) indicates that he may have had difficulty in interpreting the frequency spectrum of the sounds of certain species. Perhaps his equipment was inadequate to handle frequencies characteristic of some tettigoniid sounds. Generally, the frequencies shown in the sonagrams he displays are low, in comparison to my own, and some seem to be completely erroneous. For instance, his sonagrams of the song of Amblycorypha uhleri indicate strongly dominant frequencies from 4000 to 7000 cps with almost no frequencies above 7000 cps. My experience with A. uhleri is that the most dominant frequencies of that species' song range from 8000 to 14,000 cps with a spread of less-intense frequencies below and above the dominant range. Other of Alexander's sonagrams show similar discrepancies, but to a lesser extent. Thus, one should use caution in interpreting the frequency spectrum presented in any single sonagram of a sound. If the whole range of frequencies displayed is considered, a better idea of what frequencies really may be present in the sound will be obtained.

To determine the function of the various sounds made in solitary situations, copies of recorded natural sounds were played to individually caged, virgin females

and to males of differing age and experience. Virgin females were used because females may not be responsive to the sounds of conspecific males once they have copulated (Spooner, 1964), so much time might have been lost by working with females of unknown age and experience. Males apparently copulate more than once because they resume their acoustical activities some time after copulation (Grove, 1959, and personal observation).

In studies of responses to broadcast sounds the response arena, cylindrical cage illustrated by Spooner (1964), was used. The response arena had a half-inch plywood frame with an inside diameter of 42 inches. The entire inside surface was covered with tightly drawn bronze wire screening. The distance between top and bottom screens was four inches. The top screen was easily removable for the introduction or removal of test individuals. Sixteen equal sections were delineated by strings attached beneath the bottom screen. The four corners of the original four-foot-square piece of plywood, from which the bottom of the arena was made, were left intact to serve as loudspeaker supports.

Single kinds of sound or combinations of different kinds of sound were broadcast to test individuals using the playback system of the Ampex 351-P recorder, a Krohn-Hite Model 310AB Band-Pass Filter (Krohn-Hite Company, Cambridge, Massachusetts), an Eico HF-14 amplifier (Electronic Instruments Company, Inc., Long Island City, New York), and a University Model T-202 loudspeaker (tweeter — University Loudspeakers, White Plains, New York) which had been modified by removing the sphere in front of the diaphragm. The band-pass filter was set to filter out all frequencies below 5000 cps, the range including most extraneous noises in the recordings, and to pass all frequencies

above 5000 cps. The sounds broadcast were copies of original recordings of natural sounds made at the same temperature as that maintained in the laboratory. Continuous-play loops were made, so that the same sound was repeated at pre-determined intervals. Some of these same loops were broadcast to virgin females to record the sequence of male sound and answering female ticks. Sonagrams of the copied sounds were indistinguishable from sonagrams of original recordings. The intensity of the sounds broadcast was measured by supporting the loudspeaker vertically 6.6 inches above the microphone (Type 98B99, General Radio Company, West Concord, Massachusetts) of a sound level meter (Type 1551-B, General Radio Company - indicates the sound pressure level at its microphone in terms of a standard reference level of 0.0002 microbars at 1,000 cps) set on the "A" weighting. Because Spooner (1964) found that the female of Scudderia texensis responds differently to one conspecific male sound depending on the intensity at which she receives it, three levels of intensity were broadcast to test individuals. The highest intensity broadcast was determined from singing males by inserting a three-wire cord between the microphone and the sound level meter and holding the microphone about two inches dorsal to a singing male. Because readings thus obtained were found to be characteristically 5 decibels (db) lower than measurements of the same sounds when the microphone was connected directly to the sound level meter, I added 5 db to each measurement of the intensity of sounds produced by singing males. The intermediate intensity broadcast - in some cases the lowest intensity - was 50 db. The laboratory had a standing low-frequency noise level of 48 db, so the 50 db readings may have been somewhat in error. Nevertheless, results should

be comparable because all sound level measurements of sounds broadcast were made in the same manner at the same spot. The lowest intensity broadcast was not measurable with the sound level meter and just loud enough to be distinct about five feet away.

All of the experiments were conducted in a small laboratory, 8.3 feet x 11.0 feet, adjoining the large laboratory in which most of the recording was done. The temperature throughout the two rooms was generally uniform. Test individuals could be introduced into the arena and tested after a short adjustment period -- usually 10 minutes, but sometimes longer. To allow enough light to track test individuals, during each test a Westinghouse 7 1/2-watt red light bulb was burned in a white, porcelain receptacle on the floor beneath the center of the arena. During each test I sat behind a writing stand and noted the position of the test individual for the entire test period. A 7 1/2-watt red light illuminated the writing stand but was completely shielded from the arena.

Each test consisted of five minutes of silence followed by five minutes of broadcast sound (except in some special cases which are explained later). Each test was repeated at least four times, i. e. the same loop was broadcast to the same individual during four test periods. For each repetition the speaker position was changed to a different corner of the arena. Replications consisted of playing the same loop to different individuals, so in some cases only two replications were possible, e. g. only two virgin females were available. In other cases four replications were possible. The only females used in any tests were those which gave positive reactions -- ticked -- to the female tick-inducing sound of the species concerned. Males used in the tests were those which sang

readily in the laboratory.

These general procedures were followed during the entire course of the investigation. Deviations from the above outline were necessary at times, and such deviations will be noted under the discussions of the individual species. The original recordings made during this investigation can be obtained from the Library of Insect Sounds, Department of Entomology, University of Florida, Gainesville, Florida.

DESCRIPTIONS OF SOUNDS
AND EXPERIMENTAL RESULTS

The following is a species-by-species account of observations of the singing behaviors, descriptions of the physical characteristics of the sounds, and the results of numerous experiments to determine the function of the sounds. I have experimental data for only the first seven species. For one reason or another — for instance, no responsive females were available, or individuals of certain species would not sing in the laboratory — no experiments were conducted on the remaining species, but possible functions of their sounds are discussed later.

For an account of ecological situations and geographical distributions of most of the species, see Alexander (1956). Species not discussed there will be briefly discussed here.

Certain terms are used in this paper in describing certain kinds of sound. These terms are largely subjective but reflect differences in the method of moving the stridulatory apparatus. It was pointed out earlier that the basic unit of sound of these katydids is a pulse of sound which corresponds to a single stroke of the tegmina. The songs of the katydids described herein contain

pulse groups of varying durations and varying pulse repetition rates. A group of several pulses delivered in rapid succession is called a phrase. Phrases have pulse rates of several pulses per second. A group of pulses that are delivered slowly -- generally more slowly than one per second -- is not considered a phrase. In this case the individual pulses are functional information carrying units -- at least in the species investigated. In this latter case pulses are of two kinds. One kind is called a tick. A tick is instantaneous and involves striking only a few teeth of the stridulatory file at a fast rate (1-10 toothstrikes -- usually 1-3). The second kind of pulse which may be delivered at a very slow rate is called a lisp and involves striking a larger number of teeth over a greater interval of time, the interval of time - pulse duration - being species-specific. Another kind of sound not fitting into any of the above categories is called a click. Clicks are usually 2-pulsed sounds, the two pulses being tick-like and different from each other with respect to either intensity or duration, or both. The meanings of other terms used in the text should be self-explanatory.

Species Involved in Experiments

Inscudderia strigata (Scudder)

Adults of Inscudderia strigata start appearing about the second week of July in Alachua County, Florida and shortly thereafter may be collected in large numbers from the tops of Hypericum fasciculatum bushes. They are seldom found elsewhere.

Three distinctly different kinds of sound are made by solitary males of I. strigata, none of which has previously been described. The two sounds

commonly heard from solitary males are lisps (Fig. 2a) and ticks which are usually alternated in each acoustical performance. Lisps, delivered 1.3 - 2.2 sec. apart, variable throughout, are alternated with 1 - 7 ticks -- usually 5 - 6. The number of ticks is loosely correlated to the time interval between successive lisps. The lengths of the series vary; the recordings on hand contain 12 - 33 lisps. The intensity of the sounds and the lisp rate in each series increases slightly during the first 2 - 3 lisps. The number of ticks is often 1 - 2 initially; 1 - 2 ticks are added each time until the singer produces the characteristic 5 - 6. Often the ticks appear in pairs, but the tick rate is seldom constant. The series is usually terminated with about a dozen ticks.

Seldom is a male of this species completely isolated from other conspecific individuals. Their host plant often grows in isolated patches. When strigata has been found in one of these patches, it usually is abundant, as many as four or five having been collected in areas as small as a three-foot square. I have observed the acoustical behavior of such natural congregations, where as many as 50 individuals may have been involved, on more than ten different nights and on three different days in mid-morning. The acoustical activity appears to be the same whether in daylight or darkness. Sound production in congregations 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-in" during the 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 lipping immediately. The result is that sometimes there is almost continuous lipping 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). It seems that more continuous singing occurs when large numbers of individuals are congregated. Since the nymphal stages are as congregated as the adults, sound does not seem to be a congregating mechanism for strigata, except possibly in the case when females are acoustically active (discussed later). Table 1 shows the results of the analysis of sonagrams of lisp-tick sequences from three males. The overall average lisp duration is 77 msec. By reducing the

Table 1. Results of analysis of lisp-tick sequences from three males of Inscudderia strigata. (Time in milliseconds.)

Indiv.	° C	No. lisps analyzed	Lisp duration		Delay till first tick	
			\bar{X}	s_x	Range	\bar{X}
021-2	26.0	10	65	3	432-506	464
021-2	25.8	10	73	3	521-719	600
021-7	26.5	10	84	6	382-721	599
021-10	25.8	10	77	6	392-800	524

tape speed and, when necessary, by playing sounds into the Sona-Graph while the Sona-Graph drum turned at reproduce speed, it was possible to spread pulses of sound sufficiently to count the marks which apparently corresponded to the number of teeth of the stridulatory file struck in producing the pulses. Six lisps of individual 021-2 (see Table 1) analyzed in this manner averaged 49.5 (range = 43 - 52) teeth struck. Eight ticks from the same male averaged 7.5 (range = 4 - 10) teeth struck. The two other individuals struck 1 - 5 teeth per tick.

The least commonly produced sound — heard only once in the field, at night, and only three or four times in the laboratory, in darkness — is a low

intensity, two-pulsed click (Fig. 3). This sound is repeated in series and is produced at times of relative acoustical inactivity -- that is, periods when males sing only occasionally. Such periods are few; the males of this species are noisy almost continuously after becoming sexually mature. Only one series consisting of 13 clicks was tape recorded. It was made in the laboratory at 25.5° C. The clicks in this recording varied from 1.5 - 2.2 sec. apart and averaged 1.7 sec. apart. The second pulse of each click is much more intense than the first pulse, and the tooth strike rate of the second is greater than that of the first. Only three teeth are struck in the second pulse, whereas 3 - 5 are struck in the first pulse. The delivery rate of the two pulses within a click for the one recording averages 9.0 pulses per sec. with a standard deviation of 0.2 pulses per sec. In calculating the pulse rate, time was measured from the beginning of the first pulse to the beginning of the second pulse.

The functions of these sounds were not readily revealed by field observations so a number of individuals were placed about in the laboratory for observations. The observed laboratory acoustical behavior of males conformed to that seen in the field except when virgin females were responsive. Virgin females answered the lisps with a tick immediately after each lisp. The ticking of the males became very erratic and more intense when a female was answering. Ticks from females were emitted very shortly after each lisp when no males were ticking. Females also answered recorded lisps with or without the alternating male ticks. Table 2 shows the tick delay timing of three females. In no case was the female tick delayed until the shortest timing of a male tick.

Table 2. Results of analysis to determine the timing of answering ticks by females of Inscudderia strigata. (Time in milliseconds.)

Source of lisp answered	Indiv. female	°C	No. of responses analyzed	Tick delay		
				Range	\bar{X}	s_x
Recording	021-8	26.8	9	80-137	105	20
"	021-8	28.0	8	61-119	93	19
"	021-12	25.8	10	48-117	73	21
"	021-13	24.8	10	103-147	132	13
Singing Male	021-8	26.5	1		112	
" "	021-12	28.0	10	61-116	80	18
" "	021-13	29.0	1		119	

A series of experiments was designed to ascertain the significance of the different sounds. Continuous-play loops were made of a lisp, a lisp with ticks, ticks alone spaced as they are in normal singing, and a click. By using different lengths of leader tape to space the sounds the rate of repetition of the broadcast sounds was controlled. The lisp was broadcast once every 1.5 sec. as was the series of ticks since this was almost the modal and mean rate of alternation by males. Clicks were broadcast at a rate of one every 1.7 sec. The intensity of the sounds of five males had been previously measured at 60, 63, 64, 66 and 66 db, so each sound was played at 50 and 65 db. The lisps were played at a barely audible intensity also (see methods for intensity measurement).

The main function of the lisp appears to be the stimulation of females to tick. Three females were tested in the experimental arena, and all ticked after the lisp in whatever arrangement or intensity the lisp was broadcast. Females may move toward lisps at times in nature because each of the experimental females oriented toward the loudspeaker on at least one occasion when lisps were turned on — not all to the same intensity of sound — and two of them moved toward the loudspeaker

a short distance on one occasion each. These movements occurred at the beginning of test series, the females having been in darkness for at least ten minutes without having heard any male sounds. During succeeding tests the females either remained motionless or walked in a random pattern, always ticking after lisps.

The ticks and clicks had no visible effect on the test females at any intensity. These sounds apparently function only in male interactions.

The only reaction given by the five test males to lisps, or lisps and ticks, was ticking at the time they would have ticked in natural situations. Either no movement or random movements were seen. No orientation movements were ever seen. Often when the recorded sounds were turned off at the end of a test, the test male would give a series of lisps and ticks of his own. Very low intensity lisps almost always caused the test males to start their own lisps and ticks during the tests, whereas they only ticked in alternation with high intensity lisps. Such contrasting behavior suggested that high intensity lisps and ticks may have an inhibitory effect upon male lisping. Three series of tests -- lisps alone, ticks alone, and lisps and ticks, all at 65 db -- were run to test this idea. A group of six males were placed on a table in the experimentation room and observed as sounds were broadcast to them. The males were allowed to start their own singing, and then the recorder was turned on. The result was the inhibition of male lisp production by the recorded lisps or ticks only when a pulse of recorded sound preceded and overlapped the time the singer would have begun a lisp. This would be enough to effect the inhibition of lisping of all but one male in a congregation of singing individuals, for in the groups studied there was a modal refractory period of 1.5 sec. at 25° C between successive

lisps of a singer. This modal value was usually the minimal value, but not always. Another male, in order to start lisping, would have had to abandon the somewhat longer refractory periods between his initial lisps in order to intercede the already-singing male. The tick rate of the terminal ticks of the series observed 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.

The results of tests of the click sound are inconclusive but suggestive. All but three males had died by the time these tests were begun. The clicks were broadcast only at 55 db (arbitrarily selected). During each of these tests the males either remained motionless or moved erratically away from the speaker a short distance. One male moved away in five out of eight tests; the second male moved away in one out of five tests, and the third male moved away in two out of four tests. Such movements, compared to no movements at all during the silent part of the tests and no movements as opposed to oriented movement during other tests, certainly suggest that the click sounds function in male spacing. Not enough observations were made of the diel cycle of acoustical activity to rule out the possibility of a particular time of day in which clicking is prominent. Spooner (1964) found that males of Scudderia texensis produce a low intensity ticking sound only during the evening twilight. Ticking in S. texensis functions in male spacing by causing the males to move kinetically as long as they receive the ticking above a certain intensity, or until ticking is equal in intensity all around.

The female tick attracted males to answering females. Because of the

difficulty in producing a simulated female tick at the proper time after a male lisp it was impossible to use the same experimental technique to determine the function of the female tick. Caged females were placed, one at a time, on the corners of the arena in place of the loudspeaker. When the test males lisped the females answered. While continuing to lisp and tick, test males oriented and went directly to the answering female. To avoid the possibility of a chemical or visual stimulus causing such orientation of test males, the female was placed just outside the darkened room where she was out of sight but could still hear the test males. Her answer thus broadcast at the corner of the arena through the loudspeaker induced the same kinds of reaction from the test males.

Since in natural situations very few males are lisping at any one time, it occurred to me that non-lisping males may go to females answering lisping males. A recorded lisp and answering female tick were broadcast to test males. No male went to the speaker. A responsive female was placed on the corner of the arena and lisps were broadcast from a nearby table. The female answered the recorded lisps, and all four test males went to the female. The test males usually started their own series of lisps and ticks when the female answered so that the female answered the test males. The stridulatory file was removed from one male in order to silence him. He still went all the way to the female on each of several tests when the female answered the recording. When the female was placed outside the experimentation room and her answer to non-test males was broadcast to test males, test males still went to the corner where the sound was emitted.

One field observation supports the above data. I was standing in the

midst of a group of singing males one night and imitated a female tick by striking my fingernails together at about the proper delay timing after the lisps of the one lisping male. Not only did the lisper orient and start moving toward me, but a number of "bystanders" did also. One male about three feet in front of me almost fell off his perch when he turned suddenly after my first simulated tick.

Microcentrum rhombifolium (Saussure)

Microcentrum rhombifolium males produce two distinct kinds of sound in solitary situations -- lisps (Fig. 2d) and ticks. Both have been described by Allard (1928a), Fulton (1932, 1933), Alexander (1956, 1960), and others. The account by Grove (1959) is the most comprehensive on the acoustical activity of this species. Alexander (1960) shows sonagrams of both songs recorded at 65° F (18.3°C). This species is chiefly arboreal and thereby difficult to collect in numbers. Only three individuals, one female and two males, were studied in the laboratory.

Both lisps and ticks may be heard at any time of day or night, although more acoustical 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 be heard to give a couple of lisps in rapid succession and follow up with a series of ticks. Such behavior is the exception rather than the rule and usually occurs when a male becomes acoustically active after a period of silence.

Apparently both the lisps and ticks are made on the closing strokes of the tegmina. A single lisp (Fig. 2d) involves one closure of the tegmina at a rapid

rate. Sonagrams of four lisps (laboratory recording, 26° C) from one male showed 20 - 24 toothstrikes per lisp. The lisps in this recording were produced 2.0 - 4.1 sec. apart. The modal and mean rate of delivery was one every 3.0 sec. Ten lisps from the same recording ranged from 22 to 30 msec. duration with an average of 25 msec. ($s_x = 3$ msec). These figures indicate a toothstrike rate during the lisp of about 372 per sec. This is quite a contrast to the toothstrike rate of the ticking sound in which the individual pulses of sound (single ticks) correspond to individual toothstrikes. This phenomenon has been noted by several of the above authors. I have recorded in the laboratory three ticking series from each of two males. One male was recorded at 25° C, the other at 25.5° C. The average tick rate in the middle of each of the three series for the 25° C individual was 8.5 ticks per sec. The average tick rate for the 25.5° C individual was 8.8 ticks per sec. These males produced 22 - 34 ticks per series. Grove indicates that males produce 28 - 32 ticks in a series, and Alexander (1956) says a series consists of 15 - 30 ticks.

The ticking sound needs no detailed experimentation to resolve its function. Both Allard (1923a) and Fultor (1933) noted that females produce a low intensity tick after a series of male ticks and that males go to females when such acoustical interaction takes place. Alexander (1960) describes the acoustical interaction between a male and female caged near each other but out of sight from each other. He says the female's response was so precisely timed that her tick seemed almost a part of the male tick series. Grove and Alexander both noted that after the female answering tick, the answered male would often pro-

duce an irregular shuffling sound. Grove conjectured that this may serve to confuse the location of the female, for he observed that "listening" males would produce the shuffling sound after having heard a male-female sequence, that these males would often move toward females answering other males, and that these males may reach a female and copulate with her without having made a single sound themselves. I conducted no experiments with a recorded male-female acoustical sequence because no recording of the sequence was made before the female died. The function of the lisps has been the subject of much conjecture. Grove saw that males in cages would jump about when one male started a series of lisps, and on this evidence he postulated that the lisps exhibited a territorial function. Certainly if males were this irritable when lisps are produced, they would tend to move away from the sound. Grove also suggested that the lisps may serve to keep responsive females in the vicinity of a lisping male, and Alexander (1960) seemed to favor this idea.

I conducted three series of tests of the lisps with the one female I had -- one series each at 55, 75, and 90 db. The lisps were broadcast every three seconds during the acoustical part of the tests. At 55 db the female went immediately to the loud speaker in all four tests. At 75 db the female usually turned toward the loudspeaker, but only went toward it two times and then only part-way. At 90 db she did not move. The female made no tick to any lisp at any intensity. The tests indicated that low intensity lisps were female attracting. Two weeks after the above tests I repeated the whole experiment with the same female and she gave a similar performance -- i. e. no response to high intensity lisps but immediate orientation and movement toward the loudspeaker at low

intensity. This is a reasonable expectation since females of Scudderia texensis move toward a certain conspecific male sound only when it is received at low intensities (Spooner, 1964). This also explains why Grove never saw this function of the lisps in his caged individuals. Females close by males receive the lisps at too high intensity to be responsive.

Montezumina modesta (Bruner)

Very little is known about Montezumina modesta. I have collected it in both a sand-hill community and in a cypress head. It was equally abundant in both extremes of community-type. However, I have found it only where there is some shrub or tree cover. Nothing has been reported previously of its acoustical behavior.

Sound production of M. modesta is unique among the phaneropterines studied in terms of complication of solitary singing. In nature this species sings primarily in late afternoon and early twilight. In late twilight and darkness only occasional sounds from males and females can be heard. It is difficult to determine the acoustical activity of a group of these katydids in nature, so I will describe what I heard from one group (number unknown) observed aurally on about ten different days. As the sun began to sink behind the trees, but not below the horizon, large numbers of lisps were prominent and these were answered by ticks from both males and females. Series of lisps from different individuals varied from about 10 to about 35 in number. Lisps were spaced 0.5 - 1.0 sec. apart, and the ticks from both males and females came an instant after the lisps. No movement was ever observed from any singing individual, but few individuals

were observed due to their cryptic coloration and because of the way they perch underneath leaves and on the inner branches of shrubs. Solitary males not only lisp but most often produce a very low intensity tick immediately after each lisp in a manner such that a lisp-tick is suggestive of what sound could be produced in one opening and closing of the tegmina. Males responding to lisps of other males may produce single ticks or 3 - 4 rapidly delivered ticks.

Laboratory observations were instructive. By placing caged males and females on the table in the experimentation room and by leaving the door open for the only light source, twilight conditions were simulated, and caged individuals sang readily. I found that the males had two characteristic lisps (Fig. 4). In most lisp series the first few lisps were usually "short" lisps delivered on the average about two-thirds second apart (stop watch timings) at 25° C. The terminal lisps of most lisp series were usually "long" lisps delivered about one second apart at 25° C. Table 3 shows the results of the analysis of sonagrams

Table 3. Results of analysis of lisp-tick sequences from three males of Montezumina modesta. (Time in milliseconds.)

Type of lisp	Indiv.	°C	No. lisps analysed	Lisp duration			End of lisp to tick		Beginning of lisp to tick	
				Range	\bar{X}	s _x	Range	\bar{X}	Range	\bar{X}
Short	041-9	25.0	20	15-23	20	2	48-98	75	70-118	95
"	041-10	25.5	10	16-22	20	1	62-91	81	83-111	101
"	041-11	25.0	10	13-20	17	2	45-60	51	64- 79	68
Long	041-8	25.0	12	30-39	36	2	37-93	58	73-123	99
"	041-10	25.5	3	27-30	28	2	56-67	59	86- 88	87
"	041-11	25.0	10	23-31	28	3	36-96	68	66-119	95

of the lisp-tick sequences of three males. Short and long lisps produced without the following ticks measured the same lisp durations as those shown in Table 3. Average lisp durations for the short and long lisps were about 19 msec. and 30 msec. respectively. For those lisps analyzed there was only one case of overlap between the extremes of lisp durations, but this involved two individuals. Each individual had distinct and non-overlapping ranges of duration for the two lisps.

Table 4 shows the results of analysis of sonagrams to determine the timing of the female tick response. If time is measured from the beginnings of the lisps,

Table 4. Results of analysis of sonagrams to determine the timing of answering ticks of females of Montezumia modesta.

Type of lisp responded to	Indiv.	°C	No. of responses analyzed	End of lisp to female tick			Beginning of lisp to female tick		
				R	\bar{X}	s_x	R	\bar{X}	s_x
Short	041-7	25.7	1		38			59	
"	041-12	25.0	10	40-50	44	3	53-65	61	2
"	041-13	25.0	10	37-46	42	3	53-62	58	3
Long	041-7	25.7	2	15-24	20	4	50-54	52	2
"	041-12	25.0	7	14-25	18	4	53-65	61	4
"	041-13	25.0	10	23-35	32	2	61-68	65	2

then the female tick response timing is essentially the same -- about 60 msec. -- to both types of lisp. Response delays measured from the ends of the lisps are not the same. This phenomenon suggests to me that the females may only secondarily answer long lisps after having answered a series of short lisps. Indeed, female responses to long lisps were not nearly as vigorous (see discussion of inten-

sity of response in a later section) as they were to short lisps. Test females would answer short lisps with strong, loud ticks, and would continue answering after the male started producing long lisps (see Fig. 4), but they did not answer all the long lisps. Usually the females stopped responding before the end of a series of long lisps, and if short lisps did not begin a series, the females sometimes did not answer at all. Results from experiments with these sounds also indicate that female ticking after a long lisp is not of great importance.

The procedures outlined in the general methods for testing response to sounds were not usable with this species without modification. I was able to get responses from virgin females to recorded lisps only after filtering all frequencies below 15,000 cps from the sounds (see discussion on frequency differences). Two females were tested in the arena with lisps filtered in this manner and broadcast at 50, 55 (the maximum measured from a male), and 60 db. I reasoned that 60 db near the speaker would be 55 db or less at the test individual. The test females almost invariably answered the short lisps at all three intensities. They moved very little toward the short lisps, although they often turned immediately and oriented toward the loudspeaker. This behavior suggested that the long lisp may have been female attracting, and experience with other katydids showed that low intensities of the female-attracting sounds are important in eliciting response. Thus the initial tests with long lisps were at 50 db. The result was no reaction at any time. At 55 db both females went immediately to the loudspeaker if they were near the loudspeaker when the sound was turned on. If they were on the opposite side of the arena from the loudspeaker when the sound was turned on, they gave no response. At 60 db they always went immedi-

ately to the speaker. During these tests with long lisps only occasional answering ticks were made by the females. So, females go to high intensity long lisps. What, then, gets the sexes together from long-range in areas where the populations are low? I placed a male in the arena, a female in a small cage in place of the loudspeaker and left the door open for a twilight effect. The male sang series after series, and the female answered almost all his lisps. He heard her certainly, for he would turn and orient immediately toward the female after her first answer. But he never moved toward her. By covering the female's cage with several layers of cellucotton it was possible to muffle her answers until they were barely audible to me. At this intensity the male went rapidly to the female at whatever position I placed her. I then alternated (3 - 4 times each) placing the muffler over the female and removing it. The male never moved toward the female when she was uncovered, and he always moved toward her when she was muffled. These experiments indicate that it is the males which are attracted toward distant females in nature, and that the females make the final move to bridge the gap between the sexes by moving toward high intensity long lisps.

Scudderia cuneata Morse
and
Scudderia furcata Brunner

Scudderia cuneata and Scudderia furcata are best discussed together because of their very close relationship, overlapping geographical distributions, and similar sound productions. Alexander (1960) pointed out the problem of understanding how heterospecific males and females of cuneata, furcata and

S. fasciata Beutenmuller, 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 posed the idea that the timing of the responses of the females may be different.

Both cuneata and furcata are common in Alachua County, Florida, but for the most part they occur in different habitats and adults are present at different times of the year. Although 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. Cuneata has one generation per year, adults being found from the middle of July until early November, and furcata has two generations per year, adults being found from early May until November, but with reduced numbers in August prior to the maturation of the second generation. Thus, only those individuals of the two species found concurrently in mesic situations — and occasionally in more xeric or hydric situations — have the potentiality for confusion in pair formation. The presentation below shows that cuneata and furcata have sounds sufficiently different to allow reproductive isolation by specificity of response of males and females to conspecific sounds.

The acoustical behavior of solitary males of both cuneata and furcata is so similar that only a trained ear can usually detect which species is producing which sound in mixed populations. Without the opportunity for comparison, it is almost impossible to distinguish which species is singing when only one species occurs. Both species produce single-pulsed lisps (Figs. 2b and 2c) which they reiterate a few seconds apart in series of three or four. Different

series are spaced anywhere from 1 - 30 minutes apart. A second sound produced by both species but much less often than lisps is a short phrase (Figs. 5 and 6) in which the pulse rate is quite fast but slow enough to aurally detect its pulsing nature. The pulsed phrase is repeated at a rate of one every 4 - 5 sec. to one minute.

By slowing recordings to one-half speed and using a stopwatch, I determined the lisp rate for the two species at 25° C. The lisp rate for cuneata recordings varied from one every 1.7 - 3.0 sec. and averaged one every 2.3 sec. The lisp rate for furcata recordings was slower, ranging from one every 2.4 - 4.2 sec. and averaging one every 3.3 sec. The lisp duration of cuneata lisps at 25° C determined from 23 recorded lisps involving four males ranged from 12 to 25 msec. and averaged 16 msec. with a standard deviation of 3 msec. The lisp duration of 18 furcata lisps at 25° C involving four males ranged from 55 to 70 msec. and averaged 75 msec. with a standard deviation of 9 msec. Thus the lisp durations are distinct for the two species. I recorded several pulsed phrases from four cuneata males and a few pulsed phrases from two males of furcata. The results of the analysis of the phrases are shown in Table 5. There are not enough data to determine whether there is or is not a difference in pulse rates between the two species. The average pulse rate for cuneata between 25.2° C and 25.9° C was 35.0 pulses per sec. whereas the pulse rate for furcata at 25° C was 35.6 pulses per sec. One difference between the pulsed phrases of the two species may be the phrase duration which is reflected by the number of pulses in the phrases. Cuneata produced 2 - 4, almost always four and never more than four, pulses per phrase. Experimental evidence from both

Table 5. Results of analysis of pulsed phrases of solitary males of Scudderia cuneata and S. furcata. (Time in milliseconds.)

Species	Indiv.	° C	No. phrases sampled	Pulses per second	
				\bar{X}	s_x
<u>cuneata</u>	064-2	25.8	5	36.5	.2
"	064-6	25.2	9	32.1	1.4
"	064-6	27.4	1	37.5	
"	064-7	25.7	3	36.5	.7
"	064-7	25.9	4	38.7	.4
"	064-8	28.0	3	42.8	.6
"	064-12	27.2	2	39.0	.4
<u>furcata</u>	063-6	25.0	2	36.0	.3
"	063-9	25.0	4	35.3	.4

species (discussed later) also suggests that phrase duration may be important in eliciting responses. Other authors (Allard, 1910b, Fulton, 1932; Pierce, 1946; and Riley, 1874) have described sounds of more than one pulse from furcata, but not in detail.

The only difference between day and night acoustical 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 whether the pulsed phrases are more frequent than the lisps at some specific time of day. The descriptions presented above agree in general with those of other authors who have described furcata sounds from aural impressions, except those of Allard (1911) and Cantrall (1943) who observed more singing from furcata in the afternoon than at night.

I have heard only lisps and pulsed phrases from solitary 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 five feet away. Single "tisps" were produced every 2.5 sec. Fulton observed ticking from males of furcata in late afternoon in Oregon, the ticks being emitted 2 - 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 any ticking from solitary 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 produced answering ticks after the lisps of males, both cuneata and furcata males produced ticks irregularly in the manner described by Fulton for furcata. In the presence of responsive females male ticks were heard at almost any time except during the time when a lisp was being made and the time a female tick was 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 a slow rate. 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 "created" situations were alternately repeated a number of times, and always the results were the same; male ticking only in the presence of a responsive female. Fulton made no mention of the number of different observations he made of male ticking. Possibly Fulton noticed it only once in nature as did

Cantrall. If so, then it is possible that the presence of responsive females may have precipitated the ticking that Fulton and Cantrall heard. 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, 1964).

As mentioned above, cuneata or furcata males were almost always silent at the time when a female answering tick was expected. This agrees with the behavior of Scudderia texensis in which species the males produce a "slow-pulsed song" which the females answer at about a one-second delay at 25° C (Spooner, 1964). Listening males of texensis produce loud ticks during and immediately after the slow-pulsed song but are silent at the timing of the female tick. Occasionally a male of cuneata or furcata can be heard to produce a single tick after his own lisp at about the timing of the female tick. Sonographic analysis shows that the mean delay of the tick after the lisp in a male lisp-tick sequence is longer than the mean delay of a female tick after a lisp (see Table 6). However, the range of delays of male ticks and female ticks overlap for each species. Six lisp-tick sequences (three each from two males) of cuneata ranged from 343 to 440 msec. delay before the tick, and averaged 399 msec. with a standard deviation of 36 msec. Twenty-one lisp-tick sequences from one furcata male ranged from 1260 to 1544 msec. delay before the tick and averaged 1368 msec. with a standard deviation of 58 msec.

Table 6 shows the differences in timing of the female response to the lisps

Table 6. Results of analysis to determine the timing of the female tick after male lisps for Scudderia cuneata and S. furcata. (Time in milliseconds.)

Species	Source of lisp answered	Indiv. female	°C	Sample size	Tick delay		
					Range	X	s _x
cuneata	recording	064-4	25.0	16	332-383	361	15
"	"	064-8	25.0	10	325-408	368	23
"	"	064-10	25.0	10	270-399	325	40
furcata	singing male	063-5	24.8	10	840-1422	1054	174
"	" "	063-12	25.0	3	1110-1384	1235	137
"	recording	063-14	25.5	10	1059-1266	1147	61

of specific males. In the laboratory, response was characteristically specific for most of the adult life of the katyids. The distinctive difference between the lisps of the two species is apparently lisp duration. By standing near females of cuneata and furcata at the same time I have evoked responses from one or the other species -- but seldom from both to the same single stimulus -- by flipping my thumb across the corner of a piece of paper at different rates. The only difference between the "lisps" I thus produced was in length. Short "lisps" evoked ticks from cuneata females; long "lisps" evoked ticks from furcata females -- but, at species-specific timings. Not all such artificial lisps evoked responses. Some were uncontrollably too short or too long for either species and consequently no response occurred at all. After having been kept in the laboratory for a long period without being allowed to copulate, females would sometimes begin answering the lisps of other species, but even then at species-specific timings and with less vigor (intensity of response discussed later) than the lisps of their own males.

Controlled experiments to determine the functions of the sounds of these

two species were conducted according to the general methods outlined earlier. A maximum of 58 db was measured from lisping cuneata males, and a maximum of 62 db was measured from lisping furcata males. Thus, lisps of cuneata were broadcast at three intensities -- barely audible, 50, and 60 db -- and, lisps of furcata were broadcast at three intensities -- barely audible, 50, and 65 db. Cuneata lisps were broadcast at a rate of one every two seconds; furcata lisps: one every three seconds. The maximum intensity of the pulsed phrases was measured at 66 db for cuneata and 78 db for furcata, so these sounds were broadcast at intensities of barely audible, 50, and 65 db for cuneata; and barely audible, 55, and 80 db for furcata. Pulsed phrases for each species were broadcast at a rate of one every six seconds.

The only consistent response given in the whole series of tests with individuals of both cuneata and furcata was female ticking to conspecific male lisps. Other responses were so inconsistent between successive tests with single individuals and between individuals that no definite conclusions can be drawn from the data. A summary of the data follows. Two of the four cuneata test females oriented toward and moved toward recorded cuneata lisps in about one-half of the tests at 50 db. These same two only ticked to the same lisps at lower or higher intensities. One of these and another cuneata female always answered a cuneata four-pulsed phrase and went to the loudspeaker broadcasting the phrase. The same female which responded in the above two types of tests answered and went to a cuneata two-pulsed phrase. Also she went toward a six-pulsed phrase of furcata in five of eight tests at 80 db but never answered at 80 db. At 55 db this female answered the furcata six-pulsed phrase a few times and went to the

loudspeaker in four of four tests.

Furcata females were equally inconsistent. The six test females usually made no movements during tests other than those involved in producing ticks. All six did no more than to tick to lips at low and high intensities, but three of the six oriented and made strong movements toward the loudspeaker in about one-half of the tests when lips were played at 55 db. Only one furcata female answered the six-pulsed furcata phrase used in the tests, this at 55 db and only at two different times. At barely audible and at 80 db intensities no response was made by any furcata female to the six-pulsed phrase. At 55 db, however, five of the six females oriented toward the loudspeaker immediately when the sound was turned on and in more than one-half of the tests the females moved toward the speaker. No furcata female ever answered the cuneata four-pulsed phrase, but one female in two different tests at 55 db oriented immediately toward the loudspeaker when the cuneata four-pulsed phrase was turned on.

Cuneata and furcata females consistently answered conspecific male lips at species-specific timings. Cuneata females consistently answered cuneata four-pulsed phrases and sometimes answered furcata six-pulsed phrases, whereas furcata females seldom answered any pulsed phrase. Cuneata and furcata females often oriented and went toward medium intensity conspecific lips and pulsed phrases. Cuneata females were indiscriminate in responding to pulsed phrases of either cuneata males or furcata males.

Neither fast nor slow ticking had apparent effect on any test females of either species. However, in tests of fast ticking or slow ticking test males of both species almost always turned away when the sound was turned on and

erratically moved away from the sound. Ticking sounds from males of either species are apparently alike and both repel heterospecific males as well as conspecific males.

Another sound, not yet mentioned and heard from furcata males in situations where females were answering and several males were ticking loudly, is a high intensity, many-pulsed phrase (Fig. 7) which decreases continually in intensity and pulse rate. This sound had no apparent effect on test males and females of furcata. It may be a mechanism to release "nervous stress" in males in such a situation, for a male generally ticks more softly and at a slower rate after producing such a sound.

It would be advantageous for males that hear females answering other males to locate those females by going to ticks produced at a timing specific for that species. Since Grove found that males of Microcentrum rhombifolium sometimes locate females which are answering other males, and since I found that males of Inscudderia strigata can locate their females in this manner, I wanted to know if S. cuneata and S. furcata exhibit the same behavior. Three males of each species were tested. A test consisted of placing a caged female at the loudspeaker position and broadcasting lisps from nearby. The males of both species went rapidly to the female of their own species and made no reaction at all to the heterospecific female answer, thus proving that males are able to locate conspecific females answering other conspecific males. An imperative test is to determine experimentally if the timing of the female tick is important in attracting males to females. Casual observations suggest that it is.

Amblycorypha floridana Rehn and Hebard

Amblycorypha floridana is abundant throughout Florida from early June through July in almost any lushly vegetated area. Solitary males produce a sequence of several clicks followed by a buzz (Fig. 8), and the sequence is usually repeated several times (3 - 25 repetitions) in each series. In this text I will refer to one sequence of clicks and a buzz as an entire song (ES). When starting to sing after having been quiet for a while, a male usually clicks at a slow rate initially and increases the click rate through perhaps a dozen clicks before producing the buzz. In succeeding ES sequences only four or five clicks are usually made before each buzz. The time interval between ES sequences is usually decreased during the first three or four sequences. At the end of a series of ES sequences the interval between buzzes increases. Usually a series of clicks (perhaps a dozen or more) ends a series.

In normal singing the two clicks just before the buzz are produced in more rapid succession than are the preceding clicks, and the buzz follows the last click with almost no break. Thus I have arbitrarily divided the ES sequence into three parts -- Part I: the initial 3 - 4 clicks, given at a rate of 2 - 3 per sec., Part II: the two clicks just ahead of the buzz and given in more rapid succession than the initial clicks, and Part III: the buzz.

Most often floridana is found in congregations in favorable habitats, and in such congregations the predominant sound produced is clicking. When several males are singing close together only one male will be making both clicks and buzzes during any one period. The other males usually click loudly until the one male producing ES sequences stops buzzing. Then another male will click

and buzz while his neighbors click. Buzzing evidently inhibits sound production from the males. A male of Atlantiscus glaber Rehn and Hebard present in the laboratory at the same time, would cause floridana males to completely cease sound production with its characteristic, high intensity, high frequency buzz. I could often cause the same effect by orally producing a loud hiss. 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 abbreviate the clicking part of the ES sequences and produce only the initial 1 - 2 clicks, pause, and then buzz. Usually in the abbreviated sequences the click just before the buzz is present (although certain individuals consistently omit even this click). Thus, instead of the usual click, click, click, click, click-click-buzz, the abbreviated sequence is click, —, —, —, —, click-buzz. As indicated above, such singing occurs only when a male is acoustically isolated from other males. Such isolated males occur early in the season and in out-of-the-ordinary habitats. I have noticed that some of these solitary males fly about, singing a few sequences from each perch.

By slowing down recordings and using a stopwatch, I determined that the ES sequence in the middle of a series is repeated every 1.4 - 2.5 sec., depending on the individual. The usual rate was about one every two seconds. In an experiment to determine the effects of temperature on orthopteran sounds T. J. Walker (personal communication) found that the pulse rate of the buzz of three males of floridana from Alachua County, Florida, averaged 45.2 pulses per sec.

at 25° C (calculated from regression formula). I recorded at 24.2° C one series of ES sequences from each of seven males from different localities in Florida and made two sonagrams of each recording. Some of the results of the analysis of the sonagrams are shown in Table 7.

Table 7. Results of analysis of solitary songs of Amblycorypha floridana recorded at 24.2° C.

Location of collection in Florida	Indiv.	Pulses per buzz	Average No. pulses per sec.		Average No. sec. between beginnings of buzzes
			buzzes	clicks	
Pensacola Bay	006-24	7-8	34.4	50.3	2.0
"	006-25	7	35.9	55.8	2.0
"	006-26	6	33.6	46.4	1.4
"	006-27	9-10	33.9	55.1	1.7
"	006-29	9	38.1	49.5	1.6
Salt Springs (Marion Co.)	006-30	9-11	49.0	63.7	2.1
Guinesville	006-31	10	42.8	57.7	2.6

Those individuals from the Pensacola Bay area had somewhat slower pulse rates than the central Florida individuals. It is clear that the click pulse rate is greater than the buzz pulse rate. It is interesting also that the toothstrike rate (not shown) in the click pulses is slower than the toothstrike rate in the buzz pulses. Most often the clicks are composed of three pulses. However, the first pulse is often very weak and barely shows up on the sonagrams. Probably this first pulse corresponds to the initial opening of the tegmina. If so, the clicks consist of two cycles of opening and closing the tegmina. The relationship between floridana clicks and certain sounds of two closely related species is discussed later.

Females answer each ES sequence shortly after the buzz. I recorded

several sequences of recorded ES and answering female tick from each of four females from different Florida localities. I made sonagrams of the first ten of these male ES-female tick sequences for each female; the results are tabulated in Table 8. It seems that southern Florida females may have a longer delay period.

Table 8. Results of analysis to determine the timing of the female tick after recorded male songs of Amblycorypha floridana. (Time in milliseconds.)

Location of collection in Florida	Indiv.	° C	Tick delay	
			\bar{X}	s_x
Sanford	006-19	25.0	133	19
Gainesville	006-20	25.0	139	11
Salt Springs (Marion Co.)	006-21	25.0	143	10
Long Pine Key (Dade Co.)	006-22	26.5	161	27

To determine what part of the ES sequence was important in evoking ticks from females I broadcast recorded parts of the ES sequence — Parts I, II, and III — singly and in different combinations, to three females and noted their responses. The loudspeaker was placed one foot away from individually caged females, tested one at a time, and the sounds were broadcast at 55 db. Each part or combination of parts of the ES sequence were broadcast 50 times. Two series of tests were made with each female. The first series involved broadcasting the same randomized sequence of successive loops of tape to each female. The second series involved broadcasting a different randomized sequence of loops of tape each time a different female was tested. On the loops which had part of the ES sequence deleted a blank piece of tape was inserted to keep the remaining parts of the ES sequence normally spaced. Each female was tested twice but not twice in succession. The results of these tests are

presented in Table 9. In no case was the response to any part of the ES sequence

Table 9. Results of experiments to determine which part of the male sound sequence is important in evoking the tick response from females of Amblycorypha floridana. (Numbers in the columns represent the number of different repetitions of the sound to which the female responded. The order of the column headings reflects in no way the order the different sounds in the experiment were played.)

Test series	Indiv. female	Part of ES sequence played						
		I	II	III	I-II	I-III	II-III	ES
1	003-20	7	13	26	26	40	1	48
		10	17	19	24	33	44	45
1	003-21	0	3	9	11	21	8	36
		0	6	7	5	31	1	40
1	003-23	0	0	2	0	41	30	50
		7	5	35	1	50	48	49
2	003-20	5	0	7	8	19	23	33
		7	0	3	7	18	12	33
2	003-21	2	0	4	5	21	15	31
		4	0	6	7	19	13	34
2	003-23	7	0	9	7	22	15	47
		9	1	11	19	23	30	50

as great as to the ES sequence, and different combinations of clicks and buzzes evoked greater response than either clicks or buzzes alone. It seems that clicks and buzzes combined in sequence are important in eliciting tick responses from females. In the field females have been heard responding readily and consistently to the abbreviated ES described earlier. A logical test in these series of experiments would have been to play a simulated abbreviated ES and to have compared the results to those above. I feel that response would have been a matter of deleting a few clicks of Part I but not the first click. Thus, a female listening to an abbreviated ES sequence would hear the beginning and be primed for the end of the sequence; her response might be as if she heard the whole ES sequence. One argument against this idea is the fact that female response to Parts I, II, or I

and II was not delayed to a timing as if Part III had been present in those tests. I made several recordings of one female's answer to a recording of Parts I and II. The ensuing analysis of sonagrams showed a significantly delayed response but not enough delay to have allowed a Part III to have been completed.

Other experiments were conducted in the response arena to determine other functions of the sounds composing the ES sequence. Sounds were broadcast at 80 db (the highest intensity measured from singing males), 55 db, and barely audible. During the acoustical part of the tests, each sound was repeated every two seconds.

The first series of arena experiments was to test movement to the ES sequence. Three males were tested. No males behaved differently (other than acoustically) during the acoustical parts of the tests than they did during silence no matter what the intensity of the broadcast sound. Low intensity ES's stimulated males to sing, but they were inhibited from buzzing by high intensity ES's. This is discussed above.

The three test females ticked consistently to barely audible ES's, but either never moved or continued moving in a random pattern when the sound was turned on. All three females answered almost all ES's at 55 db, but in these tests they were apparently stimulated to move about. The test females usually remained motionless or moved very little and randomly during silence. Immediately after the 55 db ES recording was turned on all three females started moving, or if they were already moving at the start of the recording, they increased their speed of movement considerably. However, they moved about without orienting in relation to the loudspeaker. ES sequences at 80 db always

caused an immediate orientation by all three females toward the loudspeaker whether they had been still or randomly moving. Usually they proceeded directly toward the loudspeaker, although two females in two tests each went only part-way toward the loudspeaker and simply remained oriented toward it for the rest of the test period.

To get a better comparison of the responses at 55 and 80 db, I set the volume controls on the recorder so that the maximum intensity broadcast at the loudspeaker was 80 db when the volume-control knob on the loudspeaker was set to allow a maximum intensity. Then I turned the loudspeaker volume-control knob so that the sound played was 55 db. Thus I was able to carry out a 15-minute test in which five minutes were silent, five minutes were at 55 db, and five minutes were at 80 db. All that was necessary to change from 55 db to 80 db was to turn the loudspeaker volume-control knob at the 10 minute mark of the tests. The three test females exhibited the same kinds of reactions in these combined tests as they had done to separate tests of the 55 db and 80 db ES sequences. Almost invariably the three kinds of movement exhibited by the test females to the three parts of the tests were 1) no movement, 2) random movement, and 3) oriented movement toward the speaker. It is interesting that the females ticked after the ES sequence at barely audible and 55 db intensities but at 80 db they ticked only occasionally.

The next step was to determine which part of the ES sequence was important in causing the above reactions. Any part or combination of parts of the ES sequence that involved clicks caused random movements in all three females at 55 db.

The more clicks present in a particular test the greater was the amount of movement, e.g. Part II elicited only slight response. At 80 db the same sounds, those with clicks, evoked strong orientation and movement toward the loudspeaker in almost every test. Part III, the buzz, evoked no response from any female during any arena test at any intensity. Since these were the same females listed in Table 9, one would expect some ticking response to Part III. These females were about two weeks older by the time these latter tests were conducted; i.e. age may have been a factor in the difference in behavior. Part III combined with and preceded by clicks evoked ticks from the test females in the arena in about the same proportions as described earlier for the experiment to determine which parts of the ES sequence were important in eliciting ticks from females.

This species appears to be another (see discussion of Montezumina modesta) in which the females bridge the final gap between themselves and the males. Unfortunately, Amblycorypha floridana was one of the first species with which I experimented. At that time I was strongly biased with the idea that phaneropterine males go to close range answering females, so I decided to set aside the above presented data until much more time could be devoted to experiments with floridana. The result was that all my floridana males died before I realized, in my work with M. modesta, that it was possible that in some species males move toward females answering at long range and that females make the final movements in getting the sexes together. Logical experiments now to be performed are those testing male responses to different intensities of answering female ticks. I hypothesize that males move toward low intensity female ticks. A logical follow-up to all these experiments would be

to turn a male and a female loose in a room and observe which sex goes toward the other and to what extent.

I made one observation which may have bearing here. Before conducting any experiments, I opened the cage of a female floridana and placed a single, caged floridana male in the same room 12 feet away on another table. The male sang several series of ES sequences. The female answered almost every ES, climbed out of her cage, and oriented toward the male. After a few minutes she climbed down, walked immediately across the table, and leaned over the table edge toward the singing male. Later, I released the male 12 feet away from the caged female but on the same table. The male oriented immediately toward the answering female but did not move until after he had produced several ES sequences. En route toward the female he would stop and stridulate loudly for a few seconds. The closer he came to the female, the greater number of clicks he would produce between buzzes. When he finally reached the female's cage, he climbed around over it producing nothing but clicks; the female ticked occasionally. I watched this last scene for only 2 - 3 minutes before recaging the male. These observations support the hypothesis that females make the final movements in pair formation in this species. Experimentation along these lines is imperative.

Amblycorypha oblongifolia (De Geer)

Amblycorypha oblongifolia was not known from Florida before this study. T. J. Walker and I collected one female from Liberty County (western Florida) early in June, 1962, thus extending the limits of its known southern distribution.

This particular female was very responsive to the song of a single oblongifolia male collected by T. J. Walker from Berkeley County, South Carolina.

Solitary males of oblongifolia produce a short, loud, complex sound, which is repeated at varying intervals (Fig. 9). Pierce (1948) made an electronic analysis and Alexander (1956, 1960) made an audiospectrographic analysis of the sound. My analysis agrees generally with that of Alexander (1956), who says the sound is produced only at night, and that "different individuals in a colony usually sing a few minutes, alternating their chirps with one or two other individuals, then are silent for a few minutes Colonies thus sing in bursts, separated by intervals in which no individuals are singing." In the laboratory my single male sang only in darkness and at sporadic intervals, producing 10 - 20 phrases each time. The phrases were usually spaced 4 - 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." Yet, the sonagram he shows (Alexander, 1960) exhibits a short, low intensity (compared with the rest of the sound) pulse just ahead of the longer, more slowly delivered pulse that he calls the first pulse. Almost every one of the sonagrams of the phrases by the male in my laboratory have this initial, short pulse which is lower in intensity than the remaining pulses. This pulse is probably made on the initial opening stroke of the tegmina and is non-functional. Therefore, I shall retain Alexander's system of numbering the pulses. My sonagrams looked essentially like that shown by Alexander; all were three-pulsed with the first being longer than the others. Only in a few of my sonagrams

does the toothstrike rate during the first pulse increase toward the end of the pulse as Alexander indicated. Actually some phrases have decreasing toothstrike rates while others have very regular toothstrike rates during the first pulse. By measuring the time interval from the end of the long first pulse to the end of the last (third) pulse I obtained a pulse-rate value for the last two pulses from six phrases at 25° C. These averaged 20.0 pulses per sec. with a standard deviation of 0.5 pulses per sec. The average total duration of these phrases was 199 msec. The average number of toothstrikes per pulse for the three pulses comprising the phrase were 15, 10, 9 respectively. It seems that the greater duration of the first pulse is due to a combination of closing the tegmina more slowly (assuming the pulses are made on the closing strokes of the tegmina) and striking more teeth.

Unfortunately, the male died before I could conduct any experiments to determine his reactions to recorded conspecific sounds. Just before he died I noted that the male was stimulated to sing in alternation with broadcast phrases of any intensity up to 110 db. I did not measure the maximum intensity emitted by this male, but 100 db recordings sounded comparable to the sounds from the male. Long before the male died I placed him in the arena and put the caged female on the corner (loudspeaker position). The female answered his phrases and immediately the male went straight to the female in every test. Thus, it seems that males go to females at least at close range.

The female in the laboratory ticked after almost every phrase that the male made. The average delay at 25° C of the female tick after the end of six male phrases was 208 msec. with a standard deviation of 13 msec.

In order to determine which part of the complex phrase was important in eliciting the ticks from the female, I divided the phrase into two parts -- Part I: the first, long pulse, and Part II: the final two similar pulses. Surprisingly, both Part I and Part II evoked ticks from the female as well as the whole phrase (ES). Since the intensity is relatively uniform throughout the phrase, the only difference in playing the ES in reverse was the sequence of arrangement of the structural components of the ES phrase. The female gave no ticks to such a sound. However, Part I broadcast backwards elicited as much response as did the ES when broadcast forward. Part II backward evoked no response. Why? I set up a series of tests to determine if this observation could be trusted. These tests involved ES forward and backward, Part I forward and backward, Part II forward and backward, Part I forward plus Part II backward, Part I backward plus Part II forward, Part I backward plus Part II backward, Part II forward plus Part I forward, Part II forward plus Part I backward, and Part II backward plus Part I forward. Sound was broadcast every six seconds at 100 db. The sequence of broadcasting the different combinations of sound was changed in every series of tests. Five series of tests were made covering a period of about a week.

The female responded to every sound broadcast by emitting ticks, except to those sounds in which Part II was broadcast in reverse. What was it about the two terminal pulses broadcast in reverse that rendered them incapable of evoking the tick response from the female? I can only conjecture. It may be the necessity of shortening the pulse lengths in successive pulses.

In arena tests to determine what movements might be invoked by these

sounds, the female answered high intensity ES's readily, but she answered very few below 80 db. The female made no oriented movements to 95 - 100 db ES's, but she always oriented toward 75 - 80 db ES's and, in about one-half of the tests, moved toward the loudspeaker a short distance, remaining oriented and answering a few of the phrases after stopping her movement. The female died overnight after the above tests and before tests could be conducted at lower intensities. These limited studies indicate that the female may have been attracted toward low intensity ES's and would not have made any ticks to low intensity ES's. Before more definite conclusions can be made concerning the acoustical behavior of this species, data are needed involving several individuals.

Species Not Involved in Experiments

The following species were not involved in experimentation to determine the functions of their sounds. The sounds of some of these species have never been reported, so the following presentation includes descriptions of known sounds and, when known, descriptions of the singing behaviors.

Amblycorypha carinata Rehn and Hebard

Amblycorypha carinata has been located at only one small place near Gainesville, Florida. It occupies the undergrowth of a long-leaf pine flatwoods and the population density is low. It often occurs with Amblycorypha floridana.

Sound production by this species has not previously been described. Numerous observations of the single population indicate that it is a night singing species. Solitary males usually produce a two-pulsed phrase (Fig. 10) which is repeated about every two seconds in series of varying numbers. In the field I heard

one male produce 67 phrases in a continuous series. Males apparently produce the same sound whether they are completely solitary or close to, but not touching each other. Sometimes two males may alternate phrases regularly but such alternation is probably happenstance. Infrequently, males produce a series of three-pulsed phrases.

The pulses composing the phrases described above apparently correspond to single openings and closings of the tegmina, one opening and closing producing a single pulse on the closing stroke. However, close inspection reveals, in certain sonagrams, very brief pulses which probably are made on the opening strokes. Usually one of these brief pulses is the initial sound in each phrase (see Fig. 10), and evidently is made on the initial opening stroke of the tegmina. These brief pulses are not included in my counting of the number of pulses in a phrase.

I have recorded at least one series from each of several males from different localities. The results of sonographic analysis of ten phrases of each of these recordings are shown in Table 10. The analysis was made only of two-pulsed phrases except for individual 006-10 from which individual only three-pulsed phrases were recorded. A recording of a series of three-pulsed phrases from individual 006-8 was made, and the results of analysis of those phrases were similar to those depicted for 006-8 two-pulsed phrases. There were substantial differences in pulse duration between the first and second pulses of certain individuals. A bias in the calculated pulse rates for those individuals would have resulted if I had measured the time interval from the beginning of the first pulse to the beginning of the second pulse -- the time spent in the first complete cycle

Table 10. Results of analysis of the songs of some males of Amblycorypha carinata.

Location of collection	Indiv.	°C	Pulses per second		Average No. toothstrikes pulse no.			Average interval between beginnings of phrases (seconds)
			\bar{X}	s_x	1	2	3	
Gwinnett Co., Ga.	006-3	25.0	15.7	.6	16	14		1.5
" " "	006-4	25.0	17.0	.3	22	15		2.3
" " "	006-5	25.0	17.2	1.0	8	9		1.1
Alachua Co., Fla.	006-7	25.5	18.2	.4	13	13		1.7
" " "	006-8	25.5	18.0	.3	14	14		1.5
" " "	006-10	24.8	18.0	.5	17	17	16	2.9
Jackson Co., N. C.	006-9	25.0	19.6	.4	9	11		2.6

of closing and opening the tegmina -- or from the end of the first pulse to the end of the second pulse. Therefore, I measured both these time intervals and divided the averaged time interval into one hoping to obtain truer measure of the pulse rates.

There appear to be small variations in pulse rates between individuals from different localities. One striking difference between the songs of different individuals irrespective of locality is the number of teeth struck per pulse. Another difference is the toothstrike rate; generally the individuals which struck fewer teeth struck them at a slower rate than did the individuals which struck more teeth.

No responsive females of carinata were collected, so I do not know what structural unit of sound the females answer -- assuming they do produce sound in the response to male sounds -- or at what timing the females answer. The most likely unit for a female to respond to is the individual phrase.

Amblycorypha floridana, A. oblongifolia, and A. carinata are closely related and taxonomists have referred to them in different instances as species or subspecies (Rehn and Hebard, 1905, 1914b; Blatchley, 1920; Fulton, 1932). The three species are very similar to each other morphologically, in habitat preferences, and in sound production. The song similarities may not be apparent at first glance, but close inspection of a click of floridana (Fig. 8), a phrase of oblongifolia (Fig. 9), and a phrase of carinata (Fig. 10) reveals striking similarities. All sounds have an initial, low intensity pulse which probably corresponds to the opening stroke of the tegmina. Each is a short sound of two or three pulses. The biggest differences among the three sounds are between pulse rates and pulse durations and all were probably derived by modification of one basic sound.

Amblycorypha rotundifolia (Scudder)

Descriptions of the sounds of Amblycorypha rotundifolia by different authors (e.g. Allard, 1911 , 1912 , and Scudder, 1893) were inconsistent and confusing until Alexander (1960) showed that there were two species involved, separable only by their songs and partly by their geographical distributions. He described a northern "rattler" and a southern "clicker" which overlap "about 200 miles across the Appalachian Mountains." He says the song pattern in each of these two species is complex and irreversible. The song of the rattler is composed of groups of similar pulses which become progressively longer, finally terminating with a single, long pulse group usually followed by one to three short pulse groups. All of the pulses in this song are alike, and each contains six to eight toothstrikes.

In the clicker, on the other hand, the successive pulse groups in the song are of about the same length though there is a slight reduction in the rate of production as the song progresses. Each pulse group is in itself an irreversible pattern composed of three or four pulses, of which the last is much longer (contains more toothstrikes) than the first two or three.

"To the human listener, these songs appear to bear no relationship to each other. However, a closer examination reveals that they have many similar structural characteristics. Each song is composed of groups of pulse groups, and the structure of the individual toothstrikes appears to be identical. Furthermore, the songs are about the same length, they are produced in chorus in the two species in the same way, and they are produced at intervals of similar length in the singing of lone males."

The clicker has been found in Liberty and Jackson Counties, Florida. Individuals of the clicker kept in cages in the laboratory during this study sang much like the pattern indicated by Alexander but usually grouped their basic pulse groups. Figure 13 shows two basic pulse groups of the clicker. Note the increased duration at the end.

A third species of rotundifolia has been discovered by T.J. Walker (personal communication). I call it the "fast clicker" to distinguish it from Alexander's "slow clicker." The fast clicker occurs farther south than the other two species, the southernmost collection having been made at Gainesville, Florida. Both fast and slow clickers occur together, perhaps not completely overlapping in habitat preference, in Liberty County, Florida. Wherever found, the fast clicker has been very sparsely populated, whereas comparatively large numbers of the

slow clicker may be found in favorable habitats.

The song pattern of the fast clicker is diagramed in Figure 11. The click rate — basic phrase rate — is much faster than the corresponding click rate — basic phrase rate — of the slow clicker. Also there are fewer pulses in a single phrase, or click, of the fast clicker (compare Figs. 12 and 13). Since the only differences between the fast and slow clickers are the differences in basic phrase lengths — reflected by differences in the number of pulses per phrase and by differences in the pulse rates within the basic phrases — and the basic phrase repetition rates, I think such terminology (fast and slow clicker) is logical even though it is not in line with the definitions presented at the beginning of this section. Alexander has already proposed the term "clicker" and a change of that species' "name" would only add confusion. A summary of the analysis of recordings of the songs of the fast and slow clickers is presented in Table 11. On two occasions individual 001-5 almost exactly doubled his click rate in

Table 11. The results of the analysis of the songs of the "fast" and "slow" clicker forms of Amblycorypha rotundifolia.

Song form	Location of collection	Indiv.	° C	Clicks per second	Pulses per click
Fast clicker	Alachua Co., Fla.	005-6	25.8	10.2	3
" "	Leon Co., Fla.	005-4	25.8	10.4	3
" "	Stanley Co., N. C.	005-5	25.8	9.8	4
Slow clicker	Liberty Co., Fla.	001-5	25.0	2.6	4-8
" "	Jackson Co., Fla.	001-6	25.0	2.0	5
" "	" " "	001-7	25.0	2.2	4-5
" "	" " "	001-8	25.0	1.9	4
" "	" " "	001-9	25.0	2.4	5

the middle of a series of clicks. Sometimes the slow clickers produced a single-

toothstrike tick about mid-way between successive clicks for several clicks in a series.

It would be instructive to know where the female tick comes into the sequence for each of these species. Slow clicker females would almost have time enough to "squeeze in" a rapid response just behind each click, but fast ticker females would not. The most logical conjecture is that females of both species answer each group of basic phrases -- the basic pulse group of the rattler. If a male hears a female answer one of the initial short units there would be no need to produce the long, loud sequence, which could be detrimental by possibly allowing predators to locate him by sound (see Walker, 1964). If a female tick is not heard by a male after his initial, short, phrase groups, then the longer, louder series may serve to attract females toward the male from a distance.

Amblycorypha uhleri Stal
and
Amblycorypha near uhleri Stal

Amblycorypha near uhleri is an undescribed species from the coastal plains of southeastern United States. R. D. Alexander and T. J. Walker were among the first to recognize its distinctiveness from uhleri. Both occur in the same or similar habitats -- open, weedy situations such as abandoned fields or open woods. Around Gainesville near uhleri matures 3 - 4 weeks earlier than uhleri. Generally near uhleri is larger than uhleri.

Allard (1912), Fulton (1932), and Alexander (1956, 1960) have described the sound production of uhleri and all reports generally agree. A night singer, uhleri males sing from porches 3 - 4 feet off the ground. Often males are found in local, loose congregations, being spaced only a few feet apart,

in fields where there may be a much greater inhabitable area. Males apparently retain a single singing perch for an entire evening of singing except possibly in cases where they have had an acoustical interaction with a female. Congregated males may sing only in spurts, so that there are periods of singing by several males interspersed by intervals of silence.

Alexander (1960) diagrams a typical song pattern of uhleri from North Carolina and shows sonagrams of different parts of the song. The following quote from Alexander (1956) adequately describes the song. "The calling song of Uhler's katydid is a soft sound, audible only a few yards away, and is probably the most complicated sequence of sounds produced by any American orthopteran. It lasts up to 40 or 50 seconds and contains 3 or 4 distinct phases which are consistently repeated in the same sequence in every song The song begins with a rapid, tsip-i-tsip-i-tsip-i-tsip which continues for about 7 - 11 seconds, and involves pulses delivered at a rate of about 12 per second (probably 6 wingstrokes). This merges abruptly into a slower delivery of about 7 pulses per second which lasts only about 2 seconds, and ends with an abruptly louder, rattly phrase which dies away in intensity. This phrase, which contains 7 or 8 pulses delivered at a rate of about 10 per second, slowing at the end, is repeated anywhere from 3 or 4 to 10 times at intervals of 1/2 to 6 3/4 seconds (in the songs recorded). Often one or more of these phrases is preceded by a few soft ticks, apparently caused by striking individual file teeth. At least 4 different kinds of pulses are involved in the 3 different phases of this song, and there are both gradual and abrupt changes in intensity, and in speed of wing motion."

The song of near uhleri is very similar to that of uhleri. Four parts, homologous to the four parts of uhleri's song (Alexander says three parts), are involved and produced in the same sequence. But each part is much briefer in the song of near uhleri, and the third part is produced only once. Thus, near uhleri's complete song lasts 7 - 10 sec. at 25° C. Often, when first starting a series of songs, near uhleri produces only parts one and two for several sequences before producing a complete song. For instance, a series of songs may have a sequence, denoted by parts sung, of 1-2, 1-2, 1-2, 1-2-3-4, 1-2-3-4, 1-2-3-4, . . . etc. Singing males of near uhleri behave quite differently from those of uhleri. They do not usually congregate, and single males fly from perch to perch singing a short series of songs from each perch.

In his temperature experiments, T. J. Walker (personal communication) has found that each species has a characteristic pulse rate for each part of the song and the pulse rates of one species are different from the pulse rates of the other.

Recently T. J. Walker conducted some preliminary experiments in an effort to determine the behavioral significance of the different parts of the songs of these two species (personal communication). He found that no one particular part of the song by itself would evoke the tick response from conspecific females, and that females of the two species respond at strikingly different timings. In tests with the entire song, uhleri females ticked about 7.5 sec. after the end of part II. This delay allowed the production of two phrases of Part III before the female tick. Yet, apparently the timing was in relation to the initial Parts I and II because the female tick delay was characteristically about 7.5 sec.

after the initial Parts I and II whether or not one or two Part III's were produced.

In other tests the results were not completely decisive as to function, but the data did allow some strong suggestions to be made. It seems as though uhleri females may go to singing males from close range. Near uhleri females probably do not move toward males at any time. This agrees with the singing behaviors of the males of the two species. Uhleri males are stationary for long periods. Thus, uhleri females would be able to move to a single singing male easily. On the other hand, near uhleri males' behavior of moving from perch to perch would make it difficult for conspecific females to reach a singing male. Certain combinations of parts of the songs — different combination for each species — are especially important in eliciting the female tick. More work is needed concerning the behavior of these species.

Arethaea phalangium Scudder

This species has been collected in Alachua County, Florida, in very dry habitats — generally old fields and turkey oak woodlands.

No one has previously described phalangium's sound production. I have recorded two different songs from individually caged males. One song (the lisping song) consists of a series of 11 - 12 lispy pulses. The second song (the tick-lisp song — Fig. 14) is a complex one involving ticks and lisps. Every tick-lisp song contains two sequences of ticks followed by a lisp. Tick-lisp songs are usually produced 3 - 6 sec. apart in series containing as many as a dozen songs. Table 12 shows the results of sonographic analysis of recordings of the two songs of this species at room temperature. Only one typical lisping

Table 12. Results of analysis of the two songs of Arethaea phalangium.

Type of song	Indiv.	° C	No. songs analyzed	Ticks per second		Lisps per second		No. ticks before lisp		Average lisp duration (msec.)
				\bar{X}	S_x	\bar{X}	S_x	1	2	
Tick-lisp	011-2	24.8	1	45.2		3.0		7	12	54
"	011-2	25.0	5	44.4	.1	3.1	.2	8	11	55
"	011-6	25.5	6	45.3	.3	2.8	.1	7	13	50
Lisping	011-1	27.0	1			8.9				28
"	011-6	25.5	3			4.9	.4			22

song was recorded (individual 011-1); the three songs indicated for individual 011-6 were brief, containing 4, 2, and 3 pulses respectively, so that its lisp-rate is not to be taken as typical. The lisp rate of the tick-lisp song is the rate at which the two lisps were given. There was no significant difference in the number of teeth struck between individuals or between types of lisps within an individual. Therefore the shortened lisps of the lisping song are a result of increased rate of tegminal closure. This is evidenced by visually comparing the spacing of toothstrikes in the lisps of the two songs. The ticks of the tick-lisp song are evidently produced by individual openings and closings of the tegmina during which a single tooth is struck. The evidence for this is the very uniform tick rate and the fact that, in some cases, there are low intensity pulses following each tick which probably are the result of striking the stridulatory apparatus when opening the tegmina. At times only this low intensity pulse is present, indicating that the singer may have "missed" on his closing stroke (see the gap which should correspond to the sixth tick in the second sequence of Figure 14).

Nothing is known about the singing behavior in natural situations. I have heard a male singing out-of-doors only on one occasion for a period of about five minutes. It was night and the singer produced only tick-lisp songs.

I can only conjecture about the functional significance of these sounds. Perhaps the lispng song elicits female ticks -- similar to the female response to ticking in Microcentrum rhombifolium, for instance -- and the lisp-tick song attracts or spaces females and males respectively.

Inscudderia walkeri Hebard

This species is usually found around Gainesville in cypress heads as is Inscudderia strigata (discussed earlier in this section). It is my feeling that these two species are closely related. Both are restricted feeders on very resinous vegetation (strigata on leaves of Hypericum fasciculatum and walkeri on leaves of Taxodium disticum nutans) and both are morphologically similar. If they are closely related, one would expect their sound production to be similar as was shown for Scudderia furcata and S. cuneata, for the three Amblycorypha's, oblongifolia, carinata, and floridana, for Amblycorypha uhleri and A. near uhleri and for the Amblycorypha rotundifolia group. In each of those species complexes the close relationships among the species were obvious by their morphological similarities and by their acoustical behavior.

Only one sound has ever been heard from caged or wild individuals of Inscudderia walkeri by anyone in our laboratory. I call this sound a lisp, although in reality it is a two-pulsed sound (see Fig. 2e) and deviates from the definition of a lisp. However, the two pulses appear to be made in a single

opening and closing of the tegmina, the low intensity first pulse being produced on the opening stroke. Hence, my justification for calling this sound a lisp. Four males were recorded in the laboratory and the analysis of those recordings is shown in Table 13. The lisp duration is quite long whether one considers the second pulse or the entire lisp.

Table 13. Results of analysis of songs of Inseudderia walkeri. (Time in milliseconds.)

Indiv.	° C	No. lisps analyzed	Pulse duration		Total time of sound
			1	2	
022-1	26.6	2	51	130	204
022-2	27.8	2	50	156	223
022-3	26.5	3	40	151	217
022-4	25.0	2	49	154	251

Little is known of the singing behavior of walkeri. Individuals sing from the tops of the cypress trees that they frequent and produce such low intensity lisps that it is nearly impossible to make good observations when the general community resounds with the sounds of many other species of singing Orthoptera. Usually walkeri produces about four lisps in a song, these spaced 1.8 - 2.7 sec. apart. Different songs are repeated a few minutes apart.

The kinship between walkeri and strigata, as far as acoustical behavior is concerned, is not strengthened substantially by this analysis. Possibly the ancestral species was a simple "lisper," and these two species have evolved their distinctive sounds very recently. Based on the supposed close relationship between walkeri and strigata, I suspect that females of walkeri tick in response to the lisp — probably with a greater delay than females of strigata tick to lisps

of their males.

Microcentrum retinerve Burmeister

This species abounds in hydric and mesic hardwood forests of southeastern United States. It is a most difficult species to study because it inhabits and sings from treetops. A collector is most likely to catch adults of retinerve around street lights through wooded areas, for the katydid often seems to be attracted to light.

A typical song of retinerve males around Gainesville, Florida, is a series of loud, brusque phrases with decreasing numbers of pulses in each phrase. Seven is the maximum number of pulses per phrase that I have heard. Typically, a male produces a sequence of 5-, 4-, 3-, 2-, 2-, 2-pulsed phrases, the terminal two-pulsed phrases often alternated with two-pulsed phrases from another individual. Singing males fly from perch to perch singing one to a few songs from each perch.

Since captured males never sang in the laboratory, I had to rely upon analysis of field recordings made by T.J. Walker. Fortunately, he obtained three good recordings on one evening, all at 24° C. Thus, the analysis of these recordings should be comparable to analyses of recordings of other species made at laboratory temperatures (about 25° C). In my analysis I used only those phrases which contained three or more pulses. The summary of the analysis of these songs is presented in Table 14.

I have no exact data on the interval between successive songs, but observations indicate songs may be repeated 2 - 3 times per minute.

Table 14. Results of analysis of songs of three males of Microcentrum retinerve at 24° C.

Indiv.	No. phrases analyzed	Pulses per sec.		Average No. seconds between phrases
		\bar{X}	s_x	
032-3	1	12.8		2.4
032-4	5	13.8	.2	1.9
032-5	3	14.4	.2	1.6

The song of retinerve has been described by Allard (1910a, 1928a) and Alexander (1956). Alexander (1960) presents a sonagram of a complete song of retinerve from Ohio. Both Allard's and Alexander's descriptions vary from mine. Allard says the usual number of phrases is three and rarely four (Alexander, 1956, thinks Allard's observations are probably from around Washington, D. C.). On the other hand, Alexander (1956) says the song at Raleigh, N. C. and in Ohio consists of two and rarely three phrases, each phrase composed of 2 - 7 pulses. He says common sequences are 7 - 5, 6 - 4, 5 - 3, and 4 - 3 pulses per phrase. Comparisons of the geographical variations in pulse rate at the same temperature would be a valuable adjunct to these data. I suspect that the pulse rate is functionally important and the phrase length is not.

I suspect that females answer every phrase produced in a song immediately after the phrase. Since males move around at frequent intervals, I imagine that females do not locomote toward the singing males, but that males move the entire distance separating them from females once they have heard an answering female tick.

Phrixia maya Saussure and Pictet

This species is known from the United States only from three collections.

Blatchley (1920) says that Davis (1914) and Hebard (1915) each took a single specimen in Brickell's Hammock, Miami, Florida. T. J. Walker made the third collection of six individuals in 1960 near Flamingo, Florida, and made a short laboratory recording of its song.

Only one kind of sound was heard from the male recorded and that may be described as a pair of paired ticks or as a pair of clicks (Fig. 15). Every phrase has the same appearance and the phrases are repeated 2.0 - 3.5 sec. apart. Analysis of Walker's recording (containing 12 phrases) gave a pulse rate within tick pairs of 11.6 pulses per sec. with a standard deviation of 0.7 pulses per sec. The pairs of ticks within the phrases had a repetition rate of 4.5 pairs per sec. and a standard deviation of 0.3 pairs per sec.

The unusual rates of repetition of the ticks within the phrases made this sound complex within itself. Each tick probably corresponds to a single closure of the tegmina, so in producing each phrase the wingstroke rate changes twice. I will not hazard a guess as to the function of the sound, although I do think that single phrases would be the functional units. The sound is so low in intensity that it probably functions only at close range (the stridulatory apparatus of this species is very degenerate).

Scudderia curvicauda laticauda Brunner

This species is found in the pine flatwoods of Alachua County, Florida, inhabiting the herbaceous and shrub strata. I have never seen laticauda where its population density was more than about two males per acre, estimated by listening to singing individuals, and generally the density appears less than this figure. I have made very few attentive observations of its singing behavior

although I have casually heard it night-after-night during June and July for two years. It seems that the males are quite stationary for long periods while singing. I have heard only one song from laticauda, and workers in our laboratory have not reported any song from this species different from the one I have heard. It is produced only at night.

A typical song is a short series of phrases with each succeeding phrase usually containing one pulse more than the preceding phrase -- just the reverse of the pattern described for Microcentrum retinerve. The usual sequence of phrases heard contains 2-, 3-, 4-, 5-pulses per phrase. I have heard males "count" from one to seven -- never more than seven -- in some songs. Often a male will repeat phrases of a certain number of pulses producing a sequence like 2-, 3-, 4-, 4-, 5-, 5. Different songs are produced several minutes apart.

Of the recordings on hand only two were made at 25° C. One recording contains only one phrase with five pulses delivered at a rate of 5.7 pulses per sec. The second recording contains four phrases with pulse rates of 4.5, 4.7, 4.8, and 4.8 pulses per sec. Intervals between phrases varied from 3.5 to 5.5 sec. In his temperature experiment T.J. Walker obtained a pulse rate of 5.8 pulses per sec. at 25° C (calculated from the regression formula).

Several authors (e.g. Cantrall, 1943; Fulton, 1932; Rehn and Hebard, 1914a) have described the song of Scudderia curvicauda curvicauda which is a northern subspecies of S. curvicauda. Their descriptions generally agree with those given above; Alexander (1956) gives a slightly slower pulse rate, and

says that 4-, 5-, and 6-pulsed phrases are rarely heard. Fulton (1951) described a song similar to that described above. He thinks his description is of laticauda's song. Some of the writers describe a single-pulsed "tsick" or "brwzi" produced in the daytime. This could be a single pulse of the song described here.

The two males involved in the temperature experiment exhibited some interesting acoustical interactions. When one male sang songs like that described above, it often stimulated the other male to do the same thing, but not synchronously. At other times one male — either one — would give loud, slowly delivered ticks after each phrase produced by the other. Perhaps intensity of the sound received has something to do with what response is elicited.

I would suspect that females answer each phrase of the song.

Stilnochlora coulöniana (Saussure)

This large katydid is not known north of Alachua County, Florida. It is generally a tree-top dweller in hardwood forests.

No males of coulöniana have ever sung in our laboratory, and we have never seen a wild male singing. However, T. J. Walker and I have heard, in San Felasco Hammock, near Gainesville, and in hammocks of southern Florida, a long, loud, course lisp (Fig. 16), which we suppose is made by males of coulöniana.

Only one field recording suitable for analysis was made and that at 19.5° C. The five lisps of the recording were 197, 211, 248, 219, and 224 msec. duration (average = 220 msec). Two other recordings with more than one lisp were made

at 20° C and, although not suitable for analysis, I could measure the time intervals between lisps. Successive lisps were produced 6.5 - 20.0 sec. apart, but usually 13 - 15 sec. apart. I believe each lisp of this species functions as a complete song.

Turpilia rostrata (Rehn and Hebard)

This species has been found only in the subtropical hammocks and mangrove swamps of southern Florida — chiefly in the latter. Where found, it has usually been numerous.

Three songs are known from rostrata males: a ticking song, a lisping song, and a lisp-tick song. Ticking songs are produced during the evening twilight. As darkness sets in, ticking gives way to the lisping song, and still later the lisp-tick song becomes prominent. Late at night one may hear the lisping songs and the lisp-tick songs with about equal rates of occurrence. Certain individuals may produce the ticking song late at night. At times one may hear the lisp-tick song and lisping song produced in a regular sequence.

The ticking song (Fig. 18) is a series of phrases irregularly spaced 0.3 - 4.0 sec. apart and composed of 1 - 5 ticks — usually 2 - 3 ticks — per phrase. The tick rate is surprisingly uniform within the tick phrases (see Table 15). The number of ticks per phrase, however, 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. The length of a ticking song is indefinite; ticking proceeds more or less continuously until a lisping song is produced later in the twilight.

Table 15. Results of analysis of songs of Turnilla rostrata.

Kind of song	Indiv.	° C	No. phrases analyzed	Ticks sec.		Lisps/sec.		Lisp duration (msec)	
				\bar{X}	S_x	\bar{X}	S_x	\bar{X}	S_x
Ticking	071-2	26.0	10	26.0	2.1				
Lisping	071-2	26.0	1			2.5		30	2
Lisping	071-3	25.0	4			3.4	.5	31	2
Lisp-tick	071-8	24.5	5	26.1	.7	2.4	.3	35	2
2 males in cage	071-11 & -12	25.0	5	26.2	2.5				

The lisping song (Fig. 19) consists of a single phrase of 5 - 11 lisps produced at a regular rate until the last 2 - 3 lisps, at which time the lisp rate slows down. The lisp rates indicated in Table 15 are calculated from the first 5 - 7 regularly delivered lisps of each song. Intervals between songs may vary from one to several minutes.

Only one recording (laboratory) near 25° C was obtained on the lisp-tick song (Fig. 17). In this recording the singer (individual 071-8 in Table 15) added a series of lisps to each of the five lisp-tick phrases, so that the intervals — 35 - 65 seconds — between successive lisp-tick phrases were not typical. Another recording, made at 23.5° C in the field between 10 and 11 o'clock at night, had two songs of 5 and 7 lisp-tick phrases respectively. Intervals between successive phrases in those songs varied from 4.0 to 8.3 sec. and averaged 5.7 sec.

No responsive females were ever collected — at least no captured female ever gave any apparent response to any test — so I do not know to what song, or sound, the females would answer or be attracted. By the very nature of the ticking song, and on the basis that ticking in certain other species results in male

spacing, I suspect that the ticking in rostrata functions in male spacing. This idea is supported by the fact that the two males caged together in a four-inch, cubical cage produced many ticking sounds which were erratic and intense. At times the tempo from the two males would lessen and the ticks produced in those quieter periods were at a tick rate similar to the tick rates of individual 071-2 (field recording) who was assumed to be out of physical contact with another male while ticking. Contrary to this, however, is the fact that males in arena tests never made any movements during any tests. If ticking actually does function in male spacing then one would assume the lisping songs to function in male-female relationships. Indeed, I think that once the problems with rostrata are worked out, we will see that females answer individual lisps close after the lisps. As to whether females move toward singing males, I will not guess. It could be that the almost regular rate of delivery of the lisps could function in this capacity when received at low intensities.

DISCUSSION AND CONCLUSIONS

There is no instance of any species of singing Orthoptera having "learned" its sound repertoire by listening to other members of the species. Individuals which hatch and mature in the spring of each year never hear the sounds made by their parents. Yet, they produce sounds identical to those of the parents. Individuals reared in isolation do likewise. Alexander's (1962b) statement, "there is no 'culture' in cricket signalling" is applicable to katydids also.

Kinds of response to sound stimuli

When an individual hears a sound it may exhibit any one of several behavior patterns. It may do nothing different from what it was doing before it heard the sound. This is typical of the response given to most heterospecific sounds. Conspecific sounds functioning in intraspecific communication usually evoke kinesis or taxes. Kinetic reactions are evidenced by a katydid's starting to move when it hears a sound, its continued random movement — frequent turning — as long as the sound is repeated, and its stopping soon after the sound ceases. Such kinesis were typical of males of certain species in tests of ticking sounds. In natural populations such movement could result in the spacing of individuals as a result of kinetically moving in response to the ticking sounds. There may also be interspecific interaction in these respects, since many species with ticking sounds in their repertoire often occur together.

Tactic reactions, orientations toward sources of stimuli, are exhibited

when individuals are attracted to a sound. Such reactions may be more strictly termed telotaxes, for the orientations are directed toward single sources of sound when many sounds are present.

Intensity of response to sound stimuli

Different intensities of response from different individuals to the same sound and within a single individual to the same sound at different times have been noticed. At one time an individual may casually walk toward a sound if it is an attracting sound or produce one tick if it is a tick eliciting sound. At other times an individual responding to an attracting sound may alternately lean over on one side and then the other, holding up the front leg on the high side as if to more fully expose the auditory tympanum on that leg to the sound. Between successive alternations of "leaning and listening" the katydid may run a few steps toward 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 molting 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 sounds by females. In almost every species studied 5 - 7 days passed after the final molt before the insect became acoustically active. These insects would be excellent ones in which to study various hormone concentrations after their final molts.

During the first few days of the seasons in which the different species attain adulthood, certain individuals are often found far from their normal

habitats. Sometimes an individual may be heard singing in out-of-the-ordinary habitats all during the season. Such observations indicate that individuals of the species involved may disperse during the adult period prior to sexual maturity. If they do indeed fly around, it is obviously one way of intermixing the genetic material of different populations.

Stimulus situation for sound production

Almost nothing is known about what external stimuli are important in inducing an individual to produce sound. Only in a few cases are they known; for instance, certain male sounds are absolutely necessary to evoke ticking responses from females or other males. The chief problem lies in determining the nature of the stimulus situation for spontaneously producing different sounds in those species which produce more than one kind of sound in solitary situations. In many cases — e.g. in most species of Amblycorypha — low light intensity is required for sound production. In other cases — e.g. in Scudderia texensis and Turpilia rostrata — intermediate light intensities stimulate certain kinds of sound production. In still other cases — e.g. S. texensis — certain sounds may be produced principally by day, other sounds principally by 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, whether the different kinds of sound are isolated accomplishments one from another or are produced in a regular sequence? Undoubtedly, there must be a change within the singer, because, so far as it is known, external cues do not change at rates which could be correlated to the rates of change of the kinds of sound produced. I doubt that this question will

soon be answered.

Necessity of acoustical interactions in pair formation

If a species of Orthoptera had no intrinsic mechanism to aid in the formation of sexually responsive pairs, the chances of males and females of sparsely populated species coming together in nature at times when both are sexually mature and asexually responsive would be slight. In other words, casual pairing of males and females would not seem to produce a very effective breeding population unless the population density were high and the individuals of the species concerned were active. Populations with low densities, as is the case with many species of Phaneropterinae, can be very effective breeding populations if provided with a mechanism to aid in pair formation (ideas originally those of R. D. Alexander — personal communication). 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 acoustical systems of singing insects function in this capacity, and apparently very efficiently.

The thought has occurred to me that acoustical interactions may be necessary for copulation to occur in some, perhaps many, species. I know of only one bit of evidence to support such an idea — if there are published records along these lines, I have not found them. On two occasions I placed an acoustically active male and a responsive female of Scudderia taxensis in antennal contact on a table top in order to observe copulation close at hand. The only source of light was a nearby 7 1/2-watt red light. On both occasions the male and female circled each other slowly, each feeling the other with its antennae.

After 1 - 2 minutes of such behavior the two separated. A few minutes after the separation the male produced his slow-pulsed song, and the female answered with a tick. In both instances the male turned immediately toward the female, lowered the intensity of his sounds, and produced another slow-pulsed song. The female answered and he moved toward her rapidly. The sequence of low intensity, slow-pulsed song and female tick was repeated two more times and finally the male went straight to the female, moving the last 7 - 8 inches without singing. On both occasions a brief play of antennae was followed by the male's turning around, raising his wings somewhat, and the female mounting him from the rear. Copulation resulted in the first observation, but in the second observation I accidentally disturbed the pair and the male flew to the other side of the darkened room. But almost immediately he began to sing again and flew toward the female when she answered. After the male flew three times and did not alight on the table with the female, I picked him up and placed him in antennal contact with the female. This time they antennated each other briefly, the male turned around, raised his wings, and the female mounted. Thus, even though I had just handled the male they mated. These observations certainly suggest that, in S. texensis at least, mating may be the end behavior of a sequence of patterns involving acoustical interactions.

Specificity of acoustical communication systems

The descriptions of the songs of the different species presented here clearly show the specificity of the songs of each species, particularly the songs involved in male-female interactions. This is exactly what one would expect, since orientation and movement toward sound is the primary mechanism of bringing males

and females together. Not only are the male songs specific for each species, but the timing of the female response is characteristically specific among those species where similarities between heterospecific male songs are close enough to cause confusion among females of the different species concerned. Thus, the preventing of matings between males and females of different species is equally as significant a function of the acoustical communication systems as their role in pair formation. Alexander (1962a), while discussing cricket taxonomy, 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."

In the case of those species in which the males produce lisps, only one pair of species produce lisps which are nearly identical. A second pair produce lisps which are similar in duration but different in other respects. A third pair, involving one species of the second pair, produce lisps which are similar enough to cause possible confusion at times among responsive females. The three species-pairs will be discussed in order.

Males of Inscudderia strigata and of Scudderia furcata produce lisps of 77 msec. and 75 msec. (average values — see data presented earlier for each species). The frequency spectrum for each species is practically the same and the females answer the lisps in normal acoustical interactions. For the most part, adults of I. strigata, having only one generation per year, occur in the latter part of July and in August. S. furcata, on the other hand, has two generations per year, the break between generations occurring during the peak population of I. strigata. Nevertheless, at times, adults of both species are

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 results should come from such inability of females to discriminate. Males of I. strigata have been shown to go to females answering other conspecific males; perhaps males of furcata do also. The timings of the female tick response in the two species are very specific and non-overlapping. A tick with the wrong timing should elicit no orientation toward the tick by a male hearing it. Under these circumstances I see no reason why there should be any confusion between these two species in nature.

The second species-pair with similar lisps are Montezumina modesta and Microcentrum rhombifolium. The long lisp of M. modesta averages 31 msec. duration and the lisp of M. rhombifolium is 25 msec. The ranges of variations overlap at 28 - 29 msec., so there may be some confusion. However, the sounds function entirely differently in the two species. Females of M. modesta are attracted to high intensity conspecific lisps, but females of M. rhombifolium are attracted to low intensity conspecific lisps. Differences in the spacing of males and females may result in females moving toward the wrong sound at times, possibly sometimes even resulting in contact between heterospecific males and females.

Two striking differences between the lisps of the two species may serve to prevent wasteful expenditures of the time and energy. M. modesta lisps generally have much higher frequencies (dominant frequencies 12 - 18 kc) than M. rhombifolium lisps (8 - 12 kc). These differences may be enough to allow

discriminatory responses on the part of the females. Evidence for this is the fact that M. modesta females would not respond to recorded male lisps until after I had filtered all sounds below 15,000 cps. Actually this just increased the relative intensities of higher frequencies over lower frequencies. More work in this respect should clear up these questions. The second big difference between the lisps of these two species is in lisp rate. M. modesta long lisps are delivered at a rate of about one per second, whereas M. rhombifolium lisps are produced 2 - 3 sec. apart. It may be that at least minimum refractory periods are necessary to elicit proper responses from the females. -- i.e. M. rhombifolium females may not be able to respond to lisps produced faster than two per second.

The third species-pair with similar lisps is Scudderia cuneata and, again, Montezumina modesta. The lisps of S. cuneata average 16 msec. duration, and M. modesta short lisps average 19 msec. duration. The ranges, however, are broadly overlapping, but the differences in female timing are characteristic and the ranges of variation of the female timing do not overlap. The dominant frequencies present in the two species broadly overlap. Also, the rate of lisp production is slower in S. cuneata than in M. modesta. These differences may contribute to the females' ability to discriminate between the lisps of the two species.

The importance of refractory periods has been raised. In the laboratory where males of different species were lisping at the same time, I observed that a male could seemingly lisp too rapidly to get any response from listening conspecific individuals. I have already mentioned that I could rub my thumb across the edge of a piece of paper and evoke tick responses from females of several

different species, depending on the duration of the "lisp" I produced. At times, I could evoke several successive ticks from certain females. If I speeded-up the rate at which I "lisped," these females would stop answering. They would often resume answering when I produced "lisps" at the minimal lisp rate characteristic for the species involved. An important deflection in this evidence is not knowing what the actual duration of the "lisps" I produced may have been. By tape recording the interactions, this should be an easy question to answer.

Importance of toothstrike rate

In species which lisp, there is a possibility that differences in toothstrike rates within the lisps may serve as discriminatory cues for individuals responsive to conspecific lisps. I analyzed several lisps from each species and found that even though the number of teeth struck per lisp in each species was clearly different, there were only small differences in toothstrike rate except between the lisps of Inscudderia strigata and Scudderia furcata, which have lisps with identical durations and frequency spectrums. The I. strigata lisps analyzed had a toothstrike rate of 630 per sec. compared to 806 toothstrikes per sec. for S. furcata. Even with such distinct differences I doubt that toothstrike rates will be found to be important in allowing discrimination between lisps, because the insect auditory system is not believed to be able to encode such differences. Furthermore, if toothstrike rate were important, I should have obtained no response from artificial lisps produced by rubbing my thumb across the corner of a piece of paper. Here there was no toothstrike rate. Finally, toothstrike rates often vary within single lisps and from one lisp to the next.

Increase in intensity during songs

Some species increase in intensity of sound production toward the end of certain parts of songs, of certain songs, or of song sequences. Known for this are Scudderia texensis - slow-pulsed song: gradual increase; S. furcata - increase in successive hisps; and Amblycorypha uhleri and A. near uhleri - increase during Part I. One obvious advantage, at least in those species which repeat the basic functional unit of sound successively, of increasing the intensity between successive units is to allow individuals successively farther from the sound producer to hear the sound. But why increase intensities within functional units? I have some scanty evidence that such increases toward the end may be functional and therefore potentially useful in species isolation. A recording of one phrase of a S. texensis slow-pulsed song that I have does not exhibit 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 toward the end. Similarly, S. texensis females would answer a "phrase" I produced by scrubbing my finger back and forth across a piece of paper, only so long as my phrases gradually increased in intensity. S. furcata females were less finicky but seemed to answer artificial hisps" (produced by my thumb) which terminally increased in intensity.

Complicatedness of sound production

Complicatedness of sound production is measured in terms of the tegminal movements involved in producing the different kinds of sound of solitary situations. The simplest kind of katydid sound is a hisp and is made in a single opening and closing of the tegmina. Stilpnochlora coulouiana is the only species for

which a single-pulsed lisp (probably made on the closing stroke of the tegmina) is the only known solitary sound. Inscudderia walkeri makes a two-pulsed lisp by producing sound on both the opening and closing strokes of a single opening and closing of the tegmina.

Another kind of simple singing involves repetition of one kind of tegminal movement in producing single phrases. Amblycorypha carinata produces two-pulsed (or three-pulsed) phrases, the pulses of which are identical. The separate phrases of a Microcentrum retinerve song contain differing numbers of pulses, but the tegminal movements involved in producing each pulse of each phrase are identical. The ticks in the song of Phrixia maya are identical, and within tick-pairs the pulse rate is always the same. "Rattler" Amblycorypha rotundifolia belongs in this group.

Complicated sound production is of four classes. The first class involves an increase in intensity of each successive pulse in a phrase, the pulses being otherwise identical. Increases of intensity in successive pulses requires that the singer engage the stridulatory apparatus harder in each successive sound producing stroke. Scudderia curvicauda laticauda makes only this kind of sound.

The second class of complicatedness of sound production involves the producing of drastically different kinds of sound from time to time in no fixed sequence. Four of the species studied are grouped here. They are Microcentrum rhombifolium — the ticking song and the lisping song; Scudderia cuneata — lisping song and song with pulsed phrases; S. furcata — lisping song and song with pulsed phrases; and S. texensis — fast-pulsed song, slow-pulsed song, and ticking sounds. The different sounds of each of these species have no constant

relation one to another and each functions independently. Tegminal movements are identical in producing each pulse of a given kind of sound (except sometimes in intensity) but are different from one kind of sound to the next.

The third class of complication involves the producing of certain sounds independently as in the second class, and producing other sounds (or the same sounds that were produced independently) in a stereotyped pattern. Producers of this class are Arethaea phalangium -- lispng song and tick-lisp song (lisps of the latter are different from lisps of the former); Inscudderia strigata -- clicking sound and lisp-tick song; and Turpilia rostrata -- lispng song, ticking song, and lisp-tick song (the lisp and ticks of a lisp-tick phrase are identical to isolated lisps and ticks but are produced in a regular sequence), and lisp-tick-lisp song. This class of complicatedness bears special significance to reconstruction of the evolution of complicated singing (discussed later).

The fourth and last class of complicatedness involves producing two or more kinds of solitary sound in a stereotyped sequence. Eight species discussed in this paper are found in this class. They are Amblycorypha floridana -- regularly repeated sequence of clicks and buzzes; A. oblongifolia -- regular sequence of one long pulse plus two short pulses; A. near rotundifolia: "slow-clicker" -- series of phrases containing a regular sequence of several short pulses and one long pulse; A. near rotundifolia: "slow clicker" -- series of phrases containing a regular sequence of two or three short pulses and one long pulse; A. uhleri -- regular sequence of phrases, each with characteristic pulse rates, pulse durations, and pulse intensities; 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 complicatedness are discovered.

Movements involved in pair formation

Pair formation among the seven species of Phaneropterinae that I have studied in detail does not always involve the same kinds of movement on the part of males and females. In fact, the relative kinds and amounts of movement of males and females of different species can be 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 all the distance to the female. Inscudderia strigata seems to belong in this group. Evidence to date places both Scudderia furcata and S. cuneata here. The male goes to the female answering male lisps. In the second category the male produces one sound which attracts the female toward the male but not all the way to the male. Then the male produces a second sound which evokes ticks from the female. The female ticks attract the male, which moves the final distance separating the male from the female. Scudderia texensis and Microcentrum rhombifolium belong in this category. The third category includes those species in which the male produces the female tick elicitor, the female ticks, the male moves part-way to the female, then the male produces a second sound which stimulates the female to move the final distance toward the male. Montezumina modesta and Amblycorypha floridana belong in this group.

There is some evidence to allow us to predict which category Amblycorypha uhleri and A. near uhleri belong to. A. uhleri females probably go toward A.

uhleri males from close range, whereas A. near uhleri females evidently do not move at all, letting the conspecific males move the entire distance.

Amblycorypha oblongifolia may fit into either of the first two categories. Before this species can be placed definitely, more must be known about the movements of both the males and females.

It is very interesting that no phaneropterine species is known to have females which are silent and which move all the way to the males. I predict that at least one phaneropterine will be found to exhibit such behavior. Another category which one would expect is one in which the males produce a female tick eliciting sound, the females answer, and both the males and females move toward each other until contact is made. The obvious disadvantage to this kind of system is the difficulty of homing in on a moving source of sound. Since the Phaneropterinae inhabit coarse vegetation and fly toward attracting conspecific sounds, it is not likely that many, if any, cases of this category 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 straight line.

Evolution of complicated sound production

Up to this point the central theme has been the description of different kinds of sound within and between species and of how the sounds operate. Admittedly, very little has been found out, but I think enough is known to permit some tentative conclusions as to how complicated singing behavior in the Phaneropterinae evolved.

When the ancestors of the Phaneropterinae diverged from the stock which

gave rise to other groups of Tettigonidae, it was already a strong singer, probably producing a "calling" song which operated at a distance. Alexander (1962b) surmises that the calling function (attraction of females to singing males) is so widespread and so similar among Gryllidae and Tettigoniidae that it must have appeared before those two families became separate evolutionary lines. Although we are not concerned here with the origin of sound production, we must consider how the female attracting function arose, for it could have been that sounds with other functions arose in a similar manner.

Alexander (1962b) explains why the first acoustical signal of the ancestral tettigoniid was almost certainly a mediator of courtship, operating at close-range, and he suggests that the calling function arose as an outgrowth of the original courtship function (based on evidence he has collected in work with many species of crickets). This would have involved "increasing rhythmicity, intensity, and duration of the original courtship song because these characteristics enhanced the courtship function itself, through increasing consistency, range, and redundancy. Eventually, through just this kind of change, this song must have become operative at such distances that it was sometimes advantageous for the male to be triggered into stridulation without contact with the female, and sometimes advantageous for the female to be attracted by hearing the sound when she was not otherwise in contact with the male. In this way the calling function, in the approximate form that it assumes today, could have evolved." This line of reasoning seems valid. The next step would be for either the males "to develop structurally different signals, with slightly different effects, for the two situations" (close-range or at a distance or any other two different situations);

"or (perhaps originally) for the female to respond differently to the original signal that served both calling and courtship, depending on whether or not she was in contact with the male through senses other than auditory. In all likelihood these changes did take place in many cases, with the resulting development of two separate signals." Thus, in today's Gryllidae there are two characteristic signals between males and females, functional at long- and close-range respectively, or if only one signal is present it functions in the female attracting capacity, the courting function being effected by females feeding upon dorsal glands of the male.

At this point it is well to interject that in most crickets only one sound, the female-attractor, is functional at long range. Courtship activities involve males and females in contact through senses other than auditory -- e.g. tactile, olfactory, visual. In the Phaneropterinae there is no known instance of any sound production characteristic of males and females in intimate contact through whatever senses may be involved. Thus, all sounds of these katydids operate from a distance with the exception of sounds produced when males come into physical contact with one another. This is in another context, however. We are at present considering male-female interactions.

I have stated that the phaneropterine ancestors, after having become a separate evolutionary line, probably had a functional long-range female attracting song. But I doubt that these early katydids made sounds which served a courtship function as exists in many modern Gryllidae. If they did, there should be at least a few species today which retained the behavior. I really do not see why there are not some, even if the trait has secondarily evolved. More likely,

this subfamily diverged from other tettigoniid groups in which feeding upon dorsal glands of the male by the female was the principal courtship activity. In fact, the original Tettigoniidae may have diverged from a tettigoniid ancestor in which dorsal feeding was characteristic. In the few cases where mating has been observed among Phaneropterinae, "licking" of the male dorsum by the females has always been observed.

Whatever the ancestry, the point is that the original Phaneropterinae probably did not make a courtship sound. Somewhere very early in phaneropterine divergence courtship activities may have begun to include wing-jerking, or some such activity, on the part of both males and females or simply on the part of the female to the calling song when in intimate contact with the male. It is certainly reasonable to suppose that females have the ability, or could evolve the ability, to move their tegmina in the same manner as the males do in stridulation. Indeed, Huber (1962) has shown that much of the nervous and muscular system necessary for stridulation is contained in the female (from Alexander, 1962b). Wing-jerking, or other comparable signals, could have functioned initially as a visual stimulus, but almost assuredly sound would have been involved — the males with their stridulatory structures and the females simply by incidentally rubbing their wings together. The courtship could have involved alternations of signals by the males and females, the females "answering" only in response to the male signal, acoustical or otherwise. This kind of courtship activity could involve more and more sound in the signals and allow the two sexes to orient and move toward one another from close range without having seen one another. Once any kind of orientation by males toward sounds produced by females took place — even

at very close range -- the door was open for greater and greater separation.

The necessary prerequisite for the separation (as in Alexander's discussion of the evolution of the calling song) would have been for it to have been an advantage for the males to be triggered into producing the female wing-jerk eliciting sound, resulting in the female tick as it is herein termed, and for it to have been an advantage for the females to answer the sound before having had any other-than-acoustical contact with the males. Such selective advantage is obvious -- a sexually responsive male, if separated from an unknown, sexually responsive female by a relatively short distance could by-pass producing the usual female attractor, which may continue for long periods by solitary males, and immediately learn of the female's presence and proceed to court her. Retention of the female attractor is obviously advantageous. From here on all sorts of separate pathways could be taken, resulting in males moving toward females and females moving toward males in several different contexts, giving us the categories outlined under the preceding subheading.

How did the ticking sounds -- sounds that function in male-male interactions -- evolve? Alexander (1962b) postulates that aggressive sounds in crickets -- those involved in male-male interactions -- appeared as outgrowths of the calling function. His evidence is that the calling song and aggressive signals of species which have both in their acoustical repertoire are very similar, and that the calling song functions like the aggressive signals, although to a lesser extent, in interactions between males. Among the Phaneropterinae the sounds involved in male-female interactions bear little resemblance to the sounds produced in interactions between males except the ticking sounds of

Microcentrum rhombifolium, but here the resemblance is superficial; rhombifolium's ticks are regularly produced in series of 15 - 34 single toothstrikes involving a single, slow closing of the tegmina. Ticks involved in male-male interactions usually vary in the intensity from one pulse to the next, are very erratic, and are delivered at rates dependent upon the intensity of the stimulus causing their production. A single tick usually involves a complete wingstroke.

The first ticking probably arose in situations where males came into physical contact with one another. Evidence for this is that more species produce ticks in this situation than in any other. Generally males contact one another physically when they are mutually attracted toward a female. Usually such males push each other around with their front legs. In such a situation any slight movements of the tegmina may have been the result of the excited state of one of the males involved. Such behavior would have been advantageous if the tegminal movements tended to repel the other male to any degree whatever. Males not in physical contact could continue producing female attracting sounds or female tick elicitors. The genes which contributed to the tegmina-flipping and the reaction to it, whatever movement may have been involved, would have tended to have been conserved more often than not. To have subsequently involved sound -- in this case ticks -- in such tegminal movements goes almost without saying. Once ticks were made during physical encounters as males moved toward females, it would have been a decided advantage for certain males if they sometimes produced ticks after female-oriented songs of other males. Both the male which ticked and the male repelled by the ticks would have benefitted by not having come into contact and consequently having wasted time by the

encounter — time which could have been spent in producing female-oriented sounds.

To have evolved the trait of producing ticks in solitary situations might not have been as difficult as it may appear. The advantage to individual males that sometimes may have moved away from such sounds is that these males would have been spaced farther apart; each male should have had more females per area of domain than he would have had if he had not obtained the increased distance between himself and the other males. In regard to area of domain, most species which produce ticking in solitary situations are somewhat territorial while acoustically active. They occupy single perches for an entire night, but not the same perch night after night.

I have shown a possible pathway for the evolution of a female attracting song, a female tick elicitor, a female tick, and a male-spacing sound. The modifications of such sounds and their functions through speciation and development of methods of reducing confusion between species have been diverse, as evidenced by the species-specific nature of the acoustical repertoires among the species studied. To speculate on the evolution of these individual acoustical repertoires and their associated functions is unnecessary. However, one phenomenon that has not been explored, but deserves comment, is the phenomenon of regular repetitions of a stereotyped sequence of different kinds of sound. Probably no satisfactory answer can be made at this time. But a look at the different kinds of combined songs that exist today may give us a clue to how the most complex songs evolved. Certain species which produce different sounds as isolated

accomplishments — e.g. Scudderia texensis and Microcentrum rhombifolium — occasionally produce two different sounds in rapid succession, the sequence always being the same. This behavior may impart some subtle advantage to the individuals that do so, such as reducing the number of separate utterings of sound they would normally make (and consequently reduce the number of times the singer would advertise his presence to predators — Walker, 1964) and still impart the same number of demands on other individuals, or else by increasing the number of demands while not increasing the number of separate utterings of sound. Given time, the two sounds could come to be emitted more and more as a unit with a stereotyped sequence. Turpilia rostrata may represent just such a stage of evolution. It has two distinctly different sounds — lisps and ticks — which are emitted singly as characteristic songs. At other times, the two are combined in a stereotyped, lisp-tick sequence and the sequence is repeated several times in a series. Given time, perhaps the lisp-tick song will come to dominate the repertoire, leading the way eventually toward a completely stereotyped repertoire such as exists in several species of Amblycorypha.

A fitting conclusion to this discussion would be to include Alexander's (1960b) concluding remarks concerning a possible mechanism of evolutionary change in communicative systems. His summary is as follows. "In the evolution of any communicative system, whenever change of any sort occurs, there must be a change in two respects: the signal and the receiver. In the case of cricket stridulations, this means that the song of the male and the ability of the female to respond to it (correctly) must evolve together as a unit. Actually, it means

that the male's ability to respond must also change for males do respond to their own and to other males' songs. But the kinds of differences that occur among the songs of closely related species usually do not in any way involve the structure of the stridulatory apparatus (at least externally). Likewise, the differences in the ability of females to respond (properly) probably do not in any way involve the auditory apparatus itself. In both cases the difference seems to reside in the central nervous system. Indeed, . . . song differences among closely related species always (and usually only) involve those unalterable components of the patterns that must derive from the central nervous system. Is it possible that in some or many cases the genetic difference which causes the song difference — perhaps even the particular difference in the structure of the central nervous system itself — is exactly the same as the difference which causes the response difference? In this connection Huber's evidence (1962) that the components necessary for production of the song pattern reside (incompletely or completely) in the female's nervous system is particularly interesting. If there is a linkage — or an identity — here it would represent an interesting simplification of the process of evolutionary change in a communicative system — something of an assurance that the male and the female or the signaller and responder — really will evolve together, and possibly an increased likelihood through this that the entire system will persist. The question has significance in connection with speciation as well as the evolution of communication, and possibly the relationship between temperature effects on signal response as well (Walker, 1957); if this situation exists in crickets, it may exist in many kinds of communicative systems in many kinds of animals."

SUMMARY

Heretofore, the only significant work done to determine the significance of complicated sound production by any species of *Phaneropterinae* was that by Spooner (1964). This report concerns 1) an extensive analysis of the singing behaviors and the descriptions of sounds of several species of *Phaneropterinae*: 2) the results of numerous controlled experiments with seven species to determine the behavioral significance of their sounds; and 3) to show how complicated singing among the *Phaneropterinae* could have evolved. The kinds of male-female acoustical systems that exist among these species are grouped into three categories: 1) the males make a particular sound, the females answer with a tick, and the males go all the way to the females; 2) the males make one kind of sound which attracts females from a distance (but not at close-range), the males make a second sound which the females answer with a tick, and the males go to the females from close-range; and 3) the males make one kind of sound, the females answer with a tick, the males move toward the females from a distance (but not all the way), and the males produce a second kind of sound which attracts the females all the remaining distance to the males. Species which produce stereotyped sequences of different kinds of sound likewise fit into this scheme -- the difference is that the different responses may be to different sounds in the sequence.

Complicated singing behaviors probably arose from other-than-acoustical

contacts between individuals. Such contacts would have been at close-range -- i.e. physical, visual, etc. With the ability to produce sound already present, the early *Phaneropterinae* had only to develop a characteristic sound to mediate each kind of close-range encounter with other individuals. It would have been advantageous to have reduced the number of direct contacts between individuals. This was accomplished through acoustical interactions.

APPENDIX

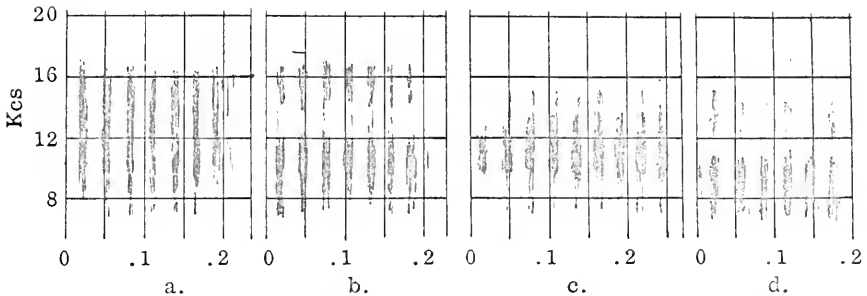


Fig. 1. Buzzes of three Amblycorypha floridana males showing variations in frequency spectrums (24.2° C). a.-b. same individual; c.-d. two other individuals.

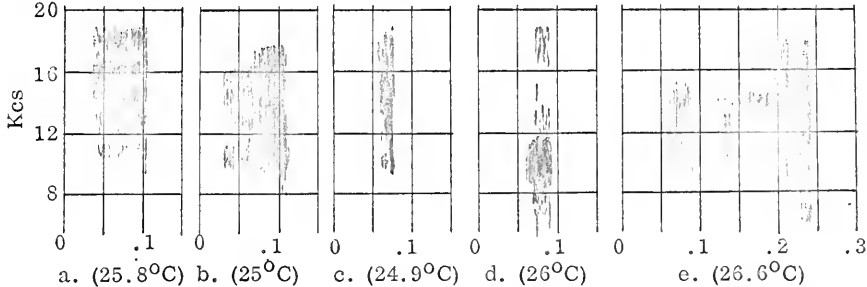


Fig. 2. Single lisps of five species of Phaneropterinae. a. Inscudderia strigata; b. Scudderia furcata; c. S. cuneata; d. Microcentrum rhombifolium; e. I. walkeri.

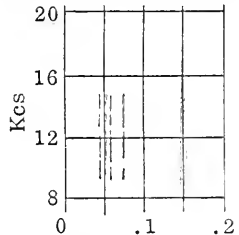


Fig. 3. Single click of Inscudderia strigata (25.5° C).

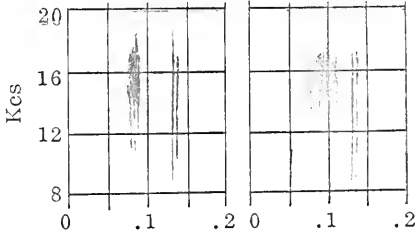


Fig. 4. Short lisp and long lisp of Montezumina modesta with answering female ticks. (25° C).

Time in seconds

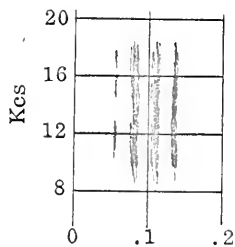


Fig. 5. Pulsed phrase of Scudderia cuneata (25.8°C).

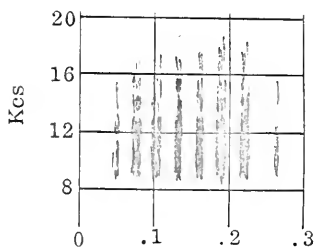


Fig. 6. Pulsed phrase of Scudderia furcata (25°C).

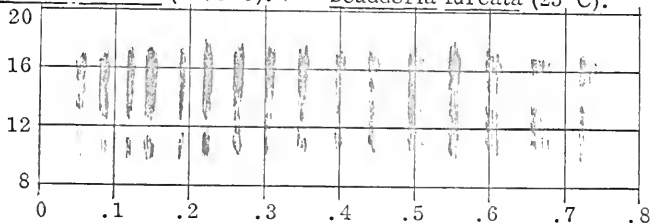


Fig. 7. Many-pulsed phrase of Scudderia furcata (24.2°C).

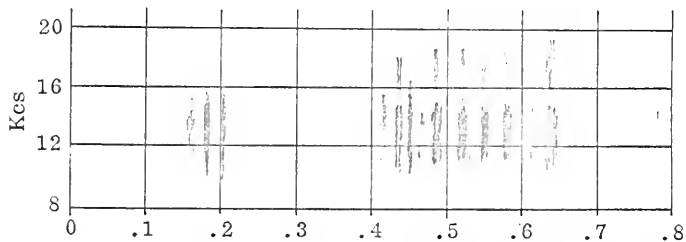


Fig. 8. Two clicks and a buzz of Amblycorypha floridana (24.2°C).

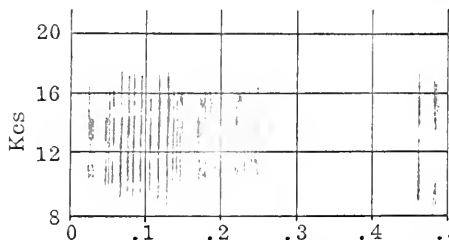


Fig. 9. Single phrase of Amblycorypha oblongifolia with answering female tick (25°C).

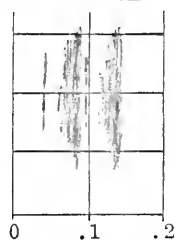


Fig. 10. Single phrase of Amblycorypha carinata (25.2°C).

Time in seconds

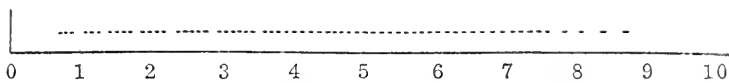


Fig. 11. Diagram of typical complete song pattern of "fast clicker" Amblycorypha rotundifolia.

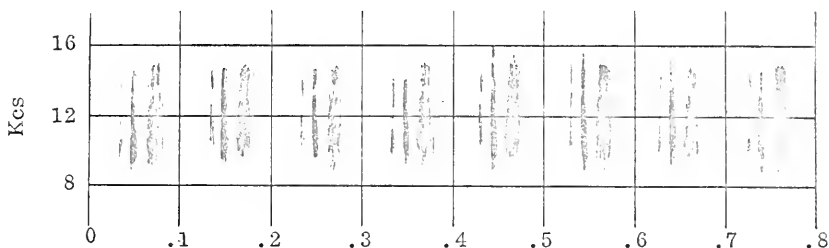


Fig. 12. Eight basic pulse groups of "fast clicker" Amblycorypha rotundifolia (25.8°C).

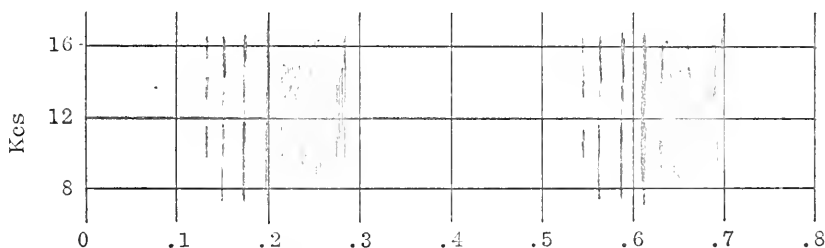


Fig. 13. Two basic pulse groups of "slow clicker" Amblycorypha rotundifolia (25°C).

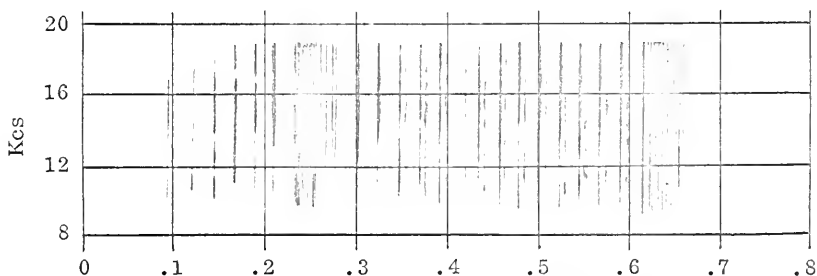


Fig. 14. Tick-lisp song of Arethaea phalangium (25.5°C).

Time in seconds

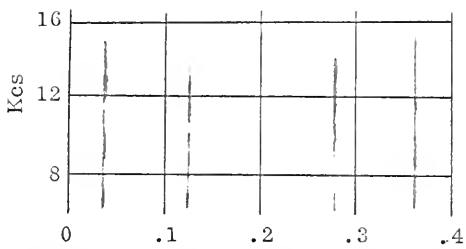


Fig. 15. Pair of paired ticks of Phrixia maya (25°C).

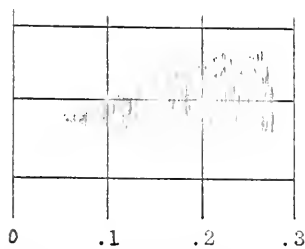


Fig. 16. Single lisp of Stilpnochlora couloniata (19.5°C).

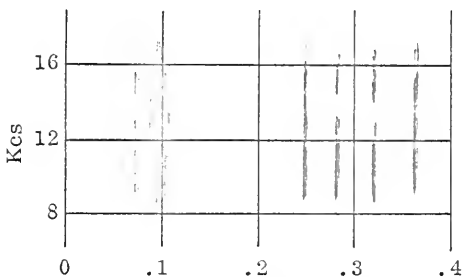


Fig. 17. Lisp-tick phrase of Turpilia rostrata (24.5°C).

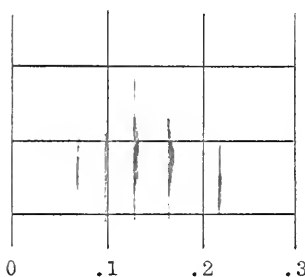


Fig. 18. One phrase of ticking song of Turpilia rostrata (26°C).

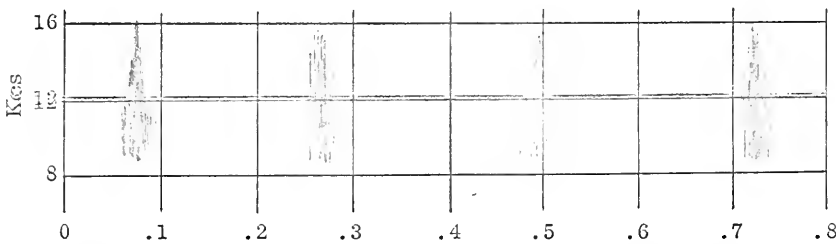


Fig. 19. Part of a lisp song of Turpilia rostrata (26.5°C)

Time in seconds

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BIOGRAPHY

John Dewey Spooner was born in Hillsborough County, Florida, on December 13, 1935. He attended public schools in Florida and Georgia and in 1953 was graduated from Douglas High School in Douglas, Georgia. He attended South Georgia College, Georgia Institute of Technology, and was graduated from Georgia State College in 1960 with a degree of Bachelor of Science, having majored in biology.

He enrolled at the University of Florida in September, 1960, and received the degree of Master of Science from the University of Florida in December, 1962.

He is a member of the Ecological Society of America, the American Association for the Advancement of Science, The Florida Entomological Society, and the Newell Entomological Society. He was president in 1963-64, and secretary in 1961-62 of the Newell Entomological Society.

The author was married to Miss Joyce Jackson on August 2, 1958 and has four children.

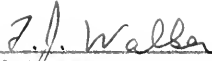
This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Agriculture and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.



Dean, College of Agriculture

Dean, Graduate School

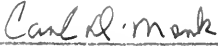
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