

THE TEXAS BUSH KATYDID—ITS SOUNDS AND THEIR SIGNIFICANCE

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Introduction

The males of many species in the subfamily Phaneropterinae (Orthoptera, Tettigoniidae) produce two or more kinds of sounds in solitary situations, that is when the singer is out of contact—with the exception in some cases of acoustical contact—with other members of the species. Furthermore, the females of several species in this group are known to produce sound. Descriptions of some of these sounds have been made, but no one previously has done any experimental work to determine the biological significance of such singing behaviour. Males of the phaneropterine *Scudderia texensis* Saussure and Pictet (1897) produce four sounds, three in solitary situations, and the females of this species make a lisping sound in response to one of the male signals. This investigation was made to determine the physical characteristics of the sounds and to establish their function.

Ecological Situation

Scudderia texensis frequents almost any open area where weeds and grasses abound such as in abandoned fields and along highway and railway embankments. This katydid has been collected in such habitats over all of eastern United States. In Florida and southern Georgia there are two generations per year, adults appearing in June and September and lingering a few weeks beyond those months. In the northern United States adults appear in early July, and there are few records late in September. Probably only one generation occurs each year in this region.

Singing Behaviour

On clear, late afternoons in early summer, wild solitary males of *S. texensis* can be heard producing long series of irregularly-spaced, short, lispy phrases. I have named such a series the *fast-pulsed song*. This song may last less than a minute and contain only a few phrases, or it may last several minutes and have many phrases. At the onset of evening twilight these solitary males begin making a soft, ticking sound (*ticking*) which can be heard only a few feet away. The ticks are delivered irregularly

and a series may last for several minutes. Ticking, interspersed with occasional fast-pulsed phrases, continues through the twilight. As darkness sets in, a third sound, the *slow-pulsed song*, becomes prominent. The *slow-pulsed song* is composed of two phrases which are longer than and delivered more slowly than the fast-pulsed phrases. After producing a *slow-pulsed song*, the singing male pauses for a couple of minutes before singing again. When he resumes singing, he almost always produces a short, fast-pulsed song and follows that with a *slow-pulsed song*. Into the night the singer produces this sequence, but with each repetition the fast-pulsed song is longer, such that late at night the fast-pulsed song may be produced for long periods (one half hour or longer) before a *slow-pulsed* one is produced.

The singing behaviour is more complex in certain situations. A singing male may change his pattern from fast-pulsed song to *slow-pulsed song* when a cloud passes over, and resume the fast-pulsed song after the cloud is gone. At times some individuals put these songs together in various combinations, abruptly changing from one song to another. Large numbers of this species may be found in favourable habitats, and the proximity of the singing males creates an interesting situation. A male which produces a fast-pulsed or *slow-pulsed song* will be answered with intense ticks by other males which hear the sound. I observed one male answering another about 100 feet away. If two males come into contact, very erratic ticking, which I call *crackling*, is produced by both individuals. Careful listening to a group of *S. texensis* reveals that females sometimes answer the *slow-pulsed song* with a short lisp. To an observer who listens for a short period of time, such singing behaviour makes it appear as if the different sounds are produced at random, but long-term observations reveal that different sounds predominate at different times over the daily period, i.e. morning and mid-day, silence; late afternoon, fast-pulsed songs; twilight, ticking and some fast-pulsed songs; early darkness, *slow-pulsed songs* and fast-pulsed songs; late night, fast-pulsed songs.

Descriptions of the Sounds

Recording and Analysis

The individuals used in this investigation were collected in the field and caged individually in cubical, screened cages four inches on a side and with a metal bottom. Each individual was assigned an identifying code number, e.g. individual 062-10, Table I and Fig. 15. The caged males were placed in cubicles in a converted book shelf which was placed in a controlled-temperature room in which the acoustics had been improved by installing four-inch-thick styrofoam walls and ceiling and by tilting the ceiling and making opposite walls non-parallel. The temperature in the cubicles for any thermostat-setting did not fluctuate more than $\frac{1}{2}^{\circ}\text{C}$. A time-switch was set to give eight hours of darkness and sixteen hours of light, the dark period falling in the normal outside daytime to allow a convenient work period. A Westinghouse $7\frac{1}{2}$ -watt red light bulb was burned overhead during recording sessions for the convenience of the recording operator.

Most of the natural sounds were recorded in this room with an Ampex Model 351-P tape recorder on low-print tape (Scotch No. 131) at 15 inches per second. The ticking noises made by solitary males were recorded in the field with a Magnemite 610A recorder (Amplifier Corporation of America). In either case a dynamic microphone was used (Model D33A, American Microphone Company, or Model MI-4048-E, Type 88A, Radio Corporation of America). The tape speed for both recorders varied less than 1 per cent. throughout the investigation. Immediately after each laboratory recording the temperature was noted by inserting a thermocouple into the singer's cage and measuring the temperature with a Leeds and Northrop Model 8663 potentiometer which had been factory-serviced a few weeks before the recording sessions. In field the temperature was taken with a mercury thermometer. Recordings were made at temperatures ranging from 15° to 38°C . The relative humidity (54 to 86 per cent.) in the recording room was measured before each recording session.

A total of 141 recordings ranging from 2 seconds to about 13 minutes in length and totaling approximately 75 minutes of recorded stridulation were obtained from 26 specimens. These recordings are in the Library of Insect Sounds, Department of Entomology, University of Florida.

Each of the four sounds of the males was analysed by making audiospectrograms, called sonagrams hereafter, with a Kay Electric Company Sona-Graph. The sonagram displays frequency along the vertical axis, time along the horizontal axis, and intensity by the darkness of the pattern. The Sona-Graph can analyse frequencies from 85 to 8,000 cycles per second. The sounds of *S. texensis* contain frequencies greater than 8,000 cycles per second so recordings were played at one-half speed into the Sona-Graph. This reduces the frequencies of the natural sounds by one-half, i.e. to a range which could be analysed by the Sona-Graph. The structural unit of the sounds of this katydid, a 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.

At least one sonagram was made of each recording. In determining the pulse rate for each sound, time was measured from the sonagrams to an accuracy of 0.01 second (by estimating to the nearest 0.001 second). The pulse rate of the fast-pulsed song (Figs. 1 to 4) was determined by measuring the time lapse from the end of the first pulse to the end of the third pulse, i.e. the time spent in two complete cycles of opening and closing the tegmina. The pulse rate of the slow-pulsed songs (Figs. 5 to 9) was determined by measuring the time lapse from the end of a pulse near the beginning of a phrase to the end of a pulse near the end of the phrase. The same technique was employed to determine the rate of tegminal movement in ticking (Figs. 10 and 11) and crackling (Fig. 12). This method was used because the beginning of a pulse was often not as distinct as its ending.

The frequency of all the sounds was determined by comparing sonagrams of the sounds with sonagrams of pure frequencies from a Hewlett-Packard Model 201 C audio oscillator.

By playing recordings at one-half speed into the Sona-Graph while its drum turned at reproduce speed (the Sona-Graph has two drum speeds—record and reproduce speed, the latter being 3.3 times faster) the pulses were spread out enough to count the marks which evidently corresponded to the toothstrikes.

Physical Characteristics of the Sounds

The fast-pulsed song (Figs. 1 to 4) consists of a series of phrases which are irregularly produced from about two seconds to 15 to 20 seconds apart. Phrases of this song usually consist of four pulses although three-pulsed phrases are

also common. In Fig. 2 the 16°C phrase is from one individual, and the 26°C and 36°C phrases are both from a second individual. The pulse rate at 25°C averages 17.3 pulses per second (computed from regression formula of Fig. 16). Sound appears to be made only on the closing strokes of the tegmina (from many observations of singing individuals). See the end of this section for a discussion of frequency variations.

The slow-pulsed song (Figs. 5 to 9) is nearly always composed of two phrases, the first usually five to seven pulses in length, the second much longer, as many as 22 pulses being recorded for a single phrase. The average pulse rate at 25°C is 11.4 pulses per second (from regression formula of Fig. 16), about 33 per cent. slower than that of the fast-pulsed song. The intensity of the sound increases toward the end of each phrase probably due to the singer's rubbing his stridulatory apparatus harder with each succeeding wingstroke. Again the pulses seem to be made only on the closing strokes of the tegmina.

Table I does not represent a statistical analysis of sonagrams of the fast-pulsed and slow-pulsed songs, but rather is a compilation of the data obtained from sonagrams of a few recordings of three males to determine the relationship between the two songs. The samples are quite biased. The fast-pulsed songs analysed were recorded at generally higher temperatures than the slow-pulsed songs shown. Also no attempt was made to keep the sample size constant. A sample size of three phrases of the fast-pulsed song means that a sonagram of three different phrases of a recorded song was made by the method described in the last paragraph under *Recording and Analysis*. Only two pulses per phrase, the second and third, are incorporated in the fast-pulsed samples. Thus a fast-pulsed sample of a total of six pulses refers to two pulses from each of three phrases. The slow-pulsed samples came from one phrase of each recording represented.

Table I gives information about the relationship between the fast-pulsed and slow-pulsed songs. By comparing tooth-strike rates at comparable temperatures it is seen that at a given temperature the tooth-strike rate is much faster in the fast-pulsed song than in the slow-pulsed song, which indicates that the singer is moving his tegmina faster, at least during the sound-producing stroke, of the fast-pulsed song. This mechanism alone could be responsible for the

greater pulse rate in the fast-pulsed song at a given temperature. However, more work must be done along these lines before concrete conclusions can be drawn. Possibly the greater pulse rate in the fast-pulsed song is due to a combination of increasing the tegminal speed and shortening the wingstroke (such that the singer would move his tegmina through a shorter distance than he does in the slow-pulsed song, and therefore could complete more cycles of opening and closing his tegmina at a given speed in a given time).

Another basic difference in the two songs is shown in Figs. 14 and 15. In the fast-pulsed song the sound producing stroke (closing the tegmina) rarely consumes more than 60 per cent. of the time required for one complete cycle of opening and closing the tegmina (Fig. 14). On the other hand, the sound producing stroke of the slow-pulsed song seldom requires less

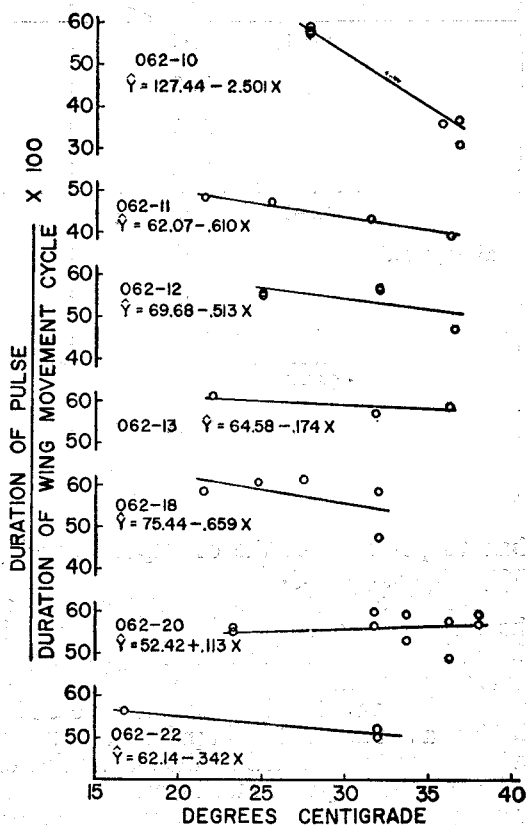


Fig. 14. Relationship between temperature and percentage of wing movement cycle spent in singing—fast-pulsed song.

Table I. Results of the Analysis of Sonagrams of the Fast-pulsed and the Slow-pulsed Songs of Three Males.

Song	Male	Temp. °C.	Sample size		No. of teeth struck		Average duration of pulse (seconds)	Average No. of Teeth struck per second	
			Phrases	Pulses	Range	Average			
Fast-pulsed	062-10	27.8	3	6	20-26	23	-0.27	852	
		35.8	2	4			-0.14		
		36.8	2	4			-0.13		
	062-11	21.5	1	2	25-32	28	-0.33	848	
		25.5	2	4	20-24	22	-0.25	870	
		31.5	1	2	21-25	23	-0.17	1353	
		36.2	1	2	25-26	25	-0.15	1667	
	062-12	25.5	2	4	25-28	27	-0.29	931	
		32.0	2	4	21-24	23	-0.22	1045	
		36.5	1	2	22-24	23	-0.17	1352	
	Slow-pulsed	062-10	17.5	1	4	29-35	32	-0.107	299
			23.8	1	4	30-37	36	-0.085	424
26.8			1	4	30-39	36	-0.065	554	
31.2			1	7	28-36	31	-0.043	837	
062-11		17.5	1	5	22-35	28	-0.111	252	
		21.5	1	4	21-33	27	-0.081	333	
		25.5	1	3	23-31	26	-0.060	433	
		31.2	1	4	22-23	23	-0.039	590	
062-12		15.0	1	8	26-24	30	-0.120	250	
		17.5	1	9	29-36	32	-0.102	313	
		26.5	1	4	26-32	29	-0.056	518	

than 60 per cent. of the corresponding wing movement cycle (Fig. 15).

The effect of temperature on the pulse rates of the fast-pulsed and the slow-pulsed songs is shown in Fig. 16. Each point in Fig. 16 represents the pulse rate of one phrase from one recording. The variation in pulse rate for each individual and the variation in pulse rate between individuals is represented by the distribution of points on the graph. A much closer fitting line would probably result if average values at different temperatures were used for each individual. In calculating the regression lines the following rules were applied to eliminate some of the bias

which would normally have been present if a figure had been used for every recording available: (1) eliminate those individuals for which separate recordings in at least a 5°C range were not made, (2) eliminate all but one point per individual in any 1°C range, using the recording which was first obtained in these small ranges. The relationship appears quite linear, but the maintenance of such a relationship is complex for each song. On the basis of the number of teeth struck (Table I), there seems to be no appreciable shortening of the distance travelled by the tegmina for either song as temperature increases, Fig. 14 indicates that in the fast-

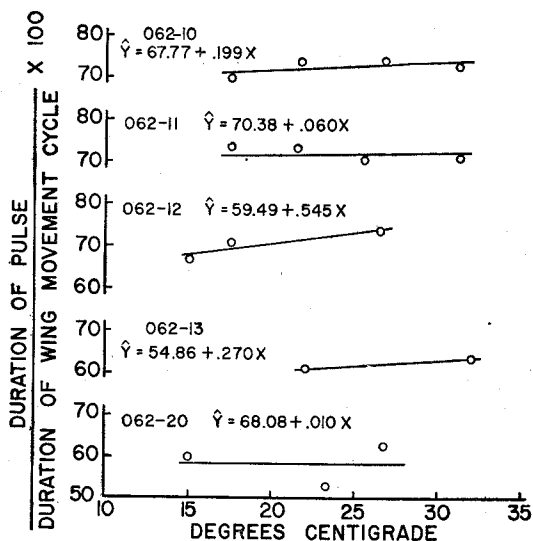


Fig. 15. Relationship between temperature and percentage of wing movement cycle spent in singing—slow-pulsed song.

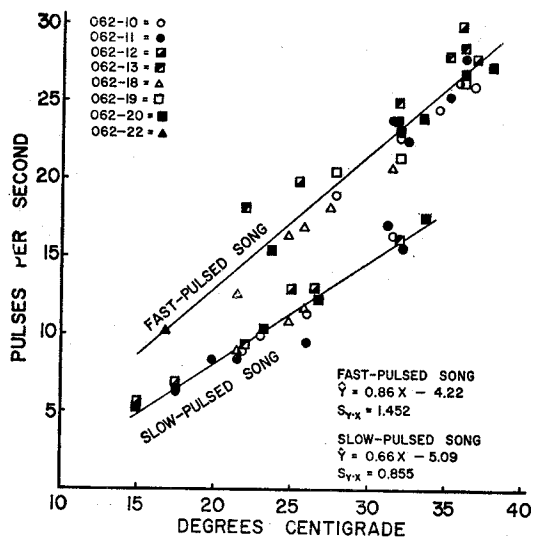


Fig. 16. The effect of temperature on pulse rate.

pulsed song, as temperature increases, less and less of the total wing movement cycle is spent in the sound producing stroke. I do not know why individual 062-20 of Fig. 14 has a positive slope. The recordings of this male sound normal and the pulse rates at different temperatures agree nicely with the trend shown in Fig. 16. Six negative slopes out of seven arbitrarily picked individuals strongly suggests that the

sound-producing stroke is quickened more rapidly than the return stroke. Yet Fig. 15 shows that in the slow-pulsed song the return stroke is quickened more rapidly than the sound-producing stroke.

Ticking (Fig. 10) appears to be made only during wing-opening strokes in which one, two, or three teeth of the stridulatory file are struck. Seldom are more than three teeth struck during a single tick. The usual number is two. This sound is less intense than any of the others.

Crackling (Fig. 12) is very similar to ticking except that crackling is much more erratic and intense. Usually more than three teeth are struck, and again there is no regular pulse rate. Sound appears to be made on both the opening and closing strokes of the tegmina (from observations), and this idea is supported by the appearance of paired pulses on the sonagram. I think the light bars correspond to wing-opening strokes.

The female lisp is a simple sound produced when the wings are opened and is sometimes repeated two or three times. (For a description of the stridulatory apparatus of female Tettigoniidae, see Fulton, 1933).

I have recorded, at a temperature of 25°C, two complete male-female sequences involving three individual females answering a male slow-pulsed song (not simultaneously answering the same male) and have one sequence involving a fourth female. The time interval from the end of the male slow-pulsed song to the initial answering female lisp for each recording of the first three females was 1.38 and 1.40 seconds, 1.06 and 1.07 seconds, and 0.98 and 0.98 seconds. The corresponding time interval for the fourth female was 1.04 seconds. Each female seconds. Each female was relatively constant with her own timing compared to the variation between individuals.

The sonagrams presented here show the presence of frequencies from 5 kcs to 18 kcs. These figures are in agreement with those of Pierce (1948) and Alexander (1960). Sonagrams of fast-pulsed phrases (e.g. those of Fig. 2) and slow-pulsed phrases (Figs. 5 and 8) show great variations in dominant frequencies, so the samples shown should not be taken as merely representative. Individual differences in dominant frequencies are often quite striking, but the range of frequencies present in the sounds of every individual is similar. A greater or lesser range of frequencies can be graphed simply by varying the input signals, marking levels, etc.

of the Sona-Graph. I tried to maintain constant VU meter readings (about —5) during graphing so that qualitative comparisons of the sonagrams would be more reliable. Depending on the individual there may or may not be changes of the dominant frequencies as temperature changes. Changes of dominant frequencies with changes of temperature are not regular, e.g. an individual may have a dominant frequency of about 11 kcs at 20°C, 15 kcs at 25°C, 12 kcs at 30°C, and 14 kcs at 35°C. Such differences perhaps can be explained in the operation of the stridulatory apparatus (Pierce, 1948, describes the stridulatory apparatus of several katydids). As the file passes over the scraper, it seems likely that the entire anal region of the right tegmen is set into vibration and that different, smaller areas, or wing cells, bounded by variously sized veins, vibrate at different resonant frequencies—due to differences in diameter, thickness, etc. A wide range of frequencies may thus be produced in a single wing-stroke. The different vibratory areas, or cells, may resonate at maximum intensities only at certain temperatures. A better understanding of the operation of the stridulatory structures of Orthoptera is sorely needed.

Function of the Sounds

Experimental Technique

To determine the function of the three sounds made by solitary males, recorded natural sounds were played to individually caged males and females of differing age and experience. Preliminary experiments showed that it was impossible to test the reaction of a group of katydids simultaneously because the close presence of one has a greater effect on another than does the recorded sound.

The cylindrical cage used (Fig. 13), called the response arena, had a half-inch plywood frame with an inside diameter of 42 inches. The entire inside surface of the arena was covered with tightly drawn bronze wire screening. The distance from the top screen to the bottom screen was four inches. The top screen was easily removable for the introduction or removal of specimens. Sixteen equal sections were delineated by strings drawn 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.

One kind of sound was played at a time using the playback system of the Ampex 351-P tape

recorder, an Eico HF-14 amplifier, and a Universal Model T-202 loudspeaker (tweeter) which was modified by removing the sphere in front of the diaphragm. Original recordings were made into loops for continuous play. The intensity of the sounds played was measured by supporting the loud speaker vertically 6.6 inches above the microphone (General Radio Co. Type 98B99) of a sound-level meter (General Radio Co. Type No. 1551-B—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 "C" weighting.

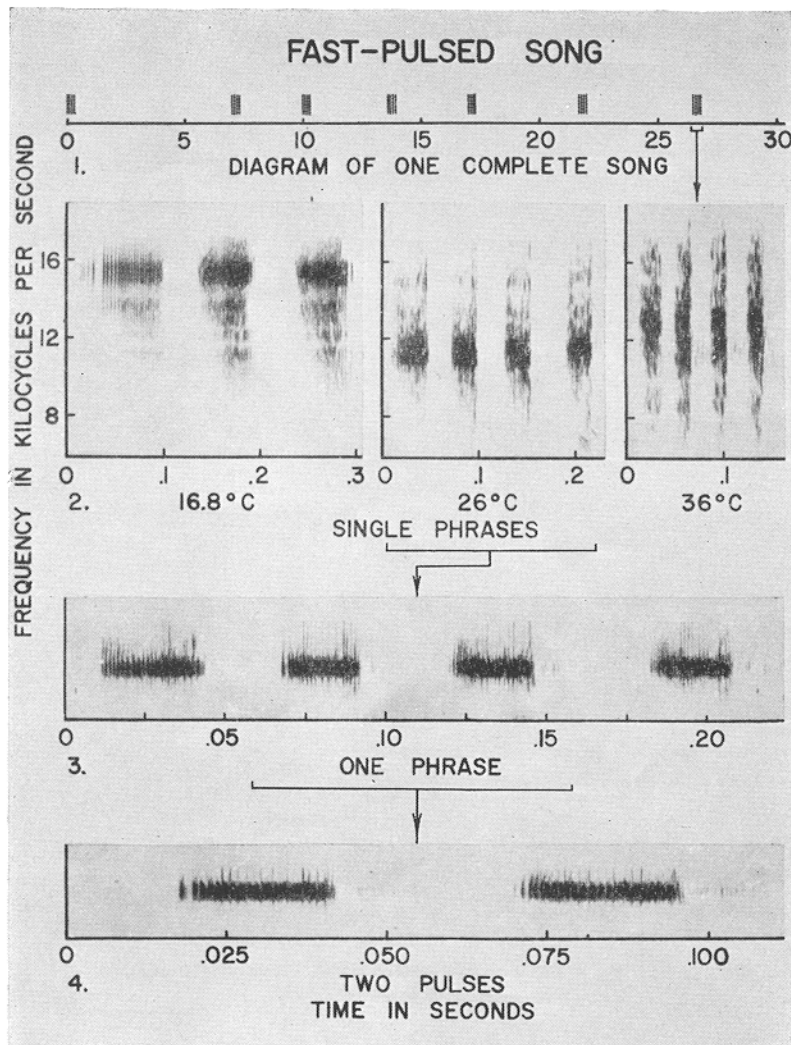
All of the experiments were conducted in the recording room. During each test a Westinghouse 7½ watt red light bulb was burned on the floor beneath the centre of the arena. This light, equal in intensity in all directions from the centre of the arena, allowed the test specimens to be tracked continuously. The acoustics in the arena were checked, and the sound level was progressively less further from the loud speaker.

During each test I sat behind a writing stand and noted the position of the test individual for the entire period of the test. A 7½ watt red light illuminated the writing stand, but was completely shielded from the arena. The data sheets had a diagram which corresponded to the top view of the arena.

The sounds were tested in no particular sequence, the randomization being the order in which the loops were picked up. For a series of repetitions of the same test the speaker position was varied about the four corners of the arena. At least four repetitions were made of each test. A test consisted of five minutes of silence followed by an equal period of sound. Each test was replicated three times in that the same loop was played to three different individuals of about the same age and experience.

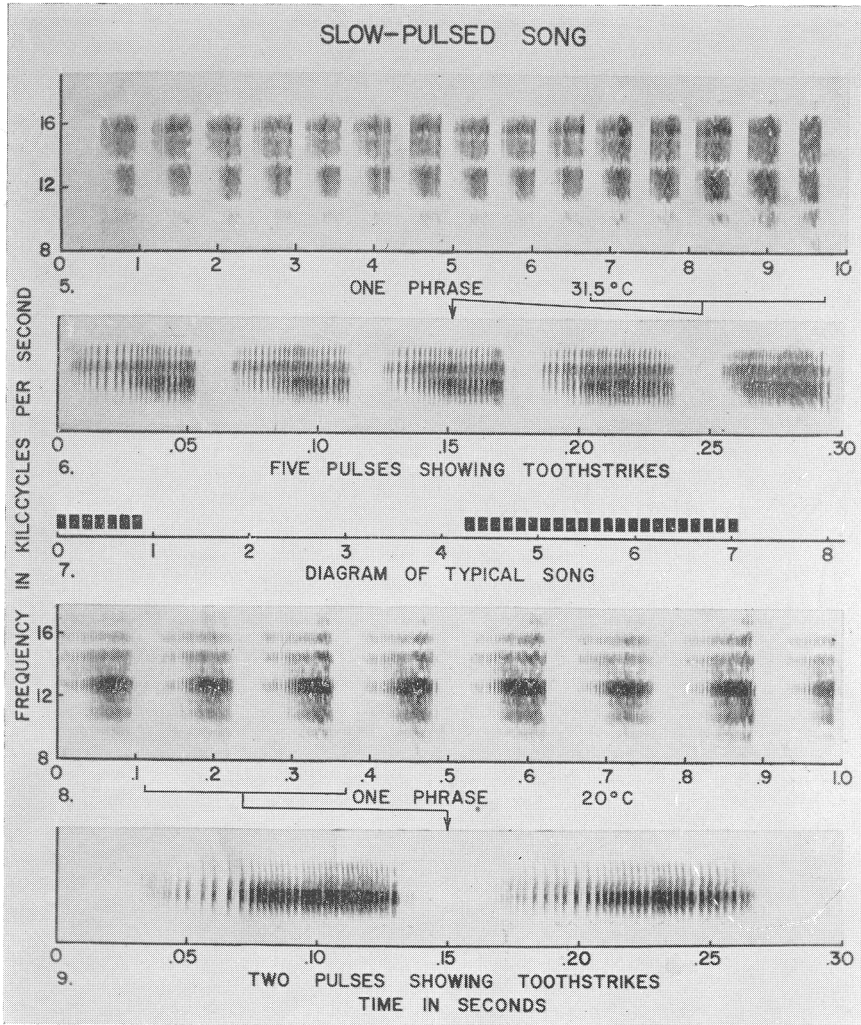
Each sound was played to virgin females, females which had copulated and laid eggs, and males and females of unknown age and experience. Two hours before a series of tests the temperature of the room was set at 25°C, which was the temperature at which the loops to be played had been recorded. This allowed the walls and arena to come to the same temperature. The temperature controls were turned off during each test to eliminate wind and noises. Just prior to each test the controls were turned on to cool the room to about 25°C, because during each test period the temperature in the room increased 1°-2°C. The test individuals

PLATE I



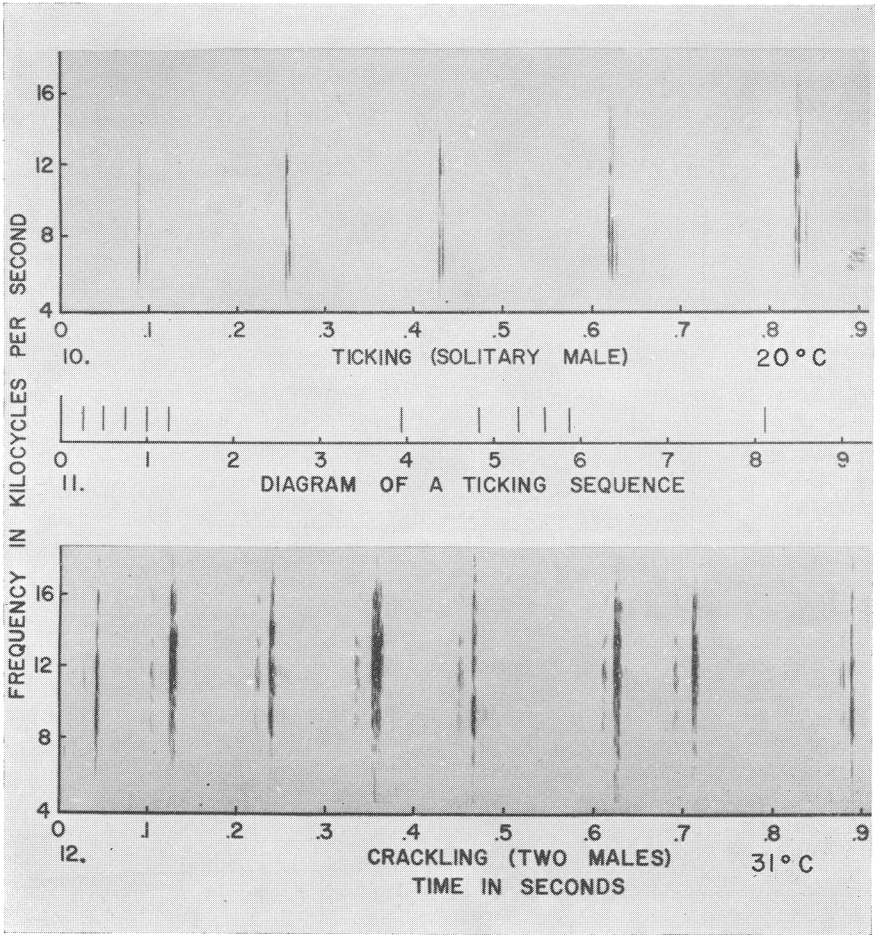
Figs. 1-4. See explanation in text.

PLATE II



Figs. 5-9. See explanation in text.

PLATE III



Figs. 10-12. See explanation in text.

PLATE IV

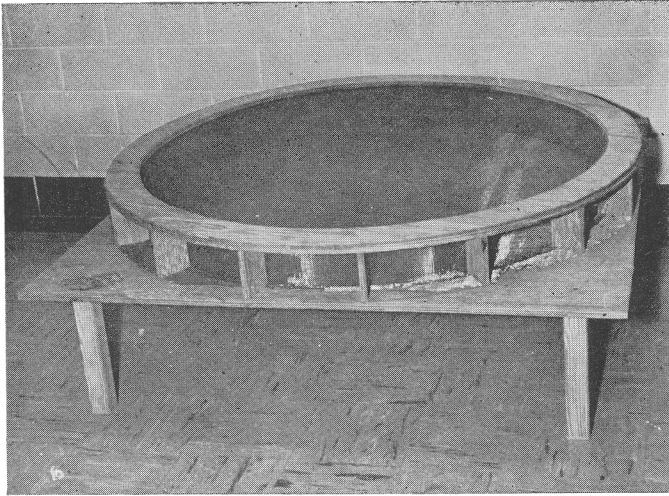


Fig. 13. Response arena used to determine the functions of the sounds.

were introduced into the arena at least ten minutes before beginning a test and this proved to be sufficient time for the individuals to adjust to their surroundings.

Four separate phrases of the fast-pulsed song were made into a single loop, the phrases spaced two seconds apart. Tests were conducted with this loop at two levels of intensity, 80 decibels and 60 decibels. In tests with virgin females two replications were made at 50 decibels. In each test after the period of silence, the loop was played continuously.

One long phrase of the slow-pulsed song was made into a loop and played such that the louder terminal part of the phrase reached a maximum of 84 decibels. After the silent period of a test the phrase was played once every minute.

The ticking loop contained a number of unevenly spaced ticks, typical of the manner in which they are produced. Two series of replications were made with this loop, the first series at a maximum of 68 decibels, some ticks being louder than others, and the second series at a maximum of 86 decibels. After the silent period the loop was played continuously.

A loop was made of a slow-pulsed phrase with an answering female lisp. This loop was played to three males to determine if males move towards females which answer other males.

Experimental Results

The only apparent reaction given by sexually mature males to either slow-pulsed phrases or fast-pulsed phrases was immediate ticking. In tests of the slow-pulsed and fast-pulsed songs the three test males acted no differently during the acoustical part of the test than during the silent part except for ticking in response to the recorded sounds. When the slow-pulsed phrase was played, answering males ticked during and immediately after the phrase; the ticking ceased less than one second after the slow-pulsed phrase ended. Ticking, when played at 68 decibels induced an apparent negative kinetic reaction. Ticking played at 86 decibels induced no movement from test males. This is much more intense than the natural ticks.

No experimental techniques were employed to determine the role of the crackling and female lisps. Crackling is produced only when two males make physical contact and is followed by their immediate separation. The female lisps guide the males to the females. The function of these sounds were deduced from many observations of reactions of individuals in the laboratory and field.

Ticking and crackling seem to function only in male spacing and have no effect on females. The slow-pulsed and fast-pulsed songs, however, did cause reactions in virgin females. Two adult females which were known to have copulated and laid eggs gave no noticeable reaction to any sounds played to them. Of three females of unknown age and experience collected as adults in the field, two gave no reactions at all, while one lisped after the slow-pulsed phrases. The one that lisped orientated directly towards the speaker when fast-pulsed phrases were played at 84 decibels. This individual may have been a virgin because three virgin females, obtained by rearing nymphs, responded positively to successive tests of the slow-pulsed and fast-pulsed songs. The slow-pulsed song always induced the virgins to produce a lisp, but there was no associated movement or orientation. From one group of 12 female nymphs, 8 normal adults (4 emerged as adults with twisted wings and legs due to insufficient space in their cages in which to suspend themselves while moulting) always answered the slow-pulsed song although they were not put into the arena. The fast-pulsed song caused either of two reactions in the virgins, depending on the intensity at which the sound was played. Low intensity sounds induced the virgins to move toward the speaker (Fig. 19) whereas high intensity sounds caused them to orientate toward the speaker but not move (Fig. 18).

The three males used to determine whether males go toward females answering other males did not move toward the speaker. One individual moved randomly during two test periods. The other two males did not move at all. All three, however, answered the slow-pulsed phrase with erratic ticks just as in tests with the slow-pulsed song alone. After the female lisp test males often gave a series of loud, slowly delivered ticks.

Discussion and Conclusions

Recently, specificity of response has been shown among certain crickets (Walker, 1957) and grasshoppers (Perdeck, 1957) to the sounds of their own species, thus showing sound to be a species-specific isolating mechanism as well as a congregating mechanism bringing the sexes together. The results of the experiments presented here show conclusively that the sounds of *S. texensis* convey definite meanings to other conspecific individuals, resulting in spacing of

males, lispings of females, and coming together of sexually receptive males and females as diagrammed in Fig. 17.

The slow-pulsed song is answered by both males and females, but at different timings, the female lisp coming after the male ticking has subsided. If a female answers a slow-pulsed song, the answered male usually lowers his intensity and produces either fast-pulsed or slow-pulsed phrases. If he produces repeated slow-pulsed phrases, the female generally answers every phrase with one, two, or three lisps. The male becomes very active and climbs over his perch until he is orientated toward the female. Then he will fly toward the female sound. If he does not alight on the same bush as the female, he produces the slow-pulsed song again, and the process is repeated. When the male alights on the same plant as the female, the female sways and shakes the substrate gently. The male does likewise and both move toward each other. Seldom is any sound made once the pair is on the same bush or small limb.

SPECIMEN: TEST FEMALE I.
SOUND TESTED: FAST-PULSED SONG.
SOUND LEVEL: 80db.

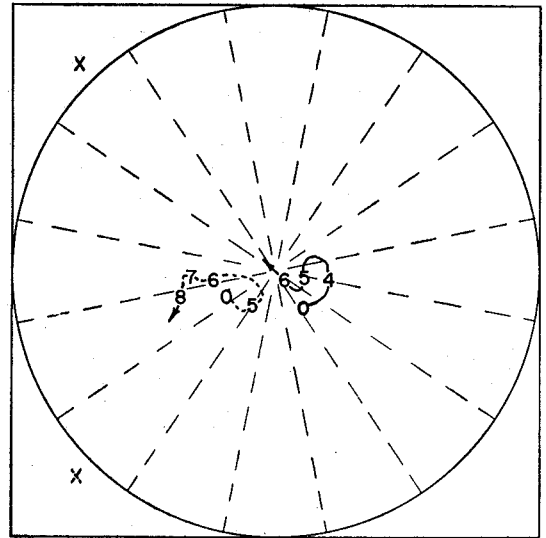


Fig. 18. Response of a virgin female to high intensity fast-pulsed phrases. Numbers indicate minutes elapsed after beginning tests, arrows show orientation at end of movement, and x denotes speaker positions.

SPECIMEN: 062-31
SEX: FEMALE
SOUND TESTED: FAST-PULSED SONG
SOUND LEVEL: 50 db.

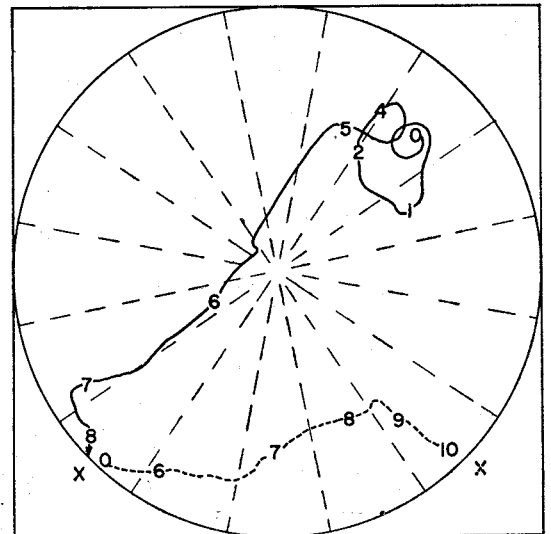


Fig. 19. Response of a virgin female to low-intensity fast-pulsed phrases. Numbers indicate minutes elapsed after beginning tests, arrows show orientation at end of movement, and x denotes speaker positions.

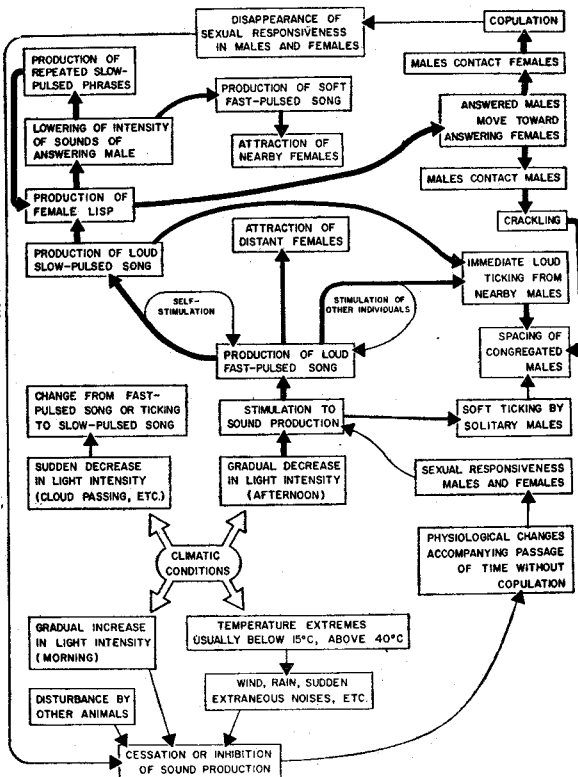


Fig. 17. Diagram of daily and seasonally singing activity of *Scudderia texensis*.

An answered male may produce soft fast-pulsed phrases instead of soft slow-pulsed phrases. This has the effect of drawing the female closer to the male. When he again produces a slow-pulsed phrase, the female will answer and a process similar to the one described above may follow.

If after a slow-pulsed song there is no answering female lisp, the male may produce a few loud fast-pulsed phrases, pause several seconds, and produce a slow-pulsed song. If again unanswered, a longer series of loud fast-pulsed phrases will be given before the process is repeated. If the male remains unanswered, he may produce the fast-pulsed song still longer. The consequence of such singing behaviour is that a singing male can attract virgin females from a distance too great for the male to hear the answering female lisps. A female will move toward the sound until it reaches a certain intensity, at which time she will orientate towards the sound until a slow-pulsed phrase is heard. At this distance, her lisping reply to a slow-pulsed phrase is usually within hearing range of the male.

Evidently, only males whose slow-pulsed songs are answered move toward females. I have yet to see males moving toward females answering other males in the field or toward laboratory recordings of male-female sound sequences. However, I am not convinced that males will not move toward females answering other males. In the laboratory, non-singing males often turned toward females answering other males, became very active in their cages, and produced loud ticks after the female sound. Grove (1958) saw males of *Microcentrum rhombifolium* attracted to females answering other males without having made any sound themselves. I have observed a male of *Inscuderia strigata* moving toward a female answering a recorded male sound, but this reaction remains to be demonstrated in *S. texensis*. This reaction is perhaps not common to all phaneropterines.

A female may answer slow-pulsed songs of several males, thus drawing them into close proximity. I have found several groups of half a dozen or more males about one foot apart in the centre of which group is usually a female. In this situation the stimulus of the female lisp is probably greater than that of the male ticking, because these males do not leave the scene even though other males are ticking nearby. Only when two males make contact and produce the

crackling, do they move away from each other, but then only a few inches. Visual and olfactory stimuli probably have little function in maintaining such an aggregation of males, for the males soon disperse in response to male ticking once the female has copulated and ceases to lisp, so that any slow-pulsed songs produced by the aggregated males are answered by male ticks only.

Complicated systems of acoustical interactions have evolved independently many times in the singing Orthoptera. These loud and persistent sounds have been selected for and elaborated hardly as a means of self-expression (as suggested by Allard, 1929), and despite some concomitant detrimental functions such as providing cues to predators (as shown experimentally for domestic cats in locating singing individuals of *Anurogryllus muticus* and *Amblycorypha uhleri* by T. J. Walker, personal communication). There are many degrees of complexity of sound repertoires in the different species of Phaneropterinae, and a study of the patterns of behaviour associated with these repertoires may lead to a reasonable hypothesis of their pattern of evolution.

Summary

The description of sounds is the only significant work done in the past on the acoustical behaviour of Phaneropterinae, a group in which many species produce two or more sounds in solitary situations. Males of the phaneropterine katydid, *Scudderia texensis*, produce four sounds, three in solitary situations, and virgin females of this species make a lisping sound in response to the slow-pulsed songs of males. Using tape recordings, sonagrams, and experimental procedures, the physical characteristics of the sounds were determined and the functions of the sounds in caged conditions were ascertained. The laboratory behaviour conformed to that seen in natural situations (Fig. 17). Two male sounds (ticking and crackling) appear to function only in male spacing. A third male sound (fast-pulsed song) causes females to (1) move toward singing males when received at low intensity, or (2) simply orientate towards males when received at high intensity. The fourth male sound (slow-pulsed song) induces responsive females to produce one to three lisps which guide males to females. Solitary males usually combine both fast-pulsed and slow-pulsed phrases in each acoustical performance.

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