

Specificity in the Response of Female Tree Crickets (Orthoptera,  
Gryllidae, Oecanthinae) to Calling Songs of the Males

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# SPECIFICITY IN THE RESPONSE OF FEMALE TREE CRICKETS (ORTHOPTERA, GRYLLIDAE, OECANTHINAE) TO CALLING SONGS OF THE MALES<sup>1</sup>

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## INTRODUCTION

A great many insect species possess specialized sound producing and receiving organs. Among these species are many which produce sounds loud enough to be noticed by man and which produce them continuously for many hours each day during their adult lives. On late summer evenings in many habitats in the eastern United States, there are twenty or more species stridulating at the same time, and the resulting din is astonishing to those unaccustomed to it. In spite of the loudness of the chorus and the fact that many of the chorusers are of economic importance, little is known about the biological significance of sound production in insects.

Loud persistent sound production is characteristic of the males of many species of Orthoptera. These males generally sing from the same place for extended periods. It is therefore supposed that the sounds attract females and result in copulation. An alternative or supplementary hypothesis is that the sounds result in spacing of the males.

If the songs of orthopteran males do cause the females to approach, a second supposition is that the sound of the male of one species attracts the females of that particular species and not those of others. That this is the case is supported by a considerable amount of circumstantial evidence. Alexander (1957) has discussed this evidence in detail, and a summary follows. First, many different species sing at the same time in the same habitat. If a female responded indiscriminantly to these sounds, she might go to several males of each of many species before she chanced upon one of her own species. This would have doubtful survival value. Second, the song of each species is characteristic of that species and different from those of all others in the same habitat.

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Special recognition is due George Potor, Jr., Division of Biophysics, Ohio State University, who generously contributed his time and skill in designing and constructing the setup which produced the artificial cricket sounds used in this study.

Thanks are given to Edward S. Thomas and Donald R. Meyer for reviewing the manuscript.

This generalization holds even for species that are so closely related as to be difficult to distinguish morphologically. Finally, there is ample evidence that the *males* of certain species of Orthoptera respond to sounds produced by their own sort and not to those of others. Several species synchronize or alternate their songs with the songs of others of the same species (Fulton, 1934) even though many species may be singing in the habitat. Males of some species group their songs so that there are periods of silence for that species followed by periods in which many males sing in close succession. Since specificity occurs among males, it is likely that it also occurs among females.

## PREVIOUS WORK ON THE BEHAVIORAL EFFECTS OF ORTHOPTERAN SOUNDS

Experimental work as to the behavioral significance of Orthopteran sounds is scanty. Probably the earliest work was by Regen (1914), who demonstrated that the female of the cricket *Gryllus campestris* L. was attracted to the sound of the male. Regen controlled the factors of olfaction and vision by transmitting the sound of the male through a telephone. The female moved toward the sound emitting from the receiver. Duijm and van Oyen (1948) found that females of the shield-backed grasshopper *Ephippiger ephippiger* Fiebiger were attracted to concealed singing males but not to males that had been silenced by gluing their wings together. Weih (1951) studied the acoustical behavior of seven species of Acrididae. He found that the species varied in their responses to the songs of other species. The males of most species would sing in alternation with males of other species, but alternation between male and female was more an intra-specific phenomenon.

With the advent of modern tape recording and high fidelity reproduction of sound, new possibilities were created for experiments dealing with the acoustical behavior of insects. Haskell (1953) played transcribed songs of the males of the cricket *Gryllus domesticus* L. to females of that species. He states that the "calling song" of the male initiates short bursts of locomotor activity, while the "courtship song" inhibits locomotor activity and results in a general passiveness of behavior.

Busnel and Busnel (1954) used modern equipment to demonstrate an attraction of the female of the tree cricket *Oecanthus pellucens* Scop. to the calling song of the male. In their experiments they either picked up the sound of a

naturally singing male and transmitted it to the testing cage with appropriate high fidelity microphone, amplifier, and speaker or played a recording of the natural song to the female.

Busnel and Dumortier (1954), in work with *Ephippiger bitterensis* Chopard, showed that the female was not only attracted to the song of the male but also to artificial signals such as notes from a Galton whistle, certain bird calls, pure frequency signals, and square wave signals. Busnel, Dumortier, and Pasquinely (1955) demonstrated that to induce a response, artificial signals must contain at least one "transient" (a sudden change in intensity).

Busnel, Busnel, and Dumortier (1956) experimented with the specificity of the songs of *Ephippigerida nigromarginata* Lucas and four species of *Ephippiger*. They found that males of each species responded to the sounds of males of the other species by singing in regular alternation or by changing the song rhythm. It is significant that none of these five species occur together in nature but were brought together for the purpose of the experiment. In experiments with *Ephippiger bitterensis* and *E. ephippiger*, females of *bitterensis* showed a more pronounced response to the song of a male of *ephippiger* than to the song of a male of *bitterensis*. This relationship was not entirely a matter of response to the song of highest intensity, nor was the response of the same nature as the response to artificial signals, since it occurred at lower intensities than the minimum intensity at which artificial sounds were effective. However, since these species do not occur together naturally, these experiments do not discredit the hypothesis that sound is an isolating factor among sympatric species.

Busnel and Loher (1954) studied the acoustical behavior of three acridids, *Chorthippus jucundus* Fisch., *C. brunneus* Thbg. (= *bicolor* Charp.), and *C. biguttulus* L. They found that artificial signals of a higher intensity than the normal song would induce responses in these species similar to the responses to natural sounds, *i.e.* alternation of song and, in *biguttulus*, phonotaxis on the part of the male. Busnel, Loher, and Pasquinely (1954) showed that for these species a transient is an essential part of an effective artificial signal. Loher (1957) gives a complete account of his work with these species. He states that there is a greater specificity in the phono-responses of *biguttulus* than in the other two species. Perdeck (1955, 1957, unpublished data) worked with two of the above species, *brunneus* and *biguttulus*, and claims that "both male and female react exclusively to the song of conspecific partners. Hence, the described orienting and releasing effect of song is lacking between a male and a female of different species. . . ."

#### SINGING BEHAVIOR OF EASTERN TREE CRICKETS

The tree crickets (Oecanthinae) of eastern

United States are well suited for a study of the specificity of response to sound in singing insects. They are abundant, and closely related species sing in the same habitat at the same time.

Among tree crickets only the males make noticeable sounds. These sounds are produced by specialized tegmina which during sound production are maintained in a plane nearly perpendicular to the axis of the body. The right tegmen overlaps the left. Near the base of the right tegmen and on its ventral surface is a vein called the file, which bears a series of teeth. Along the inside edge of the left wing is a sharp, heavily sclerotized section called the scraper. When the wings are moved mesad, the scraper engages the file, and the series of shocks produced by the striking of the teeth is transmitted to the wing membranes, causing them to vibrate. When the wings are returned to the starting position, the file and scraper do not engage and no sound is produced. When the male sings, the wings are opened and closed 15 to 100 times per second, each closure producing a *pulse* of sound of a rather pure pitch.

Male tree crickets produce sounds in several situations. The majority of the sounds are produced by solitary males which are not in contact with other individuals of the species. The song produced under these conditions is termed the *calling* song and induces a positive phonotaxis in sexually responsive females of the species. *Courtship* and *postcopulatory* songs are commonly produced when the male is in contact with a female of its species. The functions of these two types of songs have not been demonstrated, but they are assumed to stimulate the female to copulation and to continued feeding on the secretions of the metanotal glands of the male (see Jenson, 1909, for a description of behavior associated with copulation). Only the calling song will be discussed in the remainder of this paper.

The calling songs of the tree crickets of eastern United States are alike in that they consist of sequences of pulses delivered at a uniform rate. However, on the basis of the continuity of the pulse sequences, the species can be divided into three categories (fig. 1). (1) Species in which the pulse sequence continues without interruption for minutes at a time. This type of calling song will be referred to as a *continuous trill* and is characteristic of *Oecanthus latipennis* Riley, *O. pini* Beutenmuller, *O. nigricornis* F. Walker, *O. quadripunctatus* Beutenmuller, and *O. argentinus* Saussure. The last two species listed are usually classed as varieties of *O. nigricornis*, but the information presented in this paper indicates that they are distinct species. (2) Species in which the pulse sequence is discontinued and begun at irregular intervals of from one to several seconds. This type of calling song is designated a *broken trill* and is characteristic of

*Oecanthus angustipennis* Fitch, *O. exclamationis* Davis, and *Neoxabea bipunctata* (DeGeer). (3) Species in which the pulse sequence is broken into uniform bursts with uniform intervals. This type of calling song is called a *regular chirp* and is found in only one species of eastern tree cricket, *Oecanthus niveus* (DeGeer).

At any given temperature, the pulse rate of the song is characteristic for each species. However, with changes in temperature, there are corresponding changes in the pulse rate. Figure 2 shows the effect of temperature upon the pulse rates of each of the species studied. It is derived from the analysis of over 800 recordings made in the field and under controlled conditions in the laboratory. Most of the recordings were of

perature is a change in the pitch of the song. In all species the songs become lower in pitch as the temperature decreases. A certain pitch is characteristic for each species at each temperature, and the range is from 1700 to 5200 cycles per second.

Humidity, light, and air currents do not affect the pulse rate or the chirp rate in tree crickets to any readily detectable extent (unpublished data).

The habitat in which each species ordinarily is found is indicated in figure 2. Species occurring in the same habitat at the same time usually have markedly different pulse rates. *O. nigricornis* and *O. quadripunctatus* are frequently found inter-

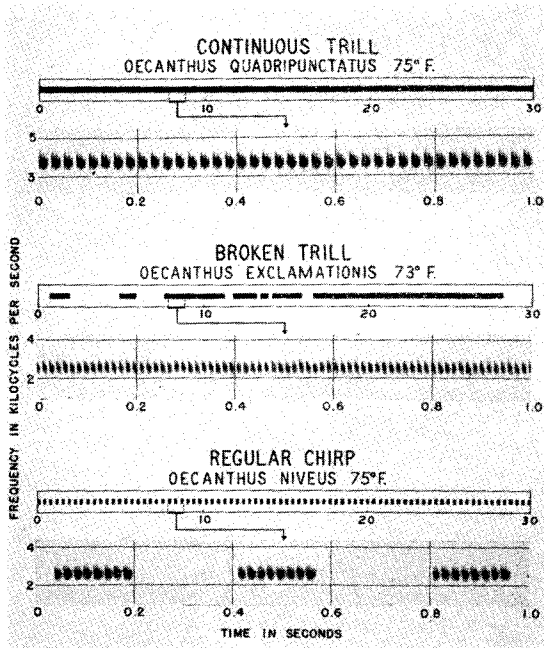


FIG. 1. Diagrams and audiospectrograms of the three types of calling songs. Note that the audiospectrograms show all calls to consist of sequences of pulses.

Ohio specimens, but recordings made in localities scattered throughout eastern United States (excepting New England) fall into the same pattern. The effect of temperature on each species appears linear, and there is only slight individual variation about the regression lines. In addition to a regular change in pulse rate with temperature, in *O. niveus* there is also a regular change in chirp rate. Since chirp rate is easily determined by counting the chirps in a specified time, it is possible to approximate the temperature by listening to a cricket of this species, and this characteristic has earned it the title of the "thermometer cricket" (see Allard, 1930, for details). Another change correlated with tem-

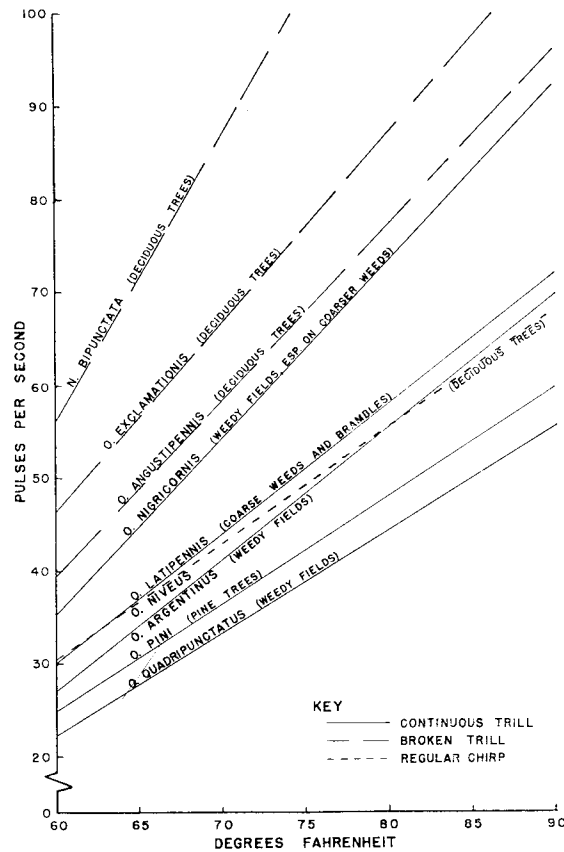


FIG. 2. Effect of temperature upon pulse rate in the calling songs of tree crickets.

mixed in large numbers in certain habitats in Ohio and Indiana, and the pulse rates of their songs are widely divergent and do not overlap. In some of the same habitats *argentinus* is also found, but it is to some extent isolated in time from the other two species. *O. argentinus* has two generations each summer in contrast to the one generation of *nigricornis* and *quadripunctatus*. The first generation of adults of *argentinus* disappears in early August at the time *nigricornis* and *quadripunctatus* begin to mature. The second generation of *argentinus* appears in mid-

September, and from then until frost adults of all three species may occur intermixed in the same habitat. The pulse rate of the song of *argentinus* never overlaps with that of *quadripunctatus* nor with that song of *nigricornis* illustrated in figure 2. However, recent work with Ohio specimens which are *nigricornis* on the basis of coloration has demonstrated that two song forms occur, the taxonomic status of which is undetermined. One form of *nigricornis* has the song illustrated in figure 2; the other has a slower song which is only slightly faster than that of *argentinus*. When the calling songs of 37 individuals were recorded under carefully controlled temperatures, 22 were found to be fast singers and 15 to be slow singers. No intermediate-type songs were recorded, and each individual produced only one of the two classes of songs. The males of the two song forms could ordinarily be separated morphologically on the basis of the number of teeth in the file. No other differences, either in morphology or biology, have been found. The

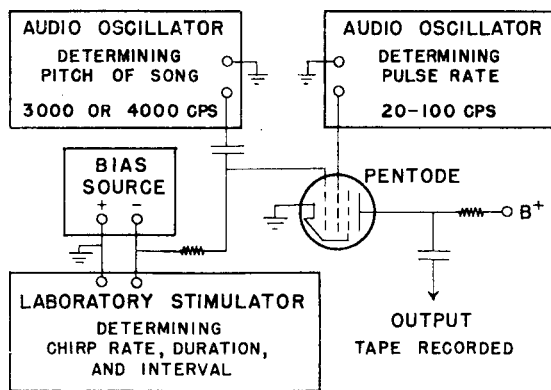


FIG. 3. Diagram of setup used to produce artificial calling songs.

females used in the experiments described in this paper were from a field in which the males were largely fast singers, and a check of the responses of the individual females showed no evidence that any of the females responded to the slower song rather than the faster one. Whether there are females which respond to the slower song is unknown.

Some interesting generalizations can be made concerning habitat, song type, and singing period of eastern tree crickets. The tree-dwelling forms sing almost exclusively at night. Forms occurring in open fields sing during both day and night; *O. latipennis* sings chiefly at night but is usually found along woodland edges. The three species with the highest pulse rates at a given temperature are the only ones which deliver broken trills, and all are tree-dwelling forms. Since they sing at night, when temperatures are low, their maximum pulse rates are not much higher than forms which sing at a lower rate at a

given temperature but which sing during the heat of the day.

#### MATERIALS AND METHODS

The sounds used in these tests were of two origins—natural and artificial. Both types were first recorded on magnetic tape and then played back to the test insects under laboratory conditions. The natural sounds were calling songs of tree crickets usually recorded in the laboratory with a Magnecorder PT63-A tape recorder mechanism and a Magnecorder PT63-J recording and playback amplifier. Some of the recordings of natural sounds were made in the field with a Magnemite 610E recorder (Amplifier Corporation

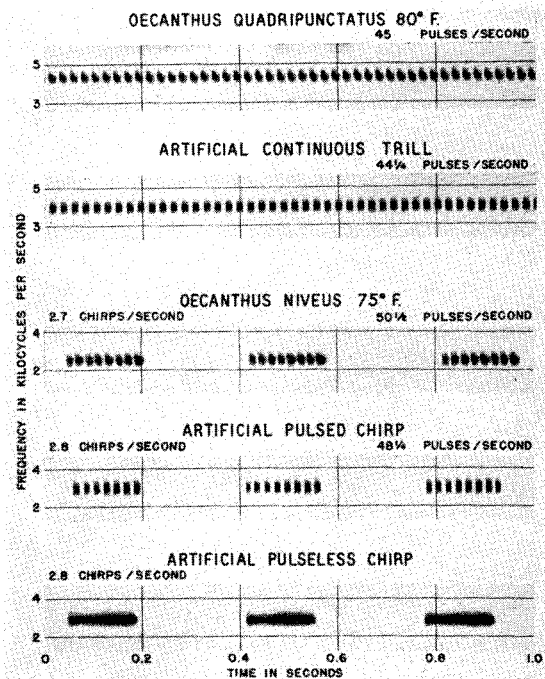


FIG. 4. Audiospectrograms comparing natural and artificial calling songs. The pulse rates given for *Oecanthus niveus* and its imitation are those within the individual chirps.

of America). In either case a dynamic microphone was used (Model D33 or D33A, American Microphone Company), and the tape speed was 15 inches per second.

Artificial tree cricket calls were produced by a device (fig. 3) designed and constructed by Dr. George Potor, Jr., Division of Biophysics, Ohio State University. The device was basically a pentode amplifier operating at 4000 (or 3000) cps, screen-grid modulated at 20-100 cps. This was grid biased by a variable DC source to that portion of the plate-characteristic curve which allowed passage of 4000 (or 3000) cps signal. The grid bias could be further switched on and off by a laboratory stimulator to provide

chirps of variable frequency and duration. Pulseless chirps could be produced by cutting out the 20–100 cps audio oscillator. Figure 4 shows audiospectrograms of artificial tree cricket calls compared with genuine ones.

From the tape recordings of the signals to be tested, loops were made by splicing the ends of seven-foot sections of tape to their beginnings. In cases of recordings of regular chirps care was taken to join the tape at an interval between chirps and in such a manner as to maintain an unbroken chirp rhythm. The uniformity of the intervals between chirps was checked by making audiospectrograms with a Kay Electric Company Vibralyzer (Borror and Reese, 1953, give a short summary of the use of this machine in sound analysis). A loop of tape made in this manner, threaded into the Magnecorder and passed over a reel as shown in figure 5, could be played continuously for as long as an experiment required.

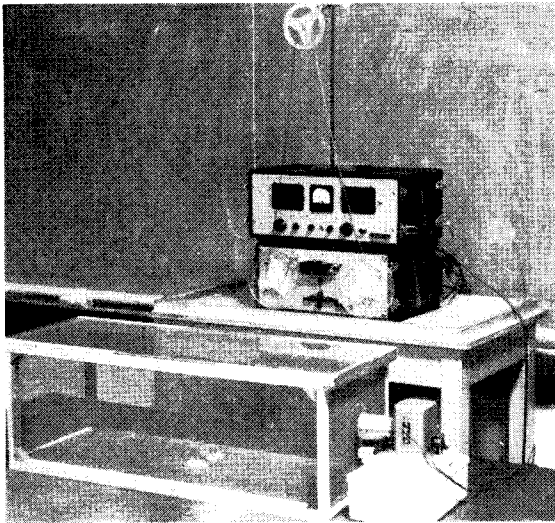


FIG. 5. Equipment used in testing the response of female tree crickets to recordings of artificial and natural sounds. The cage and speaker are in the foreground; behind them is the tape recorder with a loop of tape in place.

Each loop was marked to indicate the direction in which it should be played and was stored on a reel in a labeled envelope. The original loops are in the Library of Animal Sounds, Department of Zoology and Entomology, Ohio State University.

The speaker used in these tests was a Jensen RP-302 "super-tweeter." It was mounted with a Jensen A-402 crossover network with a 15 ohm resistor taking care of the low-pass output. The intensity of the sound emitting from the speaker was standardized for each set of experiments with the VU meter of a Magnemite 610EV tape recorder (Amplifier Corporation of America). The original standard was that reading produced on the VU meter by a naturally singing tree cricket

at one inch from the microphone. Thereafter, sounds to be tested were adjusted to give that same reading with the microphone one inch from the speaker. Later the Magnemite was calibrated with a General Radio Company Type 1551-A sound-level meter. At one inch from the outside edge of the speaker the maximum intensity was 93 db. Since the characteristics of the Magnemite as a sound-level meter vary with the voltage of its batteries, some variation from this intensity must have occurred during the several months of the tests. However, this Magnemite was seldom used except as a sound-level indicator, so the variation should not have been great. At any rate, for the tests carried out on any one night or on consecutive nights, the intensities were well standardized.

The tree crickets to be tested were confined in a cage (figs. 5 and 6) with inside dimensions 1' x 1' x 3'. The sides, bottom, and ends were made of

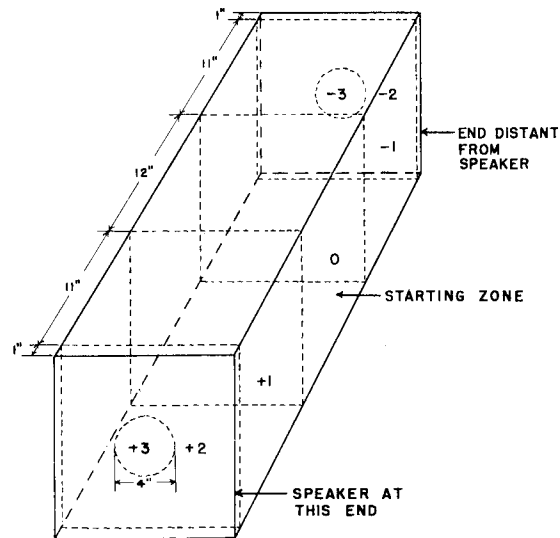


FIG. 6. Diagram of cage showing zones used in recording the positions of the crickets. The finely dashed lines indicate the boundaries of the zones, and the figures in the various zones represent the scoring system.

16 mesh plastic screening. The top consisted of three closely fitting panes of glass with the middle pane removable. The cage was constructed so that the supporting members were outside the glass and screening, leaving the inside surfaces free from obstructions. The acoustical properties of the cage were far from ideal, since standing waves were set up which caused an uneven intensity gradient from the speaker. The results of the tests indicate that the crickets were nevertheless able to orient to the sound source. In future work a cage of improved design should be used.

The crickets in these experiments were virgin females, obtained by rearing late-instar female nymphs to maturity in isolation. Virgin females

were used because they had no previous experience in responding to sounds and because they were more likely to be sexually receptive. All crickets used were from Franklin County, Ohio.

For each series of experiments the signals to be tested were selected, and two or three replicates were set up with the treatments randomized in each. At the beginning of each treatment ten virgin females of the test species were placed in the central section of the cage in a darkened room in which the temperature was held nearly constant ( $\pm 1^\circ\text{F}$ ). Previously the crickets had been marked with dots of colored paint on the pronota so that individuals could be recognized. The speaker was placed in the center of one end of the cage with the forward edge of the speaker one inch from the screening (fig. 5). From treatment to treatment the end at which the speaker was placed was randomized. The signal was played for ten minutes. At the end of this period a flashlight was used to determine the positions of the crickets in respect to the seven arbitrary zones indicated in figure 6. If a cricket was on the line of division between two zones, it was considered as in the zone farther from the starting zone. After their positions were recorded, the crickets were returned to the starting position, and the next signal was played.

The results of the tests were evaluated in two ways—an arbitrary scoring system and a chi square analysis. The scoring system involved giving the seven cage zones used in recording the position of the crickets values of +3 to -3 (fig. 6). With this system random movement on the part of the crickets would be expected to give an average score of 0. A maximum positive response for ten crickets would produce a score of about +25 and a corresponding negative response would be expected to yield a score of -25. The maximum score is estimated at 25 instead of 30, because ten crickets would not remain within a four-inch diameter circle; never were more than five observed within the circle at once. In the early stages of experimentation the +3 and -3 zones were not used in recording the positions of the crickets; therefore, the maximum score was +20. Before these scores were included in the tables of this paper, they were multiplied by 5/4 to make them more comparable with later scores.

Since the scoring system was arbitrary, the scores were not susceptible to ordinary tests of statistical significance. Therefore, a chi square test was also applied to the results. For this test the crickets which were outside the starting zone at the end of the test period were classed into two groups—*plus*, if they had moved in the direction of the speaker, and *minus*, if they had moved away from it. If the movement was non-oriented, the plus group should be equal in number to the minus group. With the chi square test, the observed distribution could then

be compared with the expected one to see if the observed deviated from the expected by more than could be accounted for on the basis of chance within certain probability limits. Since the chi square analysis takes into account only the direction of movement and not the extent, it does not utilize all the available information and is inferior to the scores as a basis of comparison between tests. It does, however, give an objective measure of the significance of the response in each test.

## RESULTS

### *Specificity of Responses to Natural Sounds*

The first problem investigated was whether female tree crickets are attracted to the calling songs of other species occurring in the same habitat. Table I shows the results of experiments with females of *O. quadripunctatus* and *O. nigricornis*, two species which occur in weedy fields. Table II shows the results of experiments with females of *O. niveus* and *O. exclamationis*, two species which live in trees. In each case a positive phonotaxis by the females to the calling songs of the male of the same species was demonstrated. No such responses were demonstrated to calling songs of other species occurring in the same habitats. It is of course possible that some response existed, but that it was too small to be demonstrated by the technique used. In any event there can be no doubt that female tree crickets show a much more pronounced positive response to calling songs of their own males than to those of males of other species singing in the same habitat.

### *Basis of Specificity among Species Producing Continuous Trills*

If female tree crickets respond to the calling songs of their own species and not to similar songs of other species in the same habitat, the question arises as to what is the basis of this specificity. The continuous trill, the simplest type of song studied, was the first to be investigated to determine what component was responsible for differential responses among females of different species.

A study of the calling songs of species producing continuous trills reveals that pulse rate is the characteristic which differs most widely among species occurring in the same habitat. Thus it seems a logical hypothesis that the female's discrimination is based on a response to certain pulse rates. The functioning of insect tympanal organs supports this contention, since their response depends on the pattern of sound intensity changes (amplitude modulation pattern) so long as the carrier frequency is within the range audible to the insect (Pumphrey, 1940). The pulses in a tree cricket trill are just such amplitude modulations.

The hypothesis that pulse rate is the song

TABLE I  
RESPONSE SCORES AND CHI SQUARE VALUES RELATING TO SPECIFICITY OF  
RESPONSE IN FEMALES OF SPECIES FOUND IN WEEDY FIELDS

	RECORDINGS TESTED		
	<i>O. quadripunctatus</i> at 74°F. 37¾ pulses/sec. 3600 cycles/sec.	<i>O. argentinus</i> at 74°F. 44¼ pulses/sec. 3500 cycles/sec.	<i>O. nigricornis</i> at 75°F. 64¼ pulses/sec. 3700 cycles/sec.
<i>O. quadripunctatus</i> females, 74°F.			
Replicate 1.....	+19	+4	-----
Replicate 2.....	+21	+1	-----
Average.....	+20	+2	-----
Chi Square.....	10.00 <sup>a</sup>	0.82	-----
<i>O. nigricornis</i> females, 75°F.			
Replicate 1.....	+1	+3	+17
Replicate 2.....	+2	+2	+19
Replicate 3.....	-3	0	+15
Average.....	0	+2	+17
Chi Square.....	0.25	1.29	19.59 <sup>a</sup>

<sup>a</sup>Significant at the 1% level.

TABLE II  
RESPONSE SCORES AND CHI SQUARE VALUES RELATING TO SPECIFICITY OF  
RESPONSE IN FEMALES OF TREE-DWELLING SPECIES

	RECORDINGS TESTED		
	<i>O. niveus</i> at 75°F. 2.7 chirps/sec. 50½ pulses/sec. 2600 cycles/sec.	<i>O. angustipennis</i> at 74°F. 53 pulses/sec. 2600 cycles/sec.	<i>O. exclamationis</i> at 76°F. 80 pulses/sec. 2600 cycles/sec.
<i>O. niveus</i> females, 75°F.			
Replicate 1.....	+10	+4	+3
Replicate 2.....	+10	+4	+1
Replicate 3.....	+14	0	-1
Average.....	+11	+3	+1
Chi Square.....	10.70 <sup>a</sup>	1.92	0.20
<i>O. exclamationis</i> females, 75°F.			
Replicate 1.....	+1	-2	+6
Replicate 2.....	0	+5	+12
Replicate 3.....	-1	-3	+6
Average.....	0	0	+8
Chi Square.....	0.00	0.17	7.36 <sup>a</sup>

<sup>a</sup>Significant at the 1% level.

component resulting in specificity of response is complicated by the fact that the pulse rate for each species varies with temperature. Different species sing at identical pulse rates if their temperatures are properly adjusted. Therefore, if pulse rate is the basis for specificity of response of the female, the female must respond to different pulse rates at different temperatures.

To test the role of pulse rate in the response of females of a species, two sorts of recordings were used: (1) recordings of songs of the species made at different temperatures and therefore having

different pulse rates and pitch and (2) recordings of artificially produced trills having different pulse rates but the same pitch. Table III shows the results of an experiment of this nature with females of *O. quadripunctatus*. It is apparent that the crickets responded to markedly different degrees to the same signals at different temperatures. At 70°F. there was a statistically significant response to the calling song of the male at 70°F. and to an artificial trill of 32½ pulses per second; there was no such response to the song of the male at 80°F. or to an artificial trill of 44½



TABLE III  
RESPONSE SCORES AND CHI SQUARE VALUES SHOWING THE EFFECT OF TEMPERATURE  
ON THE RESPONSE OF FEMALES OF *O. quadripunctatus* TO CERTAIN SOUNDS

	RECORDINGS TESTED			
	<i>O. quadripunctatus</i>		Artificial Trill	
	at 70°F. 33¾ pul/sec. 3600 cyc/sec.	at 80°F. 45 pul/sec. 4200 cyc/sec.	32½ pul/sec. 4000 cyc/sec.	44¼ pul/sec. 4000 cyc/sec.
<i>O. quadripunctatus</i> females, 70°F., 22 Aug. 1956				
Replicate 1.....	+14	+2	+18	-1
Replicate 2.....	+21	+8	+12	+7
Average.....	+18	+5	+15	+3
Chi Square.....	9.31 <sup>a</sup>	1.00	8.33 <sup>a</sup>	0.11
<i>O. quadripunctatus</i> females, 80°F., 23 Aug. 1956				
Replicate 1.....	-3	+18	0	+21
Replicate 2.....	+11	+20	-1	+12
Average.....	+4	+19	0	+16
Chi Square.....	0.50	9.00 <sup>a</sup>	1.00	11.00 <sup>a</sup>

<sup>a</sup>Significant at the 1% level.

pulses per second. At 80°F. the situation was reversed, with the females showing a response to the last two signals but not to the first two. Any role of pitch in the specificity of response seems to be eliminated by the responses to artificial trills of controlled pitch.

In a test of 74°F., again with *O. quadripunctatus* females, a positive phonotaxis was demonstrated to an artificial trill of 36½ pulses per second but not to an artificial trill of 44¼ pulses per second. These pulse rates correspond to those of males of *O. quadripunctatus* and *O. argentinus* at that temperature. This test substantiates the importance of pulse rate in explaining the data for *quadripunctatus* females in Table I.

In order to determine the extent to which females of a species respond to different pulse rates at given temperatures, *O. nigricornis* females were tested at 70° and 80°F. with artificial trills of varying pulse rates. Figure 7 shows the results of these tests. Each point on the graph represents two tests (using ten crickets each). Although the data are insufficient to give a smooth curve of response at each temperature, it is obvious that the ability to respond to given pulse rates varies with temperature and that the pulse rate producing maximum response at a given temperature approximates that produced by the male of the species at that temperature. It is also evident that at a given temperature there is a range of pulse rates to which females of a species will respond.

Before pulse rate can be singled out as the sole factor resulting in specificity of response in species producing continuous trills, another possibility

must be evaluated—the possibility of the occurrence of elements in the song of one species that

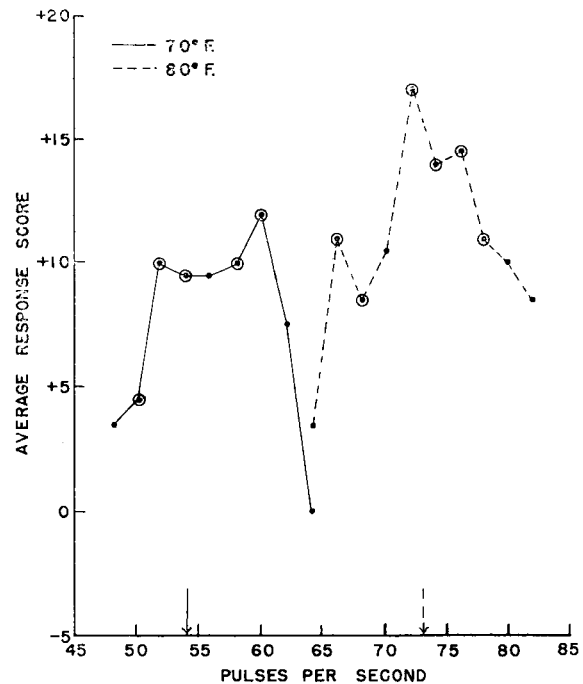


FIG. 7. Response of *Oecanthus nigricornis* females at 70° and 80°F. to artificial, 4000 cps continuous trills of different pulse rates. The encircled points are those for which chi square analysis showed a response significant at the 1% level. The arrows on the lower scale indicate the average pulse rates of the songs of the males at the two temperatures.

inhibit or repulse the females of other species. This possibility is easily checked by selecting recordings of different species singing at the same pulse rate (and hence at different temperatures) and seeing whether females of one species will respond to all songs. This was done using *O. nigricornis* females at 70°F. and recordings of *argentinus* and *quadripunctatus* at pulse rates similar to *nigricornis* at 70°F. The results are listed in Table IV. The responses of the *nigricornis* females to the songs of all three species were nearly equal, so there seems to be no inhibitory element in the song of one species to the females of another. The results of tests with the speaker turned off are given in Table IV to illustrate scores produced by movement without relation to sound. In other tests with no sound, scores as high as +4 were obtained.

#### *Specificity in Species Producing Broken Trills*

Among species with broken trills, pulse rate varies widely, and one would suspect it to be the basis for specificity of response. However, another factor which might be of importance in inducing a positive phonotaxis in the females of these species is the occurrence of discontinuities in the song. To test the effect of this latter factor, females of *O. exclamationis* were played both broken and continuous trills of their own species. A continuous trill was produced by making a loop from a recording of a pulse sequence over five seconds in length.

The results are shown in Table V, and it is apparent that the females responded at least as well to a continuous trill as to a broken trill. The data of a further test shown in Table V indicate that *O. exclamationis* females respond positively to an artificial trill of the same pulse rate as the natural song, even though the pitch is quite different. It therefore seems that the factor responsible for specificity in species producing broken trills is the same as in species producing continuous trills, *i.e.* pulse rate.

#### *Specificity in O. niveus*

In the song of *O. niveus* there are two regular rhythms—the pulse rhythm and the chirp rhythm. It is conceivable that either pulse rhythm or chirp rhythm alone induces positive phonotaxis in the female. Since the two are inseparable in the natural song of *niveus*, artificially produced signals were used to test whether one or both were responsible. Three artificial signals were played to females at 75°F.: (1) continuous trill of  $48\frac{1}{2}$  pulses per second (pulse rate similar to natural *niveus* but no chirp), (2) regular, pulseless chirp at 2.8 chirps per second (chirp rate similar to natural *niveus* but no pulse), (3) regular, pulsed chirp at  $48\frac{1}{4}$  pulses per second and 2.8 chirps per second. The pitch was imperfectly

controlled—4000 cps in (1) and 3000 cps in (2) and (3)—because more suitable recordings were not available at the time. However, in work with other species there was no indication of a role of frequency differences within this range. For instance, *O. exclamationis* females responded as well to an artificial trill pitched at 4000 cps as they did to the natural trill at 2600 cps (Table IV).

Table VI shows that the crickets did not respond significantly to the continuous trill but showed a positive phonotaxis to the pulseless chirp. This indicates that chirp rhythm is essential in the response of the female of *O. niveus*. Since pulsed chirps produced more pronounced phonotaxis than pulseless chirps, the pulse rhythm must have a supplementary effect. The prime importance of the chirp rhythm makes the response quite specific, since *O. niveus* is the only chirper with a uniform rhythm in its habitat.

The range of chirp rates to which *niveus* will respond at a given temperature was not determined. In eastern United States there is no species with a similar song, so there is no selective advantage in a narrow range of response. In western United States there is a tree cricket with a slower chirp, but it occurs in a different habitat.

#### DISCUSSION

These experiments demonstrate that insect-produced sounds may be important in the reproductive isolation of sound-producing species. Minor differences in the rhythm or rate of song may determine whether or not the female of a singing species responds to a song. If song is important in species isolation, it can play a major role in the evolution of new species. Once song differences have developed and become behaviorally significant, sibling sound-producing species can live in close contact with reduced chances of hybridization. The songs of closely related species occurring in the same habitat can be expected to differ to a greater extent than characters which do not influence the maintenance of species isolation. Most morphological characters used in classifying the Orthoptera are not directly related to the maintenance of reproductive isolation, so studies of song differences can be expected to clear up many taxonomic problems concerning sound-producing species (Fulton, 1933; Alexander, 1957a).

An example of the value of song in taxonomy is the clarification of the status of *O. quadripunctatus* and *argentinus* as species distinct from *O. nigricornis*. As pointed out above, these three species have distinctive songs, and the females are specific in their phono-responses. Other differences, in life history and morphology, exist and will be described in a later paper.

The study of the behavioral significance of insect-produced sounds is a field which has been

TABLE IV

RESPONSE SCORES AND CHI SQUARE VALUES SHOWING THE RESPONSE OF *O. nigricornis* FEMALES TO THE SONGS OF THREE SPECIES SINGING AT SIMILAR PULSE RATES

	RECORDINGS TESTED			
	<i>O. nigricornis</i> at 70°F. 53 pulses/sec. 3300 cyc/sec.	<i>O. argentinus</i> at 80°F. 56¼ pulses/sec. 3900 cyc/sec.	<i>O. quadripunctatus</i> at 89°F. 55¼ pulses/sec. 4400 cyc/sec.	No Sound
<i>O. nigricornis</i> females, 70°F.				
Replicate 1.....	+14	+11	+12	-1
Replicate 2.....	+9	+16	+10	-1
Average.....	+12	+14	+11	-1
Chi Square.....	8.33 <sup>a</sup>	10.89 <sup>a</sup>	8.00 <sup>a</sup>	0.33

<sup>a</sup>Significant at the 1% level.

TABLE V

RESPONSE SCORES AND CHI SQUARE VALUES SHOWING THE RESPONSE OF *O. exclamationis* FEMALES AT 76°F. TO CONTINUOUS AND BROKEN TRILLS

	RECORDINGS TESTED		
	<i>O. exclamationis</i> at 76°F. 80 pulses/sec., 2600 cycles/sec.		Artificial Trill 80 pulses/sec. 4000 cycles/sec. (continuous)
	Broken Trill Bursts of 2-2½ sec. Intervals of ¼-½ sec.	Continuous Trill	
Replicate 1.....	+16	+17	+19
Replicate 2.....	+15	+18	+17
Average.....	+16	+18	+18
Chi Square.....	9.00 <sup>a</sup>	8.00 <sup>a</sup>	9.00 <sup>a</sup>

<sup>a</sup>Significant at the 1% level.

TABLE VI

RESPONSE SCORES AND CHI SQUARE VALUES SHOWING THE RESPONSE OF *O. niveus* FEMALES AT 75°F. TO CERTAIN ARTIFICIAL AND NATURAL SOUNDS

	RECORDINGS TESTED			
	Artificial Trill 48¼ pulses/sec. 4000 cycles/sec.	Artificial Pulseless Chirp 2.8 chirps/sec. 3000 cycles/sec.	Artificial Pulsed Chirp 48¼ pulses/sec. 2.8 chirps/sec. 3000 cycles/sec.	<i>O. niveus</i> at 75°F. 50½ pul/sec. 2.7 chirps/sec. 2600 cyc/sec.
Replicate 1.....	+6	+5	+20	+16
Replicate 2.....	-1	+15	+20	+20
Average.....	+2	+10	+20	+18
Chi Square.....	0.40	5.40 <sup>b</sup>	16.00 <sup>a</sup>	16.00 <sup>a</sup>

<sup>a</sup>Significant at the 1% level.

<sup>b</sup>Significant at the 5% level.

neglected and promises interesting discoveries. The calling songs of tree crickets are very simple compared with those of many other species of Orthoptera. In some species different kinds of sound pulses are produced, and there are gradual and sudden changes in rhythm, rate, and intensity. Yet the sequence and nature of these changes are constant for the species. The significance of the different elements of these complex songs should be explored. Effects of songs produced by males in contact with other males or with females offer an additional field for study.

## SUMMARY

1. There is circumstantial evidence that the females of sound-producing Orthoptera respond to the songs of males of their own species and not to those of others; however, experimental evidence is scanty.

2. The calling songs of nine species of eastern tree crickets (Oecanthinae) were studied and found to consist of pulses of an almost pure pitch delivered at a uniform rate. On the basis of the continuity of the pulse sequences, the species were separated into these three groups: song a continuous trill, song a broken trill, song a regular chirp. In each species the pulse rate of the song varied directly with temperature. At any given temperature, the songs of species commonly found together had different pulse rates.

3. Experiments in which caged virgin females of four species of tree crickets were subjected to recorded natural and artificial sounds suggest these generalizations:

(1) Sexually responsive females show a positive phonotaxis to the calling songs of the males of their own species but not to the songs of other species occurring in the same habitat.

(2) In species with continuous trills, pulse rate is the determining factor in the response of the female to the calling song. The specific pulse rate to which the female exhibits greatest response varies with temperature in the same manner as does the pulse rate in the song of the male.

(3) In species with broken trills, females are equally attracted to continuous trills of the same pulse rate, and pulse rate is still the determining factor in the response of the female.

(4) In species with regular chirps, the pulse rate does not determine the response of the females, since they will respond to pulseless chirps. The response is to a regular series of sounds of longer duration than the pulses. However, the pulse rhythm may strengthen the response of females to the chirp rhythm.

4. These experiments support the contention that song is directly related to reproductive isolation among singing insects. If so, it should be of major importance in the evolution of species. The songs of closely related species occurring

together can be expected to diverge more rapidly than characters which are unrelated to reproductive isolation—such as many of the morphological characters used in taxonomy.

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