

STUDIES ON THE ACOUSTICAL BEHAVIOR OF SEVENTEEN-YEAR CICADAS

(HOMOPTERA: CICADIDAE: *MAGICICADA*)

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INTRODUCTION

In 1956 the writers studied Brood XIII of the seventeen-year cicadas in northern Illinois and firmly established the existence of two distinct species (Moore and Alexander, in press). This was not a new suggestion, but its general lack of acceptance, even among taxonomists, indicated the need for a summarization of the evidence. The most drastic differences between the two closely related and highly sympatric species were found in their songs and singing behavior, and evidence was presented to demonstrate that the song differences were behaviorally significant. The suggestion was made that the songs act as congregating mechanisms for the adult males and females of each species and concomitantly reduce the number of interspecific encounters between sexually responsive males and females. No experimental data were available. Accordingly, in late May of 1957, when it became apparent that the same two species of *Magicicada* that appeared in Brood XIII in northern Illinois were appearing in Brood XIV in southern Ohio, field tests were planned to determine more specifically the role of song in the lives of these insects. This paper reports the results of those tests.

The Songs of M. septendecim (Linnaeus) and M. cassinii (Fisher) Brood XIV

Tape recordings and analyses of the songs of Brood XIV cicadas have revealed little or no variation from the responses of Brood XIII cicadas portrayed in figures 1 to 5, and described in detail by Moore and Alexander (in press). Consequently, only brief descriptions will be given here to facilitate understanding of the experimental procedure employed and interpretation of the additional information acquired during the present study.

The congregational song (fig. 1 and 2).—This is the only song produced in

chorus by both species. The individual phrases of the congregational song of *septendecim* (fig. 1) are low-pitched buzzes lasting 2 to 4 seconds and separated by intervals of 0.5 to 2 seconds. Each buzz has a rather narrow band of frequencies between 1 and 2 kilocycles per second and drops noticeably in pitch near its end. The individual phrases of the congregational song of *cassinii* (fig. 2) consist of two parts, a series of 12 to 40 ticks delivered at 16 to 25 per second and followed immediately by a loud, shrill buzz lasting 1 to 2 seconds. This buzz has a wide band of frequencies at about 4 to 6 kilocycles per second, and rises, then falls in pitch. In the song of *septendecim* the sound pulses in the buzz (due to individual vibrations of the tymbals) are delivered at 120 to 160 per second while those in the buzz of *cassinii* are delivered at 180 to 210 per second. These descriptions are based on recordings made at 88 to 90° F.

In both species the rhythm of the congregational song involves short bursts of flight as a result of which the singing individuals continually move from perch to perch. In the songs of individual males one to five song phrases are usually delivered between flight bursts, the number becoming smaller as the species nears the peak of its chorusing activity each day.

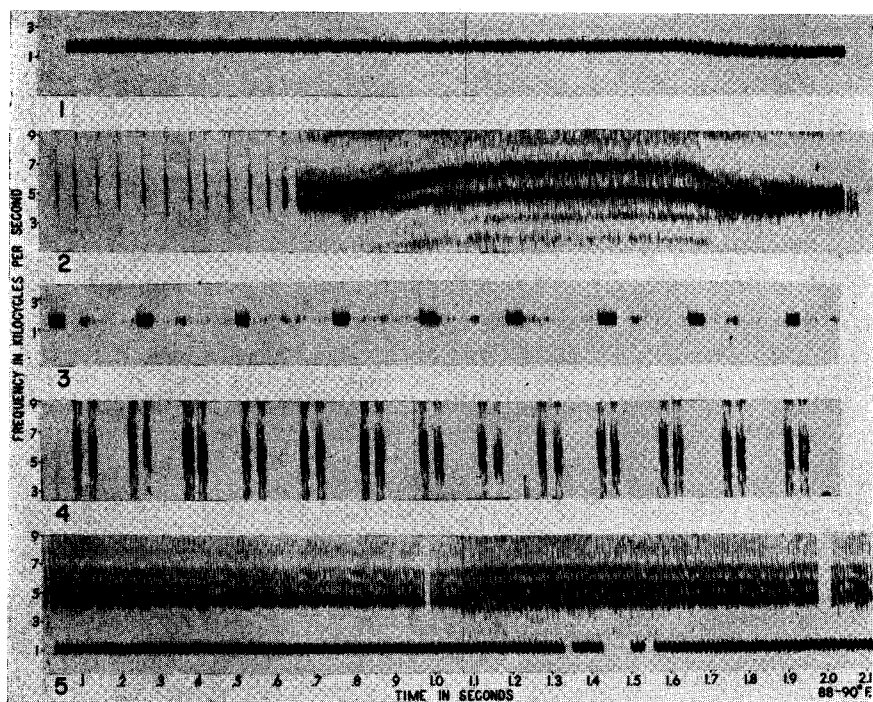
The courtship songs (fig. 3 and 4).—In 1956, a single sound for each species was heard during courtship and these were described and considered as analogous. However, during the present study an additional courtship sound has been heard for each species, and these indicate that the two courtship sounds heard in 1956 are not analogous. It is likely that these additional sounds do not reflect any difference between Broods XIII and XIV, but rather are a result of more time spent making detailed observations on Brood XIV in the field. Neither of the new sounds was recorded.

Next to the congregational songs of the two species, the most frequently heard sound in both broods was a prolonged slow ticking (3.6 to 6.7 per second) by *cassinii* males (fig. 4). The only other song noticed in Brood XIII was a rarely heard series of short buzzes by *septendecim* males produced at rates of 3.4 to 4.8 per second (fig. 3). Since these two sounds seemed to be analogous courtship songs, it was considered puzzling, both in 1956 and 1957, that the ticking should be heard so much more frequently than the buzzing. This was finally attributed to the different nature of the two sounds and the fact that the buzzing of *septendecim* is less noticeable in a chorus of its congregational song. Mention of this, however, caused two competent field observers to indicate to the writers that they had previously and independently believed the ticking to be the congregational song of a third species. Consequently, special care was taken to locate and observe males producing this sound during the present study. In all ten of such cases noticed in the field, the singing individual was a *cassinii* male courting a female or scuffling with another male. Both of the sounds heard in 1956 were also noticed to be produced in cages containing only adult males. This could possibly indicate a function other than courtship, but it should be noted that it is not unusual for a male insect to court other males. In the laboratory, five different males were heard to produce the ticking sound on one occasion and later the normal *cassinii* congregational song. These observations all appear to discount the suggestion of a third species, at least in broods XIII and XIV.

In 1957, two sounds were heard in addition to those heard in 1956. The first of these was a prolonged series of short buzzes (3 to 5 per second), apparently produced by *cassinii* males. No male was observed producing this sound, but to the ear it sounded exactly analogous in rhythm to the courtship sound already noticed for *septendecim* (fig. 3). The second new sound was a rapid production of shortened phrases resembling those in the congregational song of *septendecim*, but delivered at a rate of about one per second, with practically no intervening intervals. At first this sound was believed to be produced by an abnormal *septendecim* male since some noticeably deformed individuals had been heard producing

peculiar songs. However, after hearing this sound several times, it was realized that immediately following a series of 10 to 20 of the phrases, the short buzzes characteristic of courting males of *septendecim* were always produced. Two individuals producing the new sound were located, and in both cases the male was approaching a female two or three inches away. In both cases, as the male neared the female he extended his right foreleg and vibrated it rapidly. Then he began producing the short bursts already described for courtship and sidled close to the female. In one case the female prevented the male from mounting by extending her wing on the side from which he approached, and in the other case the female walked away and was pursued by the male until he accidentally dropped to the ground.

After these observations, we listened carefully and noticed that in the two cases heard thereafter, the intermittent buzzing of *cassinii* was produced im-



Audiospectrographs of the different sounds of *M. septendecim* and *M. cassinii* (relative intensities shown by darkness of the mark).

1. A single phrase from the congregational song of *M. septendecim*.
2. A single phrase from the congregational song of *M. cassinii*.
3. Several phrases from the song produced in advanced courtship by *M. septendecim* (faint marks are sounds of other individuals).
4. Several phrases from the song produced in preliminary courtship by *M. cassinii*.
5. Protest squawking of *M. septendecim* (lower) and *M. cassinii* (upper).

mediately following a series of slowly delivered ticks. This suggests that in both species there sometimes may be two sounds connected with courtship, and that the ticking of *cassinii* and rapid calling of *septendecim* are analogous to each other and are produced during a later stage of courtship. This suggestion fits well with the relative frequency with which each of the sounds was heard, as well as with the situations in which they were observed and with their structural relationships.

The series of rapidly delivered calls of *septendecim* is probably obscured most of the time because of its close resemblance to the congregational song.

The significance of the courtship sounds is unknown, but at least four possible functions can be suggested: (1) they may attract responsive females to individual males across short distances; (2) they may be a necessary prerequisite to successful copulation after the male and female have come into close proximity; (3) they may shorten the time between an initial encounter between male and female and subsequent copulation; and (4) a male capable of producing these sounds may successfully copulate with a female simultaneously or just previously courted by males unable to produce these sounds. The courtship sound is only produced when the male and female are in close proximity. The infrequency with which the sounds are heard suggests that they are not produced prior to every instance of copulation. These points seem to suggest the third and fourth possibilities as most likely of those mentioned.

The protest squawks (fig. 5).—In both species the males vibrate their tymbals when captured, held, disturbed into flight, or otherwise irritated. These sounds are more or less arrhythmic, but because of their frequencies and the rate of vibration of the tymbals they are just as distinctive as the other sounds produced by the two species.

The Chorusing Behavior of Seventeen-Year Cicadas

The congregational song is the only sound produced in chorus by species of *Magicicada*, and the remainder of the paper deals only with these particular sounds.

Climatic factors.—Figures 6 and 7 illustrate fluctuations in the chorusing activity of *septendecim* and *cassinii* and in concomitant climatic conditions on a clear, windless day and a cloudy, rainy day, respectively. The observations were made with the equipment set up in the middle of a clearing about 20 feet in diameter in a pasture overgrown with small trees. Temperature was read from a mercury thermometer placed horizontally in the sun (between about 6:45 A. M. and 5:30 P. M.) about six inches above the ground. Light intensity was determined with a Weston Illumination Meter, Model 603. Early and late in the day, readings were taken with the sensitive element facing directly upward. When this became impossible the element was inverted and propped in a set position facing down into the grass from a height of about four inches (fig. 6 and 7, indicatory). Wind and sun were calculated by arbitrarily setting up the categories given in the figure and then subjectively assigning conditions at the time of observation to one of the categories. Sound intensity readings were taken with a General Radio Sound Level Meter, Type 1551-A, using an Amphenol Crystal Microphone, Model 9898. All readings were taken at intervals of 15 minutes or less throughout the day. The maximum and minimum sound intensity readings were taken over a period of about ten seconds.

The nature of the chorusing activity is different for the two species. As mentioned earlier, both species have short bursts of flight incorporated into their singing rhythms as a result of which they may move from a few inches up to several yards from their previous perch. Early in the daily chorusing period, three, four, or more repetitions of the congregational song phrases are produced between flight bursts. As the number of individuals involved in song, the total intensity of the sound, and the uniformity of the sound intensity over the area occupied by the colony increase, fewer song phrases are repeated between flight bursts. In *septendecim* there is no synchronization of song phrases so that the total sound of a colony in full chorus fluctuates little in intensity. In *cassinii* the individuals synchronize their buzzes and when conditions are optimum (about 1 to 4 P. M. on cloudless, windless days and in a strong colony) an incredible degree of synchrony is achieved. Only one buzz is produced by each individual between flight bursts

at this height of activity, and most or all of the ticking is produced during the flight bursts. Almost every singing male in a woods containing tens of thousands of singers achieves synchrony with all the others, and the result gives the impression of a gigantic game of musical chairs. A treeful of these insects singing in synchrony is motionless when observed during the great burst of sound caused by all the males buzzing together, and then becomes a frenzy of activity between buzzes with nearly every individual changing perches. At such times the flutter of wings is so loud between buzzes that it almost obscures the ticking part of the song. The rate and regularity of fluctuations in sound intensity during synchrony by a chorus of *cassinii* are shown in figure 8. This is a line graph drawn from readings of time and sound intensity made simultaneously by two observers. The shape of the curves is nearly symmetrical except for a slight rise (not shown

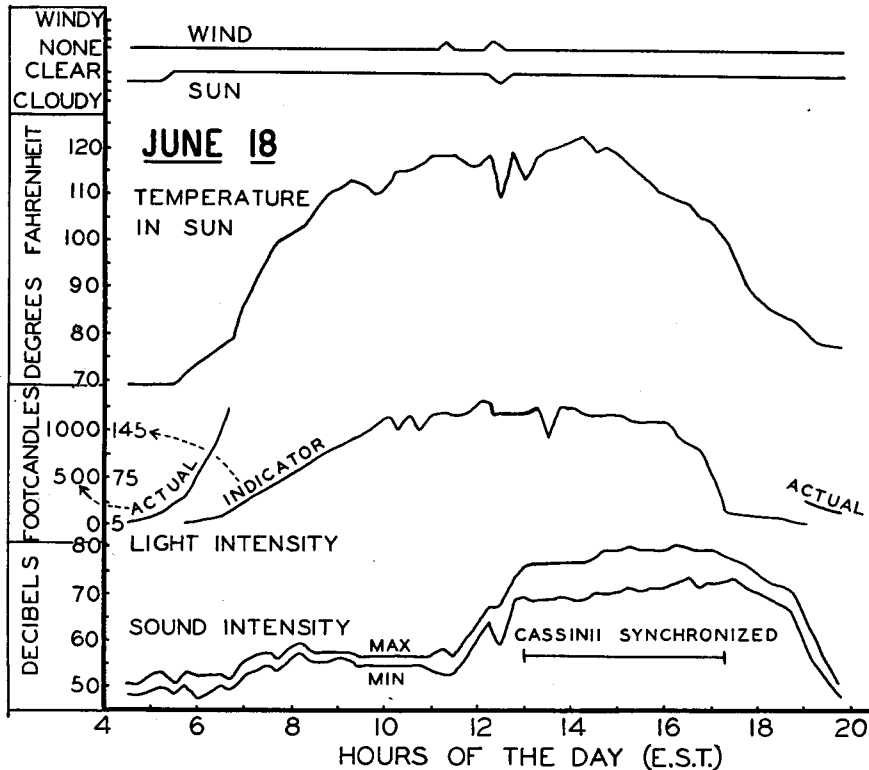


FIGURE 6. Fluctuations in the chorusing activity of *M. septendecim* and *M. cassinii* and in the concomitant climatic conditions on a clear, windless day.

in fig. 8) which occurred about one-half second after the greatest dip and held for a moment before the needle climbed steadily again to a peak. This rise in intensity apparently corresponded with the starting of ticking after the end of the previous buzz. It may be noted that the buzzes of the individual males in a colony are not perfectly synchronized since these last only about two seconds, while 5 to 6 seconds are required for the complete cycle of sound to be produced by the colony. However, the tremendous number of individuals which regularly lump their buzzes together in this short space makes this a high degree of synchrony, perhaps the most remarkable occurring anywhere in the animal kingdom.

The effect of climatic conditions on choruses of *septendecim* and *cassini* is clearly demonstrated by the various fluctuations in sound intensity in figures 6 and 7. Both species sing only during the day. They chorus more strongly on clear, windless days than on cloudy, rainy, or windy days. They are silent during prolonged rain and during brisk showers, building back up in chorusing activity if the rain stops and the vegetation dries or the sun reappears. Both species appear to be quite sensitive to changes in light intensity, increasing their chorusing activity noticeably at the appearance of the sun in the morning and dropping off in chorusing activity when the sun passes behind a cloud. When the sun reappears from behind a cloud, the intensity of chorusing activity increases, the suddenness and degree of this change corresponding to the suddenness of the reappearance of the sun and the amount of difference in light intensity before and after its reap-

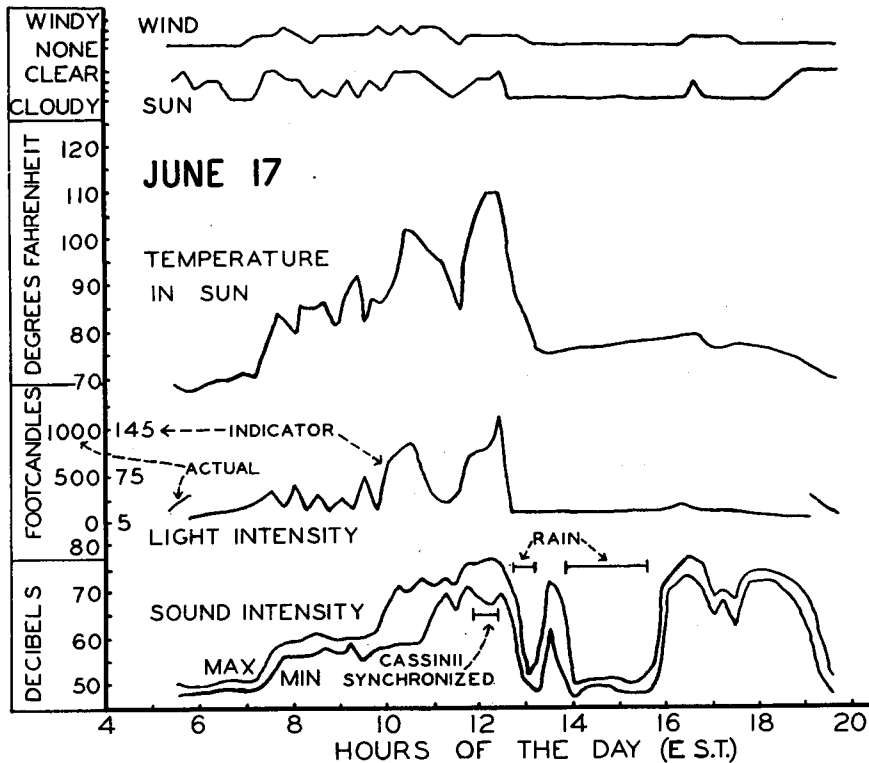


FIGURE 7. Fluctuations in the chorusing activity of *M. septendecim* and *M. cassinii* and in the concomitant climatic conditions on a cloudy, rainy day.

pearance. In the test area, *septendecim* began singing intermittently in early dawn and chorused most strongly on clear, windless days at about 11 A. M., gradually falling off in chorusing activity until only a few individuals were still singing at dusk. *Cassini* began intermittent singing rather suddenly at sunrise and on clear, windless days generally reached a peak of chorusing activity between 1:00 P. M. and 3:00 P. M., gradually falling off in chorusing activity after this until, like *septendecim*, only a few individuals were singing at dusk. Both species entirely stopped singing in late dusk, and only an occasional squawk could be heard at night. Apparently, little activity other than feeding occurs at night, with copulation and oviposition as well as all normal sound production taking place during

the day. Pairs frequently remain *in copula* during part of the night after entering into copulation in late afternoon. Both species appear to oviposit in greatest numbers in early morning and to become involved in copulation in greatest numbers about the time their chorusing activity is beginning to wane. In one case in the test area a pair of *septendecim* entered into copulation sometime between 10:00 and 10:15 A. M. and remained in copula until sometime between 3:15 and 3:30 P. M., after falling to the ground at 2:15 P. M.

The sound level when both species of *Magicicada* were silent in the morning and evening fluctuated from about 47 to 50 decibels, and all readings in figures 6 and 7 above this were caused only by the sounds of *Magicicada*. At the height of the *septendecim* chorus, about 9 to 11 A. M., and in the absence of *cassinii* chorusing, the sound level was about 55 to 60 decibels. Occasional bursts of song by small groups of *cassinii* individuals caused temporary readings during the mornings as high as 65 to 70 decibels (not shown in fig. 6), but the maximum and minimum were read for *septendecim* as long as was possible both days. After about 11:30 A. M. on June 18 and 9:45 A. M. on June 17 it was no longer possible to determine the intensity of the *septendecim* chorus because at these times the minimum readings on the sound level meter rose abruptly to a level above the maximum for *septendecim* due to the development of continuous chorusing by *cassinii*. The bursts by *cassinii* in the morning occurred erratically and with little increase in

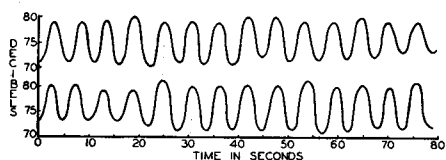


FIGURE 8

FIGURE 8. The degree and regularity of fluctuation in sound intensity produced by a synchronized chorus of *M. cassinii*.

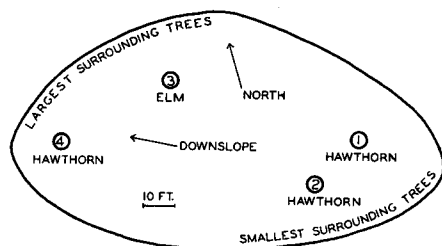


FIGURE 9

FIGURE 9. Diagram of the clearing used in the song specificity tests, showing the location of the four cage trees and the general characteristics of the area.

rate or regularity but with gradually increasing intensity (more individuals involved). On June 18 *cassinii* suddenly achieved synchrony at about 12:55 P. M. This synchrony was maintained until shortly after 5:00 P. M., when it gradually disappeared. This is illustrated in figure 6 by both the height and the degree of separation of the maximum and minimum sound intensity readings. When *septendecim* was in full chorus the fluctuation from maximum to minimum sound intensity was only 2 to 3 decibels at about 55 to 60 decibels. However, when *cassinii* was synchronized, the fluctuation was 8 to 12 decibels at about 70 to 80 decibels. These readings were taken 10 to 15 feet from the nearest singing individuals and in the area where *septendecim* was most abundant. Table 1 shows the range and mean of sound intensity readings taken about six inches from ten singing and ten protesting individuals of both species.

The development of synchrony by *cassinii* was quite sudden on June 18 (fig. 6) and seemed puzzling at the time. Plotting the data for June 18 revealed a distinct drop and rise in sunlight, temperature, and light intensity just prior to the development of synchrony by *cassinii*. Whether or not this actually triggered the sudden development of synchrony is unknown. However, the brief synchrony achieved on June 17 (fig. 7) occurred immediately following a similar fluctuation caused by a passing cloud.

Mutual stimulation.—The synchrony of *cassinii* and the development of chorusing through bursts of song by small groups of individuals demonstrates that *cassinii* is stimulated into song by hearing the singing of its own species. This was even more clearly demonstrated by playing continuous loops of tape recordings of various *cassinii* sounds to individuals released in Neotoma Valley, Hocking County, Ohio, where no seventeen-year cicadas occurred this year. The experiment was originally planned to test whether or not males and females could be attracted to a tape recorder. Unfortunately, shortly after the cicadas were released the weather became cloudy and little singing and practically no flying occurred for the rest of the day. The next two days were also rainy and cloudy, and on the third day and thereafter no cicadas could be heard or seen in the area. Due to other commitments the experiments could not be repeated. However, this cloudy weather, when the cicadas were singing little or not at all, provided an unexpected opportunity to test the possibility of stimulating cicadas into song with tape recordings.

Cicadas were released in approximately the following numbers: *septendecim*, 175 males, 100 females; *cassinii*, 250 males, 200 females. The cages containing the cicadas were upended on the edge of a woods bordered by tall weeds and sumac, and the sleeves were propped open, allowing the cicadas to crawl up and out onto the surrounding vegetation. The tape recorder and amplifier were set up on a small table about 30 feet away. The tapes played were recordings of Brood XIII made in Illinois in 1956 at 88 to 90° F, using a Magnemite Tape

TABLE I
Maximum sound intensity in decibels about six inches from ten individuals of *M. septendecim* and *M. cassinii*

	<i>cassinii</i>		<i>septendecim</i>	
	congregational song	protest squawk	congregational song	protest squawk
range	87—99	85—94	70—78	70—79
mean	94.4	89.4	74.3	73.9

Recorder, Model 610-EV, with a tape speed of 15 inches per second, and an American Microphone Company Model D-33A Microphone. The tapes were played back with a PT63J Magnecorder, using a PT63-A2HZ Amplifier for the *septendecim* sounds, and a Jensen High Frequency Unit for the *cassinii* sounds. After some experimentation it was found that the released *cassinii* responded as well to the sounds played through the Magnecorder amplifier as to those played through the high frequency unit, though they were greatly distorted in frequency to the human ear.

The *septendecim* sounds played were as follows: (1) a single congregational song phrase repeated once every six seconds, (2) a single congregational song phrase repeated twice every five seconds, (3) a chorus dominated by a single individual, (4) a homogeneous chorus (no dominating individuals), (5) continuous protesting by a single individual, (6) courtship (short buzzes as in fig. 3) by a single individual. None of these sounds produced any apparent response from the *septendecim* individuals released in the area. They were played at 10 to 11 A. M. and again at 2 P. M. While the tapes were being played, *septendecim* males were singing intermittently and individually. The sound intensity from the recordings was 65 to 70 decibels near the released cicadas. The air temperature varied from 85 to 90° F in the area.

The *cassinii* sounds played were as follows: (1) a single complete congregational phrase repeated once every five seconds; (2) same, but with the intervals between ticks and buzzes removed, thus causing the phrase to be repeated twice every five seconds; (3) same as (1) but with the ticks in the phrase following the

buzz rather than preceding it; (4) continuous ticking by a single individual at a rate of 16 to 20 ticks per second (from the congregational song phrase); (5) a single congregational song phrase with the ticking removed, repeated once every four and one-half seconds; (6) same but with the interval removed, thus repeated at a rate of 2 to 3 buzzes every five seconds, (7) an unsynchronized chorus; (8) a synchronized chorus (12 phrases per minute); (9) continuous protesting by a single individual; (10) continuous courtship ticking by a single individual at a rate of four ticks per second; and (11) same but at a rate of six ticks per second. The sound intensity near the cicadas was 75 to 80 decibels. No individuals flew to the tape recorder. However, as the first *cassinii* sounds began to play, a strong increase in the singing of the released males was noticed, and subsequently every sound except the courtship ticking increased the chorusing of the released males. There was no response to tapes played at half speed, or to *septendecim* sounds, but response occurred to tapes played backward as well as to those played forward. The released males synchronized rather imperfectly with tapes (1), (5), and (8), and produced ticks in the interval between buzzes on tape (5). They sang asynchronously and continuously, though irregularly, with tapes (2), (3), (4), (6), (7), and (9). If the recorder was stopped suddenly in the middle of a buzz of any

TABLE 2
Numbers and kinds of cicadas in each of the tree cages on the test plot during each day of the test

Cage Day	1	2	3	4
June 1	31 silenced <i>septendecim</i> ♂	200 normal <i>septendecim</i> ♂	200 normal <i>cassinii</i> ♂	61 silenced <i>cassinii</i> ♂
June 4	100 normal <i>septendecim</i> ♀	200 normal <i>septendecim</i> ♂ 100 silenced <i>cassinii</i> ♂	200 normal <i>cassinii</i> ♂ 50 silenced <i>septendecim</i> ♂	200 normal <i>cassinii</i> ♀
June 5 June 6	200 normal <i>septendecim</i> ♀	200 normal <i>septendecim</i> ♂ 200 silenced <i>cassinii</i> ♂	200 normal <i>cassinii</i> ♂ 200 silenced <i>septendecim</i> ♂	200 normal <i>cassinii</i> ♀

kind, or immediately after a buzz, there was near silence for about a half second, and then the released males started ticking in chorus. If the recorder was not again turned on, only a few of the tickers finished with a buzz. When tape (1) was played backward, the released males began ticking immediately after the recorded ticks, then buzzed slightly behind the buzz on the tape. Thus, they were silent during the last part of the ticking on the tape, and ticked while the tape played silently.

These results indicate that hearing the cessation of the buzzing part of the congregational phrase stimulates ticking, and hearing the beginning of a buzz stimulates buzzing. At least a few individuals always followed a series of ticks with a buzz, even in the cloudy weather during the tests when the ticking was stimulated artificially. A part of the mechanism of synchronization is thus demonstrated by these results. It is possible that visual as well as auditory stimulation is involved in the synchrony of *cassinii*, part of the mechanism involving active synchronization of flight bursts and part of it involving active synchronization of sound bursts. This may be associated with the ease with which *cassinii* is disturbed into flight by nearby motion, and with its failure to synchronize except in high light intensity. It could also explain in part the failure of *cassinii* to accumulate on the outside of a cheesecloth-covered tree containing singing *cassinii*, since the cheesecloth would largely prevent mutual stimulation

and synchronization of flight bursts. The percentage of singers in a colony responding to a given rhythm probably depends on the intensity of the sound and climatic conditions. Further experimentation will be necessary to determine why *cassinii* does not achieve synchrony in the morning, though this may be dependent upon light intensity alone.

Tests on the Congregational Song as an Isolating Mechanism

Our observations to this point had suggested that the congregational song causes sexually responsive males and females to move into close proximity, and that the method of movement is chiefly through flight. This indicated that any test of this hypothesis would need to be conducted in an area in which the tested cicadas could fly freely and in which the light intensity was that normally encountered outside on a clear day. It was thus considered preferable to conduct the tests in the field, and the original plan was to secure large numbers of newly emerged adults, keep the sexes separate for a week or two, and then use these virgin adults in tests in an area in which no cicadas occurred this year. However, we were completely unsuccessful in keeping cicadas alive and vigorous in cages even though they were provided daily with freshly cut branches and leaves upon which to feed. Some feeding took place in the cages, but the adults died off rapidly; only a few living longer than a week and their vigor was much below normal. They sang very sporadically and only individually after being caged a few days. There was little flight in the cages which were approximately three feet on each side. This difficulty in keeping adult cicadas alive and vigorous in cages is not unusual. We found later, as did Beamer (1938) with various species of *Tibicen*, that it is possible to keep *Magiccicada* adults in apparently normal condition in cheesecloth cages over branches of living trees. This indicates that the cicadas cannot feed satisfactorily on cut branches, perhaps because of a difference in turgor. Certainly feeding is an important consideration in spite of the surprising number of reports to the contrary in the literature. Cicadas can be observed feeding in great numbers in the field, and the defecation of a treeful of adults is like a continuous sprinkling rain. Cicadas which had remained vigorous in tree cages for a week died within two days after the trees upon which they were caged were sawed off near their bases, even though the trees were immediately placed in jars of water and did not wilt visibly until the second day. Two other tree cages of cicadas were set up at the same time and were left intact and the cicadas in these survived at least a week longer than those in the severed trees.

After these first failures it was impossible to secure virgin cicadas in numbers and with certainty from this brood. Consequently, an area was selected which contained both species in abundance and field tests were conducted to determine if uncaged cicadas from the natural population could be attracted to choruses by caged individuals, and if so, what evidence of specificity or lack of specificity of response could be obtained.

Description of test area.—The test area for this portion of the study and for the sound intensity tests already described, is located eight miles southeast of Clarksburg, Ohio, on State Route 277 in South Union Township, Ross County. It is a hillside pasture, thickly overgrown with honey locust, walnut, and ash, 20 to 30 feet tall, and with hawthorn, crab apple, and elm, 4 to 20 feet tall. There is little or no underbrush and a ground cover of bluegrass occurs over most of the area. A few large old oaks are located within 100 to 200 yards of the test plot. This area was selected because it contained both species in great abundance and because there were no large trees in the immediate vicinity. This meant that (1) the cicadas could be collected in large numbers with little difficulty, and (2) cicadas caged in trees small enough to be covered with cheesecloth and observed would be more nearly on a level with the uncaged cicadas actively flying and singing outside.

Experimental procedure.—An oval plot about 100 feet long and 50 feet wide

was cleared in the test area (fig. 9 and 10). Four small trees about 10 to 12 feet tall and similar in size and shape were left and were covered with large cheesecloth nets. Into these cheesecloth cages were placed males and females of both species in the numbers and kinds indicated in table 2. Control males were silenced by ripping their tymbals with a needle. This did not appear to affect their behavior otherwise or to hasten their death. While the normal males were singing, some of these silenced males were producing very weak sounds with their damaged tymbals and performing the other activities normally occurring during song.

After the cages had been filled with different kinds of cicadas on June 1, observations were made on June 1, 4, and 5, to determine how many and what kinds of cicadas appeared on the outside of each of the cages during the day. These results were correlated with climatic conditions, the activity of the uncaged cicadas, and the chorusing activity of the caged cicadas. On June 6 the positions of cages 2 and 3 were reversed by sawing off the trees near their bases and tying them in place in the new locations with the butts immersed in water. Observations were made for one day (June 6) with these cages in the new locations to determine the effect of position of the cages both in the clearing and with respect to the cages containing females. The results of the four days of observation are summarized in figures 11 to 16.

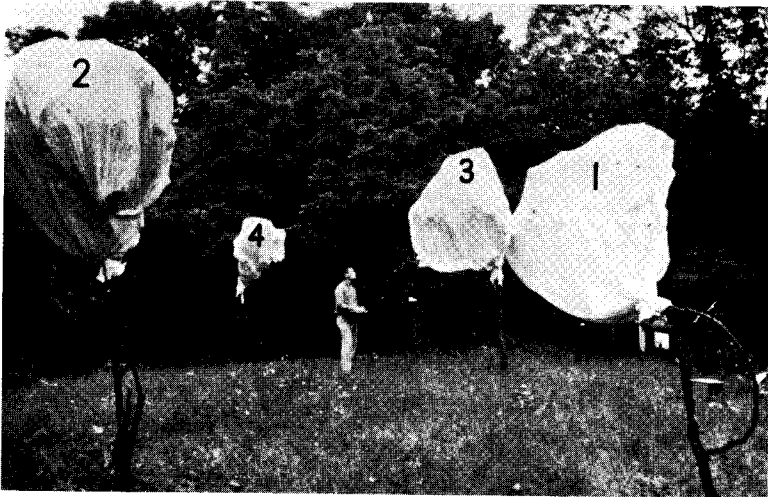


FIGURE 10. Photograph of clearing facing downslope from southeast corner.

It was originally planned to use cages 1 and 4 as controls containing silenced males. However, the silenced males were eventually placed in the test cages and those in cages 1 and 4 replaced with normal females. Due to the smaller numbers of *septendecim* in the area, it was difficult to collect enough individuals to bring the numbers up to 200 in each of the cages. However, as shown in figures 12 to 16, neither the fluctuations in numbers of cicadas in the different cages nor the reversing of position of cages 2 and 3 on June 6 had any large effect on the proportions of cicadas appearing on the outside of the cages. The numbers of cicadas inside the cages were maintained by counting the dead cicadas in the bottoms of the cages each morning and replacing these with an equal number of freshly collected live cicadas.

On June 1 we attempted to estimate in what proportions the two species were present in the area immediately surrounding the clearing. This was done by (1) circling the clearing on a cloudy morning, disturbing the bushes and trees as much as possible and then counting the numbers of cicadas which alighted on the

outsides of the cages, and (2) counting all the cicadas present on 50 different branches in the immediate surrounding area. In the first case we obtained a count of 93 *cassinii* and 11 *septendecim*. In the second case we counted 805 *cassinii* and 200 *septendecim*. These estimates were subject to large errors. *Cassinii* is much more easily disturbed into flight than *septendecim* and this undoubtedly influenced the first count. Error in the second count was caused by the fact that *cassinii* individuals were usually congregated along the main trunks and in the tops of the trees while *septendecim* individuals were most abundant on the lower branches, the only place that we could make accurate counts. It is reasonable to expect that the actual proportions of *cassinii* individuals to *septendecim* individuals was somewhere between the proportions of 8:1 and 4:1 obtained in these instances.

During the early observations on June 1, all the cicadas were caused to fly from the outside of each cage after counting them each time. Later this procedure was abandoned because cicadas which moved only as far as the next cage distorted the readings on the other cages and because there was no way of knowing that the time lapse between our observations was sufficient to allow reorientation of the disturbed cicadas. Furthermore, it was noticed that only a few individuals alighted and just sat for any length of time on a cage. The only cicadas which remained around a particular cage for any length of time were individuals which were actively singing and flying and obviously being stimulated by the chorus coming from inside the cage. A few times small choruses were begun by *cassinii* males congregated on the outside of the *septendecim* cage, and vice versa. No attempt was made to break these up because they were always of a minor nature and it was reasoned that if the cage chorus was an attractant such small groups could not compete with the choruses inside the cages.

Before beginning the observations each day, the cicadas which had climbed or alighted upon the cages during the night were removed. The numbers of cicadas of both sexes and both species alighting on the outside of each of the cages were then determined at intervals by walking slowly around the cages and counting them from the ground. After collecting large numbers of these cicadas one becomes readily able to distinguish both the species and the sexes at some distance. Our accuracy was gauged by checking each other's counts several times, and each time the same numbers were obtained by both observers. The only source of error that appeared was in the possibility of counting some very small females of *septendecim* as females of *cassinii*, and accordingly a special effort was made to positively identify any doubtful females.

Results.—Figure 11 shows the climatic conditions during each of the four test days and the status of the natural and the cage choruses of both species. This figure will allow comparison of the results obtained in the cage tests with the more objective data in figures 6 and 7 concerning the effects of climatic conditions on chorusing activity. Unfortunately, the sound level meter was not available until several days after the cage tests had been completed and the importance of precise knowledge of fluctuations in climatic conditions was not apparent until the tests were nearly completed and the data plotted.

In assessing the significance of the various numbers and kinds of cicadas present at the cages at different times of day and on different days, the following factors should be considered: 1. A slight increase should be expected in the numbers of cicadas of all kinds on all cages during the times that the uncaged cicadas were actively singing and flying. 2. Cages 2 and 3, the test cages emitting choruses of *septendecim* and *cassinii*, respectively, had a few more cicadas perched on them than control cages 1 and 4, even when there was little or no chorusing inside or outside the cages. 3. The actual numbers of cicadas attracted to the cages have little significance. The cages were competing with strong natural choruses. They were necessarily in unfavorable locations because they were in

small trees in a clearing and there is no information available as to the distance from which cicadas can be attracted by a chorus. It is likely that the cage choruses influenced only those individuals flying near the cages, accidentally alighting on them, or singing in the nearest tree which in every case was 15 to 20 feet away. The cheesecloth not only lowered the light intensity inside the cages and thus reduced the intensity of the chorusing of the caged individuals, but also there are indications that it was less suitable as a perching place for singing individuals than tree leaves and branches. Certainly the cheesecloth reduced contact between

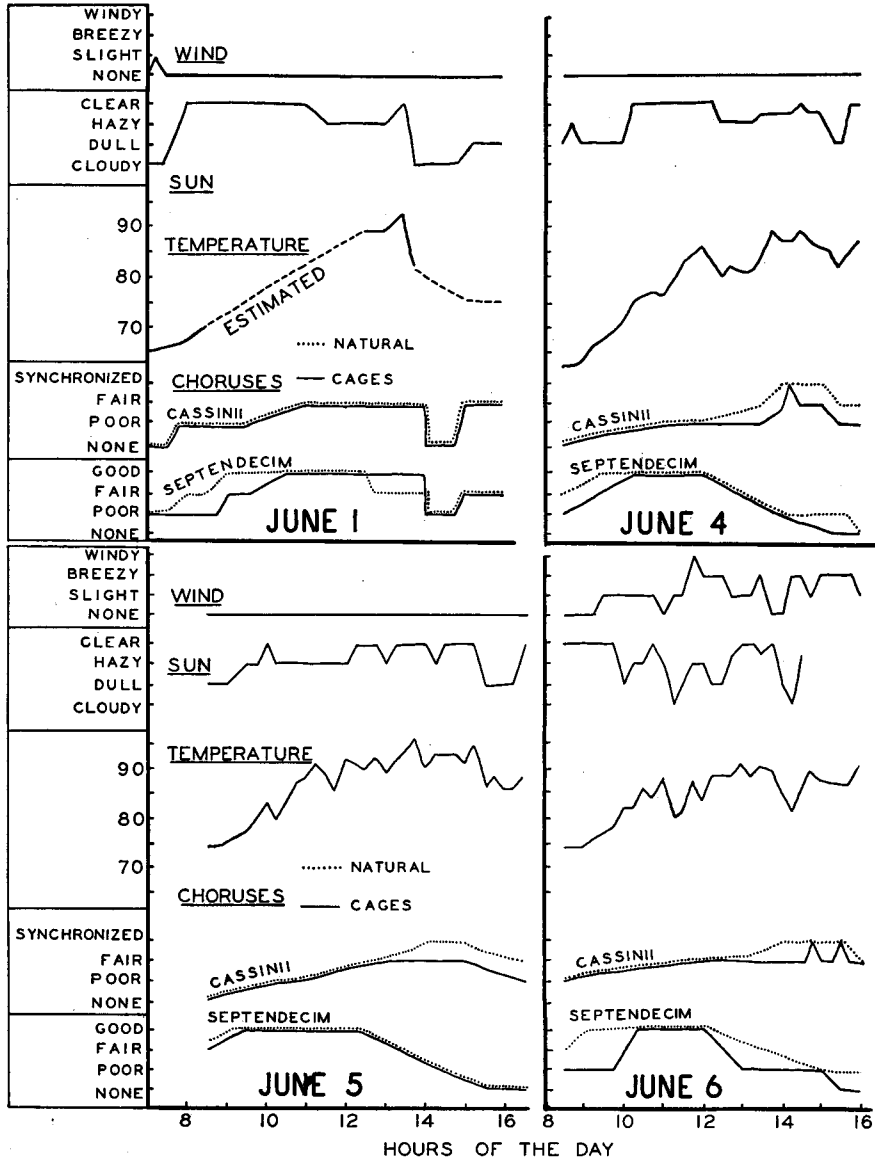


FIGURE 11. Climatic conditions and status of the natural and cage choruses of *Magicicada* during the test days.

cicadas alighting on opposite sides of the tree and between the individuals inside and those outside the cage. For these reasons the data is given in terms of proportions of individuals of each species and each sex attracted to each cage (fig. 12 to 15) and proportions of the two species attracted to cages 2 and 3 (fig. 16). 4. The activity of the cicadas on the outside of a cage, though not transmitted in figures 12 to 16, was frequently more important than the numbers of cicadas involved. Nearly all *septendecim* males remaining on the outside of cage 2, and

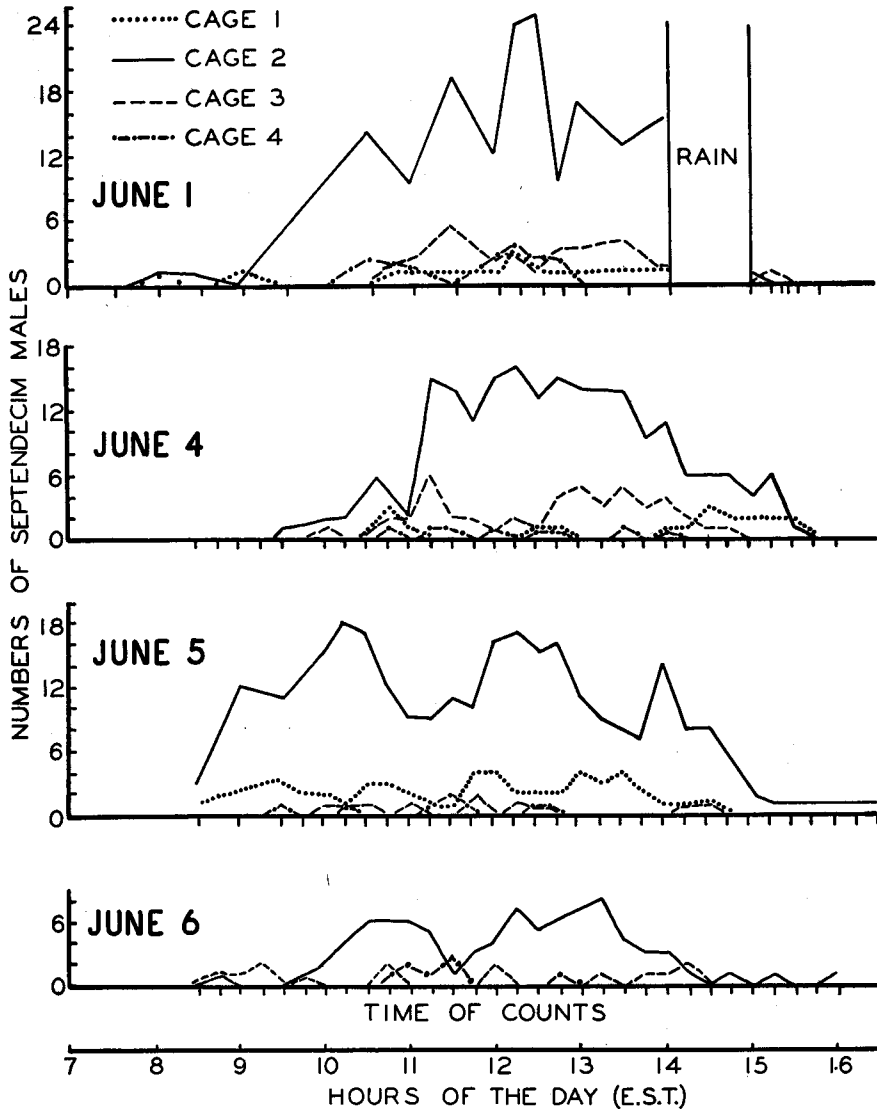


FIGURE 12. Numbers of males of *septendecim* at each cage at intervals throughout each of the test days.

cassinii males remaining on the outside of cage 3, were pursuing and courting females or singing and flying. The *cassinii* males on the outside of cage 2 and *septendecim* males on the outside of cage 3 either were not performing these activities or their stay on the cage was brief. Five instances of *septendecim* copulation were

noted on cage 2 and one on cage 1; one instance of *cassinii* copulation was noted on cage 3. No other cases were observed. Many *septendecim* individuals were missed in the counts on cage 2 because they had fallen to the ground scuffling. 5. The tests were initiated 7 to 10 days after strong chorusing by both species had begun. The large numbers of ovipositing females observed suggests that the proportion of virgin females in the area was low. This probably accounts for poor test results with females and may have caused a slight increase in the numbers of responding males.

As indicated in figures 12 to 15, the most positive data were obtained with males of *septendecim* (fig. 12). These cicadas were attracted to cage 2 in considerably higher numbers than to any other cage, even higher than to cage 1 only fifteen

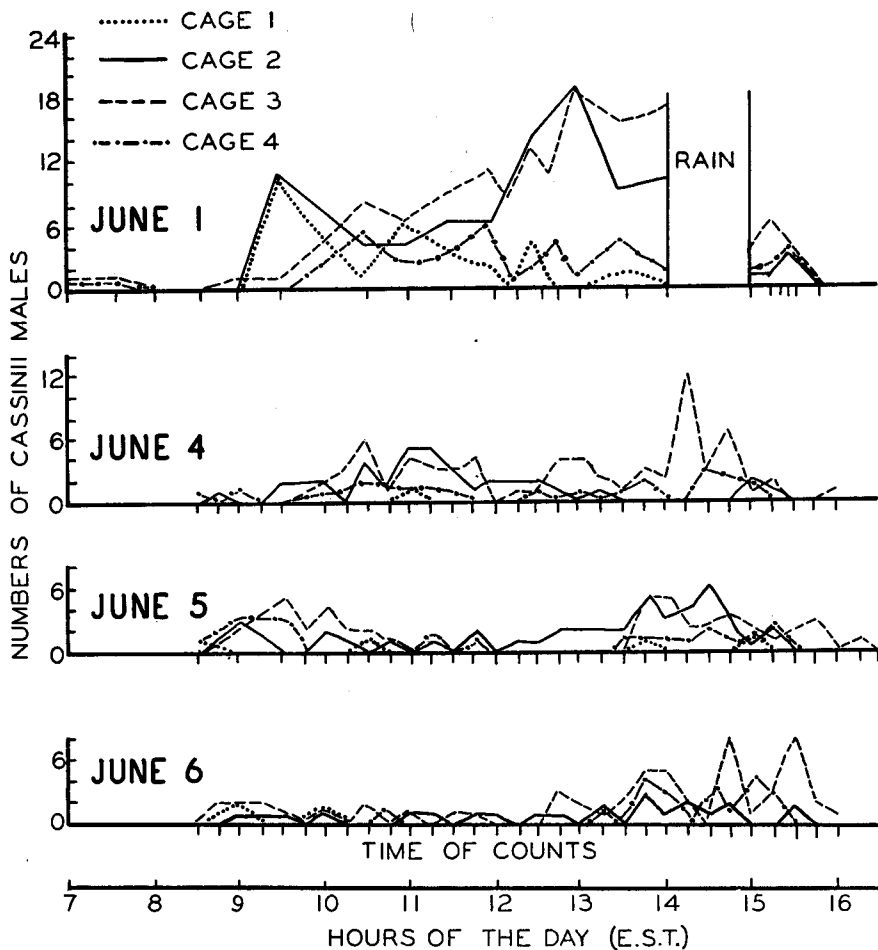


FIGURE 13. Numbers of males of *cassinii* at each cage at intervals throughout each of the test days.

feet away and containing 200 *septendecim* females. The largest numbers of individuals began to accumulate on cage 2 at about the time the cage was estimated to be developing a strong chorus (fig. 11). The subjectivity of the evaluation of the status of the cage choruses prevents precise comparison of the time

of these two events. A slight increase in numbers of cicadas on the outside of the cages occurred just prior to the development of strong choruses inside the cages due to the fact that the natural choruses generally developed before the cage choruses and caused an increase in the flying activity of the uncaged cicadas.

Cage 1 shows a slightly higher number of *septendecim* males than cages 3 and 4, apparently because of a kind of "overflow" of singing, flying males obviously being stimulated by the chorus in cage 2. On June 6, when the cage containing the *septendecim* chorus was moved away from the cage containing *septendecim* females, the latter showed not a single male at any time during the day though there should have been more sexually responsive females inside the cage than at any previous time. On June 5 the consistently higher number of *septendecim* males on cage 1 was due to a cluster of two to four males which remained on the cheesecloth directly opposite a group of three *septendecim* females for nearly the whole day. These were apparently sexually responsive females and this seems to demonstrate that a sexually responsive female in very close proximity to a male is more attractive than a nearby strong chorus by males.

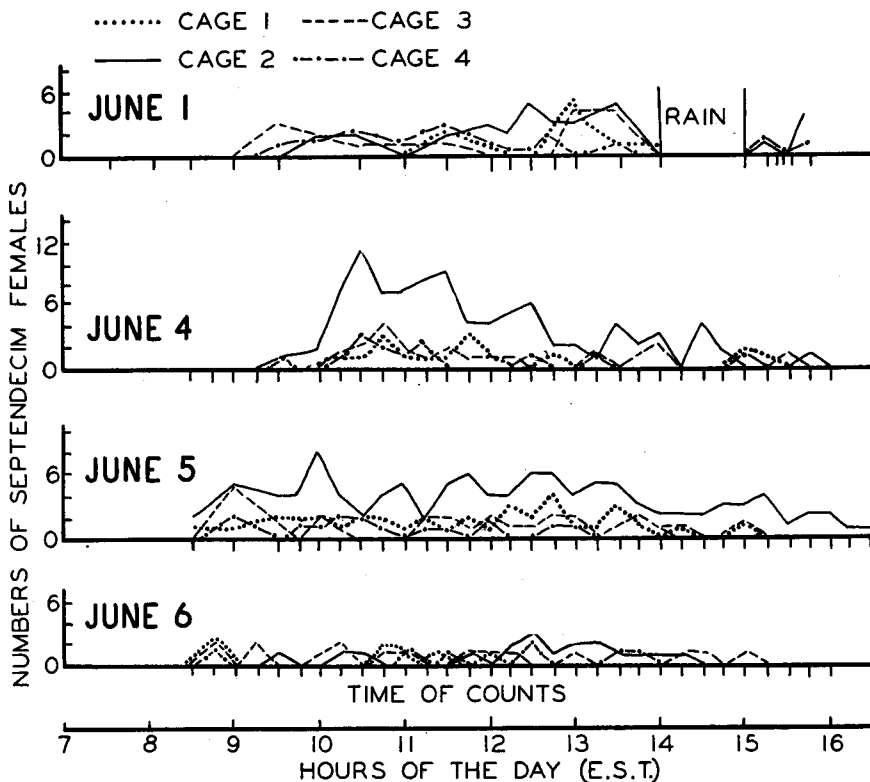


FIGURE 14. Numbers of females of *septendecim* at each cage at intervals throughout each of the test days.

As illustrated in figure 13, cage 3 was much less successful in attracting *cassinii* males than cage 2 was in attracting *septendecim* males. Although the proportions of *cassinii* individuals at this cage were usually much higher than should have been expected on the basis of estimated proportions of individuals in the total population (fig. 16), at only three times was the number of males of

cassinii much higher at cage 3 than at any other cage. These times were at 2:15 P. M. on June 4 and at 2:30 and 3:30 P. M. on June 6. Upon examining figure 11, we noted that these were the only times that the caged *cassinii* were in synchrony with the natural chorus. At no time did the caged *cassinii* achieve synchrony within the cage and not with the natural chorus. This seems to demonstrate that the pulsations in total sound intensity produced by a synchronized chorus of *cassinii* are correlated with the effectiveness of the sound as an attractant to *cassinii* individuals.

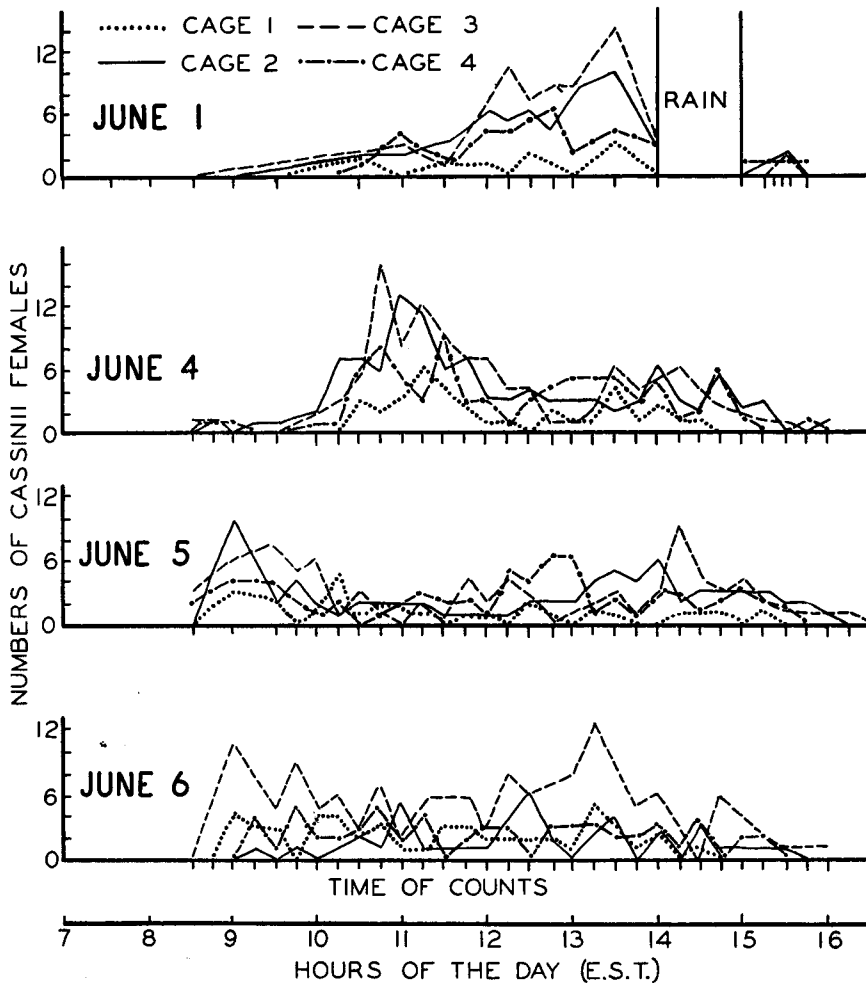


FIGURE 15. Numbers of females of *cassinii* at each cage at intervals throughout each of the test days.

There are several factors which may be involved in the general failure of the caged *cassinii* to develop synchrony and to attract more individuals. The natural *cassinii* chorus was much stronger in relation to the cage chorus than the natural *septendecim* chorus to its cage chorus. Cage 3 was in a less favorable location than cage 2, as is shown by the results obtained for both cages on June 6 when their positions were reversed. This was partly due to the original cage 3 location

being farther from the edge of the clearing and partly due to its being shorter in relation to the surrounding trees (fig. 9). In addition, singing and flying *cassinii* individuals congregate near the tops of trees while *septendecim* is usually found on the lower branches. *Cassinii* individuals flying over the clearing were usually 20 feet above the top of cage 2. Finally, the lowered light intensity inside the cheesecloth had a greater effect on the chorusing of the caged *cassinii* than on the chorusing of the caged *septendecim*.

In addition to the immediate effects of cloudy, rainy weather on the activity of *Magiccada* (fig. 11), another, cumulative effect may be visible in the results shown in figure 14. Just prior to June 1 there had been several days of fair weather during which it can be assumed that both species were chorusing well and sexually responsive females were having little difficulty in encountering

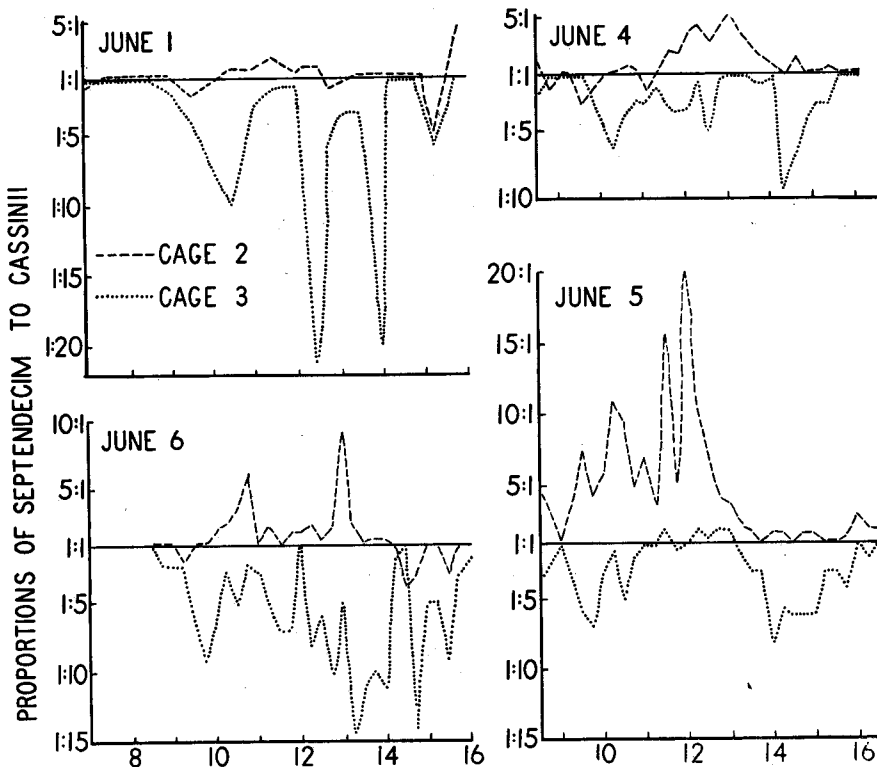


FIGURE 16. Proportions of individuals of *M. septendecim* and *M. cassinii* at cages 2 and 3 at intervals throughout each of the test days (all zeros are considered as ones).

sexually responsive males. None of the results with females were as good as those with males and it is possible that this was due to a low incidence of virgin females during the tests, as already suggested. A few cloudy, rainy days, however, should have the effect of increasing the proportion of sexually responsive females in an area because of the presence of newly emerged females and perhaps because of previously mated females again becoming sexually responsive. During June 2 and 3, as well as during part of June 1, it was cloudy and rainy and there was little chorusing activity. As shown in figure 14, a considerable number of *septendecim* females was attracted to cage 2 on June 4 and this number then dropped gradually the next two days. Likewise, the number of *septendecim*

males attracted to cage 2 (fig. 12) was greater on June 1 and 5 than on June 4, which is what would be expected if more sexually responsive females occurred in the area on June 4. The results obtained on June 6 are difficult to compare with those obtained on the other three days because of the reversal of the locations of cages 2 and 3.

The failure of the results obtained with *cassinii* females (fig. 15) to compare with those obtained for *septendecim* females (fig. 14) is probably due to a combination of the general failure to attract large numbers of *cassinii* individuals and the low number of attracted females of both species. It is probable that the June 1 data for *cassinii* males and females both are positive, this being obscured by the more favorable location of cage 2 for both cicadas.

A peak of activity by the females of each species also occurred on most days sometime prior to the peak of chorusing activity of the males. The only apparent explanation for this is that it was caused by females moving about prior to oviposition.

Figure 16 shows the proportions of individuals of the two species at the test cages, 2 and 3. A comparison of these proportions with the proportions expected through chance alone on the basis of the counts on June 1 (4 to 8 *cassinii* to 1 *septendecim*) gives a clear indication of the consistently positive results of the test. The lines for the two cages cross only once and approach each other rarely except early and late in the day when the cicadas were not active and the numbers on the cages approached zero. All large deviations were toward higher proportions of *septendecim* at cage 2 and higher proportions of *cassinii* at cage 3.

DISCUSSION

Although there have been numerous speculations as to the probable functions or lack of functions of the songs of cicadas, there have been practically no experimental investigations on the problem and none of those previously conducted have yielded positive results. In the voluminous literature dealing with the periodical cicadas only three examples are known to the writers in which some significant observation concerning this problem or some evidence based on experimentation has been presented. In 1937 Cory and Knight stated, "The cicada's song, transmitted over a carbon microphone to a loud speaker in an adjoining room, failed to orient significant numbers of virgin females." This brief report cannot be evaluated, however, because it is not known which song of which species was used, which species of virgin females was used, how old these virgins were, at what temperature the song was recorded, the temperature of the room containing the virgin females, what the light intensity of the room was, at what intensity the sound was played to the females, or whether or not the females could fly in the enclosure in which they were housed. Likewise, it is not known how long the females had been caged, or whether or not, or how, they had been fed.

In 1941 Craig speculated that periodical cicadas fly toward the greatest volume of sound and that this could account for their frequently surprisingly definite limits of distribution. This suggestion is in agreement with the results of the present study.

In 1946 Allard noted the synchronization of *cassinii* and described it accurately. This observation alone established the existence of behaviorally significant differences between the songs of the two species. Field observations of this sort have too frequently been ignored in the present surge of experimental studies on the auditory capacities of insects, some of which have led to the suggestion that insects respond indiscriminately to nearly any sound as long as it contains certain structural elements which are common to almost all animal sounds. As mentioned in an earlier paper (Alexander, 1956), this conclusion has seemed generally unwarranted due to a number of phenomena repeatedly observable in the laboratory and field behavior of singing Orthoptera and Cicadidae. A series of well-designed

experiments by Walker (1958) with different species of tree crickets in the eastern United States reveals highly discriminatory capacities in these insects and shows that the females of a given species respond only to the song of the males of their own species and not to those of any other species occurring in the same locality. There is every indication that such sensitivity is the rule in groups of insects which live together and in which song is the principal force bringing the adult males and females into breeding proximity.¹ Song has proven to be the most valuable species recognition character available in the singing Orthoptera and Cicadidae, and it is here suggested that taxonomists puzzling over morphologically ill-defined species in other sexually reproducing animals might do well to search for the mechanism responsible for bringing the sexes together in their particular groups. In some cases this character may be behavioral, in others it may be ecological, and in others it may be a complex combination (Alexander, 1957a). It might be something as obscure and remote as the odor of a host plant to a female ready to oviposit. In any case, it seems logical to expect a high degree of selective value to be attached to uniqueness in characteristics which are responsible for this kind of intraspecific congregation and, concomitantly, interspecific isolation. Such mechanisms can perhaps be regarded as the least wasteful of all possible isolating mechanisms, preventing interspecific encounters as well as wasted time and energy as a result of such encounters.

The sensitivity demonstrated in tree crickets by Walker and in two species of *Magicicada* in the present study indicates that the failure of past investigators to obtain positive results in similar experiments may have been due to failure to expect a sufficient degree of sensitivity, and thus failure to design an experiment in which such important variables as temperature, sound intensity, light intensity, and physiological condition of the test animals were properly taken into account. It seems evident that experiments with sounds which do not remotely resemble in rhythm those sounds to which the animal is subjected in nature have little or no bearing on the sensitivity of the particular animal to slight fluctuations in the rhythm of natural sounds. In such experiments, an entirely different kind of sensitivity is apparently being tested. The sensitivity demonstrated in the species tested so far with respect to natural sounds indicates that investigators working with the idea of eventually controlling an insect or altering its behavior toward some practical end will most profitably concern themselves initially with rhythm structures which fall within the narrow range which the animal encounters and to which it responds in nature.

SUMMARY

Observational and experimental field studies carried out in southern Ohio on Brood XIV of the seventeen-year cicadas, *Magicicada septendecim* (Linnaeus) and *M. cassinii* (Fisher), together with data gathered during the emergence of the same two species in Brood XIII in northern Illinois, have led to the following conclusions:

1. The whole mode of life of the seventeen-year cicadas (as also seems likely with other singing insects) is so completely tied up with the system of sound communication of the adults that an understanding of their behavior, ecology, distribution, history, and taxonomic relationships is impossible without a knowledge of how this system operates.

2. The males of each species have at least four distinct sound responses: (1)

¹Since submission of this manuscript, the following publication has appeared: Perdeck, A. C. 1957. The isolating value of specific song patterns in two sibling species of grasshoppers (*Chorthippus brunneus* Thunb. and *C. biguttulus* L.) [Orthoptera: Acrididae: Acridinae.] Leiden, Netherlands: E. J. Brill, publ., 75 pp., 9 fig., 28 tab. Perdeck's, Walker's, and the present report together confirm that species-specific song patterns operate as isolating mechanisms among closely related sympatric species in all three of the major systems of sound communication occurring in insects.

a congregational song, the production of which is regulated by daily fluctuations in climatic conditions and by hearing the songs produced by other males, (2) and (3) two courtship sounds, produced at different stages of courtship, and though apparently not produced prior to every instance of copulation probably always terminating in copulation when the female is responsive, and (4) a protest squawk, so named because it is produced by individuals captured, held, disturbed into flight, or otherwise irritated.

3. In each species these sounds are radically different in rhythm and frequency from the sounds produced by the other species in the same situations, yet the structural inter-relationships of the sounds of one species are in general analogous to the structural inter-relationships of the sounds of the other species.

4. The congregational song is the only sound produced in chorus, and in both species chorusing is most successful on clear, windless days, and least successful on cloudy, rainy days.

5. The chorusing behavior of the two species is different: *cassinii* individuals synchronize their songs while *septendecim* individuals do not, and their peaks of chorusing activity occur at different times during the day.

6. The differences in the chorusing behavior of the two species, as well as the structural differences in the songs of individuals, are behaviorally significant to both males and females.

7. The congregational song is properly named because it acts as a congregating mechanism for both males and females of each species and concomitantly reduces the number of interspecific encounters between sexually responsive males and females. It is probable that a visual stimulus is also involved in the achievement of chorus synchrony by *cassinii* and thus in congregation since the congregational chorus seems effective only when synchrony is achieved.

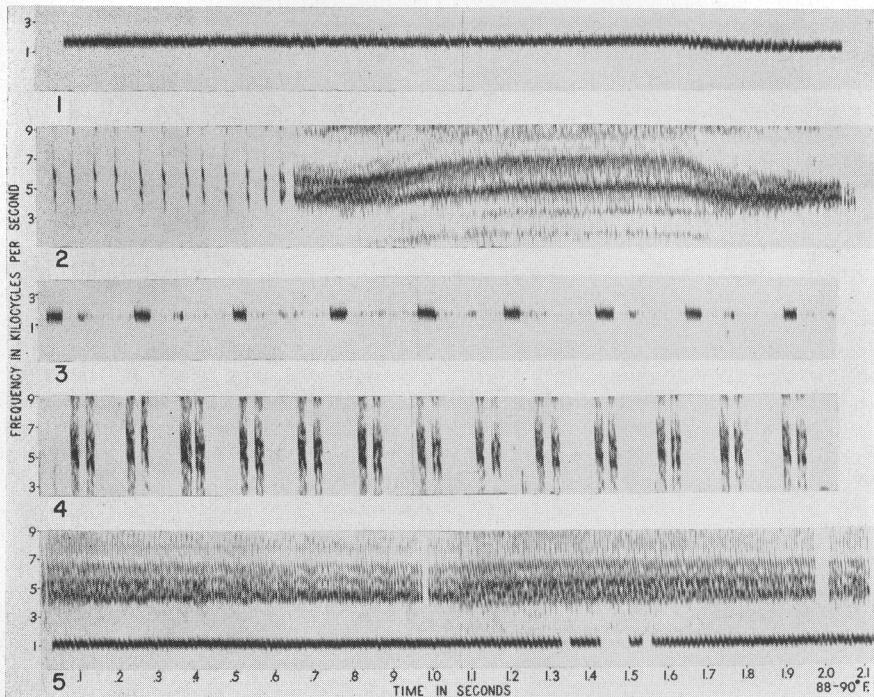
8. The chief method of congregation is through flight, and the short bursts of flight incorporated into the rhythm of the congregational chorusing facilitate this congregation, increasing the possibility that a sexually responsive female will encounter a male and decreasing the length of time involved.

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Audiospectrographs of the different sounds of *M. septendecim* and *M. cassinii* (relative intensities shown by darkness of the mark).

1. A single phrase from the congregational song of *M. septendecim*.
2. A single phrase from the congregational song of *M. cassinii*.
3. Several phrases from the song produced in advanced courtship by *M. septendecim* (faint marks are sounds of other individuals).
4. Several phrases from the song produced in preliminary courtship by *M. cassinii*.
5. Protest squawking of *M. septendecim* (lower) and *M. cassinii* (upper).

in figures 11 to 16.

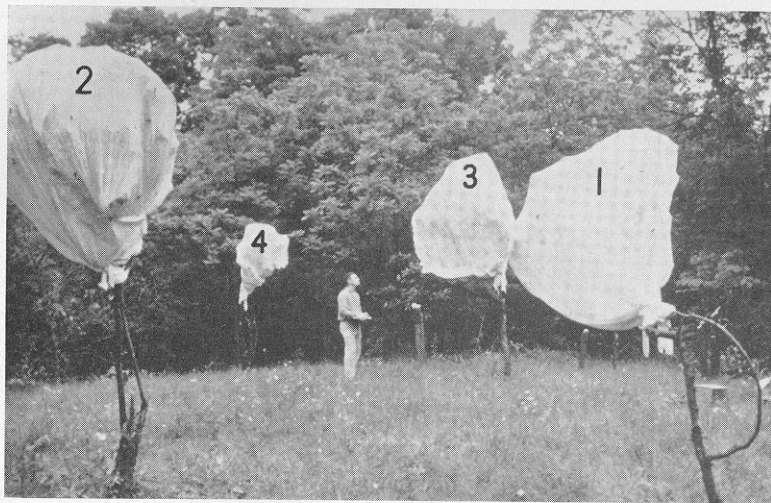


FIGURE 10. Photograph of clearing facing downslope from southeast corner.