The Periodical Cicada Complex (Homoptera: Cicadidae)

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ABSTRACT

In the more than one hundred years since Dr. J. C. Fisher described Magicicada (=Cicada) cassinii from individuals taken with specimens of Brood X of M. (=Cicada) septendecim, officially the periodical cicada, many conflicting views have been put forth concerning the validity of the specific status of the smaller form.

A map showing the localities from which we have records of Brood XIII, photographs showing color pattern and size variation in both sexes, drawings of structural differences of males found to be consistent, and analyses of the songs of both species are presented.

In general we found these two species to be sympatric, synchronic, and synhymnal, and to exhibit no tendency toward division of range other than local congregation apparently as a result of song attraction. This latter indicates that sound production and response may function as a behavioral isolating mechanism between the two species. Males of each species produce three distinctly different sounds which we have referred to as 1) the congregational song, 2) the courtship song, and 3) the protest squawk.

The recognition of M. cassinii as a species distinct from septendecim again opens the question of the status of the entities previously considered to be thirteen-year forms of the periodical cicada.

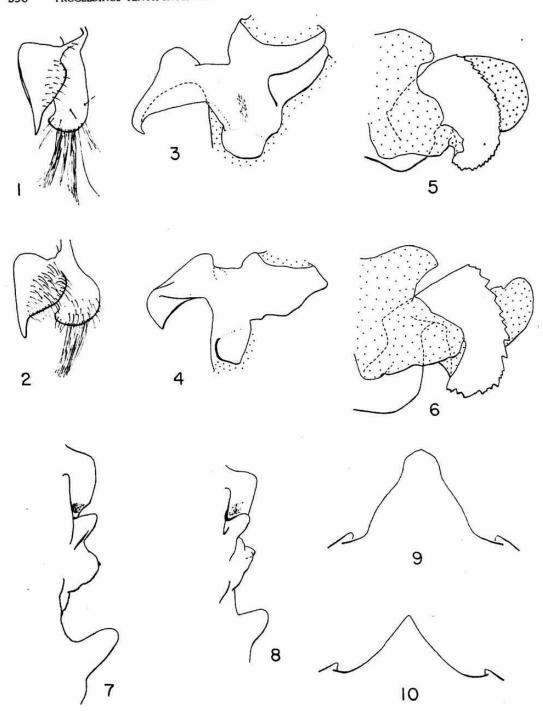
The work which we are reporting here was begun by the senior author as a project of the Illinois Natural History Survey, Urbana, and had its beginning in a cursory survey of the dispersal of Brood X in Illinois in 1953. At that time we became aware of certain song, color, and structural differences between recognizable forms in one or two places in Illinois. The emergence of Brood XIII in the spring of 1956 gave us an opportunity to check the occurrence of these forms in an emergence primarily centered in Illinois, allowing easy coverage of almost the whole range.

Magicicada cassinii was described by Fisher in 1851 (Brood X) and for a time was considered distinct from septendecim Linnaeus, 1758. Various opinions have been expounded as to the status of this entity since then, with the consensus in the last twenty years or so being that only one species, septendecim, but three forms were involved. We now believe that at least two very distinct species are involved in this complex, both of which have a seventeen year life cycle. There likely are others occurring as thirteen year forms.

Figs. 1–10 show various male structures which have proven to be consistently different between the two species. The apical aedeagal plates bearing toothed margins (Figs. 5 & 6) are best distinguished on the basis of shape, especially the angle between the top margin and the toothed edge. The teeth on the plates of cassinii are not always relatively more coarse than in septendecim. There is obviously a similarity in structure of these parts, just as one would expect to find between closely related species. The structures illustrated compare very favorably with those of specimens from Brood X taken in Illinois in 1953 and in Michigan in 1936.

Ventral abdominal color patterns are shown in Figs. 11–25. In males of M. septendecim (Figs. 11–14) the red-orange markings, indicated by the lighter areas, tend to spread basally at the margins of the sternites and these males always have rather broad orange markings. M. cassinii males which bear red-orange markings (Figs. 15–17) generally have these restricted to the apical margins of the sternites and not spreading basally at the sides. Many cassinii males have the abdominal sternites completely melanistic as in Fig. 18.

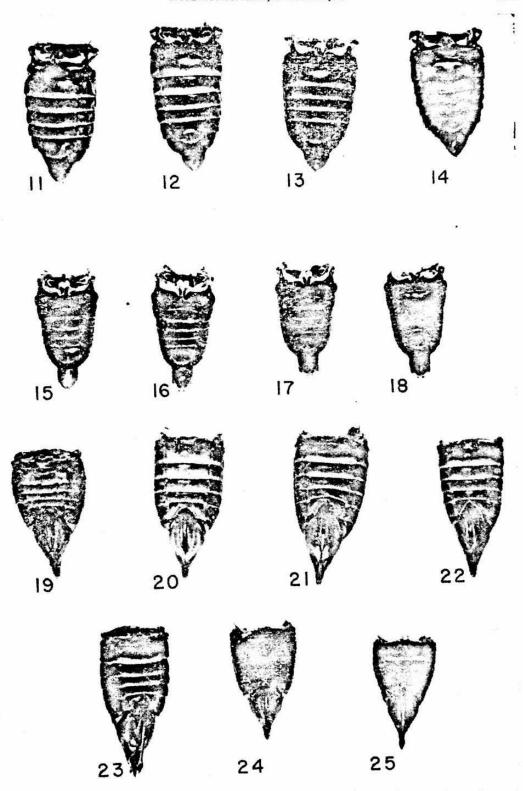
A general trend in ventral abdominal coloration similar to that shown above for males holds true for females of septendecim (Figs. 19-23). Although many specimens lack the



Figs. 1-10. Odd numbers are of M. septendecim, even numbers of M. cassinii: 1 and 2, caudal aspects of the dorsal hooks of the tenth abdominal segment; 3 and 4, lateral aspects of the same; 5 and 6, lateral aspects of the apex of the aedeagus; 7 and 8, oblique lateral aspects of the lateral margin of the ninth abdominal segment; 9 and 10, dorsal aspects of the dorsal prolongations of the ninth abdominal segment.

marginal spread, all have relatively broad apical bands of red-orange on the sternites. Females of *cassinii*, however, seldom have orange markings on the abdominal sternites, and when present they usually occur only as narrow apical bands on a few basal sternites (Figs. 24–25).

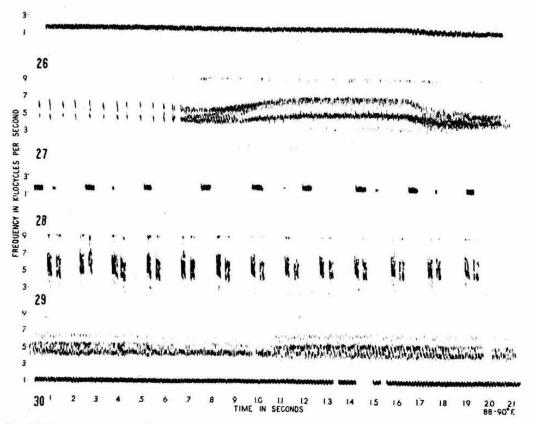
In general individuals of M. septendecim are larger than those of cassinii, but the size ranges for both sexes overlap for both species. By measuring the distance from tip of postclypeus to apex of ninth abdominal segment for males or to tip of ovipositor sheath



Figs. 11-25. Ventral aspects of abdomens: 11-14, M. septendecim males; 15-18, M. cassinii males; 19-23, M. septendecim females, 24-25, M. cassinii females.

for females and rounding off to the nearest half millimeter, we found the following average size classes for the two species: M. cassinii: σ^1-24 mm., $\varphi-25$ mm.; M. septendecim: σ^1-30 mm., $\varphi-30$ mm.

Periodical cicadas produce sounds in the three general types of situations described by Alexander (1957). Audiospectrographs of the three different sounds made by both septendecim and cassinii are shown in Figs. 26–30. The songs from which these analyses were made were recorded under natural conditions in a wooded area near Hinsdale, DuPage County, Illinois, during June, 1956. The recordings were made at a tape speed of fifteen inches per second, with a Magnemite tape recorder, Model 610EV (Amplifier Corporation of America), using an American Microphone Company D33A microphone. The audiospectrographs were made with a Vibralyzer, the use of which is explained by Borror and Reese (1953). A total of 50 minutes of recordings were made, including 201 congregational songs of 49 males of M. septendecim and 150 congregational songs of 35 males of M. cassinii. Two hundred forty-six courtship phrases of two males of M. septendecim, and 1228 courtship phrases of seven males of M. cassinii were recorded. The temperature varied from 87° F. to 97° F. during recording.



Figs. 26-30. Audiospectrographs of the songs of M. septendecim and M. cassinii. (Relative intensities are shown by darkness of the mark): 26, A single phrase of the congregational song ("Pharaoh" call) of M. septendecim; 27, a single phrase of the congregational song of M. cassinii; 28, several phrases of the courtship song of M septendecim. (The faint marks between phrases are the songs of other individuals in the background); 29, several phrases of the courtship song of Magicicada cassinii; 30, protest squawking of M. septendecim (lower) and M. cassinii (upper).

Periodical cicada males do not space themselves apart in the field and perch and sing in the same spot day after day as do the males of most singing Orthoptera. Rather, a male delivers a few calls, flies a short distance — sometimes a few inches, sometimes several yards — and sings again. A bushful or treeful of singing cicadas thus seems to be in constant motion, if watched carefully. Although the males fly much more readily than do the females, the latter fly when disturbed, and fully as well as do the males. Presumably the congregational songs function in drawing the males and females of each species together. Individual females are probably only rarely attracted to individual males by the congregational song because of the constant moving about by the males while singing, and the congregation of large numbers of males into close proximity.

Figs. 26 and 27 are audiospectrographs of single calls from the congregational songs of septendecim and cassinii, respectively. In both species these are produced in series of one to five calls which are separated by short bursts of wing motion generally resulting in flight. Within series the individual calls last two to four seconds and are produced at intervals of 0.5 to two seconds. The rhythm of the two calls is radically different, as is generally the case with the songs of closely related sympatric species of Orthoptera and Cicadidae.

The rate of pulsation due to the individual vibrations of the tymbals in the call of septendecim varies from 120 to 160 per second, while the call of cassinii involves two different pulse rates. The first part of the call sounds like a series of rapid ticks, while the second part sounds buzzy to the ear, more like the call of septendecim. The ticks are produced at a rather irregular rate of 16 to 25 per second, while the individual pulses in the buzz are produced at a rate of 180 to 210 per second. M. cassinii frequently begins the ticking part of its congregational call while walking or flying about, though, like septendecim, it does not move about during the buzzing part of the song. Occasionally an individual produces the ticking part of the call and does not follow with the buzz, or produces ticks both before and after a buzz. The two-part character of the congregational song of cassinii provides an additional rhythmic or uniform interval in the song of this species, as compared to that of septendecim.

The call of septendecim has a rather narrow band of intense frequencies located between one and two kilocycles per second. The call of cassinii is somewhat higher-pitched, and has a wider band of intense frequencies located between four and seven kilocycles per second. If the sound-producing structures are similar, a smaller insect produces a higher-pitched sound than a larger specimen, either in the same species, or in a different one. The rise and drop in pitch in the calls of these two species corresponds to a raising and lowering of the abdomen. The mechanics of this abdominal movement and associated changes in tymbal tension have been treated by Pringle (1955) for other cicada species.

A recording of a chorus of periodical cicadas made by D. J. Borror and R. W. Champlain in June, 1953, in Delaware County, Ohio, contains both of the congregational songs described here for M. septendecim and M. cassinii from Brood XIII in Illinois. Although the number of individuals singing in this recording makes it impossible to analyze the songs in detail, they seem identical to those described here.

Males of both septendecim and cassinii produce distinctive sounds under certain conditions when in close proximity to females. These will be referred to as courtship songs and are portrayed in Figs. 28 and 29 for septendecim and cassinii, respectively. The rates of delivery of the individual phrases of the courtship song varied from 3.6 to 4.8 per second in septendecim, and from 3.6 to 6.7 per second in cassinii. During courtship, and while producing this sound more or less continuously, the male crawls over the female, moving his partially extruded genitalia about on the ventral surface of her abdomen until the genitalia are engaged or he is dislodged.

The few instances of interspecific courtship observed in cages during this study were unsuccessful. An examination of more than 150 mating pairs, including approximately equal numbers of both species, yielded no cross-matings. The proportion of copulating pairs encountered in the field is highest in late afternoon.

Male cicadas almost invariably vibrate their tymbals when handled, or when captured by birds or provisioning wasps. Fig. 30 portrays the protest squawks of both septendecim (lower) and cassinii (upper) on the same audiospectrograph. The difference in frequency and pulse rate are evident. These sounds are so different that a male of either species can be identified easily by the sound he makes when captured.

The congregational song of M. septendecim, the so-called "Pharaoh" call, is produced from dawn until late afternoon, and thousands of individuals singing together produce an uninterrupted din in which the individual calls are completely indistinguishable. M. cassinii, on the other hand, sings chiefly in the afternoon, and local groups of males sing together in bursts which are separated by intervals in which none or only a few males are singing. When an individual breaks such a silent period by beginning a song, he is invariably joined by a number of males in the vicinity, and the chain reaction continues until the whole local population is involved. One by one the males finish their burst of song and drop out, and the whole cycle is repeated over and over again.

Several of the recordings made of choruses of males of M. cassinii singing together indicate that an imperfect synchronization of the ticking and buzzing parts of the song is accomplished by groups of individuals in close proximity. At any single time practically all of the males involved in song are either ticking or buzzing together. This imperfect synchronization, in which the beginning of song by one male is apparently the stimulus, also occurs in the meadow grasshoppers (Conocephalinae), which likewise produce songs that involve two distinctly different pulse rates and thus closely resemble the congregational song of M. cassinii. Synchronization of individual calls and of song bursts by cassinii both indicate that cassinii males are stimulated by their own song rather than by those of the septendecim males which are usually singing continually all around and among the cassinii individuals.

Both M. septendecim and cassinii are very sensitive to daytime changes in light intensity, and will usually stop singing if a cloud obscures the sun. On one occasion both species stopped singing after a sudden drop in light intensity during which a rather brisk rain shower began. During the shower the sun reappeared, and although the rain did not slacken, both species instantly burst into song. The light sensitivity of both species apparently changes during their daily singing period, for both begin singing at intensities quite different from those at the time that they cease singing. At night, short bursts of protest squawks by cassinii are continually heard near street lights and along roads with frequently passing cars. Males of septendecim in the same areas remain silent, even though they may be much more abundant. This may reflect a lower threshold of irritability in cassinii which is also indicated by the fact that individuals are disturbed into flight more easily than those of septendecim. These factors probably explain, at least in part, why very few specimens of cassinii are captured by the average collector.

We believe that the consistent and radical differences between the songs and singing behavior of these two otherwise quite closely related species is a strong indication that song is important in at least reinforcing their reproductive isolation. Such differences seem to appear quickly between sympatric species of singing Orthoptera and Cicadidae, often preceding noticeable differences in morphology or other characteristics (Alexander, unpublished data).

The map in Fig. 31 shows the area in which Brood XIII was expected to occur, based on Marlatt (1923), as indicated by the shaded lines. The black dots indicate the location of records taken in 1956. These records are of many types. Most of them are based on specimens collected by the authors, or are auditory records (i.e., represent localities where songs were heard by the authors). Some are based on reliable auditory or damage records made by others; some are based on specimens submitted by others; some are based on published records of occurrence appearing in the Cooperative Economic Insect Report. In practically every locality for which we have data the two species occurred together, differing in mumerical proportions sometimes from shrub to shrub, from tree to tree, or from city block to city block, but always occurring together. Our data do not indicate specific differential selection with respect to host plants, slope of terrain, soil type, drainage, or any other ecological factor.

The following is a summary of our 1956 localities and dates of collections: Illinois: Brookfield, Chicago Heights, Downers Grove, N Dwight; S Elburn, N Greenview, Henry, Hinsdale, Joliet, Kappa, LaGrange, Libertyville, Lowell Park (Dixon), Mackinaw R. along U. S. 150 (Woodward Co.), Magnolia, Marseilles, Mokena, Moline, Morris, Oregon, Ottawa, Palos Park, Paris, Park Forest, Peoria, Pontiac, River Grove, Sandwich, N E Springfield, Urbana, Western Springs; April 1—June 17 (nymphs of septendecim), May 28—July 6 (adults). Indiana: Crown Point, Lake Co., La Porte Co., Porter Co.; July 11—16 (adults). Iowa: N W Bell Plaine, Johnson Co., Lin Co., Tama Co., N E Tama; June 12—23 (adults), July 8 (damage). Ohio: Hocking Co.; June (adults). Virginia: Montgomery Co.; May 30 (adults). Wisconsin: Beloit, Grant Co., Iowa Co., Lafayette Co., Richland Co., Rock Co., Walworth Co.; June 9 (adults and nymphs).

In addition to the above, periodical cicadas were tentatively reported from an orchard in Houston County, Minnesota. Unfortunately no specimens were taken and the record cannot be verified. This is of particular importance because no verifiable record is available for that state, and because Okanagana canadensis occurs at the same time of the year in

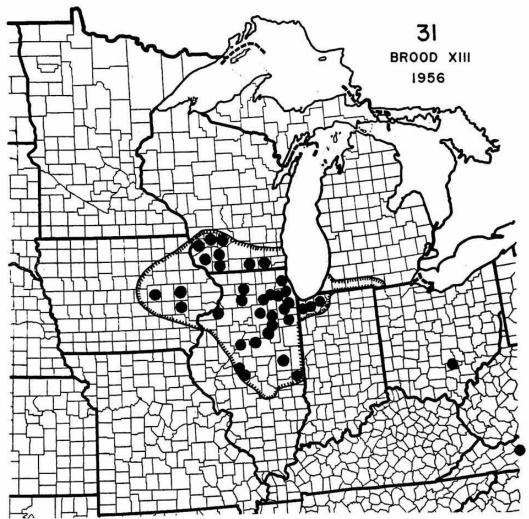


Fig. 31. Map of the expected range and location of records for both species in Brood XIII, explanation in text

that area, and closely resembles periodical cicadas in coloration, in type and appearance of damage, and in size and suddenness of emergence.

In conclusion, the recognition of two seventeen year species suggests the possibility of other species among the thirteen year forms of what formerly was considered to be one species. Both large and small thirteen year forms have been reported, too. It seems unlikely that both seventeen year species have evolved thirteen year forms maintaining similar relationships to each other. It seems more logical to expect to find additional species associated in this complex. So far we have not been able to examine sufficient authentic thirteenyear material to establish or refute the validity of this expectation. We hope to gain more information by following up Brood XIX, the largest thirteen-year brood, in 1959 in the same manner that we studied Brood XIII.

REFERENCES¹

Alexander, R. D. 1957. Sound production and associated behavior in insects. Ohio Jour. Sci. 57: 101-113, 1 Text Fig., 4 Plates.

Anon. 1956. Cooperative Economic Insect Report 6 (25): 580, 593; (26): 612; (27): 646.
Borror, D. J., and C. R. Reese. 1953. The analysis of bird songs by means of a vibralyzer. Wilson Bull. 65 (4):

Fisher, J. C. 1851. On a new species of cicada. Proc. Acad. Nat. Sci. Philadelphia 5: 272-273.

Linnaeus, Carolus. 1758. Systema Naturae. Regnum Animale. Tenth Edition. Holmiae. 824 + iii pp. Marlatt, C. L. 1923. The periodical cicada. U. S. Dept. Agric. Bureau of Ent., Bul. No. 71: 183 pp. Pringle, J. W. S. 1954. A physiological analysis of cicada song. Jour. Exp. Biol. 31: 525-560, Text Fig. 2, Plate 11.

¹Since submission of this manuscript the authors have published an experimental investigation of the functions of Magiciada songs (Ohio jour. Sci. 58: 107-127, 16 Figs. March, 1958).