# Some Facts and Theories About the Broods and Periodicity of the Periodical Cicadas[1]

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The periodical cicadas have been the subject of such a voluminous literature that it is becoming increasingly difficult to distinguish between fact and theory or for that matter between fact and fancy. Riley (17) and Marlatt (15) did a remarkable job in sorting out the older literature. Deay (10) has reviewed the status of the periodical cicadas in Indiana, and there are excellent reviews for other areas; but no one in recent years, has attempted any general review of the literature, nor an evaluation of the theories presented by Riley, Marlatt, and others. Most recent papers are devoted primarily to records of specific broods or notes upon control and biology of the cicadas.

## Some Apparent Facts and Generalizations

A number of facts concerning *Magicicada* (8) which were still problematical at the time of Marlatt's monograph (15) are now more firmly established. There are still, however, certain gaps in our knowledge.

Marlatt himself (16) reared specimens of Brood XIV from eggs collected in 1889 and obtained emergence at Washington, D. C. in 1906, thus positively establishing the 17-year period for that brood. Evidence for the 13-year cycle of the southern broods is still largely presumptive. Riley (17) (see Marlatt (15) for a summary) attempted rather elaborate experiments of transferring colonies from north to south and *vice versa*. Most of these attempted transfers resulted in complete failure, but in one case eggs presumably of the 17-year Brood X collected in 1885 in Indiana, Pennsylvania, or Michigan survived in Alabama, where adults emerged 13 years later in 1898. No 13-year brood was expected in the area that year, but the transformation of a 17- to a 13-year cycle seems doubtful. It is possible that the eggs were from cicadas of the 13-year Brood XXIII which also appeared in 1885, or that some of the eggs of Brood XXIII being sent to northern localities were misplaced in the mass shipments.

The chronological evidence for the exact periodicity of the major broods is almost irrefutable. Brood XIV has appeared every 17 years as if timed by astronomical instruments since it was first observed by the Pilgrims about 1634. The other large broods of both 17- and 13-year cycles have also been observed at the expected intervals over many years. The distinction of the cycles is also indicated by the periodicity in areas where 13- and 17-year broods overlap and would thus apparently be exposed to identical climatic conditions.

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It should be noted, however, that premature and late emergence of most of the major broods have been observed. Boyd (4) reports the emergence of a large swarm of Brood X, due in 1953, in Monmouth County, New Jersey, in 1952. This swarm extended over an area of some two square miles. This is exceptional, and most cases of premature or later emergence are minor and seem to have no influence on the major portion of the brood. Minor acceleration of emergence in clearings, in connection with forest fires, and influenced by artificial heating by underground pipes are known. Acceleration of emergence by as much as a year has also been reported in a greenhouse (15). Cory and Knight (6) showed that temperatures above normal accelerate development during the month preceding emergence, but that excessive temperatures produce many abnormalities during the final transformation. Rare fall emergence also occurs (9, 18) despite the classical polemics between Riley and Ward on this subject.

None of this evidence positively refutes the reality of a 13-year cycle in some broods and a 17-year cycle in others. No 14-, 15-, or 16-year broods are yet known although they would be expected if climate alone was the cause of the difference. It therefore seems fairly certain that the period of underground development is gentically fixed and subject to only minor modification by environmental factors.

The evidence for the unity of the various broods recognized by Marlatt (14) is not as positive as their chronology. More evidence on this subject might be obtained by a thorough search of the ephemeral literature in newspapers and other periodicals, but the technical literature has concerned itself mainly with the major broods. Determination of the unity of some of the smaller broods is also complicated by the rate at which they have declined with the clearing of the woodlands. The 13-year broods in the southeast have suffered particularly from the early and almost complete destruction of the forests in the coastal plain and piedmont areas.

There is no doubt that all of the broods have declined since the early settlement. Even Brood X which still emerges in large swarms in many areas is apparently disappearing in parts of its range (12). In Indiana, this brood is also evidently being divided into fragments as forest clearing progresses, and even in Brown County which is still extensively wooded the emergences in 1953 were not as uniformly distributed nor so great as in 1936. It is interesting that some broods seem to have declined in some areas even before extensive clearing could have been the only cause. For example, Brood XXI formerly occurred in western Florida, but has not been reported from there for many years. Similarly some apparently suitable areas lacked periodical cicadas at the time of first settlement.

The decline of the cicadas is also indicated by the decreasing frequency of reports of damage. Davis (7) points out, however, the opposition of nurserymen to the suggestion that plantings of young orchards be delayed in 1953 until after the danger of cicada damage was past. Such damage, at present, is admittedly minor and usually confined to orchard plantings along the edges of uncleared woodlands,

but all cases may not be reported because of economic pressures or lack of interest.

For many years there has been disagreement as to the status of the large form *septendecim* (L.) and a smaller form *cassini* (Fisher) which frequently occur together in mass emergences. Fisher (11) in the original description of *cassini* pointed out differences in song, genitalia and other characteristics aside from the smaller size. Riley, however, found variation in the genitalia and other characters, and most later workers agreed with him in placing *cassini* as a race or variety of *septendecim*. Beamer (3) and others have shown the considerable differences between the two forms in habitat, song, egg laying, and have emphasized the failure of the two to mate. Jacobs (13) further documents the differences in size, sex ratio, mating behavior, song, and habitat selection. Alexander and Moore (1) conclusively proved by tape recordings and experiments the distinctiveness of the songs and their influence on behavior. There is now no doubt that two distinct species are involved and that their occurrence together in the same broods is only coincidental probably being enforced by the intense predation which occurs at the time of emergence (3).

Similarly there has been dissent as to the status of the 13-year "race" *(tredecim)* as opposed to the 17-year "race" *(septendecim)*.[2] Deay (10) and others have remarked on the apparent failure of the members of different "races" to mate even when they emerge together in the same area. Taxonomically this is a different problem from that involving *septendecim* and *cassini*. The 13-year broods and 17-year broods have probably been isolated from each other for a long period of time, but they have not developed striking morphological differences. They are distinguishable on the basis of behavior, and on purely circumstantial evidence we would think that *tredecim* and *septendecim* are physiological or genetic species. But on this line of reasoning every brood, possibly every isolated colony, is probably genetically different to some degree from every other. Certainly the long nymphal life is conducive to the accumulation of mutations, and the intensive selection produced by predation at the times of emergence could be expected to lead to rapid genetic change between one cycle and the next. It is probably remarkable that we see so little evident variation.

### Some Theories and Ideas

With the decline of the broods, theorizing as to their origin and significance has also declined. Marlatt (15) summarized the theory that the periodical cicadas were originally represented by only a single great brood of 17-year periodicity. Allowing this assumption, which Marlatt admits is not the only possible one, the various broods can be derived by assuming original fragmentation due to forest fires, occurrence of unfavorable seasons, areas of unfavorable soils, and other factors and subsequent retardation or acceleration of the period by a year. The 13-year broods are assumed to derive from the 17-year

[2] A paper by R. D. Alexander and T. E. Moore in the Proc. 10th Intern. Congress of Entomology (in press) bears on this point and should be consulted.

broods by fixation of a shorter developmental period originally induced by warmer climates. Overlap of 13- and 17-year broods can be explained as the result of reinvasion by 13-year forms of the areas already occupied by 17-year broods. Marlatt presents various lines of evidence supporting these conclusions, and relates the broods by chronological and areal distribution.

This theory was not universally accepted. According to Marlatt (15) Prof. W. E. Castle suggested that some of the broods, particularly Brood VI, were extremely old, and that their distribution is the result of extinction in various portions of the original range. Brood VI, although the most widely distributed of the 17-year broods, is extremely spotty in occurrence both in area and numbers which coincides with Castle's idea. Some broods show similar fragmented distributions, and some of the small broods are extremely erratic. Other broods, although appearing in numbers where they occur, are very limited in area. Brood X shows an interesting tendency to concentrate in three distinct areas with scattered light emergences between the concentrations. Marlatt, however, rejected the theory of antiquity as an explanation in such cases in favor of derivation of the broods such as VI from swarms of diverse origin. This was very probably the way in which the original broods appeared, but does not seem to be adequate for explaining the present fragmentation.

Considering the knowledge which we now have of the Pleistocene history of the United States, the theory of a single original brood with a 17-year cycle seems less probable. The northern broods now occupy an area roughly along the edge of the area covered by the Wisconsin ice sheet and on the area exposed after the retreat of the ice and occupied by the beech-maple forest climax. This suggests that they were derived, as has been hypothesized for certain other organisms, late in the Pleistocene from southern populations of the species which spread rapidly into the newly available habitats after the glacial climates ameliorated. Certain correlations suggest, however, that the broods are much older, perhaps dating from before the ice ages.

The cicadas as a group are certainly tropical insects, and the temperate region representatives are mostly outliers of tropical groups. *Magicicada* is one of the few genera confined entirely to the temperate zone. The species are probably relicts of an originally richer fauna of the eastern forest zone. The 17-year broods still center around the mountainous areas of the Appalachian, while the 13-year broods occur mostly south of the mountains or to the west of them. The long cycles may thus have developed in connection with zonation on the mountains rather than glaciation. The 13-year cycle would presumably have evolved first, and the longer 17-year cycle later. The latter would have preadapted the cicadas possessing it for invading the colder areas north of the mountains before and during the glacial periods.

An interesting correlation of Brood XIII with the driftless area of Wisconsin and Minnesota possibly indicates great antiquity for this brood. In 1956, it was reported in damaging numbers only from Richland, Grant, Lafayette, Iowa, Crawford, Sauk, and Rock counties, Wisconsin, all in the driftless area and Walworth County just to the east.

It also occurred in Houston County, Minnesota, within the driftless area. Elsewhere in the United States, Brood XIII was reported only from Lake, Porter, and LaPorte counties, Indiana (5). The correlation may, of course, be only with edaphic and other factors and not palaeogeography.

The former occurrence of colonies of the 13-year Brood XXI in western Florida is also suggestive of great age. Periodical cicadas once occurred in Jackson, Gadsden, and Washington counties in the area around the Apalachicola River in which relict beech-maple stands and other deciduous trees occur together with remarkable tertiary relicts such as *Tumion taxifolia*, the stinking cedar. Again the correlation may be with edaphic and other ecological factors, but it would be expected on the basis of the theory that the 13-year cycle is more primitive.

The period of emergence of the periodical cicadas also coincides with the theory that the long cycles began in connection with colder climates either on mountains or in the glacial period. There is a general phenological correspondence of both *cassini* and *septendecim* and also of 13- and 17-year broods when they occur together. That is, emergence in the southern areas is earlier. In all cases, however, emergence begins while temperatures are still relatively low. Nymphs may actually be active near the surface while frosts still occur. Most other cicadas do not appear until temperatures are much higher later in the summer as evinced by such common names as "dog day" cicada. The early emergence of *Magicicada* thus seems to be an adaptation for taking advantage of a short, almost arctic or alpine, summer.

The 13-year cycle may not in itself be particularly unique. Other cicadas may have even longer periods of underground development, but since individuals appear every year no periodicity is evident. Marlatt (15) suggests that the erratically appearing *Tibicen marginata* (Say) may have a cycle extending over 20 years. Scott (19) records an unusual emergence of cicadas superficially similar to *Magicicada* in Beluchistan in 1918. The natives were apparently not familiar with this insect, and it may have appeared only at long intervals. Cicadas emerge in massive broods in many areas of Malaya and are used as fortuitous food by the natives just as *Magicada* was by the American Indians. On Okinawa in 1945, cicadas emerged in great numbers in numerous localities, but they are probably an annual occurrence even if the period of development is greater than one year. In the eastern United States the emergence of *Magicada* are impressive largely because of the irregular distribution of the broods. If they appeared every year in wide areas the periodicity would not have been so easily detected nor so astounding.

We may now hypothesize the sequence of development of periodicity and the broods as follows: The *Magicicadas* were not originally periodic in the sense that they are now, but annual emergences were probably the rule over great areas of the eastern forest. The 13-year life cycle developed slowly rather than abruptly or may represent the primitive cycle, and the cicadas were at first rather inconspicuous insects in the

forest ecosystem. Broods of different species developed in isolation emerged at first at different times, but as adaptation favored more massive emergences, and more massive emergences favored more intensive predation the broods were compacted by mass-surface effects. Gradually the annual broods became distinct in both time and area from one another, and subsequent fragmentation due to extinction in different areas accentuated the differences. Some of the original species of *Magicicada* became extinct; the survivors were forced into closer association in broods by habitat preferences and other ecological restrictions. In colder or mountainous regions the life cycle lengthened even more, at first due to environmental conditions alone, and later became genetically stabilized. The 17-year form was preadapted for invading the northern forests during and at the end of the Pleistocene, and as the broods continued to be fragmented and extirpated the condition found at the time of first settlement was established. The process of fragmentation, reduction, and extirpation continues today.

Aside from all theories the evidence now available clearly indicates that, although the periodical cicadas were probably never as portentous as some of our forefathers thought, they are still among the most interesting of Northern American insects. It is also evident that the cicadas are rapidly becoming extinct, except perhaps in a few isolated thinly settled areas (2). If we are to know much more than we now know about these wonderful insects we need to begin soon. Some of the questions which should be answered are of only abstract interest; others, however, are of far reaching significance in many fields. Unfortunately, such investigations as are needed are not the kind which can be carried on by individuals. They should be the concern of institutions which promise continuity of staff and effort over many years.

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