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A SIMPLE MENDELIAN MODEL FOR 13- AND 17- YEAR LIFE CYCLES OF PERIODICAL CICADAS, WITH HISTORICAL EVIDENCE OF HYBRIDIZATION BETWEEN THEM¹

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Periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.) are found only in the eastern deciduous forest region of the United States and have life cycles of either 13 years (Mississippi Valley and southern states) or 17 years (north and west of the 13-year range). There are no populations with intermediate life cycles. Almost every year, somewhere east of the Great Plains, a synchronized group of periodical cicadas can be found emerging. These groups, called "broods," are defined solely by their year of emergence. Whether large (covering several states) or small (covering a few counties in one state), broods tend to occupy a roughly contiguous geographic area in which local populations are patchily distributed.

Broods were numbered in chronological order (I through XVII for 17-year broods; XVIII through XXX for 13-year broods) and mapped in detail by Marlatt (1898, 1907). Of the 17 possible years in which different 17-year cicada broods could emerge, 13 have well documented broods. Of the 13 years in which different 13-year broods could emerge, only three now have confirmed broods. There is evidence of

other broods that existed in the past but are now extinct (Marlatt, 1907).

With exceptions only at the extremes of the range, each brood comprises three perfectly synchronized but distinct species: *Magicicada septendecim* (Linné, 1758), *M. cassini* (Fisher, 1851), and *M. septendecula* (Alexander and Moore, 1962). These species tend to occupy different microhabitats in a mature woodland, but become thoroughly intermixed in second-growth habitats (Dybas and Lloyd, 1962, 1974; White, 1980). Opinions differ concerning whether the 17-year and 13-year counterparts, in each case, should be regarded as different species (Alexander and Moore, 1962; Lloyd and White, 1976a). In no case can individuals of the 13-year and 17-year counterparts be distinguished by their size or morphology, or by the songs of the males. However, morphometric and allozymic techniques are now available by which two samples from different broods can sometimes be distinguished statistically, within a species (Simon, 1979a, 1983).

Once every 221 years, a given 13-year brood and a given 17-year brood will emerge in the same year. If their ranges overlap, there will be no way for the human observer to distinguish individuals that developed in 13 years from those that developed in 17 years. Evidently, the cicadas cannot make the distinction either. In 1963, 13-year Brood XXIII and 17-year

¹ This paper is dedicated to the memory of Dr. Henry S. Dybas.

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Brood III emerged in the same year, but with widely separated ranges. Lloyd and Dybas (1966) transported newly-enclosed virgins 390 km and showed that matings took place readily in large cages (3 m × 3 m × 3 m). At least some of the hybrid eggs hatched—between 13-year and 17-year forms of *Magicicada cassini* as well as between those of *M. septendecim*. Later, White (1973) showed that even different species could be induced to hybridize if confined in small cages, where the efforts of the female to rebuff advances from the “wrong” male (Dunning et al., 1979) are easily overwhelmed. The large cages used by Lloyd and Dybas would have permitted the females to avoid mating had there been any pre-zygotic isolating mechanism in operation between 13- and 17-year equivalents of a given species.

Detailed locality records of periodical cicada emergences for well over a century are now available—a byproduct of many research projects and government cooperative extension programs. It is clear that the ranges of some broods, mapped by entomologists over 100 years ago, have shifted radically in the intervening period. In 1976, an event occurred that caused us to realize the value of these extremely detailed records. Two 13-year broods were found living together in an area that had previously harbored a 17-year brood. This situation (Weldon Springs State Park, DeWitt County, Illinois), considered in the light of detailed historical records of cicada emergences in the late 19th century, suggested that the 17-year life cycle may be governed by a single dominant gene—a gene whose homologue is presumably shared by all three periodical cicada species.

Specifically, the thesis we will develop is that the situation at Weldon Springs arose from a hybridization in 1868 between 13-year Brood XIX and 17-year Brood X, after which the 17-year parent brood was eliminated from the area by competition among the nymphs underground. The only surviving progeny of the F₁ hybrids, by hypothesis, are those that genetically segregated the 13-year life cycle

in the F₂ generation and emerged in 1898. These are now 13-year cicadas of Brood XXIII, coexisting in the same woods with the parental 13-year brood (XIX).

In this paper we will (1) present the evidence that populations of two 13-year broods (XIX and XXIII) now live sympatrically at Weldon Springs and (2) give some evidence that Brood XXIII individuals at Weldon Springs are electrophoretically distinct from all others examined from the remainder of the distribution of Brood XXIII, which occupies a large portion of the Mississippi River drainage. (This would be expected if, as we hypothesize, the Weldon Springs population had a separate origin from the remainder of Brood XXIII.) We will then (3) report the historical scenario at Weldon Springs, which suggested the genetic hypothesis. The latter is not sufficient, by itself, to account for the observed pattern. We need also to postulate that 13-year nymphs have a decided competitive advantage over 17-year nymphs when they occur in the same ground. We will examine the historical evidence for (4) the rapid replacement of 17-year cicadas by 13-year ones in Missouri and Illinois, and for (5) the sudden appearance of many new populations of Brood XXIII sympatrically with Brood XIX in Illinois in 1898. Most of these have subsequently disappeared, which is also anticipated by the theory. We then (6) make nine predictions from the hypothesis which can be tested on future emergences.

One of these predictions is doubtfully contradicted by the data from Weldon Springs, but certainly contradicted by the many populations of periodical cicadas in the lower Mississippi River Valley that consist exclusively of Brood XXIII. These will be considered in a later paper, where new distributional data will be reported and the theory modified to be fully compatible with the facts.

METHODS

Cicadas write their own history, so to speak, in the eggnest scars they leave behind in the twigs of trees. Scars can be

13-yr Brood XIX	17-yr Brood X	13-yr Brood XXIII	17-yr Brood III	17-yr Brood XIII
1803*	1800	1807	1810	1803*
1816	1817	1820	1827	1820
1829	1834	1833		1837
1842		1846	1844	
1855	1851	1859	1861	1854
1868*	1868*	1872	1878	1871
1881	1885	1885	1895	1888
1894	1902	1898	1911	1905
1907		1911	1912	
1920	1919		1929	1922
1933	1936	1924		
1946*		1937	1946*	1939
1959	1953	1950		1956
1972	1970	1963	1963	
		1976	1980	1973
1985	1987	1989	1997	1990
1998	2004	2002		2007
2011		2015	2014	
2024*	2021			2024*

FIG. 1. Emergence years for six periodical cicada broods. Starred years are those in which 13-year Brood XIX emerges in synchrony with an adjacent 17-year brood.

identified to cicada species for about a year after they are made (White, 1980) and can still be found, dated, and measured for another decade after that. We used the technique of Lloyd and White (1976b) and White and Lloyd (1979) to estimate the relative numbers of adults laying eggs in the two sympatric 13-year populations at Weldon Springs, one emerging 4 years after the other.

Live cicadas from the 1976 emergence of 13-year Brood XXIII throughout the Mississippi River Valley were frozen in the field and subjected to standard electrophoretic analysis for allozymes (Simon, 1979a, 1979b). The small unexpected population from Weldon Springs was sampled fortuitously before we realized its importance. Electrophoretic analysis of this population is not reported in Simon (1979a, 1979b).

In addition to the scientific literature, archives were examined at the U.S.D.A. Bureau of Entomology in Washington, at the University of Illinois at Urbana, and at the Field Museum of Natural History in Chicago, for records of periodical cicada emergences in the late 19th century. Cicada distribution records published by Marlatt (1898, 1907) for Illinois seem to be more accurate than for most other states, owing to the work of S. A. Forbes, Illinois State Entomologist. An examination of his correspondence with L. O. Howard, Chief Entomologist, U.S.D.A., indicates that Forbes was actively involved in mapping the cicadas' distribution in 1894, 1898, and 1902.

Background

From this point onward, it will be helpful to the reader to refer to Figure 1 whenever an emergence year is mentioned. Figure 1 simply lists the scheduled emergence years, from 1800 through 2024, of broods that are relevant in the present context. The starred emergence years are those in which Brood XIX emerges in synchrony with some 17-year brood that impinges in its range. For example, 1868 was a year when Broods XIX and X emerged in the same year—something which, according to schedule, had not occurred since $1868 - 221 = 1647$ and will not occur again until $1868 + 221 = 2089$.

Figure 2 shows the distribution of periodical cicada broods in Illinois, mapped by Stannard (1975) after a decade of field work. Of special interest is a small enclave labelled "III" in three counties in east-central Illinois (DeWitt, Piatt, Champaign). This was based on Stannard's observations in 1963, the occasion when 17-year Brood III and 13-year Brood XXIII emerged in the same year (Fig. 1). Since the 13- and 17-year counterparts are indistinguishable by inspection, Stannard could only guess at whether this small enclave was III or XXIII. From its northern location and isolation—150 km from the nearest other known population of Brood XXIII—he surmised it to be Brood III. It was the discovery of Stannard's under-

standable mistake in 1976 (Kritsky and Meyer, 1976), confirmed in 1980, that called our attention to Weldon Springs and led to the present study.

RESULTS

Eggnests

Table 1 shows the counts and measurements of eggnest scars collected at Weldon Springs in 1976. Whatever process was involved in the creation of this new population of Brood XXIII, it is clear that all three periodical cicada species participated in it, since all three are well represented among the 1976 eggnests. The 4-year-old scars of Brood XIX cannot be identified to species, but there is no reason to doubt that all three species are represented in Brood XIX also, since Weldon Springs is well within the range of all three (Alexander and Moore, 1962; Dybas and Lloyd, 1974). White (1980) found all three species in abundance in 1972 near Charleston, Illinois, 100 km southeast of Weldon Springs.

The data in Table 1 are not a random sample, but a complete collection of all eggnests that could be found in one circumscribed area between heights of .5 and 2.5 m—or rather, two nearby areas collected at different times. To compare population densities in Brood XXIII versus Brood XIX, we look at centimeters of eggnests. Lumping both collections, the two broods are about equally represented: Brood XXIII is 50.3% of the total. The fact that about half the Weldon Springs population now belongs to Brood XXIII is crucial to the theoretical argument, discussed later.

To document the absence of Brood III from this area, we returned on July 1, 1980. We heard no song and found no dead adults or cast skins. We then collected, measured, and examined all sides of 50.4 m of twigs 3 mm to 11 mm in diameter in black oak, white oak, and tulip poplar without finding any eggnests of the current year. At the same time, we did find 259 cm of 4- and 8-year old eggnests attributable to Broods XIX and XXIII, in twigs ranging up to 20 cm in diameter, 28

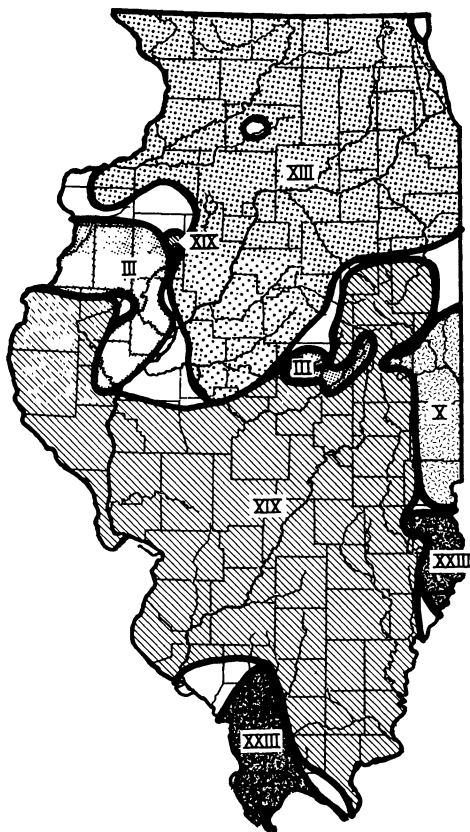


FIG. 2. The distribution of periodical cicada broods in Illinois, 1963 to 1973, unmodified from Stannard (1975) with permission. Broods III, X, and XIII are 17-year broods; Broods XIX and XXIII are 13-year broods. From field data in 1972, 1976, and 1980, it is now evident that the small enclave in east-central Illinois should be labelled, not "III," but "XIX + XXIII." When old records are considered (see Fig. 8), many of the counties mapped by Stannard as now exclusively harboring Brood XIX once contained populations of Brood XXIII, and conversely.

of the 259 cm in dead twigs still clinging to the trees.

Allozymes

The results of the electrophoretic analysis are presented in Table 2 and the collection localities mapped in Figure 3. Only one of the enzymes in one of the species shows a dramatic difference between Weldon Springs and the main part of the distribution. A fair test of statistical significance should consider all the data

TABLE 1. *Eggnest scars of 13-year Broods XIX and XXIII found in the same trees at Weldon Springs State Park, DeWitt County, Illinois, collected in July and August, 1976.*

Plant species	Eggnests of Brood XIX, 1972 (cm) ^a	Eggnests of Brood XXIII, 1976						Proportion of eggnests (cm) that are Brood XXIII
		<i>M. septendecim</i>		<i>M. cassini</i>		<i>M. septendecula</i>		
		Number	cm	Number	cm	Number	cm	
<i>Cornus drummondii</i>	20.3	4	5.2	—	—	354	360.0	.947
<i>Crataegus punctata</i>	390.5	147	148.1	91	77.3	56	61.0	.423
<i>Prunus serotina</i>	—	13	14.3	11	6.9	—	—	1.000
<i>Quercus imbricaria</i>	181.3	16	17.8	11	9.4	76	74.8	.360
<i>Quercus velutina</i>	242.1	12	14.1	17	13.7	22	22.6	.172
<i>Ulmus americana</i>	6.3	—	—	35	29.1	2	2.6	.834
<i>Ulmus rubra</i>	11.9	—	—	7	5.2	2	2.1	.380
Totals	852.4	192	199.5	172	141.6	512	523.1	.503

^a After 4 years, the individual eggnests are no longer countable or identifiable to species, but the centimeters of eggnest will not have changed, since twigs grow in length only at their tips

simultaneously, from both species and all three enzymes. We will use Fisher's (1950 p. 99) method of expressing each probability as an equivalent Chi-square value with two degrees of freedom, then adding together six of these to obtain a Chi-square with 12 *df*. As a rough statistical test, consider only the commonest allele versus the others combined. For phosphoglucosmutase in *M. septendecim*, the frequency .77 for allele 100 (Table 2) is 5.6 standard deviations below the average of the other 13 populations in the main part of the distribution, on an appropriately transformed arcsine scale ($2 \sin^{-1} \sqrt{x}$). Fisher's formula is $-2 \log_e P = \chi^2_2$, where in this case P is the (2-tailed) probability of such a large deviation, in a t -distribution with $n - 1$ degrees of freedom, where n is the number of populations sampled in the main part of the distribution. Hence $\chi^2_2 = 18.11$. The remaining five Chi-square values are 5.18 and .91 for *M. septendecim*, and 4.53, 11.36, and .20 for *M. cassini*. Altogether, we have $\chi^2_{12} = 40.3$, $P < .0001$. Had we tested *M. cassini* by itself, Weldon Springs would still be significantly different from the main part of the distribution $\chi^2_6 = 16.0$, $P = .013$. Hence, both species tested appear to have unusual allozyme frequencies at Weldon Springs.

The Model

White and Lloyd (1975) showed that 13- and 17-year cicadas differ mainly in the

earliest part of their development: 17-year cicada nymphs grow very little during their first 4 years, but after that develop at about the same rate as 13-year nymphs. Let us assume that this 4-year inhibition in development is caused by a single dominant gene; call it D . Assume that in 1868 all 17-year cicadas were DD , and all 13-year ones were dd . Under that assumption, the F_1 hybrids generated in 1868 were Dd , developed in 17 years, and emerged in synchrony with the 17-year parental Brood X in 1885. (The 13-year parental Brood XIX emerged on schedule in 1881 and was reproductively isolated from the hybrids throughout.) The hybrids would mate *inter se*, producing DD , Dd , and dd offspring, and backcross with Brood X cicadas, producing only DD and Dd . So a mixture of 13- and 17-year genotypes would enter the ground in 1885, but the proportions of each would depend on the relative numbers of Brood XIX and Brood X cicadas that had constituted the hybridizing population in 1868. Since only one-fourth of the F_2 hybrids develop in 13 years, and none of the backcross offspring do, there might be an inadequate number of 13-year genotypes to satiate predators, so the 1898 emergence would leave no offspring, or leave too few to satiate predators in 1911. The 17-year genotypes, emerging in 1902, would segregate a still smaller number of 13-year genotypes, which would again fail to satiate predators

TABLE 2. Frequencies of electrophoretic variants for three enzymes at Weldon Springs (W) compared with those from the major part of the distribution of Brood XXIII (Fig. 3).

Species and locality	Phosphoglucomutase					α-glycerophosphate dehydrogenase-1					β-esterase					
	105	100	98	95	90	n	105	100	98	95	90	n	100	95	90	n
<i>M. septendecim</i>																
W	0	.77	0	.23	0	24	0	.65	0	.35	0	24	.21	.79	0	24
IN-C	0	.891	0	.109	0	96	.005	.595	0	.400	0	96	.271	.729	0	96
IL-A	0	.953	.005	.042	0	96	.005	.552	0	.443	0	96	.203	.792	.005	96
MO-A	0	.922	0	.068	.010	96	0	.599	.030	.380	0	96	.245	.750	.005	96
KY-A	0	.969	0	.031	0	64	0	.625	0	.375	0	96	.172	.822	.006	87
TN-C	.005	.979	0	.016	0	96	0	.620	0	.380	0	96	.141	.859	0	96
TN-D	0	.964	0	.036	0	96	0	.620	.010	.370	0	96	.156	.828	.016	96
AK-B	0	.958	0	.042	0	96	.005	.552	0	.443	0	96	.219	.781	0	96
MS-A	0	.938	0	.062	0	64	0	.552	0	.448	0	96	.282	.718	0	85
MS-B	0	.953	0	.047	0	95	0	.599	0	.401	0	96	.332	.668	0	95
MS-C	0	.974	0	.026	0	96	0	.569	0	.431	0	94	.214	.776	.010	96
MS-E	0	.958	0	.042	0	96	0	.521	0	.479	0	96	.234	.765	0	96
MS-F	0	.958	.010	.032	0	96	0	.599	0	.401	0	96	.253	.747	0	96
LA-A	0	.958	.005	.037	0	96	0	.589	0	.411	0	96	.375	.625	0	48
<i>M. cassini</i>																
W	.19	.60	0	.21	0	35	0	0	0	.97	.03	35	0	.986	.014	35
IN-A	.161	.511	.031	.297	0	96	0	0	0	.937	.063	96	0	.995	.005	96
IN-C	.115	.479	.016	.385	.005	96	0	0	0	.912	.083	96	0	.974	.026	96
IL-A	.115	.458	.026	.385	.016	96	0	0	0	.927	.073	96	0	1.000	0	96
IL-B	.187	.453	.016	.344	0	96	0	0	0	.891	.109	96	0	1.000	0	96
MO-A	.163	.506	.026	.305	0	95	0	0	0	.921	.079	96	0	.990	.010	96
TN-A	.117	.500	0	.383	0	95	0	0	0	.926	.074	95	0	1.000	0	95
TN-C	.130	.526	.005	.338	0	96	0	0	0	.911	.089	96	0	.984	.015	96
TN-D	.161	.500	0	.339	0	96	0	0	0	.922	.078	96	0	.990	.010	96
MS-B	.087	.630	0	.272	0	46	0	0	0	.920	.080	44	0	.989	.011	46
MS-C	.156	.422	.010	.406	.005	96	0	0	0	.948	.052	96	0	1.000	0	96

in 1915, and perhaps not even be noticed. The *d* allele would then gradually be swept out of the 17-year population, being effectively a recessive lethal gene. We will call this "scenario (1)."

On the other hand, a successful hybrid F₂ 13-year population might have been produced if Brood XIX had been optimally abundant in 1868. In that case, there might be enough *dd* genotypes segregating and emerging in 1898 to satiate predators and form a viable new brood in their own right. We will call this "scenario (2)."

In general, in the year of joint emergence let *N* be the number of adult cicadas emerging from the ground and *p* be the proportion of these that are 13-year genotypes, *dd*. Then *pN* individuals will be *dd* and $(1 - p)N = qN$ will be *DD*. (We assume they have invaded each others' ranges less than 221 years earlier, so there

will be no heterozygotes.) For the moment we assume no competitive advantage of 13-year nymphs over 17-year ones, and that *N* represents the stable carrying capacity of the ground to produce adult cicadas of either type, or any mixture. The average fertility per adult (half the female rate, averaged over species) is *f* eggs, and the average probability of an egg becoming an adult is $1/f$. What will be the expected proportions of genotypes in future generations?

If mating is random, there will be p^2fN eggs of 13-year genotype *dd* produced, from which we expect only p^2N 13-year cicadas to emerge 13 years later. There will have been a dramatic reduction in Brood XIX from *pN* to p^2N . If *p* is low, this may not be enough to satiate predators, and the invading 13-year cicadas will become locally extinct.

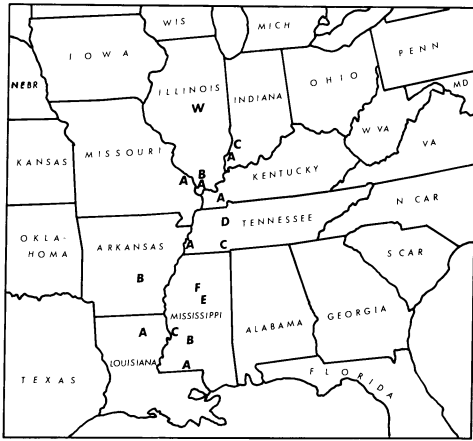


FIG. 3. Locations of sites where samples of *Magicalicada septendecim* and *M. cassini* were collected for analysis of allozymes (Table 2). Site designations are from Simon 1979b. Site "A" in Louisiana is designated "LA-A" in Table 2, site "A" in Mississippi is "MS-A," etc. Note that Weldon Springs ("W") is far removed from the remainder of the samples.

What proportion of the total N will segregate as 13-year dd genotypes when the 17-year phenotypes breed in the 17th year after hybridization? This is illustrated by Figure 4. The total 17-year population is $(1 - p^2)N$, the probability of two heterozygotes mating is $[2pq/(1 + p)]^2$, and only one-fourth of these will segregate the dd genotype. Multiplying these three factors and simplifying, we have $p^2N(1 - p)/(1 + p)$ emerging as Brood XXIII in year-30, or a proportion of $p^2(1 - p)/(1 + p)$ of the total N . This function has a maximum where $p = (\sqrt{5} - 1)/2 = 61.8\%$. Above or below that point, a relative shortage of one or the other parental genotype produces a suboptimal number of heterozygotes in year-17, from the point of view of a newly formed Brood XXIII in year-30. But when $p = .618$, Brood XXIII adults in year-30 still constitute only $p^2(1 - p)/(1 + p) = 9\%$ of the original N .

It seems unlikely that this 9% would be enough cicadas to satiate predators. Therefore, since we have one case (Weldon Springs) that we interpret as scenario (2), the genetic model demands that we relax the ecological assumption that 13-

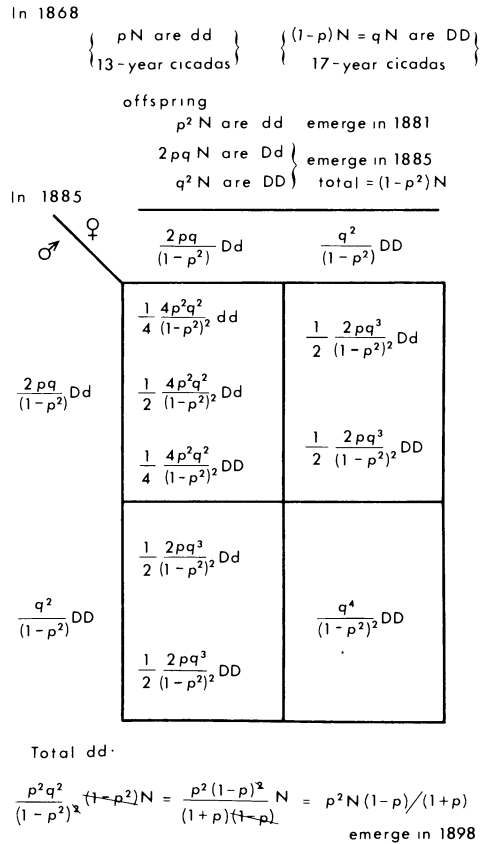


FIG. 4. A simple mendelian model for 13- and 17-year life cycles. In 1868 pN 13-year cicadas (dd) and $(1 - p)N = qN$ 17-year cicadas (DD) emerge in the same year and mate at random. Assuming N adults emerging in the next generation and that 13-year genotypes have no competition advantage, p^2N will emerge as 13-year cicadas in 1881 and $(1 - p^2)N$ as 17-year cicadas in 1885. The proportion of heterozygotes among 17-year cicadas is $2pq/(1 - p^2)$ and one-fourth of the offspring resulting when two heterozygotes happen to mate, namely $p^2N(1 - p)/(1 + p)$, segregate the 13-year genotype and emerge as Brood XXIII in 1898.

year nymphs have no competitive advantage. If the size of the emerging cicada population is limited by competition among nymphs for a limited number of feeding sites underground, and if the dd nymphs entering the ground in 1885 (Fig. 4) survive much better than the Dd and DD nymphs do, then there can be much more than 9% of N emerging in 1898—perhaps enough to satiate predators.

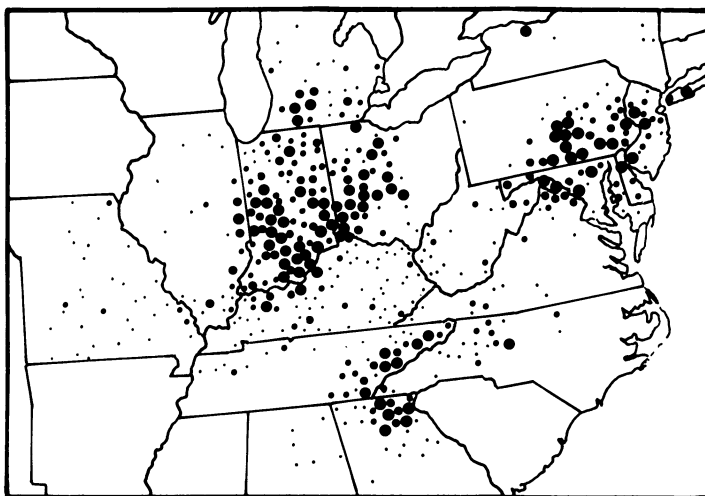


FIG. 5. The old distribution of 17-year Brood X, redrawn from Hyslop (1935). There are four sizes of dots, signifying whether, up through 1919, Brood X had been recorded only once (smallest dots), twice, three times, or at least four times (largest dots). Most of the Missouri records are for 1902; the five larger dots are for 1919. There are abundant records for Missouri in 1868 and 1885 (Haseman, 1915) but Hyslop omitted these from the maps because they could not be distinguished from Broods XIX and XXIII, respectively (see Fig. 1).

We can now summarize what we should expect the historical evidence to show, according to this model. First, there should be evidence of large-scale replacement of 17-year cicadas by 13-year ones. Second, where the historical records are good enough to detail events after 1868 in an area where Broods X and XIX hybridized and Brood XXIII later appeared, we should have the following: there should be *no* emergence in 1872 (Fig. 1), confirming that Brood XXIII was not already present when the hybridization took place; there should be an emergence 13 years later (1881, XIX); there should be one 17 years later (1885, X + F₁ hybrids); there should be one 26 years later (1894, XIX again); there should be an “unexpected” emergence 30 years later (1898, segregating XXIII). There should be only a minimal emergence 34 years later (1902, X + F₂ hybrids), and thereafter Brood X should disappear from the area. Third, even though the present-day distribution may give the impression that Broods XIX and XXIII occupy mutually exclusive territories (Fig. 2), historical records should show

both broods present in a given county at some time in the past, since, by hypothesis, XXIII was derived from XIX. Fourth, even though 13-year nymphs may have a competitive advantage over 17-year ones, the most frequent result of hybridization in 1868 should have been scenario (1), i.e., most of the Brood XXIII populations first appearing in 1898 should have failed to satiate predators and left no offspring. This is because p , the proportion of 13-year genotypes in 1868, will have been highly variable from place to place—depending on when 13-year cicadas first invaded, how many, etc.—and p will not often be in the narrow range near the optimum ($p = .618$) that leads to scenario (2).

Historical Evidence

Figure 5 shows 17-year Brood X widely distributed over the eastern two-thirds of Missouri in 1902, and scattered widely through Illinois. Brood X is now extinct in Missouri; its last appearance was in 1919 (Haseman, 1919). In Illinois, Brood X is now confined to four counties on the eastern side of the state (Fig. 2), contiguous

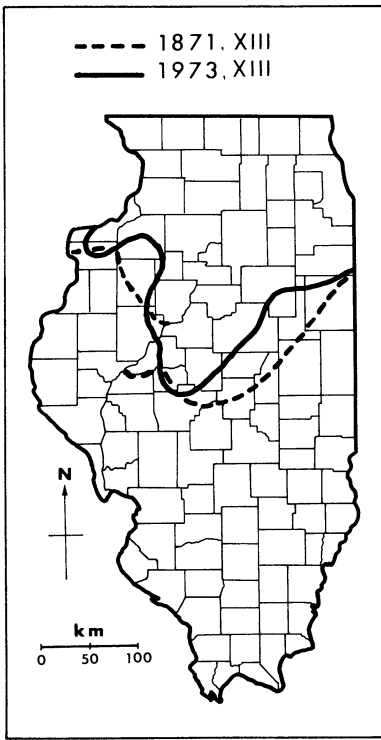


FIG. 6. The southern limit of the range of 17-year Brood XIII as mapped in 1871 by LeBaron, 1872—and in 1973 by Stannard, 1975.

with its range in Indiana. Meanwhile, by 1933, 13-year Brood XIX was abundantly occupying all the territory in Missouri and Illinois that had formerly supported Brood X (Anon., 1933).

LeBaron (1872) carefully mapped the southern edge of the range of 17-year Brood XIII in 1871. This appears as the dashed line in Fig. 6, where it is contrasted with Stannard's line for 1973, from Figure 2. In 102 years, Brood XIII has contracted its range by 50 km in some places. In east-central Illinois, the territory lost by XIII is now occupied by 13-year Brood XIX (Fig. 2). This represents an advance of about .5 km/year, or 6.5 km/generation for 13-year cicadas—all of which must take place during the brief period of adult life, i.e., during the emergence. LeBaron (1872) remarked that, "Stragglers have often been seen many

miles out upon the prairie, having been driven, sometimes by high winds, and possible being impelled by an instinct to extend their borders." White et al. (1983) found that tethered suspended *Magicicada* were exhausted after flying for 1,000 seconds, equivalent to about 2 km at 2 m/sec. Hence, at least in some areas, it appears that 13-year cicadas are replacing 17-year ones about as fast as new territory can be invaded.

Figure 7 shows that the pattern of emergences in DeWitt, Piatt, and Champaign counties conforms reasonably well with our hypothesis of the origin of Brood XXIII by genetic segregation in hybrids. These data were gathered from archives as well as from the published literature, as explained earlier. For the data to conform perfectly, we should have Brood XIX in DeWitt County in 1881 and 1894. Since it is there now (1972), we assume it was there all along, and that the 1868 record in DeWitt County includes both XIX and X. Similarly, we should have emergences in Piatt and Champaign counties in 1885, 1898, and 1911. Since XXIII is there now, we assume it was also there in 1898 and 1911, and that Brood X (plus some hybrids) was present there in 1885.

The surprise was the appearance of periodical cicadas in 1898. This was reported from Wapella, DeWitt County by an amateur, W. R. Carle, in a letter to L. O. Howard, the Chief of the Bureau of Entomology in Washington, D.C. Carle was aware that periodical cicadas were not "scheduled" to emerge there until 1902. We conjecture that, in general, scheduled emergences of periodical cicadas are more likely to be reported by professional entomologists (since that is their job) whereas unexpected ones are more likely to be reported by one of the far greater number of informed amateurs, pleased to discover something the professionals didn't know. We suppose this may be why Mr. Carle did not report the emergences that probably occurred in DeWitt county in 1881 and 1894—they were expected. County records show that Carle moved to Wapella in the 1850's and died there in 1912, es-

tablishing that he had the opportunity to observe the cicadas for 50 years. For this reason, we place some credence in the negative record from DeWitt County in 1872—that, too, would have been unexpected, and Carle would probably have reported it had it occurred. The following emergence of XXIII in DeWitt County, in 1911, was reported by a professional—Charles Hart, acting Director of the Natural History Society.

Figure 8 shows the emergence pattern for the entire state of Illinois, taken mostly from published records. The second map (1872, 1859, etc.) shows that only four counties in Illinois had evidence of Brood XXIII existing before 1868, i.e., emerging in 1872. Hence, most of the 1885 records probably represent Brood X (plus hybrids from 1868) and one can see how thoroughly sympatric they were with XIX by the many counties reporting emergences both in 1881 and 1885. Between 1885 and 1902, there was a dramatic withdrawal of Brood X from western Illinois, and a further withdrawal from southern Illinois between 1902 and 1970 (Fig. 2).

In 1898, a great many “new” populations of Brood XXIII appeared in counties where they had not been recorded in 1872 or earlier. These (to repeat) we interpret as F_2 hybrids that segregated the 13-year genotype *dd* in 1885, and hence really were new populations of XXIII. Now admittedly, a much more thorough mapping operation took place in 1898 than there had been in 1872. L. O. Howard wrote to S. A. Forbes, Illinois State Entomologist, on May 21, 1898, pointing out the confusion between X and XXIII in 1885 and urging, “It is, therefore, very desirable to have as complete records as possible made the present year.” There were two sources for Illinois cicada records in 1898. The Bureau of Entomology was receiving reports direct from Illinois citizens and Forbes directed a mapping effort through the State Entomologist’s Office. Forbes informed Howard on June 15, 1898 that he was sending an assistant to the field to check on possible cicada emergences and that he had sent a circular to “teachers and county

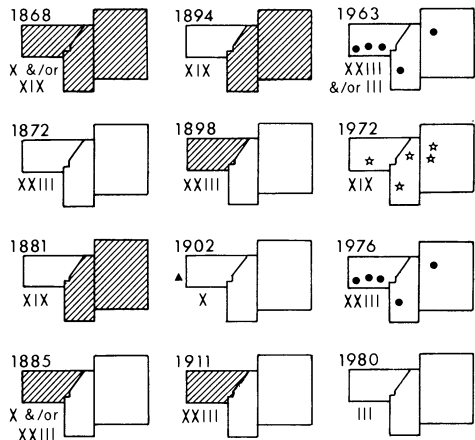


FIG. 7. Periodical cicada emergences for three counties in east-central Illinois, from west to east: DeWitt, Piatt, and Champaign. The year is given just above each diagram and the expected brood or broods (Fig. 1) just below. For the earlier records, the county is cross-hatched when an emergence occurred anywhere within it. For the later records, individual localities are shown. In 1902, there was a sparse emergence of Brood X reported at Beason (Logan County, just west of the DeWitt County line), shown by the small triangle, but none in the three diagrammed counties. The last diagram merely records the absence of Brood III in these counties.

superintendents of schools, who are more likely to take interest in these matters.” Replies started to arrive within a week and Forbes’ records were relayed to Howard in a letter dated July 2, 1898, and were published by Marlatt (1898). Forbes’ work confirmed the county reports sent to Howard and added five new county records.

In view of all this, we must assume that some of the populations of Brood XXIII first recorded in 1898 may have appeared in 1872 or earlier. On the other hand, we would urge that Forbes’ predecessor in the State Entomologist position, William LeBaron, was an extremely competent and energetic entomologist who was personally interested in periodical cicadas and corresponded extensively with amateurs in working out the detailed distribution of 17-year Brood XIII in 1871 (LeBaron, 1872). Had there been anything like the widespread proliferation of emergences of

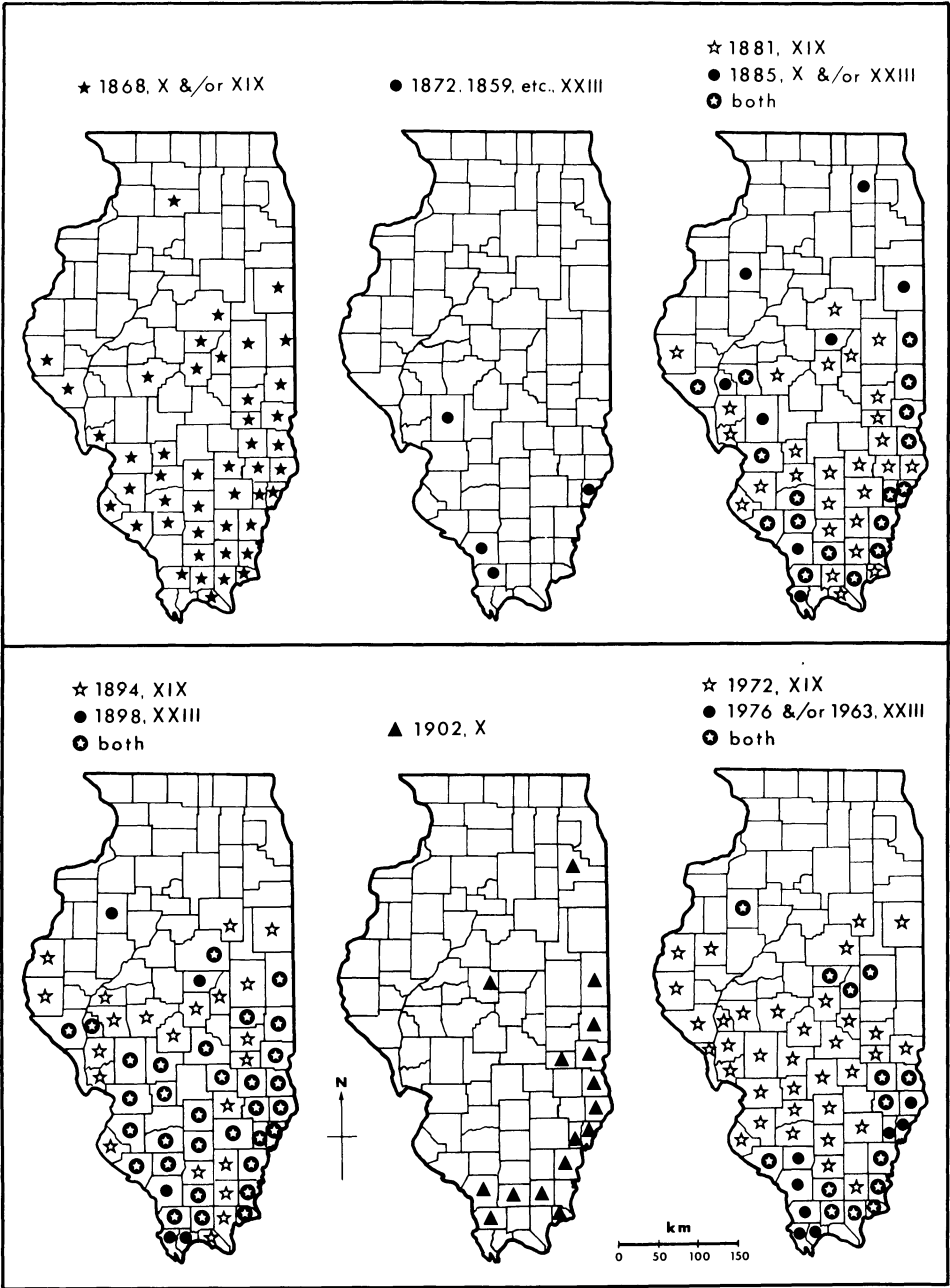


FIG. 8. Emergences in Illinois of periodical cicadas in specified years, by counties. Sources: Walsh and Riley, 1868; Riley, 1885; Marlatt, 1907; Hyslop, 1935; Anon., 1937; Stannard, 1975; Kritsky and Meyer, 1976; unpublished personal observations and returned questionnaires in 1976 (Lloyd et al., unpubl.).

XXIII in Illinois in 1872 that was later seen in 1898, it is unlikely that LeBaron would have missed it.

A series of maps very similar to Figure 8 could be constructed for Missouri, based on the published work of Riley (1885), Haseman (1915), and the U.S.D.A. Insect Pest Survey (Anon., 1933). In both Illinois and Missouri, the majority of populations of XXIII first recorded in 1898 were in counties also having populations of XIX in 1894.

Collating the records coming into the Bureau of Entomology in 1898, Marlatt (1898, 1907) was struck by an odd fact. In the main part of its distribution in the lower Mississippi River Valley (Fig. 3) Brood XXIII had the reputation (from 1872 and earlier emergences) of producing enormously *dense*, thriving populations. Yet those new records appearing in Illinois, Missouri, northwestern Arkansas, Indiana, and Kentucky—generally speaking, far away from the center of distribution—were mostly sparse populations. Marlatt used two sizes of dots in plotting the distribution of Brood XXIII: large dots for, “one or more dense swarms, in many cases several reports being received from the same county” versus small dots for, “few or scattering numbers, or at least not as abundant.” Our genetic hypothesis offers an explanation for this difference: a new emergence in 1898 did not represent a whole population, but rather a small part (necessarily less than 9%) of two hybridizing populations—the part genetically segregating the 13-year life cycle. In Illinois (Fig. 8) most of the populations of Brood XXIII first appearing in 1898 have not persisted to the present day (1976), in conformity with our theoretical expectations.

Predictions

It does not matter which 17-year brood hybridizes with Brood XIX, the result should, by hypothesis, always be the same—a new population of Brood XXIII emerging 30 years later. For example, Broods III and XIX emerged in the same

year in 1946 (Fig. 1). Wherever they occurred in the same woodland, they should have hybridized and produced a new population of Brood XXIII 30 years later in 1976. Stannard's map (Fig. 2) shows that the ranges of III and XIX are contiguous in western Illinois; this is where one would expect some interpenetration of ranges to have occurred. In particular, Stannard shows an outlier population of XIX in Knox County, just on the border between two 17-year broods—III and XIII. A check of this area in December, 1980, revealed 4-year old eggneests from 1976, in striking conformity with the prediction of our genetic hypothesis. They were easily distinguishable from the other possibilities—Brood III (1980) eggneests were fresh; those of Brood XIII (1973) and Brood XIX (1972) were respectively 7 and 8 years old. Accordingly, in Figure 8, we have plotted a 1976 emergence of Brood XXIII in Knox County. It lies 130 km northwest of the Weldon Springs population, which is itself 150 km northwest of the most northerly populations of XXIII on Stannard's map (Fig. 2).

However, it is not new: Fig. 8 also shows recorded emergences in Knox County in 1885 and 1898! Two possible explanations can be offered, both of which assume the early presence of XIX in Knox County, which was not recorded in the literature (Fig. 8): (1) if XIX was present as early as 1803, it could have hybridized with XIII and produced a population of XXIII in 1833 (Fig. 1), which might conceivably have persisted for five generations; (2) if the 1885 emergence represents Brood X in the area, then Knox County is like Weldon Springs, i.e., the 1898 emergence derives from hybridization between XIX and X in 1868. It differs from Weldon Springs, however, in one important respect—17 year cicadas (III and XIII) have not been eliminated from the vicinity. This suggests that we are dealing with an example of scenario (1) at Knox County, i.e., the population of XXIII has subsequently become extinct. In that case the 1976 record represents a second (possibly even a third) in-

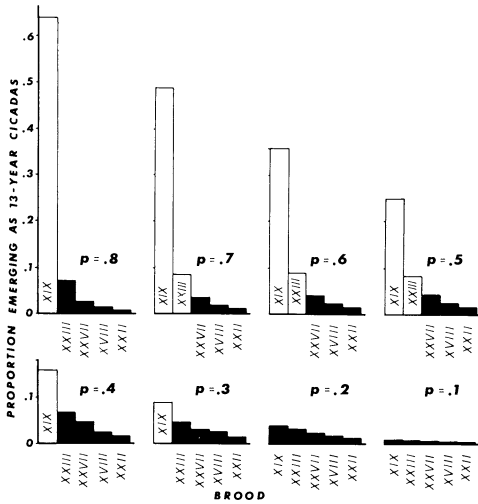


FIG. 9. The proportions of a periodical cicada population genetically segregating with a 13-year developmental period after passing through $j = 0, 1, 2, 3,$ or 4 generations with a 17-year one, i.e., emerging $17j + 13$ years after the 13- and 17-year cicadas had hybridized (according to our hypothesis that the additional 4 years is caused by a single dominant gene, D). If p is the proportion of the original population that is 13-year cicadas (dd), then $p^2(1 - p)/(1 + ip)(1 + jp)$ emerge in subsequent periods ($j = 1, 2, 3, 4, \dots, i = j - 1$). Interpreted as 13-year broods, these would be numbered XXIII, XXVII, XVIII, XXII, etc. Interpreted as 17-year broods, the genetic segregants would always be in synchrony with the brood 4 years ahead of the parent 17-year brood. Thus, if that were Brood X, all the genetic segregants would be "Brood VI." The calculations assume no competitive advantage of 13-year nymphs over 17-year ones. If such an advantage does exist and is taken into account, then the bars would be higher. All bars less than 7.5% of the total population are shaded, suggesting that these might perish from inability to satiate predators.

dependent appearance of XXIII in Knox County. This one, too, may have become extinct.

Further field work has revealed an area of several counties in northeastern Missouri, western Illinois, and extreme southeastern Iowa where Broods XIX and III are now in contact (judging by eggnest scars) and undoubtedly hybridized in 1946. In other words, our scenarios (1) and (2) are currently being reenacted between Broods XIX and III, on a large scale. We predict that in this area: (a) **further egg-nest evidence will be found for an**

emergence in 1976, (b) 1989 will see emergences of Brood XXIII where they have never been recorded before, (c) these will invariably be in the same woods where Brood XIX had previously emerged in 1985, and (d) these new populations of XXIII will be electrophoretically distinct from all others.

In the case of scenario (1), where 17-year cicadas are not eliminated by competition, how many additional 13-year genotypes should segregate in year-47, year-64, year-81, and the ensuing generations, according to our hypothesis? Iterating the calculation in Figure 4, the total emergence in year-34 is $(1 - p)(1 + 2p)N/(1 + p)$, the probability of two heterozygotes mating is $[2p/(1 + 2p)]^2$, and the expected proportion of 13-year genotypes segregating and emerging in year-47 is $p^2(1 - p)/(1 + p)(1 + 2p)$. In year-64 it will be $p^2(1 - p)/(1 + 2p)(1 + 3p)$, in year-81, $p^2 \cdot (1 - p)/(1 + 3p)(1 + 4p)$, etc.

These functions are diagrammed in Figure 9 for various values of p . The solid bars are less than 7.5% of the total original cicada population; we assume (arbitrarily) that these emergences will fail to satiate predators and be eliminated. Actually, we expect higher proportions of 13-year genotypes than are shown in Figure 9, owing to the competitive elimination of 17-year nymphs by 13-year ones, but this effect should be less and less important the smaller is p . With this 7.5% threshold for predation satiation, we expect XIX itself to be eliminated whenever it makes up less than 27% of the hybridizing swarm ($p < .27$). Where $p < .44$ we expect the segregating Brood XXIII to be eliminated. There is no p -value for which the second segregating brood, XXVII, would be expected to satiate predators. Nevertheless, an alert investigator who was present in this woods exactly at the right time might easily detect the emerging cicadas (before the birds ate them) by their song. He also might be able to locate their cast nymphal skins on the tree trunks.

This gives us a fifth testable prediction: (e) **in areas where Broods XIX and III have been in contact since 1946 (as**

evidenced by a broad zone of overlap between eggnest scars of 1980 and an emergence in 1985), there will be periodical cicadas emerging in 1993, which may be nearly as numerous as those appearing in 1985, especially if the 1985 emergence was sparse (cf. Fig. 9, $p = .2$). We visualize that, on the frontier between XIX and III, even if XIX were so reduced by the hybridization in 1946 that there were not enough to satiate predators in 1959, there would be still more Brood XIX cicadas invading later from the main part of the range—in 1972 and 1985. Meanwhile, III will have been infused with recessive *d*-alleles in 1946 (by hypothesis) and begin to segregate cicadas belonging to unheard-of broods. The year 1993 is scheduled for 13-year “Brood XXVII” and 17-year “Brood XVI.” Neither of these broods exist anywhere (Marlatt, 1907).

A similar situation exists between XIX and X on the eastern border of Illinois, in Vermillion County (the next east of Champaign Co.). There is evidence that hybridization took place there in 1868—XIX was recorded in 1881 and 1894, and XXIII appeared in 1898 (Fig. 8). Brood X was still present in 1902 and is there today, whereas XIX is not (Fig. 2), having last been recorded in 1933 (Anon., 1933). If our hypothesis is correct, then Brood X in Vermillion County should continue to segregate a few cicadas with 13-year genotypes for many generations. All of these will be in synchrony with 17-year Brood VI, since they will always appear 4 years in advance of the scheduled emergence of Brood X. Some cicadas did emerge in Vermillion County in 1932, four years ahead of the scheduled appearance of X in 1936 (Fig. 1). They were classified as “Brood VI” (Anon., 1932). Unfortunately, this particular emergence is open to the alternative interpretation of being “forerunners” of the 1933 emergence of XIX (a few stragglers appearing one year in advance of the scheduled emergence—a phenomenon which often does occur). We predict that (f) **periodical cicadas will emerge in Vermillion County again in 1983**, which is 4 years ahead of the scheduled

emergence of Brood X in 1987 (Fig. 1). If living specimens can be obtained, they should resemble electrophoretically the Weldon Springs population of Brood XXIII (Table 2). This will be seven generations after the original hybridization in 1868. Figure 9 shows that whereas the expected number of segregants declines with succeeding generations, the rate of decline is slow where p is small. As a necessary control, comparable efforts must be made to find cicadas emerging in eastern Indiana and western Ohio, where X is the dominant brood and XIX has not yet invaded. The same applies to prediction (e): comparable efforts must be made in central Iowa to find cicadas emerging in 1993.

A further precaution is necessary in testing predictions (e) and (f). It appears that 17-year cicadas can abort the 4-year inhibition in growth, i.e., develop in 13 years, in response to some unknown environmental stimulus, now believed to be crowding between the nymphs (Dybas and Lloyd, 1974). The idea was originally suggested by the geographical pattern of 17-year broods 4 years out of phase (Lloyd and Dybas, 1966). Supportive evidence has come from three independent occurrences; all in very crowded populations and none in situations where hybridization with XIX could reasonably be considered to have been an historical antecedent: (1) many individuals of Brood XIII (1973) appeared 4 years early in Chicago in 1969 (Dybas and Lloyd, 1974); (2) some individuals of Brood II (1979) appeared 4 years early in suburban yards in New Jersey in 1975 (Simon and Lloyd, 1982); (3) eggnest scars revealed 17-year Broods XIV and X co-existing in the same woodlands at 5 study sites in northern Kentucky (Lloyd and White, 1976b). There is no compelling reason, of course, why the same phenotypic aberration (a 4-year acceleration in development) could not be produced either by an environmental shock or by a gene (Waddington, 1953). We propose to distinguish between the two by the presence or absence of what we believe to be the environmental shock—extreme crowding among the nymphs.

Predictions (e) and (f) must therefore be

understood as follows: where there is a history of hybridization between XIX and a 17-year brood, and the latter has been the only survivor, it will invariably produce some individuals emerging 4 years ahead of schedule, even when population density is comparatively low. Where there has been no such history of hybridization, there may be some individuals emerging 4 years ahead of schedule, but only where population density is extremely high.

One might ask, if Brood XIX can hybridize with 17-year cicadas to produce XXIII, then why cannot XXIII do the same and produce populations of Brood XXVII (there are none—Marlatt, 1907)? The answer, by hypothesis, is that XXIII never gets a chance to do this: the hybridization between XIX and a 17-year brood, if it generates Brood XXIII, will also annihilate the 17-year brood locally. This gives us a seventh testable prediction: (g) **Brood XXIII will never be found in the same woods with a 17-year brood, although Brood XIX frequently will.**

In case of scenario (2), where the 17-year brood is eliminated and we are left with Broods XIX and XXIII living sympatrically, what is the expected proportion of cicadas in each brood? There is no reason to think that the demise of 17-year nymphs (with their programmed inhibition of growth) would favor a particular nymph of the derived Brood XXIII any more than it would favor one from the parental Brood XIX. Let us assume that the two would be equally favored.

If there were no differentially higher mortality of 17-year nymphs, then we would have had $p^2N(1-p)/(1+p)$ expected to emerge in Brood XXIII and p^2N in Brood XIX. Considering only 13-year cicadas, the proportion of the total in Brood XXIII would therefore have been $(1-p)/2$. Suppose now that we take the $(1-p)(1+2p)N/(1+p)$ 17-year cicadas emerging and eliminate their progeny by competition in a single generation. We will apportion the vacated feeding sites to individuals of the two 13-year broods with equal probability, i.e., the expected proportion going to Brood XXIII will be

$(1-p)/2$ and that to XIX, $(1+p)/2$. We have increased the emerging population of XXIII from $p^2(1-p)N/(1+p)$ to $(1-p)N/2$ and increased XIX from p^2N to $(1+p)N/2$, but the proportion in Brood XXIII among 13-year cicadas is still the same, namely, $(1-p)/2$. The same would hold if any intermediate proportion of 17-year nymphs were eliminated by competition. Hence, no matter how many or how few 17-year nymphs are eliminated, the proportion of XXIII among 13-year cicadas will be $(1-p)/2$. Now, since $0 \leq p \leq 1$, we necessarily have $(1-p)/2 \leq .50$, so this yields one more testable prediction: (h) **for newly established populations of Brood XXIII, the proportion XXIII/(XIX + XXIII) will be less than 50%.**

We can be more precise if we know how large a proportion (call it θ) of a normally dense cicada population would be just sufficient to satiate predators. Since the newly-segregating population of XXIII must satiate predators, we have $(1-p)/2 > \theta$, which sets an upper limit, $p < 1 - 2\theta$ (if p is greater than that, there will be too few 17-year genotypes in the hybridizing swarm, hence too few F_1 hybrids to generate enough F_2 segregants to satiate predators).

To arrive at a lower limit for p , it is not realistic to assume that all the 17-year nymphs will be eliminated, since there will be too few 13-year nymphs to have much effect. A conservative estimate can be obtained by assuming no benefit to 13-year nymphs from the elimination of 17-year ones. In that case, in order for Brood XIX to satiate predators, we must have $p^2 > \theta$, which sets an upper limit on the proportion of Brood XXIII: $(1-p)/2 < (1-\sqrt{\theta})/2$. For $\theta = 7.5\%$ (used to shade the bars in Fig. 9) this implies $7.5\% < (1-p)/2 < 36\%$. If more than 7.5% are required to satiate predators, then the upper limit will be lower than 36%.

Contradictions

Table 1 shows that the proportion of Brood XXIII egnests in this sample is about 50%. This implies a predator satiation threshold of essentially $\theta = 0$, which is emphatically unrealistic. Either our hy-

pothesis is wrong, or it is too simple, or the data in Table 1 are flawed.

Unfortunately, egg-nests have a patchy spatial distribution (Simon et al., 1981), which means that small samples have a high standard error. Table 1 is based on two independent samples in slightly different locations. The proportions of XXIII in the first collections (*Q. imbricaria* and *U. rubra*) were 36.1%; in the second (the remaining plant species) it was 52.1%, which gives some idea of the consistency.

There is also a systematic bias: since egg-nest damage often kills the twigs, they will sometimes fall off the trees in 4 years' time, giving an upward bias to the apparent proportions belonging to the later-emerging brood (Lloyd and White, 1976b). We have never attempted to measure the magnitude of this bias, but any correction for it would make the data more compatible with the hypothesis. Since this was in a picnic area at Weldon Springs State Park, it is even possible that maintenance personnel had trimmed off some of the egg-nest damage of XIX in 1972. The data in Table 1 establish, in a qualitative way, that XIX and XXIII exist sympatrically at Weldon Springs, and they show that all three cicada species are represented in Brood XXIII, but they do not yield a reliable estimate of the true proportion of the population that is XXIII. Nevertheless, we believe the method has great potential for future use, especially if bias corrections can be worked out.

One might wish to consider the possibility that XXIII at Weldon Springs had a double hybrid origin, involving XIX \times XIII in 1803 as well as XIX \times X in 1868 (Fig. 1). Figure 6 shows that XIII was present in DeWitt County, even as late as 1871. Assuming that the Illinois River and its tributaries are highways of invasion for cicadas, it is conceivable that Brood XIX could have worked its way up the Sangamon River and Salt Creek to Weldon Springs as early as 1803. If so, then by hypothesis they would have hybridized with XIII in 1803 and generated a population of XXIII in 1833. This could account for a relatively higher proportion of XXIII in 1972-76. We believe this possi-

bility can be discounted, for three reasons: (i) if enough 13-year cicadas had reached Weldon Springs by 1803 to generate a viable population of XXIII, i.e., scenario (2), then XIII should have been eliminated from the area long before 1871—see our prediction (g); (ii) Brood XXIII generated in 1833 would have hybridized with Brood X in 1885 and broken up the 13-year genotype again (Fig. 1); (iii) there is W. R. Carle's negative record for DeWitt County in 1872 (Fig. 7).

The most obvious way to account for the apparently high proportion of Brood XXIII at Weldon Springs is to assume that, for some intrinsic reason, nymphs of XXIII have a competitive advantage over those of XIX. If this were true, then in the six generations that have elapsed since 1898, XXIII could come to predominate over XIX and perhaps eventually displace it entirely. This possibility must be carefully considered because, in the main part of the distributions of Brood XXIII in the lower Mississippi River Valley (Fig. 3), there are many dense populations consisting entirely of Brood XXIII (Marlatt, 1907)! This is by far the most serious discrepancy between our hypothesis and the known facts. If XXIII arises by hybridizations between XIX and some 17-year brood, then how can XXIII become the only brood present?

In a later paper, we will consider in detail the competitive relationships between nymphs of two 13-year broods 4 years out of phase, as well as those between 13- and 17-year cicada nymphs. We will elaborate the genetic model to allow for double hybridizations between Brood XIX and Brood XIV, then XIX and X, because we think it probable that this phenomenon was involved in the origins of Brood XXIII in the lower Mississippi River Valley. We will also present new data on the distribution and abundance of Brood XXIII throughout its range, derived from an extensive survey in 1976.

DISCUSSION

Lloyd and White (1976) found two 17-year broods coexisting sympatrically in the same woods in northern Kentucky. In the

present study, we have found two 13-year broods in a similar situation in central Illinois. The interpretations given the two cases, however, are completely different: we believe that northern Kentucky represents one 17-year brood (XIV) gradually converting itself into another (X) by some individuals responding to an environmental shock during development, whereas we think Weldon Springs is the aftermath of hybridization between 13- and 17-year cicadas. Why cannot they have the same interpretation, i.e., why could not 13-year cicadas also undergo a 4-year acceleration in development? We believe they cannot do so, because that would mean growing to maturity in only 9 years, which we doubt would be physiologically possible, given their extremely dilute diet of xylem fluid (White and Strehl, 1978). If it could be shown that 9-year development is possible for *Magicicada*, this would disprove our theory—or at least it would demonstrate that our genetic hypothesis is not the only way to account for the known facts.

Brood XIX has also been invading the territory of 17-year Brood IV, having reached central Oklahoma and southeastern Kansas by 1933 (Marlatt, 1907; Anon., 1933). In 1981 we found evidence from old eggnest scars of XIX in northeastern Kansas (Miami Co.). Broods XIX and IV are scheduled to emerge in the same year in 1998, when they will undoubtedly hybridize. A ninth testable prediction, albeit a long-term one, is the following: (i) **in Oklahoma and Kansas, where many periodical cicadas emerged in 1981 (IV) but only a moderate number do so in 1985 (XIX), there will be none emerging in 2011 (XIX), or too few to satiate predators.** This is because the 13-year genotype will be broken up by hybridization in 1998. If we have pN 13-year cicadas mating at random in 1998, they will generate only p^2N in 2011—a reduction which, if p is low, will not be overcome by the postulated competitive advantage of 13-year nymphs over 17-year ones. By 1998, it will probably be possible to distinguish individuals of Broods XIX

and IV by electrophoresis, morphometric analysis, or some other means (Simon, 1979a, 1983).

Over a century ago, Walsh (1870) wrote an interesting essay on periodical cicadas in which he argued that the 13- and 17-year forms must be different species because they never hybridize, as evidenced by that fact that we never find life cycles of intermediate length (e.g., 15 years). He was, of course, reasoning from a premise of blending inheritance—this was 32 years before the rediscovery of Mendel's work. If our mendelian hypothesis is correct, then not only do the two hybridize, but their hybrid progeny are viable for many generations, and we think Alexander and Moore's (1962) naming the 13-year forms as separate species cannot be justified.

SUMMARY

An instance has been documented where two 13-year broods of periodical cicadas, XIX and XXIII, occur together in the same woods. Unusually good historical records suggest that this situation arose as the aftermath of hybridization in 1868 between one of the 13-year broods (XIX) and 17-year Brood X, after which the 17-year brood disappeared from the area. The evidence suggests that the 4-year inhibition in the growth of young nymphs, which characterizes the 17-year life cycle, may be caused by a single dominant gene. This simple genetic hypothesis can explain some of the facts, but an ecological factor also needs to be invoked, namely that 13-year cicada nymphs have a strong competitive advantage over 17-year ones. There is good historical evidence showing widespread contraction in the range of 17-year cicadas with the vacated territory now being occupied by 13-year ones. The theory enables us to make nine testable predictions about future observations on periodical cicadas, which can be carried out in the areas where Brood XIX now overlaps with various 17-year broods in Illinois, Missouri, Iowa, Kansas, and Oklahoma.

A major difficulty with the theory con-

cerns populations in the lower Mississippi River Valley that consist exclusively of the "derived" 13-year Brood XXIII. These will be considered in a later paper.

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ANNOUNCEMENT

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The Simpson Prize, including a cash award, will be presented annually by the Peabody Museum to a young author of a published paper judged to be an outstanding contribution to our understanding of those areas of science that have been of life-long interest to Professor Simpson.

Competition for the Second Simpson Prize is now open. Contenders for this award may submit papers of their own, or be nominated by someone else. In order to be eligible, the submitted or nominated paper clearly must be identifiable with the themes cited above, and have been published between January 1, 1981 and December 31, 1982. To encourage and give recognition to young researchers, eligibility is limited to persons under 35 at the time of submission to the publishing, refereed journal. Publication must be in English.

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