EVOLUTION IN PERIODICAL CICADAS: A GENETICAL EXPLANATION

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ABSTRACT: In contrast to prevalent thought that period length of periodical cicadas (*Magicicada* spp.) was established by ecological disasters (fungi, "parasitoids," wet soils, etc.), an alternative theory maintains that introgression of genes between populations having different (mutated) long-term periods depletes at least one of the parental stocks. Cicadas having a development period of, say, 8-, 9-, or some other number of years compared to primitive short-period cicadas, and including the two extant prime number periods (17, 13 years) may be called mutated or mutant cycle cicadas. The adverse effect of introgression resembles the introduction of lethal genes into a Hardy-Weinberg distribution. Cicadas which have had their cycles altered and emerge out of synchrony are usually so few in numbers that they are eaten by birds. Avoidance of introgression between mutant cycles is accomplished by geographic separation to some extent, but sympatric mutants are temporally isolated by the different period lengths, especially by prime-number periods. Prime-number cicadas hardly ever hybridize by coincidental emergences, and therefore they have built up huge numbers restricted neither by ordinary predation, nor by losing descendants following introgression. They gradually have eradicated any sympatric short-term cicadas (which were controlled by ordinary predation).

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Introduction

The mystery of the periodicity of the six recognized species of periodical cicadas (Cicadidae; Homoptera) has defied solution. Their long periods of underground development have been explained previously by speculative hypotheses on Pleistocene glaciation, escape from "parasitoids," or because long development is associated with great fecundity. Why does an insect live beneath the ground surface as long as 13 or 17 years? Why are both these periods prime numbers? Why are the swarms of adults comprised of such huge and easily killed insects? Why are their breeding populations so immense? How did the development periods become so well synchronized, i.e., why are there no intervening period life cycles, or non-prime periods?

As evidence accumulated to partially explain these questions, new ones arose. What process led to the evolution of periodical cicadas? Perhaps there are important ecological factors, or is there a genetical explanation for such evolution? Numerous papers by Lloyd and his associates attempt to explain many of these questions from ecological theory, but most of the fundamental questions remain. Some insights toward understanding a possible genetical basis have been mentioned (Cox and Carlton, 1988). The purpose of this paper is to develop a new hypothesis, that this is at least partially a peculiar kind of evolution which probably began, as widely assumed, as a predator-prey density phenomenon. I define here an altered life cycle which persists in its new period as a mutated or *mutant cycle*. The mutant cicadas certainly resemble their ancestors closely but seldom interbreed with them. Often they are called *sibs*. If cicadas emerged in 18 years instead of 17 (e.g., White and Lloyd, 1979) and persisted in an 18-year cycle thereafter, then the differentiated cicadas comprise a mutant cycle or sib. If the 18-year cicadas reverted to the 17-year period, I would use the prevalent term *brood*. Each of three quite distinctive species of 17-year cicadas has a corresponding 13-year sib (Alexander and Moore, 1962).

Numerous species of cicadas undergo 2-7 years of development. Incredible lengthening of the development periods even beyond 9-10 years to escape annual predation, and the evolution of synchronized emergences having enough cicadas to more than satiate normal numbers of predators (Alexander and Moore, 1962; Lloyd and Dybas, 1966; Karban, 1982), or doubtfully to elude a hypothesized "parasitoid" (Lloyd and Dybas, 1966; Dawkins, 1986), had to result from peculiar and poorly understood evolutionary phenomena.

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The periodic emergence of huge swarms proves so adaptive that shortened or extended development would seem costly if not lethal. Paradoxically, only by extended development could long periods have evolved. In this paper I will argue that introgression (hybridization of sibs, particularly of similar cicadas with different mutant periods) is a mortal sin, so to speak, resulting in the significant decimation of a cicada mutant cycle stock. Lengthening the cycle avoids much introgression. I am relying more on predictable genetical processes to explain some of the evolution of periodicity formerly ascribed to ecology.

Evolutionary Model

It has been theorized that some primitive short-term cicadas escaped predation (by birds) by lengthening the nymphal development time, thereby emerging in later years when the predators had diminished and were insufficient to limit unpredictable cicada emergences (Hoppensteadt and Keller, 1976). No mechanism has been suggested to explain how periods are lengthened, especially to prime number periods of 13 or 17 years. In this model I hypothesize that long-term nymphal development was and is strictly controlled by genes (i.e., enzymes) isolated in pure breeding stock so alleles at only one or a few loci controlled maturation, metamorphosis, and emergence. Similar genotypes led to their synchronous emergences. Cicadas synchronized to emerge together usually continued to breed among themselves. Pure breeding and inbreeding enhanced homozygosity of the genotypes. If cicadas of different periods coincidentally emerged together, the introgression probably was detrimental to at least one of the parental stocks. The number of eggs is reduced in each parental line, and competition arises with large numbers of eggs having a new development time. Introgression seems lethal to those descendants which might inherit abortive development, and also to those emerging out of synchrony, segregating out of the parental cycle in such small numbers that they were eaten by birds. Large proportions of descendants predictably emerged out of synchrony and in such small numbers they could not survive predation. If they survived, they initiated new broods or sibs sympatric with their ancestors. For practical purposes, a development gene introduced into freely hybridizing populations might be considered in a Hardy-Weinberg distribution lethal to those descendants that exit the parental cycle. Even dominant genes (which do not alter the dominant cycle in hybrids) might be stripped from the cycles by epistatic effects. Long periods, and especially long prime numbered periods, precluded much introgression (avoiding perioidic cross-breeding) and led to virtually unlimited reproduction of the pure breeding stock. The most successful mutant cycles, especially the prime periods, filled up habitats and eradicated their competitors, which also competed with one another.

Discussion

The Satiation Hypothesis. Why are the emergences so huge? The satiation hypothesis (Marlatt, 1923; Alexander and Moore, 1962; Lloyd and Dybas, 1966; Karban, 1982) seems valid that immense numbers of cicadas satiate above-ground predators leaving an enormous surplus of cicadas to breed and perpetuate the species. Convincing experimental evidence of this phenomonon was recently published by Williams et al. (1993).

Small emergences probably seldom survive. Two experiments show that transplanted cicadas, even in fairly large numbers, are entirely eaten. Alexander and Moore (1962) discussed a transplant of about 1,000 cicadas, and Marlatt (1908) mentioned transplanting approximately 10,000 with no survivors from either experiment. Lloyd (personal communciation; see Simon, 1988) reports that hundreds of thousands of 13-year sibs were all eaten up in the Chicago area, where even more numerous 17-year sibs cycle regularly.

Other species of cicadas having shorter periods of development and emerging in lower numbers are decidedly less vulnerable to bird predation (Simon, 1988; and others). Immense emergences seem related to delayed nymphal development.

Lloyd suggests a plausible reason for the slow development of such huge insects. They feed on watery xylem fluid in roots which is low in nutrients. Slow growth is one thing, but delayed synchronous emergence is something else. Perhaps the development is programmed to parallel slow growth and also to promote synchrony. Both small and large nymphs of the same brood attain a normal size and emerge simultaneously (White and Lloyd, 1975).

How might long-period cicadas compete with one another in some struggle for survival resulting in longer and longer periods? Bulmer (1977) and Lloyd et al. (1983) hypothesize that large numbers of immature nymphs compete underground to virtually eliminate sympatric broods, sibs,

and competing species. Dybas and Lloyd (1962) have shown that periodical cicadas do show specific preferences for habitat, but Alexander and Moore (1962), Bulmer (1977) and others report that all three species occasionally emerge together. It even seems adaptive to do so, in view of the aforementioned advantage of the huge emergences, amounting to a mixed species lek.

Lloyd et al. (1983) and others suggested the nymphal competition explanation (which seems reasonable considering the high densities) because they could not otherwise account for the entire loss of 17-year cicadas where two 13-year broods co-existed with them. (Cox and Carlton (1991) provide a solution to this problem, see below.) Nymphal competition or even a deadly fungus (Lloyd, personal comm.) could never be so devastating, favoring one sib to the complete exclusion of the other. Lloyd (personal comm.) also suggests wet soils probably favor one kind (the small species *Magicicada cassini*) over larger cicadas. But even when density is high there may be adequate habitat for many cicada nymphs. It is usually overlooked that following emergence of hundreds of thousands, even millions of adults the abandoned habitat is available for years for any tiny offspring (see May, 1979).

Nymphal competition does not explain abrupt and wide-spread decimation of expected progeny, the abrupt replacement of one sib by another, nor the increasingly delayed development that obviously has evolved in some sequence from short- to long-term periods.

Extended development underground of prey directly effects a decrease in numbers of predators above ground, through starvation. The periodical cicadas emerge later when predator numbers have declined. This assumes other cicadas in the same habitat, as well as the predators, in fact did become scarce.

A mutant cycle cicada may eventually build up its population enormously while its competitors cannot. In any case, there is agreement that large, synchronized emergences are adaptive because the normal bird predators are soon satiated. There is also a reasonable argument, "nymph competiton" (Lloyd et al. 1983), that huge numbers of nymphs are adaptive in eradicating competitors below ground.

Periodicity. A long life span with a short reproductive phase has been related to periodicity (Bernadelli, according to Hoppensteadt and Keller, 1976). May (1979) also mentioned that a longer life span driven by the "race of predators and prey" can cause a "balanced configuration" to become abruptly unstable and lead to periodicity. But why did such extended 13- and 17-year cycles evolve? If periodical behavior was indeed advantageous, selection would work against any cicada that added a year to its cycle. May felt a period might shorten but would not extend. My hypothesis herein is just the opposite, with the possible exception of a fortuitous shortening to a prime number (see beyond).

Time (i.e., extended development) is again hypothesized as a fitness factor by Lloyd and Dybas (1966) and reiterated by Dawkins (1986) who suggested a "parasitoid" might have become extinct when the cicadas went underground. Could the "parasitoid" not subsist on the cicadas that failed to extend development? If these other cicadas are extirpated, except the new cicada that mutated or "switched 4-years" (Lloyd and Dybas, 1966, Lloyd and White, 1976), we are either referring to wide-spread assimilation of an acquired character (but see Carlton and Cox, 1988) or possibly to a genetical phenomenon discussed below.

Hoppensteadt and Keller (1976) and Murray (1989) discussed the balance of bird predators and emerging nymphs. Their model shows how predation alone can lead in a little more than a century to synchronous emergences of 13-year cicadas. The model shows, on the other hand, that three-, four-, and seven-year forms would not exhibit synchronous emergences, and in fact, short-lived cicadas today do not have periods. There are serious problems with their model. For one, the predation would have to be relatively constant for enormous periods of time. Otherwise, the cicadas would not maintain periodicity. The population model begins with a given k, and an extended 13-year period. Attaining such a length is as important to understand as is the synchrony. How did the periods extend themselves to such length, for surely that evolution is enzymatically (genetically) controlled?

Disparaging the prime numbers (13, 17) is becoming popular, and these mathematicians cannot account for any advantage in prime cycles. My hypothesis points up the importance of all six prime periods for six existing named kinds of cicadas, because prime periods reduced opportunities for hybridization.

Hoppensteadt and Keller (1976) mentioned rigorous requirements (production of progeny must exceed predation; and the progeny cannot exceed the carrying capacity). They also show that the life span for periodicity must be as long as 10 years, and asked (but did not answer) the important

question of how 13- and 17-year life spans evolved in the first place. They also wondered about the reported four-year accelerations observed in development. May (1979) says their model can be satisfied only by a "delicate juggling of pertinent parameters."

Prime numbers. One clue related to the long periods of development is that all six periodical cicada species have prime number cycles (Lloyd and Dybas, 1966; Dawkins, 1986), too many to explain as lucky coincidence. One can, of course, consider the six species to be only three (with two potentially viable sibs each), but they also can be considered even more than six. Simon (1988) suggests on the basis of allozyme differentiation as many as nine "species"—all having prime periods.

Three forms are morphologically distinctive species of 17-year periods, and each of them has a 13-year sib. That is, in each distinctive species one kind emerges every 17 years whereas a very similar (obviously closely related) sibling form emerges in 13 years. On a phylogenetic tree the three prime-number 17-year species apparently arise from a common branch, but branching from each of the three is a prime-number 13-year branch (Alexander and Moore, 1962). That remarkable coincidence of prime period length must have some phylogenetic meaning (Alexander and Moore, 1962; Lloyd and Dybas, 1966; Dawkins, 1986; Cox and Carlton, 1988), Murray's (1989) opinion to the contrary notwithstanding.

A prime number is of course odd, and assuming the final year is for metamorphosis, then 17 might result from factors of 2 x 8 + 1, 4 x 4 + 1, and not much else. Aforementioned four year accelerations and inhibitions are, therefore, consistent with the possible mathematical factors. Four year mutations are as reasonably explained by gene-enzyme effects as by ecological disasters.

The precise timing mechanism would seem more logically to relate to observed molts between instars than to factors of two or four. However, "accelerations" or inhibitions of four-year spurts seem to be valid empirical values (Lloyd and Dybas, 1966; White and Lloyd, 1975; Lloyd and White, 1976; Martin and Simon, 1988). Obviously, one molt cannot follow another too rapidly, and successive molts do follow at established times. In most cicadas, the instars molt five times, and in periodical cicadas at approximately one, two, two, three, and then either five or nine years (Marlatt, 1923). White and Lloyd (1975) describe variation in development but 89 percent of nine-year old nymphs of 13-year cicadas compared closely in size to 86 percent of 13-year old nymphs of 17-year cicadas. They concluded that growth was inhibited several years in the second instar of the 17-year cicadas, but afterward the development was about the same rate.

Somehow irregular variation in timing is swept out of the cicada populations. Intuitively it seems plausible that periodicity is first strictly established for a cicada, and subsequently altered in a new sib.

One can hypothesize that some ancestral cicada populations evolved with periods of development closely related to the early intervals of the aforementioned cumulative instar sequence, the time of development extending somehow, evolutionarily postponing emergence. Finally a population of cicadas hit on an optimal (i.e., precluding hybridizations) number of years (in fact, a prime number).

The process of extending the early instar development in ancestral cicadas may have been different in altering regular molts (perhaps even adding some) and in maintaining growth. In later extensions of development we observe inhibition delaying the growth, apparently over four-year phases. I suspect that developmental periods indeed may be and have been altered by four- or one-year changes (see Lloyd and Dybas, 1966; Simon, 1988). Such so-called "switching" led to new mutant cycles involving the new alleles controlling them. It seems doubtful that switching becomes prevalent suddenly over a wide geographic range. But if a new mutated cycle by overcoming predation and independent proliferation succeeds in building an immense emergence it becomes a great threat to any different cicadas living in the same area. That is true not only for present day 13- and 17-year cicadas, but also for theoretical mutant cycles ancestral to those of the modern periodical cicadas.

One difference in my hypothesis and the ecological model of Lloyd and Dybas (1966) and others is that herein I try to explain long period, synchrony, and the adaptiveness of prime numbers as having a simple genetical basis. They said, to the contrary (p. 134), the explanation is "not genetical," and maintain that the answer lies in ecology instead. They also claimed the interesting facts of long period and practically synchronous emergence require a "long evolution" involving numerous alleles that help the cicadas escape the delayed density-dependent effects of the predators or the "parasitoids." But Lloyd et al. (1983) later suggested on the basis of historical

evidence and allozymes that a single pair of alleles controlled the period of existing cicadas (13 or 17 years), and indeed there was little variation observed in their enzymes (Simon, 1979).

If cicadas are emerging synchronously together, and introgression is muddling the cycles, which are only a few years in duration, then there will be no great and regular emergences. The predators will adjust to the emergences and nothing out of the ordinary transpires. Such would be the case with two-year, three-year, and four-year cicades. In 12 years they likely would have hybridized repeatedly. Evolutionarily, introgressions seem detrimental for huge synchronized emergences, and lengthening the periods of synchronized development minimizes the introgression. Somehow lengthening the periods must result in eradication of short-term sympatric cicades as well. Probably the successful long-term emergences eventually accomplish that (see below).

The last instar possibly develops in four years and emerges the next, or twice four years emerging the next (Marlatt, 1923). The enzyme that initiates emergence may appear after four years, but in the 17-year morph somehow fail, causing the four-year development to repeat. Or that enzyme may be repeatedly blocked by another gene until after four or eight years. A four-year diapause may be initiated if developmental hormone levels are below or above some critical threshold. A four-year acceleration may result from the absence of a gene. An altered cycle probably explains the co-called "switch" (Martin and Simon, 1988). Testing excavated cicadas four years prior to emergence may provide information on this point.

If altered development time is so negative, causing loss of many cicadas from the swarm, why did evolutionarily extending the time of underground development, probably several years longer at each step, seemingly have a positive effect? One reasonable answer is to minimize introgression.

If recessive, the longer period gene likely would appear first in a heterozygous cicada with normal (shorter) period for the swarm. In panmictic breeding, the pairing of the heterozygotes would be rare. Their numbers increase, but loss of homozygous mutants is infrequent. However, they regularly test the future with infrequent but pure breeding colonists.

If the longer period allele appeared as a dominant (see Lloyd, et al. 1983) it would be fortunate indeed to emerge and survive in small numbers out of synchrony. If successful, however, the new dominants might not suffer the effect of introgression from the ancestral brood. The recessives would rapidly leave the swarms in subsequent emergences.

In the early evolution involving muddled cycles none of the emergences would be large, although those ancestors were probably less vulnerable to bird predation (modern periodical cicadas are noisy and conspicuous). To escape density-dependent predation the only way seems to be the evolution of long development cycles. To maintain long, synchronized cycles leading to the great emergences, the emerging populations must be pure breeding (low heterozygosity) with long periods. Short period cicadas are put at a disadvantage (regular predation) by cicadas having prime number periods. Larger populations of successful cicades indeed would likely compete favorably with smaller populations in the nymphal stages, when one kind emerges in enormous breeding numbers and the other is limited by ordinary predation. Short-period cicadas at the same locale and emerging only one or two years later than the huge emergences would suffer the most from annual predation, which increases after an increase in prey.

If the period becomes a prime number of years, then introgression will be practically precluded in, for example, a pure rr population. The rr phenotypes, and only the rr phenotypes, will emerge many years hence. If their enzyme timing is somewhat variable, most of the deviate "stragglers" will likely become extirpated as they emerge, like a few colonists in a hostile land. The prime number cicadas will have at once established pure breeding cycles relatively free of introgression (and loss of subsequent progeny).

Even a prime number seven-year morph (two seven-year cicadas do occur in Japan, see Alexander and Moore, 1962) would hybridize with two-, three-, four-, or five-year morphs fairly regularly. The primes 11, 13, and 17 are much more secure, and a reason 11 was not hit upon by cicadas was probably that the summed development intervals for the instars probably overshot 11 years.

Genes Control Period and Synchrony. The nymphal development of a long-term cicada, lasting nearly 13 or 17 years and mostly underground, must result from numerous enzymes in a sequence precisely timed, the genomes quite similar but perhaps differing from one sib to another (e.g., 13 year versus 17 year cicadas) in only one or a few genes. There is no evidence for the complexity of the timing sequence, except intuition. There is evidence for little heterozygosity in extant cicadas (Simon, 1979; Martin and Simon 1988, 1990) and for monofactorial control of the

length of period, either 13 or 17 years. Lloyd et al. (1983) suggested that the 17-year cycle gene was dominant, but Cox and Carlton (1991) argue that the 13-year cycle probably has the dominant gene. Historical genealogies provide evidence for gene control of period length (Lloyd et al., 1983; Cox and Carlton, 1991).

If a gene caused a particular period, the offspring would inherit this gene from their parents and would emerge exactly synchronized by it. It is well known that 17-year cicadas give rise to their kind, and 13-year cicadae to their kind, with an occasional brood springing up out of synchrony but still programmed to follow the parental period. For the most part, periodical cicadas exhibit precise synchrony.

Synchrony Leads to Pure Breeding. Synchrony results in homozygosity of genomes from three proposed causes.

a) The emerging cicadas of a given period all contain at least one allele for each critical enzyme tied to the period length. Their offspring also will inherit these critical alleles and keep them to themselves.

b) Different development timing alleles that may occur in the population will segregate out of the cycle. Only those critical for the exact periods will continue in the cicada cycle. For example, a gene that shortens a 17-year period by two years somehow will exit from the cycle whenever the 15-year cicadas emerge. (Usually this different sib will perish because of small numbers and bird predation.)

c) Not only do the descendants of cicadas for any given period breed mostly among themselves, and seldom with other kinds of cicadas, but inbreeding itself regularly lowers heterozygosity.

The decreasing heterozygosity enhances the purity of the genotypes, resulting in ever more similar genomes for the synchronized periods. As the ages pass, the synchrony and pure breeding become fixed in a periodical cicada.

Hardy-Weinberg Theory. Since the 17- and 13-year sibling species are morphologically very similar, though temporally isolated from one another, we may hypothesize that a genetic difference between them (regarding development at least) is only one or a few genes. Although the three 17-year species will not freely interbreed in nature, their 13-year morphs did in captivity (Alexander and Moore, 1962). Lloyd and Dybas (1966) opportunistically transported 17-year Iowa brood III *Magicicada cassini* to Illinois and mated them with 13-year *M. tredecassini* and the females of brood III produced over 300 young. Also, they crossed *M. septemdecim* and its 13-year sib *M. tredecim* with success. Almost all the progeny were normal through the first instar. Unfortunately, some of the progeny died because of laboratory problems. The experiment was discontinued (Lloyd, personal comm.). White (1973) crossed *M. septemdecim* and *M. cassini* and found them remarkably fertile for such morphologically distinct species. The aforementioned historical study in Lloyd et al. (1983) strongly suggests hybridization occurred. Hybridization seems possible, then, among 17- and 13-year cicadas, suggesting a close genetic similarity. The concurrent emergence of 17- and 13-year sibs, however, is very seldom (17 x 13 years).

Deviants theoretically exit from the huge parent emergence. Reproductively they are dead for future perpetuation of this cycle, and so I hypothesized a recessive factor r responsible for any change in period of development as "lethal" against R with selective value as 1.0 (Dobzhansky, 1937). This is basically the same explanation of Lloyd et al. (1983) for their suggestion that a dominant gene governs 17-year development, whereas recessives exit from the swarm. This also resembles the model of Cox and Carlton (1991) which suggests the regular loss of 17-year cicadas from the swarms, based on a sound argument that the 17-year cycle is recessive.

In a mixed population RR x RR, Rr x RR, rr x RR, . . . rr x rr yield offspring emerging in both the expected R- and in a deviate (rr) period of years. The swarm is divided and has immediately lost all the rr cicadas. Furthermore, there will be a steady loss of rr from this dominant gene population until r is practically gone. The loss depends upon the f(r), but if it is a high value the loss of cicadas from the swarm is very significant. In the famous equation $p^2 + 2pq + q^2 = 1$, the frequency of rr phenotypes leaving the population is p^2 (whereas q^2=RR genotypes). Exodus of rr is rapid at first because heterozygotes (2pq) are relatively abundant. As f(r) approaches zero then p becomes very small (see Dobzhansky, 1937).

On the other hand, any different period swarm of cicadas emerging coincidentally with our R population and bringing in the deviate period allele r will suffer a drastic effect on its own cycling numbers. Since these cicadas are all rr, they combine with themselves depending on their frequency

(p x p), and if most mate with RR phenotypes, then every one that does is lost from its own population of rr period phenotypes. None of the heterozygotes will emerge with the rr cicadas in their next emergence.

Suppose a swarm of rr cycling cicadas emerged synchronously with an RR population in about the same numbers (say 5,000 of each morph). Using the simplified equation $q_n + q_o / (1 + nq)$ in its next emergence the rr population would be short the progeny of 2,500 rr cicadas because they were mated to RR cicadas and joined their cycle. By use of the simplified formula (see Dobzhansky, 1937) the f(r) is seen to drop from .5 to .25 in two generations. That is a profound selection against rr.

In a population beginning with the f(r) equals 0.1, and f(R) is 0.9, then in ten generations the small numbers of Rr will have dropped (to about 6%) so that f(r) is only .035, and f(R) is close to 97 percent. If a coincidental emergence of rr phenotypes appeared in numbers equal to our R population, it would take 20 successive pure breeding emergences to get back to our 97 percent frequency. It would take about nine generations to even get back to the original f(r) = 0.1. Synchronous emergences of cicadas with different cycles (due to particular alleles) swamp out the genetic purity of the dominant allele population and decimate the number of the recessive cicadas.

Although recessive allele cicadas are eliminated from dominant cycles, stragglers or new broods might then appear for the altered recessive allele cycles. These are descended from heterozygous progeny of hybridizing populations. However, it was difficult to perceive how dominant swarms might initiate new out-of-synch broods or lose dominant allele cicadas from the dominant gene cycles (but see epistasis below).

Both 17- and 13-year cicadas have broods, and especially the 17-year morphs (see Alexander and Moore, 1962) do. Some of these broods may have evolved before the 13-year sibs did (Simon, 1979).

Other factors such as incomplete dominance of the length of the hybrid's development also may lead to out-of-synch broods. Suppose it is the hybrids' development cycle that is altered. Then the heterozygotes are "selected" against intensely because all the hybrids are thrown out of synch. If the heterozygote has a different cycle than either parent, then the parent populations will be decimated by twice the frequencies of both alleles. If 5,000 RR emerged with 5,000 rr cicadas, then about 5,000 heterozygotes would have new development periods, and only half of each parental population would continue its cycle. The heterozygotes might foster new broods, but they also might perish, depending on the interplay of Rr and the "new" environment. If the periodicity of the hybrids is variable, then unfit stragglers will appear. There is no evidence that hybrid cicadas today generally have development out-of-synch with both of their parental stocks. What little evidence is available suggests that one cycle continues (Cox and Carlton, 1991).

Genetic control over cicada periodicity would seem a reasonable scientific explanation, even if questioned (Lloyd and Dybas, 1966: 134). A new genetical theory for periodicity merits scientific investigation. Cox (personal correspondence) suggested that the two present period lengths are probably monofactorial (or "polymorphic"), whereas in his view the accuracy of timing may be a blend of epistatic effects. For example, broods XVIII and XX dwindled and disappeared from the range of brood XIX in southeastern United States. Cox believes that XIX is the dominant 13-year cicada in the region, and that both XVIII and XX are out-of-synch broods arising from epistatic effects of timing alleles.

Possible Epistatic Development Alleles. A possibility relevant to the depletion of dominant (and of course recessive) allele cicadas is epistasis. In extended development involving molting several times, growth and carefully scheduled differentiation of cells and morphogens, all correlated by some internal clock, it seems inconceivable that only a single pair of alleles is involved. If indeed development is inhibited repeatedly, and growth deferred several years, there are very likely several genes (enzymes) at work. Teamwork by several epistatic genes may establish exactness of period, and indeed may promote dominance of a gene involved with maintaining that period.

The close resemblance in form and behavior of the modern cicadas having two periods suggests that development is closely canalized and controlled. Common sense suggests that any synchrony so precise over such a long period has very little genetic variability. What is needed is a stable genotype with little heterozygosity. Simon (1979) found periodical cicadas to have little variation and very little heterozygosity. Martin and Simon (1988, 1990) found some genetical differences from place to place but little heterzygosity in local populations. These are extremely

important findings supporting the relation of pure breeding, period length and synchronous emergences.

Once periodicity is established in a population, whatever its length of time, heterzygosity might be rapidly reduced as the different alleles separate from the cycle, either by lethal abortive development or emerging out-of-synch. As mentioned above, the proportion of alleles lost can be significant and lead to rapid fixation of one period of development.

Cicadas might be homozygous for period and homozygous also in several associated development alleles as well. Herein lies another important raison d'etre for the extended length cycles, and for prime numbers. They preclude introgression and enhance canalized synchronous development.

Assuming that each period has an important constellation of development genes, all homozygous owing to pure breeding (see above) and stripped of different alleles regularly of Hardy-Weinberg proportions that left the parent population, then we may hypothesize some homozygous recessives for the recessive gene sib may be more or less "lethal" in altering the carefully scheduled development of the dominant sib. Considering here only the hybrid progeny (with no backcrossing), then this could lead to loss even of dominant-gene cicadas from the effect of hybridization.

After recessive- and dominant-gene cycles hybridize, a doubly heterozygous hybrid generation would yield F_2 progeny in these proportions, nine dominants: seven dead or lost. That is a decrease in the ratio three dominant: one recessive cicadas due to a single pair of alleles. (Fig. 1)

If development depends upon three pairs of alleles, AaBbCc in the dominant gene sib, then hybrids that are F_1 dominant gene cicadas would segregate F_2 progeny in this ratio 27 dominant: 37 lost (either dead or segregated out). This is 58 percent lost (see Fig. 1).

The more alleles the worse it gets for the emerging cicadas of the dominant gene sib. The tetrahybrid AaBbCcDd will segregate 256 possible genotypes, 32 percent 17-year and 68 percent lost (see Fig. 1). This is a significant loss even of the dominant period cicadas from the cycling population, and probably will lead to real mortality in the altered cicadas emerging as stragglers or broods.

Some genes may control growth, others instar development or year of emergence, and still others may control the final metamorphosis. All of these and perhaps other traits must be canalized.

Obviously, the homozygosity theorized from inbreeding, purebreeding, and pioneer proportions (new broods), and the enzyme complexity of long period development raise the spectre of introgression—more profound in its effect than most ecological regulation, especially that which affects immense swarms. Prime number periods proved to be salvation against hybridization. They ensure exact periodicity and maximize the size of the emergence.

An Alternative "Switch" Hypothesis. Lloyd et al. (1983) mentioned a phenomenon of sharply decreasing numbers of progeny, in theory, by the loss from the hybrids of numerous recessive alleles. They even used the Hardy-Weinberg term "lethal," meaning that some cicadas exited from the population. Their discussion (1983) focused, however, on the supposed origin of a new 13-year brood comprised of those genotypes exiting from the hybrid generation. They did not comment on the profound evolutionary process of marked depletion of a parental population resulting from hybridization. Besides, Hardy-Weinberg provided no explanation for loss of any dominant gene life cycle (but see comments on epistasis above). The ecological factor of nymphal competition was then suggested by them as the exclusive cause of the demise of the 17-year cicadas.

Lloyd et al. (1983) and Martin and Simon (1988) suggested a sudden replacement of 17-year nymphs by more aggressive 13-year nymphs. What would be the genetic basis of this? Why would the replacement not be gradual, one sib replacing the other slowly? Cox and Carlton (1991) doubted that the replacement of a population ever happens suddenly, due to nymphal competition. They do mention "strong selection" which of course is an ecological effect.

In a brilliant reanalysis of the same history of hybridization (13- and 17-year cicadas co-emerging in 1868), Cox and Carlton (1991) disputed Lloyd et al.'s (1983) claim that the 17-year cycle was controlled by a dominant gene. They pointed out that the supposed 13-year brood segregating from the hybrids could as easily have been 17-year recessives segregating from the same hybrids, with the 13-year gene being dominant. There was a 17-year brood in 1868 + 17 years, which might have segregated a new recessive 13-year brood in 1898. Or there was a 13-year brood in 1868 + 13 years, which would have segregated 17-year recessives in 1898, if 13-year development is dominant. If the 13-year form was dominant, then the 17-year cicadas would predictably and rapidly diminish (which they did), and the 13-year cycle would continue. The 13-year cicadas, in fact, increased in numbers (my model, Fig. 2) beyond accounts for such an increase. They suggest 13-year cicadas

replace 17-year cicadas because of strong selection for the dominant gene. That agrees with Martin and Simon's (1990) suggestion that 13-year cicadas soon attain supremacy because their second instar is not retarded, thereby giving them an advantage in direct competition for the same root sites. The decline of either period cicadas could also be attributed in large part to the exit of the segregates which would be eaten as they emerged out-of-synch.

No clue is provided by the standard ecological explanations for the evolution in periodical cicadas of immense emergences, the observed stark depletion in some cycles, nor the evolution of the closely synchronized, extended development as prime-number cycles.

Martin and Simon (1988) suggested no hybridization takes place, but that over one wide range (in four states from northern Arkansas to northern Illinois) cicadas had "switched" development from 17 years to 13 years. This seems implausible.

In the "switch" hypothesis sternite color and a mitochondrial genotype A observed in these 13-year cicadas resembled the nearby 17-year cicadas more than 13-year cicadas southward and southeastward. I believe it is not surprising that adjacent and even sympatric cicadas of hybridizing cicadas possess a particular genotype in common and share similar sternite color. The critical genes that must be homozygous to control the time of synchronized development cannot be the observed genotype A, because some 13-year cicadas have it, and all the 17-year cicadas had it. This fascinating genetic variation described by Martin and Simon (1988) possibly could result from fixing of alleles, as explained below, and not necessarily be a spontaneous and wide-spread switiching. Then again, what seems to be switching may be the spread of an earlier and fit mutation, with normal selection of genotypes that gradually spread them over the four-state area. Carlton and Cox (1988) disparage the ecologically induced switching as "acquired characteristics."

The High Road to Prime Periodicity. An evolutionary model for periodicity in cacadas helps explain why there may be some stragglers, or different broods out-of-synch but following the same strictly controlled periods of development. It explains why sibling cicadas evolve as temporally isolated "species," whereas three morphologically distinct species may share mutual benefit from belonging to the same huge swarms. Hardy-Weinberg explains why hybridization is bad so long as some proportions of the progeny are severely selected against, namely any with abortive development or any segregates eaten by predators following hybridization. Since prime numbers of developmental periods having extended duration encourage pure breeding, by precluding hybridization, we find such periods enhancing fitness and encouraging great emergences.

The hypothesis of "decimation" or "depletion" by hybridization is illustrated in Fig. 2. In A, the two-year, three-year, and four-year cicadas comprise a stable population limited by bird predation (P). At H is the time of hybridization and reproduction of the mutant cycle cicadas. The pure breeding 13-year cicada rapidly builds up numbers that P cannot control, approaching carrying capacity (root availability, drought, and so on). After the short-term cicadas eventually are eradicated by the immensely successful long-period cicada, then $P_n < P$ so long as P is proportional to the annual emergences.

In B, competition between 13-year and nine-year cicadas is shown, where a seven-year cicada decimates the nine-year form once every seven generations. In about 85 years, four-year cicadas would decimate seven-year cicadas three times, in only 11 generations. If there were both four-year and seven-year cicadas cycling with a nine-year cicadas, it would be hybridized six times in nine generations. The prime-number 13-year cicada would suffer little, encountering nine-year cicadas only every 117 years (9 x 13).

If there were no short-term cicadas left, and only two in competition, say 13- and nine-year, then the nine-year cicada might even win out. Both of them might prosper sympatrically until something better came along (e.g., a 17-year prime?). Either of them might gradually lose out in competition of the nymphs for root sites (see Simon, 1988).

There exist only prime 17- and 13-year cicadas today, and both are wide spread. Some long-term periods probably have not even been tried (e.g., 11 year).

How often would long-term and non-prime cicadas suffer hybridization? In 10-year versus 12-year cicadas one might see more hybridization at work. These cicadas must, of course, hybridize every 60 years, but recessive segregates (often called pioneer broods) might do so oftener, unless they are eaten up. Either way they lose. If the 12-year period was recessive, the first brood of segregates would emerge with the dominants in 60 years. The second brood, if it survived, would emerge with the dominant cycle in 70 years. The possible hybridizations continue every 10 years. If the 10-year brood was recessive instead, segregates would emerge 60 years later, and possibly

hybridize every 12 years thereafter. Ecological and zoogeographical factors may override, of course, but prime cycles are more secure from hybridization and heterozygosity.

As mentioned above, extending development by gene-controlled enzymes may establish long-term genotypes as a regularly cycling and stable population. Assuming the normal predation (P) is constant, then H/b = P, where H is hybridization and ordinary reproduction. The denominator b diminishes H to the number of cicadas eaten. When the long-period cicadas enter into and swell the short-period population by a, only H/b cicadas are eaten,but are allocated as H/ba and H/b - H/ba. The latter are the dead long-period cicadas. It follows that the rate of predation for short-period cicadas established by stable conditions as 1/b then becomes, for the long-period cicadas (H/b - H/ba)/ aH - H, or

$$(1 - 1/a)/ (a - 1)b = 1/ab \qquad \text{Equation 1}$$

When the long-term cicadas double (a = 2) the size of the emergence, they suffer only 1/4 of the predation when 1/b = 1/2. If the swarm increases four-fold, then the long-term cicadas lose only 1/8. Predation on them is steadily reduced, and the swarm rapidly approaches carrying capacity. The short-term populations do not benefit so much, for their reproductive success results in stronger predation for a few years in their balanced system (P proportional to H).

Hybridization is costly to both mutant cycle cicadas, as discussed earlier; for example, recessive cicadas, in addition to losses from predation 1/ab, lose half their next generation if a is 2. Both adversities combined are especially costly to short-term cicadas, and they likely hybridize more often.

Short-term periodical cicadas with basically the same form and behavior cannot compete favorably with long-period cicadas, and their only hope is hybridization to mingle and hide the genes. That happens less as periods are extended, and is very seldom seen with extended prime number cycles. As the short-term cicadas move to their extinction point (e), the number of their predators (P → Pn) falls proportionately, increasing the swarms of extended cycles all the more. This proves the adaptiveness of huge emergences, the survival value of any development gene responsible for them, and for a few epistatic genes on the team as well.

Conclusions

Extending the nymphal development in a population of periodical cicadas, probably toward the end of the well-established sequence of developmental stages, minimizes both the effects of density-dependent predation and of recurring hybridization (which indeed hardly ever occurs with extended prime-number cycles). Pure breeding cicadas usually do not lose alleles from out-of-synch descendants. Pioneer broods of a new mutant cycle would show little genetic variation. Inbreeding leads soon to homozygosity, and variants disappear from the population. The evolution of the observed periodicity is fairly well predicted by Hardy-Weinberg theory involving epistatic genes expressing closely scheduled development, so long as we make several reasonable assumptions (close relatedness of the broods, extended cycles dependent upon a few epistatic alleles, the adaptive importance of huge swarms, etc.). Rather than attributing the primary selective factor in cicadas to "parasitoids," fungi, tree resistance, spontaneous "switching," and other unsubstantiated ecological factors, the chief danger to periodical cicadas having huge emergences (large enough to satiate the bird predators and produce a surplus) is the coincident emergence of cicadas of a different period having, of course, somewhat different development alleles. Subsequent emergences, of course, may be affected also by competition between developing nymphs to some extent. When the interaction of predation and prey, which under certain conditions enhances synchrony for a given life span (Murray, 1989) is joined with the process of genetical canalization of an extended life span, so the fittest population is stripped of all deviations of development period, then stringent periodicity (especially of any extended prime number period) is maintained. Owing to the temporal isolation resulting from extended development and attainment of the prime number cycles, a sympatric speciation of a special kind seems evident in periodical cicadas.

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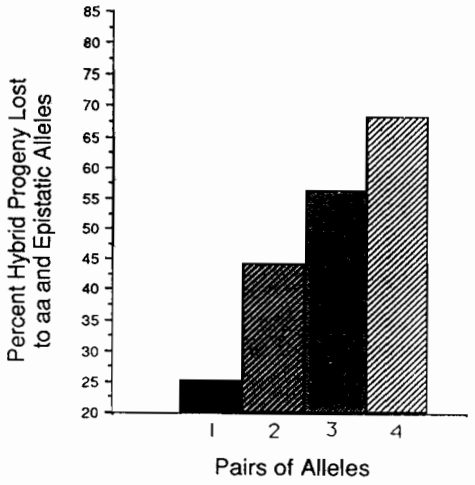

Fig. 1. Progeny of hybrids possibly lost by the effects of epistatic homozygous alleles. They may alter even the dominant gene development, combining with A- to devastate the dominant gene cycle in one generation. Instead of the A progeny emerging as scheduled, most may be lost. Recessives disappear even faster. See text.

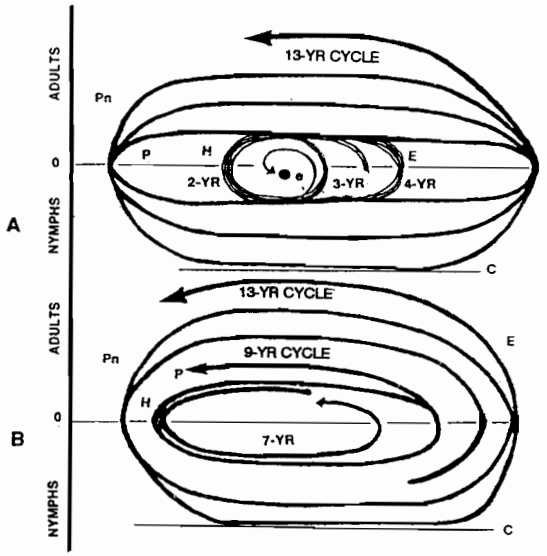

Fig. 2. Theoretical cycles of periodical cicadas. P, bird predation. H, hybridization and reproduction. E, emergences of adults above ground. C, some limiting carrying capacity, which varies from place to place but eventually limits the number of nymphs. Deviation from the zero line roughly measures the population size, which in nature varies above and below ground. Annual P drops, because of the extinction of prey (e) and becomes Pn, where Pn < P. The outermost cycles are an extended prime period. In A, short-period cicadas vanish and the 13-year cicada fills up the habitat. In B, the seven-year cicada hybridizes often with the nine-year cicada giving the advantage to an extended prime number cycle. In a sense, these are not competing kinds of cicadas, but instead competing genes. A prime-number cycle is almost a drift-like fixing of one (or a few epistatic) genes.