Evidence of Genetic Dominance of the 13-year Life Cycle in Periodical Cicadas (Homoptera: Cicadidae: Magicicada spp.)

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ABSTRACT.—Several lines of evidence suggest that the 13-year life cycle is genetically dominant over the 17-year life cycle in periodical cicadas. They are: (1) 13-year dominance best predicts the decline of 17-year Brood X, and concomitant increase in Brood XIX in the midwest, following a hypothesized 1868 hybridization with 13-year Brood XIX through assimilation of heterozygotes into Brood XIX; (2) the pattern of 4-year off-schedule emergences of recessive segregates in Illinois following the proposed 1868 hybridization is consistent with a 13-year dominance model, but is inconsistent with a 17-year dominance model; and (3) migration of a strongly selected and dominant 13-year allele best explains the synchronization and proximity of contrasting genotypes within the ranges of Broods XIX and XXIII in the midwest.

INTRODUCTION

Periodical cicadas spend 13 or 17 years as immatures feeding on xylem fluid of roots, primarily of trees, before emerging synchronously as adults to mate and deposit eggs on deciduous tree branches (White and Strehl, 1978). These life histories are among the longest of all insects. The highly predictable nature of periodical cicada (Magicicada spp.) emergence and mating makes this genus unique as a natural system for the study of gene flow and population genetics. Correct interpretation of the dominant-recessive relationships of the genes controlling the emergence schedule is critical to understanding gene flow patterns between nonsynchronized populations, and thus the gene distributions within synchronized populations.

Alexander and Moore (1962) recognized six species of Magicicada: 17-year species M. septendecula, M. septendecim and M. cassini: and respective “sibling” 13-year species M. tredecula, M. tredecim and M. tredecassini. However, because the individuals of each sibling pair interbreed freely and show a high degree of morphologic and ecologic similarity (Lloyd and Dybas, 1966; Lloyd and White, 1976a), most recent investigators treat the sibling pairs as life-cycle forms of a single species. Magicicada species emerge synchronously over a few weeks of the spring in each local population on scheduled years in eastern North America. The 13-year forms dominate in the south, and the 17-year forms in the north (Fig. 1). All periodical cicadas of a given life cycle (13 or 17 years) that emerge on the same year throughout the cycle’s range belong to the same “brood.” Thus, there are 17 possible 17-year broods (designated I through XVII) and 13 possible 13-year broods (XVIII through XXX) (Marlatt, 1907). Of the broods known to exist, many are not sympatric, and commonly only one or two are present at a given locality (Marlatt, 1907). For a more complete...
The accuracy of the life-cycle timing mechanism of periodical cicadas temporally isolates broods of the same cycle length from one another, but broods of different cycle lengths emerge synchronously once every 221 years. Lloyd and Dybas (1966) reported that caged conspecifics of 13-year and 17-year forms freely cross and produce viable eggs. Therefore, under normal circumstances, gene flow between broods occurs via sympatric broods of different cycle lengths every 221 years. Environmentally triggered off-schedule emergences (possibly due to nymphal overcrowding or climatic extremes) complicate this system to a degree. Off-schedule events are usually one or four years either behind (deceleration) or ahead (acceleration) of the scheduled emergence (Hyslop, 1935; Alexander and Moore, 1962; Lloyd and Dybas, 1966; Lloyd and White, 1976b; Maier, 1985).

The absence of intermediate life-cycle forms in the zone of overlap (Fig. 1) suggests that cycle length is a dominant-recessive dimorphism governed by a single gene (Lloyd et al., 1983). Cicadas that are heterozygous for such a unifactorial character will be synchronized with the dominant cycle length. Thus, increases in abundance of the dominant life-cycle form will follow hybridization of a 13-year brood and a 17-year brood. Beginning with this hypothesis, we present several lines of evidence in the following discussion that support 13-year genetic dominance in Magicicada. The resolution to this question is important in understanding both the present distribution of Magicicada genotypes and the evolutionary history of the genus. Previously, we have assumed 13-year dominance in a model of the evolution of four-year accelerations and decelerations (Cox and Carlton, 1988).
**Fig. 2.**—Punnett-squares for a cycle-length dimorphism following hybridization of homozygous populations of both cycle lengths. Beginning in the F<sub>2</sub> generation, crossing of heterozygotes will produce homozygous recessive segregates which will be temporally removed from the parental brood by 4 years. These low density off-schedule emergences rarely establish sustaining populations.

**Historical Evidence**

Lloyd *et al.* (1983) examined the historic records of emergences in Illinois following the widespread sympatric coemergence of 13-year Brood XIX and 17-year Brood X in 1868. The records for Illinois are particularly detailed and Lloyd *et al.* (1983) concluded that the emergence records indicate that the two broods hybridized (*but see* Martin and Simon, 1988) and that the 17-year life-cycle trait is dominant in a Mendelian hybridization model. However, we believe that a model assuming 13-year life cycle dominance more readily explains the regional trends of brood decline and expansion, and the sequences of off-schedule emergences.

**Brood Supplantation.**—Following the proposed 1868 hybridization of 13-year Brood XIX and 17-year Brood X there was a decline of Brood X and a concomitant increase in Brood XIX over the next few generations in the midwest (Lloyd *et al.*, 1983). The paucity of records of Brood XIX in the midwest prior to 1868 (Martin and Simon, 1988; Kritsky, 1989) suggests that densities for these populations were significantly lower then. Lloyd *et al.* (1983) attributed the supplanting of Brood X by Brood XIX to the faster rate of development in 13-year nymphs and a consequent advantage in feeding site competition. Simon and Lloyd (1982) suggested that nymphs compete for feeding sites on rootlets of similar size if they are in the same stage for nymphal development.

Although feeding site competition between sympatric 13 and 17-year populations may be important, we do not believe that the advantage afforded to 13-year forms is a satisfactory explanation for the decline of Brood X and the increase of Brood XIX following the 1868 hybridization. The rate of development of 13-year forms relative to 17-year forms is accelerated in the second instar during the first four years of the life cycle (White and Lloyd, 1975), and it is then that 13-year forms might gain a competitive advantage for feeding sites (Simon and Lloyd, 1982). Such an advantage would be important not only following coemergences of sympatric 13 and 17-year populations every 221 years, but also after 52, 104, and 170 years when second instar 13-year and 17-year nymphs share the same roots. Thus, the decline of 17-year broods due to nymphal competition with 13-year broods should be a gradual and relatively continuous process (less abrupt than that observed in Illinois following 1868).

The anomalous decline of Brood X in the midwest is consistent with a Mendelian model of hybridization that assumes dominance of the 13-year life cycle. This model predicts a reduction of the 17-year brood and an increase of the 13-year brood proportional to the degree of crossing between the different life-cycle forms, because heterozygotes develop as
FIG. 3.—Predicted emergences following the proposed 1868 hybridization of 17-year Brood X and 13-year Brood XIX (top = 17-year dominance; bottom = 13-year dominance). Solid dots = scheduled emergences; solid triangles = off-schedule emergences of recessive segregates; open triangles = potential emergences.

13-year forms. This decrease in densities for 17-year populations may result in a greater degree of predation and lower reproductive success (Beamer, 1931; Alexander and Moore, 1962; Lloyd and Dybas, 1966; Karban, 1982) and thus further reduction of the brood in subsequent generations.

**Recessive segregates.**—Assuming a unifactorial dominant-recessive relationship for the cycle-length character, hybridization of populations of a 13-year brood and a 17-year brood predicts a series of off-schedule subsequent emergences (Lloyd et al., 1983). Crossing will produce heterozygotes with respect to the cycle-length character in the F₁ generation (Fig. 2). These heterozygous cicadas will emerge with the homozygous cicadas of the genetically dominant brood. The F₂ generation produced from the dominant brood will include temporally segregating cicadas homozygous for the recessive cycle length (Fig. 2). Recessive alleles expressed in these segregating cicadas will have passed one generation suppressed in heterozygotes with the alternate phenotype, resulting in emergences that are 4 years off-schedule from the sympatric original brood of the same cycle length. These off-schedule emergences will rarely be large enough to establish new populations (Lloyd et al., 1983). Decreasing numbers of homozygous recessive, off-schedule cicadas will be produced in subsequent generations as the frequency of the recessive allele falls.

In 1898 widespread off-schedule emergences occurred in Illinois in the region of the proposed 1868 hybridization. Lloyd et al. (1983) interpreted these as recessive 13-year segregates of Brood X which was due in 1902. Alternatively, recessive 17-year segregates of Brood XIX (which emerged in 1894) would be due in 1898. Although other off-schedule
FIG. 4.—The proportion (k) of the genetically dominant brood that will segregate as homozygous recessives for cycle length in the $F_2$ and $F_3$ generations. $N$ = the total cicada population of the hybridizing broods; $P$ = the proportion of $N$ that is initially homozygous recessive for a unifactorial cycle-length character. $k = P^2(1 - P)/(1 + iP)(1 + jP)$, where $j$ = the number of generations after $F_1$, and $i = j - 1$ (see Lloyd et al., 1983 for derivation). This model assumes random mating and stable population size.

emergences are similarly ambiguous as evidence of 13- or 17-year dominance when considered individually (Fig. 3, triangles), the overall emergence pattern of segregating homozygous recessive cicadas is important in understanding dominance in Magicicada life-cycles.

The abundance of emerging segregates depends on: (1) the number of cicadas in the hybridizing population (13- + 17-year forms); and (2) the proportion of the hybridizing population that was homozygous for the recessive life-cycle allele. Assuming cycle length is a unifactorial dimorphism, Figure 4 shows $k$ (the percent of $F_2$ and $F_3$ offspring of the hybridizing population expected to emerge as segregates) plotted against $P$ (the percent of the hybridizing population initially homozygous recessive for cycle length). Segregates are expected to diminish in numbers through successive generations as the frequency of the recessive allele falls. Figure 5 shows the expected abundance of $F_3$ segregates relative to $F_2$ segregates plotted against $P$. Below $P = 50\%$ in a given deme, $F_3$ segregates will be increasingly greater than 50\% as abundant as $F_2$ segregates. The smaller the value $P$, the smaller the decline in abundance of segregates in successive generations.

With respect to the proposed 1868 hybridization of Broods XIX and X in Illinois, a model of 17-year dominance predicts $F_2$-generation recessive segregates emerging in 1898, 13 years after 17-year Brood X emerged in 1885, as discussed above. In areas of southeastern Illinois, segregates were recorded emerging in 1898 and Brood X emerged in 1902 (in dense
swarms in some areas) (Marlatt, 1907). For demes in which \( P < 50\% \) in 1868, a 17-year dominance model also predicts the emergences of \( F_3 \)-generation recessive segregates in these areas in 1915 (Fig. 3) that were nearly as abundant as 1898 emergences. But, there are no reports of such 1915 emergences, and we believe that this strongly contradicts the hypothesis of 17-year dominance.

Other off-schedule emergences followed the 1898 emergence by 13-year intervals and in progressively lower abundances. Lloyd et al. (1983) explained these emergences as new populations of 13-year Brood XXIII that arose in 1898 from 13-year \( F_2 \) segregates from Brood X, but declined and disappeared in a few generations. However, each of these off-schedule emergences followed an emergence of 13-year Brood XIX by 17 years, and we interpret this pattern as that of 17-year recessive segregates which decreased in successive generations of Brood XIX (Fig. 3). Because the pattern of emerging segregates predicted by a model of 13-year dominance is observed and that predicted by 17-year dominance is not, we submit that the 13-year life cycle is dominant.

Lloyd et al. (1983) present detailed data of the abundances of Brood XIX and Brood XXIII for 1972 and 1976, respectively, at Weldon Springs State Park in central Illinois, that support the hypothesis of 17-year dominance. Estimates made from eggnest scars from 1972 and 1976 suggest that Brood XXIII at this locality is a sustaining 13-year population and not 17-year segregates of Brood XIX. However, the localized example of Weldon Springs is inconclusive because environmentally triggered 4-year accelerations and decelerations may have also produced the observed emergence patterns (Lloyd and Dybas, 1966; Lloyd and White, 1976b; Maier, 1985). We believe that the evaluation of broad regional trends and long-term emergence patterns in Illinois gives better insight into the genetic controls of Magicicada life cycles.

In summary, we argue that historic records support the hypothesis of 13-year dominance in Magicicada through two lines of evidence: (1) 13-year dominance best predicts the decline
of Brood X in the midwest following the proposed 1868 hybridization through assimilation of heterozygotes into Brood XIX; and (2) the pattern of 4-year off-schedule emergences of recessive segregates following hybridization is consistent with the 13-year dominance model, but is inconsistent with the 17-year dominance model.

MOLECULAR EVIDENCE

In the upper Mississippi Valley and adjacent areas of the Ozark region of Missouri and southern Illinois, populations of 13-year Brood XIX have mitochondrial DNA (mtDNA), nuclear DNA and abdominal coloration more similar to 17-year Brood X (which occupies a contiguous range to the northeast) than to contiguous southern Brood XIX populations (Martin and Simon, 1988). This region includes that area of the midwest discussed in the preceding section where Broods XIX and X likely hybridized in 1868. The abruptness of changes in genotypes (particularly in mtDNA) (Fig. 6) led Martin and Simon (1988) to conclude that hybridization between Broods XIX and X was not responsible for these gene distributions. Rather, they proposed that a large component of the 17-year cicadas from Brood X simultaneously accelerated development by 4 years throughout Missouri and southern Illinois following the 1868 emergence, and that these cicadas retained a 13-year life cycle to become new populations of Brood XIX. They further proposed that this widespread acceleration event was synchronously triggered by nymphal overcrowding. Northernmost populations of 13-year Brood XXIII in Illinois and Indiana contiguous with Brood X also have mtDNA and abdominal coloration like that of Brood X (Chris Simon, pers. comm.), suggesting a similar relationship to Brood X. We do not concur with Martin and Simon’s interpretation of the molecular data on the basis of the following lines of evidence.

Although it is plausible that portions of populations might be triggered to accelerate due to nymphal overcrowding, the occurrence of such an event simultaneously over an environmentally diverse two state region seems highly improbable. Further, Broods XIX and XXIII are the only 13-year broods contiguous with Brood X. Given that only two areas of 17-year Brood X switch their developmental period to a 13-year life cycle, the probability that these “switched” areas will be synchronized with the only two contiguous 13-year broods is 0.006 (1/169). Considering this low probability and the unlikelihood of uniformity of population dynamics over a two state region, the likelihood of an acceleration origin for the northern populations of Broods XIX and XXIII is remote.

Martin and Simon’s interpretation dictates that the accelerated 13-year cicadas from Brood X would retain life-cycle stability in future generations, but they suggest no mechanism for the maintenance of the new cycle length. If there is a propensity in Magicicada for large portions of populations over a broad region to simultaneously change cycle length due to nymphal overcrowding, then there should be other regions of past cycle switching which are not contiguous to and not synchronized with a 13-year brood. Such regions would be easily recognized, but the continuous and largely allopatric ranges of 13 and 17-year forms (Fig. 1) contradicts this proposal.

Finally, we must briefly return to the discussion of historic emergences. Martin and Simon (1988) assert that the rapid decline of Brood X in Illinois and Missouri is evidence of widespread acceleration and concomitant decreases in population density following 1868. They cite emergence records to support their acceleration interpretation and state, “before 1868, northern Arkansas, Missouri, Illinois and southeastern Iowa were exclusively inhabited by 17-year brood X cicadas.”

However, newspaper accounts from central and southern Missouri confirm the presence of
Brood XIX in that region prior to 1868. The *St. Louis Daily Missouri Republican*, the *Cape Girardeau Patriot*, and the *Jeffersonian Republican* all reported dense swarms of periodical cicadas in the spring of 1842 (Brood XIX). The *Jeffersonian Republican* (Cole County, MO, May 21, 1842) states,

"This it appears is the year for the return of these insects [periodical cicadas]. This is the thirteenth year since they last visited the west. There is no doubt but their appearance is periodical, and perhaps once in thirteen years is the time of their coming and going. . . . It is supposed by some that locusts penetrate through the earth, visit China, and return again; but as to this we cannot hazard an opinion of our own."

Kritsky (1989) also makes reference to unpublished records of Brood XIX in this region.

In view of these accounts, we conclude that the rapid decline of Brood X was not the result of widespread cycle “switching” in 1868. The synchronization and geographic con-
tinuity of the regions of contrasting genotypes in Broods XIX and XXIII make it highly unlikely that the emergence timing of these regions is unrelated. Therefore, it is unlikely that the regions of 17-year genotypes in Broods XIX and XXIII originated by environmentally triggered cycle “switching” in Brood X at any time in the past.

We favor hybridization as the cause of the distributions described by Martin and Simon (1988). However, rather than hybridizations between invading 13-year populations from the south and indigenous 17-year populations and extensive mixing of the gene pools, we propose peripheral hybridization and selective gene flow. The strongly selected 13-year allele migrated north through previously 17-year populations following limited hybridization along the periphery of the former southern margin of Brood X (the present limit of 17-year mtDNA genotypes). Genes contributed by 13-year broods that are not strongly selected would be diluted within the range of Brood X every 221 years. Thus the nuclear genomes of new 13-year cicadas would remain similar to those in the initial 17-year populations. In addition, if the 13-year allele is dominant, these new northern 13-year populations will be synchronized with the original southern populations.

This hypothesis fails to account for the abrupt transition of mtDNA genotypes. An explanation may lie in the inheritance patterns of mtDNA. Mitochondrial DNA is inherited only from the female (without recombination). Therefore, introgression of 13-year nuclear DNA without significant introgression in mtDNA could occur if 13-year males were strongly favored over 13-year females during crossing with 17-year populations.

Periodical cicadas are relatively poor dispersers (Marlatt, 1907; Karban, 1981; White et al., 1983), but data from mark-recapture studies suggest that males may be potentially more vagile than females. The frequency of recapture is lower for males than for females. The frequency of recapture is lower for males than for females. Karban (1981) recaptured 4.5% of males released compared to 11.8% of females. Maier (1982) recaptured 6.7% of males and 9.0% of females. Of males recaptured by Karban (1981), 10.4% had moved outside the release area compared to 7.7% of recaptured females. Maier (1982) reported a greater proportion of males recaptured outside of the release area throughout a 10 day study. This proportion increased with time, and following the last release 50.0% of recaptured males compared to 30.7% of females were found outside the release area.

Lloyd et al. (1982) speculated that periodical cicadas may respond to dispersal cues in areas heavily infested with the fungal pathogen Massospora cicadina, a primary limiting factor of Magicicada populations (Soper et al., 1976; Lloyd et al., 1982; White et al., 1983). Dispersing Magicicada males may be favored reproducitively over dispersing females when escaping infestation. White et al. (1983) measured flight times of tethered Magicicada (both healthy and infected with Massospora). Healthy males flew an average of 30.4% longer than healthy females, but healthy females did not outperform infected females. Importantly, dispersal of females follows mating and fertilization (Karban, 1981; Lloyd et al., 1982), and infected females do not oviposit (Lloyd et al., 1982). Thus in areas of severe Massospora infestation, dispersing males would be more likely to encounter and mate within another population of coemerging cicadas. Postulating significantly greater infestation in the former ranges of Broods XIX and XXIII (delineated by 13-year mtDNA genotypes) than of Brood X, the cicadas most likely to disperse and mate in an adjacent population would be 13-year males escaping infestation. Under these circumstances, 13-year nuclear DNA would enter the 17-year gene pool more readily than 13-year mtDNA.

PALEOENVIRONMENTS

Although greater Massospora infestation of Broods XIX and XXIII in the midwest must be speculative, the mid-Holocene environments of this region were more favorable for
Massospora in the former ranges of Broods XIX and XXIII than Brood X. Massospora infestations are most severe in old-growth forests and absent in new growth (White et al., 1983). During the mid-Holocene dry interval (Xerothermic interval) from 8000 to 4000 years before present, forests of the midwest gave way to prairie-savannah vegetation (Tрансее, 1935; Ruhe, 1974, 1983; Wright, 1976). The mid-Holocene forest/prairie-savannah contact in this region closely corresponds to the transition in mtDNA genotypes in Magicicada (Fig. 6). 17-year mtDNA genotypes occupy the former range of prairie-savannah vegetation while 13-year genotypes occupy the former deciduous forest range. With a return to a more humid climate, prairie fires maintained a dynamic relationship between forests and prairies in the former prairie-savannah range (Gleason, 1923; Wells, 1970; Williams, 1981; Johnson, 1986). 17-year cicada populations would likely have been relatively free of Massospora infestations in these shifting stands of trees. Conversely, 13-year populations in the old-growth forests may have been severely infested.

Thus, mid- to late Holocene environments may have promoted the dispersal of 13-year males seeking mates to 17-year populations on the periphery of Brood X. If the 13-year life cycle is genetically dominant, hybrid nymphs might gain a competitive advantage during the second instar of development (enhancing their emergence abundance). Hybrids will emerge synchronized with the parental 13-year brood and will have 17-year mtDNA inherited from their mothers. Should these offspring be abundant enough to establish a sustaining population, continued nympal competition and subsequent hybridizations will effect the shift of all local cicadas to the 13-year life cycle. Further dispersal of these "new" 13-year cicadas into relatively fungal free prairie-savannah and hybridization with 17-year populations would expand the 13-year life cycle into 17-year range without significant gene flow from the synchronized original 13-year brood. Thus, genomes would remain essentially like those of the original 17-year brood.

Whether or not this prehistoric sequence of dispersal and hybridization is correct, the synchronization and proximity of areas of contrasting genotypes in Broods XIX and XXIII strongly suggest that these areas have had some degree of gene flow between them and that the 13-year life cycle is genetically dominant.

CONCLUSIONS

Diverse lines of evidence, originally interpreted with disparate conclusions, can be unified under a working hypothesis which assumes dominance of the 13-year life cycle in Magicicada. These lines of evidence are: (1) the rapid decline of Brood X in the midwest after coemerging with Brood XIX in 1868; (2) the pattern of 4-year off-schedule emergences after 1868; and (3) the ability to more reasonably explain the synchronization and geographic continuity of areas of contrasting genotypes within the ranges of Broods XIX and XXIII in the midwest by assuming the migration of a strongly selected and dominant 13-year allele.

The highly predictable emergence schedule of Magicicada provides a unique system for studies of gene flow and population genetics. We believe that the topic of genetic dominance of the life-cycle character should be debated in depth since it may control the geographic distributions of genes following hybridization between life-cycle forms. The long life cycles of Magicicada make direct testing of life-cycle dominance by artificial hybridization impractical. However, White and Lloyd (1975) documented that the difference in growth rate occurs during the first four years. This suggests the possibility that nymphs could be dug up and measured to determine dominance only four years after controlled hybridization. Future research along such lines would resolve this question.
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Literature Cited


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