THE ECOLOGY, BEHAVIOR, AND EVOLUTION OF PERIODICAL CICADAS

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ABSTRACT

Periodical cicada nymphs feed underground on root xylem fluids for precisely
13 or 17 years before emerging at any given locality synchronously and in
tremendous numbers. Populations throughout the eastern United States are
grouped into variously sized, geographically contiguous broods, which are
reproductively isolated from each other. Six distinct species represent the 13-
and 17-year life cycle forms of three morphologically and behaviorally distinct
periodical cicadas. Recent work supports and modifies previous hypotheses
concerning periodical cicada intra- and interspecific interactions, movement
patterns, juvenile development rates, life-cycle switching, the evolution of
periodicity, and the origination of broods and species. Major ecological inter-
actions of periodical cicadas include infection by a host-specific fungal patho-
gen, satiation of predators, and damage to hostplants. Central to the evolution
of periodical cicadas are four-year accelerations in development that some-
times result in switching between 13- and 17-year life cycles.

BACKGROUND

Periodical cicadas of the genus *Magicicada* (Homoptera: Cicadidae) have
fascinated biologists since they were first discussed in the scientific literature

over 300 years ago (86). They are favorite subjects in the writings of the leading early American entomologists such as Charles Marlatt, Benjamin Walsh, and Charles Riley (80, 93, 118). Many well-known 19th century naturalists, including Charles Darwin, Asa Gray, and Joseph Hooker, entered into discussions concerning the specific status of the 13- and 17-year forms. Central to this interest in periodical cicadas is their prime-numbered life cycle and amazing periodic, synchronized appearance in almost unbelievably large numbers. The evolution of a long life cycle combined with perfect synchronicity allows *Magicicada* spp. to escape the build-up of predators (12, 39, 64, 65, 84).

Although periodical cicadas are not the longest lived insects, they may have the longest juvenile development (62, 80, 110). Their life histories were first described in detail by Marlatt (80) and Snodgrass (110). Periodical cicada nymphs feed underground on root xylem fluids for 13 or 17 years. From late April to early June of the emergence year, fifth-instar nymphs emerge from the ground, crawl upwards, and eclose into adults, which are active for about 4–6 weeks. Within the first 2 weeks of the mass emergence, adults aggregate in chorus centers, i.e. places where males sing and mating takes place. The females lay eggs in pencil-sized twigs of trees, and after 6–8 weeks, nymphs hatch and rain down to the ground. There, nymphs rapidly enter the soil and begin feeding on small rootlets. Nymphal mortality can reach 98% in the first 2 years (53). As they grow, nymphs apparently move deeper below ground, feeding on larger roots (75, 125).

Broods and Life Cycles

Broods are comprised of all populations of periodical cicadas that emerge in the same year and that tend to be geographically contiguous (21); thus, broods are single-aged cohorts that are temporally isolated from other such groups. Cicada populations comprising a brood may cover areas varying from a few counties in one state to the majority of counties in as many as 15 states (98, 102). Marlatt (79) assigned Roman numeral designations to the broods, in a sequence starting arbitrarily in 1893. Designating seventeen-year broods I–XVII and 13-year broods XVIII–XXX, he noted that a given pair of 13- and 17-year broods will emerge in the same year only once every 221 years. For example, broods V and XXII emerged synchronously in 1897 but will not emerge synchronously again until the year 2118.

Seventeen-year broods generally emerge to the north, east, and west of the more southerly and centrally located 13-year broods (80, 98, 102). Although Marlatt (80) mapped 30 broods, some of them have never been well documented or are represented by only a few individuals. Moreover, some broods, including a few originally mapped by Marlatt, have gone extinct (2, 69, 98, 102). For example, brood XI, once located in the Connecticut River Valley, was last recorded in 1954 (78). Current maps of the 3 extant broods of 13-year

cicadas and the 12 extant broods of 17-year cicadas (102) indicate some recent population extinctions. However, in many instances periodical cicadas still can be found at the original locations.

Morphologically Distinct Species

Periodical cicadas have three morphologically and behaviorally distinct species, each of which has a 13- and 17-year life cycle form (2). Whether six species should be designated rather than three (using life-cycle as well as morphological factors) is still under debate and is discussed later in this chapter. The three species of 17-year cicadas are *Magicicada septendecim, M. cassini,* and *M. septendecula* (2). These species have distinctive color patterns, sizes, mating behaviors, and habitat preferences (2, 18, 19, 21, 69). In the case of the six-species designation, the 13-year forms were named *M. tredecim, M. tredecassini,* and *M. tredecula* (2).

Most broods contain all three morphologically distinct species (referred to here as Decim, Cassini, and Decula). Whereas Decim dominates northern populations, Cassini dominates Mississippi Valley and southwestern populations, and Decula is generally rare, appearing at highest densities in southern populations (21, 68, 71). By examining eggnests, White & Lloyd (125) showed that most cicadas emerge on schedule but Decula were more likely than other species to emerge as stragglers a year later, possibly because of nymphal crowding and poor competitive ability (71). Lloyd & White also proposed that intense predation on stragglers would prevent them from reproducing (71).

JUVENILE DEVELOPMENT

Emergence

The amazingly synchronous emergence of enormous numbers of periodical cicadas is one of the most predictable and fascinating of ecological phenomena. Densities of emerging cicadas (14, 19, 21, 28, 58, 61, 64, 74, 75, 76, 116, 127, 129, 130, 136) range from less than 30,000 ha^{-1} (76) to over 3.5 million ha^{-1} (19, 61). That translates into a biomass of over 0.5 metric tons ha^{-1} and represents tremendous productivity (19, 61). Most members of a population emerge within 7–10 days of each other (14, 20, 31, 60, 76, 90, 136), but emergence can be protracted by rainy or cool weather (7). In the weeks prior to nymphal emergences, periodical cicadas extend their tunnels to the soil surface, and some build mud turrets around emergence holes (5, 14, 19, 80). Physiological changes, including changes in eye (11, 75) and body (26) color, occur in the year prior to emergence.

The mechanisms for triggering the periodical emergence of cicada broods after exactly 13 or 17 years remain unknown. For most of their development,
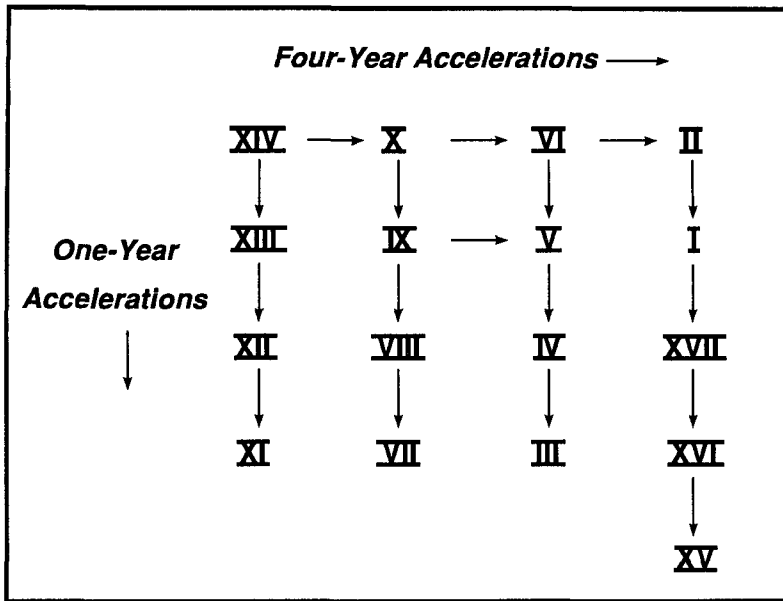
Figure 1   The hypothesis of Lloyd & Dybas (65) showing proposed relationships among the broods of 17-year cicadas. Reprinted with permission from Lloyd & Dybas (65).

periodical cicadas feed at depths [60 cm or more (11, 31, 75)] that prevent them from tracking photoperiod or detecting annual temperature fluctuations. Because these insects feed on xylem fluids, seasonally fluctuating xylem constituents, such as plant hormones or amino acids, might serve as annual cues for counting the passing years (2, 9, 124, 131). Alexander & Moore (2) noted that the north-south geographic chain formed by the adjacent broods VII, VIII, IX, and X (Figure 1) could be explained by postulating that northern cicadas counted an extra year when extreme cold periods caused early spring defoliation followed by later refoliation. Another possibility is that, rather than monitoring tree growth, periodical cicadas have an intrinsic molecular timing mechanism.

More is known about how periodical cicadas synchronize the day of emergence. Nymphs tunnel to the surface before they emerge, and because warm temperatures can accelerate emergence (5, 14, 26), photoperiod and air or soil temperatures are potential cues. Forest density and slope exposure, factors that influence soil temperature, also have been related to emergence timing (61). After examining photoperiod, air and soil temperatures, slope, and sun exposure, Heath (31) concluded that periodical cicada emergence may be triggered

when soil and cicada body temperatures at a certain depth reach a critical value.

Xylem Feeding and Development Rates

Both adult and nymphal periodical cicadas feed on xylem fluids (10, 21, 77, 117, 131) and have similar digestive organs (35, 36). Other xylem feeders include species in the Cercopidae, Coccidae, and Cicadellidae, but cicada nymphs are the only known root xylem feeders (131). White & Strehl (131) described two advantages of xylem feeding. First, xylem feeders avoid many plant defenses encountered by folivores and the accumulation of large amounts of sugar that phloem feeders must contend with. Second, excess water could be used to moisten and remold underground cells. However, excretion of amino acids in urine by nonperiodical cicadas suggests that cicadas may have to eliminate excess nonessential amino acids, just as phloem-feeding Homoptera excrete excess sugars (13, 131). However, unlike phloem feeders that tap sieve tubes, periodical cicadas must overcome large negative xylem fluid pressures, and all stages have enormous cibarial pumping muscles and valves at the base of stylets to extract xylem fluids (111, 131).

Some desert cicada species in the southwestern United States have many cuticular pores through which water obtained from xylem fluid can be actively extruded to stimulate evaporative cooling (28a, 94a, 117; K Williams, unpublished data). In contrast, long-term climate data indicate that periodical cicadas rarely encounter temperatures that require evaporative cooling, and *Magicicada* species have fewer such pores, appearing to rely primarily on passive evaporative cooling (117).

Xylem is a dilute fluid containing water, amino acids, and minerals (13, 89, 131). Because it is the only source of amino acids for periodical cicadas, several authors have proposed that this slow acquisition of nutrients causes their slow development (65, 72, 124, 131). This view is opposed by Slansky (106), who pointed out that other xylem feeders, such as spittlebugs (40), and similarly sized nonperiodical cicadas, such as *Diceroprocta apache* (27), have much shorter lives than periodical cicadas.

The uniform distribution of nymphal feeding cells (130) suggests that cicadas compete for feeding sites, which also may contribute to retarded growth and development (47, 65, 124, 125). White & Lloyd (125) reported a massive retarded emergence in which at least 50% of the population emerged in their 18th year, probably because of grossly poor nutrition. At another site where cicadas were starving, about 1% of survivors emerged after 18 years (124).

Although a population of periodical cicadas represents a single-aged cohort, nymphs of the same age can vary in size (65), possibly because of differences in food quality. Larger nymphs have been found on larger roots (124) and under fertilized trees (128), even though cicada densities tend to be greater

under fertilized trees (75, 128). Nutrition can increase developmental rates of nonperiodical cicadas dramatically (44), so White & Lloyd argued that if periodical cicada development rates depended on food quality, they should grow faster and emerge sooner when feeding on fertilized trees (128). However, since few periodical cicadas emerge one year early (62), nutritional differences in xylem fluids seem to influence nymph sizes and growth but not shorten developmental periods (128) to less than the appropriate number of years. Martin & Simon (81) related long nymphal development to the evolution of periodicity (see later), and Karban (50) suggested that slow development may enable periodical cicadas to increase fat reserves, adult body size, and potential fecundity, while avoiding host-rootlet death and allowing emergence with many conspecifics.

ADULT ECOLOGY

Adult Emergence and Mating Behavior

Adults typically emerge beginning from mid-April to the first weeks of June, depending on brood latitudes and microclimatic factors (3, 5, 14, 24, 26, 28, 31, 61, 77, 90, 100, 116, 136). Although maintaining cicadas in captivity is extremely difficult (80), adults have lived for as long as 23 days under laboratory conditions (14). In nature, adults probably live between 2 and 6 weeks, the usual duration of their activity (49, 53, 80, 102).

Adults appear to emerge with sex ratios near 50:50 (20, 52, 66, 75), although temporary biases may occur (28, 43; C Simon, personal observation). Males begin calling and adults begin mating after 5–18 days (3, 5, 28, 47, 77). Early in the emergence, predator pressure is intense (136), so the delay before mating appears to be maladaptive. However, sound-producing organs (tymbals) used by males in courtship, and ovipositors used by females to pierce twigs, apparently require several days to completely harden (47, 137). Virtually all females mate (47, 73), remaining in copula for 1 h or more (18, 52, 120) and probably do not mate again (120). During this time they receive a copualtory plug (73, 80). Males are thought to mate several times (52, 66).

The three species each have distinctive chorusing songs (1, 2, 18, 42, 96, 137), and males are attracted and stimulated to sing persistently by the singing of other males (1, 18). Sounds are produced by muscular contractions of stiff ribs covered by membranes, and although sound intensities of choruses can reach 100 dB (97, 134), calling appears to involve relatively minor energetic expense (91). Although the frequencies of Cassini and Decula songs overlap (97), the distinctive sound-making and hearing abilities acoustically isolate the three species for mating (42, 96). Visual cues also may stimulate mating, but songs appear to be more critical (1, 18).

Both males and females come to chorus centers to mate (1, 3, 18, 19, 30, 48, 66, 96, 134), possibly facilitating mate selection and predator satiation (66, 134). However, Karban found that mating rates were independent of local density (47). The patchy distribution of mating arenas, and the apparent ease with which females may reject courting males, suggest a lek mating system (47, 48, 134). Furthermore, Karban (52) found that Cassini males in copula were significantly larger than other males, indicating that females may choose large mates.

During the emergence period, chorus centers sometimes move and change composition (134). Choruses can persist at the same location for 1 to over 6 days (48, 134). Also, mating aggregations of different species can form together, further increasing sizes and sound intensities of choruses (96, 134), apparently without increasing hybridization (2, 20, 134).

After mating, females tend to disperse from choruses before ovipositing (21, 53, 73). Although the probability of predation for adults may be lower in dense aggregations (50), nymphal mortality underground appears to be higher near chorus locations (53), indicating possible selection against oviposition in chorus trees. Movement of males and females over distances of up to 300 m has been observed (20, 73, 77, 134; KS Williams, personal observation).

Habitat Preferences

While sympatric emergence of the three *Magicicada* species might enhance predator satiation effects, it also could intensify competition for resources (62, 64, 65). However, Dybas & Lloyd (21) and Lloyd & White (68) noted spatial isolation of species by habitat preferences. Decula, usually the rarest species, inhabits upland woods and oviposits in hickory and walnut trees. Decim, the most ubiquitous species, shows less host specificity than Decula, favoring trees that dominate canopies of mature upland forests. Cassini uses floodplain species such as ash, elm, oaks, and other shrubby vegetation. Within their particular habitat preferences, periodical cicadas are attracted to woodland edges and exposed aspects, especially for chorusing and ovipositing (5, 17, 21, 30, 51, 76).

Records indicate that populations of periodical cicadas have been annihilated by habitat disturbance and destruction. Populations have disappeared from parts of New Jersey (95) and Connecticut (76), apparently because of destruction of woodlands, forest fires, urbanization, or forest loss caused by the gypsy moth. Disturbance also can break down the reproductive isolation of species based on habitat preferences (21, 121). For example, Cassini may invade upland habitats when floodplains are disturbed (21). Furthermore, in disturbed areas all three species of periodical cicadas frequently use second-growth vegetation (2, 21, 62, 68, 121), which may result in intense competition and reduced densities of individual species (62, 70, 121). The smallest species,

Decula, is most susceptible to these problems (71). Habitat disturbances also could cause cicadas to use second-growth vegetation in previously unoccupied habitats (62, 73). Possible examples are periodical cicada invasions of new locations in New Jersey (95), Kansas (21), and Ohio (23). However, not all disturbances are accompanied by cicada dispersal. The distribution of periodical cicadas in undisturbed habitats has remained relatively constant during the last two centuries, as indicated by brood X in Maryland (28), brood XI in Connecticut (61), brood XIX in Arkansas (45), and broods V and VIII (23) and brood XIV (59) in Ohio.

Oviposition Behavior

Periodical cicada females begin ovipositing in small twigs 9–16 days after eclosing (28, 47, 77), depositing 20–30 eggs in each v-shaped eggnest (7, 14, 25, 43, 46, 80). Each periodical cicada species makes a morphologically distinctive eggnest (121) and tends to place different numbers of eggnests on a given twig and varying numbers of eggs in each eggnest (120), although fecundity also can be limited by larval nutrition (10). Eggs hatch after 6–10 weeks (14, 28, 49, 53, 77); then newly hatched nymphs fall to the ground and burrow into soil (within 2 min) (14) to feed on small rootlets.

Eggs are laid in, and nymphs feed on, root xylem of a wide variety of deciduous trees (7, 14, 19, 25, 43, 77, 131). Nymphs may feed on grass rootlets (5) or any other monocot, dicot, gymnosperm, or angiosperm root (72) that occurs beneath tree canopies. Lloyd (62) argued that in order for cicadas to develop population densities large enough to satiate predators, they must use a great diversity of host plants, including dominant species in mature forests and various hosts in disturbed habitats. Oviposition host preferences may differ among species (121), but 13- and 17-year forms appear to use the same hosts (6, 68, 83, 98, 99, 101). *M. tredecassini* of brood XIX exhibited no strong oviposition host preferences, but eggnest densities on eight species of trees were positively correlated with hatching success (135), indicating that host qualities may vary.

Eggs often die when their twig withers, breaks, or dies (28, 43, 122, 126), but eggs may hatch if damage occurs after about 4 weeks of development (122). Although dense aggregations may limit predation, concentrated oviposition activities can increase the probability of twig breakage and egg mortality. To explain that paradox, White (122) suggested that each species ameliorates twig damage by using differently sized twigs and eggnest arrangements. Egg mortality also may result from eggs being encased by tree growth (14, 122), or by trees producing gum or sap at wound sites (7, 25, 51, 64, 129, 133). While the intensity of such wound responses appears to be density dependent (51, 122, 133), some observations suggest oviposition preferences may be related to characteristics other than hatching success. For example, egg den-

sities were high in resin-producing persimmon trees (51, 133), yet low in other resin-producing trees (121).

Host Plant Damage

The tremendous density of periodical cicadas that occur at any location can represent a substantial herbivore load on their host plants (131). This damage can take three general forms: that caused by oviposition wounding of twigs, that caused by nymphal feeding on xylem, and that caused by pathogens vectored by the periodical cicadas. Oviposition damage has been quantified in terms of altered branch architecture (3, 7, 17, 28, 37, 107), reduced growth (37, 107, 133), and fruit crop loss (28). Nymphal feeding can reduce wood accumulation (46, 49) and flowering (107) of shrubs and trees. However, Karban (54) suggested that cicada feeding might reduce plant vegetative growth more than reproduction. Pathogenic infections of trees and shrubs also may result from oviposition wounding (87, 88, 107).

MORTALITY FACTORS

Predation

Adult periodical cicadas represent abundant, nontoxic, easily captured prey (8, 10, 65), and consequently are consumed by various predators, including birds, mammals, reptiles, and arthropods (19). The most widely noted predators, birds, include starling, common grackle, and robin (41, 50); wood thrush and blue jay (50); cuckoo (85); red-winged blackbird (34, 61, 115); English sparrow and red-headed woodpecker (41); titmouse and vireo (57); tern and laughing gull (22); and duck (5). Among the mammals reported to prey upon adult cicadas are squirrels (3), domestic cats and dogs (3), and various other small mammals (29, 60). Reptiles such as turtles (3, 19, 92) and snakes (92) also apparently feed on adults. In addition, even arthropods, including cicada killer wasps (3) and spiders (108), prey upon adult cicadas.

The reported predators of nymphs and eggs are less diverse. Moles appear to be major predators of periodical cicada nymphs underground, but they probably consume insufficient numbers to regulate cicada populations (19, 64). Above-ground arthropod predators of nymphs, such as ants, spiders, and centipedes, have also been observed (19). Although Lloyd & Dybas (65) discuss a hypothetical parasitoid that drives the life cycle of periodical cicadas, a trichogrammatid wasp is the only parasitoid reported from nature (77). Maier (77) also reported a cecidomyiid predator of periodical cicada eggs and, while none were reported to be predators, Russell & Stoetzel (94) found four orders of insects inhabiting eggnests.

Their perfect periodicity and overwhelming abundance suggests that peri-

odical cicada populations likely satiate their predators above ground (80), limiting the need for predator avoidance behavior (2, 65, 80). By escaping the numerical responses of predators (38), periodical cicadas can reproduce at the tremendous densities required to sustain their populations (65). Two studies demonstrate predator satiation by these insects. First, Karban (50) found that the frequency of predation at 16 sites in New York and Iowa did not increase as cicada density increased, although the number of cicadas consumed did increase as predator density increased. Therefore, the probability of a cicada escaping predation was higher in high-density populations. Williams et al (136) examined the intensity of predation as periodical cicada abundance changed throughout the period of adult activity at a single site in Arkansas. Heavy predation that occurred when cicada densities were relatively low declined dramatically following the rapid explosion of cicadas. Ultimately, predators consumed only an estimated 15–40% of the cicada population, and much of that probably occurred after cicadas had reproduced. Leonard (61) and Maier (77) observed similar patterns of predation.

Several examples demonstrate that predators can annihilate small populations of periodical cicadas. Both Marlatt (80) and Alexander & Moore (1) successfully transplanted eggs to new habitats, but the low densities of emerging adults (probably much less than 5000 ha^{-1}) were all consumed before oviposition (1, 63, 80). Local extinctions of small natural populations also have been reported (1, 8, 73, 90).

Although Lloyd & Dybas (65) labeled periodical cicadas as "predator foolhardy," individuals do exhibit some predator-deterring behaviors. Several authors have suggested that chorus noise levels, reaching at least 80 dB (97, 134), may repel predators (77, 96, 97), but predator responses to periodical cicada songs or choruses observed by other authors (50, 114, 115) refute that hypothesis. Nevertheless, when male periodical cicadas are alarmed, most produce a squawk call, which does seem to repel avian predators (52, 114, 115). The apache cicada, *Diceroprocta apache,* repelled mammalian predators with similar loud squawks (109).

Female periodical cicadas are larger and contain hundreds of developing eggs, and avian predators appear to feed selectively on females (52), possibly identifying them by their lack of sound (52, 114, 115). While males use sound, females apparently avoid predation by such means as flying or dropping into ground cover (114, 115).

Possibly the most important ecosystem function of periodical cicada emergence may be providing increased energy and nutrients to predators. The biomass represented by an emergence can be tremendous (19, 61), and although it apparently adds little to nutrient flux in litter fall (119), it benefits predator populations considerably. In periodical cicada emergence years, avian predators showed increased fledgling success (4, 34, 116), nestling biomass (116),

and clutch numbers and sizes (4, 34, 85). Although Anderson (4) found that foraging guilds of many avian predators of apache cicadas dissolved, Kellner et al (57) was unable to detect similar trends for predators of periodical cicadas. Despite widespread consumption of periodical cicadas by insectivorous birds in Ozark forests, Stephen et al (113) found no evidence that periodical cicadas provided any ecological release from predation for any other canopy arthropods. However, increased foraging activities resulting from numerical and functional responses to periodical cicadas (38) also may have depressed other canopy arthropod populations (113). Krohne et al (60) found that periodical cicadas enhanced reproduction of some mammalian predators (e.g. shrews, *Blarina* spp.), but not others (e.g. mice, *Peromyscus* spp.). Hahus & Smith (29) also found that *Blarina, Peromyscus,* and *Microtus* (voles) incorporated periodical cicadas into their diet, but cicada abundance seemed to produce increased intake of arthropods only for *Peromyscus.*

Fungal Infection

The only synchronized natural enemy of *Magicicada* spp. is the host-specific fungus *Massospora cicadina* (112). Infection takes place below ground (127), and after infected nymphs eclose, conidiaspores form at abdomen tips (73, 112, 123, 127). Conidiaspores are extremely infective to other adults (127), and individuals infected with them develop resting spores. In turn, resting spores are distributed as abdominal sclerites of infected individuals fall off (73), reinfecting emerging nymphs 13 or 17 years later. Because *M. cicadina* affects only the abdomen, White et al (123) found that flight speed and endurance of infected adults are not impaired, although healthy cicadas flew significantly farther. Thus, cicadas that are developing resting spores can invade new habitat, taking the fungus with them (73). Periodical cicada population dynamics are influenced by fungal infection because it reduces reproductive success of infected individuals—in that infected males may not mate and females can mate but do not oviposit (73).

   M. cicadina infection rates appear to vary among periodical cicada populations and seem to be influenced by cicada densities and habitat disturbance. Examination of infection rates and cicada densities (127) supported the suggestion that the fungus can regulate densities of periodical cicada populations (64). The fungus had relatively minor effects on adult mortality (<5–25%) in populations in New York (53), Arkansas (136), and Connecticut (77). However, those populations were considerably less dense than some that have been reported (<100,000 ha^{-1} vs >1 million ha^{-1}) (14, 19, 24, 26, 28, 61). The observation that the frequency of cicada infection increased with time since the last habitat disturbance (127) indicates that infection by fungus spores is also sensitive to disturbances. White et al (130) proposed that reduced fungal populations may allow periodical cicada populations to reach very high den-

sities (130). Stochastic natural events, such as violent summer storms, also contribute to periodical cicada mortality (5, 7, 136) and probably influence the *M. cicadina* relationship as well.

THE EVOLUTION OF PERIODICITY

The most commonly asked questions concerning periodical cicadas are, "why are they long lived?"; "why exactly 13 and 17 years?"; and "which came first, the evolution of periodicity, the evolution of the long life cycle, or the evolution of predator satiation?" We do not know the answers to these questions but experimental evidence and mathematical models have enabled us to develop some ideas.

Protoperiodicity

To be periodical a species must have a fixed development time, k, that is longer than one year, and the species must appear in a given location only once every k years (12, 33). Several authors have suggested that the evolution of periodicity in *Magicicada* spp. began with a protoperiodical condition, in which an insect that lives longer than one year is much more abundant in some years than others; this condition is common in cicadas. Soper et al (112) showed experimentally that *Okanagana rimosa* had a life cycle of 9 years, and that in the field during a 9-year period (1962 to 1970) it was extremely abundant in 4 years and scarce or absent in the other 5. Heath (32) also studied cicadas of the genus *Okanagana* and found several species that appear to be protoperiodical. Results of more than 20 years of field studies of cicada species along a transect in Arizona are expected to document that certain species are abundant in some years and rare or absent in others (M Heath & J Heath, personal communication).

Catastrophes such as weather or forest fires may have triggered periodicity in other insects (33). Lloyd & Dybas (65) postulated that the evolution of *Magicicada* spp. went through a protoperiodical stage that was initiated by variable weather conditions, and Cox & Carlton (15) and Martin & Simon (81) have expanded this hypothesis.

Once protoperiodicity has been established it can either be perfected by natural selection or dissipated by variability in life-cycle length among individuals within a population. Below, we examine factors that could have contributed to perfection of periodicity in periodical cicadas.

The Evolution of a Fixed Development Time and a Longer Life Cycle

In order to achieve periodicity, all adults of a given population must appear in the same year within a relatively short time period. Synchronization leads to higher insect densities and, coupled with a fixed predator population, results

in predator satiation (12). This safety-in-numbers strategy is selectively advantageous to individual cicadas (50, 136).

Martin & Simon (81) pointed out that selection for synchronous emergence in periodical cicadas would favor either the synchronization of nymphal development or the evolution of a waiting period in which faster-developing nymphs delayed emergence until their slower companions caught up. White & Lloyd (124) revealed that periodical cicada nymphs do not all grow at the same rate. These authors found that populations of 9-year-old nymphs consisted of three coexisting instars. Thus, nymphs reaching the fifth instar first might have to wait for as many as 4 years for the stragglers to reach the terminal instar. Based on this observation, Martin & Simon (81) suggested that perfect periodicity was achieved via life-cycle lengthening.

Long life combined with a fixed developmental period also can favor periodicity. Hoppenstadt & Keller (39) developed a model that incorporated predator satiation and a limited carrying capacity and predicted that periodicity would evolve in cicadas with a life cycle longer than 10 years. Although the fitness advantage of perfect periodicity may constitute the selective factor stimulating the increase in life-cycle length, such lengthening could have several other selective advantages, including selection for larger body size and increased fecundity (55). In addition, a longer life cycle could lead to increased survivorship during times of uncertain weather conditions, as occurred during the Pleistocene (~1–2 million years ago) (15).

The Perfection of Periodicity

The evolution of predator-foolhardy behavior in periodical cicadas must have followed the evolution of high population densities, synchronization, and associated behaviors such as male chorusing, because a predator-foolhardy cicada could only survive in the presence of many others. Furthermore, weak synchronization would favor the development of stronger synchronization because individuals that emerged in off-years would be eliminated quickly by predators (55, 65, 80), and perfection of periodicity would result.

Hoppensteadt & Keller (39) and Bulmer (12) suggested intraspecific competition as another selective factor that would favor the perfection of periodicity. Interference competition between nymphs of different year classes would create a selective disadvantage for later year classes whose first instar nymphs would be entering a habitat already occupied by the previous year's offspring. Experimental evidence has shown that nymphal cicadas may be able to cooccur without interference if the broods are separated by at least 4 years. For example, a patch of forest on Long Island containing two broods that were 4 years apart in age supported a much higher cicada population density than an adjacent patch containing only one of the broods (103). The geographic distribution of broods also supports the nymphal competition hypothesis. Lloyd

Table 1 A synthesis of hypotheses for the evolution of periodicity in *Magicicada* species[a]

Trait	Selective value or agent	Phytogenetic distribution	Reference
Xylem feeding	Allows cicadas to exploit an under-used resource	Family Cicadidae	131
Variable nymphal growth rate	Increased survivorship of offspring of one female in a variable environment (bet hedging)	Family Cicadidae	81
Long life cycle	Increased fecundity in a stable or declining population resulting from increased adult body size (achieved by lengthening nymphal period)	Family Cicadidae	55
	Increased survivorship during poor climatic conditions of the Pleistocene in the eastern United States	Eastern US Cicadas	15
Protoperiodicity	Year-to-year variation in weather conditions leads to some years with dense populations and other years with sparse populations	An unknown number of genera in Cicadidae	15, 65
Longer life cycle	Avoidance of specialist predators or parasitoids	*Magicicada*	65
	Achievement of even larger body size in temperate climates	*Magicicada*	55
	The response to selection for fixed juvenile development time. Life cycle lengthened to overcome the developmental constraint of unequal nymphal growth rates, which allows slow-growing nymphs to catch up in size and achieve synchronized emergence	*Magicicada*	81
Fixed juvenile development time; synchronization	Predator satiation: individuals that synchronize with others have higher survivorship	*Magicicada*	2, 12, 39, 55, 65, 136
High density	Improves adult survivorship; reinforces predator satiation	*Magicicada*	50, 65, 136
	Increases nymphal competition that reinforces selection against nymphs of younger, smaller year classes	*Magicicada*	12, 39, 103, 124
	Improves mating success	*Magicicada*	2

Table 1 *Continued*

Trait	Selective value or agent	Phytogenetic distribution	Reference
Predator foolhardiness	Increased mating success in large congregations	*Magicicada*	65
	Reinforces periodicity because numerical response of predators eliminates tails of the life-cycle length distribution	*Magicicada*	12, 39, 65, 136

ª Modified from Martin & Simon (81).

& Dybas (65) noted that the only 17-year cicada broods that overlap geographically are those that are separated by at least 4 years; broods that are separated by one year are often adjacent but never overlap. Table 1, modified from Martin & Simon (81), synthesizes the ideas about the evolution of periodicity in *Magicicada* spp.

Because all broods of *Magicicada* spp. are periodical, periodicity must have evolved prior to brood formation. It is difficult to determine whether periodicity evolved prior to the formation of the morphologically distinct species (102).

THE EVOLUTION OF THE BROODS VIA 4-YEAR ACCELERATIONS

Geographic Distributions of 17-Year Cicadas

Alexander & Moore (2) noted that subsets of the 17-year broods are related both geographically and temporally; consequently, many broods that appear in successive years border one another. Lloyd & Dybas (65) published a detailed scheme for the evolution of the 17-year broods (Figure 1). They discussed the one-year differences in adjacent broods recognized by Alexander & Moore (2) and agreed that the differences probably are the result of climatic factors. Furthermore, they noted that the largest broods of 17-year cicadas overlap widely (i.e. they occur in many of the same counties) and are separated by 4 years. These authors also suggested that these major broods could have been derived from one another by a 4-year shortening of the life cycle, which they suggested might have resulted from the temporary deletion of a postulated supernumerary sixth instar.

The Four-Year Dormancy Period

White & Lloyd's later study (124) of nymphal growth demonstrated that rather than possessing an extra instar, 17-year nymphs grow more slowly during the

first 4 years of life than do 13-year cicadas. Lloyd & White (69) postulated that this 4-year inhibition in growth, or dormancy period, might be broken by the stimulus of early nymphal crowding, leading part of the population to emerge 4 years ahead of schedule.

Observed Accelerations

Lloyd & Dybas's (64, 65) 4-year acceleration hypothesis gained unexpected support three years after its publication from a massive emergence in suburban Chicago of hundreds of thousands of periodical cicadas, which occurred 4 years ahead of schedule. Only one brood of periodical cicadas (brood XIII) had ever been recorded from that area, so this group must have been the source population. The remainder of the brood emerged on schedule in 1973, in enormous abundance (millions), with a few appearing during the intervening years. The thousands of cicadas that emerged in 1969 were not enough to satiate predators, and apparently they left few descendants because no egg nests could be found (69). A similar 4-year acceleration was again observed in that area in 1986 (M Lloyd, personal communication).

Since the first published report, several 4-year accelerations have been documented. In 1975, hundreds of cicadas emerged in the same suburban gardens and backlots from which hundreds of thousands later emerged on schedule in 1979 (brood II) (102). Brood VI (1983) and brood X (1987) in suburban Washington represent a similar situation, and evidence indicated a 4-year acceleration of brood X in Cincinnati in 1983 (102). Recently, Kritsky (58, 59) gathered extensive historical records that document 4-year accelerations in 20% of the counties of Indiana and 30% of the counties of Ohio. Four-year accelerations are probably responsible for the peculiar pattern of cicada broods on Long Island (104) as well.

Genetic Evidence for Massive Accelerations

Martin & Simon (82, 83) found genetic evidence for a massive, permanent 4-year acceleration in which 17-year cicadas in the Midwest switched their life cycle to 13 years. Five populations of 17-year Decim brood X and 12 populations of 13-year Decim brood XIX were surveyed for allozyme variation, mitochondrial DNA genotypes, and a morphological polymorphism—abdominal sternite coloration.

Mitochondrial genotypes outside the Midwest were found to be life-cycle specific. Analysis of eight restriction enzymes produced unvarying diagnostic patterns that consistently identified brood XIX (*M. tredecim*) or brood X (*M. septendecim*). The 13-year mtDNA genotype was designated B, and the 17-year mtDNA genotype A. In the Midwest, all individuals of brood XIX contained mitochondrial genotypes identical to the brood X mtDNA genotypes (genotype A). As the authors sampled southward, they found an abrupt tran-
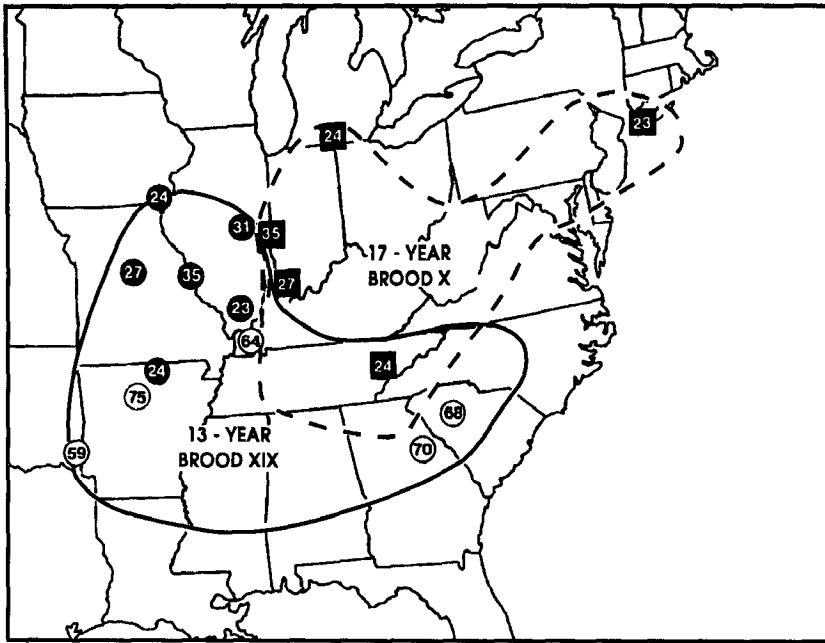
Figure 2 Map showing the spatial pattern of mtDNA genotypes and abdominal sternite coloration superimposed on the present distributions of broods X and XIX. Brood distributions are enclosed in solid black lines. Circles represent individuals sampled from brood XIX (6–12 individuals per population) and squares from brood X (4–11 individuals per population). Black circles and squares identify populations with mtDNA genotype A (characteristic of 17-year cicadas) and white circles represent genotype B (found only in 13-year cicadas). Mitochondrial genotypes represent whole genome digests, with the use of 10 different restriction enzymes. Numbers inside circles and squares represent the average abdominal color pattern for 20 individuals. Low numbers indicate primarily black coloration typical of 17-year cicadas, while high numbers indicate primarily orange coloration typical of 13-year cicadas. Redrawn from Martin & Simon (83).

sition from mtDNA genotype A to mitochondrial genotype B. In northern Arkansas they were able to localize the boundary line between two nearby counties (Searcy and Fulton) (Figure 2). Farther east, the boundary was somewhere in southern Illinois. In other words, the northern half of 13-year brood XIX was genetically identical to 17-year brood X. Results from examinations of the PGM A-allele and abdominal coloration agreed with those from the mitochondria experiments: The midwestern cicadas that were appearing once every 13 years were genetically identical and therefore recently derived from 17-year cicadas by a permanent acceleration in the life cycle.

Life-cycle switching can have important evolutionary consequences because it can result in the formation of new broods. Periodicity of cicada broods results

in reproductive isolation among broods that are separated in time, leading to genetic differentiation and incipient speciation. On the other hand, the polyphyletic nature of brood XIX indicates that life cycle switching can lead to situations in which two reproductively isolated broods that are genetically differentiated can come into contact.

THE SPECIES QUESTION IN PERIODICAL CICADAS

The Morphologically Distinct Species

The three morphologically distinct species abbreviated Decim, Cassini, and Decula are undoubtedly valid species. As mentioned above, they differ in size, coloration, song, behavior, and microhabitat preference. Furthermore, morphometric analysis of wing venation easily distinguishes Cassini from Decim, although Decula has not been examined in this regard (101). However, allozymic studies (98) found no alleles unique to any of these species. At the three most polymorphic loci, all three species shared the same common allele; the only difference was that Cassini and Decula shared a second-most-common allele that was rare in Decim, and vice versa. The extreme similarity in allozyme patterns may result from large population sizes or selection rather than recency of common ancestry. For example, mitochondrial DNA studies showed Cassini and Decula to be 7–8% divergent in DNA sequence from the Decim siblings and 3–4% divergent from each other (C Simon & A Martin, unpublished data).

Decim, Cassini, and Decula can be experimentally forced to hybridize by confining pairs in small cages. White (120) succeeded in crossing the larger Decim and smaller Cassini, producing first-instar nymphs of intermediate size. Based on hatching success results, Decim females suffered a 15% reduction in fertility when mated with Cassini males; Cassini fertility was 27% lower with Decim females. However, these morphologically distinct species appear to hybridize in nature only rarely; apparently, the distinct mating calls and associated behaviors are effective premating barriers (18). Dybas & Lloyd (20) found only 7 interspecific mating pairs out of 725 mating pairs in nature; these hybrid pairs were found in extremely dense populations. In addition, individuals are rarely found that appear to be hybrids based on a combination of coloration patterns and mtDNA (C Simon & A Martin, unpublished data).

The 13- and 17-Year Life Cycles

The first published description of 13-year cicadas (118) followed the first published record of 17-year cicadas (86) by nearly 200 years. The former record was delayed partly because the eastern range of 17-year cicadas was more heavily colonized by Europeans than the midwestern and Mississippi

Valley range of 13-year cicadas. The fact that the 13- and 17-year cicadas do not differ morphologically also contributed to this lack of recognition (101).

Differences in developmental timing between 13- and 17-year nymphs are still not fully understood. By digging up 17-year cicada nymphs, Marlatt (80) discovered that the first instar lasts for 1 year, the second 2 years, the third 3 or 4, the fourth 3 or 4, and the fifth 6 to 8 years. He reported an unpublished study that suggested that 13-year cicadas developed at a similar rate but spent only 3–4 years in the last instar. Based on this supposition, Lloyd & Dybas (65) suggested that 17-year cicadas might have a supernumerary sixth instar. However, field studies of 9-year old nymphal populations by White & Lloyd (124) contradicted the earlier ideas. They studied nymphs from three populations, northern 17-year cicadas, southern 17-year cicadas, and northern 13-year cicadas, and found that 13-year cicadas reach the fifth instar faster than 17-year cicadas. Rather than having a supernumerary sixth instar, the 17-year nymphs appeared to develop more slowly in the early instars. White & Lloyd suggested that a physiological mechanism limits growth in early instars of 17-year cicadas. Lloyd et al (67) and Cox & Carlton (16) present arguments to suggest that the 4-year difference in nymphal development rates is caused by a single dominant gene carried by either the 17-year or 13-year form.

Differences in development rates of 13- and 17-year forms do not appear to be related to climate differences. When 17-year nymphs were transplanted to a climate warmer than normal conditions, early growth of 17-year nymphs was much slower than that of 13-year cicadas (124). Conversely, when 13-year nymphs were transferred as eggs to a woodland north of their present range and within the range of 17-year periodical cicadas, they emerged on schedule 13 years later (63).

Lloyd & Dybas (65) succeeded in cross-mating 13- and 17-year forms. They transported *M. septendecim* and *M. cassini* from Iowa (brood III) and mated them with *M. tredecim* and *M. tredecassini,* respectively, from southern Illinois (brood XXIII). No barrier to cross-mating was evident, and the hybrid eggs later hatched into first-instar nymphs that appeared normal in every respect. Unfortunately, the experiment may be flawed because in retrospect the 13-year cicadas from southern Illinois fall within the anomalous region described by Martin & Simon (81, 83) where all 13-year individuals appear to be recently and secondarily derived from 17-year cicadas.

Seventeen-year cicadas were most likely formed in one developmental jump from 13-year cicadas. This scenario is suggested by the facts that stragglers are common 4 years prior to a periodical cicada emergence but not 1, 2, or 3 years prior (104), and that the jump could easily be accomplished by deletion of the second-instar 4-year dormancy period (124). In addition, Lloyd & Dybas (64) pointed out that cicadas that appeared 1 year later than the majority of their cohort would face an increased predator population. In contrast, a 4-year

increase in development time would place newly emerging adults beyond the point at which above-ground predator populations begin to diminish to their preemergence levels. Meanwhile, below-ground predators of later instars would lack suitable prey for many more years because the new generation of first-, second-, and third-instar nymphs would be well below the size range of the fifth-instar nymphs that had recently left the ground. For these reasons, Lloyd & Dybas (65) suggested that 13-year cicadas evolved first but that all then converted to a 17-year life cycle. Modern 13-year broods, they hypothesized, are secondarily derived from 17-year broods. Martin & Simon (82) present evidence from mtDNA that agrees partially with those ideas. Their data suggest that modern 13-year broods, because they are more genetically variable, are ancestral to 17-year broods and that the northernmost populations of 13-year cicadas, as described above, are secondarily derived from 17-year cicadas.

Each pair of 13- and 17-year cicada broods emerge simultaneously once every 221 years, but few 13- and 17-year broods overlap geographically. Although maps of brood distributions indicate that some 13- and 17-year cicadas live in the same counties, only three localities have been found where both forms were singing, mating, and ovipositing together on the same trees (102). Given that midwestern 13-year cicadas were recently demonstrated to be 17-year cicadas that have switched their life cycle to 13 years (82, 83), only one locality remains where true 13- and 17-year cicadas cooccur. The ranges of all broods are shrinking, so the overlap may have been greater in the past.

Broods Within a Life Cycle

Brood within life cycles are, by definition, temporally reproductively isolated. Thus, according to the biological species concept, broods would qualify as good species while 13- versus 17-year forms of the three morphologically distinct species, which have the opportunity to mate every 221 years, would not. However, lack of morphological and genetic differentiation among broods and the practical problem of naming so many different entities argues against such a designation. Allozyme studies of six of the 12 broods of 17-year *M. septendecim* showed that western broods differed significantly from eastern broods. Within broods, allele frequencies varied somewhat, but this variation showed no significant spatial patterning. Similarly, frequencies varied within and among the three 13-year *M. tredecim* broods (6) and within a *M. tredecassini* brood (56). The Cassini and Decula siblings showed no significant among-brood allozyme allele differentiation. In fact, Decula siblings displayed little or no allozyme variability at all (98). Studies in preparation examining the remaining six broods of 17-year Decim, including midwestern populations that link east and west, reveal geographic clines in gene frequency and demonstrate that allozyme frequencies are stable from generation to generation (J

Sullivan, C Simon & J Butte, unpublished data). Studies of mtDNA reveal no DNA sequence differences between eastern and western 17-year broods (105).

Isolation of broods within a life cycle is by no means perfect. For example, in 17-year broods, stragglers (i.e. cicadas appearing in off-years) are commonly sighted 1 year before, 1 year after, and especially 4 years before particularly dense emergences (69, 125). In most instances, these stragglers would be rare, unlikely to find a mate, and likely to be eaten by predators. They would not be able to join another brood because most broods do not overlap geographically. Broods separated by one year have never been found to overlap geographically (although they may come within less than a mile of each other). In all cases, the smaller brood always emerges a year earlier, thus avoiding any predator population build-up stimulated by the larger neighboring brood.

Broods only overlap geographically when they are separated by 4 or more years (58, 59, 65, 102). When populations of overlapping broods occupy the same trees, the safety-in-numbers strategy may protect accelerating individuals, and gene flow may occur through time. However, instances of exact overlap are rare, and distance can still isolate populations separated by only a few miles because movement is low (48, 73).

Are the 13- and 17-Year Siblings Valid Species?

White (132) cited periodical cicada 13- and 17-year pairs as classic examples of sibling species and suggested that broods were in effect allochronically isolated, incipient species. The above discussions clearly show that neither of those generalizations is strictly true. Specifically, brood XIV appears to be accelerating into brood X in the Midwest (58, 59), and a large section of 17-year brood X appears to have joined brood XIX (82, 83). Imperfect isolation leads to the possibility of gene flow through time.

Charles Darwin and his 19th century colleagues agreed that the 13- and 17-year life cycle forms should not be ranked as distinct species unless some differences other than the life cycles could be found (93). Martin & Simon (82, 83) found genetic differences in mitochondrial DNA between the Decim siblings that were as great as those typically found between other insect species. These results suggest the existence of two distinct genetic lineages, but that the 17-year lineage has secondarily introgressed into the 13-year. Studies of nuclear genes, currently in progress, may shed light on this problem.

FUTURE DIRECTION

Future ecological studies of periodical cicadas are needed to determine triggers for emergence, effects of nymphal competition, details of mating behavior and differential predation on the sexes, influences of *M. cicadina* fungus on cicada population dynamics, and effects of periodical cicada herbivory and damage

to host plants. While the literature on *Magicicada* spp. is extensive, very little is known about other species of cicadas in North America. Studies are underway to identify similarities and differences in host selection, mating behavior, and life cycles of *Magicicada* spp. and other native cicadas (118a; K Williams, M Heath & J Heath, unpublished data).

Ongoing studies in the laboratory of C Simon are concentrating on the differences between 13- and 17-year Decim siblings and investigating a second 13-year brood, brood XXIII, that occurs in the midwestern anomalous zone of Martin & Simon (82, 83). Populations over the range of brood XXIII are being surveyed using a combination of the polymerase chain reaction and restriction site analysis of mitochondrial DNA (105). Preliminary data suggests that life-cycle switching has also occurred in midwestern populations of brood XXIII, but the situation may be more complicated than that of brood XIX in that there appears to have been secondary integradation along the contact zone (C Simon, G Staley & J Deniega, unpublished data). This research is continuing, as are investigations into partitioning of genetic differences among broods and species.

ACKNOWLEDGMENTS

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