Debut of the Seventeen-Year-Old Cicada

This spring, brood II of the longest-lived insects will burst forth from the ground right on cue. Soon thereafter, they will "disappear" for another seventeen years

by Chris Simon

The periodical cicada is due to make an appearance this year over a wide area of the eastern seaboard—from central North Carolina to the mid-Hudson Valley. The parents of this year's generation emerged from the ground in late May 1962: first in North Carolina; later, farther north. During the intervening seventeen years, the offspring of those insects have grown from approximately six-hundredths of an inch to one inch in length.

Periodical cicadas, the subject of natural history investigations since the mid-seventeenth century, have recently proved a useful tool in studying evolutionary ecology and the problems of speciation. The most commonly asked questions about these cicadas are: Why do they emerge every seventeen years? Why do they live longer than any other insect? Why do they occur in tremendous numbers? Why are the adults synchronized in emergence time? Why don't they appear in the same year everywhere? And what do they do during their seventeen years underground? As is usually the case in scientific inquiry, the more we learn, the more interesting questions arise.

Commonly known as "seventeen-year locusts" because of their habit of emerging in plague proportions every seventeen years, periodical cicadas first received the name "locusts" in 1634 from the Pilgrims, who mistakenly equated them with the migratory grasshoppers of Biblical plagues. Since that time, both periodical and nonperiodical cicadas have been called locusts, a misnomer that has caused confusion and unnecessary panic.

True locusts are short-horned (antennaed) grasshoppers that belong to the insect order Orthoptera, along with katydids, mantids, and roaches. They possess chewing mouthparts and can destroy crops. Seventeen-year locusts are actually cicadas and belong to the order of sucking insects, Homoptera, which includes spittlebugs, leaf hoppers, aphids, scale insects, and mealybugs. The damage they cause to vegetation is considerably less severe.

Cicadas are worldwide in distribution, comprising 265 genera and 1,940 species. The diversity is immense. They range in wingspan from a little more than an inch to approximately 7½ inches. Some are brightly colored, but many are dull brown or green. The more curious species include the bladder cicadas, with their large balloonlike abdomens, and the hairy cicadas, which inhabit the cooler regions of Australia. Male cicadas are noted for their singing ability. The song is produced most commonly by the vibration of a tight, ribbed membrane (tymbal), which is moved by a pair of large muscles. However, there are species that produce sound by stridulating (with a file and scraper) or by banging their wings.

The periodical cicadas, which make up the genus *Magicicada*, occur in the United States east of the Great Plains. In addition to the seventeen-year life cycle form, a thirteen-year form inhabits the South and the Midwest. The latter was not recorded in the literature until the mid-1800s, fully 200 years after the first published reference to the seventeen-year cicada. All other cicada genera are nonperiodical: they may have long life cycles (up to seven to nine years) but they are unsynchronized, so that some individuals mature and emerge every year.

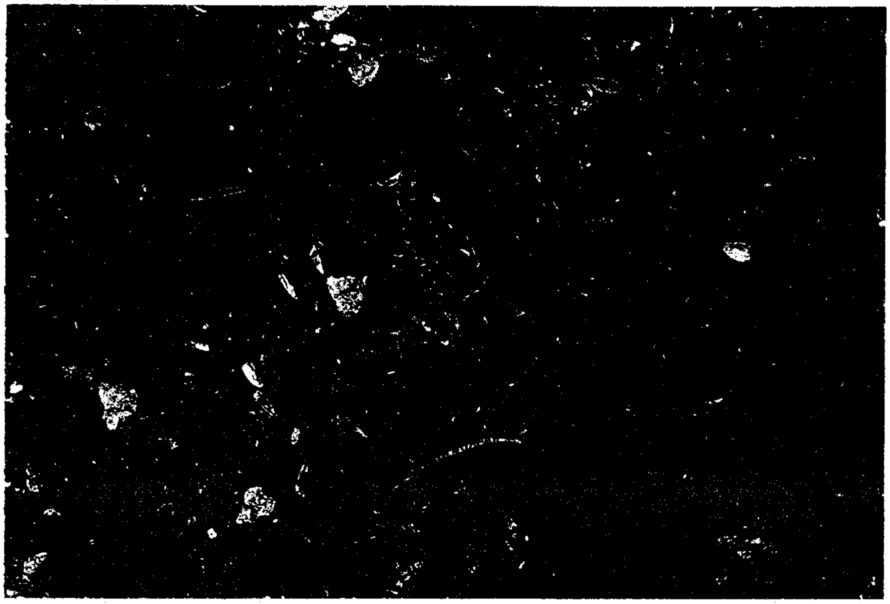
Periodical cicadas are easily distinguishable from their annual relatives as they are the only North American cicadas with red eyes and they generally emerge earlier, in May and June as opposed to July and August. Like other cicadas, the females lay their eggs in slits in tree branches using their sharp, sawlike ovipositors. The eggs hatch after one and a half to two months and hundreds of thousands of tiny millimeter-long nymphs instinctively launch themselves into space. The majority land within a few acres of where their grandparents emerged from the ground thirteen or seventeen years before. There they burrow underground and use their needlelike beaks to pierce tree rootlets and feed on dilute xylem fluid. When the rootlet dies, they search for a new one.

The subterranean nymphs pass through five stages (instars), growing with each intermediary molt. The fifth-instar nymphs emerge synchronously in a given locality, usually at dusk, often within a week or two of the emergence of their forebears 17, 34, 51 years before (or 13, 26, 39, in the thir-

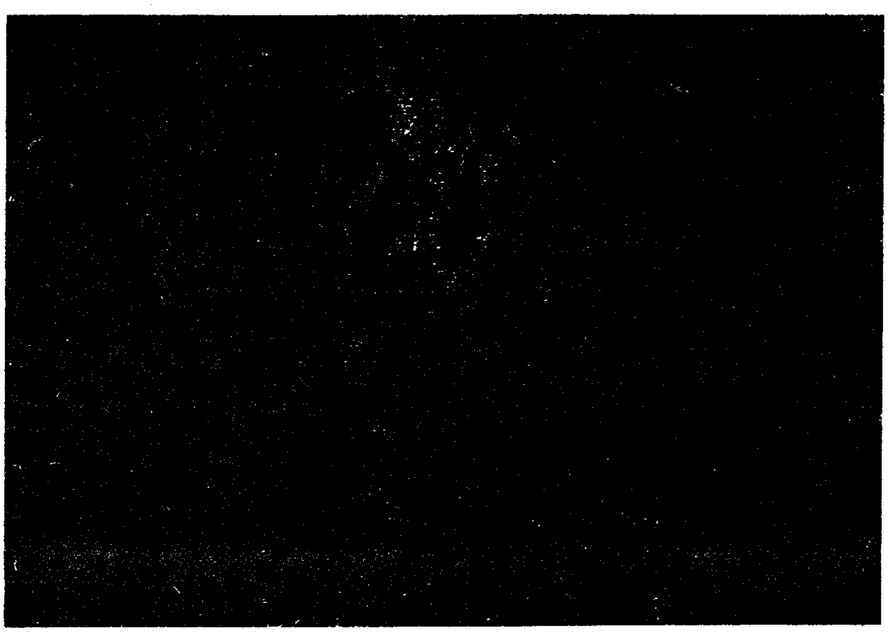
After emerging from a seventeen-year underground existence, a periodical cicada will climb any nearby vertical surface. Its aboveground life is brief; in three to four weeks it will have mated and died.

S. J. Krasemann

Karl H. Maslowski, Photo Researchers



Chris Simon



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teen-year race). When densities are particularly high, emergence may continue into the day or over a period of days.

How the nymphs "count" the years is unknown. They do not all grow at the same rate. The approximate durations of the stages are one-half to one year in the first instar; two to six years in the second (probably two years in the thirteen-year cicada and up to six years in the seventeen-year cicada); three to four years in the third; three to four years in the fourth; and the remaining time in the fifth. Thus at any given time, two or three different instars might exist in a population. Within an instar, body size may vary depending on nutrition.

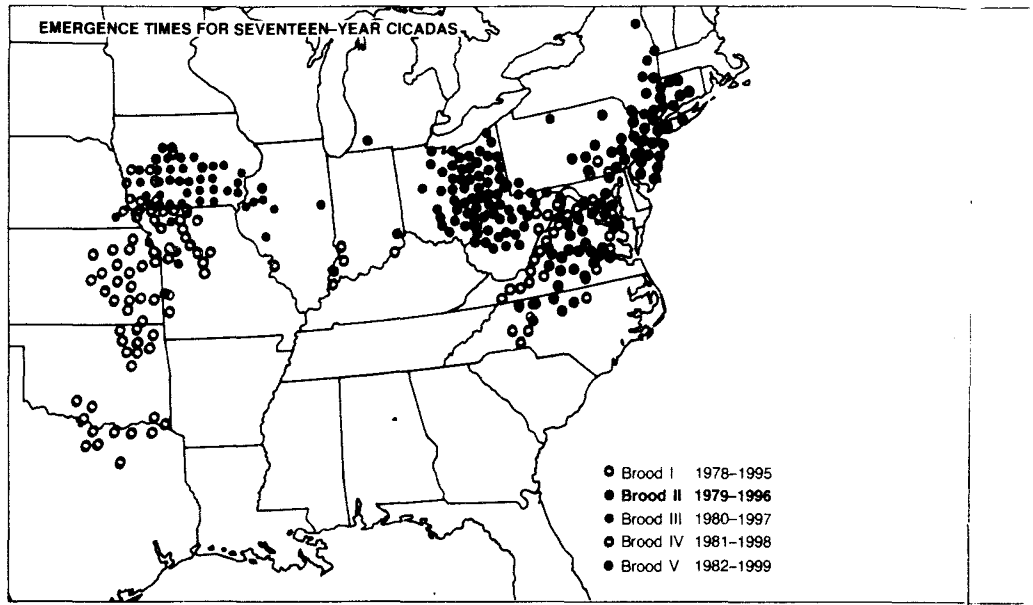
Despite varying growth rates, at the end of the allotted time all nymphs are in the fifth instar. They may construct an exit tunnel as much as a month (or even a year) early and sit just below the surface. The final precision that marks the date of emergence is impressive but less difficult to explain than the counting of the years. The crucial factor is the sum of cumulative degree days of soil temperature in the spring. James Heath, an insect physiologist at the University of Illinois, studying an emergence on a north- and south-facing wooded slope, found that a 64°F ground temperature seemed to be the final cue. Others have noticed that emergences often follow heavy rains.

Hundreds of thousands of fifth-instar nymphs emerge from the ground just after sunset and head for the nearest vertical object, which they climb. The distance they climb before eclosing depends on the object they

The exit holes of seventeen-year cicadas, top, dot the floor of a woods in Hamilton County, Ohio. Near Vicksburg, Mississippi, a newly emerged nymph of brood XXIII of the thirteen-year cicada is crawling toward a nearby tree to begin its life as an adult, center. A day after the cicadas have emerged, the base of a tree, bottom, is littered with castoff nymphal skins, dying cicadas unable to make it any farther because of injury, and a few stragglers on the ascent. Hanging from a twig, a thirteen-year cicada, right, stretches back and out of its nymphal jacket.

happen to have climbed (for example, a tall tree versus a grass stem) and probably on the level of their stored energy reserves.

The transformation to the adult stage is spectacular. The dry, golden skin, in which a nymph has been imprisoned for the previous four to eight years, splits down the back to reveal a milky white creature with bright red eyes and two square, black patches on its back (believed to be involved in the attachment of the muscles of the forelimbs). The wings, which up to this point have been folded accordianlike, are now free to expand. This is accomplished by the pumping of hemolymph through the wing vein network. The transformation may take several hours and includes hardening and darkening of the cuticle. The length of this vulnerable stage in the life cycle suggests an adaptive explanation for their dusk-timed emergence—escape from visually orienting avian predators.



By midnight, new adults can be found clinging to tree limbs, branches, blades of grass, or any other vertical object that can support their weight. Instinctively they climb upward; their wings are still too soft and the night temperature is too cool for flight. By midday the cicadas have hardened and warmed up and are capable of flight, but activity levels are generally low until the second or third day when the males begin their mating song. They prefer sunny places such as tree tops and by the end of the first week a prominent tree often becomes a chorusing center. The females fly here to mate, then disperse over short distances to lay eggs. The adults live for three to four weeks.

Egg laying can be destructive to vegetation. When densities are highest, the slits into which the eggs are laid can damage branch tips beyond repair. Although a heavy infestation may leave a forest looking brown, the ultimate effect on most trees is no more severe than a good pruning. Smaller trees, however, can be killed. When forewarned, orchard growers often plan ahead and do not plant new trees for three or four years prior to a predicted emergence. Homeowners are advised tc shake cicadas off young trees or to cover them with cheesecloth. Spraying large trees with insecticides is an expensive, dangerous, and useless exercise as the spray must contact cicadas directly to be effective. Furthermore, dying cicadas that have not escaped the poison flutter on the ground where they are eaten by unsuspecting birds, dogs, and cats.

One of the most dramatic aspects of the periodical cicada's appearance is the immensity of its populations. Often every square foot of the emergence area is pockmarked with their holes. Cicadas and empty nymphal shells can be found clinging everywhere. This immense pulse of life, preceded and followed by seventeen years of its absence, insures that no predators can specialize. The cicada strategy for survival is predator satiation, rather than predator avoidance.

Periodical cicadas cannot bite or sting. They are conspicuous, good tasting, and not always quick to fly when disturbed. These characteristics were collectively termed "predator foolhardiness" by Monte Lloyd and Henry Dybas, two evolutionary biologists who study the complex evolutionary history of the group. They pointed out that a direct consequence of this strategy is that population sizes *must* be large in order to avoid localized extinction through predation.

Rick Karban, an energetic field biologist from the University of Pennsylvania who is studying predator satiation, censused periodical cicada populations in Virginia last spring. He estimated the initial density of a population by counting emergence holes and later measured the same population's survival and reproductive success by intercepting its falling first-instar offspring in trays placed under their nest trees. His findings showed that survival, estimated by reproductive output, increased more than proportionately with population density; that is, dense populations produced relatively more offspring, presumably because a smaller proportion of the total population was eaten by predators.

Many nonperiodical cicada species fluctuate in adult abundance from summer to summer; that is, they have "good" and "bad" years. To create periodicity from such a situation, there must be natural selection against individuals emerging in years when population densities are low. The ancestral "protoperiodical" cicadas most likely had a shorter life cycle than their modern periodical relatives since all known nonperiodical cicadas have life cycles within the range of three to nine years and most other insect species have life cycles of one year or less. Seventeen years is the longest known life cycle (egg to adult) of any insect.

The classical ecological theory of predator buildup as a response to increasing prey abundance can be applied to this situation. Imagine an ancestral protoperiodical cicada species that fluctuates in adult abundance from year to year. In years when many adult cicadas succeed in emerging, the predators and parasites of these insects will feed well and produce many offspring, so the predator population will increase. Because cicadas that emerge the following year face increased predation pressure, each individual has a high probability of death. Therefore there would be selection for individual cicadas to emerge in years of high absolute cicada density. In such a situation, the probability of any one cicada being eaten is very low.

This predator-satiation strategy is not unique to cicadas. Some dragon-

The author requests that readers who see any of this year's brood, due to emerge in May and June, send her a post card with the following information:

Your name and address
Exact location and date of sighting
Number of species present (if possible)

Address cards to:

Chris Simon
Dept. of Ecology and Evolution
State University of New York
Stony Brook, New York 11794

This information will be used in precisely locating cicada populations and in helping to make distribution maps.

flies and June beetles, temperate oak trees, many tropical fruit trees, and Asian bamboos all follow the same strategy. An important component of this predator escape device is that in intervening years, prey availability must be minimal, so that predator populations drop to low levels (because of starvation) before the next pulse of prey.

Lloyd and Dybas have suggested that periodical cicadas have long life cycles as the result of an "evolutionary race through time" between the protoperiodical cicadas and a specialized parasitoid (a parasite that kills its prey). This hypothetical parasitoid presumably had a life cycle that was almost synchronized with, and nearly equal in length to (but always slightly less than), the ancestral protoperiodical cicada. As the theory goes, the cicadas finally outran their parasitoid pursuer and the poor specialized beast went extinct. The theory is tenuous in that its proof is the nonexistence of the hypothetical parasitoid. Nevertheless, no more plausible theory exists.

Once a long life cycle is achieved, the perfection and maintenance of periodicity is "easy." This mathematical problem was explored by Frank Hoppensteadt and Joseph Keller of New York University's Courant Institute of Mathematical Sciences. They demonstrated that predation and environmental carrying capacity can act in combination to bring about perfect synchrony. Synchronization is a consequence of the opposing pressures of a limiting environmental resource (in this case oviposition and nymphal-feeding sites) and the numbers of adult cicadas needed to satiate predators. When supplied with estimates of population size, fecundity, environmental carrying capacity, nymphal survival rate, and predator population size, the mathematical model predicted that cicadas with a generation time of less than ten years would be nonsynchronized and appear annually, whereas cicadas with longer life cycles would become periodical. Other parametric values could yield a different threshold for periodicity, but the general conclusion would be the same: long life cycles result in synchrony (periodicity).

Why then don't we see periodical cicadas with life cycles of, for example, twelve, fourteen, fifteen, sixteen, or eighteen years? Lloyd and Dybas have suggested that a prime number of years between emergences insures that no predators can track the cicada population by having cycles half as long and catching them every other time, or a third as long and catching them every third time, and so on. Thirteen and seventeen are prime numbers; therefore, unless the predator has a life cycle equal in length to the cicadas, the minimum number of years between predator and cicada coincidence is equal to the length of the predator's life cycle times the length of the cicada's life cycle.

Although a given population of cicadas emerges only once every thirteen or seventeen years, the thirteenth or seventeenth year differs from place to place in the eastern United States. This is because subsections of the original ancestral population somehow became displaced over time. All populations that emerge in the same year are members of a brood; a brood is simply a year class. Broods are numbered sequentially according to their year of emergence. For example, brood I adults appeared last year, II this year, and III will appear next year. Any brood numbered XVII or less is a seventeen-year brood; a brood numbered from XVIII through XXX is a thirteen-year brood. Fourteen broods of seventeen-year cicadas (at the turn of the century there were sixteen) and five broods of thirteen-year cicadas are thought to exist at the present time.

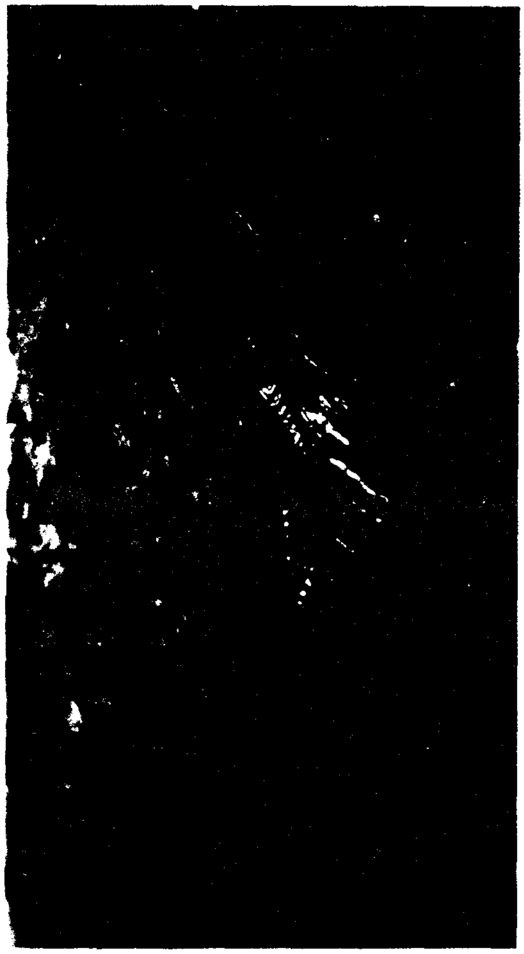
A brood is often considered to represent a loose evolutionary unit; all populations in a brood are most likely more closely related to each other than to populations occurring in other years. Some broods are large and occupy most of the eastern United States; others are small and occupy only a small corner of a state. Broods that overlap in distribution are always separated by at least four years in adult emergence time. This overlap presumably developed well after the establishment of periodicity and the demise of the hypothetical parasitoid. Adjacent broods are often separated in time by a single year.

Evidence suggesting that broods are indeed coherent units is relatively recent. My own work centers on this problem. We now know that despite the apparent superficial similarity of all broods, the members of any given brood possess more characteristics in common than they share with cicadas of other broods. These characteristics, which include the biochemical structure of their metabolic enzymes and the external shape of their body parts, can be used to construct evolutionary trees that represent the pattern of breakup of the broods of periodical cicadas.

To complicate matters, there are three morphologically distinct species of periodical cicada. Each of these is represented by thirteen- and seventeen-year life cycle forms. The largest and most common of the periodical cicadas is *Magicicada septendecim;* its thirteen-year counterpart is named *M. tredecim.* They are collectively abbreviated "Decim." The other two morphologically distinct periodical cicadas are smaller. They were lumped together and called "the dwarf form of the periodical cicada" until 1962, when Tom Moore and Richard Alexander, of the University of Michigan Museum of Zoology, demonstrated that each had a distinct mating song and unique coloration. The two smaller periodical cicadas have been named *M. cassini* (*M. tredecassini*) and *M. septendecula* (*M. tredecula*), abbreviated "Cassini" and "Decula," respectively. Cassini has a black abdomen and black tips to its legs; Decula's abdomen is black with orange stripes, while its tarsi are orange; and Decim's abdomen is entirely orange or orange-striped and its tarsi, black. In addition, Decim has a reddish patch just behind each eye.

Most broods contain all three morphologically distinct species. Decim is by far the most abundant and extends farther north than the other two species. Cassini is locally abundant in the Midwest and has its greatest densities in river bottomlands. Decula is much more common in the South than in the North but is always less abundant than the other two and never occurs alone.

Steve McDaniel: Tom Stack and Associates



Two seventeen-year cicadas mate on a maple tree in Towson, Maryland. This photograph was taken in 1970, so the pair belongs to brood X. The offspring from this mating will appear in 1987.

The three species can be identified in the field most easily by their songs. Decim's song is a hollow *pharoooh*, dramatically dropping in frequency at the end of each burst. A large chorus sounds remarkably like a fleet of flying saucers from a late fifties science fiction movie. Cassini's song is a series of *tics*, which increase in frequency and end in a loud buzz. The deafening roar of a synchronized Cassini chorus at midday is unforgettable. Decula produces a steady, tambourinelike cadence—*tschh-tschh-tschh-tschh.*

The differences in their mating songs serve to keep the species distinct. JoAnn White, an ecologist from the University of North Carolina, performed experiments in which she forced Decim, Decula, and Cassini to interbreed. White obtained hybrid eggs that later hatched into intermediate-sized nymphs. This result was not unexpected; many closely related species can interbreed. She credited the integrity of the species to the strong, behaviorally isolating influence of their unique songs. The lack of any physiological barriers to interbreeding indicated a relatively recent origin.

Few evolutionary biologists would deny that Decim, Cassini, and Decula represent distinct species, but there has been considerable debate over whether thirteen- and seventeen-year life cycle forms should be considered separate species. The biological species concept requires that separate species must not be potentially interbreeding. Thirteen- and seventeen-year forms will interbreed freely when placed together: there are no behavioral differences between them. In nature, a thirteen-year and a seventeen-year brood have the possibility of meeting every 221 years if they overlap in distribution. A few thirteen- and seventeen-year broods overlap geographically; when they do, however, they are rarely, if ever, found in the same patch of woods. From that point of view thirteen- and seventeen-year cicadas might well be called different species. But on that line of reasoning, every brood or local isolated population would qualify as a species and their taxonomy would be unreasonably complex. Clearly, the biological species definition leaves much to be desired.

Rather than arguing over species definitions, researchers are trying to understand how and why species differ. In an attempt to quantify the biochemical differences among species, evolutionary biologists have analyzed protein differences among classically defined (reproductively isolated and usually morphologically distinct) species and geographically isolated local populations of the same species. I have analyzed protein differences among the periodical cicadas and have found that compared with many other species, the morphologically distinct Decim, Cassini, and Decula are on the high end of the similarity scale. Since the three morphologically distinct species became reproductively isolated, they have accumulated very few amino acid or protein structural differences. Thirteen- versus seventeen-year forms of each of these species are even more similar: the level of variation among them is equivalent to the amount of differentiation that has occurred among local populations of most other organisms known. The various broods of a given morphologically distinct species are as distinct from each other as are any of the thirteen- versus seventeen-year forms. Local populations, in general, have not become differentiated.

Using her slender ovipositor, a seventeen-year cicada deposits her eggs in a slit in a tree branch. In one and a half to two months, the eggs will hatch and the nymphs will flutter to the ground.

There is no doubt that the numbers of periodical cicadas are dwindling in some places. Two broods are extinct: brood XI, which at one time occupied the Connecticut River Valley, and brood XXI, which used to occur along the Mississippi-Alabama border and in the Florida panhandle. The remaining broods have not decreased significantly in range, but they are made up of fewer and fewer local populations. As with most organisms, the greatest threat to the species is habitat destruction; the only sure cure for their decline is increased public awareness.

We have come a long way in our scientific understanding of the complex evolutionary relationships of the broods and species of periodical cicadas, yet they remain a needlessly misunderstood and unappreciated mystery to the majority of the people who encounter them. In the thousands of miles I have traveled in search of the periodical cicadas, I have experienced a wide variety of reactions to them. In the South, they were treated as a noisy but interesting curiosity, a reminder of childhood adventures, while many Midwesterners seemed disinterested or mildly inconvenienced by them. Northeasterners were often openly hostile or frightened; some were out to poison every last cicada, others locked themselves in their suburban homes and called the fire department.

Regional stereotyping aside, the periodical cicadas have, in general, not received the appreciation they deserve. They are the longest lived of any insect and exhibit the most precise synchronization; they occur nowhere else in the world, and their complex distribution pattern is a scientific puzzle that, when solved, will be a key contribution to understanding the speciation process. □