

How 17-year cicadas keep track of time

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Abstract

Seventeen-year periodical cicadas (*Magicicada* spp.) require 17 years to develop underground and all individuals at any location emerge synchronously within several days. The mechanisms that animals use to keep track of time are poorly understood and nothing is known about how cicada nymphs emerge after precisely 17 years. We altered the seasonal cycles of trees supporting cicada nymphs and thereby induced premature metamorphosis of the associated cicadas. This indicates that cicadas accomplish a consistently accurate 17-year preadult development time by counting host seasonal cycles and not either by the passage of real time or by the accumulation of degree days.

Keywords

17-year cicadas, biological clocks, *Magicicada*, periodical cicadas, plant–insect interactions, timing.

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An emergence of periodical cicadas is one of the great biological wonders of North America. Any given location supports only one cohort or brood consisting of many millions of individuals all of whom emerge synchronously within several days of each other (Marlatt 1907). Despite the synchronous emergence, individuals grow at very different rates and a sample of same aged nymphs contains different instars with over a 10-fold difference in size (White & Lloyd 1975). During their long, 17-year development, nymphs move little and feed actively on root xylem fluid, 15–60 cm underground (Marlatt 1907; White & Strehl 1978). Although the advantages of synchronized mass emergences are well substantiated, the mechanisms that cicadas use to keep track of time so as to emerge after precisely 17 years are completely unknown (Williams & Simon 1995). More generally, mechanisms used by insects to regulate their activities that involve time frames exceeding a single season are very poorly studied. Here we show that cicadas accomplish a consistently accurate 17-year preadult development time by counting host seasonal cycles and not by the passage of real time or by the accumulation of degree days.

Photoperiod controls many insect functions, and is usually coupled with thermoperiod in nature (Beck 1980). Insect responses to thermophotoperiod have at least three components: (1) a biological clock must recognize a cycle, (2) the number of cycles must be counted, and (3) the clock-counter must connect with neuroendocrine pathways that control the response (Takeda & Skopik 1997). Only the first two steps are considered in this study.

We asked whether 17-year cicadas were timing their development by counting host phenological cycles or by the passage of calendar or physiological time. We imposed a 6-month seasonal cycle on host plants of cicada nymphs while maintaining the accumulation of day degrees equivalent to control plants that experienced a normal 12-month seasonal cycle. Because cicadas live underground they will not experience photoperiod directly and the amplitude of daily and annual thermo-periods will be much reduced relative to air temperatures (Williams & Simon 1995). We propose that cicadas are sensitive to changes in plant phenology and associated changes in availability or quality of plant nutrients. If correct, experimentally manipulating those variables, uncoupled from the annual calendar cycle, should alter the timing of nymphal emergence. We tested this proposition by transporting 15-year-old nymphs to the roots of a judiciously selected, low-chill-requiring, peach cultivar “Tropic Sweet”, bred for subtropical climates and capable of double cropping under appropriate conditions (Dr W.B. Sherman, Department of Horticultural Sciences, University of Florida, Gainesville, FL 32611, personal communication).

MATERIALS AND METHODS

Peach trees were established in 216 m³ pots in 1996 in Davis, California. Last instar, 15-year-old cicada nymphs were collected on 6–10 September 1997 in Greene County, Pennsylvania. Nymphs were transported in potatoes and transferred to roots of peach trees on 11 September



A close up of an adult cicada.

(following Beamer 1928). Transferring nymphs to new roots is a difficult process and results in high mortality; since Beamer (1928) pioneered this technique at least three attempts to repeat his procedure by our lab and colleagues have failed. We introduced 20 nymphs to each of five trees assigned to accelerated thermophotoperiod and 15 nymphs to each of two trees assigned to normal thermophotoperiod. Trees assigned to accelerated thermophotoperiod experienced the normal photoperiod and temperature in Davis [30 years average (1961–90) for each week ([HTTP://ucipm.ucdavis.edu/WEATHER/AVERAGES/davis.txt](http://ucipm.ucdavis.edu/WEATHER/AVERAGES/davis.txt))] but with a period that was half as long as normal inside a single large growth chamber (Fig. 1). Other growing practices (fertilization, watering, and pruning) and the total annual degree-day accumulation were similar for the two treatments. Eclosed individuals were caught by netting placed over each pot.

RESULTS AND DISCUSSION

The accelerated thermophotoperiod successfully induced trees to undergo physiological changes appropriate for the simulated seasons; they abscised leaves and flowered twice each year. However, we were not successful at inducing trees to produce fruit more than once each year. Cicada nymphs transferred to roots of trees that experienced accelerated thermophotoperiod eclosed in only 16 years and nymphs transferred to trees that experienced normal thermophotoperiod eclosed in 17 years, in synchrony with the rest of their cohort. Of the original 130 nymphs, 13 survived to eclose (11/100 assigned to accelerated thermophotoperiod and 2/30 assigned to normal thermophotoperiod). No nymphs were alive in the soil at the end of the experiment. Eight nymphs from trees that experienced the additional growth cycle per year emerged 1 year early (after 17 host phenological cycles) (Fig. 1). Two nymphs emerged 6 months early from trees that experienced accelerated



The casts skins of cicada nymphs covering horsechestnut foliage during a very large emergence of 17-year cicadas.

thermophotoperiod (after 18 host cycles) and one nymph emerged after 17 years (19 host cycles) (Fig. 1). Two nymphs eclosed from trees that experienced normal host phenological cycles and both emerged after the normal 17 years (Fig. 1). Millions of cicadas emerged from the site where these nymphs were collected after 17 years; none were detected at this site emerging after only 16 years (D.C. Dunning, Department of Biology, University of West Virginia, Morgantown, WV, personal observation). Assuming each cicada nymph to be an independent replicate [an uncertain assumption (Hurlbert 1984)], a G -test for independence of emergence time and seasonal cycles indicated significant early emergence with accelerated host phenological and seasonal cycles as compared to normal seasonal cycles ($G = 4.43$, $P = 0.035$).

These results indicate that cicadas do not time their 17-year preadult development through endogenous time keeping or through accumulation of degree days but, rather, through counting the number of host phenological and seasonal cycles. Our results do not distinguish between the direct perception of seasonal cycles by the nymphs themselves or indirectly through cues provided by their host plant. We believe the latter to be likely because cicadas live underground where light and temperature fluctuations are damped and remain relatively constant year round. It is likely that cicadas use a reliable seasonal indicator that is mediated by their host as a cue for counting years, such as quality of xylem fluid (Anderssen 1929; Tromp & Ovaa 1967). The amino acid concentrations in xylem sap of mature apple trees vary quantitatively and qualitatively over the seasonal cycle with the highest concentrations occurring in spring following bud break and blossoming (Tromp & Ovaa 1967). Thus in the more rapidly cycling thermophotoperiod, the richer xylem sap spring elixir occurred twice per calendar year. Root-infesting aphids also have been shown to depend on cues from their host plants in

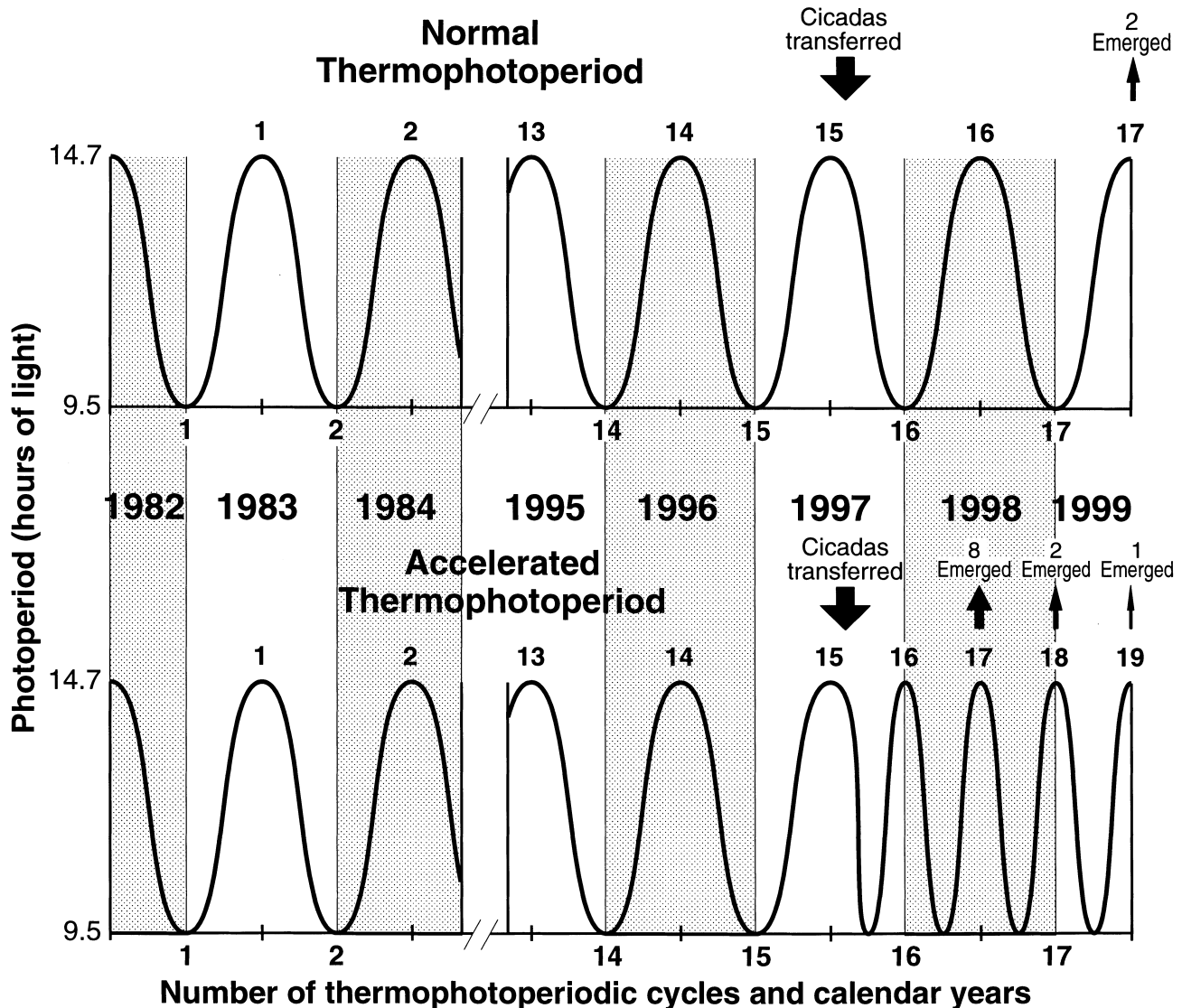


Figure 1 A summary of the experimental design and results. Cicada nymphs that were 15 years old were transferred to potted trees in 1997. The trees were subjected to one of two experimental treatments: (1) normal thermophotoperiod with one cycle per year or (2) accelerated thermophotoperiod with two cycles per year. Numbers below the x -axis indicate calendar years and those above the peaks indicate thermophotoperiodic cycles completed. Cicadas growing on trees with the normal thermophotoperiod emerged at the normal time in 1999, after 17 years. A majority (8/11) of cicadas growing on trees with accelerated thermophotoperiod emerged in 1998, after only 16 calendar years (17 thermophotoperiodic cycles).

determining their reproductive status (Sethi & Swenson 1967). Similarly, the synchronized hatch of treehopper eggs that overwinter inside of woody twigs is cued by the seasonal rise in plant sap (Wood *et al.* 1990). Our results are inconsistent with the hypothesis that cicadas track the passing of time by summing circadian cycles [the frequency demultiplication hypothesis (Gwinner 1986)]. Rather, our results indicate that environmentally linked host phenological cues occurring over longer time frames (years) are used to track time.

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BIOSKETCH

Richard Karban studies plant–herbivore interactions and has been particularly fascinated by periodical cicadas; he has dreamed about tricking them into emerging early for most of his adult life.

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