

# Evolutionary ecology of periodical insects

Kari Heliövaara, Rauno Väisänen and Chris Simon

As defined by Bulmer<sup>1</sup>, a species is periodical if the life cycle has a fixed length of  $k$  years ( $k > 1$ ) and the adults appear synchronously every  $k$ th year. Although annual insects could be thought of as periodical, their life cycles are governed by abiotic environmental factors. When it does occur, periodicity seems to be haphazardly distributed across insect orders (Table 1). There are undoubtedly more species of periodical insect than are currently known, but these remain unrecognized because relatively few insect life cycles have been carefully studied. There are many families where most species have a 1-year life cycle, but a few species live longer and therefore have the potential to be periodical. Often, however, data on juvenile development time and/or the relative abundances of adults in different years are missing. Anecdotal accounts may confuse protoperiodicity – cases in which insects are noticeably more abundant in some years than others – with true periodicity.

Periodical insects with a life cycle of  $k$  years can be divided into as many as  $k$  reproductively isolated cohorts or broods. In the most common form of periodicity, alternate-year cohorts exist as geographically distinct reproductively isolated units. This is possible, for example, when the developmental cycle is restricted to two years with two obligatory diapauses<sup>21</sup>. Box 1 details the life cycle of a typical 2-year periodical insect, the pine bark bug (*Aradus cinamomeus*). Most periodical insects have a 2-year life cycle, but periodicity can be much longer. The periodical insects with the longest life cycles are the 13- and 17-year periodical cicadas (Box 2).

## Traits associated with periodicity or protoperiodicity

Life spans can be viewed in chronological time or in physiological time, where only the number of days of growth necessary to complete development are considered<sup>30</sup>. In discussing the evolution of periodicity, it is chronological time that is important because diapausing insects are still subject to critical influences such as predation and abiotic catastrophes. Danks<sup>30</sup> points out that large body size, poor food quality and low temperatures tend to constrain developmental rates, thus lengthening life cycles. Life cycles can be especially long when several constraints coincide. The manner in which constraints interact can vary tremendously depending on chance factors and/or on differences in the genetic backgrounds of particular species.

**To be periodical, a species must have a fixed life cycle length and adults must appear synchronously, reproduce only once, and die. The consequence of this life history is that, at a given location, adults of a periodical species will be absent or rare in some years and abundant in others. The relative scarcity of periodical insect species suggests that periodicity does not evolve easily. The major obstacle to its evolution is selection favoring life cycles in which the offspring of any given female appear over a two- or three-year period. Chance events which disrupt this 'bet-hedging' strategy set the stage for periodicity. Mathematical models predict that, given certain initial conditions, intraspecific competition and predation favor its development. Recent studies suggest that periodicity is rarely perfect but that it can persist in the face of limited gene flow through time.**

Long life cycles tend to be associated with large size because bigger animals take longer to develop. This can be illustrated by cases in which the majority of insect species in a taxonomic group develop in one year while the largest members take more than one year to develop<sup>30</sup>. Large size related to long life may be selected for in situations where mortality is concentrated in the earliest instars with little risk of mortality in later instars<sup>31</sup>. Selection could then increase the number of days a juvenile can feed and thereby obtain a larger adult size leading to increased egg production.

Diets low in nutrients can result in slowed growth and/or longer life cycles. Long life has been attributed to wood-eating in beetles (up to 50 years for juvenile development<sup>30</sup>) and xylem-feeding in 13- and 17-year periodical cicadas<sup>31</sup>. Adult body size may be sacrificed to retain a fixed development time. For example, in profundal *Chironomus cucini* populations in two lakes in Northern Wisconsin, adult body size was noticeably smaller in the lake with denser larval populations (less food), although both

lakes showed the same 3-year developmental period<sup>32</sup>.

In temperate regions, species with the longest life cycles tend to be found in cool climates or microhabitats. Boreal and Arctic insect species tend to have longer life cycles than their temperate relatives<sup>30</sup>. Life cycles of seven and 14 years have been reported in arctic chironomids<sup>33</sup> and woolly-bear moths (*Gynaephora groenlandica*)<sup>34</sup>, respectively. Similarly, when a species spans a range of temperatures the life cycle can vary in response. For example, the mayfly *Habrophlebia vibrans*<sup>35</sup>, the midge *Chironomus anthracinus*<sup>17</sup> and the oak egg moth *Lasiocampa quercus*<sup>1</sup> have 2-year periodical life cycles in colder areas, but 1-year non-periodical life cycles in warmer areas. In contrast, pine-resin gall moths (*Retinia resinella*) and pine bark bugs have a periodical 2-year life cycle in warmer southern areas and a non-periodical 3-year life cycle in colder northern latitudes<sup>5</sup>.

Adversities tend to prolong the life cycle of all individuals in the population, whereas unpredictability tends to lengthen the life cycle of only some individuals<sup>30</sup>. In unpredictable environments, genetic differences in diapause characteristics among siblings can spread the risk of adult emergence in unfavorable conditions and lessen the possibility of the complete elimination of a cohort by a chance catastrophe<sup>36</sup>. This phenomenon, called bet-hedging, is

---

Kari Heliövaara is at the Dept of Applied Zoology, PO Box 27, FIN-00014, University of Helsinki, Finland; Rauno Väisänen is at the Nature Conservation Research Unit, National Board of Waters and the Environment, PO Box 250, FIN-00101 Helsinki, Finland; Chris Simon is at the Dept of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, USA.

---

Table 1. Examples of periodical insects

Species	Length of life cycle (yrs)	Host plant	Geographic area	Refs
<b>Heteroptera</b>				
<i>Aradus cinnamomeus</i>	2 (3)	<i>Pinus sylvestris</i>	Eurasia	2
<b>Homoptera</b>				
<i>Magjicada tredecim</i>	13	Deciduous trees	N. America	3
<i>M. septendecim</i>	17	Deciduous trees	N. America	3
<i>M. tredecassini</i>	13	Deciduous trees	N. America	3
<i>M. cassini</i>	17	Deciduous trees	N. America	3
<i>M. tredecula</i>	13	Deciduous trees	N. America	3
<i>M. septendecula</i>	17	Deciduous trees	N. America	3
<i>Strophingia ericae</i>	1 (2)	<i>Calluna vulgaris</i>	W. Palaeartic	4
<b>Lepidoptera</b>				
<i>Retinia resinella</i>	2 (3)	<i>P. sylvestris</i>	Eurasia	5
<i>Recurvaria starki</i>	2	<i>P. contorta</i>	W. Nearctic	6
<i>Coleotechnites milleri</i>	2	<i>P. contorta</i>	W. Nearctic	7
<i>Oeneis jutta</i>	2	Grasses	Holarctic	8,9
<i>O. nevadensis</i>	2	Grasses/Sedges	N. America	10
<i>O. macounii</i>	2	Grasses	N. America	10
<i>Erebia embla</i>	2	<i>Carex</i>	N. Palaeartic	8,9
<i>E. ligea</i>	2	Graminae	Palaeartic	8,9
<i>Lasiocampa quercus</i>	2	<i>Calluna vulgaris</i>	W. Palaeartic	1
<i>Xestia rhaetica</i>	2	<i>Vaccinium</i>	N. Eur.-Siberia	11
<i>X. okakensis</i>	2	Unknown	Holarctic	12
<i>X. n. sp.</i>	2	Unknown	E. Siberia	13
<i>X. speciosa</i>	2	<i>Vaccinium, Betula</i>	Holarctic	14
<i>X. sincera</i>	2	<i>Picea abies</i>	Palaeartic	11,15
<i>X. brunneopicta</i>	2	Unknown	N. Eur.-Siberia	13
<i>X. gelida</i>	2	<i>V. myrtillus</i>	N. Eur.-Siberia	11,13,14
<i>X. borealis</i>	2	<i>V. myrtillus</i>	N. Eur.-Siberia	11
<i>X. distensa</i>	2	Unknown	N. Eur.-Siberia	14
<i>X. laetabilis</i>	2	<i>V. myrtillus</i>	N. Eur.-Siberia	11,15
<i>X. albuncula</i>	2	Unknown	Siberia-N. America	13
<i>X. imperita</i>	2	Unknown	N. America	14
<i>X. alpicola</i>	2	<i>Empetrum, Calluna</i>	Europe	16
<i>X. lorezi</i>	2	Unknown	Holarctic	11
<i>X. tecta</i>	2	<i>Betula nana</i>	Holarctic	11
<i>X. quieta</i>	2	<i>Empetrum?</i>	Holarctic	16
<i>X. kolymae</i>	2	Unknown	Siberia-N. America	13
<i>X. ursae</i>	2	Unknown	Siberia-N. America	13
<i>X. atrata</i>	2	Unknown	Siberia-N. America	13
<i>Hyphoraia lapponica</i>	2	<i>Betula nana, Rubus chamaemorus, V. uliginosum</i>	Holarctic	16
<i>Orodemnias quenseli</i>	2	<i>Lathyrus, Taraxacum</i>	Holarctic	16
<i>Polia lamuta</i>	2	<i>V. vitis-idaea</i>	N. Eur.-Siberia	16
<i>Sympistis heliophila</i>	2	<i>Empetrum nigrum</i>	Holarctic	16
<i>S. funebris</i>	2	<i>B. nana</i>	Holarctic	16
<i>Anartomima secedens</i>	2	<i>V. uliginosus</i>	Holarctic	14,16
<i>Hada skraelingja</i>	2	Unknown	Holarctic	14,16
<i>Colostygia turbata</i>	2	<i>Galium palustre</i>	Holarctic	16
<i>Glacies coracina</i>	2	<i>B. nana</i>	Palaeartic	11
<i>Sterrhopteryx hirsutella</i>	2	Polyphagous	Palaeartic	16
<b>Diptera</b>				
<i>Chironomus anthracinus</i>	2	Phytoplankton	Holarctic	17
<b>Hymenoptera</b>				
<i>Neodiprion sertifer</i>	(1) 2	<i>Pinus sylvestris</i>	Holarctic	18
<b>Coleoptera</b>				
<i>Saperda populnea</i>	2	<i>Populus, Salix</i>	Palaeartic	19
<i>Melolontha hippocastani</i>	3,4,5,6	Deciduous trees	Eurasia	1
<i>M. melolontha</i>	3,4	Deciduous trees	Europe	1
<i>Phyllophaga rugosa</i>	3	Grasses	N. America	20

widespread in animals and plants<sup>37</sup>. Danks<sup>38</sup> lists nearly 140 insect species in which there is a low but persistent incidence of prolonged diapause. Bet-hedging constitutes a strong selective force which would have to be overcome during the evolution of periodicity.

**Development of periodicity**

Large differences in abundance among cohorts, or protoperiodicity, is common in insects<sup>2,8,11,12</sup>. For example, many long-lived cicada species are commonly more abundant in some years than others<sup>39</sup> (M. Heath and J. Heath, pers. commun.). Many other long-lived insect species show variation in abundance among cohorts (e.g. mayflies<sup>35</sup> and species of the butterfly genera *Oeneis* and *Erebia*<sup>8,9</sup>).

Variation in abundance among cohorts of a long-lived insect must in part be due to the same factors that trigger variation in abundance from year to year in annual insects, such as extreme or unseasonable cold or drought<sup>2,23,24,28,40</sup>. Other events suggested to trigger protoperiodicity include forest fires<sup>41</sup> and chance dispersal by one brood into an unoccupied territory<sup>2</sup>. The fact that the geographic locations of even- and odd-year populations of three common periodical insects in Northern Europe do not coincide argues against a few large catastrophic events and in favor of smaller taxon-specific phenomena (Fig. 1).

A fixed juvenile life span is necessary for periodical behavior. To achieve a fixed development time, individuals can spend the same amount of time in each instar or develop at different rates and catch up in the end. The latter is the most well-documented phenomenon<sup>22,33,35,36</sup> and probably reflects widely distributed bet-hedging of ancestors<sup>28</sup>. The combination of a fixed juvenile development time and a long adult life could favor the development of periodical behavior but does not guarantee it<sup>33-35</sup>.

Bulmer<sup>1</sup> pointed out the difficulty in understanding how life cycle constancy and periodical behavior could have evolved together since each presupposes the other. Martin and Simon<sup>28</sup> suggested that this difficulty can be resolved if periodicity is preceded by a chance proto-periodical condition which encourages the simultaneous and mutually reinforcing evolution of these two traits.

Synchronization of adult emergence is necessary to achieve periodicity, but many insects that show highly synchronized adult emergence are not periodical<sup>33,43</sup>. Mayflies are famous for their highly synchronized, dense, adult emergences lasting less than 48 hours<sup>44</sup>, but few species are periodical. High biomass associated with synchronized adult emergences is thought to satiate predators and increase the survival of individuals in the population – a situation analogous to mast-fruiting in plants<sup>45</sup>.

Lloyd and Dybas<sup>23,24</sup> suggested that predator satiation was the selective advantage in the evolution of highly synchronous adult emergences of periodical cicadas, because individuals that emerge a year or two late would face an increased predator pressure. Later, experimental studies conclusively demonstrated that predator satiation occurs in periodical cicada populations<sup>46,47</sup> but, as we discuss later, this alone may be insufficient to stimulate periodicity.

Predator satiation is unlikely to select for periodicity if the insect life cycle is too short to avoid the predator pulse stimulated by the previous generation, nor will it select for periodicity if predators can be recruited from outside to take advantage of the mass emergence. However, periodicity can develop in insects with short life cycles and in the absence of predator satiation<sup>1</sup>. Other factors must operate to stimulate periodicity.

Studies of periodical insect species have led to different hypotheses concerning the development of periodicity from protoperiodicity by exclusion of year-classes. These hypotheses focus on interactions with predators and parasites or on interspecific competition.

#### Host–predator/parasite interactions

According to the host–predator hypothesis, the parasitoids, predators and certain microorganisms specializing on immature stages of a species lack prey or a substrate in the year when only adults are present. The following year the predators are at low levels when the immature host numbers are again high. The same would hold for specialist predators of adult stages. Mikkola<sup>11</sup> suggested that 2-year development is an adaptation against parasitism and/or predation. However, there would be strong selection for a specialist parasitoid to adopt the same 2-year development time as their host, and if the specialist parasitoid became extinct there would be selection on the prey to resume a 1-year development time<sup>48</sup>. In the case of a generalist predator with alternative prey, the predators would increase in numbers the year following an emergence. A prey species with a two-year periodicity would be at a selective disadvantage in such a situation.

In the case of *Aradus cinnamomeus*, there are several features which argue against regulation by predators/parasitoids<sup>2,21</sup>. There is neither a gap nor decrease in the bug density in the narrow (3.5 km) transition zone between the two alternate year populations. Moreover, no significant differences were observed in parasitoid population levels (percentage of parasitized bug eggs) between mixed and alternate year populations (Fig. 2).

Several mathematical models have been explored in an attempt to understand the origin of periodicity. Hoppenstadt and Keller<sup>49</sup> showed that synchronized emergence of

#### Box 1. Periodicity of *Aradus cinnamomeus*

The pine bark bug, *Aradus cinnamomeus* (Heteroptera, Aradidae), has two or three allochronic sympatric 2- or 3-year populations (cohorts) depending on the geographical area in Europe (see Fig. 1a). In the north, the bug has a life cycle of three years. The change in the life cycle strategy seems to be correlated with the long-term means of the highest daily temperatures in mid-summer (roughly with the 21°C July isotherm). In most of Europe, there seem to be two major alternate-year cohorts that live in different geographical areas. In each area, however, there always seems to be a very small proportion of bugs (fewer than one per thousand) which reproduce in off years and are called minor cohorts. In eastern Finland, the major cohort bugs reproduce in even years, and in western Finland in odd years. The major cohorts border each other in a very narrow zone of overlap, where both are found in about equal numbers (Fig. 2).

Such a distinct numerical dominance of one cohort over the other, as in the parapatric even- and odd-year cohorts, is not apparent in the 3-year life cycle, however the three cohorts usually coexist in relatively low densities. Usually, one of them does slightly predominate, resulting in a temporally changing mosaic-like biogeographical pattern<sup>2</sup>.



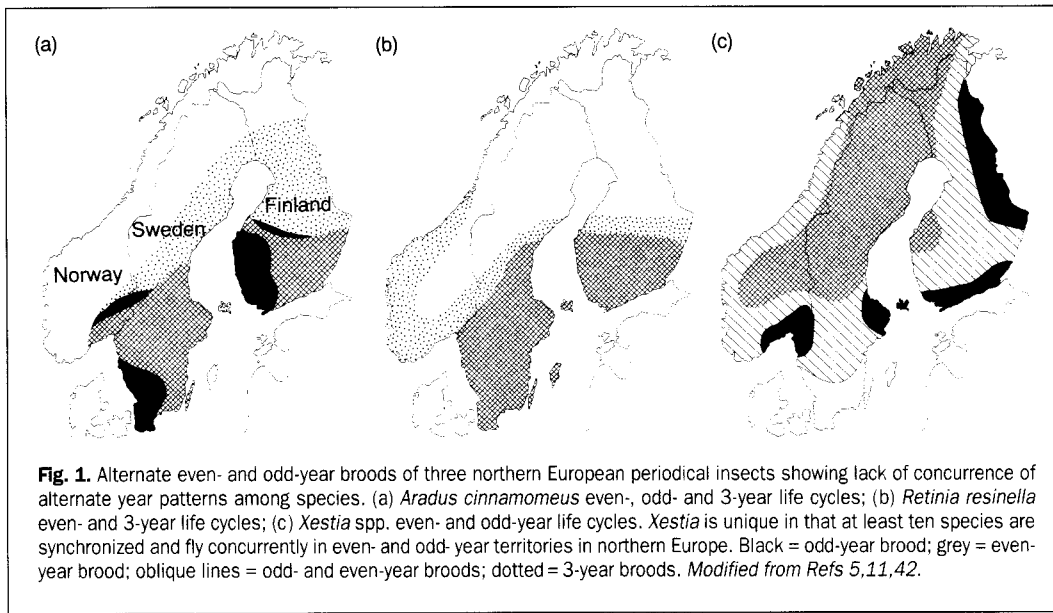
#### Box 2. Periodicity of *Magicicada* spp.

Periodical cicadas of the genus *Magicicada* are native to the United States east of the Great Plains. The 17-year cicadas are found in the northern, eastern and western edges of the distribution, and the 13-year cicadas predominate in the southern states and in the Mississippi River Valley.

There are three morphologically, behaviorally and genetically distinct periodical cicadas each of which has 13- and 17-year life-cycle types. These have been designated as six species: *M. septendecim* (illustrated here), *M. tredecim*, *M. cassini*, *M. tredecassini*, *M. septendecula* and *M. tredecula*. The difference between the two life-cycle lengths is thought to be the duration of the 2nd instar<sup>22</sup>. There is increasing evidence that periodical cicadas can switch life-cycle length<sup>23–27</sup>. Therefore, the taxonomic distinctions based on life-cycle length are not likely to represent valid species<sup>28</sup> (Fig. 3).



Periodical cicadas are divided into geographically distinct year-classes, or broods, of varying size that were numbered consecutively according to their year of emergence. The 17-year broods are numbered I–XVII; the 13-year broods are numbered XVIII–XXX<sup>29</sup>. For example, Brood VIII last emerged in 1985 and is due to emerge again 17 years later in 2002; Brood IX last emerged in 1986 and is due to emerge again in 2003. There are twelve 17-year broods and three 13-year broods currently in existence<sup>28</sup>.



**Fig. 1.** Alternate even- and odd-year broods of three northern European periodical insects showing lack of concurrence of alternate year patterns among species. (a) *Aradus cinnamomeus* even-, odd- and 3-year life cycles; (b) *Retinia resinella* even- and 3-year life cycles; (c) *Xestia* spp. even- and odd-year life cycles. *Xestia* is unique in that at least ten species are synchronized and fly concurrently in even- and odd-year territories in northern Europe. Black = odd-year brood; grey = even-year brood; oblique lines = odd- and even-year broods; dotted = 3-year broods. Modified from Refs 5,11,42.

a single year class is a possible consequence of predation given a limited environmental carrying capacity and life cycle lengths above a certain threshold value. Bulmer<sup>1</sup> also demonstrated that predation alone will not cause periodical behavior except as the accidental result of particular initial conditions. However, boosted by protoperiodicity and coupled with competition among year classes, predation can reinforce the tendency towards a periodical response.

Kettlewell<sup>50</sup> attributed periodical behavior in the oak eggar moth to parasitism. To investigate this possibility Bulmer<sup>1</sup> modeled the dynamics of host-parasite interaction for a variety of host life cycle lengths but only for the case of a parasite with a one-year life cycle. His results suggested that this type of interaction can only give rise to periodical oscillations with one brood present when the life cycle of the host is three years or shorter.

Godfray and Hassell<sup>51</sup> developed a similar mathematical model of parasitoid build-up to explain the evolution of discrete generations in tropical insects living in relatively non-seasonal environments. They demonstrated that the ratio of lengths of the host and parasitoid life cycles determines whether the model predicts discrete generations or overlapping generations.

**Competition**

According to the intraspecific competition hypothesis, the protoperiodical alternate-year cohort prevents the other cohort from spreading into its area, or prevents it from increasing if present locally. Bulmer<sup>1</sup> modeled competition in the May beetle and found that if competition is more severe between than within year classes, the system always moved to one of the *k* possible periodical equilibria with only one year-class present.

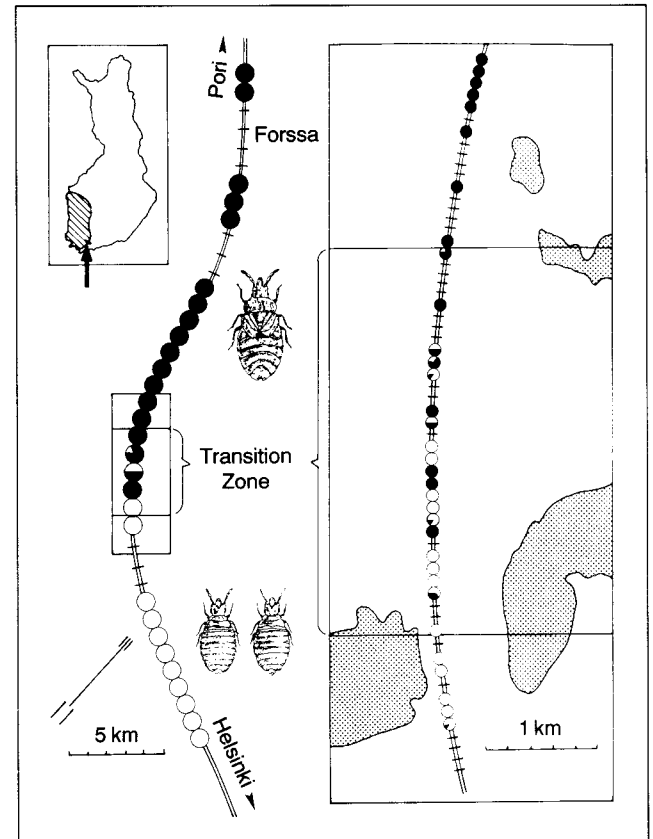
Experimental studies of competition among sap-feeding nymphs and adults of pine bark bugs forced to live in the same test bags attached to pine trunks found that the deeper-penetrating younger larvae were better exploitation competitors than older larvae or adults. Thus, competition between the two age classes, possibly reinforced by the impact of parasitism/predation, can explain, reasonably well, the parapatry of the alternate-year cohorts<sup>52</sup>.

Intraspecific competition between larvae and adults has also been suggested as the important factor maintaining exclusively even-year cohorts of the pine resin gall moth *Retinia resinella* (Lepidoptera, Tortricidae) in northern

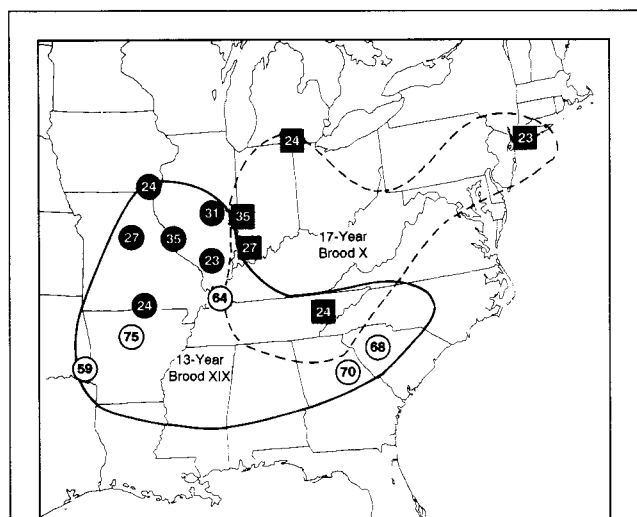
Europe<sup>5</sup>. In this case, host defenses induced by feeding larvae may make the pines uninhabitable for a year following infestation thus preventing a second cohort from becoming established. It has been suggested that the competition among cohorts which prevents cohabitation is lessened in northern 3-year non-periodical areas because the harsher climate can break down the *Retinia*-induced chemical defense mechanisms in the pine, but this has not been tested.

In a two-year periodical midge (*Chironomus anthracinus*) studied in Denmark, the density of one-year-old larvae was postulated to be

sufficient to preempt settlement of a potential odd-year cohort<sup>17</sup>. However, in the case of the 3-year non-periodical *C. cucini* in northern Wisconsin, USA, although densities of larvae exceeded those found in the periodical *C. anthracinus*, habit and foraging differences might make annual recruitment possible even in the face of high densities of established larvae<sup>32</sup>.



**Fig. 2.** The structure of the transition zone between the alternate-year populations of *Aradus cinnamomeus* along the Helsinki-Pori highway near the city of Forssa in southern Finland. The sample size was 10 specimens in each plot. First, 40 samples were taken at intervals of 1 km. Second, the transition zone was examined by taking 60 similar samples at intervals of 100 m. Filled circles = adults; open circles = larvae, in May 1983. Sample sites without bugs are indicated by small cross-lines on the highway. Redrawn, with permission, from Ref. 21.



**Fig. 3.** The spatial pattern of mtDNA genotypes and abdominal sternite coloration superimposed on the present-day distribution of broods X and XIX of *Magicicada*. Brood distributions are enclosed in solid or dashed black lines. Circles represent brood XIX (6–12 individuals per population) and squares represent brood X (4–11 individuals per population). Filled circles and squares identify populations with mtDNA genotype A (characteristic of 17-year cicadas) and open circles represent genotype B (found only in 13-year cicadas). Mitochondrial genotypes represent whole genome digests by 10 different restriction enzymes. Numbers inside circles and squares represent 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, with permission, from Ref. 27.

There is evidence to suggest that interference competition among nymphs of different periodical cicada broods might be important in the origin and maintenance of periodicity. The only broods that are known to overlap are those that are separated by at least four years<sup>3,25</sup>. Simon *et al.*<sup>53</sup> demonstrated that oak woodlands on Long Island, NY, USA, occupied by two broods with a difference in age of four years, supported twice as many cicadas as adjacent woodlands occupied by only one brood. White and Lloyd<sup>54</sup> found that cicada nymphs of Broods X and XIV were segregated by depth.

As in any biological system, it is unlikely that one factor operates free from the influence of others. Martin and Simon<sup>27</sup> created a scheme that integrated and ordered previous ideas for the evolution of periodicity and associated traits in the genus *Magicicada*. This scheme was enhanced by Williams and Simon<sup>3</sup>. They suggested that the first traits to evolve were xylem feeding, variable nymphal growth rate, and long life-cycle (7–10 years), because these traits are shared by many cicadas<sup>31</sup>. The evolution of *Magicicada*, they proposed, then went through a protoperiodical stage that was initiated by variable weather conditions<sup>23,24,40</sup>. Further lengthening of the life cycle would, in their scheme, be favored by a number of factors including avoidance of specialist predators<sup>23,24</sup>, increased survival during the uncertain climate of the Pleistocene<sup>40</sup>, and larger body size accompanied by higher fecundity<sup>31</sup>. In addition, selection for synchronization would favor a lengthening of the life cycle adding a terminal nymphal waiting period that would ensure that all nymphs were in the 5th instar and capable of emerging simultaneously<sup>28</sup>. Although predator build-up selects against life cycle lengthening, cicadas that extended their life cycle in one large jump, from 13 to 17 years, would skip over peak-density predator populations. Synchronization and fixed juvenile development

time would allow the perfection of periodicity, and predator satiation would reinforce this. Denser populations further improve adult survivorship and increase nymphal competition thus selecting against younger smaller year classes. Foolhardy behavior would be favored by increased mating success and would also reinforce predator satiation<sup>1,23,24,49</sup>.

### Imperfect periodicity – gene flow through time

Most periodical species are divided into broods, with adults appearing in mutually exclusive time periods. Such allochronic broods are, in effect, incipient species. Provided that gene flow does not disrupt the situation, these broods could go on to accumulate genetic differences that will eventually lead to speciation. The time change that produced them could be viewed in retrospect as an allochronic speciation event<sup>55</sup>. Temporal gene flow can occur in two ways: (1) via interbreeding between populations of the same species that have different life cycle lengths; or (2) via alterations of life cycles of single individuals or entire populations, which thereby travel through time and join an adjacent or overlapping brood.

Examples of interbreeding between different life cycle types include pine bark bugs where southern 2-year life cycle cohorts alternately mate with northern 3-year life cycle adults<sup>2</sup> and periodical cicadas where a given pair of 13- and 17-year broods can meet once every 221 years if they overlap geographically<sup>3</sup>. In periodical cicadas, current contact between 13- and 17-year populations is rare and distinct; 13- and 17-year genotypes over most of their range suggest no gene flow via this mechanism<sup>56</sup>. In the pine bark bug, there is no evidence for allozymic differentiation among even- and odd-year cohorts<sup>57,58</sup>. This could reflect gene flow through northern 3-year populations or recency of common ancestry. In the pine bark bugs, small populations known as minority cohorts do emerge in off-year. These minority cohorts deviate clearly in allozyme frequency from the general majority pattern, and at least morphologically from each other<sup>58</sup>. Differences between off-year and majority cohorts could reflect selection or genetic drift and suggest little or no gene flow into off-year populations despite contact with the 3-year northern populations.

Lloyd and Dybas<sup>23,24</sup> first suggested that periodical cicadas could alter their life cycle to form new broods. They suggested that the largest 17-year broods were formed from each other via 4-year changes in the life cycle in post-glacial times. Lloyd and White<sup>25</sup> studied the population dynamics of co-occurring 17-year broods and formalized the 4-year acceleration theory. Simon and Lloyd<sup>59</sup> documented that Long Island, NY is a complex mosaic of 17-year cicada broods that probably arose by 4-year acceleration in the past but are currently dwindling; they also summarized recent cases of 4-year accelerations, all of which resulted in the death of the accelerating populations. Competitive interactions among individual nymphs are thought to be the primary factor triggering life-cycle accelerations<sup>23–25,58</sup>. Accelerations are evolutionary dead ends, unless accelerating populations are large enough to satiate predators or accelerating individuals can join pre-existing broods.

In periodical cicadas, there is evidence that in the mid-western United States it is common for 17-year cicadas to temporarily accelerate their life cycle to emerge four years early and to join existing 17-year broods<sup>26</sup>. There is no reason to suspect that this gene flow through time has not existed throughout the history of the 17-year broods. It must be remembered, however, that the majority of 17-year broods are allopatric and therefore do not receive or produce successful temporal migrants<sup>3</sup>. The lack of genetic

differentiation among 17-year broods is therefore probably because of recency of common ancestry<sup>56</sup>.

Although brood geography is evidence for massive 4-year accelerations in the past, there was until lately no evidence for recent successful accelerations. Martin and Simon<sup>27,56</sup> gathered genetic evidence for a significant 4-year acceleration which converted 17-year periodical cicadas into 13-year cicadas in a large part of the midwest (Fig. 3). They found a sharp boundary between southern 13-year cicadas with typical 13-year genotypes and northern 13-year cicadas with typical 17-year genotypes. The fact that northern 13-year cicadas were genetically identical to 17-year cicadas suggested that this was a relatively recent event. The potential now exists for the exchange of 13- and 17-year genes every generation rather than only once every 221 years. Eventually, differences between 13- and 17-year lineages may be erased by this gene flow. Although evidence for life-cycle switching was only gathered for one of the three species of 17-year cicada, all three are thought to have evolved in parallel because of their peculiar predator satiation strategy<sup>3</sup>.

**Concluding remarks**

In summary, the prerequisites for the evolution of insect periodicity are associated with chance abiotic factors or food resources. The later steps in the evolution of periodicity appear to be controlled by a combination of intraspecific competition and predation. The dynamics and evolution of periodicity in different insect species are rather similar, though the patterns often show unique features. Periodicity can be maintained even in the face of limited gene flow among broods but when present this gene flow may be sufficient to prevent species formation.

Temporally isolated year-classes provide an unusual opportunity to study ecological processes in communities, since this approach provides, to some degree, replicates with similar among-site biotic and abiotic effects. Temporally isolated cohorts also offer a useful tool for evolutionary studies on the effects of isolation. Reproductively isolated cohorts are in some ways analogous to incipient species. Thus, genetic processes involved in the early stages of species formation can be examined. Studies of periodical insects can also be used to provide insight into life history evolution where past research has focused largely on insect dormancy. Future studies of insect life histories should turn up more examples of periodical species.

**Acknowledgements**

The following people contributed to the manuscript through discussions or comments on an earlier draft: Malcolm Butler, Steve Chiswell, Maxine Heath, Gene Kritsky, Kauri Mikkola, Tim Paine, Peter Turchin and David Wagner. Jonathan Leonard and Bruce Parker kindly shared their unpublished manuscript. National Science Foundations grants to C.S. provided support for this work. M.J. Spring assisted with illustrations.

**References**

1 Bulmer, M.G. (1977) *Am. Nat.* 111, 1099–1117  
 2 Heliövaara, K. and Väisänen, R. (1987) *Ann. Zool. Fennici* 24, 1–17  
 3 Williams, K. and Simon, C. *Annu. Rev. Entomol.* (in press)  
 4 Whittaker, J.B. (1985) *J. Anim. Ecol.* 54, 311–321  
 5 Heliövaara, K. and Väisänen, R. (1988) *Entomol. Gener.* 14, 37–45  
 6 Stark, R.W. (1959) *Can. J. Zool.* 37, 917–943  
 7 Furniss, R.L. and Carolin, V.M. (1980) *Western Forest Insects*. Miscellaneous Publications No. 1339. US Department of Agriculture Forest Service  
 8 Douwes, P. (1981) *Entomol. Gener.* 6, 151–157

9 Ivanov, A.I., Lukhtanov, V.A., Prasolov, V.N. and Sokolo, V.M. (1987) *Vestn. Leningr. Univ.* 2, 8–12  
 10 Pyle, R.M. (1990) *The Audubon Society Field Guide to North American Butterflies*, Alfred A. Knopf  
 11 Mikkola, K. (1976) *Ann. Entomol. Fennica* 42, 191–199  
 12 Lafontaine, J.D., Mikkola, K. and Kononenko, V.S. (1987) *Entomol. Scand.* 18, 305–331  
 13 Mikkola, K. and Kononenko, V.S. (1989) *Nota Lepid.* 12, 144–152  
 14 Mikkola, K., Lafontaine, J.D. and Kononenko, V.S. (1991) *Entomol. Fennica* 2, 157–173  
 15 Pulliainen, E. and Itämies, J. (1988) *Holarctic. Ecol.* 11, 235–240  
 16 Imby, L. and Palmqvist, G. (1978) *Entomol. Tidskr.* 99, 97–107  
 17 Jónasson, P.M. (1971) in *Dynamics of Populations* (den Boer, P.J. and Gradwell, G.R., eds), pp. 220–332, Pudoc  
 18 Pschorn-Walcher, H. (1970) *Z. Angew. Entomol.* 66, 64–83  
 19 Escherich, K. and Baer, K. (1908) *Naturwiss. Z. Land-Forstwirtschaft.* 6, 510–523  
 20 Metcalf, C.L., Flint, W.P. and Metcalf, R.L. (1951) *Destructive and Useful Insects, Their Habitats and Control*, McGraw-Hill Book Company  
 21 Heliövaara, K. and Väisänen, R. (1984) *J. Biogeogr.* 11, 491–499  
 22 White, J. and Lloyd, M. (1975) *Am. Midl. Nat.* 94, 127–143  
 23 Lloyd, M. and Dybas, H. (1966) *Evolution* 20, 133–149  
 24 Lloyd, M. and Dybas, H. (1966) *Evolution* 20, 466–505  
 25 Lloyd, M. and White, J. (1976) *Evolution* 30, 786–801  
 26 Kritsky, G. (1992) *Proc. Ind. Acad. Sci.* 101, 59–61  
 27 Martin, A. and Simon, C. (1988) *Nature* 336, 237–239  
 28 Martin, A. and Simon, C. (1990) *BioScience* 40, 359–367  
 29 Marlatt, C.L. (1898) *Misc. Results Work Div. Entomol., Bull. U.S.D.A. Div. Entomol.* 18, 52–58  
 30 Danks, H.V. (1992) *Can. Entomol.* 124, 167–187  
 31 Karban, R. (1986) in *The Evolution of Insect Life Cycles* (Taylor, F. and Karban, R., eds), pp. 223–235, Springer-Verlag  
 32 Butler, M.G. and McMillan, A.M. (1990) *Verh. Int. Verein. Limnol.* 24, 438–444  
 33 Butler, M.G. (1982) *Aquatic Insects* 4, 219–235  
 34 Kukal, O. and Kevan, P.G. (1987) *Can. J. Zool.* 65, 156–163  
 35 Lauzon, M. and Harper, P.P. (1986) *Can. J. Zool.* 64, 2038–2045  
 36 Danks, H.V. (1991) *Can. Entomol.* 123, 23–40  
 37 Philippi, T. and Seger, J. (1989) *Trends Ecol. Evol.* 4, 41–44  
 38 Danks, H.V. (1987) *Insect Dormancy: An Ecological Perspective*, (Monograph Series No. 1: Terrestrial Arthropods), Biological Survey of Canada  
 39 Soper, R.S., Delyzer, A.J. and Smith, L.F.R. (1976) *Ann. Ecol. Soc. Am.* 69, 89–95  
 40 Cox, R.T. and Carlton, C.E. (1988) *Am. Midl. Nat.* 120, 183–193  
 41 Leonard, J.G. and Parker, B.L. *Ann. Entomol. Soc. Am.* (in press)  
 42 Heliövaara, K. and Väisänen, R. (1988) *Entomol. Tidskr.* 109, 53–58  
 43 Butler, M.G. and Anderson, D.H. (1990) *J. N. Am. Benthol. Soc.* 9, 180–192  
 44 Sweeney, B.W. and Vannote, R.L. (1982) *Evolution* 36, 810–821  
 45 Kelly, D. (1994) *Trends Ecol. Evol.* 9, 465–470  
 46 Karban, R. (1982) *Ecology* 63, 321–328  
 47 Williams, K.S., Smith, K. and Stephen, F.M. (1993) *Ecology* 74, 1143–1152  
 48 Hanski, I. (1988) *Ann. Zool. Fenn.* 25, 37–53  
 49 Hoppenstaedt, F.C. and Keller, J.B. (1976) *Science* 194: 335–337  
 50 Kettlewell, H.P.D. (1973) *The Evolution of Melanism*. Clarendon Press  
 51 Godfray, H.C. and Hassell, M.P. (1987) *Nature* 327, 144–147  
 52 Heliövaara, K. and Väisänen, R. (1986) *Oikos* 47, 327–334  
 53 Simon, C., Karban, R. and Lloyd, M. (1981) *Ecology* 62, 1525–1535  
 54 White, M. and Lloyd, M. (1979) *Evolution* 33, 1193–1199  
 55 White, J. (1973) *Ecology* 54, 573–586  
 56 Martin, A. and Simon, C. (1990) *Evolution* 44, 1066–1080  
 57 Heliövaara, K., Väisänen, R., Hantula, J., Lokki, J. and Saura, A. (1988) *Hereditas* 109, 29–36  
 58 Väisänen, R. and Heliövaara, K. (1990) *Ann. Zool. Fennici* 27, 29–47  
 59 Simon, M. and Lloyd, M. (1982) *J. N.Y. Entomol. Soc.* 90, 275–301