

The Allee effect in the selection for prime-numbered cycles in periodical cicadas

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Periodical cicadas are well-known for their prime-numbered life cycles (17 and 13 years) and their mass periodical emergences. The origination and persistence of prime-numbered cycles is explained by the hybridization hypothesis on the basis of their lower likelihood of hybridization with other cycles. Recently we showed using an integer-based numerical model that prime-numbered cycles are indeed selected for among 10- to 20-year cycles. We here develop a real-number-based model to investigate the factors affecting the selection of prime-numbered cycles. We include an Allee effect in our model, such that a critical population size is set as an extinction threshold. We compare the real-number models with/without the Allee effect. The results show that in the presence of an Allee effect, prime-numbered life cycles are most likely to persist and to be selected under a wide range of extinction thresholds.

Keywords: Periodical cicada, prime-numbers, the Allee effect, hybridization, extinction thresholds

∕body

Introduction

True periodicity, involving synchronized adult emergences, fixed life cycle lengths, and intervals between emergences with no adults present, is rare among insects(1). The majority of periodical insects have life cycles of two years with geographically separated populations appearing in even and odd years respectively. The most famous periodical insects, the periodical cicadas (*Magicicada* spp.) of eastern North America, have the most extreme periodical life cycles known (1-6). The seven described species of 13- and 17-year periodical cicadas are divided into a complex mosaic of 15 largely parapatric, regional “broods” on different emergence schedules (1-6). An enduring question about these insects is why are there only two life cycles and why are these both prime numbers.

Several authors have proposed a hybridization hypothesis for the evolution of *Magicicada* life cycles that involves “weeding out” all but the long-length prime-numbered cycles from a spectrum of periodical cycles (7, 8). In the various models that have been presented, co-emergences of different life cycles lead to hybridization and production of offspring with altered life cycles that remove them from the mating population and thereby introduce a fitness cost. Thus, brood pairs that are more likely to co-emerge stand a greater chance of decline and extinction. The fact that the two extant *Magicicada* life cycles (13- or 17-years) are prime numbered means that where

broods of different life cycles are adjacent, co-emergences of adults occurs rarely (only once every 221 years). In *Magicicada*, the fitness costs of hybridization may be enhanced by predation; periodical cicadas suffer heavy mortality at low population densities, because they rely on mass numbers and a strategy of “predator satiation” for survival (9, 10). In this paper we examine the relationship between individual fitness and population density (or Allee effect (11-13)) in the evolution of *Magicicada* periodicity

In our previous studies using a simple numerical model of emergence and hybridization in periodical cicadas (14), we show that the cost of hybridization causes prime-numbered cycles to persist longer than other potential life cycles. These earlier models assume implicitly a kind of Allee effect by rounding population sizes downward, which has disproportionately large effects on small populations (14). In this paper, we present a simulation model with an explicit Allee effect in the form of an extinction threshold, or population density below which a brood becomes extinct. We use this model to investigate the potential strength of an Allee effect in the evolution of *Magicicada* periodicity.

Model

We build a deterministic discrete model of population dynamics starting with eleven pure broods of 10-20-year genetically-determined life cycles (14). All population sizes are measured as real numbers with decimals (double precision). We keep track of the population sizes of all broods/hybrids including birth year with juvenile ($N_{i,j}$) and adult stages ($N_{i,A}$). Rates of hybridization among different broods/genotypes are assumed to be proportional to the relative population sizes of co-emerging broods (15).

We apply an Allee effect to periodical cicada population dynamics (8, 11-13) in the following manner. We set a critical population size N_c , below which the population will become extinct immediately. As a control, we set $N_c = 0$ (without the Allee effect). To test the sensitivity of this extinction threshold N_c , we vary the critical population sizes, such that $N_c = 0, 10, 20, \dots, 300$ (step = 10).

In order to avoid any initial advantage to any specific cycle, the starting conditions of our model include identical population sizes for all broods ~~of. Unless specified, at the first year all the initial pure brood sizes /cycle are~~ 1000 first-instar juveniles/larva. We also test the sensitivity of the initial conditions with various equal population sizes and with various unequal population sizes. In all simulations, we explored the population

dynamics of cicadas from eleven pure broods ~~at with cycles ranging from~~ 10-20 yr ~~eyelesears~~.

Results

Selection for prime-numbered cycles appears only under the Allee effect (Fig. 1). With the Allee effect ($N_c = 100$), only a few prime-numbered cycles (17, 13, and 19) survive (Fig. 1a), and their identities depend on the initial model parameters. On the other hand, without the Allee effect (control: $N_c = 0$), the 16-year cycle increases most, but all cycles survive and some increase (Fig. 1b). We also varied the initial population sizes from 1,000 to 11,000 individuals/each cycle. When population sizes are small (<1800 individuals), prime-numbered life cycles are favored; at larger population sizes, non-prime numbered life cycles may also persist.

Parameter sensitivity ~~also analysis~~ shows that survival advantages for the prime-numbered cycles appear under the Allee effect (Fig. 2). The phase planes show the survival cycles at a thousand years for the two parameters: juvenile survival rate S and adult emergence rate E with extinction threshold $N_c = 100$ (Fig. 2a), and 300 (Fig. 2b). Here, all the broods have gone extinct under a combination of low juvenile survival rates and low adult emergence rates, while all survive when these parameters are high. Prime-numbered cycles survive at the boundaries (edge) of extinction; a single cycle at the very edge and two or more far inside with increasing number of survival cycles (Fig. 2). The difference between $N_c = 100$ and 300 is rather quantitative. The phase plane for $N_c = 300$ is more complicated. Among non-prime numbered cycles, only 14-year cycles appear near the edge of extinction (black colors in Fig. 2b). However, no non-prime numbered cycles appear at the edge of extinction when the critical population size, N_c , is set to 100 (Fig. 2a).

Without the Allee effect, we find no strict extinction in the phase plane at 1000 years, because hybrids suffer no costs (Fig. 3). Therefore, we evaluate the growth rate of populations as follows. If the populations at 1000 years are equal or more than 1000 individuals, they are considered “increasing,” while if they are less than 1000, they will be “decreasing.” The positive ~~(or negative)~~ growth is shown in the dark ~~or (light)~~ grey areas, respectively, in Fig. 3, where the total population size is increasing or ~~(decreasing)~~ from the initial 1000 individuals. At the increasing/decreasing boundary, we find an extremely narrow area where only one to three prime-numbered cycles increase, while the rest of the cycles decrease more or less (note that these colors are

コメント [CR1]: Not quite clear what this means....

different from those of Fig. 2, that indicate the survival of only one or two cycles). The increasing/decreasing boundaries are similar among all broods (Fig. 3). Thus the advantage of prime-numbered cycles does not appear when the Allee effect is ~~not at work~~ absent.

The exact tradeoff between juvenile survival rate S and adult emergence rate E is seen in the straight border of extinction (Fig. 3). The overall growth rates of populations are unity along the border. This survival border is extended largely when there is an Allee effect (Fig. 2). The individual phase plains for each cycle with $N_c = 100$ indicates that the survival areas are very large for all the prime-numbered cycles, suggesting the advantage of prime-numbered cycles (Fig. 4).

The advantage of prime-numbered cycles appears as long as there is an Allee effect, irrespective of the extinction thresholds (Fig. 5). We varied the extinction level from 0 (without the Allee effects) and 10, 20, ..., to 300 (step = 10; with the Allee effects). When the emergence rate is low ($E = 0.24$), the survival of only one prime-numbered cycle (either 17 or 19) is seen for $N_c = 20$ -250. When the emergence rate is increased slightly ($E = 0.26, 0.27$), the survival of two to three prime-numbered cycles appear in a wide range of critical population sizes ($N_c = 40$ -300; Figs. 5b and 5c). When the emergence rate is further increased ($E = 0.3$), many cycles ~~survives survive~~ at different levels of N_c (Fig. 5d), ~~but in general, prime-numbered cycles still have an advantage. We still find that the survival of prime-numbered cycles is frequently observed in all the levels of N_c . We also find some irregularity under some conditions (N_c), but general trends point to the advantages of prime-numbered cycles (Fig. 5).~~

Discussion

The hybridization hypothesis (7, 8) must explain two evolutionary processes: (1) the fixation of perfectly synchronous periodical life cycles, and (2) the selection of prime-numbered 17- and 13-year cycles. Our model addresses the processes that select for prime-numbered life cycles, or the second part of the hybridization hypothesis. To address the first part of the hypothesis and to resolve conflicts between this hypothesis and other hypotheses for the evolution of periodical cicada life cycles (5, 6, 16, 18), studies are needed on the genetic and environmental basis of periodicity.

Our results suggest that an extinction threshold Allee effect ~~could~~ facilitates the selection of prime-numbered life cycles. The various parameters in our model seem to

コメント [UC2]: Here or in the discussion, we need to explain why there should be a trade-off between juvenile survival and adult emergence rate. For example, it seems backwards that as adult emergence rate increases, juvenile survival rate decreases. Or have I misinterpreted something? How can you explain this. Higher juvenile survival should mean higher adult emergence.

コメント [CR3]: I agree with Chris' comments- this seems odd. The "Faulty eclosion in suburban backyards" paper suggests that high juvenile survival rate can affect adult success. I paper I have in the works with an undergraduate, however, shows that on a small scale at least, there is little correlation between ... 11

コメント [UC4]: We have to check to make sure all the tenses are consistent. Past tense seems to make most sense. I think I have caught most of the mistakes.

コメント [UC5]: Do you mean, "equally likely"? Otherwise it doesn't make sense. Because the word "most" should only be used when one of the levels is more likely than all the others.

コメント [UC6]: Do you mean, "under all conditions"? Not clear.

コメント [CR7]: I think that this reads slightly odd in present tense—and the methods are in present tense, too. It would all be consistent.

have little effect on the eventual outcome; under a wide range of extinction thresholds, non-prime life cycles are unlikely to persist (Figs. 1-5). In addition, the numerical advantages of prime-numbered cycles only appear when an Allee effect is at work (Fig. 3). These results suggest that the mechanism of prime-number selection is extremely stable under various environmental settings. The exact form of the Allee effect may be unimportant to the general results; this model has an explicit Allee effect, while our previous model had an implicit, ~~but untested~~ Allee effect (14). Both models ~~generated~~ ~~favoring~~ prime-numbered cycles following a process of co-emergence, hybridization, and extinction of non-prime-numbered cycles.

In the current model (~~but not our previous model~~), we assume constant clutch size ~~unlike the previous model~~ (14). This simplification is important to elucidate the mechanisms of the selection process, since the relationships among parameters and the outcomes become straightforward. The important finding is that the areas of survival of prime-numbered cycles only appear when any survival parameter is varied close to the extinction boundary (Fig. 2) and that this phenomenon is directly caused by the Allee effect.

The most unrealistic aspect of our model is that ~~is it~~ presupposes geographic overlap of periodical life cycles; ~~Among the modern-day periodical cicada broods, such life cycle overlap is virtually nonexistent; something that we do not see today~~ (1). In addition, ~~it~~ ~~our model~~ postulates the existence of ~~fixed~~ life cycles with no plasticity. Although periodical cicada life cycles are genetically determined, plasticity has been implicated in allowing periodical cicadas to switch life cycles (6, 16-18), ~~and the phenomenon of off-cycle emergences, or “straggling” is also likely a manifestation of life cycle plasticity.~~ ~~Periodical cicada life cycle plasticity may itself be subject to anything else, the degree of plasticity is subject~~ to evolutionary change (Lloyd and Dybas 1966), and we know little about the genetics ~~of~~ life cycle plasticity; thus there is no simple way to include it in our models.

Another unrealistic aspect of our model is that the extinction threshold is difficult to determine empirically and is modeled as a sharp boundary condition, while in reality, we would expect Allee effects to operate more gradually, such that small population sizes ~~are would be~~ at a higher risk of extinction than larger ones (11-13). Thus we would expect some gradual shift in the probability and intensity of the Allee effect ~~around as~~ ~~the population sizes approached~~ the extinction thresholds, unlike the ~~sharp threshold of~~

コメント [UC8]: Can we add “but untested” (to make the reviewer happy).

コメント [CR9]: Maybe for this cite some of these papers? These deal with same-cycle straggling fairly explicitly:
Dybas, H. S. 1969. The 17-year cicada: A four year mistake? Field Mus. Nat. Hist. Bull. 40:10-12.
Kritsky, G., and S. Simon. 1996. The unexpected 1995 emergence of periodical cicadas (Homoptera: Cicadidae: Magicicada spp.) in Ohio. Ohio J. Sci. 96:27-28.
Marshall, D. C. 2001. Periodical cicada (Homoptera: Cicadidae) life-cycle variations, the historical emergence record, and the geographic stability of brood distributions. Ann. Entomol. Soc. Am. 94:386-399.
White, J., and M. Lloyd. 1979. 17-Year Cicadas Emerging After 18 Years: A New Brood? Evolution 33:1193-1199.
Zyla, J. D. 2004. Reports of four year accelerated occurrences of the 2004 emergence of periodical cicadas, Magicicada spp. (Hemiptera: Cicadidae) Brood X in Maryland, Virginia, and the District of Columbia. Proc. Entomol. Soc. ... 21

コメント [CR10]: This paper: Lloyd, M., and H. S. Dybas. 1966. The periodical cicada problem. II. Evolution. Evolution 20:466-505.
Not the other one. We also elaborate on this in Marshall and Cooley 2000 (Evolution paper) and Cooley et al. 2001 (Molecular Ecology paper)

[the](#) current model. The Allee effect in our previous “round-down” integer model is more gradual (14). The round-down integer model produces relatively simple survival patterns (Fig. 2 in 14), while the current model produces much more complicated patterns (Figs. 2 and 3). Yet the general results of both models are the same: Allee effects resulting from predator satiation seem to favor prime-numbered life cycles. A numerical demonstration that Allee effects can promote the maintenance of long, prime-numbered periodical life cycles confirms our earlier, intuitive understanding of how periodical life cycles are shaped by the interactions of predators and population densities (3, 5, 7-10).

Model Specifications

The model consists of two key parameters: juvenile survival rate S and adult emergence rate E . We assume that juvenile survival (mortality) rate $S(1-S)$ per year is constant ($0 < S < 1$). Successful adult emergence rate $E(0 < E < 1)$ is kept constant, assuming emergence failure is independent of life cycle length. To make the model simple, the clutch size C is also set to be constant ($C = 25$). For simplicity, we assume that the life cycle follows a single-locus Mendelian inheritance system with shorter cycle dominance, such that genotype $[i, j]$ corresponds to phenotype i (years) if $i < j$. We do not know the genetic system of periodical cicadas, but note that the current simulation model is fairly neutral to what kind of genetic system we employ. For genotype $[i, j]$ of a given birth year, the juvenile population size of a brood at time t ($N_{i,t}$) follows the equation:

$$N_{i,t}(i, j) = S \times N_{i,t-1}(i, j) \quad (1)$$

Adult brood size $N_{A,t}$ (only appear in emergence year) is

$$N_{A,t}(i, j) = E \times N_{i,t}(i, j) \quad (2)$$

The offspring (juvenile) brood size between $[i, j]$ and $[m, n]$ is:

$$\text{Num. offspring} := \frac{1}{2} N_{A,t}(i, j) \times F(N_{A,t}(m, n)) \times C \quad (3)$$

where F is the frequency of the target brood, such that

$$F(N_A(m, n)) = \frac{N_A(m, n)}{\sum N_A}$$

where $\sum N_A$ is the sum of the population sizes of all co-emergent adults for a given year. The genotypes of hybrid offspring between broods $[i, j]$ and $[m, n]$ include four possibilities: $[i, m]$, $[i, n]$, $[j, m]$ and $[j, n]$. Thus, the offspring brood size of each genotype is determined for the sum of eq. (3). For example, the offspring brood size of genotype $[i, m]$ follows:

$$N_{i, i}(i, m) = \sum_x \sum_z \left\{ \frac{1}{2} N_{A, i}(i, x) \times F(N_{A, i}(m, z)) \times C \right\} \quad (4)$$

The other genotypes are handled in similar fashion.

Acknowledgments

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Figure legends

Fig. 1. Temporal dynamics of periodical cicadas starting with 11 pure broods at 10-20 year cycles. (a) The real-number model with the Allee effect (the extinction threshold: $N_c = 100$). All but 13-, 17-, and 19-year cycles are extinct at an early stage. The order of population sizes at the end (100 years) is: $17 > 13 > 19$. (b) Control: the real-number model without the Allee effect (critical population size, $N_c = 0$). Parameters are $S = 0.95$ and $E = 0.5$. All survive till the end (100 years), and the order of population sizes is $16 > 15 > 18 > 17 > 19 > 14 > 20 > 13 > 12 > 11 > 10$.

Fig. 2. Phase planes of thousand-year survivals for juvenile survival rate S and adult emergence rate E among 11 pure broods of 10-20 year cycles with the Allee effect. The extinction thresholds are set as: (a) $N_c = 100$, (b) $N_c = 300$. One or two cycles only (color number shown), three or more cycles (grey) and all extinction (white) are shown. The various cycles (grey) means includes hybrids.

Fig. 3. Phase planes of population sizes (relative to the initial population sizes) at-of thousand-year for survivals for juvenile survival rates S and adult emergence rate E among 11 pure broods of 10-20 year cycles without the Allee effect (control; $N_c = 0$). The population sizes are categorized as increasing or decreasing, compared with the corresponding initial population sizes ($N_0 = 1000$). The populations are shown as: three or more cycles increasing (dark grey); shown prime numbers only increasing, while the rest decreasing (colored); and all decreasing (light grey).

Fig. 4. Individual phase planes of thousand-year survivals (Fig. 2a) for each of 11 pure broods of 10-20 year cycles (numbers shown) with the Allee effect. The extinction thresholds are set as: $N_c = 100$. The two parameters are juvenile survival rates S (y-axis: range=0.91-0.97) and adult emergence rate E (x-axis: range: 0.13-0.35). The survival areas are larger in 13- and 17-year cycles, followed by 11- and 19-year cycles. Those of non prime-numbered cycles are all smaller.

Fig. 5. Surviving cycles among 11 pure broods at 10-20 year cycles along the with different levels of the Allee effect, where the extinction threshold is varied, such that N_c

コメント [UC11]: Must be consistent with previous figure caption.

コメント [CR12]: Unclear what this means....

$= 0$ (no Allee effect), 10, 20, ..., 300 (step = 10). The grey cells are surviving cycles. (a) $E = 0.24$, (b) $E = 0.26$, (c) $E = 0.27$ and (d) $E = 0.3$. Other parameters are $S = 0.944$, and $C = 25$. (a-d) correspond with the points along line $S = 0.944$ in the phase plane of Fig. 2(a).

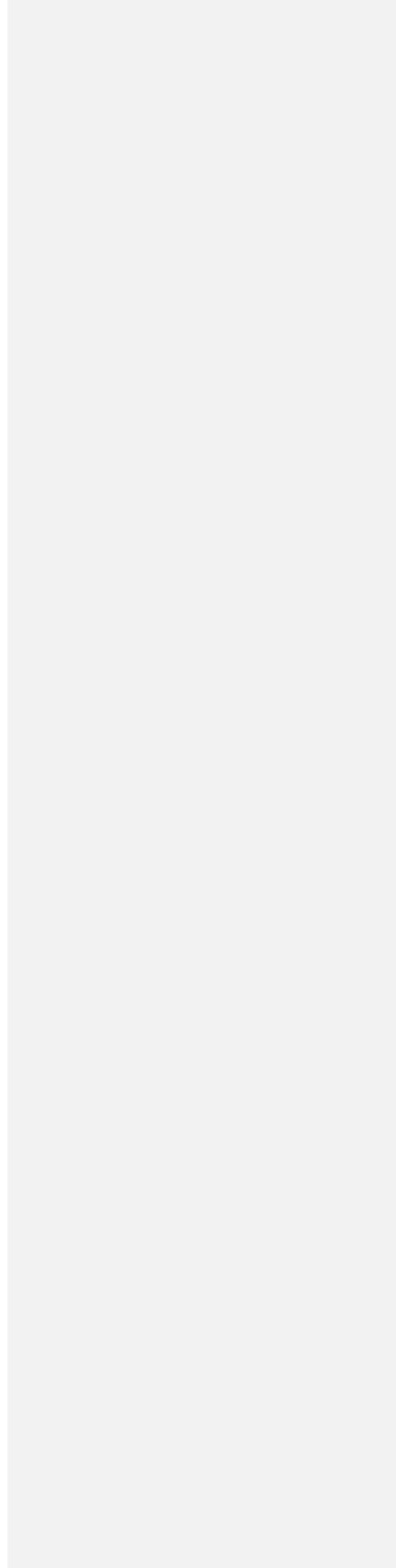
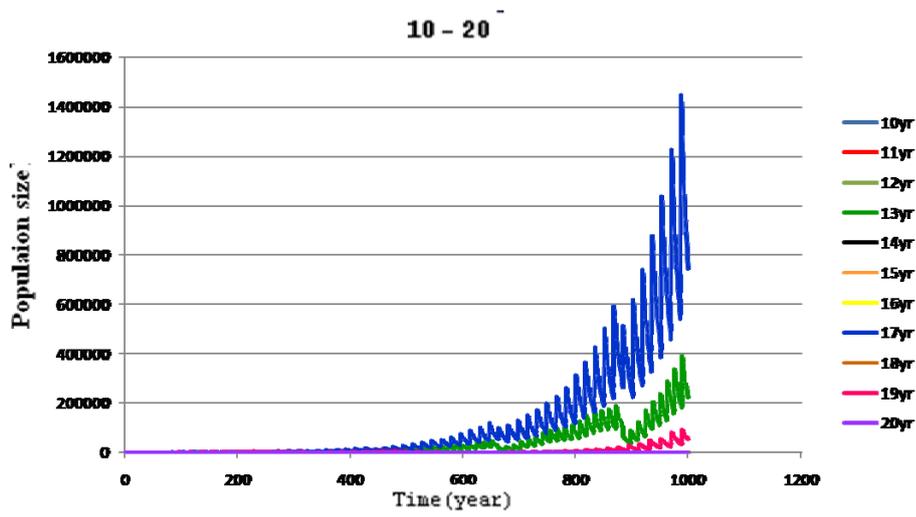


Fig.1

(a)



(b)

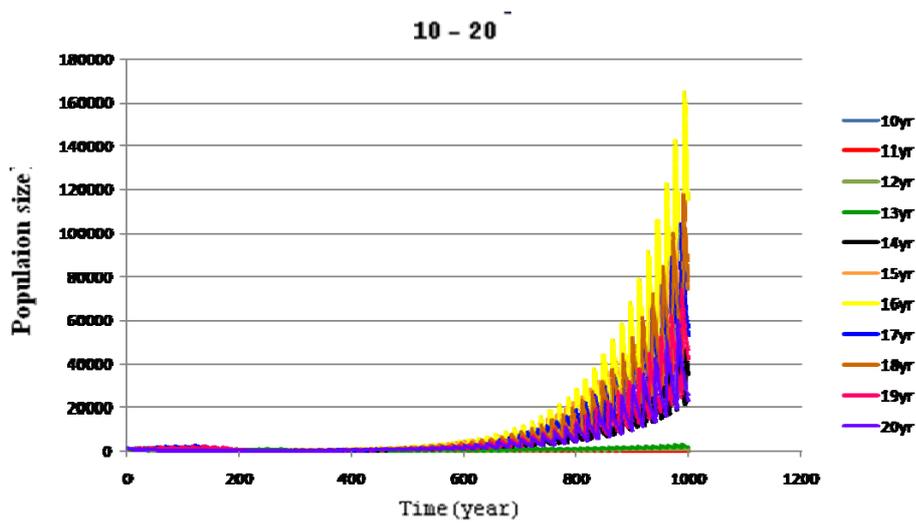


Fig.2
(a)

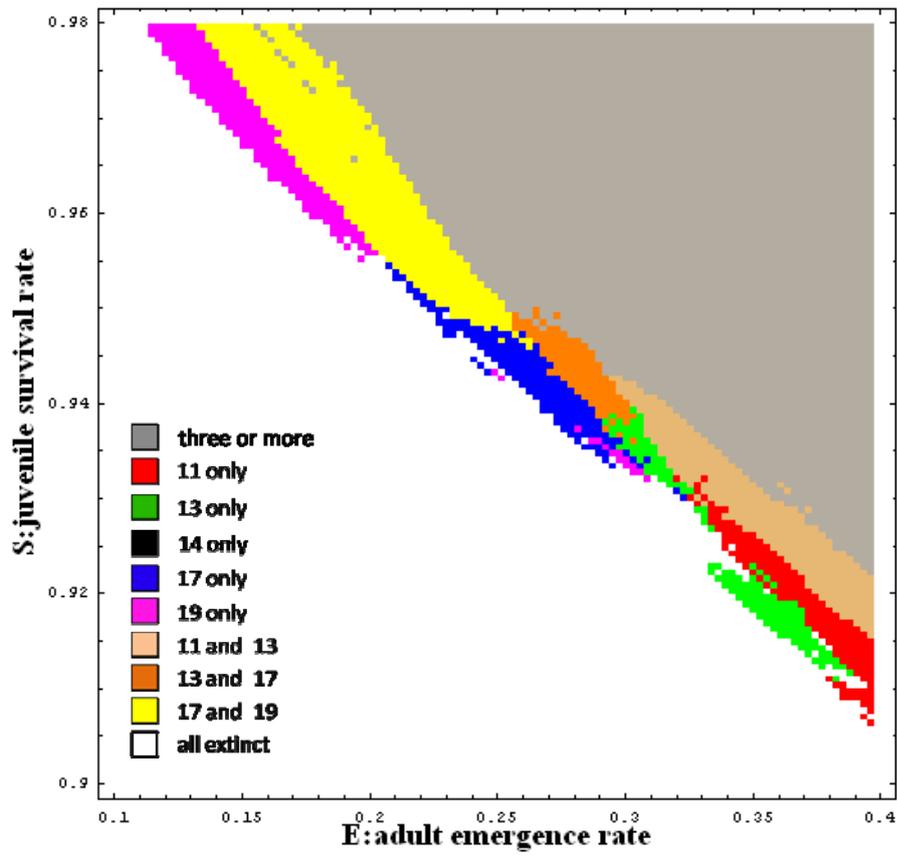


Fig. 2

(b)

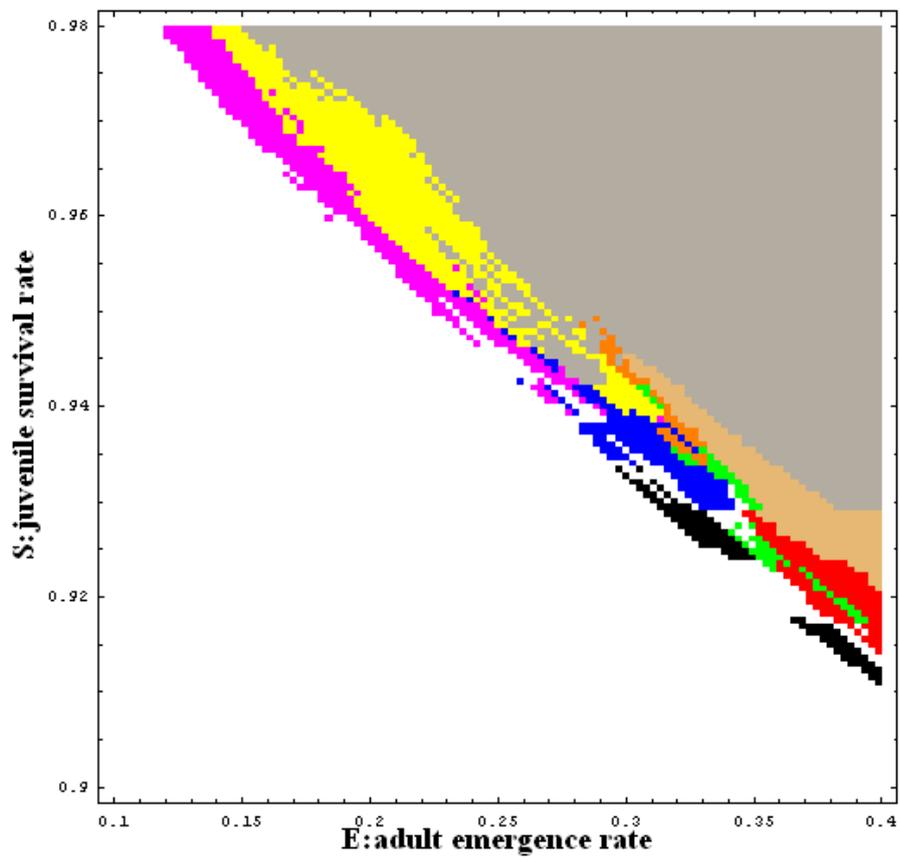


Fig. 3.

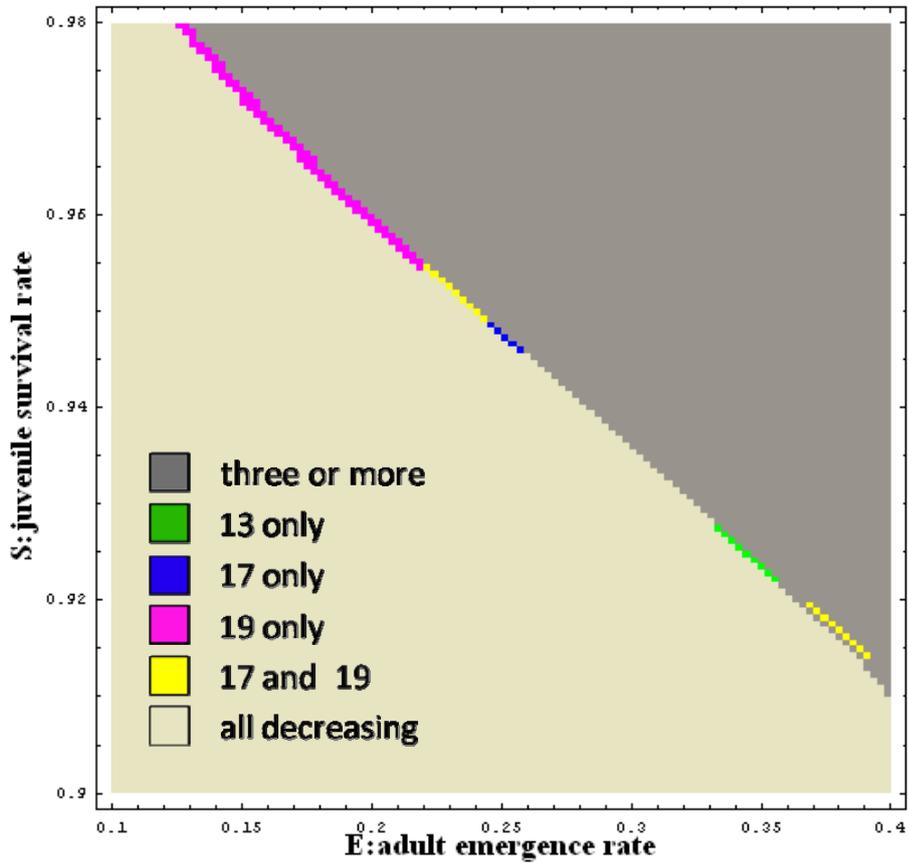


Fig. 4 10-20-year cycles

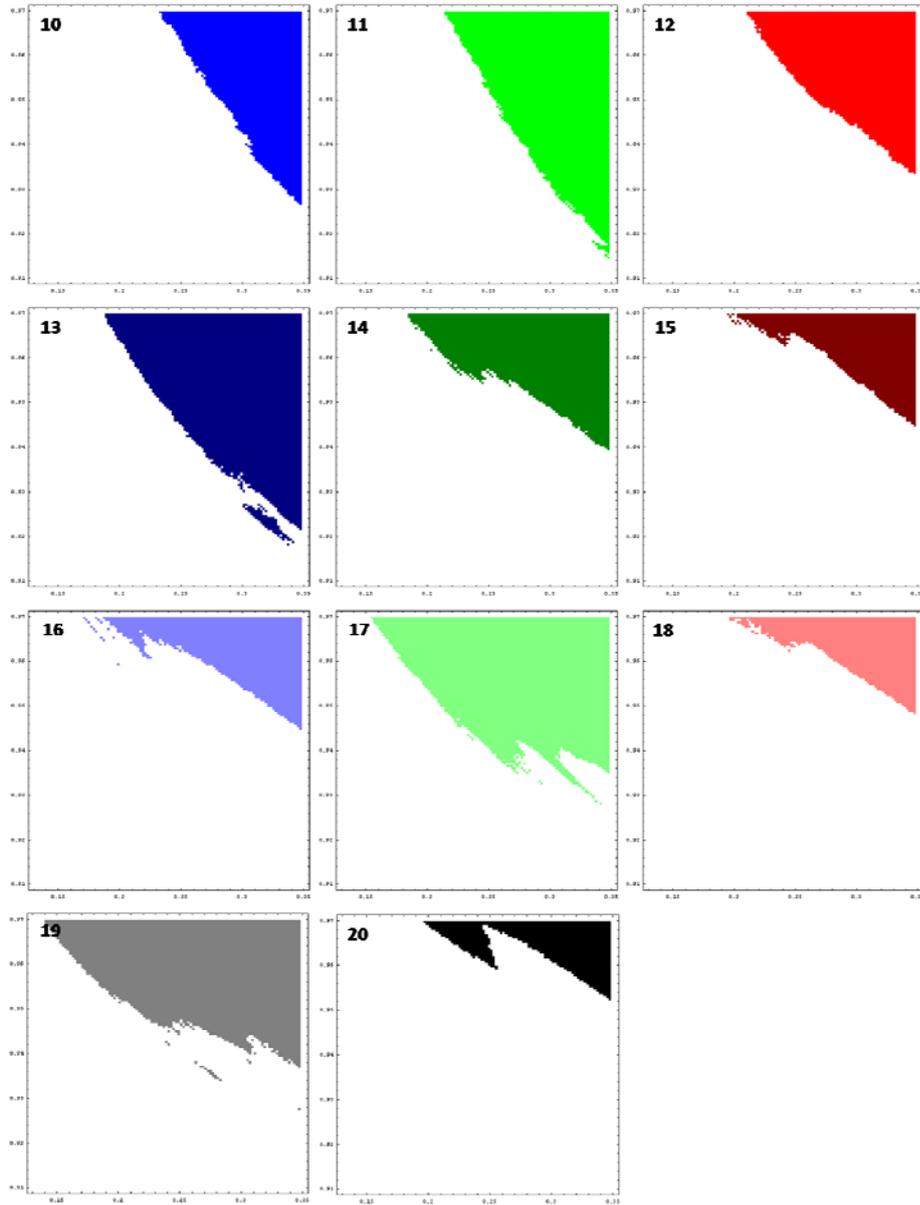
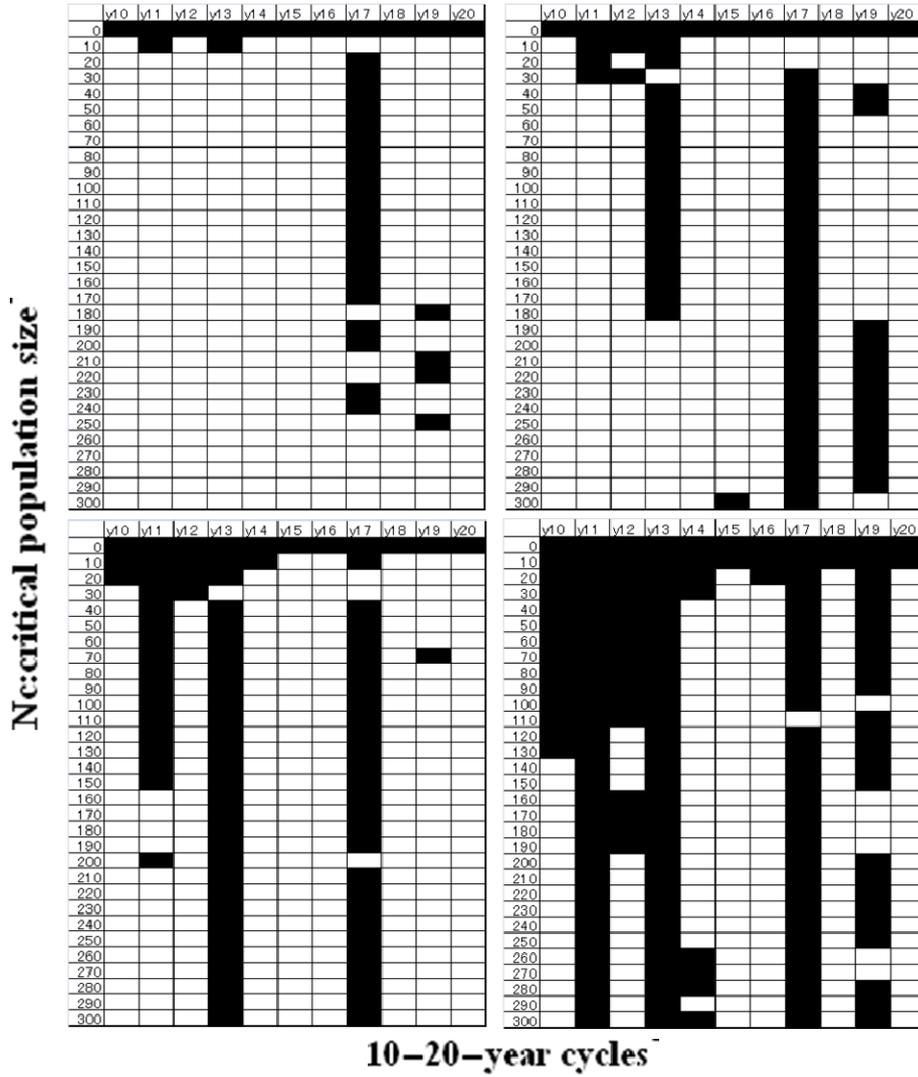


Fig. 5



I agree with Chris' comments- this seems odd. The "Faulty eclosion in suburban backyards" paper suggests that high juvenile survival rate can affect adult success. I paper I have in the works with an undergraduate, however, shows that on a small scale at least, there is little correlation between egg nest density and the density of nymphs immediately below the egg nests.

Maybe for this cite some of these papers? These deal with same-cycle straggling fairly explicitly:

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White, J., and M. Lloyd. 1979. 17-Year Cicadas Emerging After 18 Years: A New Brood? *Evolution* 33:1193-1199.

Zyla, J. D. 2004. Reports of four year accelerated occurrences of the 2004 emergence of periodical cicadas, *Magicicada* spp. (Hemiptera: Cicadidae) Brood X in Maryland, Virginia, and the District of Columbia. *Proc. Entomol. Soc. Wash.* 106:488-490.

and these deal with the general problem--

Alexander, R. D., and T. E. Moore. 1962. The evolutionary relationships of 17-year and 13-year cicadas, and three new species. (Homoptera: Cicadidae, *Magicicada*). University of Michigan Museum of Zoology Miscellaneous Publication 121:1-59.

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