Periodical Cicadas

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Background:
What is a cicada?

- An loud insect
- Periodic lifespan of 13 or 17 years
- Spends 17 years in immature stage
- Emerge synchronously (usually within 1 day, at night)
- Live as adults for 3-6 weeks to reproduce and die
- Density as high as 1 million insects/acre

Background:
Definitions

- Brood: Populations that emerge in the same year and at the same location
- Age Class: Same species and location, but different ages
- Nymph: Immature form of cicada
- Massopora: Mold spores that create infertility in adult cicadas

Background:
What is a cicada?

- Adults lay between 400-600 eggs
- Do not sting, bite or blend
- Eaten by birds
- Made infertile by Massospora
- A single male’s courtship call can reach 90 dB - equivalent to a noisy truck on the road or a kitchen blender.

Background:
What is a cicada?

- Nymphs eaten by moles, ants
- During first 2 years, settle at shallow roots then burrow deeper underground
- Competition for space and food most prominent during these first 2 years

Other Models

- Hoppensteadt-Keller (1976): First model but does allows for several age classes in a given region
- Bulmer (1977): Leslie Matrix Model. Not modeled for the particular biology of the cicada

Model Logic

- Nymphs settle on shallow roots during first 2 year before moving deeper
- Capacity limitation only at shallow roots
- Survival probability after first 2 years ~1 (required if larger periods are desired)
- Predation on cicadas is approximately constant (predation independent of density, predator saturation)

Parameters

- β-survival probability of years near deep roots
- α-yearly survival rate near shallow roots
- R-predator relaxation factor
- f-number of viable eggs per adult
- P-Predation intensity
- K-Underground carrying capacity
- A-predator growth due to cicadas
- L-period

The Model: Deterministic

Number of nymphs in year n:

$$x_n = \min(f\alpha^2(\beta^{L-2}x_{n-L} - P - Ah(\beta^{L-2}x_{n-L}, M_{n-3}))_+, K_n)$$

Carrying capacity:

$$K_n = (K - \sum_{l=1}^{L-3} x_{n-l}\beta^l)_+$$

The Model: Deterministic

Massospora density in year n:

$$M_n = RM_{n-1} + Bh(\beta^{L-3} x_{n-L+2}, M_{n-1})$$

Cicada - Massospora interaction:

$$h(x, M) = \frac{xM}{1 + CM}$$

Massospora density M_n=0 for the remainder of the talk

The Model: Deterministic

Number of nymphs in year n:

$$x_n = \min(f\alpha^2(\beta^{L-2}x_{n-L} - P)_+, K_n)$$

Carrying capacity:

$$K_n = (K - \sum_{l=1}^{L-3} x_{n-l}\beta^l)_+$$

Parameters

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$$0.97 \le \beta \le 1$$

$$0.1 \le \alpha^2 \le 0.2$$

$$0.8 \le R < 1$$

$$30 \le f \le 40$$

$$0.05 \le \frac{P}{K} \le 0.25$$

$$0 \le \frac{Ah}{K} \le 0.1$$

The Model: Deterministic

$$P^* = \alpha^2 f P/(f\alpha^2\beta^{L-2} - 1)$$

- P^* is an unstable fixed point ($0<x_n<P^*$ implies $x_{n+kL}=0$ for $k>k_0$)
- For strictly larger than P^*, solutions strictly grow until they are limited by the carrying capacity
- Need β close to 1
- $K(1- \beta^{L/2}) < P^*$

Theorem

- *In the basic deterministic model with constant predation P, M_n=0 and β approximately 1, any sequence (x_n) converges to a unique stable distribution $(\bar{x}_n)_{r=1}^{L}$. This is uniquely determined by limiting generation pattern $\mathrm{I}=\{r_1,..,r_k\}$ with $1 \le r_1 < r_2 < .. < r_k \le L$.*
- *If $r_{i0+1}-r_{i0} \ge 3$ for some r_{i0} then $r_{i+1}-r_i \ge 3$*
- *If $r_{i0+2}-r_{i0}=2$ for some r_{i0} then $\mathrm{I}=\{1, 2, \ldots, L\}$*

Theorem Conclusions

- Once a generation gap has evolved, more gaps will arise
- Long time before limiting generation pattern attained
- Approaches equilibrium quickly

Theorem

$$\overline{P}* = \underline{\alpha}^2 f \overline{P} / (f \underline{\alpha}^2 \beta^{L-2} - 1)$$

- Let predation P and yearly survival rate α^2 be stochastic, non-zero random variables.
- Then (x_n) converges to limiting sequence $(\widetilde{x_n})_{r=1}^{L}$, uniquely determined by limiting generation pattern, I. I must be feasible in $\widetilde{P*}$, instead of P*. All solutions will be synchronous if $\overline{P}* > K(\beta^{L/2} + 1)^{-1}$

Theorem Conclusion

- The stochastic model behaves just as the deterministic one
- Let's just use the deterministic one

Conclusions

- Let Q=|I| be the number of occupied age classes within each L-cycle.
- If P=.15, $\alpha^2 f$=3.5, then Q is limited to 4
- If P=.2, $\alpha^2 f$=3.5, then Q is limited to 2
- Weather and floods, which can eliminate age classes closer to the surface, can make Q smaller
- It is possible that smaller Q's increased length of L

Conclusions

- Large β, around .98, necessary for larger L and smaller Q values.
- H-K would not favor larger L
- Only possible with low mortality in later life
- Why are periods both prime numbers?

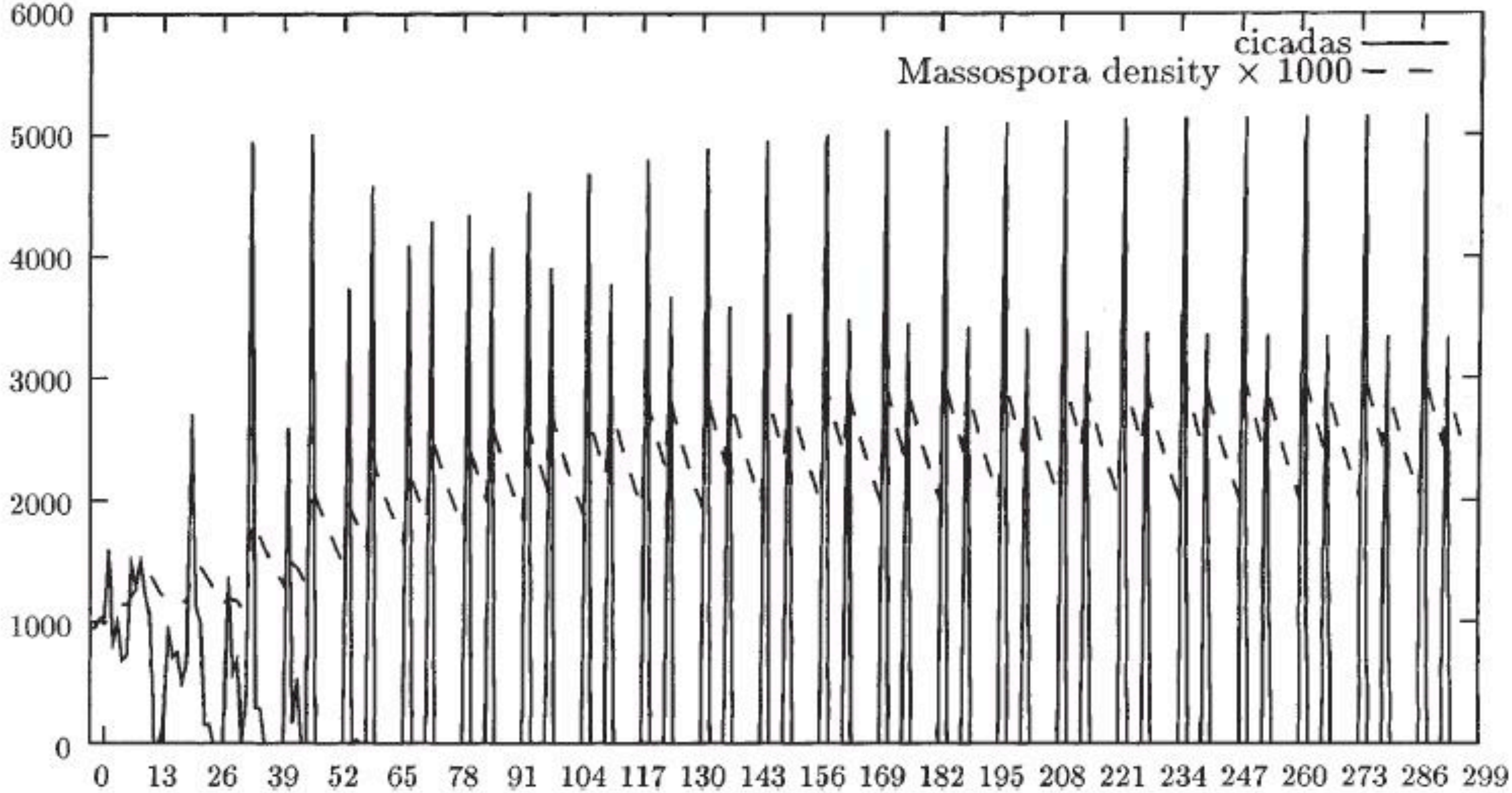

Fig. 1. Convergence in the cicada-Massospora model with constant predation and randomly chosen initial data. The parameters are $L = 13$, $\alpha^2 = .1$, $\beta = .98$, $f = 40$, $K = 10,000$, $P = .05 \cdot K$, $A = .05$, $\alpha = 4 \cdot 10^{-4}$, $R = .95$, $B = 10^{-4}$.

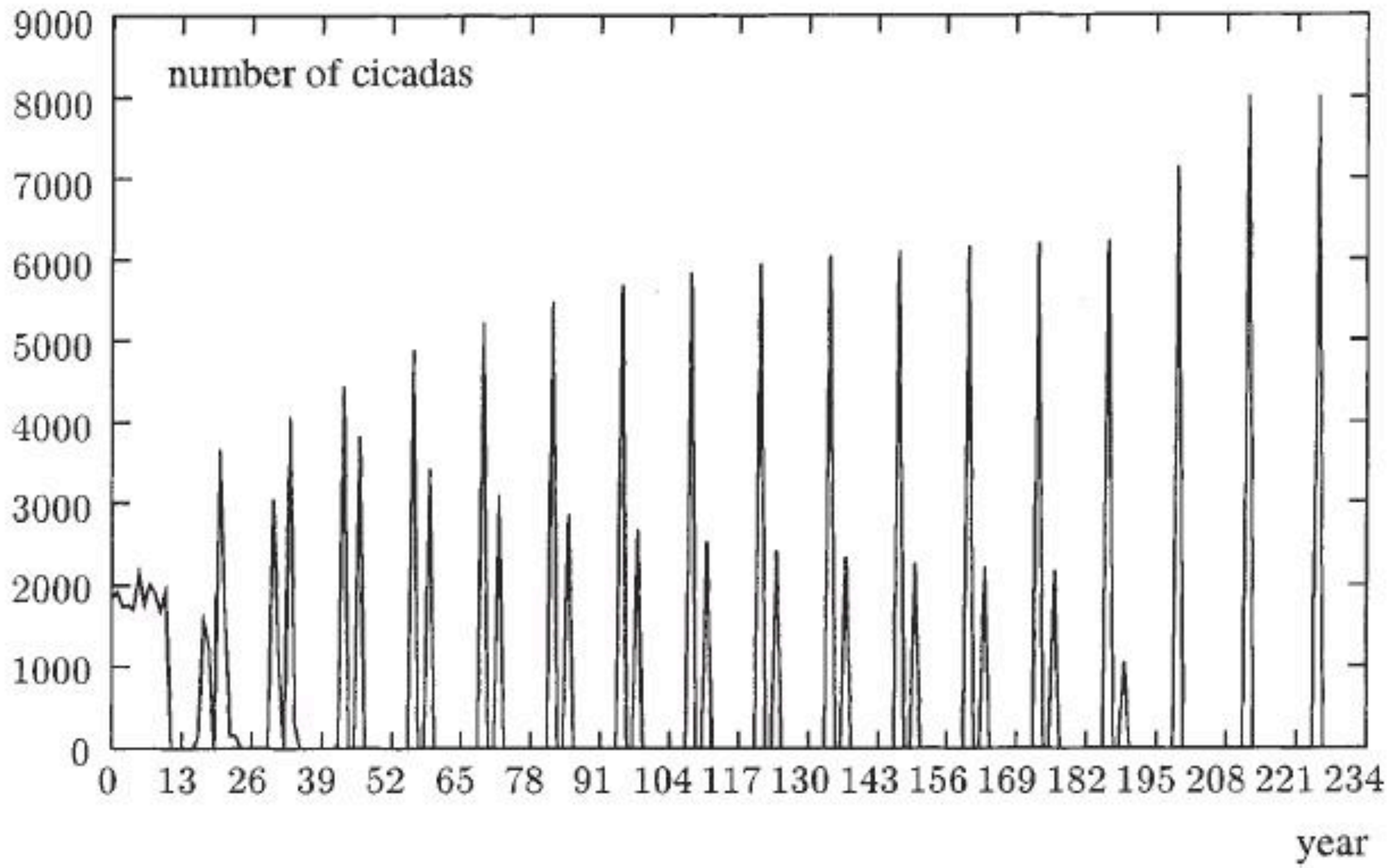

Fig. 2. The basic model with stochastically varying parameters. The solution eventually becomes synchronous. The parameters are $L = 13$, $\underline{\alpha}_1^2 = .08$, $\overline{\alpha}_1^2 = .2$, $f = 40$, $\underline{P} = 300$, $\overline{P} = 2000$, $K = 10000$.

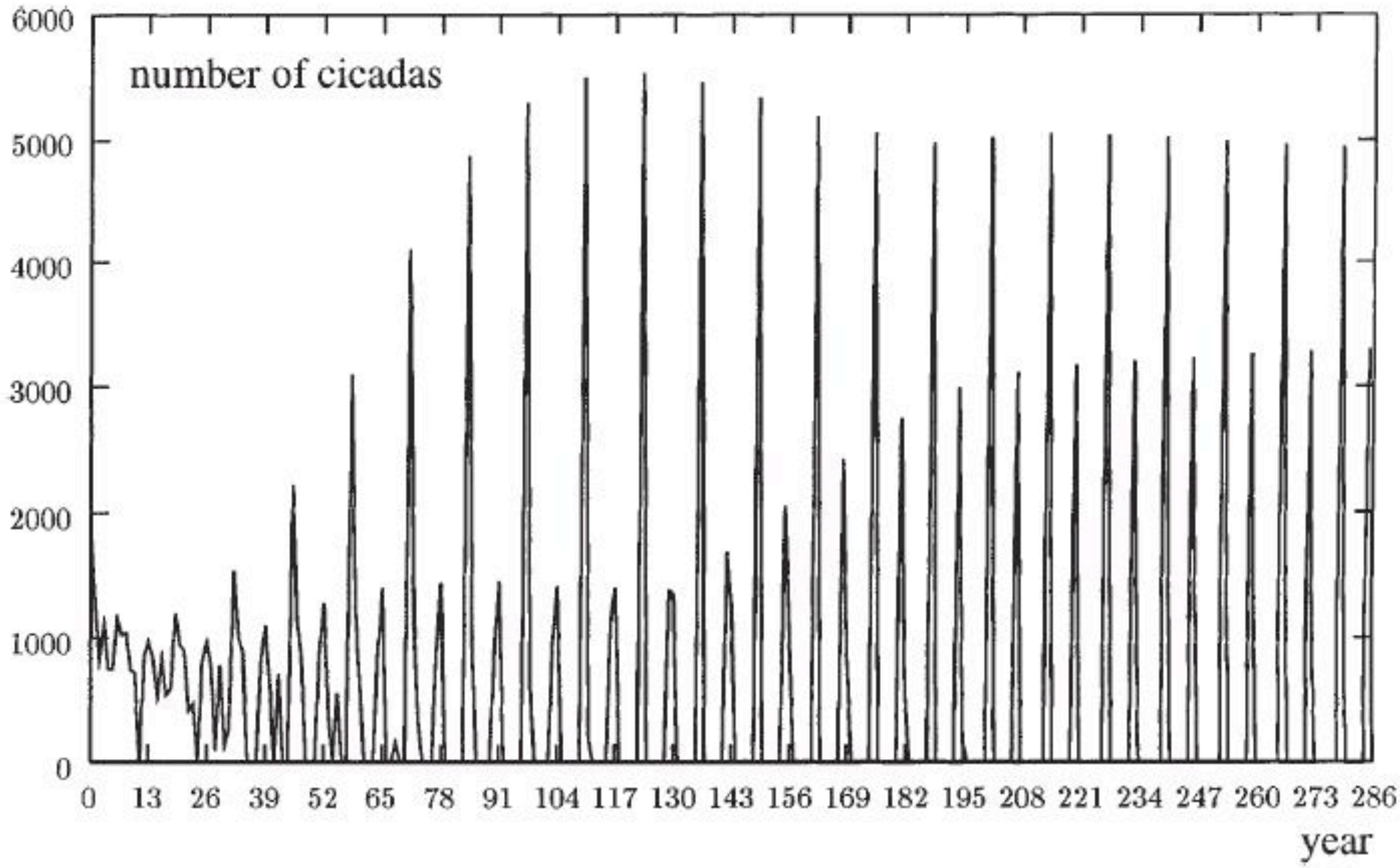

Fig. 3. A logistic type model with randomly chosen initial data. The parameters are $L = 13$, $\alpha^2 = .1$, $\beta = .98$, $f = 40$, $P = .05 \cdot K$, $\gamma = .8$, $\delta_2 = 10^{-6}$

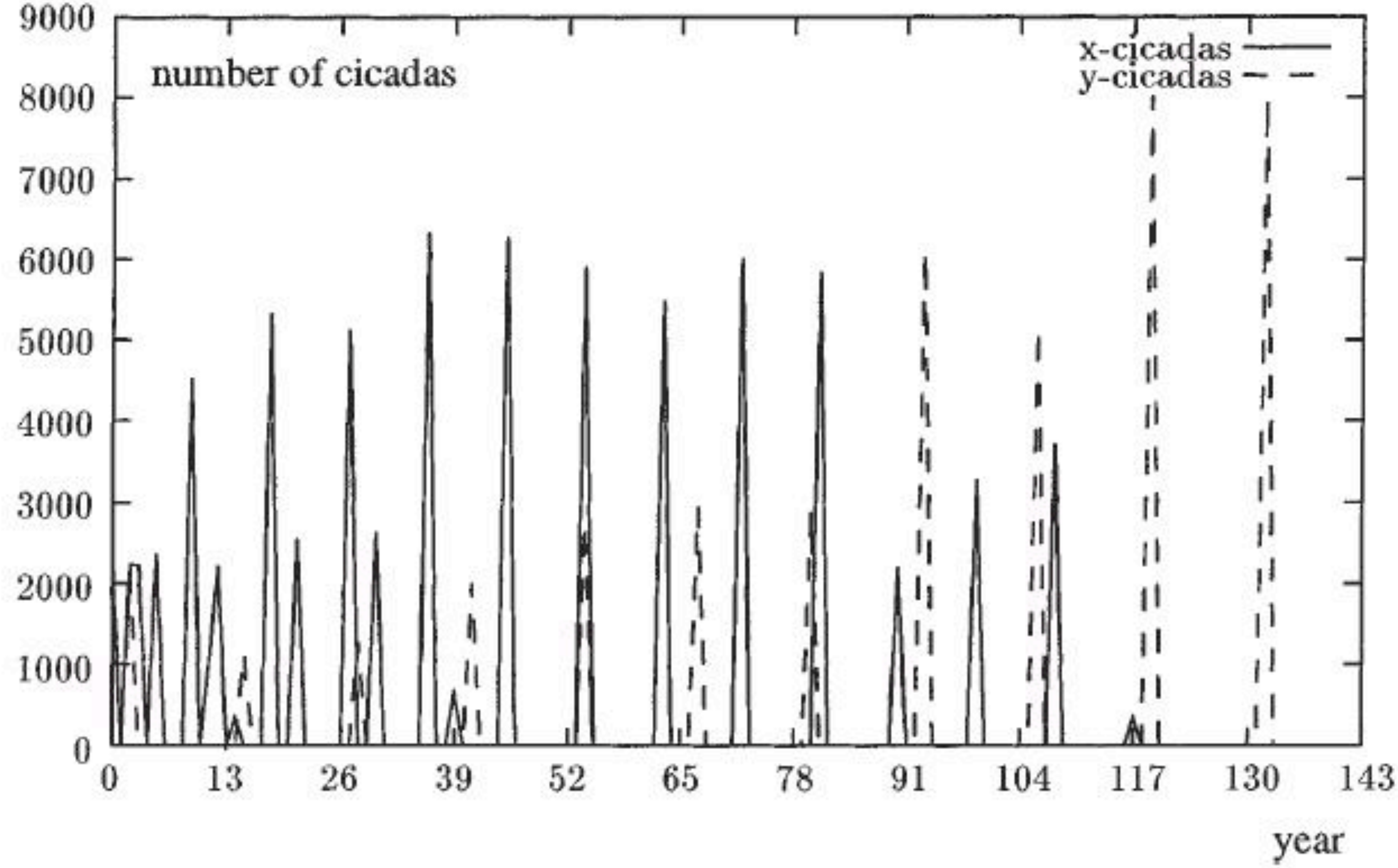

Fig. 4. Evolution in the two-species model, when one year class shifts its period

References

- Behncke, Horst. "Periodical Cicadas." JOURNAL OF MATHEMATICAL BIOLOGY. 40 (2007): 413-431. Web of Science
- Lake County Forest Preserves. “Cicada Mania.” http://www.lcfpd.org/html_lc/cicadas/sounds.html