RESEARCH ARTICLE

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Prey population cycles are stable in an evolutionary model if and only if their periods are prime

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ABSTRACT We present an evolutionary model that marks an encounter of two seemingly unrelated disciplines: population dynamics and number theory. Assuming mutations and selection of predators and prey, we show that prey cycles with non-prime lengths are unstable, while cycles with prime lenghts are stable. Allowing arbitrarily long cycles, this model is a number-theoretical tool for the calculation of large prime numbers. An extension of this purely temporal process to an evolutionary game on a spatial array leads to homogeneity, or to travelling or spiral waves having a predominance of prime prey cycle lengths. These results may be related to the appearance of cicadas (genus Magicicadae) every 13 or 17 years.

KEYWORDS: predator-prey model, cellular automata, evolutionary game, periodical cicadas.

SPATIALLY HOMOGENEOUS EVOLUTION

Definitions and assumptions

We consider populations that spend periodically a fixed number of years as larvae or dormant in one environment, and appear in another environment during a short time for reproduction. (Examples are given in Ref 1 and Ref 2). We assume a predator with period X and a prey with period Y. As shown schematically in Fig 1, we assign a momentary fitness $\phi_y(t)$ of the prey in the year t as follows: it is zero if the prey is not present, it is - 1 if both predators and prey are present, and it is + 1 if the prey is present but the predators are not. The momentary predator fitness $\phi_x(t)$ is defined analogously as for the prey, but with opposite signs (see Fig 1). The fitness F_x, resp F_y, is defined by the sum over the $\phi_x(t)$, resp $\phi_y(t)$, $t = 0, ..., XY$, divided by the number of predator, resp prey, generations. (Note that this yields an average valid for $t \to \infty$, since the process is periodic with period XY). We divide by the number of generations in order to avoid selection by virtue of the capability of frequent proliferation; we assume that each generation uses up metabolic resources (eg due to metamorphosis, mating and death), and these expenses should be minimized in the long run. Thus, our model favours infrequent emergences of the prey, as long as they are safe when they do appear. A similar reasoning applies to the predator: our model favours infrequent appearances as long as they get nourishment when they appear. Note that these assumptions do not cause divergence of the prey cycle lengths to infinity (corresponding to extinction), because these cycle lengths actually get locked into a prime number - as we will show below - bringing evolution to a stop.

We compare a prey mutating to a cycle Y' with the resident prey (cycle length Y) at constant X. Analogously, we compare mutant cycles X' with resident cycles X at constant Y. A mutant prey (resp predator) substitutes the resident if and only if $F'_y > F_y$, resp $F'_x > F_x$. Thus, in the case of fitness equality, the resident is selected. We assume that all interacting populations are synchronized, thus being all present at $t = 0$. We only allow mutations that lead to cycles obeying $1 < X < Y$ (condition K); this condition means that all cycles remain above the main diagonal $Y = X$ on the X - Y - plane.

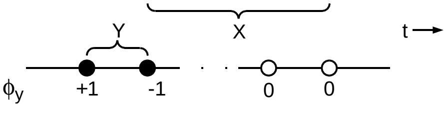

Fig 1. Scheme of the definitions of the momentary prey fitness ϕ_y and predator fitness ϕ_x (+1, -1 or 0). X: period of the predator. Y: period of the prey. A circle on the horizontal lines indicates appearance. A black circle indicates appearance of prey and predator (ϕ_y = -1, ϕ_x = +1), of predator without prey (ϕ_x = -1) or of prey without predator (ϕ_y = +1).

PROPOSITION

If Y is not a prime then there exists a sequence of mutations that will change Y ; if Y is prime then no mutation will change it.

INSTABILITY OF NON-PRIME PREY-CYCLES

Let $lcm(X, Y)$: least common multiple, $gcd(X, Y)$: greatest common divisor of X and Y . In XY years, the predator appears Y times, both predator and prey appear $XY/lcm(X, Y)$ times, thus predators without prey appear $Y - XY/lcm(X, Y)$ times. Since $gcd(X, Y)\ lcm(X, Y) = XY$, we thus obtain the predator fitness $F_x(X, Y) = 2gcd(X, Y)/Y - 1$. Analogously, we obtain the prey fitness $F_y(X, Y) = 1 - 2gcd(X, Y)/X$.

Let us assume that $Y = Y_N$ is not a prime; $F_x(X, Y_N)$ has its maximum value $2gcd(X_M, Y_N)/Y_N - 1$ at the predator period $X_M = gd(Y_N)$ ($gd(a)$: greatest divisor of a, excluding a). A sequence of random mutations keeping $Y = Y_N$ constant will eventually lead to X_M. However, (X_M, Y_N) is abandoned if mutations lead to $(X_M, Y_N \pm 1)$. In fact, $gcd(X_M, Y_N) = X_M$, implying that $F_y(X_M, Y_N) = -1$; $gcd(X_M, Y_N \pm 1)$ cannot be equal to X_M (the reason is: $(Y_N \pm 1)/X_M = Y_N/X_M \pm 1/X_M$, the first term being an integer, but the second not, so that X_M is not a divisor of $Y_N \pm 1$) and $gcd(X_M, Y_N \pm 1)$ can not be larger than X_M; thus $gcd(X_M, Y_N \pm 1) < X_M$; this implies that $F_y(X_M, Y_N \pm 1) > 1 = F_y(X_M, Y_N)$. Thus, we have shown that there exists a sequence of mutations such that prey with a non-prime cycle $Y = Y_N$ are extinguished. (Note: (X_M, Y_N) may also be abandoned by mutations larger than $Y_N \pm 1$).

STABILITY OF PRIME PREY CYCLES

Assume that Y is a prime Y_P; by virtue of condition K, any X is relatively prime to Y_P; therefore $gcd(X, Y_P) = 1$, so that starting from (X, Y_P), there exist no predator mutants that are fitter than a resident predator. On the other hand, for any X, $gcd(X, Y') \geq 1$, where Y' is a prey mutant, as compared to $gcd(X, Y_P) = 1$, so that $F_y(X, Y') \geq F_y(X, Y_P)$, ie no prey mutant is fitter than a resident. In conclusion, any initial random choice of (X, Y) and mutations fulfilling condition K will lead and lock to a prime Y after a sufficiently large number of mutations.

Note that we cannot loosen condition K because the points $(jY_P ; Y_P)$, where Y_P is prime and $j \in \mathbb{N}$, are unstable with respect to prey mutations. In fact: $gcd(jY_P, Y_P) = Y_P$, while $gcd(jY_P, Y_P - k)$ with $k \in \mathbb{N}$ cannot be larger than $Y_P - k$; thus $F_y(jY_P, Y_P) < F_y(jY_P, Y_P - k)$. This means that convergence to prey with period Y_P is not possible if mutations to the points (jY_P, Y_P) are permitted. These points are avoided by the restriction to K.

GENERATION OF VERY LARGE PRIMES

We will now use the predator-prey mechanism described above, not as a biological model, but for a numerical purpose, namely to obtain very large prime numbers. For this, we allow mutations with unbiologically large cycle changes. As an example, we considered mutations of size 10^n, where n is a random number, homogeneously distributed between 0 and 5; the result is shown in Fig 2, starting at $X = 4$ and $Y = 12$ and leading to the Euler prime $Y = E$ given in the figure caption. For mimicking this evolution process, we assumed that mutation and selection of X alternate in successive time steps with mutation and selection of Y.

SPATIALLY INHOMOGENEOUS EVOLUTION

The model

We now consider competition between neighbouring residents in a spatially extended system, instead of competition between mutants and residents. We use a cellular automaton (CA), the neighbourhoods being defined as given in Fig 3a. CA are useful tools for simulations of natural phenomena in space and time (see Refs 3-5 and references therein). The CA here evolves in a two-dimensional habitat, as follows. In each updating of the CA, the predator and the prey of each cell are replaced by the fittest among the neighbours $C_i (i = 0, 1, ...8)$. The neighbourhood of a cell C_0 is defined by the cell itself and the 8 cells around it. The momentary fitness

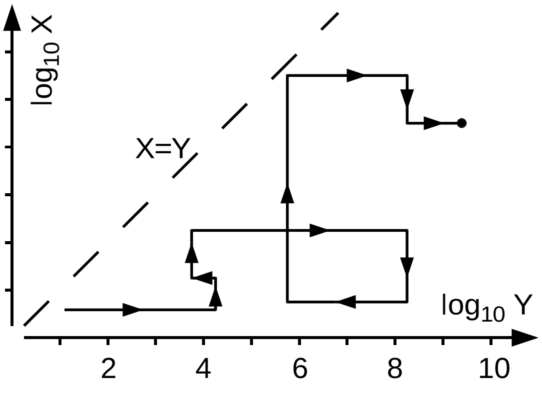

Fig 2. Evolution of X and Y by alternating mutations (size: 10^n) of X and Y, followed by selection. (n is a random number homogeneously distributed in [0,5]). Evolution stops as soon as a prime Y is reached. Here, the system locks at the Euler prime $Y = 2147483647$.

$\phi_x(t)$ of a predator at the time step t is computed here as follows: $\phi_x(t) = 0$ if the predator does not appear in that time step; if the predator appears and the number ν of cells in the neighbourhood occupied by prey is not zero ($1 \leq \nu \leq 9$), then $\phi_x(t) = \nu$; $\phi_x(t) = -p$ if the predator appears and $\nu = 0$. p is a natural number describing a "punishment" for a predator that appears but finds no prey. The momentary fitness $\phi_y(t)$ of the prey is computed analogously, but with opposite signs. The fitness F_x, resp F_y, of a predator, resp prey, are given by the sum of the $\phi_x(t)$, resp $\phi_y(t)$, over all t, t ranging from 1 to the product of all 9 cycle lengths interacting in the neighbourhood of C_0; this sum is then divided by the number of generations of the predator, resp the prey. In order to determine X and Y in cell C_0 in the next CA updating, we perform the evaluation that we just described for all 9 C_i; then, we replace X, resp Y, in C_0 by the value of X, resp Y of the cell C_i in which the largest fitness F_x, resp F_y was obtained. We use cyclic boundary conditions.

RESULTING MODES

Starting with random spatial distributions of X and Y, we obtain after a sufficient number of iterations, three types of attractors: homogeneity with a prime prey, travelling waves (as in Fig 3b) and spiral waves (as in Fig 3c). The travelling wave illustrated in Fig 3b is explained as follows. Let us call the cycles in the backround X_B, Y_B, and those in the wave X_W, Y_W. The populations in the numbered columns in Fig 3b are: X_B, Y_B in columns 1 and 6, X_B, Y_W in column 2, X_W, Y_W in columns 3 and 4, and X_W, Y_B in column 5. Note that in the case illustrated here the width of the wave is two cells (columns 3 and 4), but any width 1, 2, 3, ... (small enough to fit in the grid) is possible and does not change the present reasoning. The predator wave is always displaced one cell from the prey wave. The direction of this displacement (to the right in Fig 3b) determines the moving direction of the wave (arrow in the figure), as we will explain now. We consider that predator-prey interactions occur here only with the two immediately neighbouring columns of each column. The predator in column 5 (resp column 2) can feed on two types of prey and thus has a larger fitness than the predator in column 6 (resp column 3), which can only feed on one type of prey; therefore, the predator-wave will move one cell to the right in the next time step. The prey in column 5 (resp in column 2) can be eaten by two types of predators and thus has a lower fitness than the prey in column 4 (resp column 1), which can only be eaten by one type of predator; therefore also the prey-wave will move one cell to the right. We also found travelling waves moving diagonally; their mechanism is more complicated, but it can be understood by the same type of reasoning steps as the wave in Fig 3b.

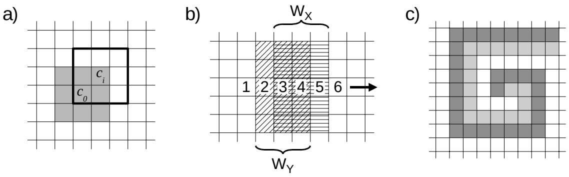

Fig 3. a: Scheme of cellular automaton neighbourhoods. For a cell C_0, the total fitness of predator and prey is determined for the 9 neighbours C_i, i = 0, 1, 2, ...8 (grey cells). The predator or prey with the largest fitness in this grey neighbourhood replaces the residents in C_0. For the determination of the fitness in a cell C_i, the interaction of all predators and prey in the 9 neighbours of that C_i (surrounded here by thick lines for the upper right C_i) is considered. b: Scheme of a planar travelling wave; W_Y : prey wave (columns 2,3 and 4; dashed obliquely); W_X predator wave (columns 3, 4 and 5; dashed horizontally). c: Scheme of a spiral wave.

The spiral wave illustrated in Fig 3c is explained by the existence of three adjacent zones, shown here white (cycle lengths: X_1, Y_1), light grey (cycle lengths: X_2, Y_2) and dark grey (cycle lengths: X_3, Y_3). The populations with cycle lengths X_1 and Y_1 are fitter than those with X_2 and Y_2, which are fitter than those with X_3 and Y_3. Those with X_3 and Y_3 are, in turn, fitter than those with X_1 and Y_1. Thus, after each updating of the CA, the light grey cells become white, the white cells become dark grey, and the dark grey cells become light gray. This causes a constant rotation of the spiral, without needing a pacemaker, so that we are dealing with a so-called autowave.

The travelling and spiral waves here show a similar behaviour to waves in prebiotic evolution[6], in host-parasitoid systems[7], as well as in excitable media (see Refs 4, 8-10 and references therein) such as chemical reactions, heart muscle and epidemics. In the latter, the black, dashed and white regions shown in Fig 3b, correspond to excited, refractory (or immune) and excitable (or resting) states, respectively.

PROBABILITY DISTRIBUTIONS OF PRIMES AND NON-PRIMES

We now determine the probabilities P of prey cycle lengths. For this we started a CA (with 10 x 10 cells) with 10^4 different initial configurations, the X and Y being chosen randomly within $2 \leq X, Y \leq 50$.

Then we evaluated the appearance of different *Y* after the CAs had reached the attracting modes. Fig 4 shows results of such analysis. The dark squares (primes) and grey squares (non-primes) were obtained setting p = 5, ie predators getting no prey lose the average of what they would gain (between 1 and 9) if they found prey in the neighbourhood; analogously, prey meeting no predators gain the average of what they would lose (between 1 and 9) if predators emerge in their neighbourhood. One clearly sees in Fig 4 much more frequent appearance of prime prey cycles (the maximum occurs at Y = 17), as compared to non-prime prey cycles (grey symbols, all being very close to the abscissa). P vs Y_P (Y_P : prime prey cycle lengths) can be well approximated by a piecewise linear function, as shown in Fig 4. This result is robust to drastic variations of the model, the results after these variations being displayed by triangles and stars in Fig 4. We also found that changing the upper bounds of X and Y from 50 to 100 or 200 also renders a peak-like shape for P vs Y with a maximum at Y = 17. This maximum is also insensitive to the "punishment" parameter p Changing the grid size of the CA to 20 x 20 cells yields a maximum of $P(Y)$ at Y = 13; however, if the grid is too small (eg 5 x 5 cells) non-prime prey cycles are selected.

DISCUSSION

We have shown that a simple predator-prey model involving mutations and selection can be used to generate very large prime numbers. This is a remarkable merging of number theory with population biology.

An extension of the model into a spatio-temporal configuration, namely a cellular automaton, yields homogeneity, travelling waves and spiral waves. Such waves allow the coexistence of different species in a spatial domain. A statistical analysis, evaluating all periods of the attracting modes resulting from a large number of initial configurations, leads to a predominance of prime prey cycles. Depending on model parameters, the probability of final prey cycle lengths has a maximum at 13 or 17. This results evokes associations with cicadas (genus Magicicadae; see Refs 1, 2, 11-19 and references therein), which have periods of 13 or 17 years.

The periodical cicadas spend most of their lives below the ground emerging and dying within a few weeks. Our model contains the hypothesis that the cycle length is a prime in order to optimally escape predators. A drawback of this hypothesis is that there are as yet no relevant periodic predators of cicadas. Nevertheless, Lloyd and Dybas[20] pointed out that

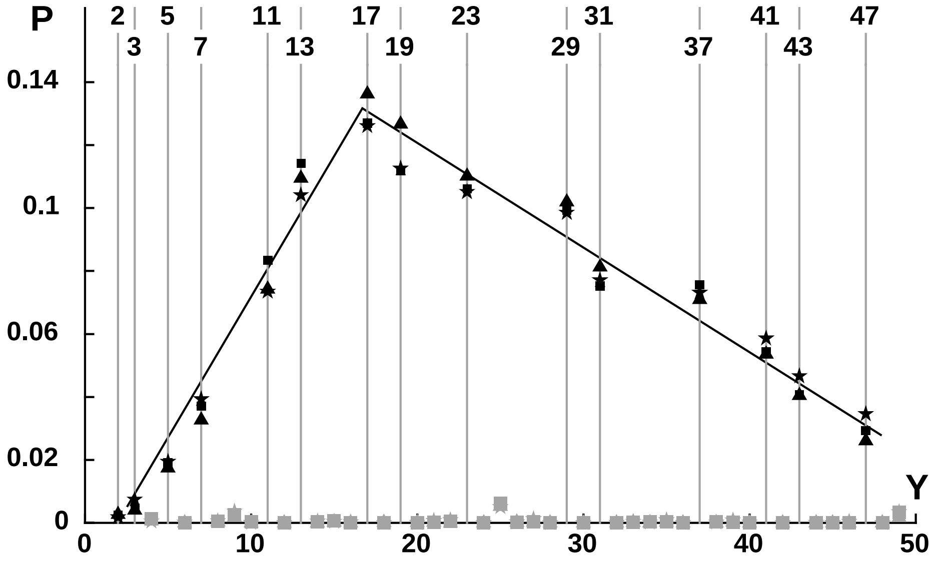

Fig 4. Probability P that prey periods Y are selected after the cellular automaton described in the text has converged to an attractor (dark squares for prime Y and grey squares for non-prime Y). Triangles: p=0, ie predators emerging but finding no prey are undisturbed, while prey emerging but meeting no predators are not rewarded. Stars: $\phi_x(t)$ = +1 if the predator emerges and finds prey, independently of the number ν of prey-populated neighbouring cells and $\phi_y(t)$ = -1 if emerging prey meets predators, no matter how many. The two straight lines are best linear fits, considering the three variations of the model (black squares, triangles and stars).

the predator hypothesis can be maintained by assuming parasitoids that attack eggs or adults; lacking their prey, these predators then go to extinction. An alternative mechanism to the predator hypothesis is given by Yoshimura[19]; he argues that prime numbers are selected because these cycles are the least likely to coemerge and hybridize, so that they prevent genetic breakdown by breeding synchrony. This mechanism has been compared[12] with that proposed by Cox and Carlton[11], which also involves advantage of prime cycles due to less frequent hybridization. In view of these proposed mechanisms, it remains an open question whether the relationship of our results with the cicada periodicity is a coincidence, or if it follows from relevant features of the model.

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