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VERHULST FACTOR IN THE PENNA MODEL OF BIOLOGICAL AGING*

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The Penna model with simplifications aimed on elimination of randomness from the system dynamics is considered. In the deterministic system resulting, the relation arising from the Verhulst factor between families constituting the population is examined. An example of self-controlling chaotic system of two-families is presented.

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1. Introduction

Although originally the Penna model was designed to reconstruct the process of biological ageing, it soon has appeared that the model is attractive to study other evolutionary facts. Attributing a family name to each individual of an initial population we can search for reasons of the mitochondrial Eve. The interest in the such effect is motivated by the following biological observation. The mitochondrial DNA — DNA existing outside chromosomes, is inherited only from mother to child, without any contribution from father [1]. Therefore, different strands of mitochondrial DNA act like different family names of the Penna model. So that, observation of the selection of one winning family in the Penna model could give insights into the hypothesis of existence of the common female ancestor, called *mitochondrial Eve*, for the whole human population. In the Penna model the selection process is easily to be observed, especially, when the population is stationary.

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It has been found that after a short period of time, when the self-organization of the population takes place to select the best fitted families (see [2] for details), the stationary state is reached. The properties of the stationary state arise from the adjustment between the basic Penna model parameters, see [3]. One of these parameters, the so-called Verhulst factor $V(t)$, seems to be responsible for the stationary evolution. As the effect of the activity of the Verhulst factor we observe the stationary evolution as it is a simple stochastic process. The evident characteristic for the stochastic branching process like surviving of one line of ancestry only, is observed. Moreover, as the Verhulst factor arises from the famous logistic map, some features originated from the logistic map can be found in the model.

The role of the Verhulst factor in the Penna model is discussed from both sides: evolutionary genetics, see [4], and system dynamics, see [3, 5]. The attempts are done, like implementing the Penna microdynamics on a lattice, see [6, 7] or considering the Verhulst which depends on age, see [10], to weaken this role. In the following paper we consider the population arising from the Penna microdynamics, however, these microrules work on a very simple collection of individuals. The simplifications introduced are aimed on elimination of randomness from the system. Then, in the deterministic system resulting, we examine the relation between two families constituting the population which is affected by the Verhulst factor. This relation is studied by manipulating with the extra parameter introduced by us, called the *conjugation parameter*. Finally, we present an example of the self-controlling evolution of the population consisting of two families.

2. The asexual Penna model

In the asexual Penna bit-string model each individual is characterized by a string of 32 bits, called *genome*. Each bit of a genome represents one subsequent period of life, called *year*. If at the age i the ith bit in the genome is set to one, the individual suffers the effect of a deleterious mutation, called *disease*, from this age on until death. If the ith bit is set to zero no disease occurs. When the total number of accumulated diseases reaches a value greater than or equal to a limit T, the individual dies. The individual can also die because of lack of food and space. This is taken into account through the Verhulst factor:

$$V = 1 - \frac{N(t)}{N_{\max}}\,, \tag{1}$$

where $N(t)$ is the current population size and $N_{\max}$ is the maximum carrying capacity of the environment, defined at the beginning of the simulation. This factor determines for each individual and independently of the individual's both genome and age, the probability to survive. After reaching the minimum reproduction age R, each year an individual generates b offspring. The baby's genome differs from the parent's one by m bits, randomly selected. Only deleterious mutations are allowed. If a selected bit is equal to one, it remains set to one in the offspring's genome. Otherwise, if the selected bit is equal to zero, the offspring carries an additional deleterious mutation when compared to its parent. To study the Eve effect, each individual obtains the name of the family, inherited from its parent.

The first presentation of this model one can find in [8], the discussion of many features together with the modifications is in [9]. The biological motivation behind the Penna model is the mutation accumulation hypothesis [11].

3. Simplified model

The process of selecting of one winning family performs in the stationary population, also. When the stationarity is gained, then the population of the Penna model can be seen as a collection of individuals of two kinds only. The first part consists of Kids waiting for the procreation age. The other part consists of Parents that, if survives, produce b offspring. Such stationary dynamics can be reconstructed by some stochastic difference equations, see [3]. Families constituting the stationary population do not differ from each other — they have the same bit-string as well as age characteristics. So that the Eve effect appears as the result of the well-known branching process.

To get other insight into the Eve effect we need to eliminate the randomness from the Penna system. Therefore, we introduced some modifications to the Penna model, namely, we assume that:

(i) all individuals are characterized by the same genetic code and

(ii) no mutation is introduced during a reproduction process. In the result of these assumptions the evolution of a population can be completely described by difference equations.

In particular, let us consider a population consisting of two families, named A and B. All individuals of both families have the same genotype of the length of 3. Hence, the maximal time of life is the same for all individuals and equals to 3. Let us assume that individuals of distinct families have different reproduction time R. Let individuals of A family start reproducing at the age of 1 and each individual within this family gives b_A offspring. Family B consists of individuals which start reproducing later than individuals of family A, namely, at the age of 2 and they give b_B offspring each reproduction year. The evolution of the families defined above is described by the following equations:

$$\begin{aligned}
x_{n+1}^{(A)} &= b_A[x_n^{(A)} - \mathrm{Int}\,(px_n^{(A)})] \\
&\quad +b_A[y_n^{(A)} - \mathrm{Int}\,(py_n^{(A)})] \\
&\quad +b_A[z_n^{(A)} - \mathrm{Int}\,(pz_n^{(A)})]\,, \\
y_{n+1}^{(A)} &= x_n^{(A)} - \mathrm{Int}\,(px_n^{(A)})\,, \\
z_{n+1}^{(A)} &= y_n^{(A)} - \mathrm{Int}\,(py_n^{(A)})\,,
\end{aligned} \tag{2a}$$

$$\begin{aligned}
x_{n+1}^{(B)} &= b_B[y_n^{(B)} - \mathrm{Int}\,(py_n^{(B)})] \\
&\quad +b_B[z_n^{(B)} - \mathrm{Int}\,(pz_n^{(B)})]\,, \\
y_{n+1}^{(B)} &= x_n^{(B)} - \mathrm{Int}\,(px_n^{(B)})\,, \\
z_{n+1}^{(B)} &= y_n^{(B)} - \mathrm{Int}\,(py_n^{(B)})\,.
\end{aligned} \tag{2b}$$

Where: $x_n^{(i)}, y_n^{(i)}, z_n^{(i)}$ are volumes of A or B family one-year-old, two-year-old, three-year-old individuals, respectively,

$$p = \frac{x_n^{(A)} + y_n^{(A)} + z_n^{(A)} + x_n^{(B)} + y_n^{(B)} + z_n^{(B)}}{N_{\max}} = \frac{N(n)}{N_{\max}} = 1 - V(n)\,. \tag{3}$$

Hence p means the probability to die because of the lack of the environment space. It is obvious that the volume of each family depends on the value of b's. Manipulating with values of b_A and b_B we can establish a stationary population with any family winning, see Figs 1(a)(b)(c). If $b_A = b_B = 1$, see Fig. 1(a), the family A is the dominant family in the population, while if $b_A = 1$ and $b_B = 3$ then the family B is the winning family, see Fig. 1(b). When the birth rates b's are sufficiently high, *e.g.*, $b_A = 3$ and $b_B = 5$ we observe the chaotic changes of the population size as it is expected in case of logistic map, see Fig. 1(c).

Eqs. (2a) describe the mutually related systems where the close conjugation is established by the Verhulst term, here in Eqs. (2a) represented by the conjunction parameter p which reads as (3). To explain better how the relation between families acts, let us rewrite Eqs. (2a), however splitting the p factor into two factors p_A and p_B with one factor for each family A and B, respectively. Let us introduce a parameter $c \in [0, 1]$, named the *conjugation parameter* to measure the family conjugation, as follows:

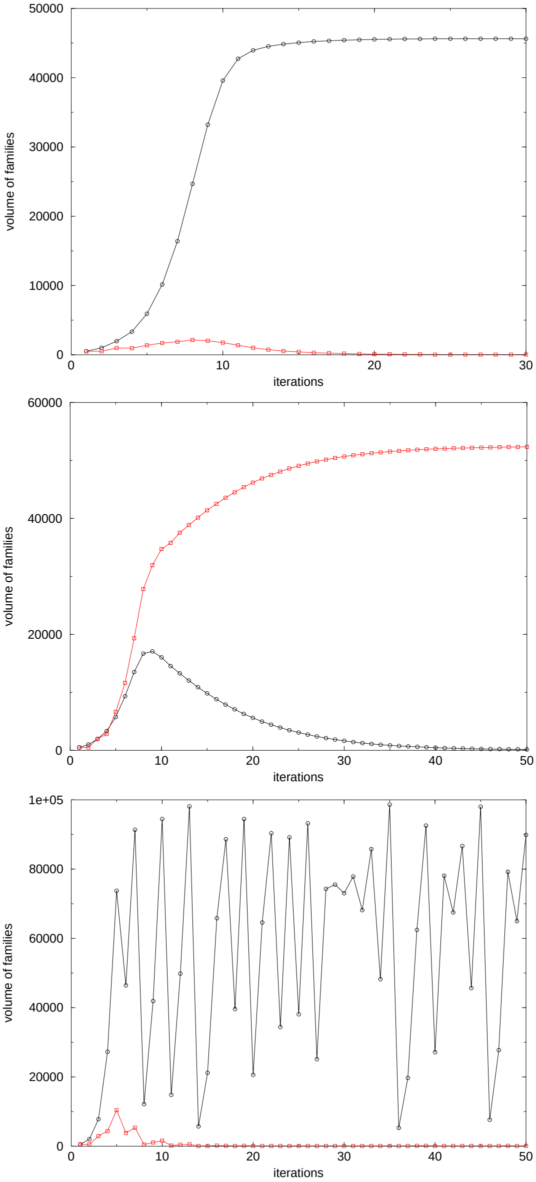

Fig. 1. Volumes of two families (circles — A, boxes — B) constituting the Penna simplified population in subsequent iterations of Eqs (2a). $N_{\max} = 100\,000$, $x_0^{(A)} = x_0^{(B)} = 100$ and $y_0^{(A)} = y_0^{(B)} = z_0^{(A)} = z_0^{(B)} = 0$, and (a) $b_A = b_B = 1$, (b) $b_A = 1, b_B = 3$, (c) $b_A = 3, b_B = 5$.

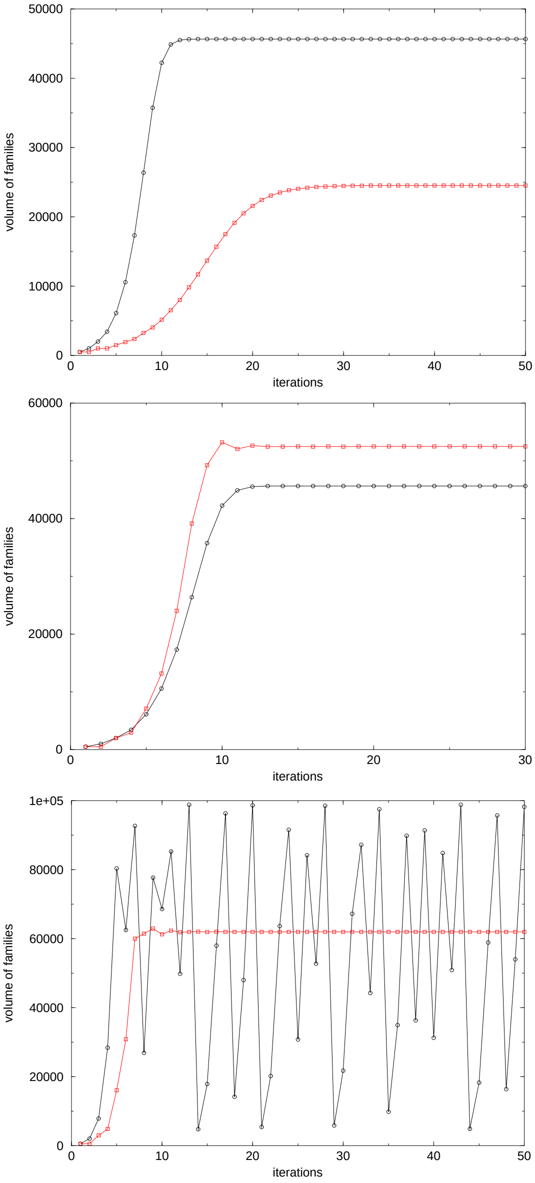

Fig. 2. Volumes of two families (circles — A, boxes — B) constituting the Penna simplified population in subsequent iterations of Eqs (2a) with the split environment , *i.e.*, $c = 0$. $N_{\max} = 100\,000$, $x_0^{(A)} = x_0^{(B)} = 100$ and $y_0^{(A)} = y_0^{(B)} = z_0^{(A)} = z_0^{(B)} = 0$, and (a) $b_A = b_B = 1$, (b) $b_A = 1, b_B = 3$, (c) $b_A = 3, b_B = 5$.

$$\begin{aligned} p_A &= \frac{x_n^{(A)}+y_n^{(A)}+z_n^{(A)}+c(x_n^{(B)}+y_n^{(B)}+z_n^{(B)})}{N_{\max}}, \\ p_B &= \frac{c(x_n^{(A)}+y_n^{(A)}+z_n^{(A)})+x_n^{(B)}+y_n^{(B)}+z_n^{(B)}}{N_{\max}}. \end{aligned} \tag{4}$$

Notice, that $c = 0$ denotes that the families evolve independently of each other, and $c = 1$ restores the relation studied in Eqs. (2a).

In Figs 2(a)(b)(c) we present the solutions to Eqs. (2a), however with p replaced by p's of (4) and for the independent dynamics, *i.e.*, with $c = 0$, and for the values of b's considered earlier. As we see dynamics of families is changed. Each of families evolves as this family is the only one in the whole surrounding. One can say that both families live together side-by-side.

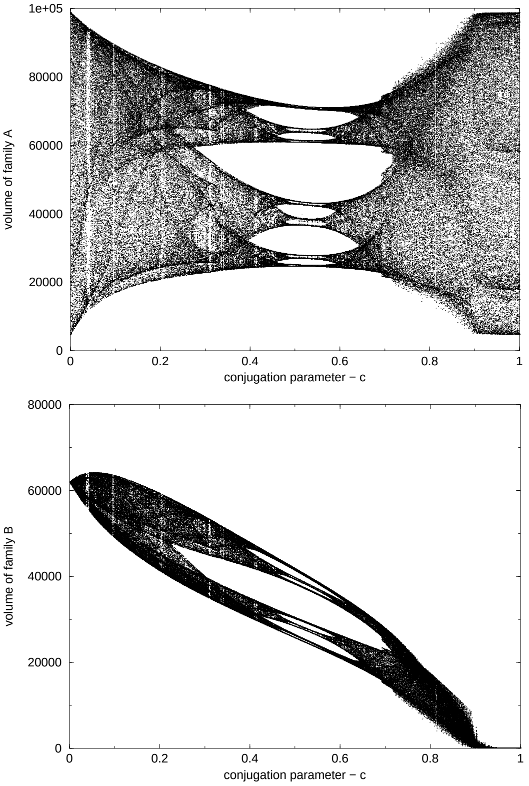

Fig. 3. Bifurcation diagram for volumes of two families (a) (A) and (b) (B), if the conjugation parameter c is changed. For each $c \in [0, 1]$ with the step $\Delta c = 0.001$ the first 500 iterations are skipped and the next 2000 points are plotted.

In Figs 3(a)(b) we present the, so-called, bifurcation diagram (see [12]) for volumes of both families versus c parameter for the chaotic region of dynamics, namely, $b_A = 3$ and $b_B = 5$. The original evolution of the family A is chaotic, while the evolution of the family B settles as the fixed point when $c = 0$, compare Fig. 2(c). With increasing of the conjugation between families $0 < c \ll 1/2$ we observe loosing the stability of the fixed point of the family B. The periodic evolution of both families is gained around the value $c = 1/2$. One can say the families control each other. When $c \to 1$ the chaotic properties of the dynamics of the family A takes over the evolution of the whole population, and, finally, we have the result that is presented in Fig. 1(c).

4. Conclusions

Although our model can be seen as a toy-model comparing to the more realistic complete Penna model, it posses the feature which allows us to get an insight into the role played by the Verhulst factor in the Penna model. We studied this role by observing the Eve effect.

In the homogeneous stationary Penna population, the only reason for the Eve effect is the randomness in the system. This randomness arises from the stochastic and independent of family membership choice of an individual to die because of environment restrictions. However, if the population is not homogeneous- the families differs from each other by, *e.g.*, the reproduction age or by the birth rate, then the Verhulst constrain causes extinction of the less suited family. To see both families alive, the environment has to be split into separate parts and each part has to be devoted to one family, only. One can say families are separated from each other. Our studies of the influence of this separation provide that manipulating with the strength of conjugation parameter we obtain a tool to control the development of both families.

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