

UDC 539.3

# Parthenogenetic Versus Sexual Reproduction: Mathematical Modelling of Population Dynamics

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Using a modified bit string aging model proposed by Penna we try to explain population dynamics of holocyclic species. In a system with two fractions (sexual and parthenogenetic) sexual population generates individuals with more genetic variability and these individuals are better adopted to the current environment. On the other hand, parthenogenetic population produces more offsprings. In our model a female can choose the best male among two randomly chosen males (i.e. with less deleterious mutations). We simulate a natural selection by this way. We show that in a system under deleterious external conditions, sexual fraction is better adopted to the current environment because of this single factor. In other words, female choice may be a unique factor responsible for the maintenance of sexual reproduction.

## Introduction

Evolutionary processes can be studied using computer simulation [1–4]. In this kind of modelling cell automations represent genomes of unicellular organisms. Bit arrays used in our simulations consist of “0” and “1” [5,6]. Unities mean mutations, i.e. damages of the genome, while zeroes symbolize undamaged fragments of DNA. By the hypothesis of Jan, Stauffer and Moseley [7], evolution has led to sexual reproduction in order to avoid extinction from very high level of deleterious mutations. But some sexual species of animals can return to reproduce in an asexual way in their life cycle although sexual way of reproducing is more perfect. For example, many species of insects and some lizards are holocyclic. (Species that produce both sexual and asexual morphs are called holocyclic).

In a system with two fractions (sexual and parthenogenetic) sexual population generates individuals with more genetic variability and these individuals are better adapted to the current environment. On the other hand, parthenogenetic population produces more offspring. A question arises: what is more important in a system with competition? The answer is not obvious. Under some conditions it is more effective to have higher fertility but under other conditions it may be more effective to have more genetic variability [8].

This complete process has been studied in reference [9]. The authors used a bit string model (a modified model of Penna [10]). In their model once a year in autumn sexual females laid winter eggs. In order to model winter (i.e. harsh condition) they used an enhanced Verhulst factor. All adult insects suffer from that enhanced factor. In spring parthenogenetic females hatch from these winter eggs. During the whole summer and autumn they reproduce by parthenogenesis and only at the end of autumn they give birth to sexual insects (females and males). In this model parthenogenetic females dominate under favorable conditions. But under unbearable conditions only sexual way of reproduction can avoid extinction.

In other works authors used a simple model for biological aging. As in many previous simulations, starting with Redfield [11,12], the sexual version does not give a clear advantage over the asexual one and additional assumptions like in [13] may be needed to justify sex.

Using a bit string model of Penna we try to explain population dynamics of holocyclic species. We have modified the original model. In our model the system consists of two fractions: sexual diploids (SD) and parthenogenetic diploids (PD). At the beginning only SD are present but later a number of PD are added too (a “parthenogenetic invasion”). A sexual female can select a male with less number of homozygous “1”’s positions. PD and SD compete between each other. As usual one fraction wins and the other fraction comes to extinction. It depends on conditions and existence or absence of the above mentioned factor of female preference. This way we simulate natural selection. The aim of this work consists in simulation of such an evolution of populations of unicellular organisms when transition to parthenogenesis occurs as a consequence of the self-organization of the system in response to external conditions.

## 1. The model

In the model proposed by Penna [10], each individual is represented by two parallel bit strings of 32 “0”’s and “1”’s. One time-step (“one year”) corresponds to read one position of all the genomes. In this way, each individual can live at most for 32 time-steps (“years”). Damages of genome (i.e. lethal mutations) are described by “1”’s.

If an individual has two bits “1”’s (homozygous) at the fifth position, for instance, it starts to suffer from a genetic disease at its fifth year of life. If it is an homozygous position with two bits “0”’s, no disease appears at that age. If the individual is heterozygous in some position, it will not get sick as well (i.e. lethal mutations are recessive). When the number of accumulated diseases of any individual reaches a threshold  $\mu$ , the individual dies.

Apart from deaths from genetic diseases, on every time step an individual can die with the probability

$$P_V = \frac{N}{N_{\max}}, \quad (1)$$

where  $N$  is the size or population at the current time step. The expression (1) is named a logistic Verhulst factor, which models the volume of ecological niche and competition of individuals for limited resources [12, 13].

Reproduction is modeled by the introduction of new genomes in the population. Each female becomes reproductive after having reached a minimum reproductive age ( $R_m$ ), after which she generates an offspring at the completion of each period of life. The meiotic cycle is represented by the generation of a single-stranded cell out of the diploid genome. To do so, each string of the parent genome is cut at a randomly selected position, the same for both strings, and the left part of one is combined with the right part of the other, thus generating two new combinations of the original genes (by this means the crossover is modeled). The selection of one of these completes the formation of the haploid gamete coming from the mother and then:

Case 1: The female selects the best male among two (randomly chosen) reproductive males, i.e. the male with less number of homozygous “1”’s positions. The male undergoes the same meiotic cycle, generating a second haploid gamete from his genome.

Case 2: The female selects any male with age more or equal to  $R_m$ . The male undergoes the same meiotic cycle, generating a second haploid gamete out of his genome.

For both regimes, the next stage of the reproduction process is the introduction of  $M$  independent mutations (i.e. “1”’s) in the newly generated genetic strands.

The two gametes, one from each parent, are now combined to form the genome of the offspring. The gender of the newborn is then randomly selected, with equal probability for each sex.

In this model at the beginning the population consists only of males and females reproducing in a sexual way, but then (after 700 time steps) we added a few parthenogenetic females which reproduce by parthenogenesis.

As a whole, manipulations with PF are the same as those described above for sexual females and males. The meiosis is represented by generation of haploid gametes

from the diploid genome. Also as for sexual fraction, crossover is performed in the gametes. Then some  $M$  randomly chosen bits are flipped from 0 to 1. PF reproduce by parthenogenesis, generating only parthenogenetic females.

The use of a single Verhulst factor for sexual population and PF leads to competition between them.

We used the following values of the parameters of the model:

- 1) minimum reproductive age:  $R = 10$ ;
- 2) total number of time steps:  $T_{\max} = 1800$ ;
- 3) maximum population size:  $N_{\max} = 300000$ ;
- 4) initial population of males and females:  $N_{0m} = 1000$ ,  $N_{0f} = 1000$ ;
- 5) threshold of lethal mutations:  $\mu = 4$  (fine conditions) and  $\mu = 3$  (harsh conditions);
- 6)  $M$  — mutation rate:  $M = 1$  (fine conditions),  $M = 3$  (harsh conditions).

## 2. Results and discussion

We begin by showing the sexual population under fine conditions (i.e low mutation rate  $M$  and high threshold of lethal mutations  $\mu$ ) in Fig. 1A. Fig. 1B represents a system with invasion of parthenogenetic population. In this case the parthenogenetic fraction wins and the sexual population becomes extinct. The similar behavior was observed in case of female preference, i.e. when a female selects a male with less number of homozygous “1”’s positions (Fig. 2). In a system under fine conditions the sexual version does not give a clear advantage over the parthenogenetic one. That also has been shown in references [11, 14].

In Fig. 3, 4 one can see a system under harsh conditions. Without natural selection (without female preference) the parthenogenetic fraction dominates (Fig. 3). The situation changes dramatically when the factor of female preference is switched on (Fig. 4). In this case the sexual fraction dominates. Data is collected as an average over many runs, and sexual males and females win in 100% percent of cases.

Typical genes (bit strings) of the winners (Fig. 4C) have  $26.26 (\pm 4.22)$  percent of heterozygous positions (and  $56.88 \pm 3.85\%$  of homozygous “1”’s positions). It may be deduced that heterozygous order of lethal mutations allows the sexual fraction to survive. Bit strings (Fig. 1) of losing sexual fraction have  $34.67 \pm 9.01$  percent of heterozygous positions and  $41.86 \pm 9.60\%$  of homozygous “1”’s positions;  $48.13 \pm 9.46\%$  of heterozygous positions and  $19.97 \pm 8.28\%$  of homozygous (Fig. 2); and  $20.96 \pm 2.96\%$ ,  $65.93 \pm 3.45\%$  for Fig. 3.

One can see, looking at Fig. 1C, Fig. 2C, Fig. 3C, that parthenogenetic females have only homozygous positions.



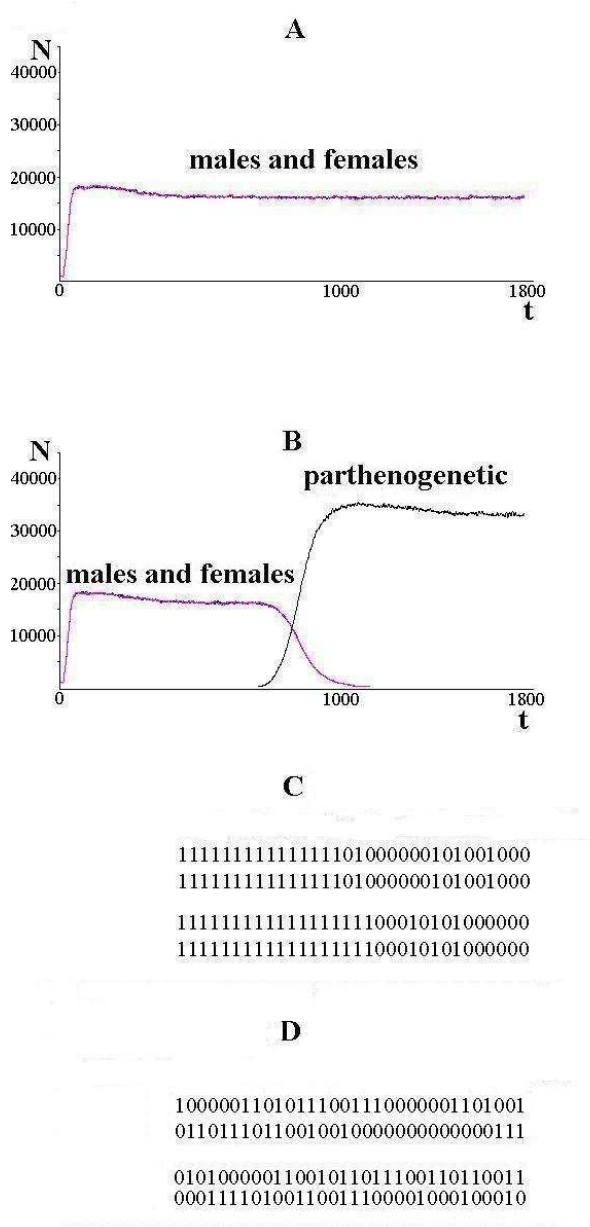


Figure 2. Population dynamics under the conditions of low rate and high threshold of lethal mutations:  $M = 1$ ,  $\mu = 4$  (“fine” conditions). The factor of female preference is switched on (Case 1). The remaining parameters are the same as in Fig. 1. A — without invasion of parthenogenetic females (PF). B — with invasion of PF. PF dominate in the system. C — typical genes of the surviving fraction (i.e. PF). D — typical genes of the dying fraction (i.e. sexual).



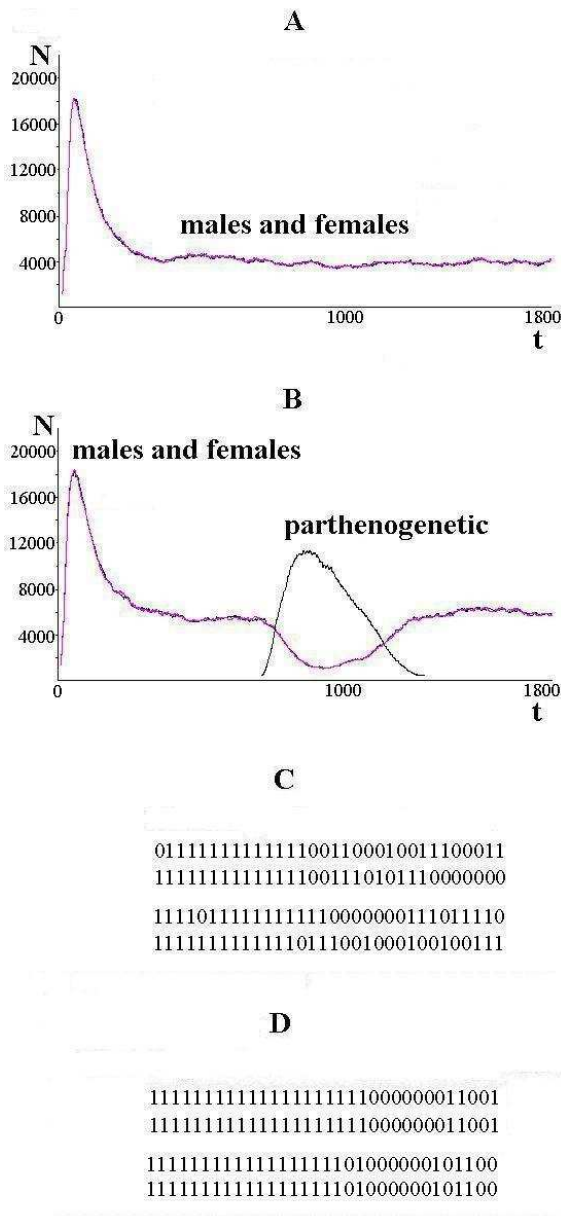


Figure 4. Population dynamics under the conditions of high rate and high threshold of lethal mutations:  $M = 3$ ,  $\mu = 3$  (“harsh” conditions). The factor of female preference is switched on (Case 1). The remaining parameters are the same as in Fig. 1. A — without invasion of parthenogenetic females (PF). B — with invasion of PF. Sexual fraction dominate in this case. C — typical genes of the surviving fraction (i.e. sexual males and females). D — typical genes of the dying fraction (i.e. PF).

So, sexual fractions demonstrate its advantages only in systems under harsh conditions with natural selection.

Analyzing bit strings of survived sexual males and females, we see that in the dominant positions of their bit strings are homozygous “1”s. But in the other positions are mostly heterozygous “1”s. So the sexual fraction can better adopt to the current environment because of a female selecting of a better genetic material (i.e. a better male).

Sexual reproduction is more efficient than parthenogenetic reproduction only in this case. On the basis of that we think that our model describes truly some significant characters of the evolution that led to the sexual reproduction.

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УДК 539.3

## Партеногенетическое воспроизводство в сравнении с половым. Математическое моделирование

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Используя модифицированную модель Пенна, мы пытаемся объяснить динамику развития голоциклических видов. В системе с партеногенетическими самками и обычными самцами и самками последние дают начало потомкам, обладающим большим генетическим разнообразием, которые лучше приспособлены к условиям окружающей среды. С другой стороны партеногенетические самки продуцируют больше потомства. В нашей модели самка может выбирать лучшего самца (с меньшим количеством мутаций) среди двух случайно выбранных самцов. Мы моделируем так естественный отбор. Мы показали, что в системе с значительным мутационным фоном, половая фракция лучше приспособлена благодаря выбору самкой лучшего самца.