Anomalous Relaxation of the Penna Model

D.N.HADDAD

T.J.P.PENNA

Instituto de Fsica, Universidade Federal Fluminense
Niteri - RJ - Brazil

tjpp@if.uff.br

Received Day Month Year
Revised Day Month Year

We simulate the response of an age-structured population face to an abrupt increasing of fertility. Contrary to the exponential decay of original model, as reported by Coe and Mao, we have found that the relaxation to the equilibrium can be algebraic under certain conditions. We show results from computer simulation for a large range of parameters, although the fertility itself seems to be the most relevant factor.

1. Introduction

The evolutionary aspects of aging have been studied with great interest on the last years[1,2]. In particular, a bit-string model[3] so-called the Penna model, after Stauffer, has appeared as the main tool for studies of the evolution of populations with age-structure. This model is based on the mutation accumulation hypothesis of Medawar[4]. It has been applied successfully to several problems on Evolution, Ecology and Population Dynamics. Although it was primarily designed for easy implementation for computer simulations, some recent papers have allowed a better understanding of the dynamics of this model[5,6,7]. A full analytic steady state solution is available but also the transient behaviour to equilibrium is developed[8].

Coe and Mao have shown that fluctuations in a population far away from equilibrium can be decomposed into a collection of decay modes which decay exponentially with time. To be able of decomposing the dynamics on independent modes, they ruled out the Verhulst factor and chose the reproduction rate as function of the number of individuals[9]. Nevertheless, under special conditions, the influence of the Verhulst factor can be weak and their treatment and conclusions can be applied. In this work, we recover the original model with the Verhulst factor. We studied systems where the population can suffer sudden changes (catastrophes). In particular, we simulated the removal of egg's predators allowing an abnormal increasing of the effective fertility. Through computer simulations, we are able to show that in these situations the decay is algebraic rather than exponential.

2. The asexual Penna model

In the Penna model[3], there is a temporal genome for each individual that is represented by a bit-string. Each bit corresponds to a time step on the individual lifetime. At each time step a bit is read from the individual's genome: if it contains 1, the individual develops a disease staying with this individual until death. If the individual accumulates T diseases, it dies. If it reaches the maturity age R, it can reproduce with probability b. In some implementations there is also an upper reproductive threshold age. As an example, the salmon reproduces only once (also known as a semelparous species[10]). Women stop reproducing at the menopause. Trees, some fish and lobsters[11] reproduces for all their lifetimes with increasing fertility. The offspring inherits the temporal genome from its parent, with a probability M of having one of its bits mutating into a 1 ($M > 1$ means deleterious mutations marked to express in more than one age).

The population is controlled by a Verhulst factor that corresponds to the death due to external (non-genetic) causes. The probability of an individual to die due to these causes is age-independent and given by

$$V = \frac{N_t}{N_{max}} \tag{1}$$

where N_{max} is the carrying capacity of the enviroment. This factor has been modified in many previous works in order to take into account different relationships between populations on populations/environment[2]. The control of the population can be done by the birth rate as well[9].

3. Punctual fertility increasing

The situation we are going to described here is similar to the evolution of the prey population in an area where predadors of their eggs are suddenly removed or if there is a protection program for the eggs. The effective fertility that means the number of offsprings that reach the first age is instantaneously increased. Situations like this one are known to have happened with the corroborre frog *Pseudophryne pengilleyi* in Australia, turtles in Brazil and many other sites. Even for humans, there reports for increases in births following the introduction of restrictions on access to abortion in eastern Europe, as in Romania (1966), Bulgaria (1968), the former Czechoslovakia (early 1970s) and Hungary (1974).

We started our simulations with a population of individuals with random bit-strings. After the population reaches a steady state, typically 5000 time steps, we allow the fertility to increase by a factor eight for only one step; it then returns to its old value. As one can see in the figure 1, the population returns to the size before the pertubation but through an oscilatory behaviour. The period of the oscillations is the maturity age, as we could expect. It is worth mentioning that no oscillations appear if we introduce new random individuals rather than offspring of those already there, so we are not talking about the introduction of foreign individuals of the same species.

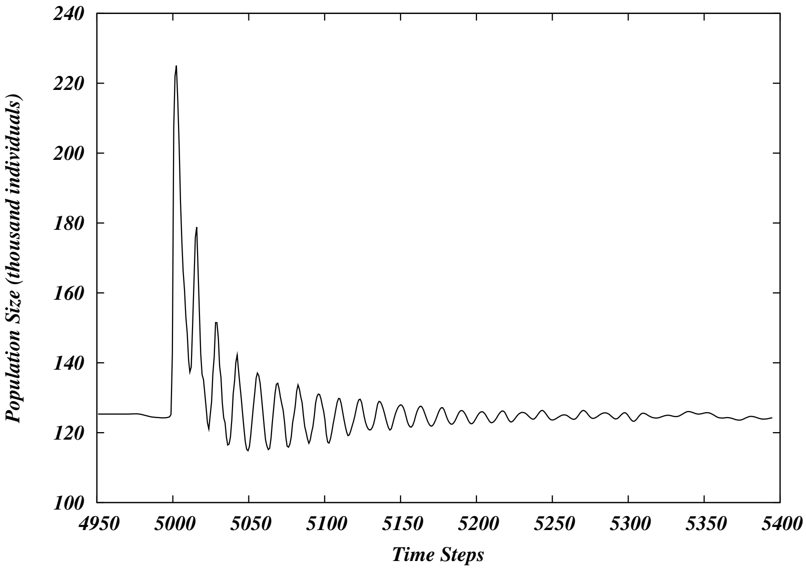

Fig. 1. Population size versus time for $m = 0.3, b = 0.7, T = 3, R = 14$. An instantaneously increasing of the fertility is introduced at $t = 5000$. The oscillations are found to have a period of R. The instantaneous increase does not change the population sizes on the steady states before/after the pertubation.

Further we check how the pertubation disturbs the distribution of genotypes on the population. It is well known the fixation of deleterious mutations on the populations at advanced ages. As shown in fig. 2, the distributions of deleterious mutations are slightly different before and after the pertubation but this difference does not change the average lifespan of the population.

The most surprising results of this work are shown in figs. 3, 4. We fit the maximum of each oscillation after the pertubation, by exponentials and power-laws curves. We have found that the algebraic decay describes that behavior better than the geometric decay in many situations we have tested. Fig. 4 corresponds to semelparous populations[10], i.e. individuals reproducing only once in lifetime as mayflies and salmon. For this case, power-laws fits better the beginning of the decays but overpredict the equilibrium population. Coe and Mao [8] have shown through analytical and simulation results that the original Penna model presents an exponential relaxation to the equilibrium if no Verhulst factor is included. To our knowledge, this is the first report of a power law decay on this model. It seems to be interesting because it shows how important is the Verhulst factor for the dynamics of the original model.

We ran many different situations and parameters and we found that the decays depends mainly on the maturity age and the reproductive threshold age. We fit the

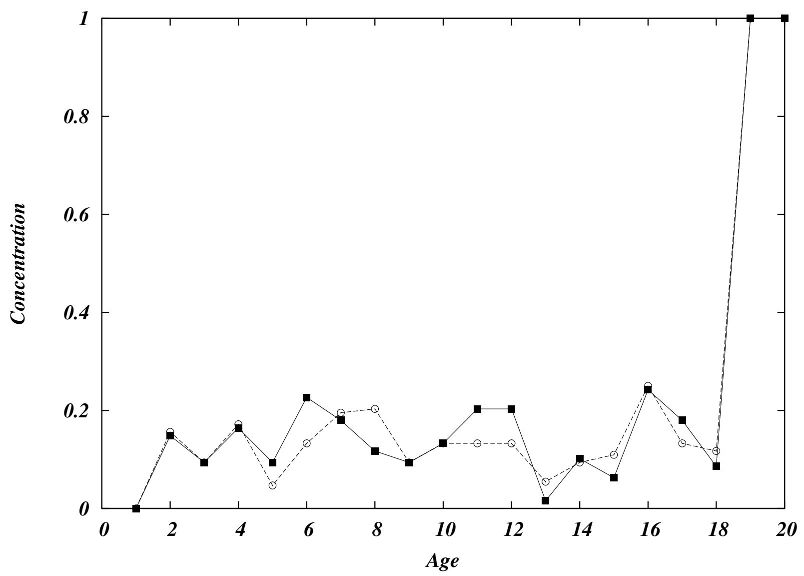

Fig. 2. Concentration of deleterious mutations on each age. The full symbols corresponds to one time step before the pertubation $t = 50000$, and the empty circles to a time step after the pertubation but in the new equilibrium state ($t = 100000$). The parameters are $L = 32$, $T = 3$, $R = 14$, $b = 0.7$ and $M = 0.3$. Here, we introduce the menopause at $Mp = 18$.

following function to the data

$$N(t) = N_0 * t^{-z} + N_\infty \tag{2}$$

where N_∞ is the population size in equilibrium after the pertubation, and N_0+N_∞ is the population one time step after the pertubation ($t = 0$). The dynamical exponent z is therefore positive. Fig. 5 corresponds to the simulation of different reproductive threshold age.

In summary, in this work we show a situation where the decay to equilibrium after a sudden change in the effective fertility, that could be caused by sudden changes in the environment or artificial changes as removal of predators, is not described by an exponential behavior as reported to happen in most situations. This anomalous behavior does not appear if the population increases by addition of new individuals chose at random but if the population is allowed to grow abnormally in a very short time. The age of maturity and the extension of its fertile period seem to be the most relevant parameters in this problem.

Acknowledgements

The authors thanks Brazilian agencies CNPq and FAPERJ for financial support and fellowships.

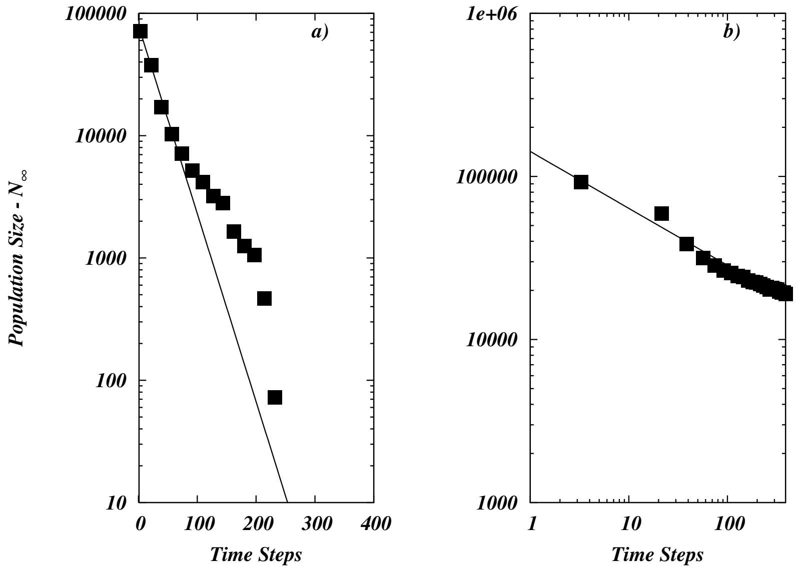

Fig. 3. Population size decay as function of the time. We present the a) exponential fitting andb) the power law fitting. The non-exponential behavior is evident in this situation. The parameters are $L = 32$, $T = 3$, $R = 15$, $Mp = 19$, $b = 0.9$ and $M = 0.3$

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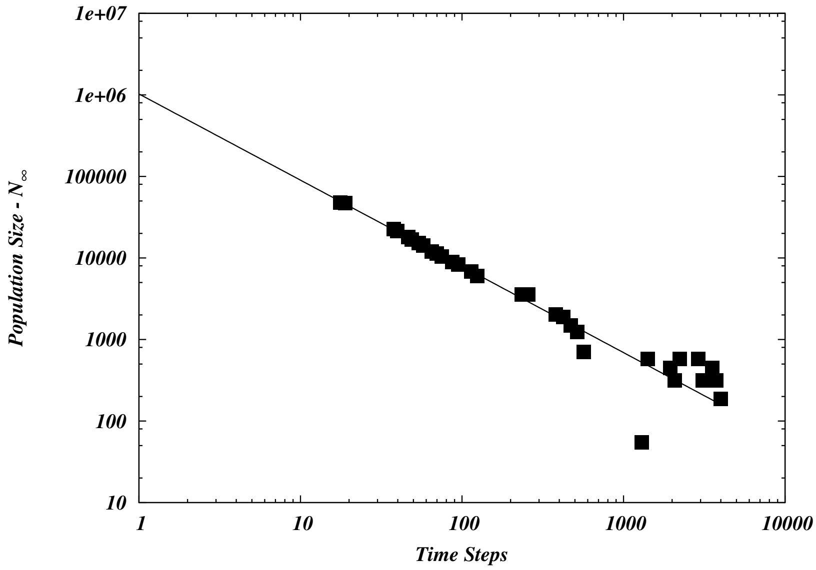

Fig. 4. Population size decay as function of the time for a semelparous population. The power law fitting is even better than for the continuosly reproducing population, shown in the previous figure. The parameters are $L = 32$, $T = 3$, $R = 15$, $b = 0.9$ and $M = 0.3$.

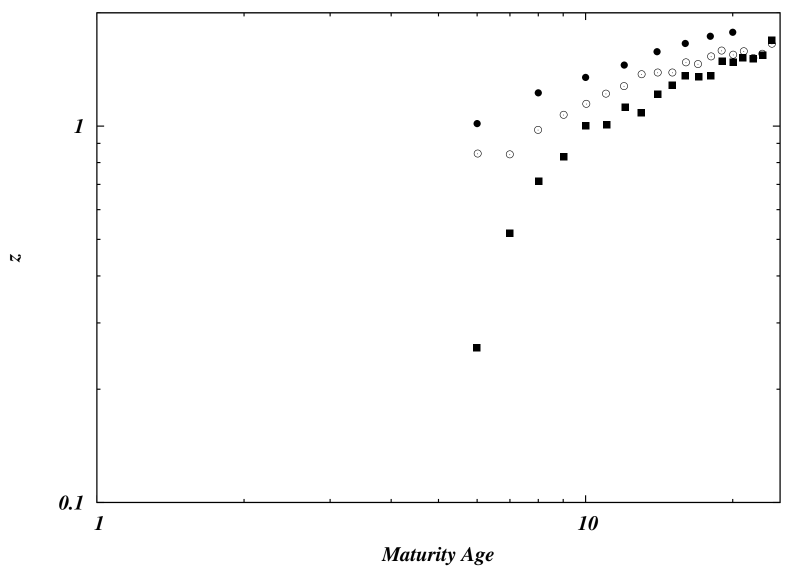

Fig. 5. Dynamical exponent z for different reproductive threshold ages ($R =$, $T = 3$, $M = 0.4$, $N_{\max} = 2.10^6$ and $b = 0.7$). Semelparous population (full squares), two ages interval (empty circles) and four ages interval (full circles) for fertility. z tends to 1.75 for both larger reproductive periods and advanced maturity ages.