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Altruism and antagonistic pleiotropy in Penna ageing model

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Abstract

The Penna ageing model is based on mutation accumulation theory. We show that it also allows for self-organization of antagonistic pleiotropy which helps at young age at the expense of old age. This can be interpreted as emergence of altruism.

Keywords: Monte Carlo; Survival; Population genetics

Introduction

How can altruism arise through Darwinian evolution of the fittest? Why does a bee kill itself but saves many other bees by stinging a large predator? This question worried biologists as well as physicists since a long time (Donato et al., 1997). For more recent models see Yamamura et al. (2004), Peck (2004), Castro and Toro (2004), and Cardia and Michel (2004). Here we check if the Penna ageing model, suitably modified, allows for self-organization of altruism in the sense that the old make sacrifices for the young, or the young for the old.

For human beings, the usefulness of altruism has been studied e.g. by game theories like the famous prisoners's dilemma. Such models require memory and

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forsight, which may not be available to that extent for simpler animals. Even on a human level, it is much easier for a government to lecture others about the need for monetary stability, then to reduce new debts in their own country or to accept punishment if they do not succeed. Egoism in the short run usually is more profitable than altruism, and Darwinian evolution does not think far ahead.

An altruism theory more than a century ago was suggested by Weissmann to explain biological ageing: We die to make place for our children. This idea is very nice and of high moral value but fails to work: To increase the number of offspring it is better to live longer and longer at a constant number of births per year, and thus Darwinian evolution would converge towards immortal parents, whose children die of starvation. In order to give a stable age distribution with a mortality increasing with age one needs an additional effect which counteracts the advantages of longevity. For example, the birth rate may diminish with increasing life span such that the total number of births for one individual stays roughly constant independent of whether the genetic death age is high or low. Such trade-offs between opposing trends, like advantageous longevity and advantageous high birth rates, are called antagonistic pleiotropy if they are controlled by genes which can be mutated to emphasize one aspect at the expense of the other.

The present note aims to explain altruism without intelligence in a biological model which does include a life history, i.e. ageing. For example, how can child care arise genetically? Moreover, we do not want to invent a new ageing model for this purpose but use an already existing and successfully tested ageing model, for which a modification then could allow for altruism. This model is the Penna ageing model (Penna, 1995; Moss de Oliveira et al., 1999; Stauffer, 2004).

The Penna bitstring model (Penna, 1995; Moss de Oliveira et al., 1999; Stauffer, 2004) assumes the chronological switching on of (at least some class of) genes, and the results of Monte Carlo simulations of the population evolution based on this model strongly support Medawar's half-century old mutation–accumulation hypothesis (Medawar, 1946): Dangerous mutations killing an organism in young age will not be transmitted to future generations, while those affecting old age will be given on to the offspring. This model gave good agreement with the exponential increase of mortality at middle age (Gompertz law). Furthermore, the age distribution of populations evolved under the parameters of the model enables the quantitative description of the fitness of organisms of any age measured as a probability giving the offspring. An alternative theory is antagonistic pleiotropy (Partridge and Barton, 1993), where the same mutation has beneficial effects in young age but detrimental effects in old age, like enhanced calcium intake producing bones for the young and arteriosclerosis for the old. Antagonistic pleiotropy was already combined with the Penna ageing model for different purposes (Sousa and Moss de Oliveira, 2001); here we use it to explain altruism. A somewhat similar theory (Stauffer, 2001; Klotz and Stauffer, 2001) explained the shorter life expectancy of men compared with women by testosterone, which makes men more aggressive to protect their family; we like this heroic interpretation better than explanations due to too much alcohol and steaks. In the next section we define our model, followed by a section of results.

Model

We start with the standard asexual Penna model program listed in Moss de Oliveira et al. (1999) and discuss here only the changes. The Verhulst deaths, due to the lack of food and space in densely populated ecosystems, were restricted to the newborn (Sá Martins and Cebrat, 2000) to make the model more realistic; an additional death probability $\pi = (1+p)/2$ at every time step kills individuals of all ages; initially p is set to an age-independent input parameter $-a$.

At every iteration a new type of inheritable mutations occurs: Randomly π is changed by an amount $+\delta/2$ for young age and by the opposite amount $-\delta/2$ for old age. The sign of δ is determined randomly for each individual at each time step, with equal probabilities for positive and negative signs. The absolute value $|\delta|$ is fixed as the input parameter b. The summation of the many mutations of π leads to a probability difference $\Delta = p(t) - p(t=0)$, which is twice the change in the death probability π. Thus a positive Δ means that the old sacrifice their lifes for the young, with a certain probability. (Mutations violating the requirement $-1+b<p<1-b$ were ignored).

The minimum reproduction age was taken as 8 age units, and thus "young" was defined as having an age below an input parameter y, while old individuals had an age above o; typically, $y=6$, $o=10$, $a=0.8$, $b=0.02$. After 2000 iterations the total population as well as the average probability difference Δ barely changed anymore, and we stopped the simulation; in one case this stabilization was confirmed by 10 times more iterations.

Results

Fig. 1 shows the emergence of altruism in the sense of the first model: With suitable parameters we mostly found the old ones to sacrifice their lives for the young, i.e. $\Delta>0$. However, one of the simulations shown there gives negative Δ where the young die for the old. In this figure we varied a and b as shown in the headline, and kept $y=6, o=10$ the same. Fig. 2 shows that varying the length of the bit-string from 8 to 64 does not change much; in order to have a surviving population we changed the minimum age of reproduction from 8 to 5, and defined young and old as 4 and 8, respectively. Fig. 3 shows that varying the limits y and o for young and old age changes the results much less than varying a and b in Fig. 1.

The standard parameters of the Penna model were taken as usual (Moss de Oliveira et al., 1999), and we know that the results of this standard model depend very little on these parameters. Fig. 2 reconfirms this effect for the length of the bit-string. In contrast, this is different for the new parameters introduced in the present model: Depending these parameters, altruism or egoism dominates as seen in Fig. 1.

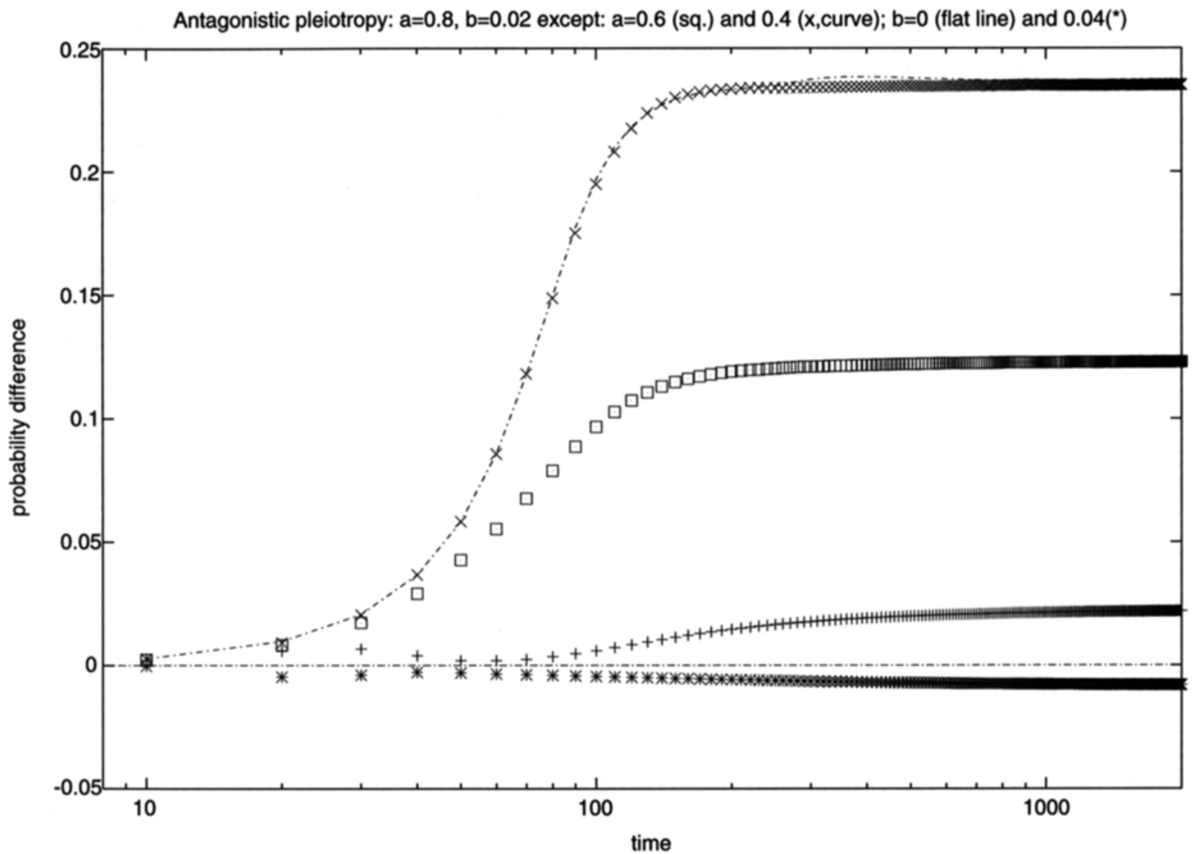

Fig. 1. Δ versus t for various choices of the probability parameters a and b; $y = 6$, $o = 10$, final population several millions. The left border of the figure gives the minimum reproduction age of 8. The line gives a ten times higher population than the x and was also (not shown) continued to $t = 20,000$. Positive Δ means the old help the young.

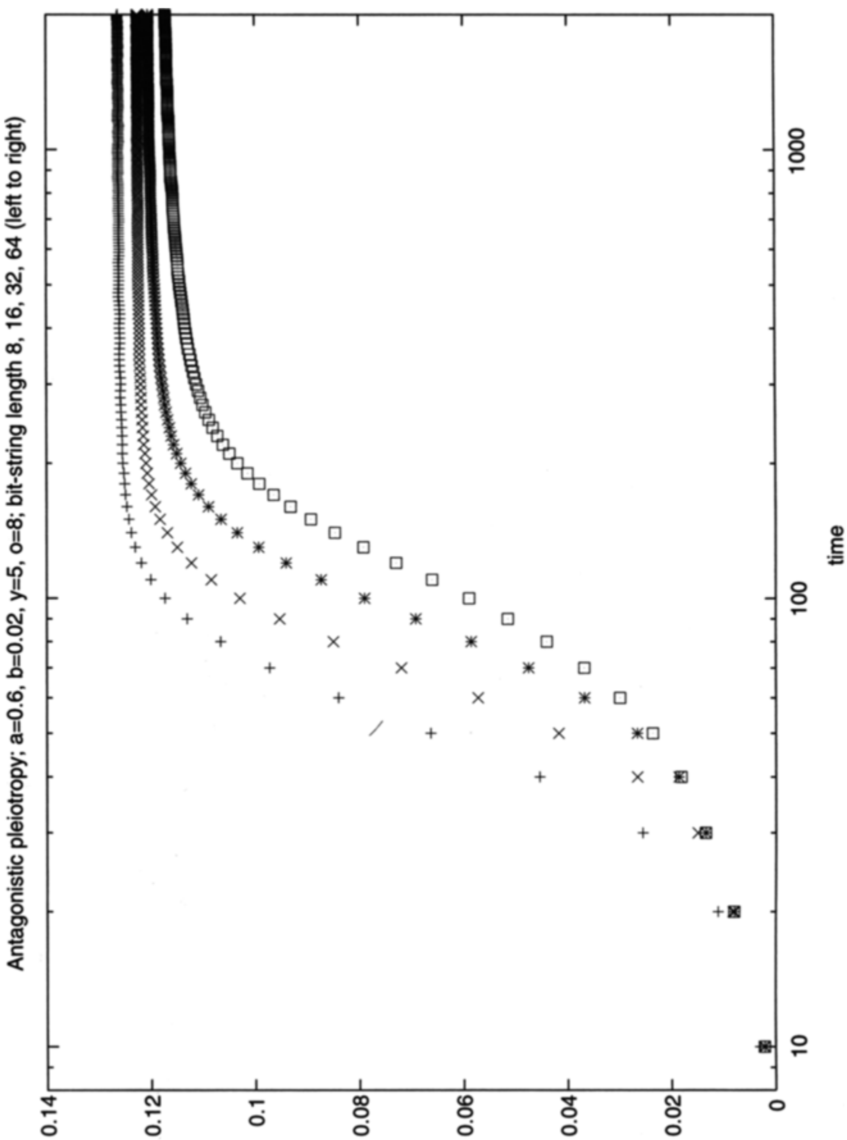

Fig. 2. Δ versus t for various lengths of the bit-strings: 8, 16, 32 (its value in the other figures) and 64; $y = 5$, $o = 8$. In all cases the old help the young.

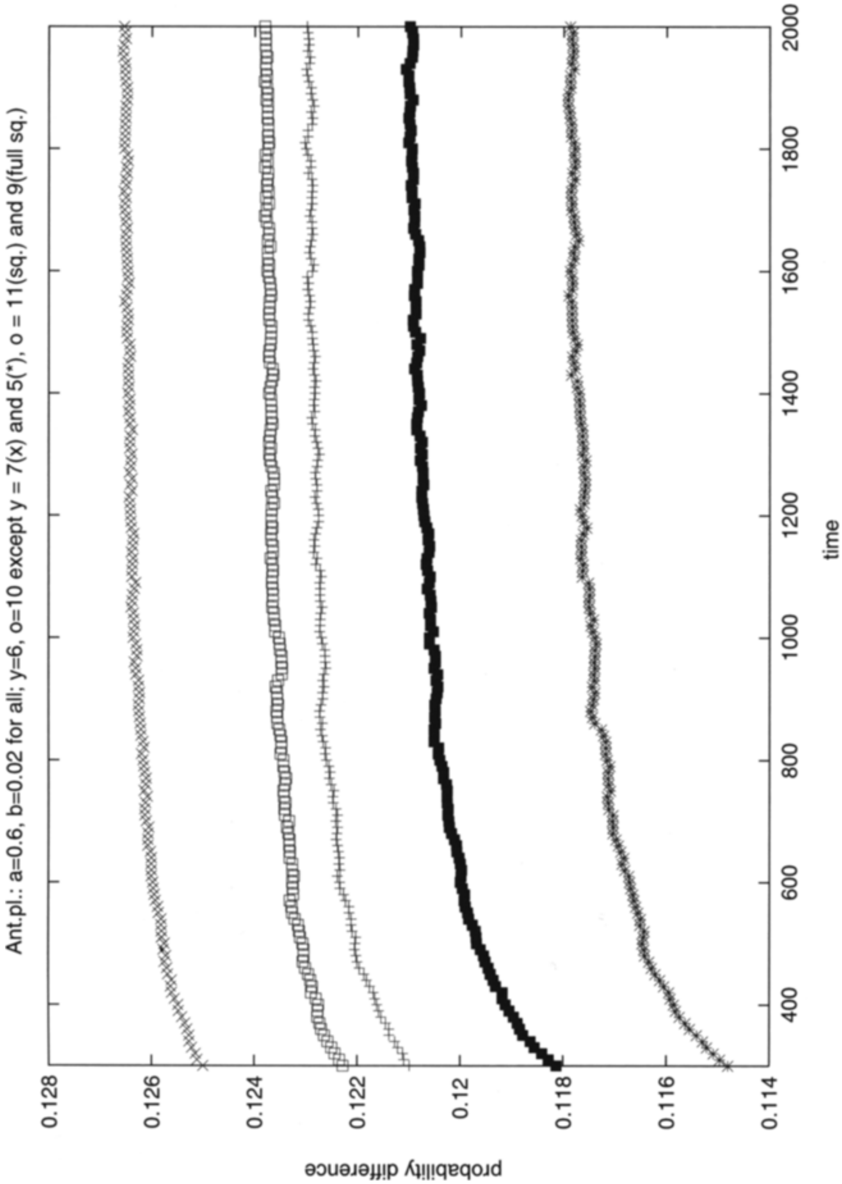

Fig. 3. Δ versus t for various choices of the age threshold y for young and o for old. Note the expanded vertical scale compared with Fig. 1. Final populations near 10^7.

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