Generalization of an Aging Model

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Here we present generalizations of a recently proposed aging model to include several ages and the "Dauer" state. The results show that increasing the number of ages does not matter in one version of the model, but matters in another version, and that the Dauer state does provide a favorable mechanism for survival.

Recently, a number of attempts have been made to tackle the problem of aging by simulating a simple model with the help of a computer (refs. 1 and 2 and references therein). These models make some crucial simplifications of the biological processes and therefore it is important to check whether the results are only the (fortuitous) outcome of the simplifications themselves. Thus, in order to take the models seriously, one has to remove some simplifications and check that the essential results still stand. This is the basic motivation of the present paper. We consider a model which has given some encouraging results recently.[1,2] This model assumes a three-age structure, following Partridge and Barton.[3] (Thus, a population is assumed to consist of babies, juveniles, and adults having ages 0, 1, and 2, respectively.) In one version (called M1 in ref. 2) the probability of survival from age 0 to 1 or 1 to 2 can have any value between 0 and 1, but in another version (called M2 in ref. 2) it can have only some discrete values (regularly spaced) between 0 and 1. With M1 one can handle only a small (100,000 or so) population, but with M2 one can simulate the behavior of an infinite population.

First we attempted to introduce more ages in M1 and M2; thus, now the population consists of individuals of ages 0, 1, 2,..., K, where $K > 2$. This

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had trivial effects in M1, but nontrivial effects in M2. Very recently a similar analysis has been made by Penna.[4] Next we tried to introduce the "Dauer" state in M1. The Dauer state provides a way[5,6] for several kinds of life forms (e.g., the nematode *Caenorhabditis elegans*) to survive hard times. (However, depending on external circumstances, the Dauer state may also prove to be a hindrance for existence, thus justifying the existence of life forms without the Dauer phase, such as human beings.) The results show that the availability of a Dauer state in the model M1 supports the survival of species for a proper choice of the parameter values.

With K ages introduced in M1, one has the following model: The population consists of individuals each having age 0 or 1 or 2 or ... or K, and each carrying survival probabilities $j_0, j_1, j_2,..., j_{K-1}$. In each time step (generation) an individual of age k suffers mutation and gets its survival probabilities j_i ($i = 0, 1, 2,..., K-1$) altered to $j_i' = j_i \exp(\varepsilon)$ and then it survives to an individual of age $k+1$ (with probability j_k') and gives birth to a baby (age $= 0$) having survival probabilities $j_0', j_1', j_2',..., j_{K-1}'$. The persons of age K die after giving birth. The quantity ε is chosen as a random number between ε_l and ε_h, which, in turn, are parameters of the model. We chose $\varepsilon_h = 0.02$ and $\varepsilon_l = -0.04$ (Fig. 1), in accordance with ref. 1. With $K = 11$ (11 ages), the result is that the population and average survival probability for ages $K \leqslant 2$ attain stationary values of reasonable magnitude and those for ages $K > 2$ vanish. Thus the extended version for 11 ages *reduces to* the one for 3 ages.

On the other hand, for an extension of the model M2 to K ages, one needs an L^{K-1} lattice in a $(K-1)$-dimensional fitness space, where L is a parameter of the model. Along the ith axis is plotted the survival probability j_i, which can have values $0, 1/L, 2/L,..., (L-1)/L, 1$. Each individual is associated with a lattice point. The effect of mutation is to keep an individual unmoved or to move it along any of the axes one step forward (thus increasing the survival probability) or one or two steps backward. The total amount of memory required depends on the parameters L, K, but not on the population, so that one can simulate an infinite population by measuring the population always in units of the initial population (some large number). However, one cannot use high values of L or K and we could use only $K = 5$ and $L = 20$ (Fig. 2), which needs 5 MB of memory and 3 hr of computation time (for 500 generations) in our machine. (This choice of L keeps the mutation rate at the same order of magnitude as in ref. 2.) Apart from L and K, there is another parameter b, which is the number of babies to which each individual gives birth after surviving a generation. We adjusted b so that the rate of growth (and decay) of the population is minimum. We found that for $b = 0.5154$, the population and survival probabilities are stationary and, unlike the case of M1, the
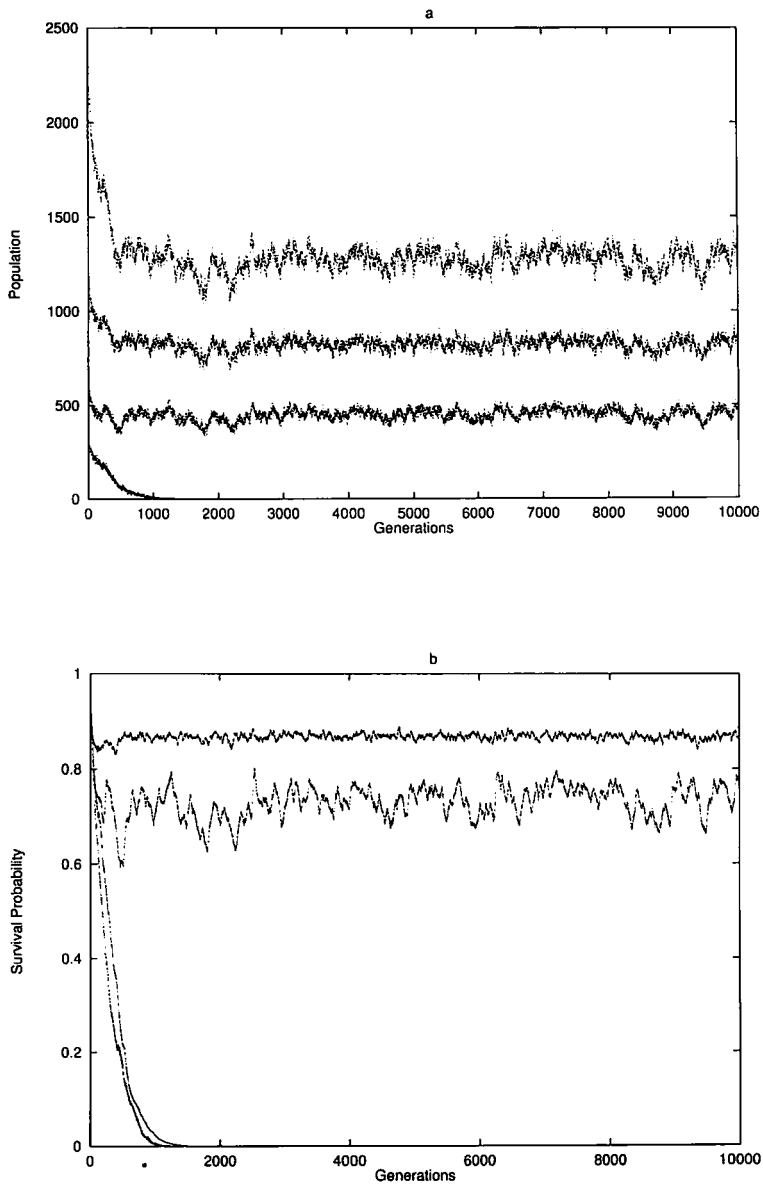
Fig. 1. (a) Population and (b) survival probabilities for ages 0, 1, 2, 3 (top to bottom, respectively) for the model M1 with the parameters $\varepsilon_h = 0.02$, $\varepsilon_l = -0.04$. We started with 4000 babies all having initial survival probability 1. The maximum possible population was 10,000 (this number is important for the food restriction factor[1,2]).
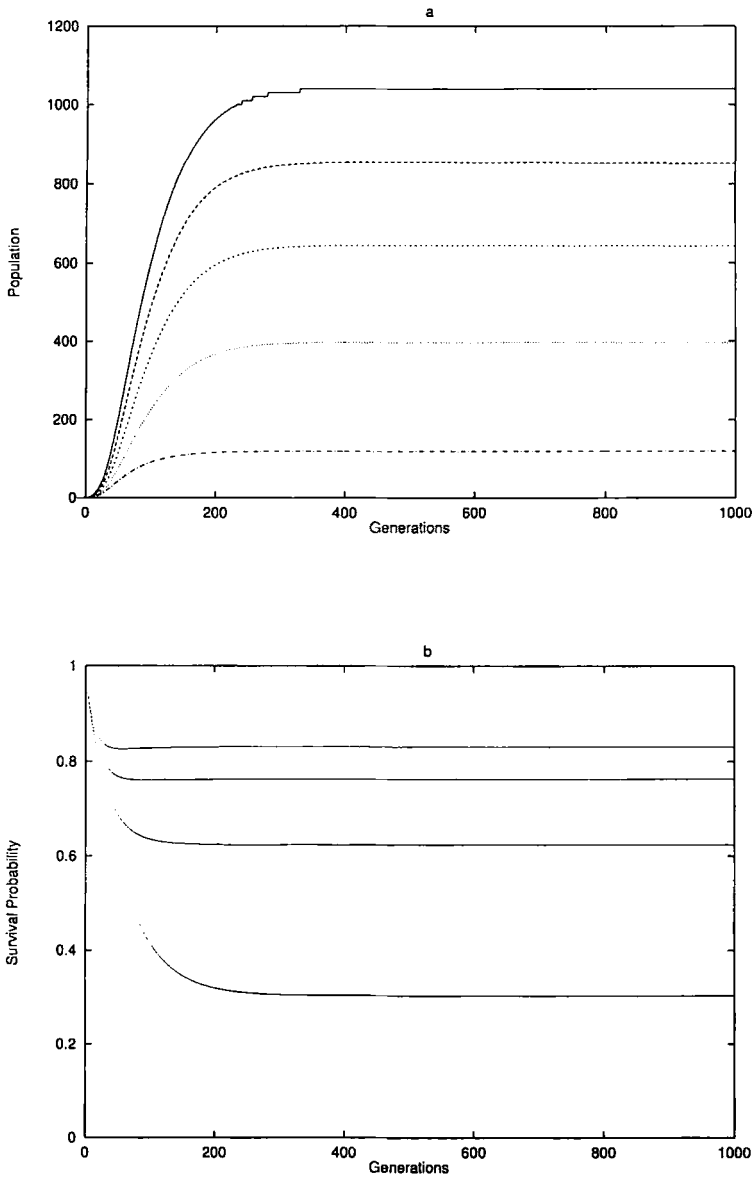
Fig. 2. (a) Population and (b) survival probabilities for ages 0, 1, 2, 3, 4 (top to bottom, respectively) for the model M2 with the parameters $L = 20$, $K = 5$, $b = 0.5154$. We started with a large number of babies all having initial survival probability 1 and measured all types of populations in units of this number.
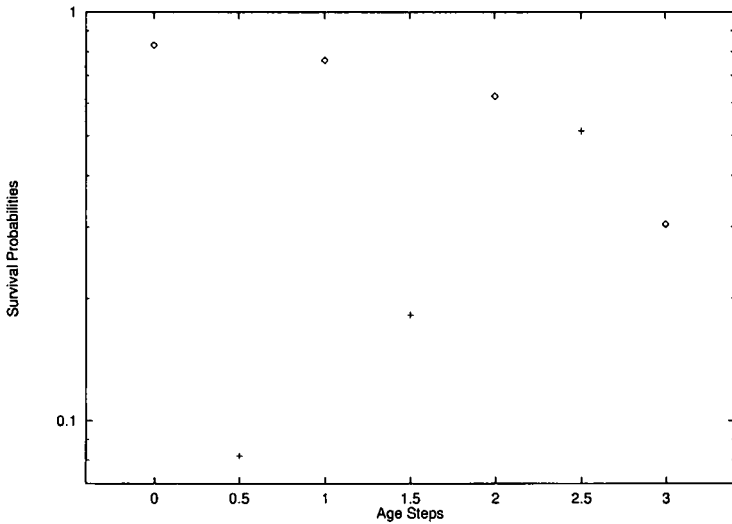
Fig. 3. Plot of the stationary values of the survival probabilities j_i (taken from Fig. 2) versus i (diamonds). The plot of $(j_i - j_{i+1})/j_i$ versus $i + 0.5$ is also shown (crosses).

stationary values are all nonzero. Thus the extended version of M2 for five ages *does not reduce to* one for three ages. It is interesting to plot the stationary values of the probabilities j_i versus i (Fig. 3), which shows a clear downward trend. Also, the plot of $(j_i - j_{i+1})/j_i$ versus i is a straight line, which indicates an exponential decrease with respect to the age.

To include the Dauer state in the Model M1 (with $K = 3$), we treated this state as a detour from age 0 to age 1 (Fig. 4). An individual of age 0 may, with probability d, go over to the Dauer state. In each generation, a
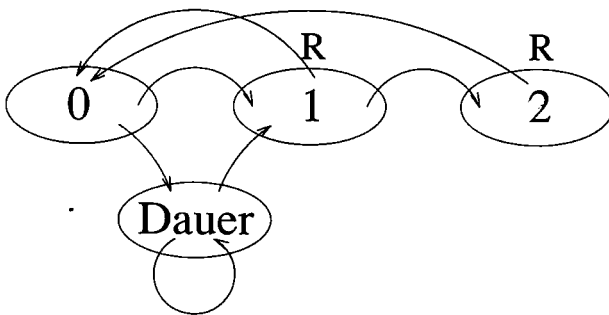

Fig. 4. Schematic diagram of the model M1 with the Dauer state (R indicates reproduction).
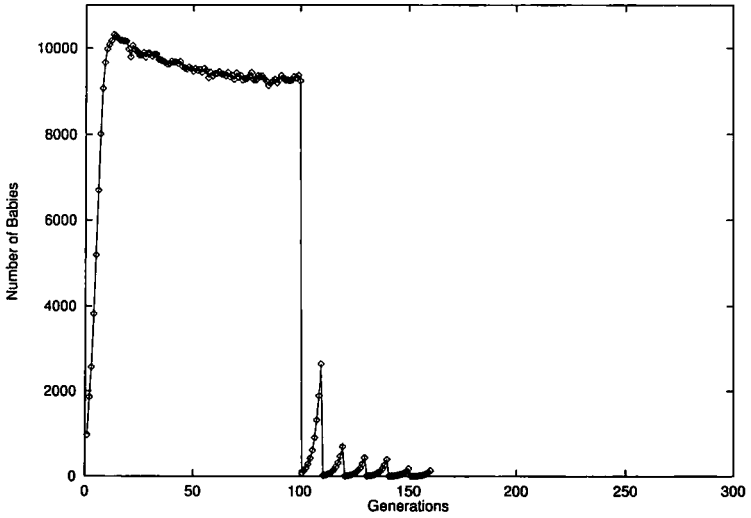
Fig. 5.   Extinction of the population without the Dauer state, $s_b = 0.01$.
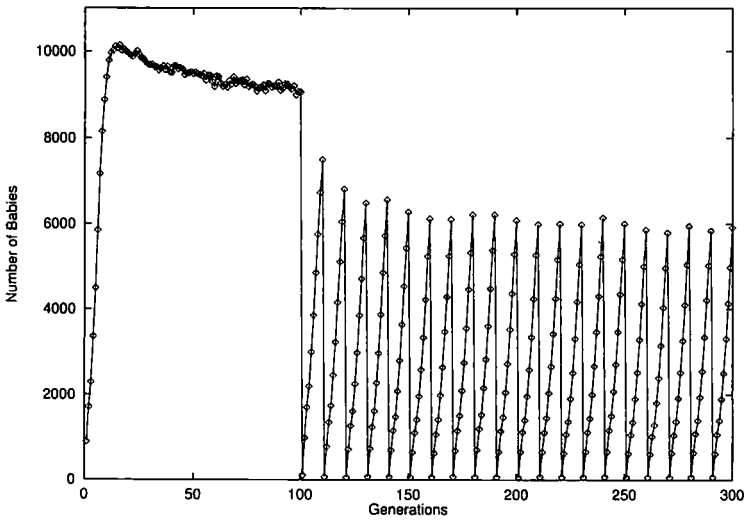

Fig. 6.   The population survives with $d = 0.1$, $s_b = 0.01$.

person sleeping in the Dauer state suffers mutation [survival probabilities are multiplied by $\exp(\varepsilon)$] and then may (with probability $1 - d$) go over to age 1 (and give birth to one baby) or stay in the same state. ε is chosen (as before) as a random number between ε_h (= 0.01) and ε_l (= −0.015). The food restriction factor (see refs. 1 and 2 for details) is now more complicated, since the individuals in the Dauer state do not consume food, but do consume space. This factor is taken to be

$$\left[1 - \left(n_t + \frac{n_d}{10} \right) \middle/ n_i \right]^2$$

where n_t is the total number of babies, juveniles, and adults, n_d is the number of individuals in the Dauer state, and n_i (= 100,000) is the initial population. The choice of this factor is somewhat arbitrary and the sole purpose of it is to prevent (in a reasonable way) the population from exceeding the available computer memory. Every tenth summer is assumed to be "bad," in the sense that all the survival probabilities are decreased by a factor s_b. We chose $d = 0.1$ and $s_b = 0.01$, and found the result that without the Dauer state, the population dies out as a consequence of the bad summers (Fig. 5), but with the Dauer state the population is sustained, according to our expectations (Fig. 6). The results remain qualitatively similar for other d values. (We always started with 1000 babies each having juvenile and adult survival probabilities equal to 1.)

Another model for the Dauer state was also tested (Fig. 7), but for higher Dauer factors ($d > 0.5$) it gives the unnatural prediction that the survival probability for adults is greater than that of the juveniles.

In short, the models M1 and M2 used in refs. 1 and 2 have been generalized to more ages and to include the Dauer state and the models have been found to stand reasonably the test of generalization.
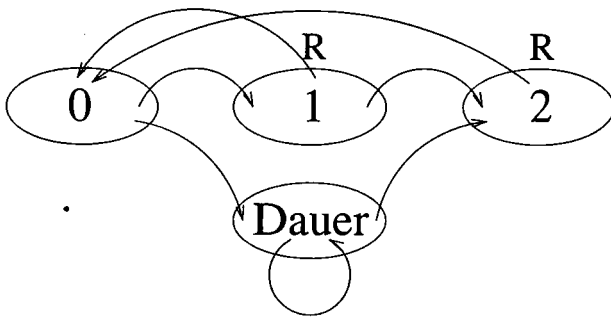

Fig. 7. Diagram of an alternative model for the Dauer state.

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