

## A Very Simple Model for Declining Mean Fitness

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**Synopsis:** We describe a large-population one-locus, two-allele model that, for certain values of viability and fertility selection parameters, displays a substantial monotonic decline in population mean fitness, concurrent with complete replacement of the allele associated with higher fitness by the allele associated with lower fitness.

**Key words:** demographic transition, selection, viability, fertility

We are in the midst of a worldwide decline in birth rate. Some evolutionary scientists (e.g., Kaplan & Lancaster 2000, Low et al. 2002) have seriously considered the possibility that this represents a genuine decline in evolutionary fitness, rather than a strategy to maximize long term descendents by better endowing fewer offspring. The model presented in this paper is not a serious attempt to interpret demographic transitions. For models of demographic transitions, see the papers cited above as well as Mace (2000) and Rogers (1995). Rather, our model is addressed to the relatively narrow technical question of whether declining population mean fitness is unconditionally inconsistent with very simple, classical, conceptions of evolution in a constant environment.

It has been known for some time that the answer is ‘no’. The traditional interpretation of Fisher’s Fundamental Theorem of Natural Selection guarantees increasing population mean fitness, but only under very restrictive conditions (Kingman 1961). Fisher’s theory has been restated in forms that are quite general, but no longer imply increasing mean fitness (Ewens 2004, pp. 64–67), and models have been identified that exhibit declines in mean fitness for particular parameter values and initial genotype probabilities (e.g., Kempthorne & Pollak 1970, Pollak 1978). This paper continues this development by presenting an extremely simple model that can exhibit a substantial and sustained mean fitness decline. Moreover the decline may occur concurrently with a complete replacement of a ‘high fitness’ allele with a ‘low fitness’ allele.

The model involves one locus with two alleles,  $A_1$  and  $A_2$ , hence three genotypes,  $A_1A_1$ ,  $A_1A_2$ , and  $A_2A_2$ . Gene proportions in zygotes are denoted  $p_1$  and  $p_2$ . The population is large and generations are discrete. Genotypes are characterized by viability parameters,  $s_{ij}$ , and fertility parameters,  $t_{ij}$ , assumed to be temporally invariant and the same for males and females. (Gene and genotype frequencies for males and

females will then be identical after an initial generation, which will be subsequently ignored.) Viability  $s_{ij}$  is the probability that an  $A_iA_j$  zygote will survive to the age of reproduction. Mates are drawn randomly from surviving adults. A mated couple  $A_iA_j \times A_mA_n$  will have  $t_{ij} + t_{mn}$  offspring on the average.

Additive fertility (considered by Roux 1977) is essential, since the comparable multiplicative fertility model will never exhibit declining population mean fitness. Zygotic genotype frequencies are in Hardy–Weinberg form in the multiplicative model (Ewens 2004, p. 56), but not in the additive model.

Genotype fitnesses  $w_{ij}$  are defined as expected numbers of offspring contributed to the next generation,

$$w_{ij} = s_{ij}(t_{ij} + E_x[t_{mn}]),$$

where  $E_x[t_{mn}]$  is the expected mate's fertility with respect to the genotype frequency distribution,  $x_{mn}$ , of survivors. Thus  $w_{ij}$  is frequency dependent. Population mean fitness,  $w$ , is the expected value,  $E_p[w_{ij}]$ , of  $w_{ij}$  with respect to the zygotic genotype frequency distribution  $p_{ij}$ . This works out to

$$w = 2E_p[s_{ij}]E_x[t_{mn}].$$

A function for calculating successive genotype frequency distributions and graphing output is posted at <http://psych.upenn.edu/~norman/model.txt>.

The function runs in the R computer environment, which can be downloaded free from <http://www.r-project.org>.

Table 1 describes the behavior of the model for five sets of parameter values. Only  $s_{11}$  varies, assuming the values 0.4, 0.5, 0.6, 0.7, and 0.8. The other viabilities are unity. The fertility  $t_{11}$  is 2; other fertilities are unity. The initial genotype frequencies are 0.99, 0.01, and 0 for  $A_1A_1$ ,  $A_1A_2$ , and  $A_2A_2$ . So  $A_1A_1$  initially predominates, and population mean fitness is initially near  $w_{11}$ , which is, in turn, near  $2 \times s_{11} \times 2 = 4s_{11}$ .

The case of greatest interest is  $s_{11} = 0.6$ , where mean fitness declines monotonically from 2.4 toward 2.0 while  $A_1$ , associated with higher fitness, is completely replaced with  $A_2$ , associated with lower fitness. Results for this case are presented graphically in Figures 1 and 2.

Table 1. Trajectories of  $A_1$  allele proportion and mean fitness

$s_{11}$	Behavior of $p_1$	Behavior of mean fitness
0.4	Declines toward 0.	Rises from 1.6 toward 2.0.
0.5	Declines toward 0.	Constant at 2.0.
0.6	Declines toward 0.	Declines from 2.4 toward 2.0.
0.7	Declines toward 0.6475.	Declines from 2.8 toward 2.33.
0.8	Rises toward 1.	Rises toward 3.2.

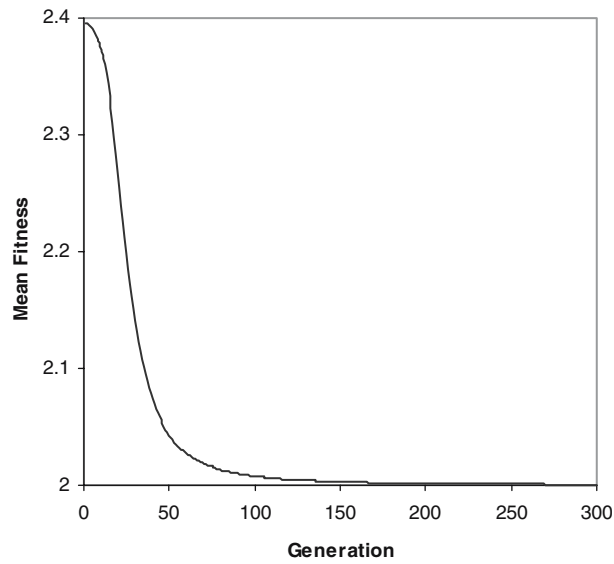


Figure 1. Mean fitness versus generation,  $s_{11} = 0.6$ .

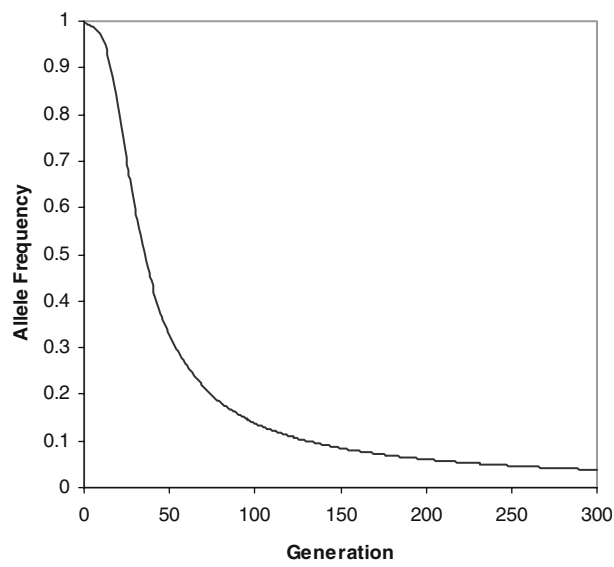


Figure 2.  $A_1$  allele frequency versus generation,  $s_{11} = 0.6$ .

The long-term decline of  $A_1$  allele frequency is very slow, reaching 0.01 only after approximately 1050 generations. Given that the decline occurs at all, it is expected to be slow, since the asymptotically predominant genotypes,  $A_1A_2$  and  $A_2A_2$ , have the same fitness.

This model is not put forward as an interpretation of demographic transitions, but the cases with declining fitness show one additional feature of some such transitions: increasing viability (from  $s_{11}$  to 1) combined with decreasing fertility (from  $t_{11}$  to 1).

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