Does dominance-recessiveness have a survival value? (draft September 26, 1997)

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1 Introduction

In this paper we describe results of a computer experiment concerning the survival value of having genes which are not expressed equally in heterozygotes, i.e., one being dominant and the other recessive. The basic idea is that this property serves for keeping genetic diversity, since recessive genes are more resistant against the selection pressure. If a recessive gene is present in a small number of individuals, it is very seldom expressed, thus it can survive for a long time under unfavorable conditions. Such a gene may save the species from extinction in case of sudden change when the environment starts to select strongly against the dominant gene. It may have other advantages, which we shall not consider here, eg. it may help the species to inhabit a territory where the environment is not suited for the dominant gene.

In this paper we are concerned with a more subtle question of a possibility of regulating dominance. The survival advantage of a recessive gene is very limited. It may save the species from extinction, but then the dominant gene dies out. The species looses its genetic diversity and a period of strong selection against the remaining gene will kill the species completely. On the other hand, if there is a possibility of switching the dominance according to the need, the dominant gene under selection pressure can switch to being recessive and thus prevent its extinction. At least in one case a shift in dominance have been actually observed. It is the case of the industrial melanism of the peppered moth. Originally, when observations started, the heterozygotes were of intermediate color, while during the industrial revolution in England the dark color became dominant [2][page 288]. Hence the possibility of switching between being dominant and recessive is not purely hypothetical.

In our computer experiments we use three types of populations with respect to a pair of alleles which we call *black* and *white*. In the first kind the genes are expressed equally, we call this type *neutral*. The second type has recessive black. The third type, called *switching type*, is able to switch the recessiveness. The switching type uses two loci with two alleles. One locus can be interpreted as controlling the colour, the second as controlling the dominance of the color alleles, the detail description will be given in the next section. The basic idea of switching is as follows. Suppose that the selection prefers the black phenotype. Then on homozygotes it does not distinguish the control genes, but on color heterozygotes it prefers the genes which make black dominant. Thus under this pressure the population not only becomes black, but also black becomes dominant in most individuals.

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We have also tried a more complicated mechanism of dominance control. The idea is borrowed from [1] and is based on the result that the frequency of a particular gene in the whole population can be, with some precision, encoded in each particular genome using only a simple crossing over mechanism (provided that frequency is kept fixed for some time). This is done, roughly speaking, by "counting" matings with mates having this gene. Then the information on the frequency of the gene is used for switching the dominance. It has turned out, however, that this kind behaves almost equally as the switching type described above. Thus we do not consider it in this paper.

Our computer experiments confirm that the recessive type can survive some changes of selection pressure which the neutral type does not and the switching type is even better, it can survive changes under which both neutral and recessive type die out. However we were able to show that only for a very special type of changes, where there is little pressure most of the time and once in a while there is a "catastrophe" where the selection works very strongly against a certain phenotype for a short period. Because of that we cannot conclude definitely that these phenomena bring some survival advantage in a changing environment. It is possible that one has to consider interaction of more genes or the presence of mutations etc. in order to get a clear explanation of the existence of unequally expressed genes.

2 Description of experiments

We consider a limited size population of diploid individuals with a pair of alleles B and W which we think of as representing the colors *black* and *white*. The phenotypes are only two, black and white, no intermediate colors. Selection will depend only on the color. The population develops in discrete generations. In each generation a certain number of pairs is chosen randomly and they mate. Each pair produces one offspring and the parents remain in the population. The number of mating pairs decreases as a function of the current size of the population N and it is chosen so that the total number of individuals after mating does not exceed a certain bound. We use the following formula for the number of mating pairs

$$\operatorname{arctg}\left(c\frac{\pi N}{2M}\right) \cdot M \cdot \frac{2}{\pi} - N,$$

where $c = 1.3$ and $M = 3000$. This means that almost 30% new individuals appear in each generation, if the size of population is close to 0. This number decreases with increasing size and at 1553 there are no mating pairs. Hence the size of population cannot exceed this number. The genotype on the locus of B and W is determined by the usual rules, e.g. BB and BW produce BB or BW each one with probability 1/2. The phenotype of BB resp. WW is black resp. white. The phenotype of a heterozygote BW is black resp. white, if black resp. white is dominant. In case there is no dominance, the color is randomly chosen with equal probability. (This is in order to have only two phenotypes and thus simplify the rules, but it is essentially equivalent to having the "gray" phenotype.)

Selection is determined by a sequence of four-tuples. A four-tuple encode the percentage of white resp. black individuals which die in each generation, the number of generations for which this takes place and the number of generation during which selection changes to the next value. Eg.

0.05 0.30 10 300; 0.30 0.05 10 300

means that in each generation die 5% black and 30% white individuals die in each of the 10 generation, then the selection gradually changes to the opposite in 300 generations etc. The gradual change is done by a cubic spline function, but linear change would likely have the same effect in most cases, due to big inertia of the changes in population. The first two numbers are always chosen positive, hence every individual will eventually die with probability tending to 1.

We consider three types of "species": (1) with no dominance, we shall call them *neutral*, (2) with one color dominant and (3) a type where dominance is switched, which we shall call *switching*. The phenotype of the first two kinds is determined as described above. The switching type has another locus with two alleles w and b. A homozygote ww (resp. bb) is dominant in gene W (resp. B), in a heterozygote bw there is no dominance of a color. The dependence of the phenotype for the switching type is given explicitly in the table below.

genotype	phenotype
xxBB	black
xxWW	white
bbBW	black
wwBW	white
bwBW	1/2 white and 1/2 black

3 Experimental results

In this section we shall describe the results of our experiments. We consider three scenarios for the selection pressure. For each scenario we test the three types. Each figure contains the graph of the selection pressure and the size of populations of particular colors in the three types. The color black is represented by a black line, white by a grey line. Higher black pressure means more black individuals die. Vertical lines mark 10 generations. Since the simulation is a random process, the chosen selection functions do not determine the run; in each case we present a typical run.

Scenario 1 – periodically changing environment, Fig. 1. The selection is given by: 0.15 0.15 50 10; 0.35 0.10 10 10; 0.10 0.35 10 10; repeat{0.45 0.05 10 10; 0.05 0.45 10 10}, ie., periodically changing short periods of strong selection against one color. In the neutral type both colors survive for ever. The periods are too short to extinguish a color and in the next period the gene is able to use the favourable situation to spread quickly. The type with recessive black dies out very fast. The white is wiped out easily because of its dominance, then there are no heterozygotes to save the black from the strong pressure in the following periods and the black goes away too. The switching type struggles for a longer time, as it is closer to the neutral type, but also eventually dies out. The recessiveness slows down recoveries, thus both colors gradually decrease.

Scenario 2 – white catastrophes, Fig. 2. The selection is given by: repeat{0.05 0.15 200 5; 0.45 0.05 80 30}, ie., long periods with small selection pressure and slight white preference alternate with short periods when there is strong pressure against white. In the neutral type black color dies out before the first white catastrophe which kills the remaining white. When black is recessive, it survives the initial period and then remains for ever, since without a competition with white the pressure is not strong enough to extinguish it. In the switching type, black becomes recessive in the initial period, hence it survives to the white catastrophe. Unlike in the previous type, white is not extinguished in the white catastrophe, since it is switched to recessive. The preference of white in the next period causes white to spread out and black become recessive. At the next white catastrophe the situation repeats itself an it goes on.

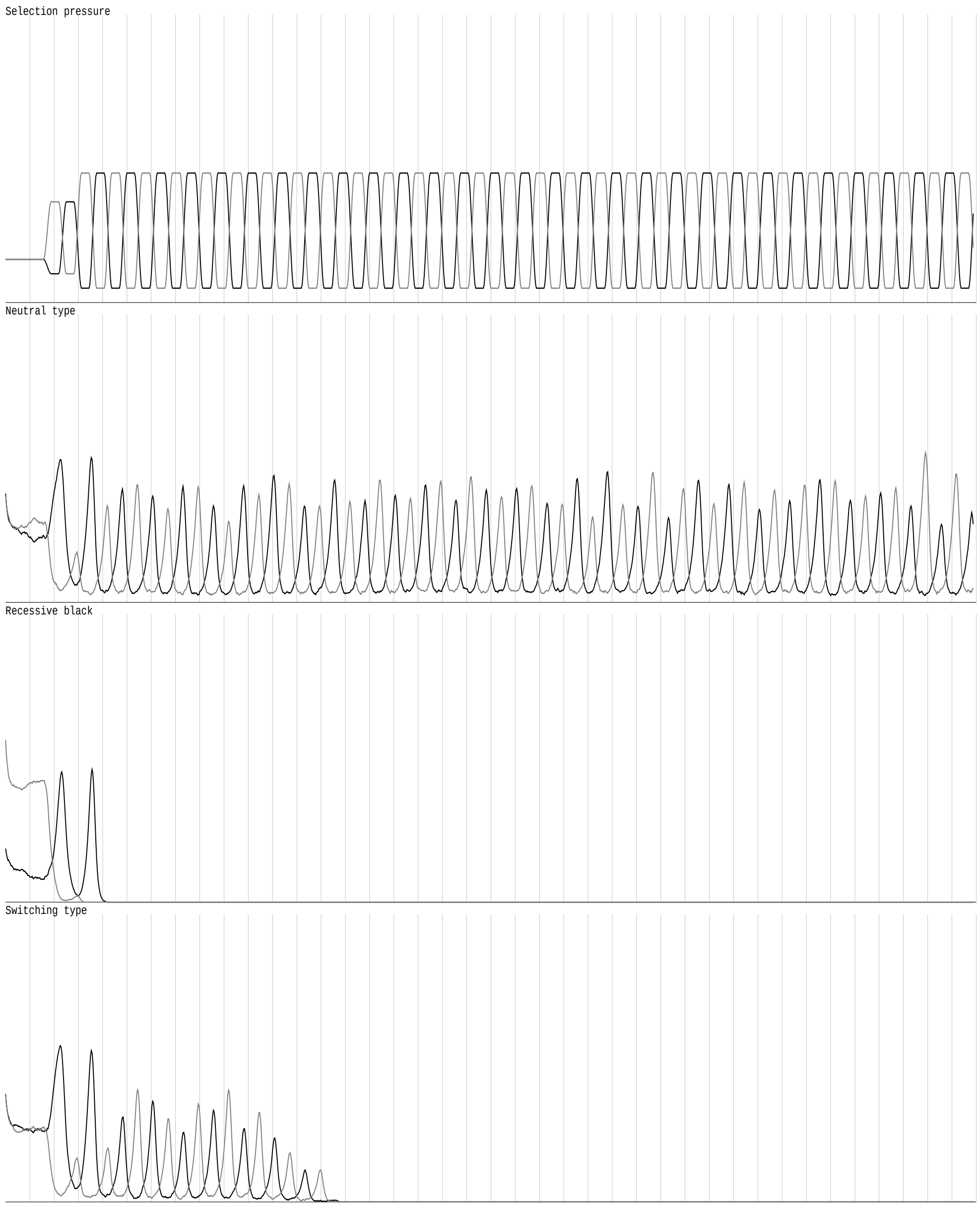

Figure 1: Scenario 1

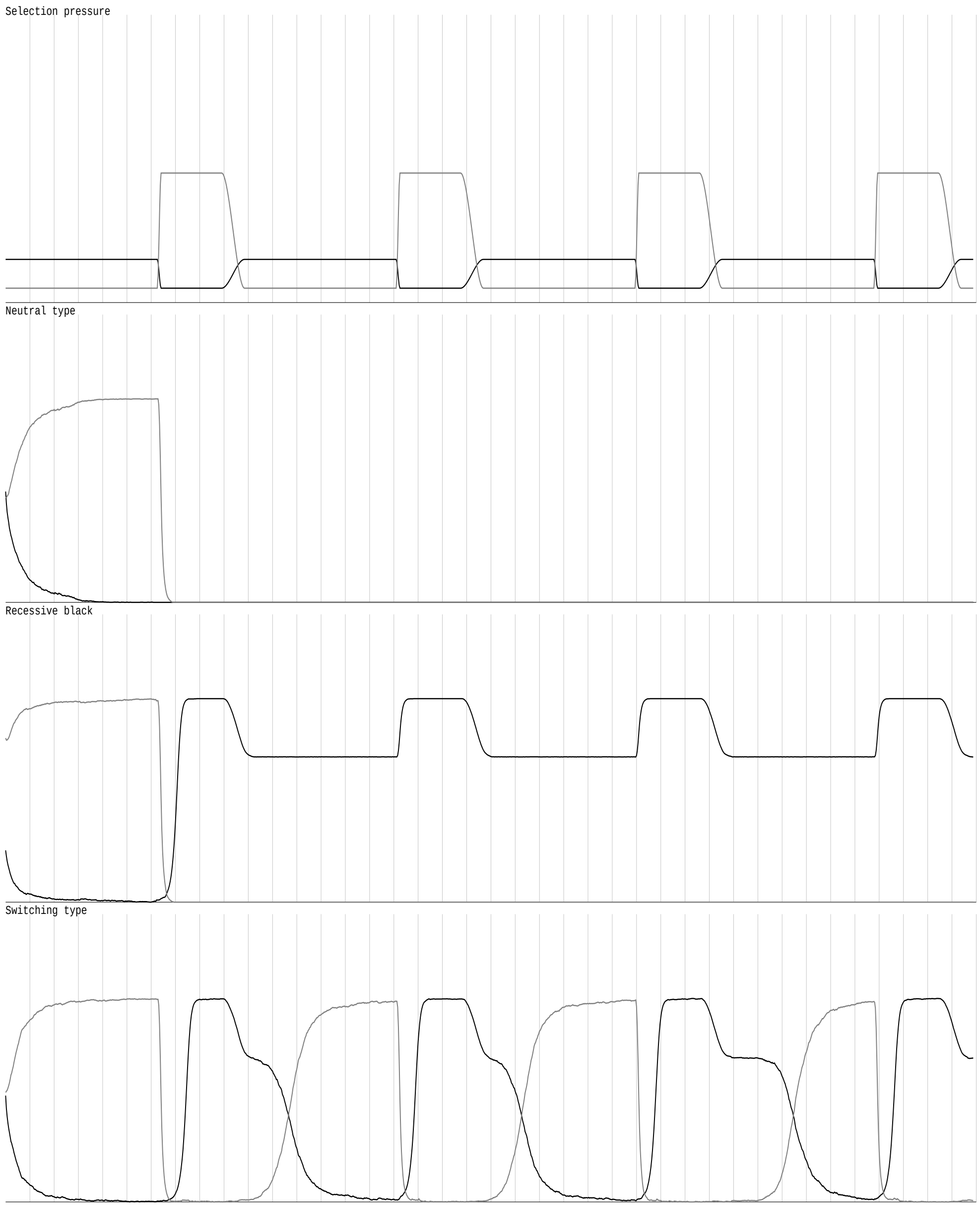

Figure 2: Scenario 2

Scenario 3 – alternating white and black catastrophes, Fig. 3. The selection is given by: 0.05 0.05 200 5; repeat{0.40 0.05 35 25; 0.06 0.05 200 5; 0.05 0.40 35 25; 0.05 0.06 200 5}. This is similar to the previous case except that after each catastrophe the role of the colors is interchanged, the catastrophes are shorter and the preference between catastrophes is not so strongly expressed. In this case the switching type usually survives much longer than the others. The switching mechanism helps to survive the catastrophes as in the previous case. The neutral type behaves in a very similar way, but it is more sensitive to the catastrophes, thus dies out soon. In the population with recessive black, the dominant white is extinguished during the first white catastrophe. The next black catastrophe kills the remaining black, because there are no heterozygotes which can save the black gene.

Scenario 4 – alternating black and white catastrophes, Fig. 4. The selection is the same as in the previous case, but the colors are interchanged. Thus the first catastrophe is black. Because of the symmetry, the neutral and switching types behave in the same way as in the previous scenario. (In the particular run shown in Fig. 4 the neutral type lasted only till the third catastrophe, while in Fig. 3 till the fourth one. This is due to the randomness of the process.) The type with recessive black lasts longer than in the previous case, because the first black catastrophe does not extinguish the black gene. After that, however, the fate of the species is the same as in the previous case.

References

[1] P. Pudlák, *Complexity theory and genetics (preliminary version),* in Proc. Structure in Complexity Theory, ACM, 1994

[2] W.D. Stansfield, *The Science of Evolution,* Macmillan Publ. Co., 1977

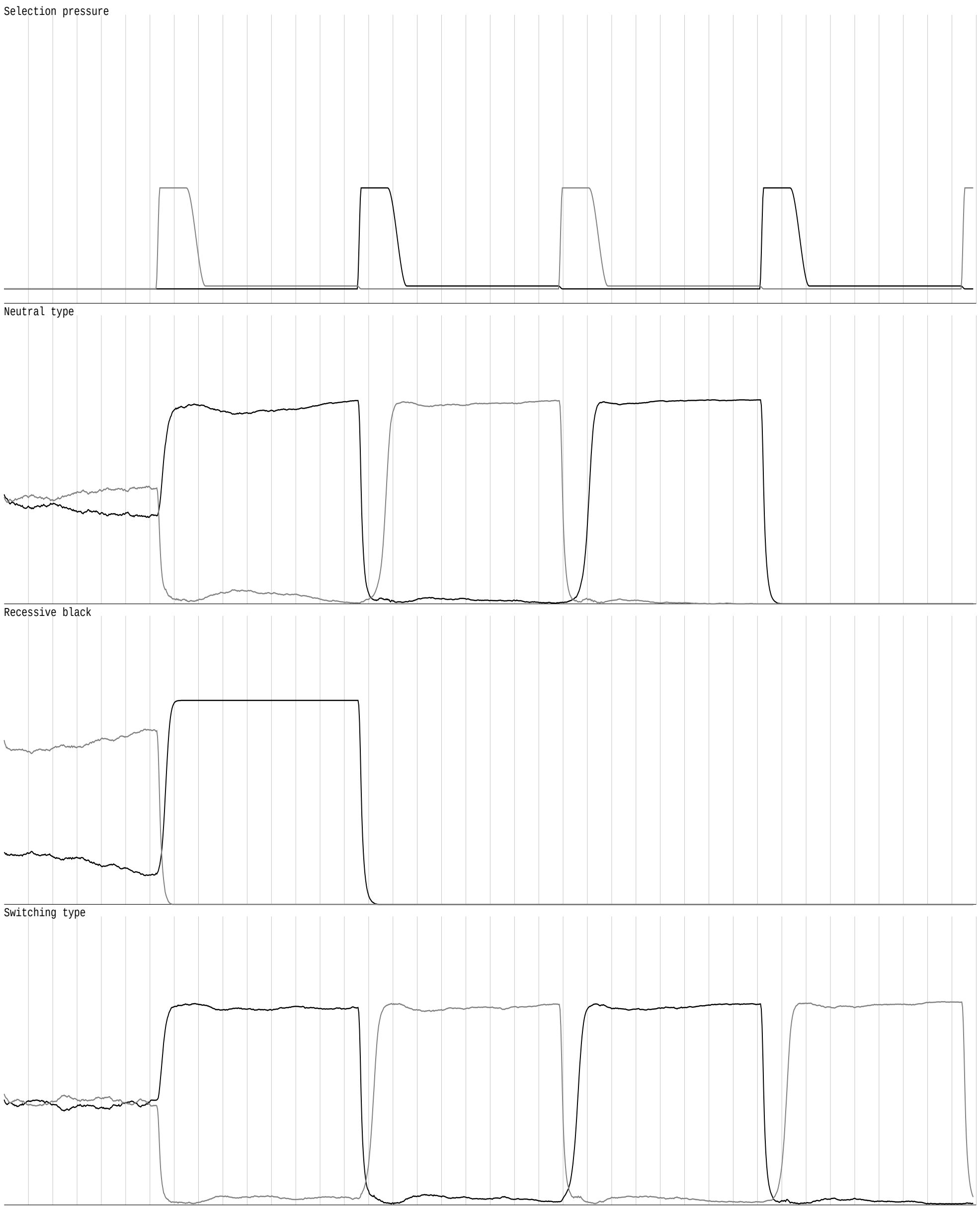

Figure 3: Scenario 3

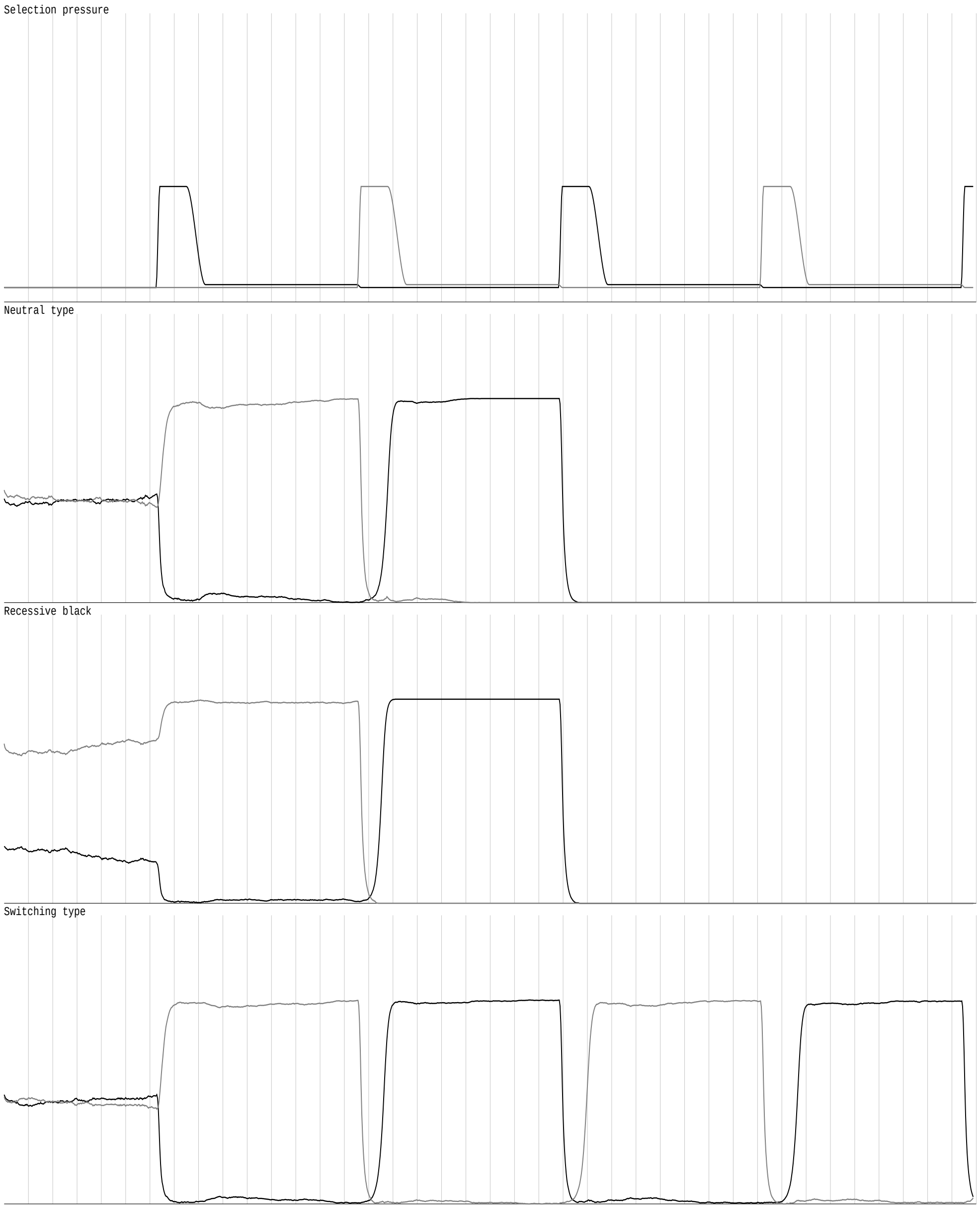

Figure 4: Scenario 4