

The Effect of Fluctuations in Population Size on the Response to
Directional Selection

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ABSTRACT: Ford (1964) and Carson (1968) have argued, on intuitive grounds, that fluctuations in population size due to periods of temporarily relaxed selection (flush) followed by periods of intense selection (resulting in a crash) can enhance the rate of evolution of the population. Because of the exponential nature of unrestricted growth, a population undergoing such a flush would require a greater overall selection intensity to reduce it to its original size at the end of a cycle than would have sufficed to maintain the population constant in size over an equivalent number of generations. To determine the effect which this difference in total selection intensity might have on the rate of evolution, I develop a simple model comparing the relative responses to directional selection for a phenotypic trait in a population which undergoes such a cycle with one which remains stationary in size. The model shows a lower selection response by the fluctuating population than the stable one, a deficiency which becomes more intense with wider population fluctuations. Any alternative mechanism, such as the production of rare mutants or recombinants, must be effective enough to override the retarding effect demonstrated here.

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One obvious property of natural populations is that they do not remain constant in size over time. Examples of dramatic changes in population numbers include populations of multivoltine insect species responding to seasonal cycles (Andrewartha and Birch, 1954), vole populations undergoing cycles of abundance over periods of several years (Krebs and Myers, 1974) and Tertiary mammal faunas undergoing expansion and contraction over millenia (Simpson, 1944). Fluctuations in abundance must involve changing selection intensities and therefore may have an important effect on the rate of evolutionary change.

Population geneticists have dealt with varying selective values (e.g., Haldane and Jayakar, 1963; Hoekstra, 1975), but since they deal only with gene frequencies, normalizing them each generation, the models simply shift the burden of selection from one genotype to another. In these models, a temporary relaxation of all fitness differences results in a dull interlude with no changes in genotype frequencies.

Ford (1964) and Carson (1968) have suggested that numerical fluctuations per se, can greatly increase the rate of evolution. They argue that the number of individuals in a population will increase when selection is relaxed, allowing the production of an increased range of phenotypes for selection to act upon. It is therefore necessary to distinguish two phases:

1. A period in which the population increases (called a "flush" by Carson) during which there is no change in the population mean; and
2. A period of intense selection ("crash") reducing the population to its initial size.

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Clearly the hypothesis requires that the selective advance occurring during phase 2 more than makes up for time lost during phase 1.

A possible mechanism for such a result is inherent in the nature of population growth. A fluctuating population, because of compound interest effects during the growth phase, would require more intense selection to reduce it to its original size, than the total amount of selection which would be required to maintain an identical population constant in size for the same number of generations. To determine whether this mechanism can produce the result suggested by Ford and by Carson, a model is developed to compare the response to directional selection on a phenotypic trait for a population which is maintained stable in size with a constant selection intensity on a given trait each generation to that of a population which undergoes cycles of abundance due to alternate periods of flush followed by crash.

The Model

1. Response to selection. Consider a normally distributed, quantitatively inherited trait. The trait can be any morphological or physiological character, but not fitness itself. Assume that the phenotypic variance of the trait each generation before selection, σ^2 , is at all times greater than zero and that the genetic component of the variance is due to segregation at a large number of loci, with each having only a small effect. During the generations in which selection occurs, a constant, truncated proportion of the phenotypic distribution is retained as parents of the subsequent generation (figure 1).

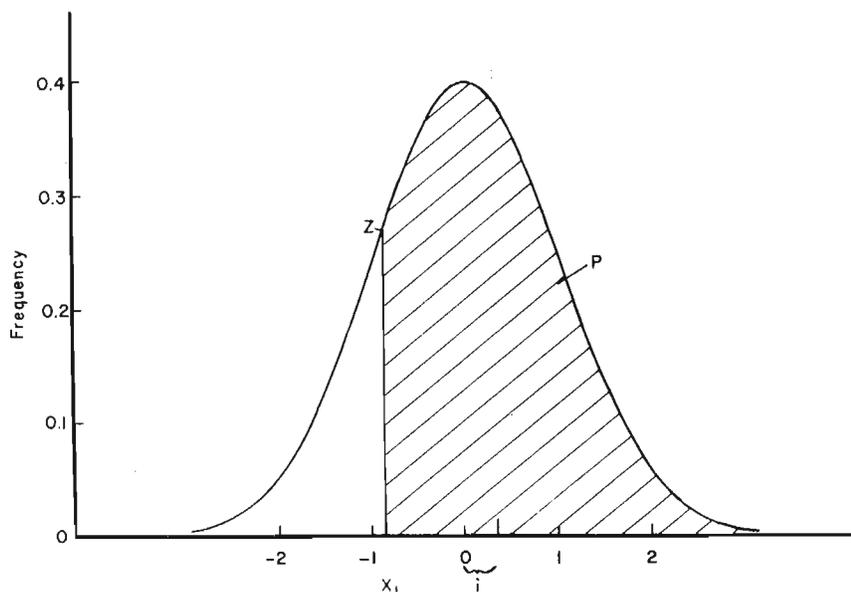


Figure 1. Truncation selection for a trait with normal phenotypic distribution. All individuals with values to the right of x_1 are retained as parents of the subsequent generation. The difference between the means of the original and truncated distributions is i .

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The parents are assumed to mate at random. Truncation selection may seem unduly restrictive as a model for natural selection, but for the purposes of comparison, we need only consider the "potential intensity" of selection as

where the subscript F refers to the fluctuating regime and S to the stable one. We now need expressions for p_S and p_F .

2. The proportion selected in the stable regime. Assume the model for growth in a population with discrete, non-overlapping generations (Crow and Kimura, 1970). If the number of individuals serving as parents in any generation is N_0 , then the number of offspring in the subsequent generation before selection can be written as

$$N_1 = N_0(1+s), \quad s > 0.$$

Denote the number of individuals remaining after selection in the j^{th} generation as N'_j . Since $N'_1 = N_0$, the proportion selected is

$$\frac{N'_1}{N_0(1+s)} = \frac{1}{1+s}.$$

We need not consider s to be the total growth rate of the population, but only the excess culled by selection for the trait under consideration. Thus it would be the growth rate of the population if selection for that trait alone is relaxed.

3. The proportion selected during the crash phase of the cycling population. Assume that the length of a complete cycle is t generations, including c generations in which selection for the trait is relaxed and $d=t-c$ generations of constant directional selection of the intensity required to reduce the population to its original size after selection in generation t . If N_0 is the initial size of the population, then its size at the crest of the cycle before selection in the first generation of selection is given by

$$N_{c+1} = N_0 (1+s)^{c+1}.$$

The proportion retained as parents of the subsequent generation is

$$p_F = \frac{N'_{c+1}}{N_0(1+s)^{c+1}}$$

so that

$$N'_{c+1} = p_F N_0 (1+s)^{c+1}.$$

Since $N_{c+2} = N'_{c+1}(1+s)$, and since we assume p_F to be constant,

$$p_F = \frac{N'_{c+2}}{N'_{c+1}(1+s)} = \frac{N'_{c+2}}{p_F N_0 (1+s)^{c+2}}.$$

Therefore

$$p_F^2 = \frac{N'_{c+2}}{N_0(1+s)^{c+2}}.$$

After d generations of selection, since the population size at the end of the cycle is N_0 ,

$$p_F^d = \frac{N_0}{N_0(1+s)^t} \quad \text{and} \quad p_F = \frac{1}{(1+s)^{t/d}}.$$

The proportion selected in each generation of the crash phase depends only on

s and the ratio t/d. Thus, for example, the case where t/d=2 [and therefore d/t=1/2 in equation (2)], covers all patterns where the number of generations in the expansion phase equals that in the decline phase.

4. The response to selection in stable and fluctuating populations.
 Substituting the values for p_F and p_S into equation (2) gives

$$\frac{R_F^{(t)}}{R_S^{(t)}} = \frac{d}{t} \frac{z_F}{z_S} \frac{(1+s)^{t/d}}{1+s} = \frac{d}{t} \frac{z_F}{z_S} (1+s)^{(t-d)/d},$$

$$\frac{R_F^{(t)}}{R_S^{(t)}} = \frac{d}{t} \frac{z_F}{z_S} (1+s)^{c/d}. \tag{3}$$

This equation is independent of population size, as a direct result of the assumption that selection is slow enough for σ and h^2 to remain constant. Since, in addition, the terms in the summation of equation (1) can be rearranged in any order without affecting the result, equation (3) also holds for the patterns of oscillation depicted in figure 2B and 2C.

The values of z_F and z_S are uniquely determined by p_F and p_S respectively and can be obtained from tables of the normal distribution relating, for any phenotypic truncation point, x_i , the height of the curve, $z_i = f(x_i)$ with the area of the curve truncated to the left at x_i [that is, $p_i = \int_{x_i}^{\infty} f(x)dx$]. Figure 3 gives the ratio $R_F^{(t)} / R_S^{(t)}$ as a function of selective value, s, for various

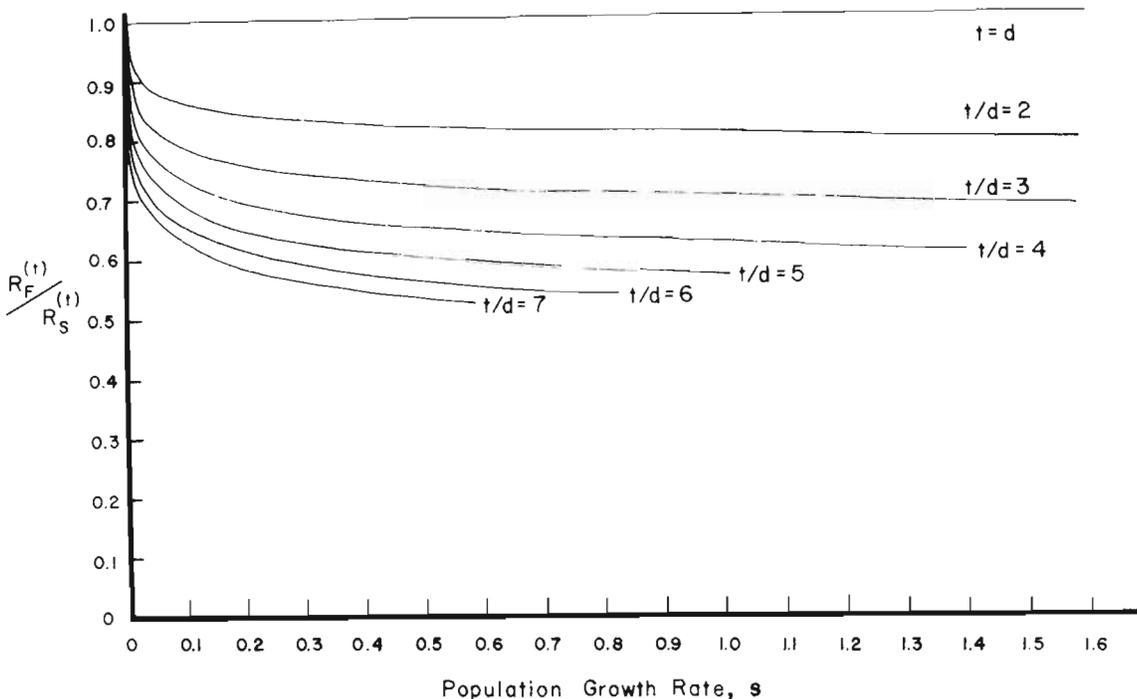


Figure 3. Ratio of the response to selection after t generations, for fluctuating and stable population size patterns, as a function of s, the growth rate of the populations in the absence of selection on the trait. The number of generations in the decline phase of the fluctuating regime is given by d.

values of t/d .

Contrary to Ford's (1964) and Carson's (1968) intuitive arguments, the overall response to selection in the oscillating pattern is less than that of the stable pattern (figure 3). Furthermore, for every value of s , the ratio of the responses decreases with increasing values of t/d , that is, as the decline during the crash phase becomes sharper.

Discussion

Under the conditions of the model developed here, the rate of evolution of a quantitative character, as measured by the response to directional selection, is less in a population which undergoes cycles of abundance, expanding when selection for the trait is relaxed and contracting due to intensified selection, than one which remains stable due to a constant selection pressure each generation. This deficiency increases with wider fluctuations in size (with large s , large values of t/d , or both).

A major restriction of the model deserves comment. It was assumed that neither σ nor h^2 changed as selection progressed. Both parameters may decline by fixation of alleles, either because of selection or due to inbreeding. If loci are fixed by selection, the population having the greater total response (the stable regime) will suffer greater reduction in σ and h^2 . Fixation of alleles can therefore reduce the difference between the two patterns, but the qualitative result, that selection response is retarded in the oscillating population, will not be changed. If loci are fixed by inbreeding, we must distinguish between the patterns depicted in figure 2A, 2B, and 2C. Consider the pattern shown in figure 2A. Since inbreeding effects of a variable population are dominated by the minimum point in the cycle, the effect on σ and h^2 should be roughly similar in the two patterns and should not affect the outcome. For the pattern depicted in figure 2C, inbreeding should have a greater effect on the oscillating population (reducing σ and h^2) than on the stable one. Thus the differences in selection response should be accentuated, not reduced.

An important aspect of Ford's and Carson's arguments is not covered in this model: the production of rare recombinant individuals and new mutants. If this aspect of evolution is sufficiently important that it exceeds the deficiency in selection response found here, then cycles in population abundance could enhance the rate of evolution by this mechanism. However, to the extent that evolution occurs by the steady accumulation of small changes, cycles of abundance must retard, not enhance, response.

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