The Effect of Selection on the Phenotypic Variance

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ABSTRACT

We consider the within-generation changes of phenotypic variance caused by selection \( W(X) \) which acts on a quantitative trait \( x \). If before selection the trait has Gaussian distribution, its variance decreases if the second derivative of the logarithm of \( W(X) \) is negative for all \( x \), while if it is positive for all \( x \), the variance increases.

The action of selection on a quantitative trait can be characterized from many different points of view. Traditionally, the difference between stabilizing (one mode close to the population mean), directional (monotonic fitness curve), and disruptive (two modes) selection is emphasized (see Bulmer 1980). Here we will consider another important feature of selection—its effect on the population variance. Selection may be called narrowing or widening, depending on whether it decreases or increases the phenotypic variance.

The effect of selection on the population variance depends both on the shape of the fitness curve and on the distribution of the trait. Nevertheless, stabilizing and directional selection are usually narrowing, while disruptive selection is widening (Bulmer 1971). This is true, for example, of Gaussian (stabilizing), truncation (directional), and “double truncation” (disruptive) selection (Bulmer 1980, p. 156). However, this connection is not absolute. For example, exponential directional selection does not change the variance of a trait with a Gaussian distribution (see Charlesworth 1990).

Here we demonstrate a sufficient condition for narrowing or widening selection on Gaussian traits. The effect of selection on the phenotypic variance is important, for example, for the evolution of sexual reproduction and recombination (see Kondrashov 1988; Charlesworth 1990).

RESULT AND PROOF

Consider a quantitative trait \( x \) whose distribution in the population \( p(x) \) is Gaussian. Assume without loss of generality that \( p(x) \) is standardized, i.e., its mean \( M[p] = 0 \) and its variance \( \text{Var}[p] = 1 \). How does selection, with fitness function \( w(x) \), influence the variance of this trait? We shall prove that if

\[
(\ln w(x))'' = (w'(x)/w(x))' < 0 \quad \text{for all } x,
\]

then

\[
\text{Var}[P] = I_2/I_0 - (I_1/I_0)^2 < \text{Var}[p] = 1
\]

where \( P(x) = w(x)p(x)/\int w(x)p(x)dx \) is the distribution of \( x \) after selection and \( I_k = \int x^k w(x)p(x)dx \) (here and below integrals are taken from \(-\infty \) to \( \infty \)).

If \( p(x) \) is Gaussian, then, as \( p(x)w(x) \) tends to 0 when \( x \) tends to \(-\infty \) or \( \infty \),

\[
I_1 = \int w(x)(-p'(x))dx = \int w'(x)p(x)dx
\]

and

\[
I_2 = \int xw(x)p(x)dx = -\int xw'(x)p(x)dx = \int w(x) + xw'(x)p(x)dx.
\]

From (4) we obtain

\[
I_2/I_0 = 1 + (1/I_0)\int xw'(x)p(x)dx.
\]

Thus, the statement we want to prove is equivalent to the inequality

\[
J = I_0\int xw'(x)p(x)dx - (I_1)^2 < 0.
\]

Let us rewrite the expression for \( J \) as

\[
J = \int w(y)p(y)dy \int xw'(x)p(x)dx - \int xw(x)p(x)dx \int w'(y)p(y)dy
\]

or, in a double integral form

\[
J = \int \int xw(y)w'(x) - w(x)w'(y)p(x)p(y)dxdy.
\]

The last integral may be also written as

\[
J = \int \int yw(y)w'(x) - u(y)u'(x)p(x)p(y)dxdy
\]

The sum of these two integrals is

\[
2J = \int (x - y)w'(x)w(y) - w(x)w'(y)p(x)p(y)dxdy.
\]

The expression under the integral sign may be rewritten as

\[
(x - y)w'(x)/w(x) - w'(y)/w(y)p(x)p(y)w(x)w(y)dxdy.
\]
The condition \( (w'(x)/w(x))' < 0 \) implies that \( w'(x)/w(x) - w'(y)/w(y) < 0 \) if \( y < x \). Consequently, the two parentheses in the expression under the integral have different signs, so that the expression is negative, which completes the proof. Evidently, if \( (w'(x)/w(x))' > 0 \), \( \text{Var}[P] > \text{Var}[\mathcal{F}] \). A similar result for continuous time and fitness functions that can be expanded into Taylor series follows from Equations 4.9 and 4.4 of Burger (1991).

**DISCUSSION**

To our knowledge, criterion (1) provides the first general condition for narrowing and widening selection, although for any given \( w(x) \) the effect of selection on the phenotypic variance can be easily found (e.g., Bulmer 1980, pp. 147–156). It shows that most "reasonable" forms of stabilizing and directional selection are narrowing. The examples are Gaussian selection \( w(x) = \exp(-(x - m)^2/2V) \) where \( (w'(x)/w(x))' = -1/V \), and linear selection \( w(x) = ax + b \), where \( (w'(x)/w(x))' = -(a/(ax + b))^2 \). Although criterion (1) cannot be directly applied to truncation selection, which involves a discontinuous selection function, such selection can be approximated to an arbitrary degree by other narrowing fitness functions. Exponential selection does not change the variance because here \( (w'(x)/w(x))' = 0 \), while disruptive selection is usually widening. Of course, criterion (1) cannot be applied to "mixed" fitness functions where \( (\ln w(x))'' \) has different signs with different values of \( x \).

Our analysis does not depend on the nature of the genetic control of the trait. If, however, the trait is genetically determined, some further implications should be considered. Suppose that an individual carries a large number of genetic factors each of which can be in two alternative states, \( I \) and \( II \), and \( x \) is the number of factors \( II \) in the individual's genotype. In this case selection changes the variance exclusively by creation of associations between distributions of factors, and not by changes in their frequencies [the infinitesimal model of Bulmer (1971, 1980, pp. 147–150)]. Then, the decrease of variance means that selection creates repulsion associations between distributions of factors in the same state, in the sense that such factors are distributed more uniformly than randomly. In contrast, an increase of variance reflects creation of coupling associations.

Strictly speaking, criterion (1) can be applied when the number of factors in the genome is large and factors are either distributed independently before selection, or, at least, only pairwise associations exist (non-zero higher-order associations would make \( \mathcal{F}(x) \) non-Gaussian). In practice, the assumption of a Gaussian distribution seems to give a good approximation (Bulmer 1980, p. 157). The within-generation changes of the phenotypic variance, which are considered here, are, of course, related to its between-generation changes (Bulmer 1980, p. 154–156).

Criterion (1) is analogous to the results with a small number of factors. Suppose that an individual carries only two factors. Then selection creates repulsion association if \( w_0 w_2 < w_1^2 \) (so that \( w_0/w_1 < w_1/w_2 \) were \( w_i \) is fitness of individuals carrying \( i \) factors \( I \), while if \( w_0 w_2 > w_1^2 \), selection creates coupling association (Felsenstein 1965).

As far as changes of the variance and creation of associations between genetic factors are important, criterion (1) justifies using the second derivative of the logarithm of the fitness function in the definition of epistasis under directional selection (Kondrashov 1988; Charlesworth 1990). Epistasis is synergistic (diminishing returns) if each new increment of the trait leads to a larger (smaller) change in the relative fitness. Then, if \( w'(x) \geq 0 \), for example when \( x \) is the number of beneficial alleles at a set of fitness loci, selection is narrowing with diminishing returns epistasis, i.e., if addition of each new allele leads to a smaller increase of relative fitness. In contrast, if \( w'(x) \leq 0 \), and \( x \) is the number of deleterious alleles, selection is narrowing under synergistic epistasis, i.e., if addition of each new allele causes a larger decline of relative fitness.

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**LITERATURE CITED**


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