ON THE COST OF NATURAL SELECTION
IN FINITE POPULATIONS

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ABSTRACT

Haldane's concept of the cost of natural selection or the substitutional load has been extended to deal with finite populations and finite time of gene substitution. Results indicate that the load of gene substitution depends not only on the initial gene frequency of the favorable gene (as in infinite populations) but also on the population size and selection coefficient. The expected amount of selective elimination in a changing environment (such as a polluted environment) is increased with a decrease in the initial frequency of the favorable allele, a decrease in population size, an increase in the selection intensity against the unfavorable allele or an increase in the time of population exposure to the new environment.
Haldane (1957) defined the cost of natural selection as the proportion of non survivors to survivors in the process of substituting an allele for another. The process of gene substitution can occur in a nonchanging environment as a result of a new mutant arising that is more fit than its existing allele; or it can occur as a result of a shifting balance (to use Wright's terminology) between alleles due to a deteriorating environment. Environmental pollution, for example, is an important factor in changing the environment. Assume an enzyme b, which is produced by an allele b, to be an optimal enzyme in the normal environment. However, enzyme b has little ability to handle the pollutants in a polluted environment. Hence, there may be an increase in the rate of mortality. A positive association between the amount of pollutants and the rate of mortality has been reported (Lave and Seskin, 1973). If enzyme B which is produced by allele B has a greater ability to handle the pollutants, B will be favored over b and the frequency of allele B will increase at the cost of allele b due to natural selection.

Whether gene substitution occurs in the old or in the new environment, the original type of individuals can be replaced by a new optimal type due to natural selection without appreciably affecting the size of the population. Haldane (1957) showed that the cost of natural selection or the substitutional load over the whole process of gene substitution in an infinitely large population depends only on the initial frequency of the favorable allele.

In extending Haldane's concept to finite populations, several definitions of load have been adopted. As pointed out by Ewens (1972), Kimura and Maruyama (1969) defined the load to be the average load until a gene is lost or fixed in a population divided by the probability that a gene is fixed. Ewens considered
in addition a conditional load, that is the average load in a population resulting from a gene substitution that is eventually fixed in the population. In both these definitions, the load is finite. Felsenstein (1971) argued that Haldane's concept of a substitutional load is only meaningful in a deteriorating environment, and that the load will be then infinite if there is a positive probability that the favorable allele is lost from the population due to drift. It is finite, however, if mutation to the favorable allele is introduced into the model.

We do not intend here to argue the biological merits on nonmerits of each of these definitions. A case can perhaps be made for each of these different concepts. Our aim in this study is to formulate a theory of substitutional load in finite populations that will predict the load at any generation $t$ and in the limit of the process of gene substitution. Existing load theory in finite populations has been limited to far to studying the load after the process of gene substitution has been in operation for an infinite number of generations.

**SELECTION IN HAPLOID**

Let the population consist of two types of individuals who have alleles $B$ and $b$, and denote $p(i)$ and $1 - p(i)$ their respective frequencies in the population at the $i^{th}$ generation. In a normal environment the $b$ allele is the more favorable allele; however, the $B$ allele becomes the more favorable allele in a polluted environment. Fitness of the two types $B$ and $b$ will be assumed to be $w$ and $w(1-s)$ respectively. Relative to the $B$ type, a fraction $s$ of the $b$ type will fail to survive or their rate of reproduction will be decreased by an equivalent amount due to the effect of environment. In the whole population the ratio of individuals not transmitted to those that are transmitted at the $i^{th}$ generation will be
\[ R(i) = \frac{s[1 - p(i)]}{1 - s[1 - p(i)]} \]

The cost of selection which is the sum over all of the generations involved is

\[ D = \sum_{i=0}^{t} R(i) \]

where \( t \) is the number of generations. When we consider finite populations

\[ R(i) = \frac{s[1 - \bar{p}(i)]}{1 - s[1 - \bar{p}(i)]} + \frac{-s[p(i) - \bar{p}(i)]}{(1 - s[1 - \bar{p}(i)])^2} + \frac{2s^2[p(i) - \bar{p}(i)]^2}{2!(1 - s[1 - \bar{p}(i)])^3} + \ldots \]

Where \( \bar{p}(i) \) is the mean gene frequency at the \( i^{th} \) generation. Considering only the sum of the first three terms of this series, the expected value of \( R(i) \) is

\[ E[R(i)] = \frac{s[1 - \bar{p}(i)]}{1 - s[1 - \bar{p}(i)]} + \frac{s^2}{(1 - s[1 - \bar{p}(i)])^3} \sigma_p^2(i) \]

Where \( \sigma_p^2(i) \) is the variance of gene frequency at the \( i^{th} \) generation. Hence the expected cost of selection is

\[ E(D) = \sum_{i=0}^{t} \left[ \frac{s[1 - \bar{p}(i)]}{1 - s[1 - \bar{p}(i)]} + \frac{s^2}{(1 - s[1 - \bar{p}(i)])^3} \right] \sigma_p^2(i) \ldots \quad (1) \]

To evaluate the expected cost of selection we need to know the mean gene frequency and the variance of gene frequency at each generation.
The change of mean gene frequency at the $i$th generation is approximately

$$\frac{dp(i)}{di} = s \bar{p}(i)[1 - \bar{p}(i)] - s \sigma^2 \bar{p}(i)$$

The drift variance is given by $\bar{p}(i)[1 - p(i)][1 - (1 - \frac{1}{Ne})^i]$, where $Ne$ denotes the effective population size. Substituting the drift variance for $\sigma^2 \bar{p}(i)$ yields

$$\int_{\bar{p}(0)}^{\bar{p}(t)} \frac{dp(i)}{\bar{p}(i)[1 - \bar{p}(i)]} = s \int_0^t (1 - \frac{1}{Ne})^i di$$

Hence

$$\bar{p}(t) = \frac{e^{xl(t)}}{1 + e^{xl(t)}} \quad \ldots$$

(2)

where

$$xl(t) = \frac{s[(1 - \frac{1}{Ne})^t - 1]}{\ln(1 - \frac{1}{Ne})} + \ln \frac{\bar{p}(0)}{1 - \bar{p}(0)}.$$

The variance considering selection and drift is

$$\sigma^2 \bar{p}(i) = \bar{p}(i)[1 - \bar{p}(i)] - \frac{1}{s} \frac{dp(i)}{di}$$

$$= \frac{e^{xl(i)}}{[1 + e^{xl(i)}]^2} [1 - (1 - \frac{1}{Ne})^i] \ldots$$

(3)

Wright (1969) stated that effective population size is defined as that function of the observed numbers that most accurately replaces $N$, the actual population size in the formula

$$\frac{\bar{p}(i) [1 - \bar{p}(i)]}{N}.$$
Using his definition the effective population size from selection and drift can be computed by the relationship

\[
\frac{\tilde{p}(i)[1 - \tilde{p}(i)]}{N_e} = \frac{\tilde{p}(i+1)[1 - \tilde{p}(i+1)]}{N}
\]

Hence the effective population size considering selection and drift for the above equations will be approximately

\[
N_e = \frac{N}{1 + s[1 - 2\tilde{p}(i)]}
\]

(4)

The cost of selection can be computed using equations (1), (2), (3) and (4).

If the population is infinite, \(q^2_{p(i)}\) is zero. Hence the expected cost is

\[
E(D) = \sum_{i=0}^{t} \frac{s[1 - \tilde{p}(i)]}{1 - s[1 - \tilde{p}(i)]}
\]

Taking a generation as a unit of time,

\[
\frac{d\tilde{p}(i)}{di} = \frac{sp(i)[1 - \tilde{p}(i)]}{1 - s[1 - \tilde{p}(i)]}
\]

The expected cost is approximately

\[
E(D) = \int_{0}^{t} \frac{s[1 - \tilde{p}(i)]}{1 - s[1 - \tilde{p}(i)]} di
\]

\[
= \int_{\tilde{p}(0)}^{\tilde{p}(t)} \frac{1}{\tilde{p}(i)} d\tilde{p}(i)
\]

\[
= \ln \tilde{p}(t) - \ln \tilde{p}(0)
\]

(5)
When we consider infinite number of generations and an infinite population, \( \bar{p}(t) \) will approach 1.0. Hence the expected cost of selection is

\[
E(D) = -\ln \bar{p}(0)
\]

This is the result obtained by Haldane (1957). Since \( \sigma^2_{p(i)} \) is zero for an infinite population, the mean changing rate of allele frequency at the \( i \)th generation is approximately

\[
\frac{dp(i)}{dt} = sp(i) \left[ 1 - \bar{p}(i) \right]
\]

Hence in (5)

\[
\bar{p}(t) = \frac{e^{x2(t)}}{1 + e^{x2(t)}}
\]

where

\[
x2(t) = st + \ln \frac{\bar{p}(0)}{1 - \bar{p}(0)}
\]

**SELECTION IN DIPLOID**

Consider a pair of alleles B and b in a random mating population of N diploid individuals with frequency \( p(i) \) and \( 1 - p(i) \) respectively at the \( i \)th generation. In a normal environment the allele b is the favored gene; however, the allele B becomes the more favorable gene in a polluted environment. Fitness of the three genotypes BB, Bb and bb will be assumed to be \( w \), \( w(1 - \frac{s}{2}) \) and \( w(1-s) \) respectively.

The cost of selection can be defined as

\[
D = \sum_{i=0}^{t} \frac{1 - \bar{w}(i)}{\bar{w}(i)}
\]

where \( \bar{w}(i) \) is the mean fitness of the three genotypes at the \( i \)th generation. Hence

\[
D = \sum_{i=0}^{t} \frac{s[1 - p(i)]}{1 - s[1 - p(i)]}
\]
The expected cost of natural selection due to environment pollution is approximately

\[ E(D) = \sum_{i=0}^{t} \left( \frac{s[1 - \bar{p}(i)]}{1 - s[1 - \bar{p}(i)]} + \frac{s^2}{\{1 - s[1 - \bar{p}(i)]\}^3} \frac{\sigma^2_p(i)}{\bar{p}(i)} \right) \]  

(7)

To evaluate equation (7) we need to know \( \bar{p}(i) \) and \( \sigma^2_p(i) \) for diploid populations. Park (1977) showed the expected mean gene frequency is approximately

\[ \bar{p}(t) = \frac{e^{x3(t)}}{1 + e^{x3(t)}} \]  

(8)

where

\[ x3(t) = \frac{s[(1 - \frac{1}{2Ne})^t - 1]}{2}\ln(1 - \frac{1}{2Ne}) + \ln(\bar{p}(0)) \]

By the same procedure as in the previous section we get

\[ \sigma^2_p(i) = \frac{e^{x3(i)}}{1 + e^{x3(i)}} \frac{[1 - (1 - \frac{1}{2Ne})^i]}{[1 - \bar{p}(i)]} \]  

(9)

The effective population size considering selection and drift in the diploid equations will be approximately

\[ Ne = \frac{N}{1 + \frac{s}{2}[1 - 2\bar{p}(i)]} \]  

(10)

Equations (8), (9) and (10) were evaluated extensively by Park and Nassar (1977). They found the above equations to be generally accurate.

When we consider an infinite population \( \sigma^2_p(i) \) is zero. Hence equation (7) is reduced to
\[ E(D) = \sum_{i=0}^{t} \frac{s[1 - \bar{p}(i)]}{1 - s[1 - \bar{p}(i)]} . \]

The changing rate of mean gene frequency at the \( i \)th generation is
\[ \frac{d\bar{p}(t)}{di} = \frac{1}{2} s \frac{\bar{p}(i)[1 - \bar{p}(i)]}{1 - s[1 - \bar{p}(i)]} . \]

The expected cost of natural selection is approximately
\[ E(D) = \int_{0}^{t} \frac{s[1 - \bar{p}(i)]}{1 - s[1 - \bar{p}(i)]} \, di = \int_{\bar{p}(0)}^{\bar{p}(t)} \frac{2}{p(i)} \, d\bar{p}(i) = 2[\ln \bar{p}(t) - \ln \bar{p}(0)] \quad \cdots \quad (11) \]

when \( t \to \infty \), \( \bar{p}(t) \) will approach 1.0. Hence the expected cost of selection due to environmental pollution is
\[ E(D) = -2 \ln \bar{p}(0) , \]

which is also reported by Haldane (1957).
\[ \frac{d\bar{p}(i)}{di} = \frac{1}{2} s \frac{\bar{p}(i)[1 - \bar{p}(i)]}{1 - s[1 - \bar{p}(i)]} \]
\[ \int_{\bar{p}(0)}^{\bar{p}(t)} \frac{d\bar{p}(i)}{\bar{p}(i)[1 - \bar{p}(i)]} = \frac{1}{2} s \int_{0}^{t} di \]

Hence the gene frequency at the \( t \)th generation in (11) is
\[ \bar{p}(t) = \frac{e^{x_4(t)}}{1 + e^{x_4(t)}} \quad \cdots \quad (12) \]
where \( x_4(t) = \frac{1}{2} st + \ln \frac{\hat{p}(0)}{1 - \hat{p}(0)} \)

**NUMERICAL EVALUATIONS**

The cost of natural selection is evaluated numerically to understand clearly the effects of different population sizes in a polluted environment, selection coefficients as a function of mortality, initial gene frequencies as an initial proportion between the favorable and the unfavorable types, and generation number.

Table 1 is computed from equations (1), (2), (3) and (4) for finite haploid populations and (5) and (6) for infinite populations with initial B gene frequency of .1 and selection coefficient .1. We wish to see the effect of population size at each generation on the cost of natural selection. If one million individuals are living in a polluted environment, the number 2.503 at generation infinity indicates that there were about 2.5 million deaths to keep one million survivors in the process of substituting the unfavorable gene for the favorable gene at a locus. The number .93 at the 10th generation indicates 930,000 individuals should die in 10 generations to adjust to the new environment.

When the population size is 10 the ultimate fixation probability of the B allele is .214. In this case the expected cost of natural selection will approach infinity as generation time approaches infinity since there is a .786 probability that only the unfavorable gene \( b \) will exist in the population.

This is seen from the series in (1). If \( \hat{p}(i) \) does not approach 1 as \( t \) approaches \( \infty \), the series in (1) diverges. On the other hand, if \( \hat{p}(i) \rightarrow 1 \) as \( t \rightarrow \infty \), \( \sigma^2_{F_i} \) approaches also zero and the series converges to a finite sum. For the case where \( \hat{F}(\infty) < 1 \) the load will be infinite if we argue that the load does not stop once the favorable allele is lost. The load will be finite, however, if we follow the implicit assumption in Kimura and Maruyama (1969) that the load...
is defined only over the time until the favorable gene is fixed or lost. In the latter case, the summation in (1) will be over a finite time $t$. To state that a load is infinite might not be also completely true, since a population might go to extinction in a finite time if the unfavorable environmental conditions persist for a long time and no mutation to the favorable allele occurs.

Table 1 shows that if the number of individuals is decreased, the expected cost of natural selection increases. However, the effect is negligible unless the size of the population is extremely small. The table also shows that after 40 generations the load is not much different from that in the limit.

Table 2 is computed from equations (7), (8), (9) and (10) for finite diploid populations, and (11) and (12) for infinite populations with initial gene frequency $1$ and selection coefficient $1$. The table shows that the expected cost of natural selection is almost the same between haploid and diploid for early generations; however, the total cost in the limit is about twice in the diploid case. The approach to the limit is also slower in the diploid than in the haploid case.

Tables 3 and 4 show the effect of initial gene frequency on the cost of natural selection. The tables show, as expected, that if the favored gene in a new environment is shifted to a relatively high proportion, the cost of natural selection will be relatively small. In this regard, tables show little difference between haploid and diploid.

Tables 5 and 6 show the effect of selection intensity, which is related to death rate, due to various levels say of environmental pollution. The tables indicate that if the selection intensity is increased the cost of natural selection is also increased.
The equations for the prediction of the expected cost of natural selection have been tested extensively and found to closely agree with the results from simulation. A representative result is given in Table 7. Kimura and Maruyama (1969) obtained the cost of selection with finite populations and an infinite time interval from the numerical solution of the Kolmogorov backward equation. Their results are in reasonable agreement with the results of the above prediction equations. For example they calculated the cost as 5.50 with initial gene frequency .01, selection coefficient .1 and population size 100. Their simulation showed the cost of selection as 5.73. However, the prediction from our equations was 5.86.

The advantages of our equations to existing ones in the literature are that they provide the cost of natural selection at the intermediate generations, and they give the effects of the selection coefficient and the population size separately, not as a product.
Table 1

The cost of natural selection with initial gene frequency .1 and selection coefficient .1. The table shows the effect of population size and generation time in haploid populations.

<table>
<thead>
<tr>
<th>Gener</th>
<th>10</th>
<th>100</th>
<th>1,000,000</th>
<th>∞ (Haldane)</th>
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Table 2

The cost of natural selection with initial gene frequency .1 and selection coefficient .1. The table shows the effect of population size and generation time in diploid populations.

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Table 3

The cost of natural selection with selection coefficient .1 and population size 10. The table shows the effect of initial gene frequency and generation time in a haploid population.

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Table 4

The cost of natural selection with selection coefficient .1 and population size 10. The table shows the effect of initial gene frequency and generation time in a diploid population.

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Table 5

The cost of natural selection with population size 10 and initial gene frequency .1. The table shows the effect of selection coefficient and generation time in a haploid population.

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Table 6

The cost of natural selection with population size 10 and initial gene frequency .1. The table shows the effect of selection coefficient and generation time in a diploid population.

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Table 7

The cost of natural selection with selection coefficient .1, initial gene frequency .1 and population size 20. The table compares the computer simulation results to the theoretical predictions from the equations for a diploid population.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Simulation</th>
<th>Theoretical</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>.098</td>
<td>.098</td>
</tr>
<tr>
<td>5</td>
<td>.490</td>
<td>.480</td>
</tr>
<tr>
<td>10</td>
<td>.969</td>
<td>.965</td>
</tr>
<tr>
<td>20</td>
<td>1.885</td>
<td>1.879</td>
</tr>
<tr>
<td>30</td>
<td>2.761</td>
<td>2.740</td>
</tr>
<tr>
<td>40</td>
<td>3.609</td>
<td>3.557</td>
</tr>
</tbody>
</table>
LITERATURE CITED


Felsenstein, J., 1971  On the biological significance of the cost of gene

Haldane, J.B.S., 1957  The cost of natural selection.  Jour. Genetics,
   55: 511-524.

Kimura, M.T. and Maruyama, 1969  The substitutional load in a finite

Lave, L.B. and E. P. Seskin, 1963  An analysis of the association between

Park, Y.C., 1977  Variance of gene frequencies from recurrent selection in

Park, Y.C. and R. F. Nassar, 1977  Response and variance of response to
   selection.  International Conference on Quantitative Genetics.  Iowa State

Wright, S., 1969  Evolution and the genetics of the populations Vol. 2.  The