A STABLE EQUILIBRIUM WITH MINIMUM AVERAGE FITNESS

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IN population genetics the average fitness of a Mendelian population containing genotypes $G_1, G_2, \dots, G_n$ is defined by the expression:

$$\bar{W} = \sum f_i W_i \quad i = 1, 2, \dots, n$$

where f_i is the frequency of genotype G_i and W_i its relative fitness. If two alleles are segregating in a random mating diploid population, $\bar{W}$ is known to be maximized at equilibrium by selection when the W 's are constants. This paper will present a simple model in which $\bar{W}$ is actually minimized by selection when the W 's are not constants, but functions of gene frequency.

When two alleles B and b with frequencies q and $1-q$ are segregating in a random mating diploid population, all individuals fall into one of three genotypic classes as shown in Table 1. The W 's must be positive so $4 \geq a \geq -1$.

$$\bar{W} = 4 + a[q^2 - 2q(1-q) + (1-q)^2] = 4 + 4a(\frac{1}{2} - q)^2$$

When $q = \frac{1}{2}$, $\bar{W}$ is maximal if $a < 0$ and minimal if $a > 0$.

The expected frequency of allele B in the progeny population is

$$q_1 = \frac{q^2(a + 1/q^2) + q(1-q)[-a + 1/q(1-q)]}{\bar{W}}$$

$$= 2[-q(\frac{1}{2} - q)a + 1]/\bar{W}$$

and the change in gene frequency

$$\Delta q = q_1 - q = 2[-q(\frac{1}{2} - q)a + 1 - 2q - 2aq(\frac{1}{2} - q)^2]/\bar{W}$$

$$= 4(\frac{1}{2} - q)[1 - aq(1-q)]/\bar{W}$$

Since $[1 - aq(1-q)] > 0$, equilibrium ($\Delta q = 0$) occurs only when $q = \frac{1}{2}$.

The stability of the equilibrium can be seen by examining the sign of Δq for gene frequencies greater than or less than $\frac{1}{2}$. Since the sign of Δq is the same as the sign of $(\frac{1}{2} - q)$

TABLE 1

Frequency and relative fitness of genotypes

	Genotype		
	$B B$	$B b$	$b b$
Frequency	q^2	$2q(1-q)$	$(1-q)^2$
Relative fitness (W)	$a + 1/q^2$	$-a + 1/q(1-q)$	$a + 1/(1-q)^2$

$$\Delta q < 0 \text{ if } q > 1/2$$

$$\Delta q > 0 \text{ if } q < 1/2$$

A stable equilibrium occurs at $q = 1/2$ for all values $4 \geq a \geq -1$, and in particular $\bar{W}$ stabilizes at its minimum value when $4 \geq a > 0$. In this model symmetry exists between the fitnesses of the homozygotes. The rare genotype enjoys great selective advantage. The model might describe a population in which selection is based on predator recognition of the most common type.

The model is made more general in Table 2 by introducing two new parameters s and t . The range of a is $4 \geq a \geq \max[-s^2/t^2, -t^2/s^2]$.

Let $r = s + t$

$$\bar{W} = r^2 + a(rq - s)^2$$

If $q = s/r$, $\bar{W}$ is maximal for $a < 0$ and is minimal for $a > 0$.

$$\Delta q = r(s - qr) [1 - aq(1 - q)] / \bar{W}$$

Equilibrium occurs when $q = s/r$ provided that s and t have the same sign; of course if $s = t = r/2$, $q = 1/2$. Since the sign of Δq is the same as the sign of $r(s - qr)$, the equilibrium is stable, i.e.,

$$\Delta q < 0 \text{ if } q > s/r$$

$$\Delta q > 0 \text{ if } q < s/r$$

At equilibrium the three fitnesses are $r^2 + at^2$, $r^2 - ast$, $r^2 + as^2$ for BB , Bb , and bb . If $a < 0$ the heterozygote is superior to both homozygotes and if $a > 0$ the heterozygote is inferior to both homozygotes, but the equilibrium is stable in either event. LEWONTIN (1958) has shown that heterozygote superiority is neither a necessary or sufficient condition for a stable equilibrium when the selective values (W 's) are functions of gene frequency. Although the positive range of a is independent of the values of s and t , the negative range is greatly reduced if either s/t or t/s is small. WRIGHT (1955) discusses a similar model where the W value of a rare genotype becomes very large, however in his model $\bar{W}$ is a constant.

Table 3 presents the opposite situation, i.e., the maximum fitness coincides with an unstable equilibrium. In this model s , t , and c are all positive constants. As in Table 2, $r = s + t$. Also let $\hat{q} = s/r$.

Then

$$\bar{W} = [1 - (q - \hat{q})^2] [tq^2 + s(1 - q)^2] + c$$

and the maximum value of $\bar{W}$ occurs when

$$q = \hat{q} = s/r.$$

$$\Delta q = q(1 - q) [(1 - [q - \hat{q}]^2)] (qr - s) / \bar{W}$$

TABLE 2
Frequency and relative fitness of genotypes

	Genotype		
	BB	Bb	bb
Frequency	q^2	$2q(1 - q)$	$(1 - q)^2$
Relative fitness	$at^2 + (s/q)^2$	$st[-a + 1/q(1 - q)]$	$as^2 + [t/(1 - q)]^2$

TABLE 3

Frequency and relative fitness of genotypes

	Genotype		
	<i>B B</i>	<i>B b</i>	<i>b b</i>
Frequency	q^2	$2q(1-q)$	$(1-q)^2$
Relative fitness (W)	$t[1-(q-\hat{q})^2] + c$	c	$s[1-(q-\hat{q})^2] + c$

and

$$\Delta q = 0 \text{ when } q = \hat{q} = s/r.$$

Since Δq has the same sign as $(qr - s)$, the equilibrium is unstable, i.e.,

$$\Delta q > 0 \text{ if } q > \hat{q}$$

$$\Delta q < 0 \text{ if } q < \hat{q}$$

The concept of an adaptive topography based on the $\bar{W}$ surface has been criticized by MORAN (1964). He has shown for a two-locus model with constant W 's that gametic equilibrium need not coincide with a local maximum of the $\bar{W}$ surface. Furthermore, $\bar{W}$ may be either increased or decreased by selection depending on the initial gametic frequencies. KIMURA (1965) has shown that $\bar{W}$ does eventually increase if there is loose linkage between the loci and if gene frequencies as well as gametic frequencies are changing. If a state of quasi linkage equilibrium exists $\bar{W}$ is either maximized or almost maximized at equilibrium by selection. This paper shows that difficulties can be encountered with the concept of an adaptive topography even for the single locus model if the W 's are functions of gene frequency. In fact LI (1955) has shown, for the single locus model, that the equilibrium value of gene frequency (q) is not in general the value that maximizes $\bar{W}$. He suggests an alternate function

$$G(q) = \int \left[\Sigma W \frac{df}{dq} \right] dq + \text{constant.}$$

Unfortunately, this function lacks any obvious physical meaning although it provides a surface with local maximum that corresponds to stable equilibrium points. The author feels the concept of an adaptive topography based on the W surface requires more attention. If discrepancies arise even with a single locus model, one should expect even more exceptions when multilocus models are investigated.

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SUMMARY

This paper discusses two models of selection at a diploid locus when relative fitnesses of the different genotypes are functions of gene frequency. In one model, selection leads to a unique stable equilibrium gene frequency that corresponds to the minimum value of the average fitness. In the other model, the value of gene frequency that maximizes the average fitness corresponds to an unstable

equilibrium. These two cases are discussed in connection with recent criticism of the adaptive topography concept.

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