§4.3 Fundamental Theorem of Natural Selection

The essence of the theory of evolution through selection is that in any population there will exist genetic variation between individuals and that those genotypes which are better suited to the environment than others will contribute rather more than their fair share of offspring to the following generation. Thus the genetical make-up of the following generation will differ somewhat from that of the parent generation, leading to substantial changes over large numbers of generations.

Such evolution depends on the existence of genetical variation in the population, so that it might be expected that the greater the variation, the greater will be the changes which occur. Further, it appears that in some sense the process leads to an 'improvement' in the population. The theory which has so far been developed allows a more precise quantitative examination of these intuitive notions.

Random-mating populations

Consider firstly the case where only two alleles A_1 and A_2 are allowed at the locus in question. Using the notation developed in the previous two chapters, if the frequency of A_1 in any generation is p, and that of A_2 is $q = 1 - p$, the frequency p' of A_1 in the following generation is

$$p' = (w_{11} p^2 + w_{12} pq) / W , \tag{3.1}$$

where $W = w_{11} p^2 + 2 w_{12} pq + w_{22} q^2$.

The mean fitness W' of the population in the second generation is

$$W' = w_{11} (p')^2 + 2 w_{12} p' q' + w_{22} (q')^2 , \tag{3.2}$$

and the increase ΔW in mean fitness between the two generations is

$$\begin{aligned} \Delta W &= w_{11} \{(p')^2 - p^2\} + 2 w_{12} \{p' q' - pq\} + w_{22} \{(q')^2 - q^2\} \\ &= (p' - p) \{w_{11} (p' + p) + 2 w_{12} (1 - p - p') + w_{22} (p + p' - 2)\} . \end{aligned} \tag{3.3}$$

Writing $\Delta p = p' - p$ and using the expression (3.1) for p', it is possible after some manipulation to reduce eqn. (3.3) to the form

$$\Delta W = (\Delta p)^2 \{ w_{11} - 2w_{12} + w_{22} + wW(pq)^{-1} \}$$
$$= 2pq\{ w_{11}p + w_{12}(1 - 2p) - w_{22}q \}^2$$

$$\{ w_{11}p^2 + (w_{12} + \tfrac{1}{2}w_{11} + \tfrac{1}{2}w_{22})pq + w_{22}q^2 \}W^{-2}. \qquad (3.4)$$

Clearly ΔW is always non-negative, so that we can conclude that gene frequencies move, under natural selection, in such a way as to increase, or at worst maintain, the mean fitness of the population.

If, furthermore, the w_{ij} are close to unity, eqn. (3.4) may be approximated by

$$\Delta W = 2pq\{ w_{11}p + w_{12}(1 - 2p) - w_{22}q \}^2 = 2pq\{ E_1 - E_2 \}^2, \qquad (3.5)$$

where

$$E_1 = w_{11}p + w_{12}q - W \qquad (3.6)$$

and

$$E_2 = w_{12}p + w_{22}q - W. \qquad (3.7)$$

The quantities E_1 and E_2 can be given the following interpretation. If the heterozygotes A_1A_2 are divided into two halves, the first half going to form a group with the homozygotes A_1A_1 and the second half going to form a group with the homozugotes A_2A_2, then E_1 and E_2 represent respectively the deviations from the mean fitness of the population of the mean fitnesses of the two groups. The quantity $E_1 - E_2$ is called the 'average excess' of A_1 (Fisher, 1930).

It was remarked earlier than it is expected that ΔW will be related in some way to the variation in fitness in the population. This possibility is now investigated more closely. It is clear from eqn. (3.5) that if $E_1 = E_2$, that is to say if

$$p = p^* = \frac{w_{12} - w_{22}}{2w_{12} - w_{11} - w_{22}}, \qquad (3.8)$$

then $\Delta W = 0$. In the case when w_{12} exceeds both w_{11} and w_{22}, p^* is, as we know, a stable equilibrium point, so that it could have been anticipated that W will remain unchanged when $p = p^*$. But the total variance in fitness, namely

$$\sigma^2 = w_{11}{}^2 p^2 + 2w_{12}{}^2 pq + w_{22}{}^2 q^2 - W^2 \qquad (3.9)$$

will be positive when w_{12} exceeds both w_{11} and w_{22}. Thus if ΔW is to have some interpretation as a variance, it can only be as some component of the total variance of fitness.

To guide us in trying to isolate some component of σ^2 which is related to ΔW, it is useful to consider the particular case $p = q = \frac{1}{2}$, $w_{11} = w_{22} = 1$, $w_{12} = 1 + c$. Different values of c lead to different values of σ^2, but irrespective of c it is always true that $\Delta W = 0$. This suggests that it would be useful to isolate some component of σ^2 which is zero irrespective of the value of c. A component of σ^2 fulfilling this requirement is that part of the total variance which is removed by fitting a weighted least-squares regression line to the fitnesses w_{ij}. It is therefore reasonable to consider generally the effect of fitting such a line. Any regression line will yield fitness value $W + 2x$, $W + x + y$, $W + 2y$ for $A_1 A_1$, $A_1 A_2$, and $A_2 A_2$, and the least-squares regression line is that line for which

$$D = p^2 (w_{11} - W - 2x)^2 + 2pq(w_{12} - W - x - y)^2 + q^2 (w_{22} - W - 2y)^2$$

is minimized with respect to variation in x and y. The required solutions for x and y are

$$x = E_1 - W, \quad y = E_2 - W, \qquad (3.10)$$

where E_1 and E_2 are defined by eqn. (3.6) and (3.7). Standard regression theory shows that the sum of squares removed by fitting this least-squares line is

$$\sigma A^2 = 2pq(E_1 - E_2)^2, \qquad (3.11)$$

which is identical to eqn. (3.5). Thus to the order of approximation used the increase in mean fitness of the population is identical to that part of the total genetic variance which can be accounted for by fitting a weighted least-squares regression line to the fitnesses. For this reason, this component is called the 'additive' part of the total variance.

Two sex viability models with two alleles. Consider next a population divided into males and females, mating randomly subject to viability selection where the fitness coefficients may differ between the sexes. The array in Table 1 describes the process (assuming male and female offspring are produced with equal probability).

Sex		Male				Female	
Gamete		A	a			A	a
Frequency		p	q			P	Q
Genotype	AA	Aa	aa	AA	Aa	aa
Fitness coefficients (viabilities)	σ	1	τ	s	1	t
Relative frequencies after random mating and selection	σpP	$pQ+qP$	τqQ	spP	$pQ+qP$	tqQ

Table 1

With Mendelian segregation we obtain for the gene frequencies in the next generation the transformation equations

$$p' = \frac{\sigma pP + \frac{1}{2}(pQ+qP)}{\sigma pP + pQ + qP + \tau qQ}, \quad P' = \frac{spP + \frac{1}{2}(pQ+qP)}{spP + pQ + qP + tqQ}, \qquad (2.5)$$

Where the denominators are the required normalization factors (cf. Model 1).

In the case at hand it is more convenient to express the changes of gene frequencies over successive generations in terms of the equivalent pair of variables $x = p/q$,

$y = P/Q$, $0 \le x$, $y \le \infty$. We obtain

$$x' = \frac{\sigma xy + \frac{1}{2}(x+y)}{\tau + \frac{1}{2}(x+y)} = f(x,y), \quad y' = \frac{sxy + \frac{1}{2}(x+y)}{t + \frac{1}{2}(x+y)} = g(x,y). \quad (2.6)$$

Write T for the mapping defined in (2.6). The fixed point $0 = (0,0)$ corresponds to the pure population of only aa genotypes and $\infty = (\infty,\infty)$ represents the pure population of AA genotypes.

We wish to ascertain the character of all equilibria of T and their domains of attraction. The analysis of T and its iterates is much facilitated by exploiting the feature that T is monotone, i.e., where $z = (x,y) \le \tilde{z} = (\tilde{z}, \tilde{y})$ holds (the ordering signifies the inequality for each coordinate). Then we have

$$Tz \le T\tilde{z} \quad \text{with strict inequality in each coordinate unless } z = \tilde{z}. \quad (2.6a)$$

The stability nature of any equilibrium is customarily ascertained by analysis of the local linear approximation to the non-linear mapping T in the neighborhood of the fixed point. More specifically, we examine the matrix transformation given by the gradient matrix

$$\|\partial T\| = \begin{Vmatrix} \dfrac{\partial f}{\partial x} & \dfrac{\partial g}{\partial x} \\ \dfrac{\partial f}{\partial y} & \dfrac{\partial g}{\partial y} \end{Vmatrix}$$

evaluated at the fixed point $\hat{z} = (\hat{x}, \hat{y})$.

All equilibria can be determined in general, and for some special cases, viz., $\lambda = \mu$, $\lambda = 1 - \mu$, $\lambda = 0$ or 1, the full convergence behavior can be analysed.

Thus, when $\mu = 0$, $x^{(n)} \to 1$ rapidly.

When $\lambda + \mu = 1$ and $\lambda > \frac{1}{2}$, again we find $x^{(n)} \to 1$.

For $\lambda = \mu$ and $\lambda < \frac{1}{2}$, then it can be proved that

$$x^{(n)}; \quad z^n \rightarrow \frac{1 - \sqrt{1 - 2\lambda(1 - 2\lambda)}}{2(1 - 2\lambda)}.$$

The following can be readily checked. Assume by symmetry $(0 < \mu \leq \lambda < 1)$ then:

(i)   For $0 < \mu \leq \lambda < \frac{1}{2}$, there exists a unique locally stable polymorphism.

(ii)   For $0 < \mu < \frac{1}{2} < \lambda < 1$, there exists no internal equilibrium. It can be proved that fixation in the A_1 allele occurs.

(iii) If $\frac{1}{2} < \mu \leq \lambda < 1$, there exists a unique internal non-stable equilibrium.

The global convergence behavior of (2.20) for arbitrary parameters λ, μ is in general unsettled.

SOME MODELS OF POSITIVE ASSORTATIVE MATING

Consider a two-allele (A and a) single locus population displaying certain preferences in mating behavior. We consider here the case where the preference is exercised by one of the sexes, say the female sex, (this covers most situations of insect and mammal populations).

A model of assortative mating. Assume that A is dominant to a so that phenotypically AA and Aa are alike. The degree of partial assortative mating in the phenotypes is measured by two parameters: α $(0 \leq \alpha \leq 1)$ will be the fraction of dominant females preferring to mate with their own kind and β $(0 \leq \beta \leq 1)$ that of recessive females preferring their own kind. Thus a fraction, $1 - \alpha$, of $\overline{A}$ (of AA or Aa) females mate indifferently, i.e., at random. We assume all females are fertilized (i.e., find a suitable mate). This happens if the males. Consider the genotypes AA, Aa, aa (A dominant) with the frequencies u, v and w respectively in the female population.

When the prohibitions of assortative mating are operating, it is obligate that each mate of an aa individual is of the same genotype so that the frequence of the $aa \times aa$ mating type is w. Therefore the frequency of the matings of the dominant phenotypes is $1 - w = u + v$. Among the matings of dominants the frequency of occurrence considering of the $AA \times AA$ mating type is u^2 and its frequency of occurrence considering all admissible mating is then $u^2/(1-w)$. The frequencies of the mating types are listed in Table 3.

	Frequencies	
Mating Type	Of Assorting Types	Random Mating
$AA \times AA$	$\alpha u^2/(u+v)$	$(1-\alpha)u^2$
$AA \times Aa$	$2\alpha uv/(u+v)$	$2(1-\alpha)uv$
$AA \times aa$		$(2-\alpha-\beta)uw$
$Aa \times Aa$	$\alpha v^2/(u+v)$	$(1-\alpha)v^2$
$Aa \times aa$		$(2-\alpha-\beta)vw$
$aa \times aa$	βw	$(1-\beta)w^2$

Table 3

The corresponding recurrence relations connecting genotype frequencies over successive generations in accordance with Mendelian segregation laws become

$$u' = (\frac{\alpha}{u+v} + (1-\alpha))(u + \tfrac{1}{2}v)^2$$
$$v' = \frac{\alpha uv}{2(u+v)} + \tfrac{1}{2}v + (1-\alpha)u(\tfrac{1}{2}v + w) + (1-\beta)w(u + \tfrac{1}{2}v), \qquad (3.1)$$
$$w' = \beta w + \frac{\alpha v^2}{4(u+v)} + (1-\alpha)\tfrac{1}{2}v(\tfrac{1}{2}v + w) + (1-\beta)w(\tfrac{1}{2}v + w).$$

Introducing the A gene frequency, $p = u + \tfrac{1}{2}v$, and for the next generation, $p' = u' + \tfrac{1}{2}v'$ and, letting p_n denote the frequency of the gene A in the nth generation, we drive, from (3.1), the relationship

$$p' = p[1 + \tfrac{1}{2}(\alpha - \beta)w].\tag{3.2}$$

The following inferences can now be made:

(i)   For $\alpha > \beta$, p_n increases to 1, the pure homozygous AA state. The rate of convergence is algebraic.

(ii)   For $\alpha < \beta$, the population ultimately fixes in the pure homozygous aa state and convergence occurs with an asymptotic factor of decrease per generation $\lambda = 1 + \tfrac{1}{2}(\alpha - \beta)$.

When $\alpha = \beta$ it is readily checked that $p^{(n)} = p^{(0)}$ for all n. Then v' simplifies to

$$v' = \frac{vp\alpha}{p + \tfrac{1}{2}v} + (1 - \alpha)2pq = f(v), \quad (q = (1 - p)),$$

where p is the constant gene frequency. Thus $f(v)$ is a linear fractional transformation and therefore the nth generation frequencies $v_n = f_n(v_0) = f(f_{n-1}(v_0))$ can be explicitly evaluated. Indeed we have

$$\frac{v_n - \gamma_1}{v_n - \gamma_2} = K^n(\frac{v_0 - \gamma_1}{v_0 - \gamma_2}),$$

where γ_1 and γ_2 are the fixed points of $f(v) = v$ and

$$K = \frac{\gamma_1}{\gamma_2}\left[\frac{2(1 - \alpha)pq - \gamma_1}{2(1 - \alpha)pq - \gamma_2}\right].$$

Because $f(v)$ is concave increasing, we deduce $v_n \to \gamma_1$. For the case $\alpha = 1$ we obtain $v_n = 2pv_0 / (nv_0 + 2p)$ so that $v_n \to 0$ at an algebraic rate.