A mathematical theory of natural and artificial selection. Part III.

By Mr J. B. S. Haldane, Trinity College.

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In this part the cases of a single but incompletely dominant factor, and of several interacting factors are considered. Mating is supposed to be at random, populations to be very large, and generations not to overlap. The notation is, so far as possible, that of Part I (1).

Selection of an incompletely dominant autosomal character.

Let the nth generation be formed from female gametes in the ratio $u_n A : 1a$, male gametes in the ratio $v_n A : 1a$. The nth generation is therefore in the proportions $u_n v_n AA : (u_n + v_n) Aa : 1aa$. Let the ratios after selection has occurred be:

$$\begin{aligned} &♂\ \ u_n v_n AA : (1 - K_m)(u_n + v_n) Aa : (1 - k_m)\, aa,\\ &♀\ \ u_n v_n AA : (1 - K_f)(u_n + v_n) Aa : (1 - k_f)\, aa, \end{aligned}$$

where K_m, K_f, k_m, k_f are small.

$$\therefore \quad u_{n+1} = \frac{2u_n v_n + (1 - K_f)(u_n + v_n)}{(1 - K_f)(u_n + v_n) + 2 - 2k_f}.$$

Hence, since $\frac{u_n - v_n}{u_n}$ is clearly small,

$$\Delta u_n = \frac{v_n - u_n}{2} + \frac{u_n (K_f u_n - K_f + k_f)}{1 + u_n}, \text{ approximately,}$$

and $$\Delta v_n = \frac{u_n - v_n}{2} + \frac{u_n (K_m u_n - K_m + k_m)}{1 + u_n}, \text{ approximately.}$$

Δu_n and Δv_n can be shewn to differ by a small quantity of the second order.

$$\therefore \quad \Delta u_n = \frac{u_n (K u_n - K + k)}{1 + u_n} \quad \ldots\ldots\ldots\ldots\ldots (1{\cdot}0)$$

where $$K = \tfrac{1}{2}(K_f + K_m);\ k = \tfrac{1}{2}(k_f + k_m).$$

Equilibrium can only occur when $\Delta u_n = 0$, i.e. u_n tends either to zero, infinity, or to $1 - \frac{k}{K}$. Hence for equilibrium to be possible $\frac{k}{K} < 1$. If K be positive, i.e. heterozygotes are at a disadvantage compared with pure dominants, then $\Delta u_n \gtrless 0$ according as $u_n \gtrless 1 - \frac{k}{K}$. Hence the equilibrium is unstable if it exists. If K

be negative the equilibrium is stable if it exists. We have thus three cases to consider. In each

$$\frac{du_n}{dn} = \frac{u_n(Ku_n - K + k)}{1 + u_n} \text{ approximately,}$$

and the proportion of recessives $y_n = (1 + u_n)^{-2}$.

(*a*) No equilibrium, $\frac{k}{K} > 1$.

$$\therefore \quad (k - K)n = \log_e u_n + \frac{k - 2K}{K} \log_e \left(\frac{Ku_n - K + k}{k}\right) \ldots (1{\cdot}1)$$

making the usual convention that $u_0 = 1$.

Hence the values of u_n lie between two geometrical series, and selection is therefore vastly more efficacious on recessives than when dominance is complete, as in equations 2·4 and 4·3 of Part I.

(*b*) Stable equilibrium, $k > K$, $0 > K$.

$$\therefore \quad (K - k)n = \log_e \left(\frac{u_n}{u_0}\right) + \frac{2K - k}{K} \log_e \left(\frac{Ku_n - K + k}{Ku_0 - K + k}\right) \ldots (1{\cdot}2).$$

We must take $u_0 \gtrless 1 - \frac{k}{K}$ according as $u_n \gtrless 1 - \frac{k}{K}$.

Here again successive values of u_n lie between two geometrical series, so that the population proceeds fairly rapidly towards equilibrium. As Fisher (2) has pointed out, such cases probably occur in nature in connexion with factors governing size, where the heterozygote is at an advantage as compared with either type of homozygote.

(*c*) Unstable equilibrium, $K > 0$, $K > k$.

The population proceeds towards homozygosis in one direction or the other. This case can hardly occur in nature, as any mutants, either in an *AA* or an *aa* population, would be weeded out while still few in number.

Selection of an incompletely dominant sex-linked character.

The female sex is throughout supposed to be homogametic; if the male is homogametic the argument is the same, *mutatis mutandis*. Let the *n*th generation be formed from ova in the ratio $u_nA : 1a$, female-producing spermatozoa in the ratio $v_nA : 1a$. Let the ratios of the *n*th generation after selection be:

$$♀ \quad u_n v_n AA : (1 - K)(u_n + v_n) Aa : (1 - k)\, aa,$$
$$♂ \quad u_n A : (1 - k')\, a,$$

where K, k and k' are small.

$$\therefore \quad u_{n+1} = \frac{2u_n v_n + (1-K)(u_n + v_n)}{(1-K)(u_n + v_n) + 2 - 2k},$$

$$v_{n+1} = \frac{u_n}{1-k'}.$$

$$\therefore \quad \Delta u_n = \Delta v_n = \frac{u_n}{3+3u_n}\left[(2K+k')\,u_n - 2K + 2k + k'\right],$$

approximately, ...(2·0)

and $u_n = v_n$, approximately.

Hence u_n tends to zero, infinity, or $\frac{2K-2k-k'}{2K+k'}$. Equilibrium is possible if $\frac{k+k'}{2K+k'} < \frac{1}{2}$. It is stable if $2K+k'$ be negative, unstable if this quantity be positive. In each case

$$\frac{du_n}{dn} = \frac{u_n\,(2Ku_n + k'u_n - 2K + 2k + k')}{3\,(1+u_n)}, \text{ approximately,}$$

and the proportion of recessive females is $(1+u_n)^{-2}$, of recessive males $(1+u_n)^{-1}$. Three cases occur.

(*a*) No equilibrium, $\frac{k+k'}{2K+k'} > \frac{1}{2}$.

$$\therefore \quad \frac{2k+k'-2K}{3}\,n = \log_e u_n + \frac{2k-4K}{2K+k'}\log_e\left(\frac{2Ku_n + k'u_n - 2K + 2k + k'}{2k+2k'}\right)$$

......(2·1),

putting $u_0 = 1$. Selection therefore proceeds much as according to equation 7·2 of Part I.

(*b*) Stable equilibrium, $0 > 2K + k'$, $2k + k' > 2K$.

$$\therefore \quad \frac{2K-2k-k'}{3}\,n = \log_e\left(\frac{u_n}{u_0}\right) + \frac{2k-4K}{2K+k'}\log_e\left(\frac{2Ku_n + k'u_n - 2K + 2k + k'}{2Ku_0 + k'u_0 - 2K + 2k + k'}\right)$$

......(2·2)

where $u_0 \gtrless u_\infty$ according as $u_n \gtrless u_\infty$.

The results of Robertson (3) suggest that milk-yield in cattle depends on one or more sex-linked factors which act most effectively when heterozygous, besides autosomal factors. If so human effort in this case has given K a negative value, while k and k' are nearly zero. Hence an equilibrium should be reached.

(*c*) Unstable equilibrium, $2K + k' > 0$, $2K > 2k + k'$.

The population proceeds in one direction or the other to homozygosis. This case can hardly occur in nature.

Multiple factors.

Many cases exist in nature where several factors are needed to ensure the appearance of a character. Thus in wheat Nilsson-Ehle (4) found that any one of three dominant factors will produce redness, that is to say a white plant must be a triple recessive. On the other hand Saunders (5) found that in Matthiola three dominant factors are needed for slight hoariness, four for complete hoariness, so that a hoary plant is a multiple dominant. In other cases the effects of factors are merely additive, and selection will act on each independently of the others. It will be shown later that linkage between factors, unless very strong, is unimportant. We shall therefore at first consider unlinked factors, and shall confine ourselves to the case of complete dominance.

Selection of a multiple autosomal recessive character.

Let $A_1, A_2, \ldots A_r, \ldots A_m$ be m autosomal dominant factors, each of which produces the same effect, so that the multiple recessive alone competes with the other genotypes. Let $1-k$ of this type survive for every one of the others. Let y_n be the proportion of multiple recessives in the nth generation, formed from gametes in the proportion ${}_ru_n A_r : 1 a_r$, and similarly for the other factor pairs. Then the nth generation consists of zygotes in the ratios:

$$ {}_ru_n^2 A_r A_r : 2\,{}_ru_n A_r a_r : 1 a_r a_r, \text{ etc.} $$

$$ \therefore \quad y_n = \prod_{r=1}^{m} (1 + {}_ru_n)^{-2}. $$

Of the $a_r a_r$ zygotes only $y_n (1 + {}_ru_n)^2$ are multiple recessives. Hence

$$ {}_ru_{n+1} = \frac{{}_ru_n (1 + {}_ru_n)}{1 + {}_ru_n - k y_n (1 + {}_ru_n)^2}. $$

$$ \therefore \quad \Delta_r u_n = k y_n \, {}_ru_n (1 + {}_ru_n), \text{ approximately, if } k \text{ be small.} $$

Putting $x = kn$ we have approximately:

$$ \left.\begin{array}{l} \dfrac{d\,{}_1u_n}{dx} = y_n \, {}_1u_n (1 + {}_1u_n) \\ \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots \\ \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots \\ \dfrac{d\,{}_ru_n}{dx} = y_n \, {}_ru_n (1 + {}_ru_n) \\ \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots \\ \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots \end{array}\right\}. $$

To eliminate the u's from these m equations put $s_r = \dfrac{{}_ru_n}{1 + {}_ru_n}$.

$$ \therefore \quad \frac{ds_r}{dx} = y_n s_r. \qquad \therefore \quad \log s_r = \int y_n \, dx + \log a_r. $$

$\therefore\ s_r = a_r s$, where a_r is an integration constant independent of n and given by the initial state of the population.

$$\left.\begin{aligned} \therefore\quad y_n &= \prod_{r=1}^{m} (1 - a_r s)^2 \\ kn = x &= \int \frac{ds}{s y_n} \end{aligned}\right\} \quad \ldots\ldots\ldots\ldots\ldots(3{\cdot}0).$$

The latter equation is integrable, and the elimination of s gives the required relation between y_n and kn.

$$\frac{dy_n}{dx} = -2y_n^2 \sum_{r=0}^{m} {}_r u_n,$$

whereas if only one factor is concerned,

$$\frac{dy_n}{dx} = -2y_n^2 u_n.$$

Now comparing these rates for equal values of y_n in the two cases, we note that since $y_n^{-\frac{1}{2}} = 1 + u_n = \prod_{r=1}^{m} (1 + {}_r u_n)\ \therefore\ u_n > \sum_{r=1}^{m} {}_r u_n$. Hence selection is slower than in the case of a character determined by one factor only. When however dominants are very rare, or when one a_r greatly exceeds the rest, i.e. one recessive factor is far commoner than the others, selection proceeds at about the same rate in the two cases. It is slowest when all the a_r's are equal.

Selection of a multiple sex-linked recessive character.

If $A_1, A_2, \ldots A_r, \ldots A_m$ are sex-linked (the female being homogametic) the nth generation formed from eggs in the ratios ${}_r u_n A : 1a$, etc., and female-producing spermatozoa in the ratios ${}_r v_n A : 1a$, etc., while z_n is the proportion of multiple recessive males, y_n of such females, and k is the coefficient of selection.

$$\therefore\quad {}_r u_{n+1} = \frac{2\,{}_r u_n\,{}_r v_n + {}_r u_n + {}_r v_n}{{}_r u_n + {}_r v_n + 2 - 2k y_n (1 + {}_r u_n)}.$$

$${}_r v_{n+1} = \frac{{}_r u_n}{1 - k z_n (1 + {}_r u_n)}.$$

$$y_n = \prod_{r=1}^{m} (1 + {}_r u_n)^{-1} (1 + {}_r v_n)^{-1}.$$

$$z_n = \prod_{r=1}^{m} (1 + {}_r u_n)^{-1}.$$

$\therefore$ Approximately ${}_r u_n = {}_r v_n,\ y_n = z_n^2$.

$$\therefore\quad 3\Delta\,{}_r u_n = k\,{}_r u_n (1 + {}_r u_n)(2z_n^2 + z_n).$$

As above, putting $kn = x$, $\dfrac{{}_ru_n}{1 + {}_ru_n} = a_r s$, we have a_r constant, and

$$\left.\begin{aligned} z_n &= \prod_{r=1}^{m} (1 - a_r s) \\ kn &= x = 3 \int \frac{ds}{s z_n (2z_n + 1)} \end{aligned}\right\} \quad \ldots\ldots\ldots\ldots\ldots (4{\cdot}0).$$

This again is soluble in finite terms by the elimination of s.

$$\frac{dz_n}{dx} = -\tfrac{1}{3} z_n^2 (2z_n + 1) \sum_{r=1}^{m} {}_ru_n,$$

while in the single factor case

$$\frac{dz_n}{dx} = -\tfrac{1}{3} z_n^2 (2z_n + 1)\, u_n, \text{ where } u_n = z_n^{-1} - 1.$$

Comparing these rates for equal values of z_n, we find as above $u_n > \Sigma\, {}_ru_n$. Hence selection proceeds more slowly with many factors than with one. When, however, dominants are very rare or one a_r much larger than the rest, selection proceeds as with one factor.

Selection of a multiple autosomal dominant character.

When each of m autosomal dominant factors is needed to produce a character, we find, using the same notation as above except that y_n is the proportion of dominants,

$$y_n = \prod_{r=1}^{m} [1 - (1 + {}_ru_n)^{-2}],$$

$$\frac{d\, {}_ru_n}{dx} = \frac{y_n (1 + {}_ru_n)}{2 + {}_ru_n}, \text{ with } m - 1 \text{ similar equations.}$$

$$\therefore \quad (1 + {}_ru_n)\, e^{1 + {}_ru_n} = e^{\int y_n dx} = a_r s.$$

Hence the problem can be reduced to the elimination of s between:

$$\left.\begin{aligned} y_n &= \prod_{r=1}^{m} [1 - \{\phi (a_r s)\}^{-2}] \\ kn &= x = \int \frac{ds}{sy} \end{aligned}\right\} \quad \ldots\ldots\ldots\ldots\ldots (5{\cdot}0)$$

where ϕ is defined by the equation $t = \phi(t)\, e^{\phi(t)}$.

Numerical integration would be possible for known values of a_r,

$$\frac{dy_n}{dx} = 2y_n^2 \sum_{r=1}^{m} \frac{1}{{}_ru_n (2 + {}_ru_n)^2},$$

while in the single factor case

$$\frac{dy_n}{dx} = \frac{2y_n^2}{u_n (2 + u_n)^2}.$$

Now when one a_r is very much smaller than the rest these two rates are nearly equal for equal values of y_n. When all the a_r's are equal,

$$\frac{dy_n}{dx} = my_n^2\left[\left(1 - y_n^{\frac{1}{m}}\right)^{-\frac{1}{2}} + 1\right]^{-2}\left[\left(1 - y_n^{\frac{1}{m}}\right)^{-2} - 1\right]^{-1}.$$

The ratio of this rate to the rate with a single factor (putting $t^m = y_n$) is

$$\frac{mt^{m-1}(1 + \sqrt{1 - t^m})(1 - t)^{\frac{3}{2}}}{(1 + \sqrt{1 - t})(1 - t^m)^{\frac{3}{2}}}.$$

When t is small this tends to the small mt^{m-1}; when t is nearly unity, to $m^{-\frac{1}{2}}$ which is also small. The ratio when all the a_r's are equal is, by Purkiss' theorem, the minimum value. Hence it would seem that in general natural selection acts more slowly on a multiple dominant than a single dominant. The case of a multiple sex-linked dominant and various more complicated cases present still greater difficulties to analysis, though of course individual cases could always be solved numerically.

Linkage.

Consider two autosomal factors A, B, linked with such intensity that the cross-over value is $100l$ in the female, $100l'$ in the male sex. Let the nth generation be formed from:—

eggs $\quad p_n AB : q_n Ab : r_n aB : s_n ab,$
spermatozoa $\quad p_n' AB : q_n' Ab : r_n' aB : s_n' ab,$

where $p_n + q_n + r_n + s_n = p_n' + q_n' + r_n' + s_n' = 1$.

The nth generation therefore consists of:—

$$p_n p_n' ABAB : (p_n q_n' + p_n' q_n) ABAb : (p_n r_n' + p_n' r_n) ABaB$$
$$: q_n q_n' AbAb : (p_n s_n' + p_n' s_n) AB.ab : (q_n r_n' + q_n' r_n) Ab.aB$$
$$: r_n r_n' aB.aB : (q_n s_n' + q_n' s_n) Abab : (r_n s_n' + r_n' s_n) aBab$$
$$: s_n s_n' abab.$$

If no selection occurs they produce gametes in the proportions:

$$2p_{n+1} = p_n + p_n' + l(q_n r_n' + q_n' r_n - p_n s_n' - p_n' s_n)$$
$$2q_{n+1} = q_n + q_n' - l(q_n r_n' + q_n' r_n - p_n s_n' - p_n' s_n)$$
$$2r_{n+1} = r_n + r_n' - l(q_n r_n' + q_n' r_n - p_n s_n' - p_n' s_n)$$
$$2s_{n+1} = s_n + s_n' + l(q_n r_n' + q_n' r_n - p_n s_n' - p_n' s_n),$$

whilst the values of p_{n+1}', etc., are given by the same expressions with l' substituted for l. Hence after one generation

$$\frac{p_n + q_n}{r_n + s_n} \text{ and } \frac{p_n' + q_n'}{r_n' + s_n'}$$

have the same constant value u, while

$$\frac{p_n + r_n}{q_n + s_n} = \frac{p_n' + r_n'}{q_n' + s_n'} = v.$$

We may therefore write:

$$p_n = \frac{uv}{(1+u)(1+v)} + x_n; \quad q_n = \frac{u}{(1+u)(1+v)} - x_n;$$

$$r_n = \frac{v}{(1+u)(1+v)} - x_n; \quad s_n = \frac{1}{(1+u)(1+v)} + x_n.$$

$$p_n' = \frac{uv}{(1+u)(1+v)} + x_n'; \quad q_n' = \frac{u}{(1+u)(1+v)} - x_n';$$

$$r_n' = \frac{v}{(1+u)(1+v)} - x_n'; \quad s_n' = \frac{1}{(1+u)(1+v)} + x_n'.$$

$$\therefore \quad q_n r_n' + q_n' r_n - p_n s_n' - p_n' s_n = -2(x_n + x_n').$$

$$\therefore \quad 2x_{n+1} = (1-2l)(x_n + x_n'); \quad 2x_{n+1}' = (1-2l')(x_n + x_n').$$

Hence if $x_0 + x_0' = c$,

$$\therefore \quad \left.\begin{aligned} x_n &= (\tfrac{1}{2} - l)(1 - l - l')^{n-1} c \\ x_n' &= (\tfrac{1}{2} - l')(1 - l - l')^{n-1} c \end{aligned}\right\} \quad \ldots\ldots\ldots\ldots(6{\cdot}0).$$

Hence the proportions of the various types of gamete approach asymptotically those which would be reached in one generation without linkage, the ratio of successive differences from the final values being $1 - l - l'$. Hence if either l or l' is larger than k the effects of linkage are unimportant. A similar proof holds for a pair of sex-linked factors.

Selection in a tetraploid organism.

In a tetraploid race which is stable, i.e. yields only diploid gametes, five types of zygote and three of gamete exist. Gregory (6) and Blakeslee, Belling and Farnham (7) have shown that zygotes produce gametes as follows:

Zygotes	Gametes
$AAAA$	AA
$AAAa$	$1AA : 1Aa$
$AAaa$	$1AA : 4Aa : 1aa$
$Aaaa$	$1Aa : 1aa$
$aaaa$	aa

Gregory thought that $AAaa$ gave $1AA : 2Aa : 1aa$, but his results, as well as theory, suggest the above ratio. As in Part II we first consider tetraploidy without selection, and then the process of selection in a population which would be in equilibrium but for that selection. Let the mth generation be formed from gametes in the ratios $p_m AA : 2q_m Aa : r_m aa$, where $p_m + 2q_m + r_m = 1$, and $u_m = \dfrac{p_m + q_m}{q_m + r_m}$. They form zygotes in the ratios:

$$p_m^2 AAAA : 4p_m q_m AAAa : (4q_m^2 + 2p_m r_m) AAaa$$
$$: 4q_m r_m Aaaa : r_m^2 aaaa.$$

$$\begin{aligned} \therefore \quad p_{m+1} &= p_m + \tfrac{2}{3}(q_m^2 - p_m r_m) \\ q_{m+1} &= q_m - \tfrac{2}{3}(q_m^2 - p_m r_m) \\ r_{m+1} &= r_m + \tfrac{2}{3}(q_m^2 - p_m r_m). \end{aligned}$$

Hence $u_{m+1} = u_m = u$, and when equilibrium is reached $q_\infty^2 = p_\infty r_\infty$.

Hence $p_\infty = \dfrac{u^2}{(1+u)^2}$, $q_\infty = \dfrac{u}{(1+u)^2}$, $r_\infty = \dfrac{1}{(1+u)^2}$,

and the population in equilibrium is in the ratios:

$$\frac{u^4}{(1+u)^4} AAAA : \frac{4u^3}{(1+u)^4} AAAa : \frac{6u^2}{(1+u)^4} AAaa$$

$$: \frac{4u}{(1+u)^4} Aaaa : \frac{1}{(1+u)^4} aaaa.$$

Putting $\theta_m = q_m^2 - p_m r_m$, we find $\theta_{m+1} = \frac{1}{3}\theta_m$, $\therefore \theta_m = 3^{-m}\theta_0$.

$$\begin{aligned} \therefore \quad p_m &= p_{m-1} + \theta_{m-1} \\ &= p_0 + \sum_{r=0}^{m-1} \theta_r \\ &= p_0 + \tfrac{3}{2}(1 - 3^{-m})\,\theta_0 \\ &= p_\infty - \frac{3^{1-m}}{2}\,\theta_0 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (7\cdot 0). \end{aligned}$$

Hence the ratios of the different classes converge very rapidly to their final values. Under selection of a population which has reached such an equilibrium, if A is completely dominant,

$$\begin{aligned} u_{n+1} &= \frac{p_n + q_n}{q_n + r_n - k r_n^2} \\ &= \frac{u_n}{1 - k(1+u_n)^{-3}}, \end{aligned}$$

$$\therefore \quad \frac{du_n}{dn} = \Delta u_n = \frac{k u_n}{(1+u_n)^3}, \text{ approximately, if } k \text{ be small.}$$

$$\therefore \text{ if } u_0 = 1, \; kn = \log_e u_n + 3u_n + \tfrac{3}{2}u_n^2 + \tfrac{1}{3}u_n^3 - 4\tfrac{5}{6} \ldots (7\cdot 1),$$

Hence when dominants are few u_n changes at the same rate as in a diploid organism; when they are many, much more slowly. To compare the change in the number y_n of recessives we find

$$kn = \log_e(1 - y_n^{\frac{1}{4}}) - \tfrac{1}{4}\log_e y_n + y_n^{-\frac{1}{4}} + \tfrac{1}{2} y_n^{-\frac{1}{2}} + \tfrac{1}{3} y_n^{-\frac{3}{4}} - 6\tfrac{2}{3} \ldots (7\cdot 2),$$

$$\therefore \quad \frac{dy_n}{dn} = -4k y_n^2 (y_n^{-\frac{1}{4}} - 1),$$

while in a diploid population

$$\frac{dy_n}{dn} = -2k y_n^2 (y_n^{-\frac{1}{2}} - 1).$$

Hence here too the rate is always slower in the tetraploids, though not much so when recessives are few.

If dominance is incomplete, as is usual in tetraploid organisms, and after selection the zygotes are in the ratios:

$$u_n^4 AAAA : 4(1-k_1)u_n^3 AAAa : 6(1-k_2)u_n^2 AAaa \\ : 4(1-k_3)u_n Aaaa : (1-k_4)\,aaaa,$$

$$\therefore\quad \Delta u_n = \frac{k_1 u_n^4 + 3(k_2-k_1)u_n^3 + 3(k_3-k_2)u_n^2 + (k_4-k_3)u_n}{(1+u_n)^3},$$

approximately, if the coefficients are small. The possible equilibria, if any, are given by the roots of

$$k_1 u_\infty^3 + 3(k_2-k_1)u_\infty^2 + 3(k_3-k_2)u_\infty + k_4 - k_3 = 0.$$

The various possible cases, and their stability, could easily be investigated. If the advantage of the various genotypes increases or decreases with the number of dominant factors they contain, so that $k_4 > k_3 > k_2 > k_1 > 0$, or $0 > k_1 > k_2 > k_3 > k_4$, no equilibrium is possible,

$$\therefore\quad n = \int \frac{(1+u_n)^3\,du_n}{k_1 u_n^4 + 3(k_2-k_1)u_n^3 + 3(k_3-k_2)u_n^2 + (k_4-k_3)u_n} \quad\ldots(7\cdot3).$$

If $k_1 = 0$ this contains a term proportional to u_n or u_n^2. If $k_1 \neq 0$ all the terms are logarithmic and selection is always rapid. But $AAAa$ is more likely to resemble $AAAA$ than Aa to resemble AA. Hence polyploidy diminishes the probability of a rapid selection in populations where recessives are few. Since stable polyploidy is only known in hermaphrodite plants there is no need to discuss cases of sex-linkage or different intensities of selection in the two sexes. The theory can readily be extended to the higher forms of polyploidy.

SUMMARY.

Expressions are found for the changes caused by slow selection in populations whose characters are determined by incompletely dominant, multiple, or polyploid factors, and for the equilibria attained in certain of these cases.

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