SELECTION ON BOTH HAPLO AND DIPLOPHASE

FRANCESCO M. SCUDO

*International Laboratory of Genetics and Biophysics, Pavia Section,
c/o Institute of Genetics, University of Pavia, Pavia, Italy*

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IN most organisms, for the largest part of their chromosome complement, the phase between fertilization and meiosis is diploid and that between meiosis and fertilization is haploid. Further, most organisms fall into two contrasting categories: in "lower" organisms multiplication is confined to the haplophase, which is much more extended than the diplophase; in "higher" ones, the reverse occurs.

Organisms in which the two phases show a comparable extension and/or multiplication occurs in both, are called haplo-diplonts or haplo-diploids. The former term should be preferred since the latter is also applied to sexual dimorphism for ploidy, as in bees. Examples of such intermediate organisms can be found among Algae and Foraminifera.

This paper is concerned with two deterministic models for sex-independent selection on a pair of alleles. As such, they apply, in a strict sense, only to lower organisms and haplo-diplonts proper which are sexually undifferentiated even in the haplophase. They would be a reasonable approximation for sexually differentiated organisms if selection were almost sex independent in both phases, which does not seem to occur. In *Lilium callosum*, for example, a strong selection favoring a supernumerary chromosome seems to be confined to egg cells; this balances a strong selection against the chromosome in the plant (KIMURA 1961). The cases of a series of *T* alleles in the house mouse (DUNN 1959) and of the *SD* alleles in *Drosophila melanogaster* (HIRAIZUMI, SANDLER and CROW 1960) are rather similar; they are harmful to the zygotes but strongly favored in the sperm of the heterozygous males.

The distinction between lower and higher organisms is also relevant for the timing of selection in one phase with respect to selection in the other. In most lower organisms the haplonts are just the products of the fission of the monocellular diplonts; thus selection on the former operates wholly "after" selection on the latter. Also, the distinction between the adaptive values of a genetic system in the haplo and in the diplophase will be very clear-cut.

Thus the mean adaptive value in both phases must be taken into account in assessing the overall adaptive value of a genetic system.

Matters can differ in higher organisms where, in a loose sense, the higher the organism, the higher the fraction of the haploid cycle which is spent "inside" or, somehow, "attached to" the diploid parent. Thus selection for some genes in the haplonts (gametophase) could, in principle, occur while the haplonts are still in the diploid and, at the same time, selection for the *same* genes has not yet

started operating on the diploid itself. In this case selection on the haplophase would operate wholly "before" that on the diplophase. Many results for this case have been derived by HIRAIZUMI *et al.* (1960) and HIRAIZUMI (1962, 1964); some of them will be discussed in an Appendix. The more general case in which gametic selection operates, partly after and partly before zygotic selection, will not be considered.

It will become apparent that, contrary to the case of mutation, it makes quite a difference whether haploid selection acts after or before zygotic. This leads to some interesting implications for higher organisms. In turn, some details of the life cycle in such organisms can help conjecture the possible relevance for them of these two types of selection, on which very little evidence is available.

(1) *Selection on haplonts after that on diplonts*: Only the statics of the system will be worked out, for nonoverlapping generations. Also, mutation is assumed to be negligible in its effect, compared to selection.

The haplont types (gametes), their frequencies and relative adaptive values are denoted by

$$\begin{array}{lll} A: & p & \rho \\ a: & q & 1 \end{array}$$

The genotypes, their frequencies and their relative adaptive values in the diploid phase alone, are denoted by

$$\begin{array}{lll} AA: & X & 1 \\ Aa: & Y & \sigma \\ aa: & Z & \tau \end{array}$$

The heterozygote is assumed to segregate 1:1, differences at meiosis being accounted for by ρ . Consider first, random union of haplonts; random mating of zygotes, leading to the same result, will be treated later.

Denoting the mean adaptive value of the population in the diplophase by

$$W_D \equiv X + \sigma Y + \tau Z, \quad (1)$$

the frequency of *A* haplonts before selection will be

$$p = \frac{X + \frac{1}{2}\sigma Y}{W_D}. \quad (2)$$

By applying selection and random union of haplonts, zygote frequencies in the next generation will be

$$X' = \frac{\rho^2 p^2}{(\rho p + q)^2} \quad (3,1)$$

$$Y' = \frac{2\rho p q}{(\rho p + q)^2} \quad (3,2)$$

$$Z' = \frac{q^2}{(\rho p + q)^2}. \quad (3,3)$$

It is slightly more convenient to work in terms of haplont ratios, that of *A* to *a* being denoted by

$$u \equiv \frac{X + \frac{1}{2}\sigma Y}{\tau Z + \frac{1}{2}\sigma Y} \quad (4)$$

In the neighborhood of $Z = 1$, the reciprocal of (4) should be used.
In terms of (4), system (3) becomes

$$\begin{aligned} X' &= \left(\frac{\rho u}{\rho u + 1} \right)^2 \\ Y' &= \frac{2\rho u}{(\rho u + 1)^2} \\ Z' &= \frac{1}{(\rho u + 1)^2} \end{aligned}$$

whence the recurrence equation for u

$$u' = \rho u \frac{\rho u + \sigma}{\rho \sigma u + \tau} \quad (5)$$

The system will be at equilibrium when:

- i. $u=0$ if $\rho=0$ or when $\rho \frac{\rho u + \sigma}{\rho \sigma u + \tau} = 1$
namely for
- ii. any value of u if $\rho=\sigma$ and $\tau=\sigma^2$
- iii. $\hat{u} \equiv \frac{\tau - \rho\sigma}{\rho(\rho - \sigma)}$ or $u=0$ if $\rho \neq \sigma$.

Case (i) says that a lethal haplont is eliminated in one generation while case (ii), a family of solutions with the same mechanics as for the Hardy-Weinberg Law, seems to be of very little practical value. Case (iii) gives as equilibrium states the fixation of α and a polymorphism if $\hat{u} > 0$ namely either

$$\left. \begin{aligned} \tau &> \rho\sigma \\ \rho &> \sigma \end{aligned} \right\} \quad (6)$$

or

$$\left. \begin{aligned} \tau &< \rho\sigma \\ \rho &< \sigma \end{aligned} \right\} \quad (7)$$

For the stability of the two solutions, consider the condition

$$\frac{u'}{u} \equiv \rho \frac{\rho u + \sigma}{\rho \sigma u + \tau} > 1 \quad (8)$$

which is satisfied by

- i. $u > \hat{u}$ if $\rho > \sigma$
- ii. $u < \hat{u}$ if $\rho < \sigma$. Namely the polymorphic solution is unstable inside the region of the ρ, σ, τ space defined by inequalities (6) and stable in that defined inequalities (7).

In the region

FIGURE 1.—Static properties of a pair of alleles when selection on the haplophase acts “after” that on the diplophase. ρ is the adaptive value of A with respect to a , σ and τ are those of Aa and aa with respect to AA . Haploid selection is held constant ($\rho = \frac{2}{3}$), namely this is a section of the parameter space ρ, σ, τ with the plane $\rho = \frac{2}{3}$. The straight lines $\sigma = \frac{2}{3}$ and $\tau = 2\sigma/3$ divide the σ, τ plane into four regions; each region is characterized by the solution (s) which is (are) stable within. Polymorphic equilibria having the same gene ratio lay in a straight line passing through $\sigma = 2/3$, $\tau = 4/9$; some of them are drawn (dashed). The parabolae are lines of constant mean adaptive value at the polymorphic equilibria, in the case of multiplicative interaction (formula 11). The parabola $\hat{W} = \frac{2}{3}$ degenerates into the straight lines $\sigma = 1$ and $\sigma = \frac{2}{3}$.

$$\left. \begin{array}{l} \tau < \rho\sigma \\ \rho > \sigma \end{array} \right\}$$

inequality (8) is always satisfied being $\hat{u} < 0$; here fixation of A is stable, that of a is not. Just the reverse occurs in the region

$$\left. \begin{array}{l} \tau > \rho\sigma \\ \rho < \sigma \end{array} \right\}$$

These four regions, specified by their stable solutions, are drawn in Figure 1 for a fixed value of $\rho (\frac{2}{3})$. In this representation, the condition $u = \text{constant}$ is a family of straight lines centered at $\sigma = \rho$, $\tau = \rho^2$; some of these are also drawn.

The mean adaptive values in the two phases, at the polymorphic equilibrium, turn out to be, for the diplophase

$$\begin{aligned} \hat{W}_D &\equiv \hat{X} + \sigma\hat{Y} + \tau\hat{Z} \\ &= \frac{\rho^2\hat{u}^2 + 2\rho\sigma\hat{u} + \tau}{(\rho\hat{u} + 1)^2} \end{aligned}$$

$$= (\tau - \sigma^2) \frac{\tau + \rho^2 - 2\rho\sigma}{\{\tau + \rho - (\rho+1)\sigma\}^2} \quad (9)$$

and for the haplophase

$$\begin{aligned} \hat{w} &= \rho\hat{p} + \hat{q} \\ &= \frac{\rho\hat{u} + 1}{\hat{u} + 1} \\ &= \rho \frac{\tau + \rho - (1+\rho)\sigma}{\tau + \rho^2 - 2\rho\sigma} \end{aligned} \quad (10)$$

According to the relative extensions of the two phases of an organism, these two quantities will have different weights in determining the overall adaptive value of the system. We might, for instance, assume that adaptive values in the two phases influence the performance of the population only through their product. This turns out to be, at equilibrium

$$\hat{W} \equiv \hat{W}_D \hat{w} = \rho \frac{\tau - \sigma^2}{\tau + \rho - (\rho+1)\sigma} \quad (11)$$

In the subspace ρ constant, the lines $\hat{W}$ constant are a family of parabolae passing through $\sigma = \rho$, $\tau = \rho^2$. They have upward concavity for $\hat{W} < \rho$, downwards one for $\hat{W} > \rho$, reducing to the straight lines $\sigma = 1$ and $\sigma = \rho$ for $\hat{W} = \rho$. The lower bound for $\hat{W}$ in the stable region is $2\rho^2/(\rho+1)$ (see Figure 1). This special case lends itself to an interesting comparison with the second model in this paper.

The treatment of random mating has been left to the end since the case deserves some special comment. For this purpose, the relative contribution in gametes (before gametic selection) and the relative contribution to zygotes per gamete must be worked out for each mating type. For the sake of simplicity, only the case of hermaphrodites is explicitly considered. The population can thus be described by the array in Table 1).

By combining the contribution in gametes with the contribution in zygotes per gamete and the segregation ratios, the proportions of zygotes are first obtained. Normalization of them leads again to recurrence (3).

It seems rather unlikely that the case might have any application. Since spermatozoa always far outnumber eggs, selection in the former should always be more intense than in the latter. It seems even less probable that a gene might effect in the same direction the survival and the chance of union of eggs and sperm. The same arguments apply to all organisms with a strong gametic dimorphism. Other arguments will be given later against a common occurrence of gametic selection, whether sex dependent or not, in higher organisms.

(2) *Selection on haplonts before that on diplonts:* If haplonts spend a relevant fraction of their cycle inside diplonts, haploid selection can be completed before dispersal or mating or before diploid selection starts operating. It might, for

TABLE 1

Population array for random mating of zygotes with gametic selection occurring after zygotic selection or mating

Mating types	Contribution in gametes	Contribution to zygotes per gamete	Segregation ratios		
			AA	Aa	aa
AA × AA	X^2/W_D^2	ρ^2	1	0	0
AA × Aa	$2\sigma XY/W_D^2$	$\rho \frac{\rho+1}{2}$	$\frac{\rho}{\rho+1}$	$\frac{1}{\rho+1}$	0
AA × aa	$2\tau XZ/W_D^2$	ρ	0	1	0
Aa × Aa	$\sigma^2 Y^2/W_D^2$	$\left(\frac{\rho+1}{2}\right)^2$	$\left(\frac{\rho}{\rho+1}\right)^2$	$\frac{2\rho}{(\rho+1)^2}$	$\frac{1}{(\rho+1)^2}$
Aa × aa	$2\sigma\tau YZ/W_D^2$	$\frac{\rho+1}{2}$	0	$\frac{\rho}{\rho+1}$	$\frac{1}{\rho+1}$
aa × aa	$\tau^2 Z^2/W_D^2$	1	0	0	1

instance, occur at some stage of meiosis, prior to phenotypic manifestation on the genes involved.

In this case haploid selection does not affect the haplophase proper but only the relative adaptive values of the genotypes and segregation in the heterozygote. In such a case, the population can be described by the following array:

Genotypes	Frequencies	Adaptive values	Segregation	
			A	a
AA	X	$1-s$	1	0
Aa	Y	1	$(1+d)/2$	$(1-d)/2$
aa	Z	$1-t$	0	1

Here $s \leq 1$, $t \leq 1$ and, without loss of generality, $0 \leq d \leq 1$.

Denoting by

$$W \equiv (1-s)X + Y + (1-t)Z$$

the mean adaptive value of the population, the frequency of A haplonts will be

$$p = \frac{(1-s)X + (1+d)Y/2}{W}$$

whence both by random union of gametes and random mating of zygotes we obtain the Hardy-Weinberg frequencies in the next generation.

Again it is more convenient to work in terms of haplont (gamete) ratios, that of A to a will be noted by

$$u = \frac{(1-s)X + (1+d)Y/2}{(1-t)Z + (1-d)Y/2}$$

The recurrence equation for this quantity is easily derived as

$$u' = u \frac{(1-s)u + 1 + d}{(1-d)u + 1 - t} \quad (12)$$

Its fixed points are:

- i. any u if $s = d = -t$;
- ii. $u = \frac{t+d}{s-d} \equiv \hat{u}$ or $u = 0$ if $s \neq d$; in terms of A frequency, $\hat{p} = \frac{t+d}{s+t}$.

Case (i) is a Hardy-Weinberg-like family and the same discussion as in the first model leads to a split of the parameter space into four domains, characterized by different stability properties of the solutions (ii):

1. $(-d < t \leq 1, d < s \leq 1)$: $\hat{u}$ is stable, both fixations are unstable;
2. $(t < -d, s < d)$: $\hat{u}$ is unstable, both fixations are stable;
3. $(-d < t \leq 1, s < d)$: $\hat{u} < 0$, fixation of A is stable, that of a unstable;
4. $(t < -d, d < s \leq 1)$: $\hat{u} < 0$, fixation of A is unstable, that of a stable.

In the subspace d constant, the condition $\hat{p}$ constant is a family of a straight lines centered on $s=d$, $t=-d$. See Figure 2 (dashed lines) for $d=1/3$; the four regions defined above are specified by their stable solutions.

The mean adaptive value at the polymorphic equilibrium will be

$$\begin{aligned}\hat{W} &= (1-s)\hat{X} + \hat{Y} + (1-t)\hat{Z} \\ &= \frac{(1-s)\hat{u}^2 + 2\hat{u} + 1-t}{(1+\hat{u})^2} \\ &= 1 - \frac{st+d^2}{s+t}\end{aligned}\quad (13)$$

In the subspace d constant, the lines $\hat{W}$ constant are a family of hyperbolae;

FIGURE 2.—The same as in Figure 1 but when haploid selection acts “before” zygotic; s and t are the selection coefficients on AA and aa with respect to Aa . The distortion in the heterozygote is measured by d , which is held constant ($1/3$). The straight lined $t = -1/3$, $s = 1/3$ divide the s , t plane into four regions; each is characterized by the solution (s) stable within. Polymorphic equilibria with equal gene frequencies lay on straight lines passing trough $t = -1/3$, $s = 1/3$; some of them are drawn (dashed). The branches of hyperbolae are lines of constant mean adaptive value at the polymorphic equilibria; that for $\hat{W} = 1-d$ degenerates to $s=d$ and $t=d$.

for $\hat{W} > 1-d$ the meaningful branches pass through $s=d$, $t=-d$; the condition $\hat{W}=1-d$ is satisfied by the two straight lines $s=d$ and $t=d$. The lower bound for $\hat{W}$, which occurs in the stable region, is $(1-d^2)/2$.

It might be of some interest to compare two systems, otherwise identical, with different distortion; this is done in the Appendix. It turns out that distortion results in a loss of adaptive value at stable equilibria, provided they are not the same in both cases, with respect to a pair in which the same zygotic section acts, but no distortion. This is just a slight extension of what was pointed out in (3) where it is also noted that the reverse might occur with fixed inbreeding.

Comparisons of this kind have a meaning only if, according to the magnitude of selection, there is such an excess of gametes that selection on them does not influence the adaptive values of the zygotes.

It must be noted that the hypothesis of sex independence in gametic selection seem even less plausible than for the first model. If it operates after meiosis, further reasons for sex dependence are the often large differences in timing between male and female gametogenesis (see, e.g. 6). This, together with the well known diversity of the cytoplasmic events in the sexes, seems to leave very few chances for a gene to alter the two meiotic processes (segregations) in the same way.

Although this model appears to be of very little practical value, if any, it is theoretically interesting to examine a special case in which it shares some property with the first one. This happens when:

- i: haploid selection does not depend on the haploid genotype, and
- ii. the adaptive value of haplonts (the mean one in the heterozygote), W_1 , interacts in a multiplicative way with the conditional adaptive values of the genotypes, W_2 , in determining their overall adaptive values, W_T .

The population can thus be described by the following array:

Genotype	Frequency	W_1	W_2	W_T	Segregation	
					A	a
AA	X	ρ	1	ρ	1	0
Aa	Y	$\frac{1+\rho}{2}$	σ	$\sigma \frac{1+\rho}{2}$	$\frac{\rho}{1+\rho}$	$\frac{1}{1+\rho}$
aa	Z	1	τ	τ	0	1

Under random mating or union of haplonts, the recurrence for

$$u \equiv \rho \frac{X + \sigma Y/2}{\tau Z + \sigma Y/2}$$

turns out to be

$$u' = \rho u \frac{u + \sigma}{\sigma u + \tau}$$

It is characterized by the polymorphic solution

$$\hat{u} = \frac{\tau - \rho\sigma}{\rho - \sigma}$$

and the same stability properties as the first model. The mean adaptive value at the polymorphic equilibrium turns out to be the same as in the case of multiplicative interaction between the mean adaptive values in the two phases for the first model (11).

DISCUSSION

That selection on the haplophase of an organism is much more efficient than that on the diplophase has been a well known fact since the oldest paper on the subject (HALDANE 1924). For instance, equal selection on both kind of gametes gives the same result as a twice larger selection on the homozygote and intermediate heterozygote. Thus, if selection on a gene operates, with similar intensities, in both phases of an organism, it is not surprising that the outcome is more heavily determined by selection on the haplophase.

This paper analyzed two models in which selection is sex independent in both phases. In the first, selection on the haplophase occurs after that in the diplophase has been completed. Here the relative adaptive values of the genotypes and of the haplont types, in their phases, must be separately defined. Also, the overall adaptive value of a genetic system will be determined by the mean adaptive values in the two phases.

The relative efficiency of the two forms of selection, when they act separately, is only slightly altered by their joint action. Thus, for instance, a relative adaptive value ρ in the A haplont balances the adaptive values ρ in Aa and ρ^2 in aa .

This model will apply to lower organisms with sexually undifferentiated haplophase. Whenever gamete dimorphism occurs, it seems *a priori* rather unlikely that selection might have the same intensity and/or direction in both kinds. An even stronger view is held in HALDANE's 1924 paper: "Except in homosporous plants, the intensity (*of selection*) must be different in gametes of different genders. . . ." The little observational evidence so far available fully supports this stand. On the other hand, the occurrence of selection in one kind of gametes rather than in both makes a very large difference, as shown again by HALDANE (1924). For these reasons it seems unlikely that the model might be a reasonable approximation for gametic selection in higher organisms.

The second case in this paper deals with selection on the haplophase before that on the diplophase (or dispersal or mating). Such selection (which includes the case of meiotic drive) seems to be possible only in rather high organisms. It is not likely, however, that this model can be applied to them, for the same reason as given for the previous one. It has nevertheless been discussed at some length, mainly for reference to HIRAZUMI (1962, 1964), where great emphasis is given to the possible role of such a mechanism in the evolution of higher organisms.

Again, the relative efficiency of distortion and genotypic selection are much the same as when acting separately. Thus, distortion balances a selection twice its magnitude on the homozygote and dominance ratio $\frac{1}{2}$. It might thus lead to fixation of rather deleterious genes or greatly slow down the accumulation of favorable ones. It seems unlikely that this may be compensated by its possible effect in speeding up the fixation of favorable genes. Differences in selection between

the two kinds of gametes should lead to a rather different situation. Special cases of this kind are treated by HIRAZUMI *et al.* (1960) and by KIMURA (unpublished).

Sex differences apart, it seems of advantage for higher organisms to reduce the chances of gametic selection to a minimum. The occurrence of genetic modifications counteracting the distortion of the *SD* locus in *Drosophila melanogaster* (HIRAZUMI *et al.* 1960) are in agreement with such a view. This would also imply that gametes of higher organisms should not be allowed to express their haploid phenotype, or very little of it. The delay of the last meiotic reduction in the majority of such organisms, as late as postfertilization in female insects might be indirect evidence (see, for instance, WHITE 1961). This view is also supported by the little direct evidence so far available (see, for instance, McCLOSKEY 1966).

From the above arguments, one should expect that the relative amount of selection in a phase of a organism should be roughly proportional to the weight of the phase in determining the overall adaptation of the population. While such models seem to have little practical value for higher organisms (especially animals), they might help in elucidating some aspects of the evolution from haploidy to diploidy.

Most of these considerations apply only to proper gene mutations. There are, in fact, hints of a very active selection, probably against gross chromosome abnormalities, in the sperm of higher animals. This occurs after insemination which, according to PEACOCK and ERICSON (1965), is also the case with *SD* alleles. Meiotic drive seems, on the other hand, a very plausible mechanism in producing large chromosome modifications. This is pointed out by KIMURA (1962), especially for the aneuploid type of increase in chromosome number.

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SUMMARY

This paper treats two deterministic models for natural selection on a pair of alleles when it acts both on the haplo- and diplophase of an organism. Since selection is assumed to be sex independent in both phases, it is argued that the models should never apply, in practice, to organisms with gametic dimorphism.—The difference between the two models lies in the timing of haploid selection with respect to zygotic. The first model assumes that selection on haplonts occurs after they have separated from the zygote, which should mainly apply to lower organisms. Adaptive and mean adaptive values must be accounted separately in the two phases.—Conditions for polymorphic equilibrium, its stability and the corresponding mean adaptive values in the two phases, are derived. Haploid selection is about twice as efficient as zygotic. Thus a relative adaptive value ρ in the *A* haplont exactly balances the adaptive values ρ in *Aa* and ρ^2 in *aa*, giving a Hardy-Weinberg-like equilibrium.—Selection on haplonts might also occur while they are still carried by the zygote and, at the same time, the trait has not yet been selected in the zygote. This is the assumption in the second model in which

haplont selection enters only through distortion in the heterozygote, adaptive values being as usual. It is argued that such a situation, altogether impossible in the lowest organisms, should be uncommon even in high ones.—Polymorphic equilibrium, conditions for its stability and corresponding mean adaptive value are derived. Again distortion is about twice as efficient as zygotic selection, so besides “lowering” the mean adaptive value of stable polymorphisms, it can slow down the accumulation of favorable genes or even produce the fixation of unfavorable ones. This is at variance with HIRAIZUMI’s conclusions on the evolutionary role of prezygotic selection.

APPENDIX

Comparison between distortion (the second model in this paper) and the usual Mendelian situation will be sketched; some reservations on its meaning have already been given.

The lowering of population fitness in a polymorphism maintained by distortion has already been emphasized by KIMURA and others. On the other hand, its effect on gene substitution does not seem to have been properly understood. HIRAIZUMI (1964), for instance, gives several examples of distortion speeding up substitution of favorable genes but not a single one of distortion slowing down such a substitution or producing substitution of a deleterious gene (“substitutional load” = $+\infty$).

It is convenient to introduce the quantity *loss of adaptive value, due to distortion, at a stable equilibrium*.

$$\Delta W(s, t, d) \equiv \hat{W}(s, t, d=0) - \hat{W}(s, t, d \neq 0) \quad (14)$$

Here $\hat{W}$ is given by (13) when the polymorphic equilibrium is a stable one, is $1-s$ when fixation of A is stable or $1-t$ when that of a is so.

The six regions of the parameter space d constant in which stable equilibria differ or can differ between the Mendelian and distorted situation are given in Figure 3 (dotted areas). On

FIGURE 3.—In the s, t plane a case with constant d ($1/3$) is compared with the Mendelian case ($d=0$). The continuous lines define the regions of the plane where the stable solutions differ in the two cases (dotted areas). ΔW measures the loss in mean adaptive value, at stable equilibria, due to distortion (see Appendix); bounds for its values within each region are given. The more heavily dotted area is where unfavorable genes tend to be fixed by distortion.

the interior points of each of them, upper and lower bounds for the quantity (14) are easily calculated; they are also given in Figure 3. Consider, for instance, the domain

$$(-d < t < 0, 0 < s < d);$$

here fixation of A is stable in the population with distortion, that of a in the distortion-free one. In this region $\Delta W = s - t$ whose bounds are 0 and $2d$.

Proceeding in the same way for the other regions it is proved that: "Except when both populations are in the same stable equilibrium, a population with distortion will have, almost everywhere in s, t , a lower adaptive value, at a stable equilibria, than a distortion-free one with the same values of s and t ."

Some dynamics of such system will be discussed with the usual approximation by differential equations. Neither its accuracy as such, nor its own merits as an overlapping generations model will be discussed.

For equation (12) it gives

$$\frac{du}{d\tau} = u \frac{(d-s)u + d + t}{(1-d)u}$$

which, by separation, integrates to

$$-\tau = \frac{1}{t+d} \left\{ (1-t) \ln \frac{u}{u_0} + \left(\frac{st+d^2}{s-d} - \hat{u} \right) \ln \frac{u-\hat{u}}{u_0-\hat{u}} \right\}$$

where u_0 is the initial gene ratio and $\hat{u} = (t+d)/(s-d)$.

As an example, the number of generations required for a change in the ratio of A to a genes from 10^{-3} to 10^3 is, for $s = -.4, t = .3$ and different values of d

d	Number of generations
.2	60.66
.1	82.10
0	111.27
-.1	161.01
-.2	290.22

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