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## COMPONENTS OF FITNESS

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## I. FITNESS AND BIOLOGICAL PROGRESS

The substance of this paper is concerned with an analysis of the components of fitness and may stand as such without reference to biological progress. Nevertheless, the general definition of fitness here presented was derived from some thought concerning the meaning of biological progress, and it is perhaps well, therefore, to give it its original context.

The problem of arriving at a satisfactory definition of biological progress has recently received the attention of a number of authors, notably of Julian Huxley (1942, 1947), who has steadily endeavoured to push the problem before us as one of great importance and has derived from some detailed discussion a definition of progress that is of considerable interest. This definition is broadly increasing adaptation to life in general, rather than to any particular mode of life, one of the important features being increasing independence of the environment. It is derived from a consideration of the characteristics distinguishing dominant groups from both their non-dominant contemporaries and their dominant predecessors. A definition quite similar in principle (and apparent derivation) has been put forward by J. Z. Young (1951).

These definitions of progress, however, seem to have one essential weakness, for they involve the initial assumption that there is or has been progress, which leaves only the question of deciding in what directions change must be if it is to be labelled progressive. This may be justifiable if we appeal to our intuitive feeling that progress has occurred, but it does not seem entirely justifiable to some. Simpson (1950), for instance, does not seem to be satisfied. He points out that it is possible to define progress in relation to any end, and then find evidence of the progress so defined.

Though this is true it seems too extreme and, furthermore, involves the use of the word progress in a different sense from that of Huxley. It involves using the word progress in its general sense of unidirectional change, rather than giving the word its particular meaning of change toward a higher state.

There does, however, seem to be an approach to a definition of progress that avoids the assumption that progress has occurred, and at the same time does not permit us to define progress entirely as we will. This

approach involves the initial consideration of the general conditions of living and the deduction from these of the kinds of change that, whether they have occurred or no, must be labelled progressive.

Thus approaching the problem, we are forced to begin with the axiom that survival is essential to life, and hence that progress must be increase in fitness for survival, provided only that fitness and survival be defined as generally as possible.

It is therefore the purpose of this paper to put forward a general definition of fitness and to analyse the components of fitness. A progressive change will be one that increases this fitness. One which decreases it will be retrogressive, and a change that does not alter it will be mere change, however much it is part of a unidirectional trend.

## II. UNITS OF EVOLUTION

The word fitness is of course used in many ways. These differ largely in the level to which the word is applied—individual, population or species, or in the time scale to which it is applied. For our present purpose it is not satisfactory to restrict the meaning of the word to fitness for the *contemporary* environment, since the fitness of a group must include its capacity for future survival in future environments. We cannot, therefore, discuss directly the fitness of individuals or populations or species, for to do so we should have to put entirely arbitrary limits on the time during which survival is to occur. If we are not so to limit this time, then the fitness of contemporary individuals or populations cannot be defined without reference to their offspring. Therefore the fitness of each generation is dependent to some measure on the mates of its descendants and we are forced to define fitness for survival in relation to that contemporary group of individuals which will some time in the future have common descendants. These we may call the contemporary representatives of a unit of evolutionary continuity or for the sake of brevity a *unit of evolution*.

It is, of course, well-nigh impossible to determine just where the boundaries of such a unit lie, because of the variation and variability\* of breeding structures (Thoday, 1952). Where isolating barriers may in the future break down, where introgressive hybridization may occur, or where allopolyploids may arise, the unit of evolution must comprise more than one taxonomic species and often more than one biological species. On the other hand, where sexual reproduction has been permanently lost the representative at any one time of a unit of evolution must be an individual. There are all possible intermediate conditions.

\* In this paper the words variation and variability are strictly distinguished. Variability is used to mean *capacity to vary*.

However, though it may for this reason seem unsatisfactory to relate fitness to such units of evolutionary continuity, we are nevertheless forced to do so, and we must therefore remember that the various contemporary and future components of a unit belong to the unit whether or no they exhibit such morphological variation that they receive more than one specific or generic name, and that a species which is as species extinct may nevertheless have left descendants and may be more successful than another species that survives as such.

### III. STABILITY AND VARIABILITY

The probability that such a unit of evolution will survive for a given long period of time, such as  $10^8$  years, that is to say will leave descendants after the lapse of that time, is the fitness of the unit. It depends upon a number of components that may be called adaptation, stability, variability and the rate of environmental change.

Such a unit has to be imagined as existing in a slowly changing environment. Its members are of course selected so as to become adapted to their contemporary conditions. The more perfectly adapted they become, the greater will be the advantage of producing offspring like themselves, and there will therefore be selection for *genetic stability*. However, during any long period of time considerable environmental change will occur, and the unit of evolution must be capable of variation so that it may meet this change. There will therefore be selection for *variability*. Thus the fitness of the unit depends not only upon adaptation to the present environment, but also upon adaptation to change in that environment. Short-term survival depends upon adaptation and stability; long-term survival depends upon short-term survival and upon variability; the capacity to change.

These general conditions of survival have of course been widely realized, and, especially since the publication of Darlington's (1939) *Evolution of Genetic Systems*, it has further been realized that there is some antagonism between the two conditions of survival here expressed as stability and variability. Darlington expressed the antagonism in terms of 'fertility' and 'sterility', and he discussed a number of examples illustrating the effects that selection for stability and variability have had on genetic systems. Mather (1943) has also discussed the matter in terms of 'fitness' and 'flexibility', and these authors have contributed much to our sense of the compromise between stability and variability necessary to a genetic system that is to be successful.

## IV. PHENOTYPIC FLEXIBILITY

The discussions of both these authors have been concerned almost entirely with genetic mechanisms, and thus the component of variability they discuss is *genetic flexibility*. However, this is not the only form of variability that can permit a unit of evolution to survive environmental change.

One of the general properties of life is what we sometimes call its antagonism to its environment. By this we mean that an individual organism is capable of adapting itself to varying external conditions so that by reaction to the environment it maintains its characteristics. In other words, organisms are buffered against environmental variation. Now though this buffering is a general characteristic of life, nevertheless, some organisms are buffered against a wider range of environmental conditions than others.

It is evident that such variation in the range of environmental conditions in which the individual members of different units of evolution can successfully function must mean variation in the range of environmental change the units can survive without the necessity of genetic change, and hence without the necessity of genetic flexibility. There is therefore a component of variability which is independent of genetic flexibility. For this we may use the term *phenotypic flexibility*, to underline the relationships between the two. A unit of evolution which had complete phenotypic flexibility could be perfectly fit, for it could have complete genetic stability, and nevertheless its members could function in all possible environments and hence meet all possible environmental change.

## V. COMPONENTS OF FITNESS

Of necessity, most organisms which survive are well adapted to their contemporary environments, though there may be varying lags in adaptation. Therefore the first component of fitness, adaptation to contemporary conditions, is likely to vary least. Thus the relative fitness of different units of evolution is likely to be largely independent of adaptation, and increase of fitness, which is biological progress, must be brought about largely by changes which increase either genetic stability or variability without bringing about corresponding decrease in the other component. A progressive change is thus one that increases the sum of these components.

Since variability is divisible into two components, genetic and phenotypic flexibility, and since genetic stability and genetic flexibility are partially antagonistic, it will be clear at once that increase of fitness might be brought about either by changes in the genetic system that affect the relationship between genetic flexibility and genetic stability or by changes that increase phenotypic flexibility.

## VI. THE GENETIC SYSTEM AND FITNESS

Some resolution of the conflict between genetic stability and genetic flexibility is possible, for, in many organisms, much genetic variation is not of necessity expressed as phenotypic variation. Such suppressed genetic variation or, as Muller (1949) has called it, cryptic genetic change may be a source of variability which does not involve equivalent loss of stability.

This suppression may be a result of diploidy and dominance, or of dominance in heterokaryons. In either state recessive genes may be carried as a hidden source of variability that does not affect stability by causing phenotypic variation. The various life cycles and some of the sex-determination mechanisms of plants and animals may be considered in this light. Plants with an alternation of haploid and diploid generations must have their variability limited primarily in the haploid phase, and from this point of view, *Fucus* and the Liliaceous and Plumbaginaceous forms that have reduced the haploid phase to one division in the female have thereby increased fitness most. Similar considerations apply to haploid tissues such as the endosperm of gymnosperms, to haploid sexes, and to haploid parts of the chromosome set. However, care must be taken in applying such a criterion. The elimination of a haploid endosperm may have been one major source of advantage to angiosperm ancestors. Nevertheless, the limit imposed by a haploid tissue, or a haploid phase in the life cycle, must in part depend on the variability and complexity of the environment to which that tissue or phase is exposed. For example, the haploid endosperm of a gymnosperm may limit fitness of gymnosperms much less than the gametophyte phase of a fern limits the fitness of ferns, for the environment of the endosperm is partly under sporophyte control.

The development of balanced polygenic systems as discussed by Mather (1943) may also be regarded as resulting in increase of fitness, for it permits variation of genotype that does not necessarily result in phenotypic variation. Within populations relational balance permits variation of genotype accompanied by relative uniformity of phenotype, and hence the maintenance of adaptation and at the same time of adaptability. Likewise internal balances that are different in different populations provide a source of variability, that though fixed, may be freed when, perhaps as a result of environmental change, the populations meet. This brings us to the question of genetic diversity in the unit of evolution. Such a unit, if it is composed of many partially isolated populations, or even completely isolated populations provided the isolation is not permanent, will come to consist of many

lines, each stable, but each capable, if the environment changes, of contributing sources of variation to the common pool of variability. Such concepts have been discussed by Wright (1940) and Stebbins (1950), who has pointed to the freeing of fixed variability consequent upon hybridization.

Thus the unit of evolution whose genetic component of fitness is greatest will be that in which the ratio of the number of genotypes to the number of phenotypes in any particular environment is greatest and in which there are the largest number of temporarily isolated subunits. Hence the fission of the unit, sometimes synonymous with speciation, must reduce the fitness of the unit and is therefore biologically retrogressive unless it happens in such a way that it either increases phenotypic flexibility or permits part of the unit to establish in some more stable environment.\*

Finally, among aspects of the genetic system there are mechanisms that permit stability when the environment is stable and variation when variation is required. These depend either on factors that operate on recombination rate or on the existence of what may be called dual breeding systems. Factors that operate on recombination rate to affect fitness in this way may be rare. However, the crossover frequency of *Drosophila* does vary in such a way as to be minimal in optimal temperature conditions (Plough, 1917), and this would make possible greater stability in optimal conditions and increased variation when conditions deviate widely from optimal.

Dual breeding systems are those which involve both sexual and asexual reproduction, whether together or alternating. Asexual reproduction of course involves high stability, and forms that are only reproduced this way can only survive environmental change by virtue of such phenotypic flexibility as they may possess. But forms reproduced by both means, such as facultative apomicts and many herbaceous perennial angiosperms, may have high stability and variability together. Such a breeding system must be particularly advantageous to sessile organisms, for sexual reproduction will permit variation among the offspring that must colonize more distant and different environments, and asexual reproduction will permit the locally successful form to spread locally.

It is not the purpose of this paper to present any detailed analysis of the components of fitness. Rather is it the purpose to present a synthesis of the components. Hence this brief discussion of genetic systems and fitness must suffice. The subject has been discussed extensively by many others.

\* It is perhaps worth pointing out that some authors' conclusions depend upon the assumption that permanent fission of the unit is the end or an essential means of progressive evolution. For instance, much of the argument in Keith's (1946) *Essays on Human Evolution* depends upon this unjustified generalization.

## VII. FITNESS AND PHENOTYPIC FLEXIBILITY

Though the importance of genetic flexibility is widely realized and discussed, little attention has been given to phenotypic flexibility in the context of evolution theory, or even as a desirable characteristic for economic plants. Furthermore, phenotypic flexibility is often entirely ignored, and the view is expressed that without genetic flexibility a form is doomed to extinction. This view implies that genetic evolution is the only means whereby organisms can meet environmental change. It is particularly misleading when applied to man whose high phenotypic flexibility has made social inheritance and variation of utmost importance (Thoday, 1951). In man stability and variability must largely be a question of tradition and new ideas.

The term phenotypic flexibility is used here in the sense in which Salisbury (1940) has used plasticity, that is, to describe the capacity of the individual organism to function in a range of environmental conditions. Such phenotypic flexibility may be classified into two types, *developmental flexibility* and *behaviour flexibility*.

An individual or organism may be said to possess developmental flexibility either if its genotype is such that it can develop different phenotypes in different environments, each phenotype better adapted than the others to the environment that evokes it, or if its genotype is so balanced that development is buffered against environmental variables and hence apparently the same adaptive phenotype results in a range of environmental conditions. Such flexibility will be of particular advantage in heterogeneous habitats, and, hence, is most likely to be selected for in such habitats.

An individual organism may be said to possess behaviour flexibility if it can react temporarily to environmental change so that it adapts reversibly, or if, being mobile, it can choose the environment to which it is best adapted.

(a) *Developmental flexibility*

The relative developmental flexibility of different forms must be difficult to assess, for, though apparent examples of such flexibility may be easy to find, the demonstration that developmental flexibility is truly involved may be difficult. The difficulty arises because morphological plasticity, as the term plasticity is used by, for example, Marsden-Jones & Turrill (1930, 1938), may sometimes be evidence for developmental flexibility, but is just as likely to be evidence of lack of such flexibility. To take an example, a plant that produces different forms in sunny and in shady situations has morphological plasticity. But to show that it has developmental flexibility it would be necessary to show that the development of a shade form in

shady situations, and of a sun form in sunny situations, is a positive advantage to the plant. It may well be that the sun form might be a better adaptation to the shady situation, but the plant is incapable of developing that form in that environment.

To take a specific example, we may consider briefly the shade form var. *lobata* of *Dactylis glomerata*. Turresson (quoted by Salisbury, 1940) reports that, like so many ecotypes, var. *lobata* is sometimes genetically fixed, but in other areas it is a modification, and if transplanted to a well-lit situation produces the more normal narrow leaves. Now if it be supposed that a broad leaf is advantageous in the shade and a narrow leaf in the sun, a supposition that requires to be tested experimentally, then the form of var. *lobata* that is *not* genetically fixed would appear to be at an advantage in both situations, for it develops the appropriate phenotype in the appropriate conditions. Seeds falling in open situations and seeds falling in shady situations will both fall in suitable environments. Furthermore, the removal of the source of shade will leave the young plants in a situation to which they are adaptable. The genetically fixed form, on the other hand, will only find a suitable environment when the seeds fall in shady situations and while the shady environment itself survives. It is therefore possible that the genetical fixing of the shade form is a disadvantage.

In fact, the whole problem of the genetical basis of modifications has been neglected. For too long environmentally caused phenotypic variation has been regarded by geneticists as a nuisance interfering with their proper study of genetic variation, whereas in fact knowledge of the genetic situations that control the extent to which development can be affected by environmental variables may prove of the utmost value both to students of evolution and to the plant and animal breeder.

Fortunately, there are signs that steps are being taken to remedy this deficiency. When I was discussing the problem of developmental flexibility with Prof. Mather some time ago he was good enough to tell me of his observations on asymmetry in *Drosophila*, as measured by sternopleural bristle number. He had not only shown that it was possible to select effectively for high and low asymmetry, but also that  $F_1$ 's between the highly inbred strains Samarkand and Oregon were less asymmetrical than their parents. Now the prime cause of difference between the two sides of a fly must be difference between the environments to which the sides are exposed. Hence we reach the conclusion that these heterozygous flies are better buffered against environmental variables than are their highly homozygous parents. Mather (1950) has made similar observations on inbred strains of *Primula sinensis* which have a greater within-plant variance of style length than outbred plants.

Evidence that leads to a similar conclusion is accumulating from the study of the variances of  $F_1$  individuals and of the individuals of the parental strains. Mather (1949) has quoted one example from a species cross between *Petunia axillaris* and *violacea*. The variance in corolla length of  $F_1$  is lower than that of either parent, which again must mean that the hybrid is less affected than its parents by environmental variables. Another example, pointed out to me by Mr Riley of Sheffield University, is provided by Sax's data quoted by Mather (1949) as evidence of linkage between major genes and polygenes. Sax's experiment involved crossing *Phaseolus vulgaris* strains differing in seed size and by a single major gene affecting colour. The coefficients of variation in seed size, calculated from the standard errors and numbers given, are 6.5 and 6.1 for the two sets of  $F_2$  beans homozygous for the colour factors and 4.6 for the set heterozygous for the colour factors. Hence it seems that heterozygosity for a particular chromosome or chromosome segment can significantly reduce environmentally caused variation. Similar conclusions are suggested by the interesting results of Hagberg (1952) with *Galeopsis* and of Rasmuson (1951) with *Drosophila* bristles, and striking results have been described by Robertson & Reeve (1952) showing that variance in body size in *Drosophila* increases with the number of chromosome pairs that are made homozygous. It is of the greatest importance that such investigations be extended to naturally inbreeding species.

From the present point of view Mather's experimental studies of asymmetry are of great interest. Interest in developmental flexibility makes us not only desire to study the genetical basis of environmentally caused phenotypic variation, but also require some means of determining whether or not the environmentally caused variation we measure is due to developmental flexibility. The problem will always be to decide whether a particular environmentally caused morphological change is evidence of developmental flexibility or of lack of efficient buffering of the organism. There is, however, a way out if the characteristic studied is amenable to quantitative study that will give estimates of both intra-individual and inter-individual variation. Intra-individual variation when there should be symmetry, such as difference of size of the two wings of a fly, may be taken as a measure of poor organization of the individual. Hence where high inter-individual variation of, for example, wing size is correlated with high asymmetry, we may plausibly suppose that the inter-individual variation is evidence of low developmental flexibility. On the other hand, high inter-individual variation correlated with high symmetry would suggest high developmental flexibility. This is summed up in Fig. 1, which specifically refers to comparisons between heterozygotes and homo-

zygotes, but is applicable to any two or more genetically homogeneous samples.

A concrete example may serve to illustrate the application of these principles. Preliminary studies of sternopleural bristle number in two highly inbred lines of *Drosophila* (Oregon and Samarkand)\* and their two

Variation of heterozygotes relative to corresponding homozygotes		Inter-individual variation (within clones or genetically homogeneous populations)	
		Greater	Less
Intra-individual variation (asymmetry)	Less	Better organization of heterozygous individuals indicating high inter-individual variation is due to developmental flexibility that depends on physiological mechanisms with morphological effects	Better organization of heterozygous individuals indicating low inter-individual variation is due to developmental flexibility that depends on physiological mechanisms without morphological effects
	Greater	Poorer organization of heterozygous individuals indicating high inter-individual variation is due to low developmental flexibility	Poorer organization of heterozygous individuals indicating low inter-individual variation is due to low developmental flexibility

Fig. 1. Interpretation of non-genetic variation

reciprocal  $F_1$ 's grown at various temperatures,† indicate that both variance and asymmetry of bristle number are higher at 30 than at 25° C., but that the increase in variance and asymmetry brought about by the increase in temperature is much less for  $F_1$ 's than for the inbred lines. We conclude that the increase in variance is due to increased disorganization of development, and that the relatively heterozygous flies withstand the extreme environment much better than the inbred flies; the  $F_1$ 's have greater development flexibility than the inbred lines.

The conclusion, hence the technique, may be tested by determining the viability of the flies in the different environments; it passes the test.

Fig. 2 illustrates the mean numbers of flies emerging as adults from cultures containing ten eggs each. Viability is low at 30° C., but it is clear that the  $F_1$ 's survive this extreme environment far better than the parents. In fact, the  $F_1$  flies have clearly greater developmental flexibility with

\* The author is indebted to Prof. K. Mather, F.R.S., who kindly made these stocks available.

† It was not possible to control humidity for these experiments. High temperature may not, therefore, have been the important factor determining the effect of the extreme environment.

regard to temperature than the inbred strains, or, if it is preferred, greater 'resistance' in Timofeeff-Ressovsky's (1940) sense.

Interestingly enough, an example where  $F_1$ 's between pure lines show, relative to the parents, high intra-individual variation and low inter-individual variation has recently been published by Hagberg (1952). The

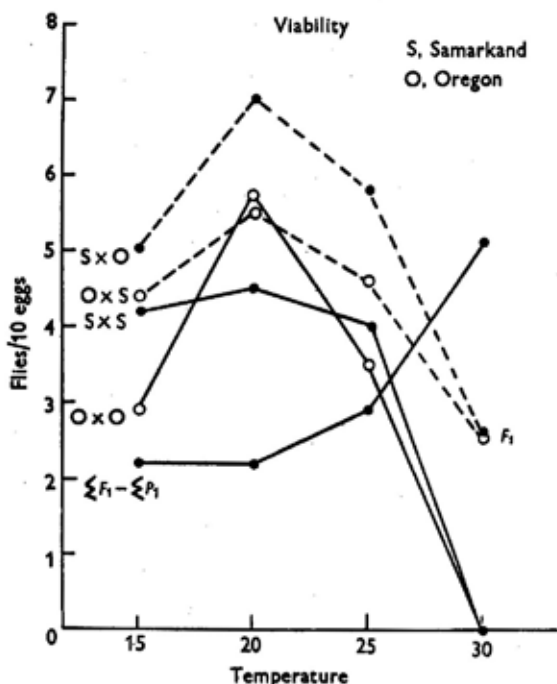


Fig. 2. Temperature and viability of inbred and  $F_1$  *Drosophila*. Each point represents the mean number of adults emerging from twelve tubes in each of which ten eggs were planted. O x O, Oregon stock. S x S, Samarkand stock. O x S, Oregon x Samarkand  $F_1$ . S x O, Samarkand x Oregon  $F_1$ .  $\Sigma F_1 - \Sigma P_1$  (mean number of O x S adults + mean number of S x O adults - mean number of O x O adults - mean number of S x S adults): measure of the viability of  $F_1$ 's relative to the parental inbred types.

plants are forms of *Galeopsis tetrahit* and the character stomatal size. These results would not, however, necessarily indicate that the parental lines have higher developmental flexibility than the relatively heterozygous  $F_1$ . There is no *a priori* reason to suppose that uniformity of stomatal size is necessarily a measure of a high degree of organization of the individual. In fact, there is some evidence that the most efficient stomatal size may vary with the position of the stoma (see Yapp, 1912). For a character to be suitable for this purpose there must be very good reason to suppose complete symmetry to be desirable.

It may be felt by some that these examples are merely demonstrations of yet another aspect of hybrid vigour. In a sense, of course, this is so, but it seems to be a matter that may be of fundamental evolutionary importance. Heterozygosity in naturally occurring organisms is usually the result of out-breeding systems, and the prevalence of such systems is plausibly explained in terms of the genetic flexibility that results. Nevertheless, this plausible explanation is not necessarily the sole explanation. Heterozygosity *must* have some advantage of a general nature other than that arising from the resulting segregation, for mechanisms fixing heterozygosity are too common. The evolution of a genetic system that permits heterozygosity must, therefore, sometimes confer advantages on the individual as well as the population. It may be that the genetic complexity involved permits relatively high developmental flexibility.

Perhaps we have here an explanation of the success of amphidiploids. Amphidiploidy is more and more clearly demonstrated to be a widespread phenomenon among plants. Often the amphidiploid species has, as parents, species whose ranges are small. For some reason the amphidiploid spreads rapidly. Now it is clear that the rapid spread of the amphidiploid species, relative to its diploid parents, cannot be explained in terms of genetic flexibility because the amphidiploid by nature of its origin cannot segregate and must have a smaller population size than the parent species. However, though from the point of view of segregation the amphidiploid must be completely homozygous until mutants arise, from the point of view of gene action it may be highly heterozygous, containing different alleles or differently balanced chromosomes in the different genomes. It may be therefore that developmental flexibility is conferred upon it by this heterozygosity, and that it is this that permits it to spread.

#### (b) *Behaviour flexibility*

Of behaviour flexibility there is no need to say much. The term is here used to include all those *reversible* changes by which an individual organism can adapt itself to environmental change. The category is highly heterogeneous, including the ability of the individual to migrate from a place that is becoming less suitable for it and find a more suitable place, such an ability as that of *Mimosa pudica* to survive tropical rainstorms by folding up, the ability of deciduous trees and northern mammals to change as the seasons change, the ability of beavers and man to control their local environment, and thousands of other specific abilities, all of which permit temporary adaptation to temporary environmental conditions.

It is, however, a moot point where we must classify ability to control the environment. We may if we wish regard the ability to control part of the

High phenotypic flexibility permitting, as it must, relatively high genetic stability, must have a profound effect on the reaction of a population to gradual environmental change, for it will mean that there is a considerable lag in genetic change. When, however, genetic change begins, the balance upon which the phenotypic flexibility depends may often be lost, and hence the organisms may be placed in a position where relatively radical genetic change is required rather suddenly. We may thus get evolution proceeding rather in fits and starts though these may be on a small scale. 'Quantum evolution', as discussed by Simpson (1949), is likely to be a phenomenon involving more radical genetic changes, but since we have little idea how important phenotypic flexibility may be, we cannot say.

(c) *Revolutionary environmental changes*

Such changes are those which involve the comparatively rapid disappearance of a habitat and may usually be brought about by sudden invasion by a new type of organism, or the sudden disturbance of an ecological system often as a result of the activity of man or the death of a parasite's host. Very often the environments subject to such changes will be local environments, such as the habitats occupied by mosses in woods, isolated ponds or rubble piles and other open or disturbed small areas. These types of environment are in one way unstable, for they appear and disappear at a given locality, but in another way they are stable for they always exist somewhere. Units of evolution that occupy such habitats may therefore be highly stable provided that they are efficient migrators. Among the appropriate plants, therefore, we find many, such as apomicts, with very efficient dispersal mechanisms but relatively low genetic flexibility. Such environments might well be labelled ephemeral. Desert environments also present a situation in which conditions of growth may be said to be ephemeral, and here ephemeral plants are correspondingly common. Furthermore, many of the desert perennial species are capable, if the rainy season is short, of developing as ephemerals, though it requires to be demonstrated whether these are the same genotypes that can establish as perennials in more favourable seasons. The ephemerals proper must be presented with considerable difficulties by such variable seasons, for they must by some mechanism ensure that the first rains do not bring about the germination of all seeds. Otherwise in a season when there is insufficient rain to permit fruiting the population must be exterminated. Delicate switch mechanisms determining germination (which may be classed as behaviour flexibility) may be the most usual means of ensuring that only a proportion of the seeds germinate in any one year, but other means may be discovered.

## IX. PROGRESS, FITNESS AND ENVIRONMENTAL CHANGE

We began with an attempt to determine the meaning of fitness as applied to a unit of evolution, since increase of such fitness is what we define as biological progress. Such fitness may be analysed into a number of components all affecting either the ability of the unit to retain its adaptation and its ability to accommodate to environmental change or the amount of environmental change it may meet. Fitness so considered is compounded of stability and variability, and increase in fitness becomes a resolution of the antagonism between stability and variability. This resolution may be brought about either by changes of the genetic system that increase the amount of cryptic genetic variation, or by increase of the range of environmental conditions to which the individual is adaptable or adapted, or by adaptation to a stable environment. The fitness of a unit at any one time may therefore be represented in the first analysis as increasing with the number of genotypes in the unit, decreasing with the number of phenotypes, increasing with the mean phenotypic flexibility of the individual members of the unit, and decreasing with increase in the rate of change to which the environment of the unit is liable. Alteration of any of these factors will alter the probability that the unit will survive a given long period of time, and one factor may have a strong influence on the effects of selection on the others, for all the components of fitness must be interrelated so that:

(i) In a relatively uniform and stable environment there will be little selection for genetic or phenotypic flexibility, and selection will primarily be for adaptation and stability.

(ii) In a heterogeneous environment there will be strong selection for phenotypic flexibility, especially among organisms with a long generation time. It is of some importance in relation to contemporary population studies to consider that the smaller a population is the more uniform (relatively) its environment is likely to be, and, hence, small populations, especially small island populations, may be subjected to more powerful selection for adaptation, whereas the larger mainland populations, occupying a relatively heterogeneous environment, must be subject to less powerful selection for local adaptation, and more selection in favour of generally successful, developmentally flexible types.

(iii) In an unstable environment there will be strong selection for genetic flexibility, but the greater the phenotypic flexibility the less selection there will be for genetic flexibility.

This definition of fitness and the implied definition of progress put strong stress upon the capacity of units of evolution to deal with environmental change. This seems justifiable, for life could not arise except in

a changing world, and once arisen life itself is change and must accommodate itself to the change of which it becomes part cause. Mutation, segregation, reproduction and death are adaptations to that change, and progress of life must come about by the means whereby these are manipulated and made less necessary.

Except verbally the conclusions are little different from those of Huxley, for phenotypic flexibility is largely similar to Huxley's independence of the environment, and Huxley's adaptation to life in general rather than to any particular mode of life is essentially adaptation to the more stable aspects of the environment. In one respect, however, Huxley's progressive trends have to be treated with reserve, for he has included increasing rate of change as such a trend. This, however, may not necessarily be justifiable, for increasing the rate of change of one unit of evolution, such as that of which we ourselves are members, may well mean so great an increase in the rate of change of the environment that fitness is in effect decreased.

Finally, it may perhaps be suggested that the best measure we have of the range of future change a unit of evolution can survive is in fact the range of contemporary environmental conditions the members of the unit can occupy. This then may be a legitimate approximation to a definition of progress for immediate purposes.

## X. SUMMARY

1. It is argued that fitness for survival cannot be completely defined except as applied to a 'unit of evolution', that is, the unit comprising all the contemporary individuals that will have common descendants.
2. The fitness of such a unit is its probability of leaving descendants after a given long period of time. Biological progress is increase in such fitness.
3. Such fitness has a number of components:
  - (a) adaptation,
  - (b) genetic stability,
  - (c) variability, which comprises
    - (i) genetic flexibility,
    - (ii) phenotypic flexibility,
  - (d) the stability of the environment:
4. Increase of fitness can come about:
  - (a) by resolution of the antagonism between genetic stability and genetic flexibility which is possible by the development of genetic systems permitting increased cryptic genetic variation, or by division of the unit into temporarily isolated subunits,
  - (b) by increase of phenotypic flexibility (increase of the range of environments in which the individual can function),
  - (c) by adaptation to a stable environment.

5. Within populations and species the various components of fitness will be balanced. Thus a heterogeneous or unstable habitat will lead to selection for variability; this may result in a flexible genetic system or a flexible developmental system or both. The more flexible the developmental system, the less flexible the genetic system need be, and the strength of selection for the two types of flexibility must depend largely upon the relations between generation time, the rate of environmental change and the heterogeneity of the environment.

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