

I

THE NATURE OF INHERITANCE

The consequences of the blending theory, as drawn by Darwin. Difficulties felt by Darwin. Particulate inheritance. Conservation of the variance. Theories of evolution worked by mutations. Is all inheritance particulate? Nature and frequency of observed mutations.

But at present, after drawing up a rough copy on this subject, my conclusion is that external conditions do extremely little, except in causing mere variability. This mere variability (causing the child not closely to resemble its parent) I look at as very different from the formation of a marked variety or new species. DARWIN, 1856. (*Life and Letters*, ii, 87.)

As Samuel Butler so truly said: 'To me it seems that the "Origin of Variation", whatever it is, is the only true "Origin of Species".' W. BATESON, 1909.

The consequences of the blending theory

THAT Charles Darwin accepted the fusion or blending theory of inheritance, just as all men accept many of the undisputed beliefs of their time, is universally admitted. That his acceptance of this theory had an important influence on his views respecting variation, and consequently on the views developed by himself and others on the possible causes of organic evolution, was not, I think, apparent to himself, nor is it sufficiently appreciated in our own times. In the course of the present chapter I hope to make clear the logical consequences of the blending theory, and to show their influence, not only on the development of Darwin's views, but on the change of attitude towards these, and other suppositions, necessitated by the acceptance of the opposite theory of particulate inheritance.

It is of interest that the need for an alternative to blending inheritance was certainly felt by Darwin, though probably he never worked out a distinct idea of a particulate theory. In a letter to Huxley probably dated in 1857 occur the sentences (*More Letters*, vol. i, Letter 57).

Approaching the subject from the side which attracts me most, viz., inheritance, I have lately been inclined to speculate, very crudely and indistinctly, that propagation by true fertilization will turn out to be a sort of mixture, and not true fusion, of two distinct individuals, or rather of innumerable individuals, as each parent has its parents and

ancestors. I can understand on no other view the way in which crossed forms go back to so large an extent to ancestral forms. But all this, of course, is infinitely crude.

The idea apparently was never developed, perhaps owing to the rush of work which preceded and followed the publication of the *Origin*. Certainly he did not perceive that the arguments on variation in his rough essays of 1842 and 1844, which a year later (1858) he would be rewriting in the form of the first chapter of the *Origin*, would on a particulate theory have required him entirely to recast them. The same views indeed are but little changed when 'The causes of variability' came to be discussed in Chapter XXII of *Variation of Animals and Plants* published in 1868.

The argument which can be reconstructed from these four sources may be summarized as follows:

- (a) with blending inheritance bisexual reproduction will tend rapidly to produce uniformity;
- (b) if variability persists, causes of new variation must be continually at work;
- (c) the causes of the great variability of domesticated species, of all kinds and in all countries, must be sought for in the conditions of domestication;
- (d) the only characteristics of domestication sufficiently general to cover all cases are changed conditions and increase of food;
- (e) some changes of conditions seem to produce definite and regular effects, e. g. increased food causes (hereditary) increase in size, but the important effect is an indefinite variability in all directions, ascribable to a disturbance, by change of conditions, of the regularity of action of the reproductive system;
- (f) wild species also will occasionally, by geological changes, suffer changed conditions, and occasionally also a temporary increase in the supply of food; they will therefore, though perhaps rarely, be caused to vary. If on these occasions no selection is exerted the variations will neutralize one another by bisexual reproduction and die away, but if selection is acting, the variations in the right direction will be accumulated and a permanent evolutionary change effected.

To modern readers this will seem a very strange argument with which to introduce the case for Natural Selection; all that is gained

by it is the inference that wild as well as domesticated species will at least occasionally present heritable variability. Yet it is used to introduce the subject in the two essays and in the *Origin*. It should be remembered that, at the time of the essays, Darwin had little direct evidence on this point; even in the *Origin* the second chapter on 'Variation under Nature' deals chiefly with natural varieties sufficiently distinct to be listed by botanists, and these were certainly regarded by Darwin not as the materials but as the products of evolution. During the twenty-six years between 1842 and 1868 evidence must have flowed in sufficiently at least to convince him that heritable variability was as widespread, though not nearly as extensive, in wild as in domesticated species. The line of reasoning in question seems to have lost its importance sufficiently for him to introduce the subject in 1868 (*Variation*, Chapter XXII) with the words 'The subject is an obscure one; but it may be useful to probe our ignorance.'

It is the great charm of the essays that they show the *reasons* which led Darwin to his conclusions, whereas the later works often only give the *evidence* upon which the reader is to judge of their truth. The antithesis is not so heterodox as it sounds, for every active mind will form opinions without direct evidence, else the evidence too often would never be collected. Impartiality and scientific discipline come in in submitting the opinions formed to as much relevant evidence as can be made available. The earlier steps in the argument set out above appear only in the two essays, while the conclusions continue almost unchanged up to the *Variation of Animals and Plants*. Indeed the first step (*a*), logically the most important of all, appears explicitly only in 1842. In 1844 it is clearly implied by its necessary consequences. I believe its significance for the argument of the *Origin*, would scarcely ever be detected from a study only of that book. The passage in the 1842 MS. is (*Foundations*, p. 2):

Each parent transmits its peculiarities, therefore if varieties allowed freely to cross, except by the *chance* of two characterized by same peculiarity happening to marry, such varieties will be constantly demolished. All bisexual animals must cross, hermaphrodite plants do cross, it seems very possible that hermaphrodite animals do cross—
conclusion strengthened:

together with a partly illegible passage of uncertain position,

If individuals of two widely different varieties be allowed to cross,

a third race will be formed—a most fertile source of the variation in domesticated animals. If freely allowed, the characters of pure parents will be lost, number of races thus [illegible] but differences [?] besides the [illegible]. But if varieties differing in very slight respects be allowed to cross, such small variation will be destroyed, at least to our senses—a variation just to be distinguished by long legs will have offspring not to be so distinguished. Free crossing great agent in producing uniformity in any breed.

The proposition is an important one, marking as it does the great contrast between the blending and the particulate theories of inheritance. The following proof establishes it in biometrical terms.

Let x and y represent the deviations in any measurement of the two parents from the specific mean; if the measurement is affected not only by inheritance, but by non-heritable (environmental) factors also, x and y stand for the heritable part of these deviations. The amount of variability present in any generation of individuals will be measured by the variance, defined as the mean value of the square of x , or of y . In purely blending inheritance the heritable portions of the deviations of the offspring will be, apart from mutations, equal to $\frac{1}{2}(x+y)$; in the absence of such mutations, therefore, the variance of the progeny generation will be the mean value of $\frac{1}{4}(x^2 + 2xy + y^2)$.

The mean values of x and y are both zero, since they are both defined as deviations from the mean of the species; consequently, in the absence of selective mating, the mean value of xy is also zero, and the variance of the progeny generation is found to be exactly half the variance of the parental generation. More generally the ratio is not $\frac{1}{2}$ but $\frac{1}{2}(1+r)$, where r is the correlation between x and y . r cannot exceed unity, else the average value of the positive quantities $(x-y)^2$ would have to be negative, and can only be unity, if they are all zero, that is, if the size of each individual prescribes exactly the size of its possible mates. Darwin's 'except by the chance of two individuals characterized by same peculiarities happening to marry' is his way of rejecting high correlations as improbable.

The effect of correlation between mates is to hasten, if the correlation is negative, or to retard if positive, the tendency of blending inheritance to reduce the variance; such effects are not of importance, for even if the correlation were as high as 0.5, and mates had to be as much alike as parent and child usually are, the rate of decay would

be little more than halved. The important consequence of the blending is that, if not safeguarded by intense marital correlation, the heritable variance is approximately halved in every generation. To maintain a stationary variance fresh mutations must be available in each generation to supply the half of the variance so lost. If variability persists, as Darwin rightly inferred, causes of new variability must continually be at work. Almost every individual of each generation must be a mutant, i. e. must be influenced by such causes, and moreover must be a mutant in many different characters.

An inevitable inference of the blending theory is that the bulk of the heritable variance present at any moment is of extremely recent origin. One half is new in each generation, and of the remainder one half is only one generation older, and so on. Less than one-thousandth of the variance can be ten generations old; even if by reason of selective mating we ought to say twenty generations, the general conclusion is the same; the variability of domesticated species must be ascribed by any adherent of the blending theory to the conditions of domestication as they now exist. If variation is to be used by the human breeder, or by natural selection, it must be snapped up at once, soon after the mutation has appeared, and before it has had time to die away. The following passage from the 1844 essay shows that Darwin was perfectly clear on this point (pp. 84-6).

Let us then suppose that an organism by some chance (which might be hardly repeated in 1,000 years) arrives at a modern volcanic island in process of formation and not fully stocked with the most appropriate organisms; the new organism might readily gain a footing, although the external conditions were considerably different from its native ones. The effect of this we might expect would influence in some small degree the size, colour, nature of covering, &c., and from inexplicable influences even special parts and organs of the body. But we might further (and this is far more important) expect that the reproductive system would be affected, as under domesticity, and the structure of the offspring rendered in some degree plastic. Hence almost every part of the body would tend to vary from the typical form in slight degrees, and in no determinate way, and therefore *without selection* the free crossing of these small variations (together with the tendency to reversion to the original form) would constantly be counteracting this unsettling effect of the extraneous conditions on the reproductive system. Such, I conceive, would be the unimportant result without selection. And here I must observe that the foregoing remarks are equally applicable to

that small and admitted amount of variation which has been observed in some organisms in a state of nature; as well as to the above hypothetical variation consequent on changes of condition.

Let us now suppose a Being with penetration sufficient to perceive differences in the outer and innermost organization quite imperceptible to man, and with forethought extending over future centuries to watch with unerring care and select for any object the offspring of an organism produced under the foregoing circumstances; I can see no conceivable reason why he could not form a new race (or several were he to separate the stock of the original organism and work on several islands) adapted to new ends. As we assume his discrimination, and his forethought, and his steadiness of object, to be incomparably greater than those qualities in man, so we may suppose the beauty and complications of the adaptations of the new races and their differences from the original stock to be greater than in the domestic races produced by man's agency: the ground-work of his labours we may aid by supposing that the external conditions of the volcanic island, from its continued emergence, and the occasional introduction of new immigrants, vary; and thus to act on the reproductive system of the organism, on which he is at work, and so keep its organization somewhat plastic. With time enough, such a Being might rationally (without some unknown law opposed him) aim at almost any result.

Difficulties felt by Darwin

The argument based on blending inheritance and its logical consequences, though it certainly represents the general trend of Darwin's thought upon inheritance and variation, for some years after he commenced pondering on the theory of Natural Selection, did not satisfy him completely. Reversion he recognized as a fact which stood outside his scheme of inheritance, and that he was not altogether satisfied to regard it as an independent principle is shown by his letter to Huxley already quoted. By 1857 he was in fact on the verge of devising a scheme of inheritance which should include reversion as one of its consequences. The variability of domesticated races, too, presented a difficulty which, characteristically, did not escape him. He notes (pp. 77, 78, *Foundations*) in 1844 that the most anciently domesticated animals and plants are not less variable, but, if anything more so, than those more recently domesticated; and argues that since the supply of food could not have been becoming much more abundant progressively at all stages of a long history of

domestication, this factor cannot alone account for the great variability which still persists. The passage runs as follows:

If it be an excess of food, compared with that which the being obtained in its natural state, the effects continue for an improbably long time; during how many ages has wheat been cultivated, and cattle and sheep reclaimed, and we cannot suppose their *amount* of food has gone on increasing, nevertheless these are amongst the most variable of our domestic productions.

This difficulty offers itself also to the second supposed cause of variability, namely changed conditions, though here it may be argued that the conditions of cultivation or nurture of domesticated species have always been changing more or less rapidly. From a passage in the *Variation of Animals and Plants* (p. 301), which runs:

Moreover, it does not appear that a change of climate, whether more or less genial, is one of the most potent causes of variability; for in regard to plants Alph. De Candolle, in his *Geographie Botanique*, repeatedly shows that the native country of a plant, where in most cases it has been longest cultivated, is that where it has yielded the greatest number of varieties.

It appears that Darwin satisfied himself that the countries in which animals or plants were first domesticated, were at least as prolific of new varieties as the countries into which they had been imported, and it is natural to presume that his inquiries under this head were in search of evidence bearing upon the effects of changed conditions. It is not clear that this difficulty was ever completely resolved in Darwin's mind, but it is clear from many passages that he saw the necessity of supplementing the original argument by postulating that the causes of variation which act upon the reproductive system must be capable of acting in a delayed and cumulative manner so that variation might still be continued for many subsequent generations.

Particulate inheritance

It is a remarkable fact that had any thinker in the middle of the nineteenth century undertaken, as a piece of abstract and theoretical analysis, the task of constructing a particulate theory of inheritance, he would have been led, on the basis of a few very simple assumptions, to produce a system identical with the modern scheme of Mendelian or factorial inheritance. The admitted non-inheritance of

scars and mutilations would have prepared him to conceive of the hereditary nature of an organism as something none the less definite because possibly represented inexactly by its visible appearance. Had he assumed that this hereditary nature was completely determined by the aggregate of the hereditary particles (genes), which enter into its composition, and at the same time assumed that organisms of certain possible types of hereditary composition were capable of breeding true, he would certainly have inferred that each organism must receive a definite portion of its genes from each parent, and that consequently it must transmit only a corresponding portion to each of its offspring. The simplification that, apart from sex and possibly other characters related in their inheritance to sex, the contributions of the two parents were equal, would not have been confidently assumed without the evidence of reciprocal crosses; but our imaginary theorist, having won so far, would scarcely have failed to imagine a conceptual framework in which each gene had its proper place or locus, which could be occupied alternatively, had the parentage been different, by a gene of a different kind. Those organisms (homozygotes) which received like genes, in any pair of corresponding loci, from their two parents, would necessarily hand on genes of this kind to all of their offspring alike; whereas those (heterozygotes) which received from their two parents genes of different kinds, and would be, in respect of the locus in question, crossbred, would have, in respect of any particular offspring, an equal chance of transmitting either kind. The heterozygote when mated to either kind of homozygote would produce both heterozygotes and homozygotes in a ratio which, with increasing numbers of offspring, must tend to equality, while if two heterozygotes were mated, each homozygous form would be expected to appear in a quarter of the offspring, the remaining half being heterozygous. It thus appears that, apart from dominance and linkage, including sex linkage, all the main characteristics of the Mendelian system flow from assumptions of particulate inheritance of the simplest character, and could have been deduced *a priori* had any one conceived it possible that the laws of inheritance could really be simple and definite.

The segregation of single pairs of genes, that is of single factors, was demonstrated by Mendel in his paper of 1865. In addition Mendel demonstrated in his material the fact of dominance, namely that the heterozygote was not intermediate in appearance, but was almost or

quite indistinguishable from one of the homozygous forms. The fact of dominance, though of the greatest theoretical interest, is not an essential feature of the factorial system, and in several important cases is lacking altogether. Mendel also demonstrated what a theorist could scarcely have ventured to postulate, that the different factors examined by him in combination, segregated in the simplest possible manner, namely independently. It was not till after the rediscovery of Mendel's laws at the end of the century that cases of linkage were discovered, in which, for factors in the same linkage group, the pair of genes received from the same parent are more often than not handed on together to the same child. The conceptual framework of loci must therefore be conceived as made of several parts, and these are now identified, on evidence which appears to be singularly complete, with the dark-staining bodies or chromosomes which are to be seen in the nuclei of cells at certain stages of cell division.

The mechanism of particulate inheritance is evidently suitable for reproducing the phenomenon of reversion, in which an individual resembles a grandparent or more remote ancestor, in some respect in which it differs from its parents; for the ancestral gene combination may by chance be reproduced. This takes its simplest form when dominance occurs, for every union of two heterozygotes will then produce among the offspring some recessives, differing in appearance from their parents, but probably resembling some grandparent or ancestor.

Conservation of the variance

It has not been so clearly recognized that particulate inheritance differs from the blending theory in an even more important fact. There is no inherent tendency for the variability to diminish. In a population breeding at random in which two alternative genes of any factor, exist in the ratio p to q , the three genotypes will occur in the ratio $p^2 : 2pq : q^2$, and thus ensure that their characteristics will be represented in fixed proportions of the population, however they may be combined with characteristics determined by other factors, provided that the ratio $p : q$ remains unchanged. This ratio will indeed be liable to slight changes; first by the chance survival and reproduction of individuals of the different kinds; and secondly by selective survival, by reason of the fact that the genotypes are probably unequally fitted, at least to a slight extent, to their task of

survival and reproduction. The effect of chance survival is easily susceptible of calculation, and it appears, as will be demonstrated more fully (Chapter IV), that in a population of n individuals breeding at random the variance will be halved by this cause acting alone in $1.4 n$ generations. Since the number of individuals surviving to reproduce in each generation must in most species exceed a million, and in many is at least a million-fold greater, it will be seen that this cause of the diminution of hereditary variance is exceedingly minute, when compared to the rate of halving in one or two generations by blending inheritance.

It will be seen in Chapter IV that selection is a much more important agency in keeping the variability of species within limits. But even relatively intense selection will change the ratio $p : q$ of the gene frequencies relatively slowly, and no reasonable assumptions could be made by which the diminution of variance due to selection, in the total absence of mutations, would be much more than a ten-thousandth of that ascribable to blending inheritance. The immediate consequence of this enormous contrast is that the mutation rate needed to maintain a given amount of variability is, on the particulate theory, many thousand times smaller than that which is required on the blending theory. Theories, therefore, which ascribe to agencies believed to be capable of producing mutations, as was 'use and disuse' by Darwin, a power of governing the direction in which evolution is taking place, appear in very different lights, according as one theory of inheritance, or the other, is accepted. For any evolutionary tendency which is supposed to act by favouring mutations in one direction rather than another, and a number of such mechanisms have from time to time been imagined, will lose its force many thousand-fold, when the particulate theory of inheritance, in any form, is accepted; whereas the directing power of Natural Selection, depending as it does on the amount of heritable variance maintained, is totally uninfluenced by any such change. This consideration, which applies to all such theories alike, is independent of the fact that a great part of the reason, at least to Darwin, for ascribing to the environment any considerable influence in the production of mutations, is swept away when we are no longer forced to consider the great variability of domestic species as due to the comparatively recent influence of their artificial environment.

The striking fact, of which Darwin was well aware, that whole

brothers and sisters, whose parentage, and consequently whose entire ancestry is identical, may differ greatly in their hereditary composition, bears under the two theories two very different interpretations. Under the blending theory it is clear evidence of new and frequent mutations, governed, as the greater resemblance of twins suggests, by temporary conditions acting during conception and gestation. On the particulate theory it is a necessary consequence of the fact that for every factor a considerable fraction, not often much less than one half, of the population will be heterozygotes, any two offspring of which will be equally likely to receive unlike as like genes from their parents. In view of the close analogy between the statistical concept of variance and the physical concept of energy, we may usefully think of the heterozygote as possessing variance in a potential or latent form, so that instead of being lost when the homozygous genotypes are mated it is merely stored in a form from which it will later reappear. A population mated at random immediately establishes the condition of statistical equilibrium between the latent and the apparent form of variance. The particulate theory of inheritance resembles the kinetic theory of gases with its perfectly elastic collisions, whereas the blending theory resembles a theory of gases with inelastic collisions, and in which some outside agency is required to be continually at work to keep the particles afloat.

The property of the particulate theory of conserving the variance for an indefinite period explains at once the delayed or cumulative effect of domestication in increasing the variance of domesticated species, to which Darwin calls attention. Many of our domesticated varieties are evidently ill-fitted to survive in the wild condition. The mutations by which they arose may have been occurring for an indefinite period prior to domestication without establishing themselves, or appreciably affecting the variance, of the wild species. In domestication, however, not only is the rigour of Natural Selection relaxed so that mutant types can survive, and each such survival add something to the store of heritable variance, but novelties of form or colour, even if semi-monstrous, do undoubtedly attract human attention and interest, and are valued by man for their peculiarity. The rapidity with which new variance is accumulated will thus be enhanced. Without postulating any change in the mutation rates due to domestication, we should necessarily infer from what is known of the conditions of domestication that the variation of domesticated

species should be greater than that of similar wild species, and that this contrast should be greatest with those species most anciently domesticated. Thus one of the main difficulties felt by Darwin is resolved by the particulate theory.

Theories of evolution worked by mutations

The theories of evolution which rely upon hypothetical agencies, capable of modifying the frequency or direction in which mutations are taking place, fall into four classes. In stating these it will be convenient to use the term 'mutation', to which many meanings have at different times been assigned, to denote simply the initiation of any heritable novelty.

(A) It may be supposed, as by Lamarck in the case of animals, that the mental state, and especially the desires of the organism, possess the power of producing mutations of such a kind, that these desires may be more readily gratified in the descendants. This view postulates (i) that there exists a mechanism by which mutations are caused, and even designed, in accordance with the condition of the nervous system, and (ii) that the desires of animals in general are such that their realization will improve the aptitude of the species for life in its natural surroundings, and also will maintain or improve the aptitude of its parts to co-operate with one another, both in maintaining the vital activity of the adult animal, and in ensuring its normal embryological development. The desires of animals must, in fact, be very wisely directed, as well as being effective in provoking suitable mutations.

(B) A power of adaptation may be widely observed, both among plants and animals, by which particular organs, such as muscles or glands, respond by increased activity and increased size, when additional physiological calls are made upon them. It may be suggested, as it was by Darwin, that such responses of increased functional activity induce, or are accompanied by, mutations of a kind tending to increase the size or activity of the organ in question in future generations, even if no additional calls were made upon this organ's activity. This view implies (i) that the power which parts of organisms possess, of responding adaptively to increased demands upon them, is not itself a product of evolution, but must be postulated as a primordial property of living matter: and requires (ii) that a mecha-

nism exists by which the adaptive response shall itself tend to cause, or be accompanied by, an appropriate mutation.

Both these two suggested means of evolution expressly aim at explaining, not merely the progressive change of organic beings, but the aptitude of the organism to its place in nature, and of its parts to their function in the organism.

(C) It may be supposed that the environment in which the organism is placed controls the nature of the mutations which occur in it, and so directs its evolutionary course; much as the course of a projectile is controlled by the field of force in which it flies.

(D) It may be supposed that the mutations which an organism undergoes are due to an 'inner urge' (not necessarily connected with its mental state) implanted in its primordial ancestors, which thereby directs its predestined evolution.

The two last suggestions give no particular assistance towards the understanding of adaptation, but each contains at least this element of truth; that however profound our ignorance of the causes of mutation may be, we cannot but ascribe them, within the order of Nature as we know it, either to the nature of the organism, or to that of its surrounding environment, or, more generally, to the interaction of the two. What is common, however, to all four of these suppositions, is that each one postulates that the direction of evolutionary change is governed by the predominant direction in which mutations are taking place. However reasonable such an assumption might have seemed when, under the blending theory of inheritance, every individual was regarded as a mutant, and probably a multiple mutant, it is impossible to let it pass unquestioned, in face of the much lower mutation rates appropriate to the particulate theory.

A further hypothetical mechanism, guiding the evolution of the species according to the direction in which mutations are occurring, was suggested by Weismann. Weismann appreciated much more thoroughly than many of his contemporaries the efficacy of Natural Selection, in promoting the adaptation of organisms to the needs of their lives in their actual habitats. He felt, however, that this action would be aided in a subordinate degree if the process of mutation could acquire a kind of momentum, so that a series of mutations affecting the increase or decrease of a part should continue to occur, as a consequence of an initial chance tendency towards such increase or decrease. Such an assumed momentum in the process of mutation

he found useful in two respects: (i) it would enable an assumed minimal mutation in an advantageous direction to be increased by further mutations, until it 'attains selection value'; (ii) it explains the continuous decrease of a useless organ, without assuming that each step of this decrease confers any advantage upon the organism manifesting it.

The concept of attaining selection value, which is fairly common in biological literature, seems to cover two distinct cases. In the first case we may imagine that, with increasing size, the utility of an organ shows no increase up to a certain point, but that beyond this point increasing size is associated with increasing utility. In such a case, which, in view of the actual variability of every organism, and of the parts of related organisms, must be regarded as somewhat ideal, we are really only concerned with the question whether the actual variability in different members of the species concerned, does or does not reach as far as the critical point. If it does not do so the species will not be able to take the advantage offered, simply because it is not variable enough, and the postulate of an element of momentum in the occurrence of mutations, was certainly not made in order to allow organisms to be more variable than they would be without it.

The second meaning, which is also common in the literature, depends upon a curious assumption as to the manner in which selective advantage increases with change of size of the organ upon which this advantage is dependent; for it is sometimes assumed that, while at all sizes an increase of size may be advantageous, this advantage increases, not continuously, but in a step-like manner; or at least that increases below a certain limit produce an advantage which may be called 'inappreciable', and therefore neglected. Both the metaphor and the underlying idea appear to be drawn from psychophysical experience. If we compare two physical sensations such as those produced by the weights of two objects, then when the weights are sufficiently nearly equal the subject will often be unable to distinguish between them, and will judge them equal, whereas with a greater disparity, a distinct or appreciable difference of weight is discerned. If, however, the same test is applied to the subject repeatedly with differences between the weights varying from what is easily discernible to very much smaller quantities, it is found that differences in the weights, which would be deemed totally inappreci-

able, yet make a significant and perfectly regular difference to the *frequency* with which one is judged heavier than the other. The discontinuity lies in our interpretation of the sensations, and not in the sensations themselves. Now, survival value is measured by the

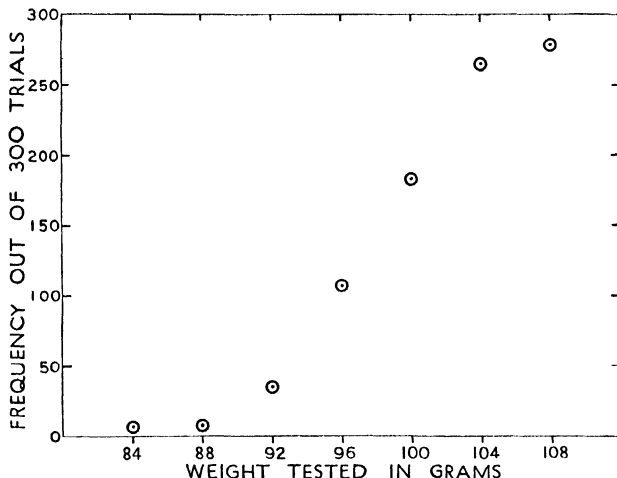


FIG. 1. The frequency with which test objects of different weights are judged heavier than a standard 100 gram weight. (Urban's data, for a single subject.) Illustrating the fact that with a sufficient number of trials, differences in weight, however 'inappreciable', will affect the frequency of the judgement.

frequency with which certain events, such as death or reproduction, occur, to different sorts of organisms exposed to the different chances of the same environment, and, even if we should otherwise be in doubt, the psychophysical experiments make it perfectly clear that the selective advantage will increase or decrease continuously, even for changes much smaller than those appreciable to our own senses, or to those of the predator or other animal, which may enter into the biological situation concerned. If a change of 1 mm. has selection value, a change of 0.1 mm. will usually have a selection value approximately one-tenth as great, and the change cannot be ignored because we deem it inappreciable. The rate at which a mutation increases in numbers at the expense of its allelomorph will indeed depend on the selective advantage it confers, but the rate at which a species responds to selection in favour of any increase or decrease of parts depends on the total heritable variance available, and not

on whether this is supplied by large or small mutations. There is no *limen* of appreciable selection value to be considered.

The remaining advantage which Weismann sought in postulating his mechanism of germinal selection was to supply an explanation of the progressive diminution of useless organs, even when these are of so trifling a character that the selective advantage of their suppression is questionable. The subject is an interesting one, and deserves for its own sake a more extended discussion than would be suitable in the present book. For our present purpose it will be sufficient to notice (i) that to assert in any particular case that the progressive suppression of an organ brings with it no progressive selective advantage appears to be very far beyond the range of our actual knowledge. To take a strong case from Weismann—the *receptaculum seminis* of an ant is assuredly minute; but the ant herself is not very large, nor are we concerned only with the individual ant, but with the whole worker population of the nest. As an economic problem we certainly do not possess the data to decide whether the suppression of this minute organ would or would not count as an appreciable factor in the ant polity. Human parallels might be given in which the elimination of very minute items of individual waste, can lend an appreciable support to social institutions which are certainly not negligible. I do not assert that the suppression of the *receptaculum* has been useful to the ant, but that in this as in other cases, if we pause to give the matter due consideration, it is at once apparent that we have not the knowledge on which to base any decided answer. (ii) In the second place Weismann's view that in the absence of all selection a useless organ might diminish, degenerate, and finally disappear, by the cumulative action of successive mutations, and especially his view that this is the only type of progressive change, which could take place by mutations only, without the guidance of Natural Selection, is fully in accordance with modern knowledge of the nature of mutations. The special mechanism, however, by which he sought to explain the successive occurrence of degenerative mutations must be judged to be superfluous. It is moreover exposed to the logical objection that the driving force of his mechanism of germinal selection is an assumed competition for nutriment between the chromatin elements which represent the degenerating organ, and those which represent the rest of the body. The degenerating organ itself is assumed to be so unimportant that

its demands upon the general nutrition of the body are to be neglected ; and it may well be asked if it is legitimate to bring in, in respect of the well-nourished germ cell, the factor of nutritional competition which is to be ignored in the occasionally ill-nourished body.

Is all inheritance particulate ?

The logical case for rejecting the assumption that the direction of evolutionary change is governed by the direction in which mutations are taking place, and thereby rejecting the whole group of theories in which this assumption is implicit, would be incomplete had not modern researches supplied the answer to two further questions: (i) May it not be that in addition to the mechanism of particulate inheritance, which has been discovered and is being investigated, there is also, in living organisms, an undiscovered mechanism of blending inheritance ? (ii) Do the known facts within the particulate system render a mechanism, which could control the predominant direction of mutation, inoperative as a means of governing the direction of evolutionary change ?

On the first point it should be noted briefly that, whereas at the beginning of the century there were several outstanding facts of inheritance which seemed to demand some sort of blending theory, these have all in the course of research been shown, not only to be compatible with particulate inheritance, but to reveal positive indications that such is their nature. The apparent blending in colour in crosses between white races of man and negroes is compatible with the view that these races differ in several Mendelian factors, affecting the pigmentation. Of these some may have intermediate heterozygotes, and of the remainder in some the darker, and in some the lighter tint may be dominant. The Mendelian theory is alone competent to explain the increased variability of the offspring of the mulattoes.

The biometrical facts as to the inheritance of stature and other human measurements, though at first regarded as incompatible with the Mendelian system, have since been shown to be in complete accordance with it, and to reveal features not easily explicable on any other view. The approximately normal distribution of the measurements themselves may be deduced from the simple supposition that the factors affecting human stature are approximately additive in their effects. The correlations found between relatives of different

degrees of kinship are, within their sampling errors, of the magnitudes which would be deduced from the assumption that the measurement is principally determined by inheritance, and that the factors controlling it show, like most Mendelian factors, complete or almost complete dominance. The presence of dominance is a Mendelian feature, which is shown in the biometrical data by the well-established fact that children of the same parents are, on the average, somewhat more alike than are parent and offspring.

So far we have merely established the negative fact that there are no outstanding observations which require a blending system of inheritance. There is, however, one group of modern researches which, at least in the organisms investigated, seems to exclude it, even as a possibility. In certain organisms which are habitually self-fertilized, as Johannsen was the first to show with a species of bean, it is possible to establish so-called pure lines, within which heritable variability is, apart from exceptional mutations, completely absent. Within these lines the selection of the largest or the smallest beans, even where this selection was continued for ten or twenty generations, constantly produced offspring of the same average size. This size differed from one line to another, showing that heritable variability existed abundantly in the species, and among the thousands of beans examined two distinct mutants were reported. If, however, any appreciable fraction of the variance in bean size were ascribable to elements which blend, the mutations necessary to maintain such heritable variability would, in ten generations, have had time to supply it almost to its maximum extent, and must inevitably have been revealed by selection. Experiments of this type seem capable of excluding the possibility that blending inheritance can account for any appreciable fraction of the variance observed.

Nature and frequency of observed mutations

The assumption that the direction of evolutionary change is actually governed by the direction in which mutations are occurring is not easily compatible with the nature of the numerous mutations which have now been observed to occur. For the majority of these produce strikingly disadvantageous deformities, and indeed much the largest class are actually lethal. If we had to admit, as has been so often assumed in theory, that these mutations point the direction of evolution, the evolutionary prospects of the little fruit-fly *Drosophila*

would be deplorable indeed. Nor is the position apparently different with man and his domesticated animals and plants; as may be judged from the frequency with which striking recessive defects, such as albinism, deaf-mutism, and feebleness of mind in man, must have occurred in the comparatively recent past, as mutations. Mutant defects seem to attack the human eye as much as that of *Drosophila*, and in general the mutants which occur in domesticated races are often monstrous and predominantly defective, whereas we know in many cases that the evolutionary changes which these creatures have undergone under human selection have been in the direction of a manifest improvement.

In addition to the defective mutations, which by their conspicuousness attract attention, we may reasonably suppose that other less obvious mutations are occurring which, at least in certain surroundings, or in certain genetic combinations, might prove themselves to be beneficial. It would be unreasonable, however, to assume that such mutations appear individually with a frequency much greater than that which is observed in the manifest defects. The frequency of individual mutations in *Drosophila* is certainly seldom greater than one in 100,000 individuals, and we may take this figure to illustrate the inefficacy of any agency, which merely controls the predominant direction of mutation, to determine the predominant direction of evolutionary change. For even if selective survival were totally absent, a lapse of time of the order of 100,000 generations would be required to produce an important change with respect to the factor concerned, in the heritable nature of the species. Moreover, if the mutant gene were opposed, even by a very minute selective disadvantage, the change would be brought to a standstill at a very early stage. The ideas necessary for a precise examination of the nature of selective advantage will be developed in Chapter II; but it will be readily understood that if we speak of a selective advantage of one per cent., with the meaning that animals bearing one gene have an expectation of offspring only one per cent. greater than those bearing its allelomorph, the selective advantage in question will be a very minute one; at least in the sense that it would require an enormous number of experimental animals, and extremely precise methods of experimentation, to demonstrate so small an effect experimentally. Such a selective advantage would, however, greatly modify the genetic constitution of the species, not in 100,000 but in

100 generations. If, moreover, we imagine these two agencies opposed in their tendencies, so that a mutation which persistently occurs in one in 100,000 individuals, is persistently opposed by a selective advantage of only one per cent., it will easily be seen that an equilibrium will be arrived at when only about one individual in 1,000 of the population will be affected by the mutation. This equilibrium, moreover, will be stable; for if we imagine that by some chance the number of mutants is raised to a higher proportion than this, the proportion will immediately commence to diminish under the action of selection, and evolution will proceed in the direction contrary to the mutation which is occurring, until the proportion of mutant individuals again reaches its equilibrium value. For mutations to dominate the trend of evolution it is thus necessary to postulate mutation rates immensely greater than those which are known to occur, and of an order of magnitude which, in general, would be incompatible with particulate inheritance.

Summary

The tacit assumption of the blending theory of inheritance led Darwin, by a perfectly cogent argument, into a series of speculations, respecting the causes of variations, and the possible evolutionary effects of these causes. In particular the blending theory, by the enormous mutation rates which it requires, led Darwin and others to attach evolutionary importance to hypothetical agencies which control the production of mutations. A mechanism (Mendelism) of particulate inheritance has since been discovered, requiring mutations to an extent less by many thousandfold. The 'pure line' experiments seem to exclude blending inheritance even as a subordinate possibility. The nature of the mutations observed is not compatible with the view that evolution is directed by their means, while their observed frequency of occurrence shows that an agency controlling mutations would be totally ineffectual in governing the direction of evolutionary change.

The whole group of theories which ascribe to hypothetical physiological mechanisms, controlling the occurrence of mutations, a power of directing the course of evolution, must be set aside, once the blending theory of inheritance is abandoned. The sole surviving theory is that of Natural Selection, and it would appear impossible to avoid the conclusion that if any evolutionary phenomenon

appears to be inexplicable on this theory, it must be accepted at present merely as one of the facts which in the present state of knowledge seems inexplicable. The investigator who faces this fact, as an unavoidable inference from what is now known of the nature of inheritance, will direct his inquiries confidently towards a study of the selective agencies at work throughout the life history of the group in their native habitats, rather than to speculations on the possible causes which influence their mutations. The experimental study of agencies capable of influencing mutation rates is of the highest interest for the light which it may throw on the nature of these changes. We should altogether misinterpret the value of such researches were we to regard them as revealing the causes of evolutionary modification.

II

THE FUNDAMENTAL THEOREM OF NATURAL SELECTION

The life table and the table of reproduction. The Malthusian parameter of population increase. Reproductive value. The genetic element in variance. Natural Selection. The nature of adaptation. Deterioration of the environment. Changes in population. Summary.

One has, however, no business to feel so much surprise at one's ignorance, when one knows how impossible it is without statistics to conjecture the duration of life and percentage of deaths to births in mankind. DARWIN, 1845. (*Life and Letters*, ii, 33.)

In the first place it is said—and I take this point first, because the imputation is too frequently admitted by Physiologists themselves—that Biology differs from the Physico-chemical and Mathematical sciences in being 'inexact'. HUXLEY, 1854.

The life table

IN order to obtain a distinct idea of the application of Natural Selection to all stages in the life-history of an organism, use may be made of the ideas developed in the actuarial study of human mortality. These ideas are not in themselves very recondite, but being associated with the laborious computations and the technical notation employed in the practical business of life insurance, are not so familiar as they might be to the majority of biologists. The textbooks on the subject, moreover, are devoted to the chances of death, and to monetary calculations dependent on these chances, whereas in biological problems at least equal care and precision of ideas is requisite with respect to reproduction, and especially to the combined action of these two agencies in controlling the increase or decrease of the population.

The object of the present chapter is to combine certain ideas derivable from a consideration of the rates of death and reproduction of a population of organisms, with the concepts of the factorial scheme of inheritance, so as to state the principle of Natural Selection in the form of a rigorous mathematical theorem, by which the rate of improvement of any species of organisms in relation to its environment is determined by its present condition.

The fundamental apparatus of the actuary's craft is what is known

as a life table. This shows, for each year of age, of the population considered, the proportion of persons born alive who live to attain that age. For example, a life table may show that the proportion of persons living to the age of 20 is 88 per cent., while only 80 per cent. reach the age of 40. It will be easily inferred that 12 per cent. of those born alive die in the first 20 years of life, and 8 per cent. in the second 20 years. The life table is thus equivalent to a statement of the frequency distribution of the age of death in the population concerned. The amount by which each entry is less than the preceding entry represents the number of deaths between these limits of age, and this divided by the number living at the earlier age gives the probability of death within a specified time of those living at that age. Since the probability of death changes continuously throughout life, the death rate at a given age can only be measured consistently by taking the age interval to be infinitesimal. Consequently if l_x is the number living to age x , the death rate at age x is given by:

$$\mu_x = -\frac{1}{l_x} \frac{d}{dx} l_x = -\frac{d}{dx} (\log l_x),$$

the logarithm being taken, as in most mathematical representations, to be on the Natural or Naperian system. The life table thus contains a statement of the death rates at all ages, and conversely can be constructed from a knowledge of the course taken by the death rate throughout life. This in fact is the ordinary means of constructing the life tables in practical use.

It will not be necessary to discuss the technical procedure employed in the construction of life tables, the various conventions employed in this form of statement, nor the difficulties which arise in the interpretation of the observational data available in practice for this purpose. It will be sufficient to state only one point. As in all other experimental determinations of theoretical values, the accuracy attainable in practice is limited by the extent of the observations; the result derived from any finite number of observations will be liable to an error of random sampling, but this fact does not, in any degree, render such concepts as death rates or expectations of life obscure or inexact. These are statements of probabilities, averages &c., pertaining to the hypothetical population sampled, and depend only upon its nature and circumstances. The inexactitude of our methods of measurement has no more reason in statistics than it has

in physics to dim our conception of that which we measure. These conceptions would be equally clear if we were stating the chances of death of a single individual of unique genetic constitution, or of one exposed to an altogether transient and exceptional environment.

The table of reproduction

The life table, although itself a very comprehensive statement, is still inadequate to express fully the relation between an organism and its environment; it concerns itself only with the chances or frequency of death, and not at all with reproduction. To repair this deficiency it is necessary to introduce a second table giving rates of reproduction in a manner analogous to the rates of death at each age. Just as a person alive at the beginning of any infinitesimal age interval dx has a chance of dying within that interval measured by $\mu_x dx$, so the chance of reproducing within this interval will be represented by $b_x dx$, in which b_x may be called the rate of reproduction at age x . Again, just as the chance of a person chosen at birth dying within a specified interval of age dx is $l_x \mu_x dx$, so the chance of such a person living to reproduce in that interval will be $l_x b_x dx$.

Owing to bisexual reproduction a convention must be introduced into the measurement of b_x , for each living offspring will be credited to both parents, and it will seem proper to credit each with one half in respect of each offspring produced. This convention will evidently be appropriate for those genes which are not sex-linked (autosomal genes) for with these the chance of entering into the composition of each offspring is known to be one half. In the case of sex-linked genes those of the heterogametic parent will be perpetuated or not according as the offspring is male or female. These sexes, it is true, will not be produced in exactly equal numbers, but since both must co-operate in each act of sexual reproduction, it is clear that the different frequencies at birth must ultimately be compensated by sexual differences in the rates of death and reproduction, with the result that the same convention appears in this case to be equally appropriate.

A similar convention, appropriate in the sense of bringing the formal symbolism of the mathematics into harmony with the biological facts, may be used with respect to the period of gestation. For it will happen occasionally that a child is born after the death of its father. The children born to fathers aged x should in fact be credited to males aged three-quarters of a year younger. Such corrections are

not a necessity to an exact mathematical representation of the facts, but are a manifest convenience in simplifying the form of expression ; thus with mankind we naturally think of the stage in the life-history as measured in years from birth. With other organisms the variable x which with man represents this age, may in some cases be more conveniently used to indicate rather the stage in the life history irrespective of chronological age, merely to give greater vividness to the meaning of the symbolism, but without altering the content of the symbolical statements.

The Malthusian parameter of population increase

If we combine the two tables giving the rates of death and reproduction, we may, still speaking in terms of human populations, at once calculate the expectation of offspring of the newly-born child. For the expectation of offspring in each element of age dx is $l_x b_x dx$, and the sum of these elements over the whole of life will be the total expectation of offspring. In mathematical terms this is

$$\int_0^{\infty} l_x b_x dx,$$

where the integral is extended from zero, at birth, to infinity, to cover every possible age at which reproduction might conceivably take place. If at any age reproduction ceases absolutely, b_x will thereafter be zero and so give automatically the effect of a terminating integral.

The expectation of offspring determines whether in the population concerned the reproductive rates are more or less than sufficient to balance the existing death rates. If its value is less than unity the reproductive rates are insufficient to maintain a stationary population, in the sense that any population which constantly maintained the death and reproduction rates in question would, apart from temporary fluctuations, certainly ultimately decline in numbers at a calculable rate. Equally, if it is greater than unity, the population biologically speaking is more than holding its own, although the actual number of heads to be counted may be temporarily decreasing.

This consequence will appear most clearly in its quantitative aspect if we note that corresponding to any system of rates of death and reproduction, there is only one possible constitution of the population in respect of age, which will remain unchanged under the action of this system. For if the age distribution remains unchanged the

relative rate of increase or decrease of numbers at all ages must be the same; let us represent the relative rate of increase by m ; which will also represent a decrease if m is negative. Then, owing to the constant rates of reproduction, the rate at which births are occurring at any epoch will increase proportionately to e^{mt} . At any particular epoch, for which we may take $t=0$, the rate at which births were occurring x years ago will be proportional to e^{-mx} , and this is the rate at which births were occurring at the time persons now of age x were being born. The number of persons in the infinitesimal age interval dx will therefore be $e^{-mx}l_x dx$, for of those born only the fraction l_x survive to this age. The age distribution is therefore determinate if the number m is uniquely determined. But knowing the numbers living at each age, and the reproductive rates at each age, the rate at which births are now occurring can be calculated, and this can be equated to the known rate of births appropriate to $t=0$. In fact, the contribution to the total rate, of persons in the age interval dx , must be $e^{-mx}l_x b_x dx$, and the aggregate for all ages must be

$$\int_0^{\infty} e^{-mx} l_x b_x dx,$$

which, when equated to unity, supplies an equation for m , of which one and only one real solution exists. Since e^{-mx} is less than unity for all values of x , if m is positive, and is greater than unity for all values of x , if m is negative, it is evident that the value of m , which reduces the integral above expressed to unity, must be positive if the expectation of offspring exceeds unity, and must be negative if it falls short of unity.

The number m which satisfies this equation is thus implicit in any given system of rates of death and reproduction, and measures the relative rate of increase or decrease of a population when in the steady state appropriate to any such system. In view of the emphasis laid by Malthus upon the 'law of geometric increase' m may appropriately be termed the Malthusian parameter of population increase. It evidently supplies in its negative values an equally good measure of population decrease, and so covers cases to which, in respect of mankind, Malthus paid too little attention.

In view of the close analogy between the growth of a population supposed to follow the law of geometric increase, and the growth of capital invested at compound interest, it is worth noting that if we

regard the birth of a child as the loaning to him of a life, and the birth of his offspring as a subsequent repayment of the debt, the method by which m is calculated shows that it is equivalent to answering the question—At what rate of interest are the repayments the just equivalent of the loan? For the unit investment has an expectation of a return $l_x b_x dx$ in the time interval dx , and the present value of this repayment, if m is the rate of interest, is $e^{-mx} l_x b_x dx$; consequently the Malthusian parameter of population increase is the rate of interest at which the present value of the births of offspring to be expected is equal to unity at the date of birth of their parent. The actual values of the parameter of population increase, even in sparsely populated dominions, do not, however, seem to approach in magnitude the rates of interest earned by money, and negative rates of interest are, I suppose, unknown to commerce.

Reproductive value

The analogy with money does, however, make clear the argument for another simple application of the combined death and reproduction rates. We may ask, not only about the newly born, but about persons of any chosen age, what is the present value of their future offspring; and if present value is calculated at the rate determined as before, the question has the definite meaning—To what extent will persons of this age, on the average, contribute to the ancestry of future generations? The question is one of some interest, since the direct action of Natural Selection must be proportional to this contribution. There will also, no doubt, be indirect effects in cases in which an animal favours or impedes the survival or reproduction of its relatives; as a suckling mother assists the survival of her child, as in mankind a mother past bearing may greatly promote the reproduction of her children, as a foetus and in less measure a sucking child inhibits conception, and most strikingly of all as in the services of neuter insects to their queen. Nevertheless such indirect effects will in very many cases be unimportant compared to the effects of personal reproduction, and by the analogy of compound interest the present value of the future offspring of persons aged x is easily seen to be

$$v_x = \frac{e^{mx}}{l_x} \int_x^{\infty} e^{-mt} l_t b_t dt.$$

Each age group may in this way be assigned its appropriate

reproductive value. Fig. 2 shows the reproductive value of women according to age as calculated from the rates of death and reproduction current in the Commonwealth of Australia about 1911. The Malthusian parameter was at that time positive, and as judged from

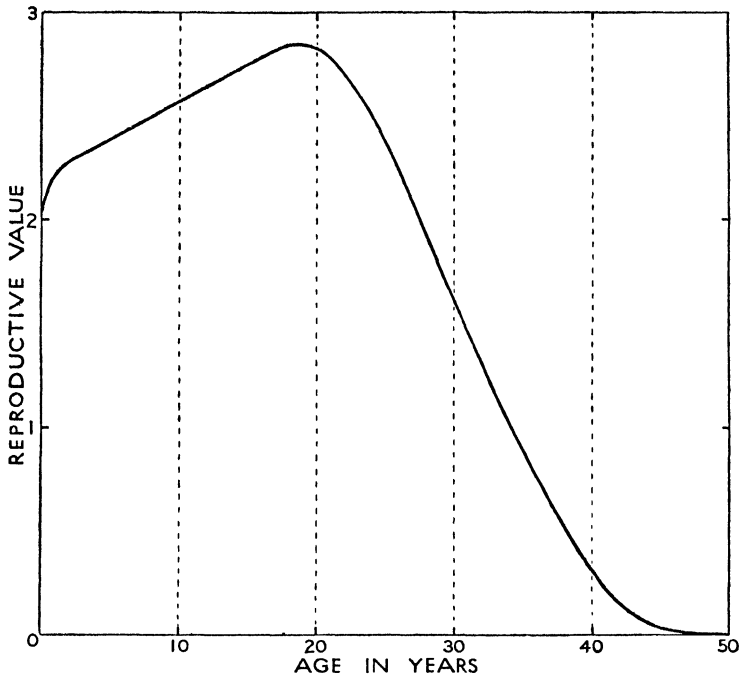


FIG. 2. Reproductive value of Australian women.

The reproductive value for female persons calculated from the birth- and death-rates current in the Commonwealth of Australia about 1911. The Malthusian parameter is $+0.01231$ per annum.

female rates was nearly equivalent to $1\frac{1}{4}$ per cent. compound interest; the rate would be lower for the men, and for both sexes taken together, owing to the excess of men in immigration. The reproductive value, which of course is not to be confused with the reproductive rate, reaches its maximum at about $18\frac{1}{2}$, in spite of the delay in reproduction caused by civilized marriage customs; indeed it would have been as early as 16, were it not that a positive rate of interest gives higher value to the immediate prospect of progeny of an older woman, compared to the more remote children of a young girl. If this is the

case among a people by no means precocious in reproduction, it would be surprising if, in a state of society entailing marriage at or soon after puberty, the age of maximum reproductive value should fall at any later age than twelve. In the Australian data, the value at birth is lower, partly by reason of the effect of an increasing population in setting a lower value upon remote children and partly because of the risk of death before the reproductive age is reached. The value shown is probably correct, apart from changes in the rate since 1911, for such a purpose as assessing how far it is worth while to give assistance to immigrants in respect of infants (though of course, it takes no account of the factor of eugenic quality), for such infants will usually emigrate with their parents; but it is overvalued from the point of view of Natural Selection to a considerable extent, owing to the capacity of the parents to replace a baby lost during lactation. The reproductive value of an older woman on the contrary is undervalued in so far as her relations profit by her earnings or domestic assistance, and this to a greater extent from the point of view of the Commonwealth, than from that of Natural Selection. It is probably not without significance in this connexion that the death rate in Man takes a course generally inverse to the curve of reproductive value. The minimum of the death rate curve is at twelve, certainly not far from the primitive maximum of the reproductive value; it rises more steeply for infants, and less steeply for the elderly than the curve of reproductive value falls, points which qualitatively we should anticipate, if the incidence of natural death had been to a large extent moulded by the effects of differential survival.

A property that well illustrates the significance of the method of valuation, by which, instead of counting all individuals as of equal value in respect of future population, persons of each age are assigned an appropriate value v_x , is that, whatever may be the age constitution of a population, its total reproductive value will increase or decrease according to the correct Malthusian rate m , whereas counting all heads as equal this is only true in the theoretical case in which the population is in its steady state. For suppose the number of persons in the age interval dx is $n_x dx$; the value of each element of the population will be $n_x v_x dx$; in respect of each such group there will be a gain in value by reproduction at the rate of $n_x b_x v_o dx$, a loss by death of $n_x \mu_x v_x dx$, and a loss by depreciation of $-n_x dv_x$, or in all

$$n_x \{ (b_x v_o - \mu_x v_x) dx + dv_x \},$$

but by differentiating the equation by which v_x is defined, it appears that

$$\frac{1}{v_x} \frac{dv_x}{dx} + \frac{1}{l_x} \frac{dl_x}{dx} - m = \frac{-l_x b_x e^{-mx}}{\frac{v_x}{v_0} l_x e^{-mx}} = -\frac{b_x v_0}{v_x},$$

or that

$$dv_x - \mu_x v_x dx + b_x v_0 dx = m v_x dx.$$

Consequently the rate of increase in the total value of the population is m times its actual total value, irrespective of its constitution in respect of age. A comparison of the total values of the population at two census epochs thus shows, after allowance for migration, the genuine biological increase or decrease of the population, which may be entirely obscured or reversed by the crude comparison of the number of heads. The population of Great Britain, for example, must have commenced to decrease biologically at some date obscured by the war, between 1911 and 1921, but the census of 1921 showed a nominal increase of some millions, and that of 1931 will, doubtless in less degree, certainly indicate a further spurious period of increase, due to the accumulation of persons at ages at which their reproductive value is negligible.

The genetic element in variance

Let us now consider the manner in which any quantitative individual measurement, such as human stature, may depend upon the individual genetic constitution. We may imagine, in respect of any pair of alternative genes, the population divided into two portions, each comprising one homozygous type together with half of the heterozygotes, which must be divided equally between the two portions. The difference in average stature between these two groups may then be termed the average excess (in stature) associated with the gene substitution in question. This difference need not be wholly due to the single gene, by which the groups are distinguished, but possibly also to other genes statistically associated with it, and having similar or opposite effects. This definition will appear the more appropriate if, as is necessary for precision, the population used to determine its value comprises, not merely the whole of a species in any one generation attaining maturity, but is conceived to contain all the genetic combinations possible, with frequencies appropriate to their actual

probabilities of occurrence and survival, whatever these may be, and if the average is based upon the statures attained by all these genotypes in all possible environmental circumstances, with frequencies appropriate to the actual probabilities of encountering these circumstances. The statistical concept of the excess in stature of a given gene substitution will then be an exact one, not dependent upon chance as must be any practical estimate of it, but only upon the genetic nature and environmental circumstances of the species. The excess in a factor will usually be influenced by the actual frequency ratio $p : q$ of the alternative genes, and may also be influenced, by way of departures from random mating, by the varying reactions of the factor in question with other factors; it is for this reason that its value for the purpose of our argument is defined in the precise statistical manner chosen, rather than in terms of the average sizes of pure genotypes, as would be appropriate in specifying such a value in an experimental population, in which mating is under control, and in which the numbers of the different genotypes examined is at the choice of the experimenter.

For the same reasons it is also necessary to give a statistical definition of a second quantity, which may be easily confused with that just defined, and may often have a nearly equal value, yet which must be distinguished from it in an accurate argument; namely the average effect produced in the population as genetically constituted, by the substitution of the one type of gene for the other. By whatever rules mating, and consequently the frequency of different gene combinations, may be governed, the substitution of a small proportion of the genes of one kind by the genes of another will produce a definite proportional effect upon the average stature. The amount of the difference produced, on the average, in the total stature of the population, for each such gene substitution, may be termed the average effect of such substitution, in contra-distinction to the average excess as defined above. In human stature, for example, the correlation found between married persons is sufficient to ensure that each gene tending to increase the stature must be associated with other genes having a like effect, to an extent sufficient to make the average excess associated with each gene substitution exceed its average effect by about a quarter.

If a is the magnitude of the average excess of any factor, and α the magnitude of the average effect on the chosen measurement, we shall

now show that the contribution of that factor to the genetic variance is represented by the expression $pqaa$.

The variable measurement will be represented by x , and the relation of the quantities a to it may be made more clear by supposing that for any specific gene constitution we build up an 'expected' value, X , by adding together appropriate increments, positive or negative, according to the natures of the genes present. This expected value will not necessarily represent the real stature, though it may be a good approximation to it, but its statistical properties will be more intimately involved in the inheritance of real stature than the properties of that variate itself. Since we are only concerned with variation we may take as a primary ingredient of the value of X , the mean value of x in the population, and adjust our positive and negative increments for each factor so that these balance each other when the whole population is considered. Since the increment for any one gene will appear p times to that for its alternative gene q times in the whole population, the two increments must be of opposite sign and in the ratio $q : (-p)$. Moreover, since their difference must be a , the actual values cannot but be qa and $(-pa)$ respectively.

The value of the average excess a of any gene substitution was obtained by comparing the average values of the measurement x in two moieties into which the population can be divided. It is evident that the values of a will only be properly determined if the same average difference is maintained in these moieties between the values of X , or in other words if in each such moiety the sum of the deviations, $x - X$, is zero. This supplies a criterion mathematically sufficient to determine the values of a , which represent in the population concerned the average effects of the gene substitutions. It follows that the sum for the whole population of the product $X(x - X)$ derived from each individual must be zero, for each entry qa or $(-pa)$ in the first term will in the total be multiplied by a zero, and this will be true of the items contributed by every factor severally. It follows from this that if X and x are now each measured from the mean of the population, the variance of X , which is the mean value of X^2 , is equal to the mean value of Xx . Now the mean value of Xx will involve a for each Mendelian factor; for X will contain the item qa in the p individuals of one moiety and $(-pa)$ in the q individuals of the other, and since the average values of x in these two moieties differ by a , the mean value of Xx must be the sum for all factors of the

quantities pqa . Thus the variance of X is shown to be $W = \Sigma(pqa)$ the summation being taken over all factors, and this quantity we may distinguish as the *genetic* variance in the chosen measurement x . That it is essentially positive, unless the effect of every gene severally is zero, is shown by its equality with the variance of X . An extension of this analysis, involving no difference of principle, leads to a similar expression for cases in which one or more factors have more than two different genes or allelomorphs present.

The appropriateness of the term genetic variance lies in the fact that the quantity X is determined solely by the genes present in the individual, and is built up of the average effects of these genes. It therefore represents the genetic potentiality of the individual concerned, in the aggregate of the mating possibilities actually open to him, in the sense that the progeny averages (of x , as well as of X) of two males mated with an identical series of representative females will differ by exactly half as much as the genetic potentialities of their sires differ. Relative genetic values may therefore be determined experimentally by the diallel method, in which each animal tested is mated to the same series of animals of the opposite sex, provided that a large number of offspring can be obtained from each such mating. Without obtaining individual values, the genetic variance of the population may be derived from the correlations between relatives, provided these correlations are accurately obtained. For this purpose the square of the parental correlation divided by the grandparental correlation supplies a good estimate of the fraction, of the total observable variance of the measurement, which may be regarded as genetic variance.

It is clear that the actual measurements, x , obtained in individuals may differ from their genetic expectations by reason of fluctuations due to purely environmental circumstances. It should be noted that this is not the only cause of difference, for even if environmental fluctuations were entirely absent, and the actual measurements therefore determined exactly by the genetic composition, these measurements, which may be distinguished as *genotypic*, might still differ from the genetic values, X . A good example of this is afforded by dominance, for if dominance is complete the genotypic value of the heterozygote will be exactly the same as that of the corresponding dominant homozygote, and yet these genotypes differ by a gene substitution which may materially affect the genetic potentiality

represented by X , and be reflected in the average measurement of the offspring. A similar cause of discrepancy occurs when gene substitutions in different factors are not exactly additive in their average effects. The genetic variance as here defined is only a portion of the variance determined genotypically, and this will differ from, and usually be somewhat less than, the total variance to be observed.

It is consequently not a superfluous refinement to define the purely genetic element in the variance as it exists objectively, as a statistical character of the population, different from the variance derived from the direct measurement of individuals.

Natural Selection

The definitions given above may be applied to any characteristic whatever; it is of special interest to apply them to the special characteristic m which measures the relative rate of increase or decrease. The two groups of individuals bearing alternative genes, and consequently the genes themselves, will necessarily either have equal or unequal rates of increase, and the difference between the appropriate values of m will be represented by a , similarly the average effect upon m of the gene substitution will be represented by a . Since m measures fitness to survive by the objective fact of representation in future generations, the quantity pqa will represent the contribution of each factor to the genetic variance in fitness; the total genetic variance in fitness being the sum of these contributions, which is necessarily positive, or, in the limiting case, zero. Moreover, any increase dp in the proportion of one type of gene at the expense of the other will be accompanied by an increase adp in the average fitness of the species, where a may of course be negative; but the definition of a requires that the ratio $p : q$ must be increasing in geometrical progression at a rate measured by a , or in mathematical notation that

$$\frac{d}{dt} \log \left(\frac{p}{q} \right) = a$$

which may be written

$$\left(\frac{1}{p} + \frac{1}{q} \right) dp = a dt,$$

or

$$dp = pqa dt$$

whence it follows that,

$$adp = pqa dt$$

and, taking all factors into consideration, the total increase in fitness,

$$\Sigma(\alpha dp) = \Sigma(pqaa)dt = Wdt.$$

If therefore the time element dt is positive, the total change of fitness Wdt is also positive, and indeed the rate of increase in fitness due to all changes in gene ratio is exactly equal to the genetic variance of fitness W which the population exhibits. We may consequently state the fundamental theorem of Natural Selection in the form:

The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time.

The rigour of the demonstration requires that the terms employed should be used strictly as defined; the ease of its interpretation may be increased by appropriate conventions of measurement. For example, the ratio $p : q$ should strictly be evaluated at any instant by the enumeration, not necessarily of the census population, but of all individuals having reproductive value, weighted according to the reproductive value of each.

Since the theorem is exact only for idealized populations, in which fortuitous fluctuations in genetic composition have been excluded, it is important to obtain an estimate of the magnitude of the effect of these fluctuations, or in other words to obtain a standard error appropriate to the calculated, or expected, rate of increase in fitness. It will be sufficient for this purpose to consider the special case of a population mating and reproducing at random. It is easy to see that if such chance fluctuations cause a difference δp between the actual value of p obtained in any generation and that expected, the variance of δp will be

$$\frac{pq}{2n},$$

where n represents the number breeding in each generation, and $2n$ therefore is the number of genes in the n individuals which live to replace them. The variance of the increase in fitness, $\alpha \delta p$, due to this cause, will therefore be

$$\frac{1}{2n} (pq\alpha^2),$$

and since, with random mating, the chance fluctuation in the different gene ratios will be independent, and the values of a and α are no longer distinct, it follows that, on this condition, the rate of increase

of fitness, when measured over one generation, will have a standard error due to random survival equal to

$$\frac{1}{T} \sqrt{\frac{W}{2n}}$$

where T is the time of a generation. It will usually be convenient for each organism to measure time in generations, and if this is done it will be apparent from the large factor $2n$ in the denominator, that the random fluctuations in W , even measured over only a single generation, may be expected to be very small compared to the average rate of progress. The regularity of the latter is in fact guaranteed by the same circumstance which makes a statistical assemblage of particles, such as a bubble of gas obey, without appreciable deviation, the laws of gases. A visible bubble will indeed contain several billions of molecules, and this would be a comparatively large number for an organic population, but the principle ensuring regularity is the same. Interpreted exactly, the formula shows that it is only when the rate of progress, W , when time is measured in generations, is itself so small as to be comparable to $1/n$, that the rate of progress achieved in successive generations is made to be irregular. Even if an equipoise of this order of exactitude, between the rates of death and reproduction of different genotypes, were established, it would be only the rate of progress for spans of a single generation that would be shown to be irregular, and the deviations from regularity over a span of 10,000 generations would be just a hundredfold less.

It will be noticed that the fundamental theorem proved above bears some remarkable resemblances to the second law of thermodynamics. Both are properties of populations, or aggregates, true irrespective of the nature of the units which compose them; both are statistical laws; each requires the constant increase of a measurable quantity, in the one case the entropy of a physical system and in the other the fitness, measured by m , of a biological population. As in the physical world we can conceive of theoretical systems in which dissipative forces are wholly absent, and in which the entropy consequently remains constant, so we can conceive, though we need not expect to find, biological populations in which the genetic variance is absolutely zero, and in which fitness does not increase. Professor Eddington has recently remarked that 'The law that entropy always increases—the second law of thermodynamics—holds, I think, the

supreme position among the laws of nature'. It is not a little instructive that so similar a law should hold the supreme position among the biological sciences. While it is possible that both may ultimately be absorbed by some more general principle, for the present we should note that the laws as they stand present profound differences— (1) The systems considered in thermodynamics are permanent; species on the contrary are liable to extinction, although biological improvement must be expected to occur up to the end of their existence. (2) Fitness, although measured by a uniform method, is qualitatively different for every different organism, whereas entropy, like temperature, is taken to have the same meaning for all physical systems. (3) Fitness may be increased or decreased by changes in the environment, without reacting quantitatively upon that environment. (4) Entropy changes are exceptional in the physical world in being irreversible, while irreversible evolutionary changes form no exception among biological phenomena. Finally, (5) entropy changes lead to a progressive disorganization of the physical world, at least from the human standpoint of the utilization of energy, while evolutionary changes are generally recognized as producing progressively higher organization in the organic world.

The statement of the principle of Natural Selection in the form of a theorem determining the rate of progress of a species in fitness to survive (this term being used for a well-defined statistical attribute of the population), together with the relation between this rate of progress and its standard error, puts us in a position to judge of the validity of the objection which has been made, that the principle of Natural Selection depends on a succession of favourable chances. The objection is more in the nature of an innuendo than of a criticism, for it depends for its force upon the ambiguity of the word chance, in its popular uses. The income derived from a Casino by its proprietor may, in one sense, be said to depend upon a succession of favourable chances, although the phrase contains a suggestion of improbability more appropriate to the hopes of the patrons of his establishment. It is easy without any very profound logical analysis to perceive the difference between a succession of favourable deviations from the laws of chance, and on the other hand, the continuous and cumulative action of these laws. It is on the latter that the principle of Natural Selection relies.

The nature of adaptation

In order to consider in outline the consequences to the organic world of the progressive increase of fitness of each species of organism, it is necessary to consider the abstract nature of the relationship which we term 'adaptation'. This is the more necessary since any *simple* example of adaptation, such as the lengthened neck and legs of the giraffe as an adaptation to browsing on high levels of foliage, or the conformity in average tint of an animal to its natural background, lose, by the very simplicity of statement, a great part of the meaning which the word really conveys. For the more complex the adaptation, the more numerous the different features of conformity, the more essentially adaptive the situation is recognized to be. An organism is regarded as adapted to a particular situation, or to the totality of situations which constitute its environment, only in so far as we can imagine an assemblage of slightly different situations, or environments, to which the animal would on the whole be less well adapted; and equally only in so far as we can imagine an assemblage of slightly different organic forms, which would be less well adapted to that environment. This I take to be the meaning which the word is intended to convey, apart altogether from the question whether organisms really are adapted to their environments, or whether the structures and instincts to which the term has been applied are rightly so described.

The statistical requirements of the situation, in which one thing is made to conform to another in a large number of different respects, may be illustrated geometrically. The degree of conformity may be represented by the closeness with which a point A approaches a fixed point O . In space of three dimensions we can only represent conformity in three different respects, but even with only these the general character of the situation may be represented. The possible positions representing adaptations superior to that represented by A will be enclosed by a sphere passing through A and centred at O . If A is shifted through a fixed distance, r , in any direction its translation will improve the adaptation if it is carried to a point within this sphere, but will impair it if the new position is outside. If r is very small it may be perceived that the chances of these two events are approximately equal, and the chance of an improvement tends to the limit $\frac{1}{2}$ as r tends to zero; but if r is as great as the diameter of the

sphere or greater, there is no longer any chance whatever of improvement, for all points within the sphere are less than this distance from A . For any value of r between these limits the actual probability of improvement is

$$\frac{1}{2} \left(1 - \frac{r}{d} \right),$$

where d is the diameter of the sphere.

The chance of improvement thus decreases steadily from its limiting value $\frac{1}{2}$ when r is zero, to zero when r equals d . Since A in our representation may signify either the organism or its environment, we should conclude that a change on either side has, when this change is extremely minute, an almost equal chance of effecting improvement or the reverse; while for greater changes the chance of improvement diminishes progressively, becoming zero, or at least negligible, for changes of a sufficiently pronounced character.

The representation in three dimensions is evidently inadequate; for even a single organ, in cases in which we know enough to appreciate the relation between structure and function, as is, broadly speaking, the case with the eye in vertebrates, often shows this conformity in many more than three respects. It is of interest therefore, that if in our geometrical problem the number of dimensions be increased, the form of the relationship between the magnitude of the change r and the probability of improvement, tends to a limit which is represented in Fig. 3. The primary facts of the three dimensional problem are conserved in that the chance of improvement, for very small displacements tends to the limiting value $\frac{1}{2}$, while it falls off rapidly for increasing displacements, attaining exceedingly small values, however, when the number of dimensions is large, even while r is still small compared to d .

For any degree of adaptation there will be a standard magnitude of change, represented by d/\sqrt{n} , and the probability of improvement will be determined by the ratio which the particular change considered bears to this standard magnitude. The higher the adaptation the smaller will this standard be, and consequently the smaller the probability that a change of given magnitude shall effect an improvement. The situation may be expressed otherwise by supposing changes of a given magnitude to occur at random in all directions, and comparing the rates of evolutionary progress caused by two opposite selective agencies, one of which picks out and accumulates all changes which

increase the adaptation, and another which similarly picks out and accumulates all which diminish it. For changes very small compared to the standard, these two agencies will be equally effective, but, even for changes of only one-tenth of the standard, the destructive selection is already 28 per cent. more effective than the selection favouring

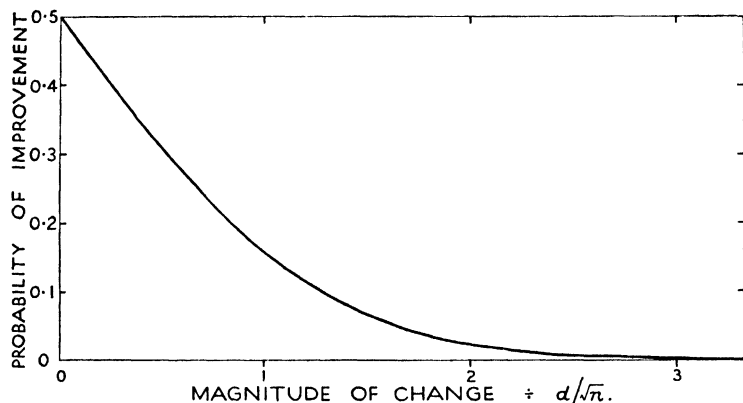


FIG. 3. The relation between the magnitude of an undirected change and the probability of improving adaptation, where the number of dimensions (n) is large

$$p = \frac{1}{\sqrt{2\pi}} \int_x^{\infty} e^{-t^2} dt, \quad x = r\sqrt{n}/d.$$

adaptation. At one half the standard it is over three and a half times as powerful, at the standard value itself, at which the probability of improvement is still, as the diagram shows, nearly one in six, the selection destroying adaptation is thirteen times as effective as that building it up, and at twice and three times the standard value the ratio has risen to the values 236 and 7,852 respectively.

The conformity of these statistical requirements with common experience will be perceived by comparison with the mechanical adaptation of an instrument, such as the microscope, when adjusted for distinct vision. If we imagine a derangement of the system by moving a little each of the lenses, either longitudinally or transversely, or by twisting through an angle, by altering the refractive index and transparency of the different components, or the curvature, or the polish of the interfaces, it is sufficiently obvious that any large derangement will have a very small probability of improving the adjustment, while in the case of alterations much less than the smallest

of those intentionally effected by the maker or the operator, the chance of improvement should be almost exactly half.

Deterioration of the environment

If therefore an organism be really in any high degree adapted to the place it fills in its environment, this adaptation will be constantly menaced by any undirected agencies liable to cause changes to either party in the adaptation. The case of large mutations to the organism may first be considered, since their consequences in this connexion are of an extremely simple character. A considerable number of such mutations have now been observed, and these are, I believe, without exception, either definitely pathological (most often lethal) in their effects, or with high probability to be regarded as deleterious in the wild state. This is merely what would be expected on the view, which was regarded as obvious by the older naturalists, and I believe by all who have studied wild animals, that organisms in general are, in fact, marvellously and intricately adapted, both in their internal mechanisms, and in their relations to external nature. Such large mutations occurring in the natural state would be unfavourable to survival, and as soon as the numbers affected attain a certain small proportion in the whole population, an equilibrium must be established in which the rate of elimination is equal to the rate of mutation. To put the matter in another way we may say that each mutation of this kind is allowed to contribute exactly as much to the genetic variance of fitness in the species as will provide a rate of improvement equivalent to the rate of deterioration caused by the continual occurrence of the mutation.

As to the physical environment, geological and climatological changes must always be slowly in progress, and these, though possibly beneficial to some few organisms, must as they continue become harmful to the greater number, for the same reasons as mutations in the organism itself will generally be harmful. For the majority of organisms, therefore, the physical environment may be regarded as constantly deteriorating, whether the climate, for example, is becoming warmer or cooler, moister or drier, and this will tend, in the majority of species, constantly to lower the average value of m , the Malthusian parameter of the population increase. Probably more important than the changes in climate will be the evolutionary changes in progress in associated organisms. As each organism increases in fitness, so will its enemies and competitors increase in

fitness; and this will have the same effect, perhaps in a much more important degree, in impairing the environment, from the point of view of each organism concerned. Against the action of Natural Selection in constantly increasing the fitness of every organism, at a rate equal to the genetic variance in fitness which that population maintains, is to be set off the very considerable item of the deterioration of its inorganic and organic environment. It is only if the former of these agencies exceeds the latter that there can be any actual increase in population, while in the reverse case the population will certainly decrease.

Changes in population

An increase in numbers of any organism will impair its environment in a manner analogous to, and probably more definitely than, an increase in the numbers or efficiency of its competitors. It is a patent oversimplification to assert that the environment determines the numbers of each sort of organism which it will support. The numbers must indeed be determined by the elastic quality of the resistance offered to increase in numbers, so that life is made somewhat harder to each individual when the population is larger, and easier when the population is smaller. The balance left over when from the rate of increase in the mean value of m produced by Natural Selection, is deducted the rate of decrease due to deterioration in environment, results not in an increase in the average value of m , for this average value cannot greatly exceed zero, but principally in a steady increase in population.

The situation is represented by the differential equation

$$\frac{dM}{dt} + \frac{M}{C} = W - D$$

in which M is the mean of the Malthusian parameter, C is a constant expressing the relation between fitness and population increase, and defined as the increase in the natural logarithm of the population, supposed stationary at each stage, produced by unit increase in the value of M , W is the rate of actual increase in fitness determined by natural selection, and D is the rate of loss due to the deterioration of the environment. If C , W and D are constant the equation has the solution

$$M = \frac{W - D}{C} + Ae^{-t/C}$$

in which A is an arbitrary constant, dependent upon the initial conditions. C has the physical dimensions of time, and may therefore be reckoned in years or generations, and the equation shows that if C , W , and D remain constant for any length of time much greater than C , the value of M will approach to the constant value given by

$$M = \frac{W - D}{C}.$$

In this steady state the whole of the organism's advantage or disadvantage will be compensated by change in population, and not at all by change in the value of M .

A word should perhaps be said as to the form of statement of selection theory which ascribes the 'struggle for existence' to the excessive production of offspring, supposedly to be observed throughout organic nature. If the numbers of a species are adjusted to that level at which each adult produces on the average just two offspring which attain the adult state, then, if there is any mortality whatever in the previous life stages, either through inorganic causes, or by reason of predators and parasites, it necessarily follows that young must be produced in excess of the parental numbers. If the mortality is high, then the ratio of this excess will be large. Having realized this situation, if we now imagine an ideal world in which all these offspring attain maturity and breed, it is obvious that in such a world the numbers of the species considered will increase without limit. It is usually added, though this is logically irrelevant, that the increase will be in geometrical progression. We may in this sense speak of the production of offspring as 'excessive', and the geometrical rate of increase with its impressive picture of over-population, has been widely represented as a logical basis of the argument for natural selection. However, it should be remembered that the production of offspring is only excessive in relation to an imaginary world, and the 'high geometrical rate of increase' is only attained by abolishing a real death rate, while retaining a real rate of reproduction. There is something like a relic of creationist philosophy in arguing from the observation, let us say, that a cod spawns a million eggs, that *therefore* its offspring are subject to Natural Selection; and it has the disadvantage of excluding fecundity from the class of characteristics of which we may attempt to appreciate the aptitude. It would be instructive to know not only by what physiological mechanism a just

apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life-history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction. The historical fact that both Darwin and Wallace were led through reading Malthus's essay on population to appreciate the efficacy of selection, though extremely instructive as to the philosophy of their age, should no longer constrain us to confuse the consequences of that principle with its foundations.

It will have been apparent in the earlier sections of this chapter that the actuarial information necessary for the calculation of the genetic changes actually in progress in a population of organisms, will always be lacking; if only because the number of different genotypes for each of which the Malthusian parameter is required will often, perhaps always, exceed the number of organisms in the population, in addition to the fact that this parameter is very imperfectly known even in human population aggregates, for which vital statistics are in some degree available. If, however, we are content to consider not in full detail exactly what changes are in progress, but quite broadly to what extent an organism is holding its own in the economy of nature, it is only necessary to determine the numerical values of the four quantities W , D , C , and M , which enter into the equation of population growth. Our ignorance as to these is, of course, profound, but, regarding the problem in this limited aspect, it is by no means obvious, with respect to organisms of sufficient importance to deserve detailed study, that it could not largely be removed by systematic and well-directed observations. The quantity C , for example, which is a period of time, measuring the facility with which, with increased fitness, the population is allowed to increase, must be intimately related to the course of population increase or decrease, with which the numbers of an organism exposed to new influences, approach an equilibrium value, which over short periods may be regarded as stationary. An organism introduced into a new environment, to which it is well suited, will increase in numbers rapidly for a comparatively few years, and somewhat rapidly attain its equilibrium density. The same must be true of the decrease of a population exposed by man to new causes of destruction. In these cases it is probable that the process of attaining equilibrium is sufficiently rapid for the changes due to organic evolution, and the natural deterioration of

the environment, to be neglected, and further changes in the extent of human intervention could, for experimental purposes, be suspended locally. In such cases, at their simplest, the course of population change would be represented by the equation $M = Ae^{-t/C}$, or, since M is the relative or logarithmic growth rate of the population, by $\log N = \log N_0 - ACe^{-t/C}$, where N is the size or density of the population, and N_0 the steady value to which it is tending. Observations of N will then determine, at least approximately, the value of the time constant C . It should be noticed that for such comparatively large changes of population density as could be measured with sufficient precision, important changes will often take place in the numbers of associated organisms. The simple relation obtained above will only be satisfactory if these associated changes take place rapidly in comparison to the change we are studying. Otherwise it would be necessary to take account by direct observation of the changes in numbers of at least the more important of the associated organisms, and so to determine the constants of the more complex system of differential equations by which their interactions may be represented.

With respect to the other constants, the practical difficulties appear to be greater, though, seeing how little attention in general has been paid to the quantitative study of organisms in their natural habitats, it would be rash to assume that their determination is beyond human endeavour. Though it would be out of place here to outline a programme of research, it is perhaps worth while to indicate a few possibilities. The density of populations of animals and plants may be studied in relation to the climatic and other environmental factors of their habitats. Knowledge of this kind, even if only approximately complete, would indicate to what extent physical changes now in progress can be improving or impairing the environment. If the constant C is also known, these effects may be translated directly into terms of fitness. In certain cases, such as the slow changes in composition of plant associations, the value of M might be directly determined, and in conjunction with more or less trustworthy determinations of C and D , this would lead to a more or less exact estimate of the evolutionary factor W . The direct determination of the latter quantity would seem to require a complete genealogy of the species for several generations, and this will only be possible in Man. Moreover, owing to the rapid changes which man is making in his environment, it may be foreseen that human genealogies on a national or

international scale, such as has been undertaken in Sweden, while throwing an immense amount of light on the current conditions of human reproduction and survival, will offer special difficulties in the determination and interpretation of the evolutionary value W .

Summary

The vital statistics of an organism in relation to its environment provide a means of determining a measure of the relative growth-rate of the population, which may be termed the Malthusian parameter of population increase, and provide also a measure of the reproductive values of individuals at all ages or stages of their life-history. The Malthusian parameter will in general be different for each different genotype, and will measure the fitness to survive of each.

The variation in a population of any individual measurement is specified quantitatively by its variance, and of this, taking account of the genetic composition of all possible individuals, a definite amount may be recognized as genetic variance.

The rate of increase of fitness of any species is equal to the genetic variance in fitness, and the standard error of this rate of progress even over a single generation, will (unless the latter is so exceedingly minute as to be comparable, when time is measured in generations, to the reciprocal of the number of organisms in the population) be small compared to the rate of progress.

Adaptation, in the sense of conformity in many particulars between two complex entities, may be shown, by making use of the geometrical properties of space of many dimensions, to imply a statistical situation in which the probability, of a change of given magnitude effecting an improvement, decreases from its limiting value of one half, as the magnitude of the change is increased. The intensity of adaptation is inversely proportional to a standard magnitude of change for which this probability is constant. Thus the larger the change, or the more intense the adaptation, the smaller will be the chance of improvement.

Against the rate of progress in fitness must be set off, if the organism is, properly speaking, highly adapted to its place in nature, deterioration due to undirected changes either in the organism, or in its environment. The former, typified by the pathological mutations observed by geneticists, annul their influence by calling into existence an equivalent amount of genetic variance. The latter, which are

due to geological and climatological changes on the one hand, and to changes in the organic environment, including the improvement of enemies and competitors, on the other, may be in effect either greater or less than the improvement due to Natural Selection.

Any net advantage gained by an organism will be conserved in the form of an increase in population, rather than in an increase in the average Malthusian parameter, which is kept by this adjustment always near to zero.

Although it appears impossible to conceive that the detailed action of Natural Selection could ever be brought completely within human knowledge, direct observational methods may yet determine the numerical values which condition the survival and progress of particular species.