It is vital that we should keep population trends, ecological problems and food supply problems in the public eye. But it will not help to provoke despair.

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EVOLUTION AND THE GENETICS OF POPULATIONS. VOLUME 2: THE THEORY OF GENE FREQUENCIES. Sewall Wright. University of Chicago Press. Pp. 511. £6, 15s.

It is a platitude of mathematical population genetics that the subject's development is principally due to Fisher, Haldane and Wright. The order is alphabetic; but it is also the order in which they are leaving the scientific stage, and the order in which they have published their major books on the subject. Fisher gave us *The Genetical Theory of Natural Selection* in 1930 (Fisher, 1930*a*, 1958) and Haldane *The Causes of Evolution* in 1932 (Haldane, 1932*b*, 1966); but we have had to wait until now, full forty years after *The Genetical Theory*, for Professor Sewall Wright to distil his contribution into a major book. Happily he has been given the time and strength to perform this work; without it the perspective in which he views, and wishes us to view, mathematical population genetics would have remained indistinct.

This volume owes something to an earlier work of Wright's *Statistical Genetics in Relation to Evolution* (Wright, 1939*b*), a slim book published in Paris on the eve of war, and consequently not widely known. But it is very much larger, and includes the fruits of thirty years' more work; it is also much more partisan. The author spares no efforts to remind us of his early contributions, sometimes with startling effect: on p. 417, for example, we read that he " dealt with analysis of covariance as well as variance " in 1917. My impression had been that Fisher did not introduce the word *variance* until 1918 (Fisher, 1918); here is meat for historians.

With Haldane's contribution Wright deals generously, but this only emphasises the conflict with Fisher. Not for him Haldane's epithet " brilliant" in describing *The Genetical Theory* (Haldane, 1966, p. 13)*. The wounds inflicted in this sad battle must lie deep. Only the scientific drama, however, concerns us at present, and it is never far from the surface. Sometimes Wright avoids mentioning Fisher altogether, as in " Correlations between Relatives in the Presence of Dominance " (p. 433), a principal topic of Fisher's 1918 paper *The correlation between relatives on the supposition of Mendelian inheritance*. The " correlation array " used by Fisher is attributed correctly to Pearson (1904) (it is the only paper of Pearson quoted), and the " 1918 " paper is not cited at all, merely earning a critical mention in the next section because Fisher neglected the environmental correlations when analysing Pearson's data on human stature. But that was 53 years ago.

The old battlegrounds of adaptive surfaces, self-sterility alleles, the evolution of dominance, inbreeding, and the rate of fixation, are revisited. Naturally, the author presses his own points of view, and this is not the place to question matters of opinion. But the kernel of the book is the concept of the adaptive surface, a concept which Fisher never accepted and Haldane,

* I have since discovered that Wright once wrote of *The Genetical Theory*. "It is a book which is certain to rank as one of the major contributions to the theory of evolution". (*J. Hered.*, *21*, 349, 1930).

I think, never used. The dispute concerns a matter of fact, not opinion, and we must pursue it. The adaptive surface is the hero—or villain—of the piece; it reminds us of the scientific drama at each appearance.

The problem is as follows. On p. 39, Wright reveals his famous formula for the change in the frequency q_x of the xth of a series of alleles in one generation under natural selection:

$$\Delta q_x = q_x(1-q_x)\frac{\partial \bar{W}}{\partial q_x} / 2\bar{W}.$$

$\bar{W}$ is the " mean fitness ", and the partial derivative is the slope of the function $\bar{W}$ in the direction of the corner of the simplex* corresponding to a population all A_x, the xth allele. No one, as far as I know, disputes the formula, though many feel that the introduction of the derivative of $\bar{W}$ is somewhat artificial; but Wright, of course, is going to hang a whole theory on $\bar{W}$ and its derivatives.

Now if all the Δq_x are zero, we have an equilibrium point, by definition; that is, the gene frequencies all remain unchanged from one generation to the next. Similarly, if the gene frequencies are such that $\bar{W}$ is a stationary point with respect to them, all the $\frac{\partial \bar{W}}{\partial q_x}$ are zero, and hence all the Δq_x zero. Thus the non-degenerate equilibrium gene frequencies and the gene frequencies at the stationary point of $\bar{W}$ *with respect to variation in the* q_x are one and the same thing. So far so good.

Now (p. 41) Wright finds the conditions under which the stationary point of $\bar{W}$ is a maximum *with respect to variation in the* q_x. He does so correctly, though it might be neater to use the theory of constrained derivatives. But what has this to do with changes in the q_x *with respect to time* under natural selection? All that the above equation tells us is that, since Δq_x and $\frac{\partial \bar{W}}{\partial q_x}$ are of the same sign, the *direction* of gene-frequency change is such that a very small step in that direction would lead to an increase in $\bar{W}$.† The direction of the change is not even necessarily along the line of steepest ascent on the $\bar{W}$ surface; but, more important, there is nothing in the equation itself which makes it obvious that the *magnitude* of the gene-frequency change is going to be sufficiently small for it to count as a " very small step ".

Imagine yourself on the side of a smooth hill in a fog. Your " equation of motion " guarantees that (1) the size of your step is proportional to the gradient, reducing to zero at the top, and (2) the direction of each step is such that, were you to proceed a very small distance—but not a whole step—in that direction, you would certainly move to a higher point. Would you necessarily arrive at the top of the hill? No, because the actual size of any

* A simplex is the generic name for the sequence of geometrical figures " point, line, triangle, tetrahedron . . ." on or in which we may represent the frequencies of genes at a locus with 1, 2, 3, 4 . . . alleles.

† On reflection, even this generally accepted statement requires proof. Though it is obviously true for two alleles, it is not obviously true for three or more, because the element " ∂q_x " refers to the direction towards the " x "-apex of the simplex, whilst the element " Δq_x " refers to the direction perpendicular to the flat opposite the " x "-apex. These directions only coincide at the centre of the simplex, or when there are but two alleles. However, Mr E. F. Harding and I have obtained a proof, which we propose to publish shortly.

step might be such that it would take you over a shoulder of the hill to a *lower* point. The ony certain way to arrive at the top under this scheme would be to make the steps infinitesimally small, for then each shuffle would necessarily take you a little higher. Alternatively, you might examine the equation of motion in more detail to see whether, hidden in it, was the assurance that even with man-sized steps you would necessarily gain height with each step.

So it is with Wright's " surface of mean fitness " or " adaptive topography ". In order to identify the problem of whether the equilibrium gene-frequency points are stable or unstable with the problem of whether the stationary points of $\bar{W}$ are at a maximum or a minimum of the $\bar{W}$ surface, we must either assume such weak selection that each step can be shown to be small enough for $\bar{W}$ to certainly increase, or we must prove that, for any magnitude of selection, and hence for large step sizes, $\bar{W}$ does in fact increase. Wright does neither: in connection with the multiple-allele case with a particular fitness matrix, he simply jumps to the statement (p. 43), " It is fairly obvious and easily verified that equilibrium is stable ($\bar{W}$ maximum) ". But what is " fairly obvious " in this case is that $\bar{W}$ is a maximum with respect to variations in gene frequency, from which it does not necessarily follow that the equilibrium is stable.

With just two alleles we can easily prove that $\bar{W}$ always increases (or, to be precise, never decreases), for we merely have to show that there is a single stationary point of $\bar{W}$, which is a trivial matter, and that the direction of gene frequency change is monotonic towards, or away from, the stationary point, which is clear from Fisher's (1930*a*) treatment. But with three or more alleles, although $\bar{W}$ still has only one stationary point, being a quadratic function of the gene frequencies, one cannot appeal to monotonicity in gene frequency change.

Wright refers to the work of Kimura (1956*b*) and Penrose, Smith and Sprott (1956) for the establishment of the multiple-allele stability conditions, and also to Mandel (1959), but in fact Mandel was at pains to point out that both Kimura and Penrose *et al.*, had assumed a continuous-time model which " is justified only in the case of infinitesimally slow selection ". As we have seen, with such very small steps in gene-frequency change, $\bar{W}$ must increase, as it will whenever selection is so slow that we can effectively treat populations of genes rather than of genotypes.

The nettle of what happens with selection of any magnitude and discrete generations, which is precisely Wright's model, was first grasped by Owen (1954) who correctly gave the stability conditions for the three-allele case, though without proof. The proof, actually for any number of alleles, was supplied by Mandel and Hughes (1958), who arrived at the conditions by showing that, sufficiently near the equilibrium point, $\bar{W}$ is in fact a non-decreasing function. They also " conjecture that the mean viability $\bar{W}$ increases each time the population undergoes the process of mating, but to prove this statement generally appears to be a matter of considerable mathematical difficulty ". This difficulty was overcome, and the increasing nature of $\bar{W}$ finally established, by Scheuer and Mandel (1959), Mulholland and Smith (1959), and Atkinson, Watterson and Moran (1960), and in 1961 Kingman sealed the matter by giving a greatly simplified proof.

One might have supposed that Wright would have eagerly siezed on the above work as in part validating the concept of an adaptive topography, at least for the case of a single autosomal locus in a diploid organism undergoing random mating, with any number of alleles and constant genotypic fitnesses. But in fact he completely ignores all the above papers, in spite of them being cited in Moran's (1962) book. This omission is significant, because if Wright were to admit the existence of the problem, he would have to prove $\bar{W}$ an increasing function in every case to which he applied the concept of an adaptive topography, and so far a proof has only been obtained for a single autosomal locus. Indeed, as soon as one proceeds to the next most complex case, two loci with epistacy, a counter-example is known (Moran, 1964), though Wright dismisses Moran's criticism as " based on a misunderstanding of the concept " of an adaptive surface.

In the case of selection with inbreeding, Li (1967) notes that " the peak-and-valley theory of natural selection no longer holds ", but adds that " Wright is well aware of the fact ". It appears that at equilibrium the gene frequencies are at a stationary point of the " modified average fitness $\bar{W}^*$"; but that does not justify a new " peak-and-valley " representation, because $\bar{W}^*$ may not be an increasing function. Weir (1970) is not hopeful on the point. In the case of autotetraploids " the average fitness does not necessarily increase under selection " (Li, 1967); nor does it with linked loci. For a multi-allelic sex-linked locus neither a proof nor a counter-example is known to me, though Cannings (1968) is of the opinion that the use of a potential function " would probably be misleading ". The situation is similar when the fitnesses differ between the sexes, where there may be two distinct stable equilibria (Owen, 1953), whilst with frequency-dependent selection " the concept of adaptive peak ceases to apply " (Li, 1967).

This is not an auspicious foundation for a general theory. By ignoring the fundamental problem, Wright inevitably forfeits our sympathy in his attempts, later in the book, to treat more complex situations by fitness functions, sometimes specially constructed. He tries to sustain a general theory by distinguishing between the peaks of the special " fitness functions " and the peaks of the mean fitness functions, which do not, in general coincide. But by this stage in the argument I am forced to conclude that the concepts merely obscure the issues, and are best abandoned. Fisher (1941), in a paper which all who seek to resolve this controversy for themselves should study, says " Wright's conception embodied in equation (6) [that quoted above] that selective intensities are derivable, like forces in a conservative system, from a simple potential function dependent on the gene ratios of the species as a whole, has led him to extensive but untenable speculations ". Fisher was no doubt familiar with potential theory, since he read mathematics in Cambridge before the first war, but his " Fundamental theorem of natural selection " (Fisher, 1930*a*) was as far as he would travel along that road. This theorem, which is a very restricted continuous-time theorem, tells us all that we can hope to learn about the increase in fitness in a general way, and serves to emphasise, rather than to obscure, the essential peculiarities of selection in *diploid* populations. It preceded Wright's (1932) concept of an adaptive topography; Wright devotes three lines to it (p. 121).

To sum up this discussion on the core of Wright's book, the general theory of gene-frequency change cannot be satisfactorily treated by appealing to the concept of an adaptive surface, because the mean fitness is not necessarily an increasing function (unless selection is so slow that we can no longer call the theory general); in the single case in which we know the mean fitness does increase, the concept is hardly necessary, and misleading to the extent that populations do not climb the surface by the steepest route; in more complex cases the stationary points of the adaptive surface may not correspond to the equilibrium gene frequencies, so that for a potential theory representation other " fitness functions " have to be found. These appear to offer no conceptual advantage, and the demonstration that they are in fact potential functions requires the solution of the problem of interest in any case, unless selection is so slow that, again, the theory is no longer general. Finally, the concept obscures the fact that in a diploid population the interests of the individual and of the population do not usually coincide.

The book is refreshingly well-written, direct and to the point. The introduction is an admirably concise précis; Chapter 2 opens at such a pace that the author does not even mention that he is dealing with the large-population theory initially, and it is not long before the reader is confronted with some samples of an unfortunate characteristic of Wright's mathematical work: the proliferation of subscripts. This " underwriters' disease " reaches epidemic proportions at times, a peak being reached on page 469, with the subscript WW(E)W(E1)W(E2). Subscripted subscripts, and even superscripted subscripts, occur. Indeed, the use of path coefficients as a method of analysis often seems to relegate the essential difficulties to the subscripts, rather than to illuminate the problem.

Chapter 3—Systematic change of gene frequency: single loci—has already drawn extensive comment above. We may additionally note that the section " Unequal selection in males and females " does not mention Owen's (1953) interesting work; and that the conditions for stable equilibrium at a sex-linked locus appear to have been first given by Bennett (1958), and proved by Mandel (1959*a*), Kimura (1960) and Edwards (1961), by different methods. None of this work is mentioned; nor does Wright consider genes which affect the sex-ratio in the way suggested by Fisher (1930*a*).

In Chapter 4 the concept of an adaptive surface is extended to multiple loci, and in Chapter 5 to frequency-dependent selective values. A general " fitness function " is introduced in order to handle those cases in which the stationary points of the mean fitness are not the same as the points of genetic equilibrium. In effect the fitness function is found by determining the expression for Δq in the particular case under consideration, equating it to $q(1-q)\dfrac{\partial F}{\partial q}\,/\,2F$, and then solving for F. " The set of formulas for the Δq's has the important property that these show by their form that within their range of approximate validity the set of gene frequencies tends to move up the gradient of the ' surface ' $\log \bar{w}$, except as qualified by the positive factor, $0{\cdot}5q(1-q)$, and thus tends to approach a ' peak ' in this surface " (p. 121). The " important property " is the one mentioned earlier in this review, which Wright does not prove; it is interesting to find him suggesting that the factor $0{\cdot}5q(1-q)$ might upset it (in fact it does not).

Thus for slow selection F plays the role of $\bar{W}$ in simple models, and may be regarded as an adaptive surface which " would determine the course of evolution of the system ". But the truth of the matter is that what happens to F, or $\bar{W}$, is a consequence of evolution and not a determinant. The general theory for which Wright seeks is a will-o'-the-wisp, and solving for F is simply a mathematical juggle designed to rescue the concept of an adaptive topography from oblivion. That may by now be impossible, but at least the demise of $\bar{W}$ draws attention to the fact that the *average effect* and the *average excess* are not, in general, the same (Fisher, 1930*a*).

Chapter 6 deals briefly with cytoplasmic inheritance, and in Chapters 7-11 Wright treats the theory of inbreeding, to which he has contributed so much. Naturally, the treatment is by path coefficients. There need be no controversy about the correctness of the approach, though it is fruitful to reflect on ways in which the presentation might be improved. The major advance since Wright's early work on the subject is undoubtedly the replacement of the definition of the inbreeding coefficient as the " correlation between uniting gametes " by the " probability that the two uniting genes are identical by descent ". It is understandable that Wright should not adopt the more modern treatment, but his treatment suffers correspondingly. He barely mentions Malécot's work, and Cotterman (1941), to whom is due the concept of gene-identity by descent, is not mentioned at all. Kempthorne's (1957) contributions are not discussed, though Fisher is frequently (and justifiably) taken to task for his 1949 book. But on the whole we may share the reaction of Rupert Brooke:

> " So shall I curb, so baffle, so suppress
> This too avuncular officiousness,
> Intolerable consanguinity ".

Chapter 12—Population structure—shows the use of the inbreeding coefficient at its best, and Chapters 13 and 14 deal with the stochastic distribution of gene frequencies, with a long digression on self-incompatibility alleles. Chapters 15 and 16 are on components of variability, path coefficients being used freely. Chapter 17 is a summary of the entire book.

One may readily sympathise with Wright in his desire to give us a lasting account of his contributions to the subject of mathematical population genetics, but in this volume he renders himself a disservice. By offering us a general treatise which adheres so closely to his own earlier work he runs the risk of having this work too harshly criticised. His coverage of the literature is extensive but also, as we have seen, selective. His treatment of some topics is not along lines which are generally adjudged the most illuminating, and his insistence on relying so heavily on the concept of an adaptive surface creates more problems than it solves.

There is no doubt that his contribution to the subject has been great, but if his wish is that future generations should fully understand and appreciate this contribution, it would have been better to have presented us with a historical account than to offer us a treatise so biassed in favour of his own particular approaches. For it is generally true that the study of the foundations of a subject enhance one's opinions of the founders, whereas the realisation that earlier views are being too closely followed has the reverse effect. We must view this book in a historical setting, for it would be a disservice to the subject and to Professor Wright if we were to regard it as an account of the contemporary state of mathematical population genetics.

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" INSTINCT " AND " INTELLIGENCE "—THE BEHAVIOUR OF ANIMALS AND MAN. S. A. Barnett. Penguin Books, 1970. Pp. 328. 10s.

One of the boom subjects in post-war zoology has been the study of animal behaviour. Ideas originating with the Continental ethologists, particularly Konrad Lorenz, found fertile ground in this country and the United States and have grown into a strong and healthy discipline. One of the best introductions to this field is Anthony Barnett's book " *Instinct* " *and* " *Intelligence* " which was first published three years ago in hard covers and now appears in a revised Pelican edition.

As is characteristic of the field, the emphasis is on " instinct ". Nowadays this term is used descriptively to refer to those aspects of behaviour which are more or less common to all members of a species. Nothing is implied about the development of such behaviour. The old heresy that " instincts " represent the behaviour that is " fixed by the genes " has long been abandoned by British workers, though it still persists on parts of the Continent.

Barnett's book is organised around the traditional functional categories of behaviour (orientation, exploration, courtship, mating, etc.), and some major questions about mechanisms (the development of behaviour, motivation, learning). There is a useful section on the anatomy and physiology of the nervous system. Throughout the book there are restrained and sensible comments about human behaviour—quite unlike the more colourful and widely publicised claims of some of the human ethologists.

From sixth form level onwards, this book may be recommended to anyone who wishes to follow the zoologists in their study of behaviour.

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