NATURAL SELECTION, HEREDITY, AND EUGENICS

Including selected correspondence of R.A. Fisher with Leonard Darwin and others

Edited with an introduction
by
J.H. BENNETT
Professor of Genetics,
University of Adelaide, South Australia

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PREFACE

This volume consists of a selection from R.A. Fisher's letters on natural selection, heredity, and eugenics, along with such comments and other material as are required for the elucidation of the correspondence and for giving continuity to the whole.

The structure of the book has been greatly influenced by Fisher's extensive correspondence with Leonard Darwin over more than 20 years. Many of their letters in the period 1915-29 were concerned with questions later considered in Fisher's book *The genetical theory of natural selection* (1930). This fact and the considerable influence of that book on much of the other correspondence have necessitated a somewhat lengthy introduction. Chapter 1 is concerned with the circumstances in which *Genetical theory* was written, its main features, the reception it was given, and its impact on evolutionary thought. Chapter 2 contains two unpublished papers by Fisher from 1911-12 dealing with Mendelism, biometry, and selection. The Darwin-Fisher letters, separated into pre- and post-*Genetical theory* periods, are presented in Chapters 3 and 4, respectively, and Fisher's letters to other correspondents in Chapter 5. Fortunately, it has been possible to add to the interest of this material by including in Chapters 3 and 4, extracts from Darwin's letters to Fisher and, in Chapter 5, some relevant correspondence from a few of the eminent individuals to whom Fisher was writing. Before 1930 Fisher had very little correspondence on natural selection and heredity with anyone other than Darwin, whereas after *Genetical theory* was published, various readers wrote with questions and comments stemming from the book. A number of Fisher's letters in Chapters 4 and 5 may be seen as providing an extension or elaboration of arguments contained in *Genetical theory*. Of the four appendices in the present volume, A and C comprise reprints of two reviews by Fisher referred to in the text, whilst B and D contain material hitherto unpublished—a review by Fisher of J.B.S. Haldane's book *The causes of evolution* and Fisher's last paper on natural selection which he read at a meeting in Adelaide in 1959. In this article he contrasts the scope and magnitude of Charles Darwin's achievements with the work of those who are still sometimes put forward as the progenitors of his ideas.

A graphic description of how *Genetical theory* was written has been given by Joan Fisher Box (1978) in her outstanding biography of her father, *R. A. Fisher. The life of a scientist* (John Wiley, New York).

Like his other genetical work, it was done at home with his wife. He would stride about the room, or mull over a pipe, as he dictated and she took down his words in longhand ... Fisher seemed to know exactly what he wished to say, holding the whole ordered argument in his head, and even his deliberation over the detailed expression of his thoughts did not often give pause to the pen of his amanuensis. Yet, once he had set a passage down on paper, he rarely changed a word or needed to rearrange the order or insert omissions. His capacity to hold in mind the numerous details of a complex argument was remarkable, as was his precision in expressing what he meant.

This passage could equally well describe Fisher dictating letters to his secretary. The letters provide a fascinating record of one of the most brilliant intellects in modern evolutionary biology discoursing in characteristic manner on numerous subjects, many of them complex, with great care, precision, and some subtlety, and showing at the same time much good humour and charm.

The Darwin-Fisher letters are presented in chronological order but the letters in Chapter 5 are arranged, for ease of reference, in alphabetical order according to the names of the correspondents. My object when selecting correspondence has been to include material of scientific or historical interest, avoiding unnecessary repetition and personal references of no scientific relevance. Editorial insertions in the correspondence have been kept to a minimum; such material is shown in square brackets. When a word or passage has been omitted, this is indicated by the symbol ... . Occasional changes in punctuation or spelling have been made without comment.

I am indebted to Lady Barlow and Professors E.B. Ford and S. Wright for their gracious permission to reproduce material from their letters to Fisher as shown in Chapter 5; to Lady Barlow and Professor H.B. Barlow for their kind assistance with Leonard Darwin's letters; to Naomi Mitchison, Laura Huxley, Anthony Huxley, and Unity Sherrington for permission to reproduce material from the letters of Professor J.B.S. Haldane, Aldous Huxley, Sir Julian Huxley, and Sir Charles Sherrington, respectively; to Dr W.B. Provine for kindly sending copies of Fisher-Wright correspondence; to the Oxford University Press for information on the sales of *Genetical theory* and for permission to reproduce extracts from Mr K. Sisam's letters to Fisher concerning publication of that book; to the Secretary of the Royal Society of Edinburgh for information on the refereeing of Fisher's 1918 paper on the correlation between relatives; to the Eugenics Society and *Nature* for permission to reprint the material in Appendixes A and C respectively; and to the University of Adelaide for permission to quote various passages from *R. A. Fisher correspondence* held at the University.

Mrs Joan Fisher Box kindly read the whole work and made many valuable suggestions. I am indebted to Professors W.F. Bodmer and D.J. Finney for their comments on the typescript and to Professor R.J. Berry for reading and commenting on Chapter 1. Special thanks are due to Miss Georgette Psaltis for her patient and careful assistance in the preparation of material for the publisher.

J.H.B.

Adelaide, South Australia
September 1982

CONTENTS

EDITOR'S ABBREVIATIONS

CP — *Collected papers of R.A. Fisher* (ed. J.H. Bennett). University of Adelaide (1971-4). (Numbered references to papers can be identified from the reference list on p. 298.)

FLS — *R.A. Fisher. The life of a scientist* by Joan Fisher Box. John Wiley, New York (1978).

GTNS — *The genetical theory of natural selection* by R.A. Fisher. Clarendon Press, Oxford (1930); 2nd edn, Dover Publications, New York (1958). (Page numbers refer to the 1958 edition.)

1 INTRODUCTION

Since Charles Darwin developed the theory of natural selection in ignorance of the true nature of heredity, it was inevitable that it should be redeveloped later on a genetical basis. However, the relevance of genetics for an understanding of evolutionary theory was not widely appreciated by biologists until well into the twentieth century. Fisher's (1930) book *The genetical theory of natural selection* was the first major work to provide a general synthesis of Mendelism and Darwinism. Written at a time when Darwinism was neglected or ignored, it marked an important turning point in the development of evolutionary thought, leading to the emergence of neo-Darwinism.

To appreciate fully what it was that Fisher accomplished with this book we must recall the general attitude of biologists to natural selection and evolution in the period 1920-30. D.M.S. Watson in his Presidential Address to the Zoology Section of the British Association for the Advancement of Science in 1929 expressed it as follows.

> Whilst the fact of evolution is accepted by every biologist the mode in which it has occurred and the mechanism by which it has been brought about are still disputable.
>
> The only two 'theories of evolution' which have gained any general currency, those of Lamarck and of Darwin, rest on a most insecure basis; the validity of the assumptions on which they rest has seldom been examined and they do not interest most of the younger zoologists.

Such views were widely held by botanists as well as zoologists. D.H. Scott in his Presidential Address to the Botany Section of the British Association in 1921 said,

> There is a strong tendency in these days to admit natural selection only as a 'merely negative force' and as such it has even been dismissed as a truism.
>
> It may be that the theory of natural selection as Darwin and Wallace understood it may some day come into its own again: but in our present total ignorance of variation and doubt as to other means of change we can form no clear idea of the material on which selection has had to work and we must let the question rest. For the moment, at all events, the Darwinian period is passed. We can no longer enjoy the comfortable assurance which once satisfied so many of us that the main problem had been solved. All is again in the melting pot. By now a new generation has grown up that knows not Darwin.

E. W. MacBride,[1] writing in 1927, explained his view of natural selection as 'a purely negative agent': 'it weeds out but does not create; it accounts for the elimination of the unfit, but not for the appearance of the fit.'

The above quotations have come from British biologists but the views involved were widespread and general. Similar comments can be found in the writings of contemporary scientists from North America and elsewhere. For example, in 1926 the American paleontologist, H.F. Osborn, in an article in *Science* entitled, 'The problem of the origin of species as it appeared to Darwin in 1859 and as it appears to us today', concluded, 'The causes of "variation", to use the term (Darwin) employed for the evolutionary process, lie in the way before us. They may be resolved or they may prove beyond human solution.' R.K. Nabours[2] gave frank expression to the general view in 1930: 'We are still in a morass, it may as well be admitted, with regard to the ultimate problems of evolution.'

Amongst the few biologists who accepted natural selection as an agency of adaptive modification—a positive force for evolutionary change—there was often confusion and lack of understanding of the means by which it could work. C. Tate Regan in his Presidential Address on Organic Evolution to the Zoology Section of the British Association in 1925 said, 'I am inclined to accept Darwin's theory as a whole, including both natural selection and the inherited effects of use and disuse, at any rate until some better explanation of the facts is forthcoming.'

Biological variation and inheritance

Confusion as to the role of natural selection in evolution had become widespread among biologists in the generation after Darwin. The basic difficulty was an inadequate understanding of the nature of biological variation. There were really three closely connected problems involved here for what was missing in Darwin's theory of natural selection was (i) a satisfactory distinction between the different *types* of biological variation, especially heritable versus non-heritable and continuous versus discontinuous (or discrete) variation, (ii) a convincing explanation for the *origin* or causes of heritable variation, and (iii) an adequate theory of the *inheritance* of such variation. Darwin had seen that it was essential for there to be heritable variation if evolution by natural selection were to occur. He distinguished between 'individual differences' which were small and occurred frequently and 'sports' which were large and occurred rarely. He suggested that natural selection acts on the individual differences which he thought were mostly heritable. As to the origin of new variation, Darwin imagined that 'changed habits' produced individual differences which were heritable. On heredity, he wrote in the first edition of the *Origin of species* in 1859, 'The laws of inheritance are quite unknown'; in the fifth edition (1869), he replaced 'quite unknown' in this sentence by 'for the most part unknown'.

In 1868, in *The variation of animals and plants under domestication*, Darwin had put forward his 'provisional hypothesis of pangenesis'. This was a vague and speculative proposal to explain the hereditary transmission of individual differences including those caused, as Darwin believed, by environmental effects. Each part of an organism was imagined to throw off small invisible particles called gemmules. These supposedly came together in the germ cells from where they were transmitted to the next generation. Some gemmules, he thought, controlled the development of various parts of the new organism although many remained in a dormant state to be transmitted to the next generation. Although this scheme of inheritance was in a sense particulate, Darwin did not conceive of his gemmules as particles segregating unchanged throughout successive generations. Hybridization, he thought, led to a blending of the parental differences. Pangenesis did not lead to any change of approach in the *Origin* where Darwin in effect accepted the traditional view of heredity as involving a blending of the parental contributions.

Darwin's theory of natural selection had a profound influence on his half-cousin Francis Galton who was intensely interested in variation of all kinds. Seeing the central place which biological variation had in Darwin's theory, Galton carried out a number of investigations into heredity. He soon perceived that Darwin's theory of pangenesis was unsatisfactory. A very important contribution was his demonstration of the role of heredity in continuous variation. In attempting to measure the intensity of heredity in Man, Galton was led to introduce the concept of regression and to develop the analysis of correlations. In this way he helped lay the foundations of biometry. His law of ancestral heredity[3] was formulated in an attempt to predict the average value of a character in an individual from a knowledge of the given character in the ancestors. He suggested that the average contribution of each parent to its offspring is one-quarter or, in other words, that half of the qualities of the child can be accounted for when we know the father and mother; likewise, the four grandparents together contribute one-quarter and so on.

In his celebrated paper of 1865 on experiments in plant hybridization, Gregor Mendel[4] wrote,

> It requires indeed some courage to undertake a labour of such far-reaching extent; this appears, however, to be the only right way by which we can finally reach the solution of a question the importance of which cannot be overestimated in connection with the history of the evolution of organic forms.

Did Mendel appreciate the importance of his particulate theory of heredity in understanding the evolutionary process? Whilst he does not mention Darwin in his 1865 paper, four years later in the paper on *Hieracium*, he refers to 'the spirit of the Darwinian teaching'; he clearly knew of Darwin's work. But can we be sure that he was referring to Darwin's work in the above passage? Fisher evidently thought so. He wrote to D.J. Finney on 19 November 1948,

> Evolutionary problems were, of course, not the subject of Mendel's paper, but as a side issue he points out that the view of inheritance at which he had arrived does

remove one of the principal difficulties which Darwin and others had felt about the theory of selection. Indeed, Mendel was so clear about the theoretical implications of the particulate view of inheritance, that one rather wishes he had written a paper on the theory of evolution.

Mendelism, Darwinism, and biometry

Following the rediscovery of Mendel's paper in 1900, the question as to whether ancestral heredity was consistent with Mendelism soon aroused much interest and controversy. It was not till more than 30 years later that biologists generally came to realize that Mendel's work provided a firm foundation for Darwin's theory of natural selection.

How did it come about that this general understanding of the importance of Mendelism for natural selection took so long to follow the Mendelian rediscovery of 1900? A major reason must be that some of the most influential early advocates of Mendelism were found amongst those who were already opposed to Darwin's theory of natural selection by small variations. In an unfortunate chapter in the history of biology, Mendelism became involved in a bitter controversy as though its principles were basically opposed to natural selection. As Fisher (*CP* 165, 1939) put it,

> The Mendelian discovery, since it embodied some facts unknown to Darwin, was eagerly seized on, and an antagonism between these facts and Darwin's theory was assumed and asserted, though never conscientiously examined. The early advocates of Mendelism, such as Bateson, had already before its discovery embroiled themselves in anti-Darwinian controversy.

In his book, *Materials for the study of variation treated with special regard to discontinuity in the origin of species*, William Bateson had written in 1894 (p. 567), 'the Discontinuity of which Species is an expression has its origin not in the environment, nor in any phenomenon of Adaptation, but in the intrinsic nature of organisms themselves, manifested in the original Discontinuity of variation.' Whereas Darwin had suggested that natural selection acts generally and gradually on small individual differences which he assumed were for the most part inherited, Bateson maintained that the evolutionary process was a discontinuous one which depended essentially on the occurrence of large, definite or discontinuous differences between individuals. It is not altogether surprising then that, when Mendel's work was rediscovered in 1900, Bateson mistakenly seized on the discontinuity in heredity as supporting evidence for his own ideas of the discontinuity of the evolutionary process.

In 1901, Hugo de Vries,[5] on the basis of what he thought were mutations in the evening primrose, put forward a general explanation for the origin of heritable variation which could itself account for evolutionary change. He claimed that species arose by saltations or single large mutations and that the small individual differences observed in natural populations had nothing to do with the origin of species. Although the variants in the evening primrose were later shown to involve chromosomal rearrangements and not mutation at all, de Vries' mutation theory of evolution had a considerable influence on many biologists and it led to a widening of the gap not only between Mendelism and Darwinism but also between Mendelism and biometry. Bateson[6] wrote of de Vries that 'for the first time he pointed out the clear distinction between the impermanent and non-transmissible variations which he speaks of as *fluctuations*, and the permanent and transmissible variations which he calls *mutations*' which are 'those alone by which permanent evolutionary change of type can be effected'. Thus the early Mendelians came not only to regard mutation as involving discontinuous or large differences which determined directly the course of evolutionary change, but also to think of fluctuations or continuous variation as non-heritable.

At the same time a bitter controversy developed in England between the biometricians and the Mendelians over the question as to whether the correlations between relatives could be accounted for in terms of Mendelian inheritance. Karl Pearson[7] and his associates, the biometricians, maintained that the observed correlations for continuous characters could not be accounted for in terms of Mendelism where they assumed complete dominance to be essential. Pearson accepted Darwin's view that evolution proceeded gradually by selection acting on small or continuous differences whereas, as we have seen, Bateson rejected Darwinism and believed in discontinuity in evolution. It thus came about that Mendelism was represented as opposed to both biometry and Darwinism. The feud which developed between the Mendelians and the biometricians had serious repercussions on ideas of the relevance of genetics for an understanding of evolutionary theory well into the twentieth century.[8]

Though G.U. Yule[9] had suggested in 1902 that, with a multiple-factor hypothesis for continuous characters, ancestral heredity was reconcilable with Mendelism, it was not until 1918 with the publication of Fisher's comprehensive paper, 'The correlation between relatives on the supposition of Mendelian inheritance' (*CP* 9), that Mendelism and biometry were brought properly together. In this paper Fisher developed the basic quantitative theory for the analysis of the variation in a population for a continuous character affected by a large number of genes. He took account of the most general assumptions as to the individual peculiarities of the genes (for example, in respect of dominance, gene frequency, and magnitude of the gene effects) and showed that the genetical behaviour to be observed does not become more complex as the number of genes is increased. Fisher established that with such a general system there was very good agreement between the correlations of relatives actually found and those calculated.

He showed how the variance (a term which Fisher introduced with this paper) could be partitioned into heritable and non-heritable fractions and that the heritable variance could itself by analysed into various genetically meaningful components attributable to additive gene effects, dominance, and other genic interactions. This analysis was of particular importance, for selection can act directly only on the additive genetic component.

Whilst the 1918 paper rightly marks the grand synthesis of Mendelism and biometry, and the birth of biometrical genetics, Fisher had already in 1911, at a meeting of the Cambridge University Eugenics Society, pointed out the essential basis for the synthesis of biometric results and Mendelian theory (see *FLS*, p. 1). Fisher's 1911 paper on Mendelism and biometry was not published but at least two typewritten copies have survived; an uncorrected copy is in the Minute Book of the Cambridge University Eugenics Society kept at the office of the Eugenics Society in London, whilst the other is Fisher's corrected copy complete with illustrations and footnotes. We are indebted to Mrs Joan Fisher Box not only for first drawing attention to the existence of this paper but also for giving the corrected copy for safe keeping with the Fisher Papers in Adelaide. This copy has been used for the reproduction included in Chapter 2.

By 1911 Fisher not only appreciated that the results of the biometricians could be accounted for in terms of the simultaneous action of many genes with additive effects, but he also saw the valuable contributions to be made to the study of quantitative characters by both biometrical and genetical methods of analysis. His 1911 paper contains a number of original ideas quite apart from those taken up in the 1918 paper on the correlation between relatives. For example, it is interesting to see the way in which Fisher suggests that the concepts of population genetics can be used in the study of inbreeding. After referring to the large number of dominant defects known in Man, he says that there must be a still larger number of recessive defects 'by one or more of which almost everyone is affected'. He indicates how a knowledge of the frequencies of defective children born to consanguineous unions may be used to estimate the number of recessive genes for serious defects which are carried in the heterozygous state by a healthy member of the population. He also shows that with cousin marriage and uncle-niece unions the probability of any progeny having two genes identical by descent from a gene in a common ancestor is 1/16.

Fisher's 1911 paper is not concerned directly with evolution but it contains a clear reference to the basic relationship of Mendelism and biometry to evolution and to the need to involve population and statistical studies: 'The value of biometrical work is largely due to the fact that the actual evolution of new species in the past is a question of populations, and must have taken place in the way indicated by statistical methods.' In view of this, we may certainly share Fisher's regret, expressed in his introductory remarks, that he has made no mention of de Vries' mutation theory of evolution—even though we might well wonder why he should refer to de Vries' theory at all in a paper on Mendelism and biometry. Perhaps it is significant in this connection that Fisher ends his introductory remarks by saying that his object has been to give a fair view of the merits of the two methods (i.e. Mendelism and biometry) 'whose advocates have shown so little appreciation of the other school'.

Fisher had received no formal education in either of these new disciplines. His undergraduate education at Cambridge was in mathematics and physics but at the same time he maintained and extended biological pursuits begun in his schooldays. After his election to the Royal Society in 1929, Fisher wrote to Arthur Vassal, who had been his biology master at Harrow,

> It would have worked out much the same, I fancy, if I had taken your suggestion and taken biology for Scholarship purposes at school. I still think the scholarship would have been more chancy and I suppose, without being sure, that a mathematical technique with biological interests is a rather firmer ground than a biological technique with mathematical interests, like D'Arcy Thompson.

Joan Fisher Box (*FLS*, p. 19) records how Fisher had excelled at school in biological and physical science as well as mathematics. The choice of some of the numerous books awarded as school prizes reflects his early and developing interest in biology. At the age of 11 he was given E. Stanley's *A familiar history of birds*, and a year later Gilbert White's *Natural history and antiquities of Selborne*, both as prizes for mathematics. His prizes at Harrow include O. Schmell's *Introduction to zoology* and G. J. Romanes' *Jelly-fish, starfish and sea urchins*. In 1909, during his last year at Harrow, Fisher chose for one of his prizes the complete works of Charles Darwin. His choice of these 13 volumes was of special significance. As he later recorded (*CP* 217), 'it was the year in which the centenary of Darwin's birth and the jubilee of the publication of the *Origin of species* were being celebrated'. Later in 1909 when he went up to Cambridge, Fisher eagerly seized on three remarkable books, all published at just that time by the Cambridge University Press: (i) *The foundations of the origin of species: two essays written in 1842 and 1844 by C. Darwin* (ed. F. Darwin); (ii) *Darwin and modern science* (a collection of essays assembled by A.C. Seward); and (iii) *Mendel's principles of heredity* by W. Bateson. Fisher's copy of the *Foundations*, a gift from C.S. Stock, his friend and contemporary at Cambridge, bears the inscription, 'In memory of many delightful conversations on the subject matter of this book, June 1913'. *Darwin and modern science* was given to Fisher as a College prize. Bateson's book he bought as a freshman (see his Bateson Lecture, *CP* 248, 1951). Another book published in 1909, which seems also to have come under Fisher's early scrutiny, was W.C.D. and C.D. Whetham's *The family and the nation*, which emphasizes the selective effect of differential birth-rates, a subject to which Fisher himself later attached much importance.

To judge from his 1911 paper on Mendelism and biometry, Fisher's knowledge of heredity at that time was determined to a very large extent by his reading of Bateson's book. Bateson, who had been appointed as Professor of Biology at Cambridge in 1908, was in the forefront of workers in 'genetics', to use the name he had himself chosen for the new discipline in 1905. There can be little doubt that Fisher would have noted with ready approval Bateson's statement on p. 288. of his book that, 'With the discovery of the (Mendelian) factors precise analytical treatment can at length be applied to the problem of Evolution.' On the very next page, however, Bateson says, 'The conception of Evolution as proceeding through the gradual transformation of masses of individuals by the accumulation of impalpable changes is one that the study of genetics shows immediately to be false.' The reference to evolution in Fisher's 1911 paper suggests that he had by then seen not only that Bateson's position on this last point was wrong, but also how Mendelism and Darwinism would have to be brought together in a quantitative theory of natural selection. Fisher's introductory remarks suggest that he also saw that it would be difficult to obtain a fair view of the matter in the controversial atmosphere for which Bateson and Pearson were largely responsible.

In 1910 Bateson left Cambridge to become the first Director of the John Innes Horticultural Institution and his colleague R.C. Punnett was appointed as Professor of Biology in his place (the title was changed to Genetics in 1912). Punnett had been a Fellow of Caius College since 1901 and in 1911 he must have known Fisher, not only as a Caius Scholar, but also as one of the small group responsible for the formation of the Cambridge University Eugenics Society, a fellow Council member of the Society, Chairman of its undergraduate committee, and the author of original ideas on Mendelism, biometry, and evolution. (Like Fisher after him, Punnett was a Scholar and then Fellow of Caius College, and also Professor of Genetics at Cambridge.) In 1911 Punnett was only 36 years old and it may well be that Fisher was thinking of the possibility of new and exciting developments for genetics and evolution in Cambridge following Bateson's departure. If these were Fisher's dreams it must have soon become clear that they were not to be realized. In 1915, when Punnett's book *Mimicry in butterflies* was published by Cambridge University Press, it included a mutationist's explanation for the evolution of complex mimetic resemblances between members of unrelated species. The evolution of mimicry was later described by Fisher as the greatest post-Darwinian application of natural selection.

Punnett's references to selection in his book on mimicry are of particular interest. Central to his discussion is an appendix with a table (prepared by

H.T.J. Norton) showing the numbers of generations required for various selective intensities (0.50, 0.25, 0.10, and 0.01) to bring about given alterations in the frequencies of the three genotypes in a dimorphic population mating at random. Punnett commented (p. 96), 'it is remarkable in how brief a space of time a form which is discriminated against, even lightly, is bound to disappear. Evolution, in so far as it consists of the supplanting of one form by another, may be a very much more rapid process than has hitherto been suspected, for natural selection, if appreciable, must be held to operate with extraordinary swiftness where it is given established variations with which to work.' Punnett referred to evidence from the study of melanism in the peppered moth *Biston betularia* in some parts of England as confirmation that such rapid changes in the constitution of a dimorphic population exhibiting Mendelian heredity do take place and he concluded that the melanics must have some selective advantage over the pale form. He also mentioned the experience of breeders who found that melanics were 'somewhat hardier, at any rate in captivity'. After suggesting that 'it is not at all improbable that the establishing of a new variety at the expense of an older one in a relatively short space of time is continually going on', Punnett wrote, 'a census of a polymorphic species, if done thoroughly, and done over a series of years at regular intervals, might be expected to give us the necessary data for deciding whether the relative proportion of the different forms was changing—whether there were definite grounds for supposing natural selection to be at work, and if so what was the rate at which it brought the change about.' Punnett's book is thus noteworthy for calling attention not only to the remarkable efficacy of selection as a factor for change in a population involving what E.B. Ford later called *transient* polymorphism, but also to the value of regular field surveys in such a situation. That these interesting early suggestions on selection by Punnett have not received greater recognition may, perhaps, be due to the curious circumstance that he included them in his book in support of his mutationist explanation of mimicry. As no rapid change had been recorded in the frequencies of the different mimetic forms in the various populations under observation, Punnett suggested that natural selection must be non-existent in this case. In fact, as Fisher showed in 1922 (*CP* 24), a quite different situation exists with a stable selectively balanced polymorphism, as when selection favours the heterozygote, the genetic composition of the population being maintained unaltered from generation to generation. Then the stability of the gene ratios of factors controlling the polymorphism could be seen as implying not the absence of selection, as Punnett had imagined, but the existence of selective differences (possibly large differences) between the different forms. In 1927, Fisher (*CP* 59) suggested not only that polymorphic mimicry in butterflies was an example of such a selectively balanced equilibrium but also that the polymorphism could itself undergo evolutionary development by the selection of modifying factors. The twin concept of allelic genes acting to switch on one or another of the possible alternatives in a polymorphism and of the alternatives themselves being subject to modification by selection in the course of evolution were entirely novel in 1927. These suggestions were later confirmed by field and laboratory studies.

Fisher's view of the role of selection in the maintenance of balanced polymorphisms represented a marked change not only from Punnett's approach but also from Darwin's attitude to common differences. In Chapter II of the *Origin*, Darwin refers to an 'extremely perplexing' point concerning species presenting 'an inordinate amount of variation' and he suggests these are variations 'which are of no service or disservice to the species and which consequently have not been seized on and rendered definite by natural selection'. Again, in Chapter VII of *The descent of man,* he says, 'The great variability of all the external differences between the races of man ... indicates that they cannot be of much importance; for if important, they would long ago have been either fixed and preserved or eliminated.' He then refers to polymorphic forms 'which have remained extremely variable, owing, as it seems, to such variations being of an indifferent nature, and to their having thus escaped the action of natural selection'. With blending inheritance, common differences maintained in a population could only be seen as selectively neutral. Fisher's demonstration in 1922 that a polymorphism can result from a balance of selected forces was important in showing that selection can maintain genetic variation in a population with a constant homogeneous environment.

Norton's table in Punnett's book provided an early demonstration of the value of a mathematical treatment of the effect of selection in population genetics. Both J.B.S. Haldane and the Russian geneticist S.S. Chetverikov acknowledged the stimulus it supplied when they began their work in population genetics. Norton was a mathematician who during the period 1910-15 was a Fellow of Trinity College, Cambridge. He worked on various problems in population genetics but it seems his only publication was his 1928 paper,[10] 'Natural selection and Mendelian variation', describing work he had completed many years earlier. It is interesting to speculate on what the early development of genetics at Cambridge might have been like if Punnett had sought the mathematical assistance he needed from Fisher rather than Norton. Perhaps it was Punnett's friendship with the mathematician G.H. Hardy of Trinity which led to Norton being asked to consider genetical problems. We know that in 1908 Punnett had taken the problem of the genotypic frequencies to be expected in a random mating population to Hardy who as a result published his note,[11] 'Mendelian proportions in a mixed population'. Fisher apparently did not know about Norton or the work on which he was engaged in Trinity, right alongside Caius; he wrote to R.F. Harrod in 1951 that he had not heard of Norton till he read about him in Harrod's book[12], *Life of John Maynard Keynes.*

Fisher's early interest in and original approach to the evolutionary process are clearly evident in a number of his writings apart from the 1911 paper on Mendelism and biometry. For example, in his 1912 paper on Evolution and Society (see p. 58), he considers the possibility of selection acting generally on *any* entities having the properties of variation and heredity; after discussing the co-ordination of individuals into groups or societies, he touches on the evolutionary problem presented by altruism. In 1916, commenting upon an article by W.E. Castle entitled, 'Is selection or mutation the more important agency in evolution?', he wrote, 'Mendelian characters take their place within the Darwinian scheme; they can be modified by selection and no doubt have come into existence by that agency.'[13] Apparently Fisher was already thinking of Mendelian characters as the product of previous selection in the gene-complex. This was a remarkable departure from the generally accepted view. Had not Bateson[14] written in 1909 that the order in heredity 'cannot by the nature of the case be dependent on Natural Selection for its existence, but must be a consequence of the fundamental chemical and physical nature of living things'? In 1920, at the end of a review of H.J. Muller's 1918 paper on balanced lethals, Fisher raised the possibility of the evolution of a co-adapted gene complex; 'The process of evolution would seem to require that selection should act separately upon many minute variations, but as soon as mutual adjustment and adaptation is obtained, it might thereafter be advantageous if the whole group were cemented into a single factor.'[15] Reviewing *The relative value of the processes causing evolution* by A.L. and A.C. Hagedoorn, Fisher (*CP* 17, 1921), wrote, 'The whole process is worthy of a thorough discussion, but the authors evidently lack the statistical knowledge necessary for its adequate treatment.' Fisher's two papers, 'On the dominance ratio' (*CP* 24) and 'Darwinian evolution by mutations' (*CP* 26), both published in 1922, mark the start of his thorough quantitative discussion of the evolutionary process, a work which went on growing and led ultimately to the production of *GTNS.*

Major Leonard Darwin and the Eugenics Society

By 1911 Fisher had clearly seized on the essentials of both biometry and Mendelism and saw the important role which both of these disciplines were destined to play in developing a proper understanding of natural selection. It was natural that he should follow these ideas through to questions of ultimate human concern. Mankind was becoming responsible for the future course of human evolution. The recognition of excellence and its promotion for future generations were clearly most important. What could an understanding of Mendelism, biometry, and natural selection contribute to a discussion of the future path of human evolution?

The improvement of the biological inheritance of man, or eugenics as Galton called it, was a subject that attracted increasing attention in the years following the Mendelian rediscovery in 1900. Galton not only had arranged for the establishment of a Eugenics Laboratory at University College London and financed the appointment of a Research Fellow but also, on his death in 1911, he left an endowment for a Chair in Eugenics with Karl Pearson designated as the first incumbent. A separate organization, the Eugenics Education Society (later called the Eugenics Society), was formed in London late in 1907 with the object of spreading a knowledge of eugenics and the laws of heredity among the public; shortly afterwards Galton became its President. The Cambridge University Eugenics Society was set up in 1911 with the aim of increasing the awareness of eugenics and heredity in members of the University; its Council included A.C. Seward[16] (President), Horace Darwin, R.C. Punnett, W.C. Dampier Whetham, J. Maynard Keynes (treasurer), C.S. Stock (secretary), and Fisher. The First International Eugenics Congress was held in London in 1912 with Leonard Darwin as president; Fisher attended as a steward. The two men had met before this in Cambridge but it was perhaps at the London Congress that Fisher had his first opportunity to appreciate fully the unusual qualities of Leonard Darwin. A man of exceptional character, intellect, and background, Darwin soon came to exert a profound influence on Fisher's life and work.

Leonard Darwin (1850-1943) was the second youngest and the longest surviving of Charles Darwin's five sons. For 20 years in the Royal Engineers he was engaged mostly with teaching and administration but also occasionally as a member of scientific expeditions. He resigned from the army at the age of 40 with the rank of Major, and then entered public life, serving for three years as a member of the House of Commons. Shortly after Galton retired as President of the Eugenics Education Society in 1909, Leonard Darwin succeeded to this office. In this position he found when he was over 60 that he was at last doing work which he felt to be of importance. For 18 years as president he devoted all his energies to the welfare of the Eugenics Society.

Leonard Darwin was, by all accounts, a remarkable man. Sir Arthur Keith[17] has written of him, '... in physical appearance, ... in his attitude to life and in the disposition of his mind he bore a closer resemblance to his father than did any of his brothers. He had his father's honesty of expression, openness of mind, charitable disposition, subjection of self, an excess of candour, and also his father's happy sense of humour. He was completely devoid of personal ambition.' Gwen Raverat, in her enchanting book, *Period piece*, about life in the Darwin family, includes the following verse on 'Uncle Lenny':

> Serenely kind and humbly wise,
> Whom each may tell the thing that's hidden,
> And always ready to advise,
> And ne'er to give advice unbidden.

When, shortly after Leonard Darwin's death, another niece, Margaret Keynes, sent Fisher a copy of a memoir she had written about her uncle, Fisher in writing to her said, 'My very dear friend Leonard Darwin ... was surely the kindest and wisest man I ever knew.'

Fisher acknowledges his indebtedness to Darwin in several of his early papers (*CP*9, 10, 70). His study of the correlation between relatives (*CP*9) was first undertaken, he says, at Darwin's suggestion and it was to Darwin's 'kindness and advice' that it owed its completion. *GTNS* itself was dedicated to Darwin 'in gratitude for the encouragement given to the author during the last fifteen years by discussing many of the problems dealt with in this book'. The advice and encouragement of Charles Darwin's son Leonard must have provided a powerful stimulus for Fisher to press on with the big job of work involved in laying the foundations for the neo-Darwinian synthesis.

From 1915 for about 20 years, Fisher and Darwin met and wrote to each other frequently, exchanging their views on natural selection, heredity, eugenics, and many other questions. During much of this time they corresponded with one another every few days. Fisher kept most of the letters which Darwin sent him. He also kept carbon copies of the typewritten letters which he sent Darwin from about 1928 onwards. Unfortunately, Fisher's earlier handwritten letters to Darwin, which would be of the greatest interest, seem not to have survived. Sometimes, however, it is possible to catch a reflection in Darwin's letters of ideas and suggestions which Fisher must have introduced previously.

Darwin's earliest letters in 1915 set out various problems which he hoped Fisher would solve; these are concerned mostly with biological variation and inheritance, Galton's law of ancestral heredity, parental correlation and regression, as well as natural selection and mutation. Darwin said he was 'building up ideal conditions and seeing how far they work like nature does work'. He was especially anxious to know if Galton's work on ancestral heredity could be given a Mendelian interpretation. In 1902, Bateson[18] and Weldon[19] had each suggested that Mendelism and ancestral heredity were inconsistent. Yule[9] had criticized this view and suggested instead that Mendelism and ancestral heredity were 'perfectly consistent the one with the other and may quite well form parts of one homogeneous theory of heredity'. This problem must have come forcefully to Leonard Darwin's attention in 1914 when his brother Francis[20] gave the first Galton Lecture before the Eugenics Education Society. Francis said that Mendelism requires that we 'look at variation in a very different way to that of Galton' and that whilst 'a progressive study of heredity must necessarily be on Mendelian lines', it 'does not follow that the laborious and skilful work of Galton and his school is wasted'. Biometrics, he said, 'may illuminate a problem which cannot as yet be solved in Mendelian fashion'. Leonard apparently judged that Fisher could provide the light that was needed. From 1915 onwards, he unfailingly gave stimulus, support, and encouragement to Fisher for his mathematical studies of biometry, heredity, and selection, constantly plying him with questions and suggestions, and sending various notes and papers of his own on evolution with requests for Fisher 'to pull them to pieces'. Fisher was always glad to hear Darwin's ideas, for as he once wrote, 'I have been learning bit by bit that there is generally the germ of something uncommonly well worth thinking about in what you say.' After receiving Fisher's detailed counter-notes to his suggestions, Darwin sometimes referred to his difficulty in 'sucking the whole juice' out of Fisher's letters, and to his concern that Fisher took so much trouble and treated his suggestions so seriously.

Some of Darwin's early letters show the kind of clarification which he thought was needed in the ideas surrounding biological variation. Others show how he was ready with wise counsel when Fisher encountered difficulties in getting his papers published. This had some important consequences. For example, we can see that it was only because of Darwin's interest, initiative, and support that Fisher's big paper on the correlation between relatives, after having effectively been rejected by the Royal Society of London in 1916, was published by the Royal Society of Edinburgh in 1918. In August 1920, when Fisher's paper, 'On the probable error of a coefficient of correlation deduced from a small sample' (*CP* 14), was refused publication in *Biometrika* and then in the *Journal of the Royal Statistical Society,* Darwin wrote at once with helpful advice. Early in 1923, when Darwin agreed that the Royal Statistical Society had treated Fisher badly in refusing to publish a paper on χ^2, he wrote to Fisher, 'You may well feel that I preach to you unwarrantedly but please remember it is friendship to you which makes me risk annoying you'; he urged Fisher to 'push on quietly avoiding as far as possible all controversy'. Darwin said that at home he was brought up to believe controversy with individuals was a great waste of time and should be avoided. Here and elsewhere in Darwin's letters, we find ourselves reminded of his father, if not explicitly, then perhaps by the ideas or sentiments expressed or by the use of a particular turn of phrase. Sometimes we find Fisher urging Darwin to try and recall his father's spoken words, 'especially when explaining his dissent from some view which he felt, rather than saw, to be unsound'. The Darwin-

Fisher letters thus shed light not only on the development of Fisher's thinking in natural selection and related areas, but also to some extent on Charles Darwin's writings and ideas. They also reveal the growth of the fascinating friendship which developed between these two exceptional men—Leonard Darwin, President of the Eugenics Society, himself with two happy but childless marriages, and Ronald Fisher, 40 years younger, initially an unknown and rather isolated schoolmaster, producing brilliantly original papers which could not be published in England because of opposition from the leading authorities in biometry and genetics. For Fisher the friendship with Darwin, with his close links with Charles Darwin and Francis Galton, had special significance. It seems that Darwin soon became as a revered father whose counsel on many questions was eagerly sought and always greatly respected. Darwin's nobility of character, his modesty, and charm shine through his letters. He repeatedly excuses himself for being 'muddle-headed' and 'stupid about mathematical things'. His letters to Fisher were, he said, an opportunity to 'let off steam'—'I like blowing off steam to you and expect you to take *no* notice of it.' The Darwin-Fisher letters were certainly not written with an eye to posterity or publication. They were exchanges between trusted friends who knew well how to receive them. They are, however, full of good things and are of interest not only for the scientific content but for the stimulating discussion of a great many general questions as well as for the personal touches and expressions of humour. There are fascinating exchanges on chance, indeterminism, and free will, the economic and social order, family allowances, tropical agriculture, food production, the level of population, and many other questions of lasting interest. Darwin wrote that he always liked getting Fisher's letters because they made him *think*. He once summed up his feelings on receiving a letter from Fisher as 'somewhat like that of a pig genuinely admiring a necklace of pearls, but not knowing quite how to put it on and feeling sure that he had not deserved such a present'. There are indeed many gems in this correspondence and much to make the reader *think*.

From 1914 onwards, Darwin encouraged Fisher to write reviews, mostly of biological books and articles, for the *Eugenics Review*, a quarterly journal published by the Eugenics Society. Fisher no doubt appreciated the ready access to genetical and other literature thus provided. Over the next 20 years he published about 200 reviews in this journal. During much of this time Darwin was president of the Society and Fisher was an honorary secretary. It seems that one of Fisher's major objectives in his work with the Society was to get it re-organized as a predominantly scientific body. He wished to see it encouraging and promoting scientific research in human heredity. There is an interesting exchange of letters with Darwin on this theme in October 1930 when Fisher was exploring the possibility of diverting funds from publicity into research. Fisher wrote that he was concerned to answer the question, 'Are there any ways in which I can do good through my connection with the Society?' Fisher's concern on this score seems to have grown as Darwin's influence on the Society diminished. Darwin retired as president in 1928, and before long, Fisher became increasingly disillusioned with those who took control. Writing to Darwin on 16 November 1933, he referred to 'the small group of non-scientifics who control the Society' and said he was 'more than ever convinced that Eugenics will make no progress ... unless it has widespread sympathy and some active support from professional men of Science.' Fisher was then a vice-president of the Society and his recent appointment to the Galton Professorship as Pearson's successor had given Darwin much pleasure. When Pearson was in charge of the Laboratory, relations with the Society were badly strained. Fisher tried to encourage co-operation between the two groups. Shortly after he took over from Pearson, the Society agreed to share the cost of publishing the Laboratory's *Annals of Eugenics*; from 1934 till 1941, the *Annals* was issued jointly by the Laboratory and the Society. Pearson's subtitle for the *Annals*, a journal 'for the scientific study of racial problems', was replaced by Fisher's new description of it as one 'devoted to the genetic study of human populations'. Fisher had helped prepare the Society for the opportunity to support a journal of human heredity. In December 1932, the Society's council had agreed to take the initiative in forming 'a non-propagandist organization to study human heredity' and its Human Heredity Committee had been authorized to enquire into the financial aspects of initiating and running a journal devoted to this subject. When Fisher became Galton Professor and editor of the *Annals*, the Society dropped these plans and supported the *Annals* instead. In 1934, Fisher persuaded the Society to support post-graduate research by funding studentships in honour of Leonard Darwin. Several of these were later awarded to individuals who worked in the Galton Laboratory.

The Eugenics Society was able to greatly extend its financial commitments at that time because of a large bequest from Henry Twitchin. For about six years before his death in 1929, Twitchin, a grazier in Western Australia, had been giving £1000 annually to the Society to help it extend the knowledge of eugenics among the general public. During those years, Darwin helped maintain Twitchin's interest in the Society by writing to him about its work and occasionally meeting him or his solicitor in London. Twitchin[21] died on 19 March 1929, leaving an estate valued at about £80 000 to the Society. This bequest not only made possible a much larger annual expenditure but also led to increased discussion about the Society's programme. It is against this background that we should see Fisher's letters to Darwin in October 1930 pressing the case for the Society to fund research in human heredity. Though Fisher failed in 1930 to win Darwin to the view that Twitchin money should be used to support research, in particular on human blood groups, yet by 1934, as we have seen, he had gained Society support for funding research scholarships and sharing the costs of publishing the *Annals*. However, by a strange irony, Fisher came to feel at about that time that those who had gained control of the Society were 'almost without eugenic knowledge or ideas'. C.P. Blacker had become general secretary of the Society in 1931 and, with his active encouragement, Society funds went more and more to support work on chemical contraception, whilst the grant in support of the *Annals* was gradually reduced and finally removed altogether. Writing to P.F. Fyson in September 1938, Fisher said the directors of policy in the Society were strongly entrenched and 'almost impervious to scientific advice'; he had therefore not attended the Council for some years though he had allowed his name to remain as vice-president. After 1937 Fisher was no longer vice-president; he remained a member of the Society's council till 1942 but apparently attended no meeting in this period. He resigned from the council in 1942, shortly before Leonard Darwin's death. Fisher's involvement with the Eugenics Society over many years seems to have derived much of its strength from the close bond he had formed with Darwin and it did not last long after Darwin's strong influence on the Society came to an end.

All the evidence from Fisher's published work, his biography, and his correspondence, shows, I believe, that his biological interests were primarily in natural selection (which had aroused his interest at school), secondly in heredity (which had stirred his imagination as a freshman at Cambridge in 1909), and that, from these, stemmed his interests in human heredity and eugenics. After he was awarded the Darwin Medal of the Royal Society in 1948, Fisher wrote to D.J. Finney that this was 'an immense satisfaction ... as I have worked for a good many years, and indeed saw the need nearly forty years ago, to reverse the trend then prevalent of misrepresenting and minimizing the importance of Darwin's achievement'. Recently, however, several writers have proffered a different view of Fisher's priorities and aims in his biological work, based upon a sociological or ideological approach. B. Norton[22] has written about the neo-Darwinian synthesis, 'Fisher's decision to become involved in this sort of work has remained somewhat mysterious'; he then suggests that the 'mystery' would be removed if one were to accept his belief that 'Fisher's problems were ideological rather than biological'. The classic 1918 paper on the correlations between relatives (*CP* 9) should now be seen, Norton says, 'predominantly as a contribution to the hereditarian social ideology of eugenics'. According to Olby,[23] 'Fisher was both a eugenicist and a Mendelian biometrician but not an evolutionary biologist', while MacKenzie[24] believes Fisher 'sought not to *reconcile* Mendelism and biometry but to *use* Mendelism to vindicate biometric eugenics'. I hope that the contents of this volume will help readers in judging what weight should be given to these different views.

The writing of *GTNS*

The first indication that Fisher was writing a book on selection occurs as early as 1919 when he prepared several chapters dealing with the selective situation in Man. Although never completed it was probably a useful preparation for the writing of *GTNS* ten years later. In August 1919, Darwin wrote, 'it wants more orderliness. It is worth taking great pains with your first book, even though a book is an awful grind. ... You must not take your facts only when they fit your theories and neglect theoretical conclusions when facts are not available.' In some respects, Darwin seems to have filled a role not unlike that of a research supervisor. Over several years, he tried to stir Fisher 'to write a great work on the mathematics of evolution'. In August 1921, he told Fisher that papers are of comparatively little use in permanently affecting opinion and that he hoped 'when you are fully ready—not before—you will put your ideas into a book'. He kept returning to this point urging Fisher on at a time when the leading biologists saw no need or place for mathematical arguments. A few years later Darwin wrote, 'You will have a small audience, but it will gradually be realized that many of these problems [of selection] can be attacked in no other way.' In 1928, when Fisher began to put together material for *GTNS*, he lost no time in seeking Darwin's comments, especially on his reconstruction of Charles Darwin's arguments which was to have an important place in his first chapter.

Except for the mathematical chapters (IV and V), the whole manuscript of *GTNS* was written out by Mrs Fisher at Fisher's dictation between October 1928 and June 1929. Fisher's letters to Darwin at this time tell us about the author's attitude to the work in progress. On 13 November 1928, after thanking Darwin for the care he had given to reading Chapter I, he wrote, 'I wish I could believe it was worth the trouble. I have decided to write on, sometimes ahead of my convictions, with a view to subsequent careful revision, which I hope may be less difficult than making a fresh start.' On 18 February 1929, when sending Chapters IV and V, he wrote, 'I have made an abominable mess of the whole thing and failed to get out an adequate solution of nearly all the problems, but I hope that it may at least show what further work is needed.' Darwin replied, 'if you have not covered the whole surface, it is because the ground is very very stiff. In pioneer work of this kind, no one can be expected to solve all the problems.' Within a few months, Fisher had done much of the further work needed and in October 1929 he was able to incorporate it in Chapter IV. As Fisher recorded both in *GTNS* (p. 95) and *CP* 86 (p. 458), during 1929 he had received from Sewall Wright in manuscript a study in which 'while confirming many other conclusions of my [1922] paper [*CP* 24], he arrives at a time of relaxation of only $2n$ generations' instead of $4n$ and this 'has led to a more exact examination of the whole problem.'

On 19 March 1929, when sending Darwin the first of the chapters on Man (Chapter VIII) Fisher wrote, 'I do not expect you to agree that I am necessarily right about Man, but only that I am approaching the subject in a rational spirit.' It was to be another three months before the further chapters on Man were finished, and by then, on the basis of what they had seen of the early part of the book, the Clarendon Press, Oxford, had agreed to publication.

Although Fisher viewed his deductions regarding Man as 'strictly inseparable' from the more general chapters, he was concerned that the publishers, who had agreed to publication after seeing only Chapters I-VIII, might view Chapters IX-XII rather differently. When sending the final chapters on Man, he therefore told them that they must feel perfectly free to change their mind about publication. Their reply, however, was quick and encouraging. They recognized Fisher's quantitative genetical theory of natural selection as an outstanding and lasting achievement. But they also saw that the book would require a considerable effort from the reader. They no doubt paused at some of the long, complicated sentences—sentences which had led Darwin to recommend to Fisher 'one idea—one sentence' as a good rule to follow. The letters which passed between Fisher and Kenneth Sisam of the Clarendon Press show not only the encouraging responses and the helpful suggestions of the publishers, but also the author's characteristic reactions to the particular questions raised.

K. Sisam to Fisher: 13 May 1929

Our representative, Mr. Crowther, has safely delivered to us part of your MS. in which you examine statistically the theory of natural selection, etc. Our advisers are very much interested, and it would help me, for short reference, if you could give me an idea of the title you propose (which ought to be explicit). From reading a little of the MS., I assume that you would preface it by an introductory chapter on aims and methods, and I understand that the chapters on Man are still to be completed. I have not yet had time for a detailed report from our advisers, but I am sure the Delegates will be interested in this new method of approach.

Fisher to K. Sisam: 14 May 1929

I should call the book something like

THE GENETICAL THEORY OF NATURAL SELECTION

I cannot easily get the words statistical or mathematical into the title, but genetical is essential. My impudence in treating the subject as a branch of mathematics, I must justify in a preface; very short and historical, was my intention, not dealing there with methods, and only hinting at aims.

There will be four or five chapters on Man as the subject is generally shirked by geneticists, and I know of no historian who knows what Natural Selection means.

K. Sisam to Fisher: 28 May 1929

Our advisers have now had an opportunity of reading the chapters of *Natural selection*, which they find full of good things. They urge two points very strongly in the interest of the book:

(1) That the Introduction on its scope and results should not be too brief or too stiff.
(2) That, as the text at present is decidedly hard reading, it would be improved if you could get a comparative layman in the subject to go over it, and if you could then meet his difficulties. They do not suggest that the book could be make intelligible to a person who knew no mathematics, but they think that the exposition could sometimes be easier without loss of accuracy. The matter itself they consider well chosen.

In its present form the book would be very useful to specialists; but—though it could never be 'popular'—the circle of readers would be increased considerably (especially in America) if the treatment were simplified in hard places, so as to bring more of it within reach of those not highly equipped already.

These are suggestions for making the book more successful, which would be in your interest and ours. But if you say the present treatment is the only one possible to you, we should still be ready to publish for the narrower group of specialists only. ...

I hope this will enable you to go on and finish the work, which will, we are sure, be of great value to biologists, not many of whom have the full command of statistical method.

Fisher to K. Sisam: 31 May 1929

Many thanks for your letter of May 28. I shall do my best to improve the presentation in the way you suggest, though of course most of what you say is so probably true that I have worried about it a good deal already. ...

I want to get a largish class of biological teachers who often do not know what to say about the present position of Selection Theory, and in consequence say nothing to the point.

Fairly large print is a real antidote to stiff reading, though of course I must do my best too.

K. Sisam to Fisher: 4 June 1929

Thank you for your Preface; I shall take advice upon it. I am afraid we did not keep notes of particular passages, but our advisers did feel that in the interests of brevity, you plunged into the middle of the subject, and that an introductory guide to the purposes of your research would help a reader to follow. ...

K. Sisam to Fisher: 24 June 1929

We find, and our advisers find, your Preface interesting and original, though we still think that a little more explanation of the scope of the work is desirable, even if it is only a single paragraph. At least we suggest that each chapter should have a short summary heading, indicating the thread of its content. You see, our whole concern is to help the reader to follow your argument easily, instead of having to double back on his tracks in order to pick up points he has missed at the outset.

I am returning the Preface, and we shall be very glad to set to work upon your completed MS. ...

Fisher to K. Sisam: 25 June 1929

I have now completed the part on Man and it comes to 5 chapters (VIII to XII). I will send them when I have the MS in order (quite soon).

I am conscious that the Chapters on Man will, from your point of view, tend to alter the character of the whole book, and I want you to feel perfectly free to change your mind about publication. In particular I had great hesitation in writing Chapter XII at all, and would willingly stop at the end of Chapter XI, if it seemed at all possible.

I think the provision of contents at the beginning of each Chapter is an excellent suggestion. I have also selected quotations for most of them.

I think two colour plates should be enough, but will put the point to Poulton.

K. Sisam to Fisher: 1 July 1929 [sic]

Thank you for your letter of 27th June with the good news that your chapters on Man are complete. We shall look at them with interest when they come, but on the whole our nerves are strong and I hope no reasonable and well-based position will lead us into difficulties. If we have any suggestions, I shall let you know as soon as possible after the MS comes in. But I hope that we shall be able to proceed with the composition almost at once.

K. Sisam to Fisher: 25 July 1929

Thank you for your letter of 22nd July, in accordance with which we have returned Chapter VII for revision.

So far we are brave enough for the later chapters, but in order to save time we are having them set straight up into slip proofs, without previous reference to our official advisers, and it is just possible that they may have some suggestions to make. To me personally your latter chapters were of very great interest, and I know no reason why biologists should not consider the ultimate ends of their science.

Fisher to K. Sisam: 27 July 1929

Thanks for your letter. I am glad you are not prostrated. We have had no contract yet, but I suppose you will send one, when you have been more fully advised.

Fisher to K. Sisam: 15 October 1929

I send herewith corrected galley proofs completed, and have indicated the positions of Figs. 6-11. The first five are in the part you already have, and I think their positions are clear. The end of Chapter IV has been rewritten, and the new versions of Figs. 6 and 8 will follow soon. I have not yet heard, however, of further progress with colour plates.

I am exceedingly sorry to have to make a big alteration at this stage, which is in every sense due to my own fault. I became convinced that my mathematical treatment was all wrong, and I am lucky to have the chance to put it right. Of course I must pay for it.

Fisher's choice of title for his book was doubly significant. It served not only to direct the attention of biologists back to the theory of natural selection as the mechanism of evolution but also to emphasize the genetical basis for this theory. Fisher had rethought the whole of Darwin's theory in terms of genetics. In *GTNS* the theory of natural selection was considered for the first time on its own merits. The work of biologists during the 70 years after publication of the *Origin* had thrown very little light on the evolutionary process. Natural selection was neglected or ignored. Leonard Darwin himself had written at the start of his *Organic evolution*[25] that 'evolution is the great thing, not natural selection' and he even suggested 'if a recollection of about 50 years standing may be trusted', that his father had once expressed this view. Fisher gently revealed his response to this when writing to Darwin on 28 March 1929: 'I am particularly anxious to avoid misrepresenting your father's views; though I do not agree in emphasis with the earlier pages of *Organic Evolution*. *If* Lamarckism had seemed acceptable I think it would have done all that your father said about Natural Selection and would therefore have been as important as Natural Selection really is. To me it all hangs on the if.'

When *GTNS* appeared in April 1930, Fisher promptly sent copies to a number of friends. Included amongst these was James Davidson, an entomologist and a former colleague at Rothamsted who had taken up a post at the University of Adelaide. From the covering letter which Fisher sent him, we can catch a glimpse of what the Rothamsted fellowship, at once stimulating and congenial, had meant to the author when considering the problems dealt with in *GTNS*. During the previous ten years as statistician at Rothamsted, Fisher was daily in close touch with some very able research biologists. The role of natural selection in evolution must have come into a number of their discussions. It was, no doubt, after one such discussion that Davidson tried to get Fisher to talk at the 1925 meeting of the British Association for the Advancement of Science when Tate Regan gave his presidential address to the Zoology Section on Organic Evolution, but Fisher says he 'funked it quite shamelessly'. However, Regan's Lamarckian conjectures to account for some observations on vertebra numbers in fishes aroused Fisher's interest. In 1927, the year in which Regan became Director of the British Museum of Natural History, Fisher sent him an alternative interpretation involving selection. This correspondence, which apparently made no impression on Regan, is of special interest because it contains the first known outline of the argument which later became the subject of Chapter I of *GTNS*.

Some features of *GTNS*

The first two chapters of *GTNS* were considered by Fisher to be the most important. Chapter I involves a comparison of the consequences of blending and particulate inheritance for the theory of natural selection. With the traditional blending theory accepted by Charles Darwin, heritable variation is shown to be rapidly dissipated, whereas with Mendelian or particulate inheritance it is conserved. With particulate inheritance the mutation rates needed to maintain a given amount of variation are therefore considerably smaller than those required with blending inheritance, where new variation would have to be snapped up by selection within a few generations before it disappeared. Fisher suggests that it was because Darwin accepted the logical consequences of blending inheritance that he was led into considerable speculation as to how new variability could be generated. Although Darwin thus came to believe that increased food and changed conditions were causes of variation, he was clear that, as regards evolutionary change, such factors were unimportant compared with selection. Fisher supports his contention by a masterly reconstruction and analysis of Darwin's reasoning, based largely on the rough essays of 1842 and 1844.

Darwin's essays were published in *The foundations of the origin* in 1909 and we know that Fisher studied them carefully when he was a student at Cambridge. A suggestion from Leonard Darwin may have provided the stimulus for Fisher to undertake his reconstruction of Charles Darwin's reasoning. He wrote to Fisher in the autumn of 1926 that his father's extremely modest nature led him to pay too much attention to criticism and therefore his earlier opinions should perhaps be given not less but more weight than the later ones. The analysis which Fisher carried out shed light not only on Charles Darwin's concern with new variation and especially with environmentally induced modification but also on the early Mendelians' view of the role of mutation in evolution. He alluded to these two aspects through the quotations he inserted below the heading to Chapter I.

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 (C. Darwin, 1856).

As Samuel Butler so truly said: 'To me it seems that the "Origin of Variation", what ever it is, is the only true "Origin of Species".' (W. Bateson, 1909).

The first quotation indicates that although Darwin believed that almost every individual must involve new variation (or mutation as we would now say), he nevertheless drew a sharp distinction between the origin of variation and the origin of species. The second quotation shows that over half a century later Bateson was proclaiming that the origin of species was the same as the origin of variation. As Fisher (*CP* 279) later commented, Darwin 'showed a deep understanding in resisting the easy notion that evolutionary progress was, so to speak, worked by mutation'.

These carefully chosen quotations placed in thought-provoking juxtaposition at the start of the book seem particularly apt when one considers that the introductory chapter contains a comprehensive discussion showing that the bearing of Mendelian inheritance on evolutionary theory is indeed the opposite of that which the pioneers of Mendelism such as Bateson took it to be. The author's presentation of this argument is a model of clarity. Nevertheless it has not always received the attention it deserves. In two books on evolution published in 1963 and 1976, Mayr[26] describes the quotation from Bateson as the 'motto' for Chapter I of *GTNS* and claims that it shows Fisher believed that mutation is the only true origin of species! In reality, as any reader of *GTNS* can see, the very opposite is the case. One of Fisher's aims in Chapter I was to dispose of the point of view represented by Bateson's statement and so prepare the way for a discussion of the pioneering advances in selection theory made possible by developments in population genetics. The early Mendelians had ignored the distinction between mutation and ~~evolution~~ selection latent in Charles Darwin's work and 'thought of Mendelism as having dealt a deathblow to selection theory whereas in reality it had swept the field of all its competitors' (Fisher, *CP* 279).

Fisher had shown that the logical argument on which Darwin relied, and which governed the opinions expressed in the *Origin*, finds expression only in the essays of 1842 and 1844. Writing to M.J. Feldstein in 1929, Fisher related his finding to a more general question in the history of science: 'The history ... of the development of fundamental ideas has been much obscured by the hesitation of great men to publish incomplete work ... The bearing of Mendelism upon evolutionary theory could scarcely have been so misunderstood as it has been, if these essays had first put Darwin's views incompletely before the world.'

Chapter II, which Fisher described as 'heavy', is noteworthy for three reasons: (i) the development of the quantitative ideas necessary for a precise examination of the nature of selective advantage; (ii) the derivation of the Fundamental Theorem of Natural Selection; and (iii) the discussion of the nature of adaptation. Fisher first shows how to take account of the age structure of a population to define what he called the 'Malthusian parameter of population increase' to represent the fitness of the population. A Malthusian parameter may be defined similarly for any genotypic class in the population so giving a measure of that genotype's fitness. In this formulation, which involves an integral equation and age-specific birth- and death-rates, each age group is weighted by what Fisher called its *reproductive value.* This is a measure of the extent to which persons of given age contribute to the ancestry of future generations. This concept was entirely new with *GTNS*. As Medawar and Medawar[27] ascribe the Malthusian parameter to A.J. Lotka and say it was 'borrowed without acknowledgement by R.A. Fisher in his treatise on the Genetical Theory of Natural Selection', it should perhaps be noted that Fisher has recorded that he developed these concepts independently of Lotka. In fact, the intrinsic rate of population increase, which Lotka introduced into demography in 1925, has the same value as Fisher's Malthusian parameter if, ignoring all differences in reproductive value, it is assumed that the population has attained its steady-state age distribution.

Fisher wrote to Darwin on 27 June 1929 with an interesting application of his new concept: 'The reproductive value at different ages must determine the extent to which parental care pays.' He considers the case of an old oak in a forest having a greater expectation of posterity than a young one and concludes that 'it would be a bad bargain for the father oak to benefit his offspring unless he could do so by losing considerably less than the offspring gains.' For crocodiles, assuming they could recognize their mature progeny, 'I suppose they would co-operate with them not only on terms of mutual advantage, but on terms of joint advantages so long as the loss of either did not exceed half the gain of the other. Hence society starts with the family.'

In a short section headed, 'the genetic element in variance', Fisher (*GTNS*, p. 30) shows how, taking account of the genotypic composition of the population, a part of the population variance for a quantitative character may be identified as the genetic variance (now widely called the additive genetic variance), being the variance of the relative genetic values (also called the additive genetic or breeding values) which are built up of the average effects of the genes. He sets this out for the general case of a non-random mating population, introducing the concepts of average excess as well as average effect of a gene or gene substitution. Fisher then applies this method of analysis to the case where fitness is the quantitative character and arrives at what he calls the Fundamental Theorem of Natural Selection: 'the rate of increase in fitness of any organism at any time is equal to its [additive] genetic variance in fitness at that time.' The fundamental theorem specifies the relationship between the instantaneous rate of evolutionary advance in fitness and the additive genetic variance in fitness when *all* genes are taken into account. In an interesting article entitled, 'Fisher's "fundamental theorem" made clear', G.R. Price[28] came close, I believe, to Fisher's meaning in a number of respects but he went on to describe Fisher's 'device of treating non-additive gene effects as "environment"' as a 'defect'. Writing to O. Kempthorne in 1955, Fisher elaborates on his reasons for regarding the components of fitness attributable to dominance, epistasis, and environment as 'all in the same boat' in respect of their effect on the evolution of the species. He says these components cannot by themselves have any evolutionary effect on the species but they may induce selection in favour of genes which enable the organism to exploit these components of variance in fitness. He considers the situation in which, by the extinction of certain insects, a plant species rapidly becomes self-fertilized and homozygous; the genotypic frequencies are changed but, so long as the gene frequencies are unaltered, Fisher suggests that the plant cannot be said to have evolved but is just reacting passively to its changed environment. Fisher's letters to M. Kimura throw further light on these questions.

In considering Fisher's achievement with the quantitative analysis of selection in Chapter II, it should be remembered that the concept of individual characteristics being advantageous or adaptive, even when strikingly cryptic or warning coloration was involved, was not generally accepted in 1930. For many biologists adaptation remained as a puzzle. In 1909, Bateson had written 'Mendelism ... provides no fresh clue to the problem of Adaptation' and 'we look on the manner and causation of adapted differentiation as still wholly mysterious',[29] and again in 1924, 'modern discoveries have given little aid with the problem of the origin of adaptation'.[30] The early Mendelians regarded large mutations as the stuff of progressive evolution. Believing there was no evidence for large differences resulting from many small changes, they saw it simply as a matter of chance that a mutant should arise conforming closely to its environment in a great many particulars. Some biologists regarded the high degree of improbability of such an event as an argument against Darwinism. Writing to A.J. Nicholson in 1955, Fisher said '... I feel sure that Darwin would never have made his discovery had he not been remarkably strongly impressed with the reality and intensity of adaptations. It was, I think, only the fading of this impression towards the end of the nineteenth century which opened the door to theories of de Vries' "mutation theory" type.' In Chapter II, Fisher considers adaptive improvement as an interaction between the organism and its environment and concludes that it must generally involve many separate differences and also a large number of small evolutionary steps. With a well-adapted organism, large mutations must be harmful. Small mutations were thus seen to have far greater biological importance than those of large extent. This was contrary to the belief of the early Mendelians; according to Bateson, 'the smaller the steps, the less could Natural Selection act upon them'.[31] Having earlier shown that Lamarckism, orthogenesis, and other theories of evolution worked by mutation are inconsistent with the observation that the great majority of mutations are deleterious, Fisher concludes that natural selection is the only known mechanism which can gradually accumulate and combine the various contributory changes. Since natural selection leads to combinations of genes which otherwise would be extremely unlikely, it could be described as a mechanism for generating an exceedingly high degree of improbability. Such an outlook involved a fundamental change from the earlier description of evolution as a chapter of accidents. The objection that the principle of natural selection depends on a succession of favourable chances is, Fisher says (*GTNS*, p. 40), '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'. His opinion of the supreme importance of Darwin's conception of natural selection is perhaps best summarized in the following sentence (*CP* 258), '... it was Darwin's chief contribution, not only to Biology but to the whole of natural science, to have brought to light a process by which contingencies *a priori* improbable, are given, in the process of time, an increasing probability, until it is their non-occurrence rather than their occurrence which becomes highly improbable.'

Chapter III on the 'Evolution of dominance' was written in November 1928 only a few months after Fisher had first developed the relevant theory (*CP* 68). Dominance, he suggests, should be regarded as a modifiable property of the phenotype, which, in suitable circumstances, could have evolved over a long period through selection acting on modifying genes in the genetic background of the organism. It will be advantageous for the organism if rare deleterious mutants, repeatedly produced over a great many generations and generally carried in a single dose, are rendered recessive. Most mutants are deleterious and are thus expected to be recessive but with selectively neutral or advantageous mutants the theory gave no reason for expecting dominance or recessiveness to have evolved.

Fisher's theory of the evolution of dominance provoked much discussion. It was first criticized by Wright[32] who questioned whether there were modifier genes sufficiently numerous and so nearly neutral in relation to all other evolutionary forces for Fisher's proposed scheme to give a plausible explanation for the common phenomenon of dominance. This comment reflected a basic difference between Fisher and Wright regarding the efficacy of minute selective intensities. We shall return to this point later.

Fisher's theory of the evolution of dominance was based on the same principle which he had applied in 1927 to account for the evolution of mimicry, the essential idea being that the genes of an organism comprise an interacting system, the effect of any gene being capable of gradual modification by selection acting on the rest of the genetic system. This work led the way to a wider recognition of the importance of interactions of numerous genes in the evolutionary process. Elsewhere in *GTNS* Fisher draws on the same principle in considering the selective modification of linkage values. These discussions of the role of selection in the evolutionary modification of mimicry, dominance, and linkage values contributed in an important way to the growth of the concept of the gene-complex. Fisher's work in this area is also noteworthy for drawing attention to the valuable contribution which evolutionary theory can make to an understanding of genetic phenomena—as distinct from the contribution which genetic theory makes to an understanding of evolutionary phenomena.

Fisher had found that when two factors in the same chromosome are both in equilibrium in a population in such a way that each greatly affects the selective advantage of the other, selection will tend to produce progressively closer linkage. If the genotype is not to congeal, this tendency to closer linkage must be counterbalanced in some way. Fisher suggested in *GTNS* that such an agency 'may be found in the advantage of combining different advantageous mutations which, unless they occur consecutively, can only be done by recombination', although he observed that this would probably mean that 'the stream of favourable mutations would need to be a considerable one'. Writing to Wright on 25 October 1930, he said 'the apparently non-mathematical parts [of *GTNS*] where I have left the mathematics undone, are often of the greatest ultimate interest' and he referred to the 'elusive problem of the effect of a stream of gene substitutions in loosening the linkage' mentioned in Chapter V. Writing to R.K. Nabours on 22 March 1933, Fisher said he had never been able to see how his suggested linkage-loosening agency could be great enough quantitatively but it 'might, I suppose, be much enhanced in a species which had recently experienced great changes in environment either by spreading into new habitats or by its ecological situation, including its predators, being much affected by human occupation. ... Perhaps the ideal form of selection for loosening linkage in general would be one in which one set of pattern combinations was highly selected for a few generations and a totally different complementary set were just as highly selected a few generations later. Seasonal selection, e.g. fertility in summer versus viability in winter, might perhaps really work in some such way ...' He was urging Nabours to collect suitable field data with his grouse locusts which might shed light on this problem. Writing to J.S. Huxley on 5 July 1954, Fisher said he was rather puzzled in 1930 as to 'how, in spite of such widespread tendency to closer linkage, free recombination had in fact been retained, as is needed if different improvements are to be combined, though I find it difficult to understand how this *effect* is itself effective in promoting recombination.'

The stage was now set for Fisher to present (in Chapters IV and V) a quantitative assessment of the consequences of Mendelian heredity for the maintenance of population variability taking into account selection, mutation, and finite population size. This was essential for the rehabilitation of natural selection, for as Fisher later put it (*CP* 258), 'Darwin had no deductive basis from which to infer the quantitative efficacy of a selective process in producing evolutionary change ... [and] he was undoubtedly led consistently to underrate the rapidity with which, in favourable circumstances, evolutionary changes can be brought about by natural selection.'

The problem of the survival of an individual mutant gene in a large population is examined using the branching-process model and functional iteration. So long as there are few copies of the mutant present, chance effects predominate in determining survival. For a mutant with a selective advantage s, the probability is approximately $2s$ that it will ultimately sweep through the entire population. It follows that an advantageous mutant can occur only a small number of times before its substitution in the population becomes practically certain. Fisher attached much importance to this result.

In *CP* 24 (1922), Fisher had initiated the study of change in population gene frequency as a random process evolving in time. Treating gene frequency as a continuous variate, he introduced the chain binomial model and diffusion methods involving partial differential equations into the study of gene frequency distributions in a population. In particular, he considered the effect of random sampling of gametes in a small population on both gene frequency and the decrease of variability—the case of steady decay—as well as the statistical equilibrium established between a supply of neutral mutants and the causes of extinction of such genes. In *GTNS*, this work is greatly extended. Noting that the solution of the diffusion equation for steady decay and neutral mutation give gene frequency distributions whose integrals fail to converge, Fisher derives the exact forms for the terminal class frequencies using the method of functional equations. Considering the statistical equilibrium maintained in a finite population by a supply of mutations each having a small selective advantage, he develops some far-reaching conclusions concerning the selective process. Perhaps the most important is that in a species with n individuals living to reproduce in each generation, selective intensities greater than $1/n$ exert entirely regular and calculable effects. He wrote (*GTNS*, p. 102),

The very small range of selective intensity in which a factor may be regarded as effectively neutral suggests that such a condition must in general be extremely transient. The slow changes which must always be in progress, altering the genetic constitution and environmental conditions of each species, must also alter the selective advantage of each gene contrast. Slow as such changes in selective advantage must undoubtedly be, the zone separating genes possessing a definite selective advantage from those suffering a definite selective disadvantage is so narrow, of the order of the reciprocal of the breeding population, that it must be crossed somewhat rapidly. Each successful gene which spreads through the species must in some measure alter the selective advantage or disadvantage of many other genes. It will thus affect the rates at which these other genes are increasing or decreasing, and so the rate of change of its own selective advantage. The general statistical consequence is that any gene which increases in numbers, whether this increase is due to a selective advantage, an increased mutation rate, or to any other cause, such as a succession of favourable seasons, will so react upon the genetic constitution of the species, as to accelerate its increase of selective advantage if this is increasing, or to retard its decrease if it is decreasing. To put the matter in another way, each gene is constantly tending to create genetic situations favourable to its own survival, so that an increase in numbers due to any cause will in its turn react favourably upon the selective advantage which it enjoys.

Writing to E.B. Ford on 24 March 1930, Fisher described this as 'rather a subtle principle'.

Fisher's theoretical deduction that the more numerous species tend to be the more variable genetically gave support to Darwin's suggestion that abundant species make the most rapid evolutionary progress. He wrote (*GTNS*, p. 132), 'An evolutionary consequence of some importance is that in general a smaller number of large species must be increasing in numbers at the expense of a larger number of small species, the continuous extinction of the latter setting a natural check to the excessive subdivision of species which would ensue upon a too fine and detailed specialization.'

In 1922, in the first discussion of selectively balanced polymorphism, Fisher (*CP* 24) suggested that factors involving heterozygote advantage would accumulate in the stock and should therefore be commonly found. In *GTNS* (p. 113), he considers the more general situation of a polymorphism where 'one gene has a selective advantage only until a certain gene ratio is established, while for higher ratios it is at a selective disadvantage'. He emphasizes that selective differences and therefore the conditions of stability must change during evolution. Such polymorphisms cannot therefore be absolutely permanent but as there is a tendency for them to accumulate, they must exist 'with a frequency quite disproportionate to the probability of occurrence of the conditions on which the stability is based' (*GTNS*, p. 114). Fisher suggests in several letters that he would have included more about polymorphism if *GTNS* had been written a little later. In 1929 he began corresponding with Nabours on genetical and ecological aspects of his work with polymorphic grouse locusts. His letters to Nabours contain many suggestions which were then quite novel. On 8 August 1932, he told Nabours that it would be 'of the very highest interest if you found that the proportion of dominants, and therefore the selective advantage of the colour pattern, varied from place to place, for this would open up a whole new field in the quantitative study of ecological conditions.'

In Chapter VI, 'Sexual reproduction and sexual selection', Fisher at first discusses a question he had touched on in 1922 (*CP* 26), namely the evolutionary advantage of sexual reproduction. He suggests that evolution will occur more rapidly with sexual than with asexual reproduction because beneficial mutants involving different gene loci can more readily be brought together in a single individual. Writing to Wright in October 1930, Fisher says he had shirked the quantitative treatment of this problem. However, he does offer the following conclusion which is surely remarkable for 1930: 'the only groups in which we should expect sexual reproduction never to have been developed, would be those, if such exist, of so simple a character that their genetic constitution consisted of a single gene.' (*GTNS*, p. 137).

After considering the concept of a species as a natural group whose members are bound together by a constant interchange of their germ plasm via sexual reproduction, Fisher turns to the question of how it is possible for selection acting on small individual differences to lead to speciation. Noting that it is 'characteristic of unstable states that minimal causes can at such times produce disproportionate effects', he remarks that this problem 'involves complexities akin to those that arise in the discussion of the fission of the heavenly bodies'. He suggests that selection acting differently on different parts of a species will generate genetic heterogeneity and that an element of instability may then be introduced by genetic modification affecting gene flow between the parts. Under sufficiently intense selection, this would lead to speciation 'even in the absence of geographical or other barriers'. Fisher examines these ideas using a model of speciation with a geographical gradient in gene frequency, the gradient gradually becoming steeper until fission occurs.

An important means of fission in higher animals may be provided, Fisher suggests, by sexual preference where females in different parts of a species display a preference for differently characterized suitors. He is then led into a discussion of Darwin's theory of sexual selection. As Fisher wrote to E. Selous in 1932, he 'had ventured to add an excrescence of my own on the psychic evolution, through the same selective process, of female taste'. Fisher had discussed the evolution of sexual preference in 1915 (*CP* 6) but in *GTNS* he takes the argument much further and shows that in certain circumstances sexual selection will act by increasing the intensity of preference to which it is due and so lead to a 'runaway process which, however small the beginnings from which it arose, must, unless checked, produce great effects, and in the later stages with great rapidity'(*GTNS*, p. 152). In such a situation, sexual selection might ultimately be checked by natural selection.

Also in Chapter VI, Fisher uses his concept of reproductive value to show

how natural selection will lead to a sex ratio which equalizes the parental expenditure devoted to the production of the two sexes. He thus solves the problem of the influence of natural selection on the sex ratio, of which Darwin wrote in *The descent of man*, it is 'so intricate that it is safer to leave its solution for the future'.

Mimicry, the subject of Chapter VII was seen by Fisher as having special interest because of 'the great disparity between the views formed by the pioneers of Mendelism and those of selectionists' (*GTNS*, p. 187). The question of how the polymorphic mimetic resemblances for colour pattern in butterflies could have evolved presented a considerable challenge to the early Mendelians because the different forms not only mimicked models belonging to different genera or families but also were controlled by a single gene switch mechanism. Punnett's suggestion that the mimicry could be explained by parallel mutations in model and mimic required, as Fisher had noted (*CP* 59, 1927), 'the gratuitous assumption that no evolutionary change has taken place in the two alternative forms since the dimorphism was first established'. Fisher's explanation, which has been fully substantiated by later work, involved the gradual evolution of a gene-complex by selection operating on an interacting genetic system.

The rest of *GTNS* (Chapters VIII-XII), comprising one-third of the book, is devoted to the selective situation in civilized man. Fisher had first intended social selection in human fertility to follow sexual selection and mimicry as a third application of natural selection. He found, however, that the argument in this case needed more extensive development and as this section grew in size he was concerned that the reader might not easily see it as a whole.

Fisher begins with the assertion that human characteristics, whether of a physical, mental, or moral kind, have evolved under natural selection and may be studied just as are the characteristics of any other organism. In particular, individual differences in human behaviour, especially those associated with fertility, must be seen as capable of leading to important evolutionary changes. In examining the main agencies at work in the evolutionary modification of man and his social organization, genetical variation must be considered equally with sociology and the historical record. The rise and fall of numerous civilizations calls for some very special explanation. The advantages of civilization would surely be enhanced and prolonged 'if, as it was formerly thought could be safely assumed, life in the civilized condition, as in the barbaric state, favoured the survival and reproduction of those human types who could most effectively promote the prosperity of their society and who on the other hand were most apt temperamentally to appreciate and exploit its advantages' (*GTNS*, p. 199). Why, then, has it been otherwise?

Fisher first considers the role of selection in the evolution of co-operative behaviour and specialization of labour in civilized man and in the social insects. In his 1912 paper on social selection, he had said that in the social insects, 'there is no conflict between the interests of family and the nation, which in human society constitutes the central problem in Eugenics: where those individuals who are of most use to the state, and who will sacrifice themselves most readily for the common good, are often prevented by that very sacrifice from procreating their valuable kind.' In insect communities, reproductive specialization has eliminated intracommunal selection as an evolutionary agent. In *GTNS*, Fisher suggests that when human societies adopted an economic system of individualizing property, this might have been expected to control intracommunal selection in a socially advantageous way, with social success and accumulated wealth reflected in high fertility. However, this expectation has not been realized. Fisher says that differences in behaviour associated with fertility have been of major importance in the evolution of human societies. He suggests that the human species is unique in having differential fertility instead of mortality as the main factor affecting selection and, on the evidence available, he concludes that there is an important genetical component in fertility differences. In Chapter X Fisher considers the relation between fertility and social class; for all civilized societies for which data are available he says the birth-rate has a larger value in the lower than in the higher social classes. He suggests that it is important that we recognize 'the absolute failure of the economic system to reconcile the practice of individual reproduction with the permanent existence of a population fit, by their mutual services, for existence in society', for in his view it is the inversion of the birth-rate with respect to social class which has led to the decline of apparently successful civilizations.

In Chapter XI Fisher develops his theory of the selective process by which the inversion of the birth-rate becomes established in civilized societies. The two essential elements are (i) the social promotion of the less fertile and (ii) a genetical component in characteristics affecting reproduction. He points out that in primitive societies having a tribal organization the more eminent individuals are generally the more fertile and the effects of natural selection are greatly enhanced by social and sexual selection. Altruistic qualities such as those associated with heroism, recognized as socially valuable in such groups, may then be developed considerably further than could be ascribed to individual advantage alone. Fisher suggests that the higher mental qualities of man, and especially his appreciation of them, may also be ascribed to social selection acting in a similar way.

Having found that in civilized man the main selective influences act through the birth-rate and that such selection is very intense and against all the factors of social success, Fisher in the final chapter offers his suggestions for countering the social promotion of infertility so as to provide conditions thought necessary for a permanent civilization. The financial burden of raising children should not rest with the parents but should be distributed equally throughout the members of the same social class by means of family allowances *proportional to income*. If this were done, there should be an equal standard of living for equal work irrespective of the size of the family. When the introduction of family allowances was being widely discussed in Britain after the First World War Fisher argued against flat allowances and for a system of proportional allowances to be regarded as an integral part of wages and salaries. Such allowances, he suggested would be comparable in principle with the proportional deductions made widely for superannuation benefits. Fisher attached great importance to proportional family allowances as part of a long-range population policy. It is a subject which comes into a number of his letters to Darwin and other correspondents.

In developing his argument that there is a biological basis for expecting the decline of civilized societies in which there is a reduced fertility amongst those who are socially successful (where socially valuable qualities making for leadership, enterprise, high endeavour, etc., are generally most frequent) Fisher referred to the economic system of individualizing property, 'which, diverse as are the opinions which different writers have formed about it, appears to the writer to be one of the unconscious triumphs of early human organization' (*GTNS*, p. 201). Writing to C.V. Drysdale on 4 October 1929, he said, 'free competition is invaluable in stimulating the production of wealth, but should be excluded on economic and eugenic grounds from the question of the reproduction of children. Unless it is so excluded, you cannot fail to recruit the next generation preferentially from the least prudent, or the most bigotted.' After reading *GTNS*, J.B.S. Haldane told Fisher that he regarded this part as 'highly controversial' and that if he were convinced by it, he would have to become an extreme form of socialist. J.S. Huxley reacted to the final section of *GTNS* by suggesting that to work against individualism was eugenic.[33] Aldous Huxley wrote on 26 September 1931 that 'after reading in your book about the effects on the human stock of a social organization based on economic reward I think we have a right to a good deal of gloom and alarm'. Fisher's response to his finding that class differences were an essential feature of the dysgenic process in civilized life was quite different. As he wrote to Darwin on 16 March 1931, he had tried to conceive of biologically progressive societies which were classless, but he found this always led to an impasse: 'Man's only light seems to be his power to recognize human excellence, in some of its various forms... Promotion must be a reality.' Fisher's attitude is consistent with his general view of the human condition and the nature of evil which he expressed when writing to Bishop Barnes on 12 January 1952: 'Man is in process of creation, and that process involves something we can call improvement, in which Man's own co-operation is necessary. Hence the need to become acutely conscious of evil or quasi-evil in ourselves and in the world, just as the increase of natural knowledge requires a corresponding consciousness of ignorance. Complacency in either respect would seem quite deadly to progress.'

Reception of *GTNS*

With its novel approach to the theory of natural selection, *GTNS* presented a challenge to readers and reviewers. Fisher wrote to L.C. Dunn in 1930,

> The book will be really difficult to review owing to new arguments being developed (though from a central viewpoint) on questions which hitherto have been discussed in isolation, and which consequently appear at first sight to be very distinct. If I had to review it I should waver much between giving the reader an idea of Chapter I, and alternatively, of the arguments in Chapter VI. The human chapters are more manageable being really the development of a new evolutionary argument as to social selection, comparable with such developments as Sexual Selection and Mimicry; and it is done more fully as is necessary in breaking new ground.

The review in *Nature* by Punnett[34] was a great disappointment to Fisher. Punnett's approach was revealed in his opening paragraph: 'Probably most geneticists today are somewhat skeptical as to the value of the mathematical treatment of their problems' believing that 'in their own particular line it is, after all, plodding that does it'. Most readers, he said, would find the final section of *GTNS* dealing with Man, 'the brightest part of the book for apart from the absence of mathematical formulae, it is full of shrewd comments and odd bits of learning'. The significance of *GTNS* evidently went unrecognized: 'Throughout the book one gets the impression that Dr. Fisher views the evolutionary process as a very gradual, almost impalpable one, in spite of the discontinuous basis upon which it works.' When Darwin read this, he wrote at once to Fisher saying how sorry he was that *Nature* had picked 'an old discontinuous stick-in-the-mud like Punnett'. Then, characteristically, he added 'to get 5 columns is an excellent advertisement. My father would have been much pleased by such a review of the *Origin*, and merely carefully noted the points to answer in his next edition'. However, Fisher thought he should tidy up such 'troublesome trifles' at once; he published a rejoinder to Punnett in the same volume of *Nature*.

Some biologists realized quickly the worth of Fisher's book. Writing in the *Eugenics Review* under the heading 'Mathematical Darwinism', Haldane[35] said *GTNS* laid the foundations of a new branch of science and that 'no serious future discussion, either of evolution or eugenics can possibly ignore it ...; during the next generation any discussions of the problem of gradual evolution which are likely to be of permanent value will take the form of a development, discussion, and perhaps in some cases, a refutation of the arguments stated in the book before us.' In a review in the *Mathematical Gazette,* Haldane[36] wrote that *GTNS* 'should serve not only to raise the discussion of the evolution problem to a higher level but to introduce mathematicians to a new growing point of their subject'. Interestingly enough, Haldane added that Fisher's runaway process (*GTNS*, p. 152) had special value in explaining orthogenesis and he believed this process was more important than Fisher's 'fundamental theorem'.

Long and favourable reviews of *GTNS* were published in a number of English periodicals. An anonymous reviewer in *The Times Literary Supplement* of 28 August 1930 described it as 'the most important contribution to biological theory which has appeared in any country in the last quarter of a century', and added, 'it may well be the beginning of a new phase in the endeavour to understand the living world'. A reviewer in *The Spectator* of 24 May 1930 said the task of considering the theory of natural selection on its own merits 'certainly has never been performed with anything like the skill and subtlety now brought to bear upon it' in *GTNS*. C.G. Darwin wrote in the *Eugenics Review* that the 'masterly quality of the book can be seen even by reading the four short pages of the Preface'. A. Bradford Hill in a long review in the *Journal of the Royal Statistical Society* quoted from Fisher's preface, 'no efforts of mine could avail to make the book easy reading' and then commented, 'From Dr. Fisher this is no mean threat; anyone at all conversant with his scientific works knows that they are invariably difficult to read—though, equally invariably, exceedingly well worth the effort demanded.'

Upon publication of *GTNS*, Fisher had arranged for complimentary copies to be sent to a number of American scientists, including L.C. Dunn, H.H. Laughlin, T.H. Morgan, H.J. Muller, R. Pearl, E.B. Wilson, and S. Wright. Whilst the book was not unknown in America in 1930, it appears to have taken longer there than in England for it to be widely appreciated. According to Dobzhansky, Ayala, Stebbins, and Valentine,[37] 'The reception of Fisher's book is a clear indication of the climate of its time. One searches in vain through the issues of *Science* for 1930 and 1931 for a review of it. Apparently the editors did not consider it important enough to be worth reviewing.' At least two American journals carried reviews of *GTNS*. In the *Quarterly Review of Biology,* of which R. Pearl was editor in 1931, it was dismissed in a brief note, which described as 'paradoxical' Fisher's conclusion that the direction of evolution is determined not by the direction of mutation but by that of selection. The *Journal of Heredity* published a long review by Wright[38] who described *GTNS* as 'a book which is certain to take rank as one of the major contributions to the theory of evolution'. He went on to give a critical discussion of Fisher's concept of evolution which he described as 'pure Darwinian selection' and indicated that in his view less weight must be given to what individual selection is doing.

Shortly after publication of *GTNS*, Fisher's interest in the role of selection turned to the exciting possibilities opened up by the study of polymorphisms and the human blood groups. Several early readers, noticing that blood groups were not referred to in *GTNS*, wrote seeking Fisher's views on the role of selection, mutation, and migration in determining the different racial frequencies of the ABO blood types. When R.R. Gates suggested that these serological differences were apparently without selective effect, Fisher replied (1 July 1930), 'There are a good many climatically limited blood diseases, such as malaria and yellow fever, so I would not be too sure of the absence of selection.' On 18 October 1934, Fisher wrote to W.C. Boyd, 'I cannot see any escape from the view that the frequencies have been determined by more or less favourable selection in different regions, governed not improbably by the varying incidence of different endemic diseases in which the reaction of the blood may well be of slight but appreciable importance.' These must be some of the earliest suggestions put forward for natural selection acting via climatically limited endemic blood diseases in the maintenance of human polymorphism.

When Charles Todd's work on the individuality of red blood cell antigens in chickens was brought to Fisher's attention, he wrote at once (23 April 1930) suggesting that Todd was detecting primary gene products and proposing further experiments. A. H. Sturtevant[39] in his book *A history of genetics* says that Todd's remarkable results were 'soon interpreted to mean that the antigens were close to immediate gene products, and might furnish useful materials for the study of the action of genes, relatively free of the complications of developmental interactions. It is not clear who first formulated this idea; I first heard it in conversation with Haldane in the winter of 1932-1933. However, the results of this assumption have been of far-reaching importance in the study of the developmental effects of genes.' Several of Fisher's letters to Todd and Haldane in 1930 shed interesting light on this question.

Fisher was soon predicting on the basis of Todd's work that serological methods would uncover many genic differences in Man and that this would lead to a revolution in human genetics. He was anxious to see a start made in 1930 and tried in vain to persuade Darwin that the Eugenics Society should support a research worker in this area. In 1933, Fisher moved to the Galton Laboratory and shortly afterwards he set up the Serum Unit which soon made important contributions to knowledge of the human blood groups, especially with the Rhesus system.

Fisher's early interest in blood groups stemmed largely from his ideas on the evolution of dominance. His letters to Todd and Boyd show that he was at first contemplating the possibility of many, if not most, genes being detectable via serological effects. An excellent account of the development of his ideas in this area is provided by Joan Fisher Box in Chapter 13 of *FLS*.

Second edition of *GTNS*

Shortly before publication of *GTNS*, Darwin had written telling Fisher not to be disappointed at a small sale. It was, he said, 'the kind of book to work through others'. In fact, there was a gratifying early demand for *GTNS* and more than one-third of the 1500 copies printed were sold in the first 12 months. However, sales soon declined markedly and the last copies of *GTNS* were not sold until 1947.

In 1930 Darwin repeatedly urged Fisher to prepare extra material in readiness for a second edition. Early in 1931 Fisher wrote a review of the criticisms raised against the theory of natural selection 'with a view to repairing something like an omission from my book'. He thought of including this as an extra chapter in a proposed German translation of *GTNS*. However, as sales of *GTNS* fell away, the prospects of a German translation and a second English edition receded. In November 1931 Fisher sent a copy of the article to Julian Huxley and asked if he knew an editor who would care for it. The paper remained unpublished and Fisher filed it away. Twenty years later he brought it out and sent if off as his contribution to *Evolution as a process*, a volume of essays on evolution published in honour of Huxley. Unfortunately, Fisher did not add a note explaining when and why he had written this paper, 'Retrospect of the criticisms of the theory of natural selection' (*CP* 258, 1954). In 1980 it was cited by Mayr[40] as an example of 'post-synthesis literature' with 'an extraordinary amount of space ... devoted to the refutation of anti-Darwinian arguments'.

When Fisher sent this article to Ford in 1951, he dismissed the possibility of a second edition of *GTNS*: 'the most I should be inclined to attempt would be a book of essays taking up particular topics such as this one'. In 1955 Dover Publications expressed interest in reprinting the original text. When their paperback edition of *GTNS* appeared in 1958, it contained various changes and additions supplied by the author. Though widely referred to as the second edition, Fisher did not like to call it that. Whilst he acknowledged that he could not give the amount of work necessary to bring the original text up to date in its various aspects—genetical, evolutionary, sociological, etc.—it was probably also his historical sense which led him to prefer that *GTNS* should stand as 'the first attempt in strictly genetical terms to appraise the weight of evolutionary theories going back for nearly a century'.

The additions and alterations introduced with the Dover edition were collected up from the author's interleaved copy of *GTNS* where he had noted them down as they occurred to him over the years. Some of this material had been prepared a quarter of a century earlier. As slightly smaller print was used for the new material in the Dover edition, it is not difficult to see where changes or additions have been made. There was no major alteration but several of Fisher's additions deserve comment. In Chapter II, when considering the analysis of genetic variance, he introduces a more general formulation taking account of multiple alleles which he had developed about 1930. Unfortunately, the presence of a number of typographical errors detracts from the presentation of this new material.[41] An insertion which should not be overlooked occurs on page 40 where Fisher explains how, in his Fundamental Theorem of Natural Selection, the evolutionary effects ascribable to the dominance component of the genotypic variance are credited to gene substitutions at other loci.

An addition of particular interest is the reference to individual and group selection on page 49. As Fisher wrote to A.G. Lowndes on 23 June 1945, '... natural selection will only explain adaptations insofar as they are effective in preserving the germ plasm of the individuals concerned.' In the Dover edition, he says it is doubtful if any character, with the possible exception of sexuality itself, could be interpreted as having evolved for specific rather than for individual advantage. In his letter to Lowndes, Fisher emphasized that individual selection 'does not preclude adaptations which are effectual through the survival of relatives, for these share to a great or less extent the germ plasm of the individual'.

The most extensive changes in the book are in Chapter III on the evolution of dominance where Fisher said the tentative and apologetic approach adopted in 1930 was inappropriate in 1958, given the progress made during that period in understanding the important role of systems of interacting genes in evolution.

A significant addition to Chapter VI (p. 153) is Fisher's non-genetic early nesting model which he developed in order to account for Charles Darwin's suggestions on sexual selection in monogamous birds. This was the subject of several letters between Fisher and Leonard Darwin who wrote (20 August 1930) that he thought his father would have been 'a bit surprised that such a complicated explanation was needed'. There are several slips in the passage as printed which make it hard to follow but Fisher's letters to Darwin (27 June and 7 August 1930) show what he intended and also how some of the slips came about. Also in Chapter VI Fisher added a section referring to butterflies of the genus *Limenitis* in the eastern USA as 'an example of a species in process of fission, in which sexual preference is evidently playing an important part' (*GTNS*, pp. 145-6). Fisher was doubtful about the validity of this example, the information on which had come to him from E.B. Poulton about 1935. Late in 1955 when preparing material for the Dover edition, he sought advice on this from E.B. Ford and L.P. Brower. The passage which was ultimately inserted in *GTNS* in its original form was later criticized by Platt and Brower (1968).[42] Referring to examples of phenotypic intergradation in areas of geographic overlap between populations which are elsewhere distinct and relatively homogeneous, as a key to understanding the process of the origin of species, they say,

> one of the most historically significant concerns two North American nymphaline butterflies of the genus *Limenitis*, *L. arthemis* Drury and *L. astyanax* Fabricius. Fisher (1930) regarded the available data on these butterflies as evidence for their being incipient species on the verge of attaining complete genetic isolation. This example proved important to understanding not only the role of sexual selection in interspecies evolution (Huxley, 1938a, b) but also laid the foundation for Dobzhansky's (1937) theory that, following allopatric separation and divergence, speciation can be completed by selection in the zone of secondary overlap. Notwithstanding the absence of subsequent substantiating data, this interpretation of the *arthemis-astyanax* complex was accepted by Hovanitz (1949), reasserted by Fisher (1958), and again put forward by Mayr (1963).

Platt and Brower found that mating occurs at random in the zone of overlap of *L. arthemis* and *L. astyanax*, and they offer a plausible explanation for the maintenance of this narrow zone based on mimicry. Evidently Fisher was right to have had misgivings about the passage on *Limenitis*, but despite what Platt and Brower suggest in the above quotation, his insertion of this passage in the Dover edition of *GTNS* in 1958 can scarcely have misled other writers on this subject in publications which appeared 10 or 20 years earlier.

Fisher, Haldane, and Wright

The publication of *GTNS* was followed shortly afterwards by S. Wright's (1931) paper, 'Evolution in Mendelian populations', and J.B.S. Haldane's (1932) book, *The causes of evolution*. Wright's view of the role of selection in evolution differed markedly from Fisher's. This difference, described by Fisher and Ford (*CP* 239, 1950) as 'the widest disparity which ... has so far developed in the field of Population Genetics', became the subject of much argument. Can Fisher's correspondence add to our understanding of the issues involved?

It seems that Fisher first wrote to Haldane and Wright when they published criticisms of his theory of the evolution of dominance in 1929-30. The correspondence with Haldane continued for many years but that with Wright stopped in June 1931. The Fisher-Wright letters, however, are of great value for the light they shed on the development of their differing views of the roles of selection and random drift in evolution.

As far as we know, Fisher first wrote to Haldane on 15 March 1930 enclosing a draft of his paper on the evolution of dominance in certain polymorphic species (*CP* 87). Fisher clearly valued the stimulus provided by Haldane's suggestions in this area. Over the next ten years they seem to have enjoyed exchanging letters, discussing questions of natural selection, and sometimes sending drafts of their papers to one another for comment. Their letters are perhaps of greatest interest for what they reveal of their relationship in that decade, especially in 1933 when Fisher was about to join Haldane at University College London and again in 1940 when Haldane was about to join Fisher at Rothamsted.

Fisher first wrote to Wright on 6 June 1929 with a draft reply to Wright's paper criticizing dominance theory.[32] Wright had claimed that the selective pressures on the modifying genes were too small to be effective. When Wright replied that this criticism rested on the assumption that modifiers would nearly always be subject to other selective pressures more important than those concerned with dominance modification, Fisher wrote back encouraging him to publish a second paper since, he said, others also might have missed this point in the earlier paper. When Wright published a second paper,[43] he introduced the suggestion that the most important selective action on a gene is not necessarily the controlling factor. I think this exchange may be seen as the first of a series of misunderstandings between Fisher and Wright. Wright was proposing that natural populations are often of such restricted sizes that random drift is important in determining the frequencies of genes subject to very small selective differences. Fisher wrote (13 August 1929) questioning the importance of this factor; he suggested that in considering the interference of population number n with selection, n must be based on the entire species unless isolation in districts were substantially complete.

Now Fisher had met Wright in 1924 during a visit with a party of mathematicians to the US Department of Agriculture centre at Beltsville. Almost 30 years later, when writing to a friend about organization of the biological sciences, Fisher recalled that occasion.

> In the Dark Ages of 1924, I had the pleasure of visiting a research centre at Beltsville ... and was impressed even then to find that there was a department for research on horses and one for cows, and I think there was also one each for sheep, pigs and poultry, but none for Physiology or for Pathology or for Parasitology, Nutrition, etc. There was, however, newly injected and shining like a star, Sewall Wright with a Department of Genetics, an enormous corrugated iron building crammed from floor to roof with guinea pigs. I am afraid I held up the progress of the party sitting in the hot sun outside this building surrounded by tiers and tiers of guinea pig skins.

Later in 1924 Fisher sent Wright a copy of his 1922 paper (*CP* 24) dealing with gene frequency distribution in populations. In 1929 Wright wrote to Fisher that, stimulated by that paper, he had himself made a comparable study and had arrived at the value $1/(2n)$—instead of $1/(4n)$ as given by Fisher (*CP* 24)—for the rate of decay of gene frequency in a random mating population of n individuals with no mutation or selection. On 13 August 1929, the same day as that on which Fisher wrote to Wright suggesting that the relevant population number must be that for the whole species, Wright wrote to Fisher enclosing a copy of his manuscript on gene frequency distribution. He sought Fisher's comments saying that he was not clear as to the cause of the discrepancy between $1/(2n)$ and $1/(4n)$. Two weeks later, replying to Fisher's letter of 13 August 1929, he agreed that the population number n must be based on the entire species, unless isolation in districts is substantially complete, and he acknowledged that isolation would need to be much more nearly complete than he had at first realized if it were to lead to random fixation of strains. Was not Wright suggesting that he now saw isolation as a less important factor affecting gene frequency than he did when he wrote the big manuscript? Perhaps this was what Fisher had in mind when he wrote (9 September 1929) that Wright's letter of 28 August 1929 'is not only exceedingly interesting in itself, but helps me to understand the larger paper, which I have been puzzling over occasionally for some time'. I think this exchange contained the germ of a second misunderstanding since Wright's later writings showed that he continued to regard the relevant population number n as that for the local population and not the species.

The discrepancy between $1/(2n)$ and $1/(4n)$, which Wright found, required Fisher to re-examine the diffusion approach used in his 1922 paper (*CP* 24). He soon found that he had neglected a small term in the diffusion equation; when this was included there was complete agreement with Wright's result for the case of no mutation and selection. This experience led Fisher to undertake a more detailed study of the terminal class frequencies using the method of functional equations which he had outlined in *CP* 24. He took the opportunity to include an account of this work and the corrected diffusion equation in *GTNS* at the proof stage in October 1929.

On 1 January 1930, Wright read a short paper, 'Evolution in a Mendelian population', to a meeting of American geneticists. The published abstract ends with the following passage.[44]

> In too large a freely interbreeding population, there is great variability but such a close approach of all gene frequencies to equilibrium that there is no evolution under static conditions. ... With intermediate size of population, there is continual random shifting of gene frequencies and consequent alteration of all selection coefficients, leading to relatively rapid, indefinitely continuing, irreversible, and largely fortuitous, but not degenerative changes, even under static conditions. The absolute rate, however, is slow, being limited by mutation pressure. Finally, with a large but subdivided population, there is continually shifting differentiation among the local races, even under uniform, static conditions, which, through intergroup selection, brings about indefinitely continuing, irreversible, adaptive, and much more rapid evolution of the species as a whole.

Wright's concern with the lack of evolution in a large freely interbreeding population under 'uniform, static conditions' is plainly evident, as is the way this led him to propose an important role for population subdivision and intergroup selection in his 'shifting balance theory of evolution', as he later called it. On 10 June 1930, writing to thank Fisher for a copy of

GTNS which he had just received, Wright suggested that the above abstract —written before he saw *GTNS*—exaggerated the differences between them since 'I was forced by limitation of space to express my views in a balder and more unqualified form than I would care to maintain fully.' Shortly afterwards, when reviewing Fisher's book, Wright spelt out clearly a basic difference in their points of view. He wrote,[38] 'throughout the book (Fisher) overlooks the role of inbreeding as a factor leading to the non-adaptive differentiation of local strains, through selection of which, adaptive evolution of the species as a whole may be brought about more effectively than through mass selection of individuals.' Wright emphasized that, in his view, inbreeding has an essential role in the theory of evolution. His confident statement on this point seems to have come as a surprise to Fisher. Upon seeing the review, he wrote at once to Wright (19 January 1931):

> You must really take some later opportunity to set out your views more fully, for I am willing to be convinced, not of the importance of subdivision into relatively isolated local colonies, which I should agree to at once, but that I have overlooked here a major factor in adaptive modification which is what at present I am not convinced of. The point is very well worth going into in detail. I fear though that an adequate discussion will be above the heads of many biologists.

Evidently, Fisher expected Wright to have developed a mathematical theory justifying his view of isolation as a primary factor in adaptive modification. Writing on the same day to E.B. Ford for his opinion on this question, Fisher said that whilst he could see that random survival in small isolated colonies may be of special importance in some cases, he did not appreciate how it could *generally* favour a more rapid progress in *adaptive* modification, and he added, 'at present I doubt if the adaptive modification of the species as a whole would in general be at all retarded by a complete mixture of every generation.' In fact, Fisher seems to have come to the conclusion well before this that isolation would have to be very extreme to be worth anything genetically. He had written as much to Darwin on 15 January 1929 and to Wright himself on 13 August 1929. Now, however, that Wright had published such a definite statement about partial isolation as a primary factor in adaptive modification, Fisher was inclined to emphasize that the different views of Wright and himself on this point were ones held 'at present'. On 20 April 1931, for example, he wrote to A.B.D. Fortuyn,

> As far as I can see at present, isolation, whether geographical or physiological, whilst of immense importance to the problem of fission, is not a primary factor in adaptive modification, save in the subordinate sense that fission is a necessary condition for divergent adaptation. Sewall Wright, however, at present thinks otherwise, and there are very few men who have a better right to form their own opinions.

At the end of May 1931, when Fisher arrived at Ames, Iowa, for a six-week period as visiting professor, he wrote at once to Wright in Chicago asking when he could visit him there. No doubt Fisher was anxious to hear about Wright's theory, to judge for himself what significance should be given to it, and to see if they could then agree on the role of random survival in adaptive evolutionary modification. Fisher's next letter, written after he had visited Chicago, was evidently the last one he sent Wright. After thanking the Wrights for their kindness and hospitality, Fisher gives a hint of exasperation that his visit to Chicago, made especially to talk with Wright, and which no doubt involved long and searching discussions, had not led him to a better understanding of Wright's views on those points on which they differed. There is a rare touch of finality about Fisher's remark that he saw no chance of ever understanding Wright's views on those points which he had discussed with J.L. Lush in Ames. Perhaps it is significant that, shortly afterwards, when reviewing Wright's paper, 'Evolution in Mendelian populations', Fisher drew a distinction between Wright's 'scientific conclusions' and his 'philosophical observations on the nature of the evolutionary process, which are of great interest, although necessarily more personal and subjective' (See Appendix A, p. 287). Commenting on Wright's concern with the lack of evolution in large outbreeding populations under uniform static conditions, Fisher said that not only had Wright overlooked the advantages of a large population with respect to mutation, but also that, since the environment must be continually changing, static conditions in the evolutionary sense do not occur.

In 1932, both Fisher and Wright were in Ithaca, New York for the Sixth International Congress of Genetics. Fisher's paper, 'The evolutionary modification of genetic phenomena' (*CP* 97), included the following reference to Wright: 'Sewall Wright, if I understand him, has suggested ... that very small selective intensities do not, as one would naturally assume, exert effects proportional to their magnitude; but I have so far found it impossible to set up any reasonable scheme of genic interaction which would justify this conjecture.' Wright, in his paper, 'The roles of mutation, inbreeding, crossbreeding and selection in evolution', concluded, 'The course of evolution through the general field [of possible gene combinations] is not controlled by direction of mutation and not directly by selection, except as conditions change, but by a trial and error mechanism consisting of a largely non-adaptive differentiation of local races (due to inbreeding balanced by occasional cross breeding) and a determination of a long time trend by intergroup selection ... the average adaptiveness of the species thus advances under intergroup selection, an enormously more effective process than intragroup selection.'

In June 1933, when Wright took up again his criticism of Fisher's theory of the evolution of dominance, he appeared to place the argument in a wider setting.[45]

Fisher used the observed frequency of dominance as evidence for his conception of evolution as a process under complete control of selection pressure, however small the magnitude of the latter. My interest in his theory of dominance was based in part on the fact that I had reached a very different conception of evolution (1931) and one to which his theory of dominance seemed fatal if correct. As I saw it, selection could exercise only a loose control over the momentary evolutionary trend of populations. A large part of the differentiation of local races and even of species was held to be due to the cumulative effects of accidents of sampling in populations of limited size. Adaptive advance was attributed more to intergroup than intragroup selection.

Replying, Fisher (*CP* 119, 1934) quoted Wright's statement that 'there should always be other evolutionary pressures of greater magnitude acting in one direction or the other' on the modifiers, and he added, 'Wright appears to think that this implies that a selective intensity of lesser magnitude has therefore no effect', but such an argument, Fisher claimed, was fallacious. Wright[46] replied that he could not follow Fisher's reasoning but probably more significant for their future relationship were the complaints he included in this paper about Fisher's handling of his 1929 manuscript. Though this question had not been mentioned in any of a dozen letters which had passed between them since 13 August 1929, Wright evidently came to believe that Fisher had made use of his manuscript without adequate acknowledgement. After this exchange, there was, it seems, little chance of reconciliation.

Fisher certainly had reason to be immensely grateful to Wright for sending his manuscript in August 1929. Fisher wrote as much to Wright on 15 October 1929 and he included acknowledgements to Wright in *GTNS* (p. 95) and *CP* 86 (1930). These acknowledgements might, perhaps, have been more happily constructed but there is nothing in the Fisher-Wright letters, or elsewhere that I know of, indicating that Fisher had done anything more or less with Wright's manuscript than he stated.

Fisher's next major reference to Wright's work was in 1941 (*CP* 185) when he questioned Wright's concept of an adaptive surface and his formulation of selective tendencies in terms of a potential function $\bar{W}$—with the implication that selection is governed by the average condition of the species or interbreeding group rather than by its action on individuals. Fisher had touched on the first of these points in a letter to Wright on 31 May 1931. His letters to E.B. Ford (2 May 1938) and M. Kimura (3 May 1956) also refer to these questions. In one of his last references to this subject, Fisher wrote (*CP* 277, 1958), 'the existence of such a "potential function" as that which Wright designates by $\bar{W}$ is not a general property of natural populations ... selective tendencies are not, in general, analogous to what mechanicians describe as a conservative system of forces. To assume this property is one of the gravest faults of Wright's formulation.

The only other major references to Wright's work in Fisher's later publications concern the question of selection and random drift. They occurred in two papers with E.B. Ford—*CP* 219 (1947) and *CP* 239 (1950)—and in a prefatory note written for the reprinting in 1950 of Fisher's paper, 'The distribution of gene ratios for rare mutations' (*CP* 86, 1930). In this note Fisher recorded that he did not share Wright's 'conviction that evolutionary progress is favoured by the subdivision of a species into small, imperfectly isolated populations, save in the case stressed by Darwin in which the environmental conditions of these are sufficiently diverse to induce divergent evolutionary tendencies. Wright, on the other hand, has maintained that random survival in such populations leads to the testing of a greater variety of genotypes, and to the more rapid discovery of successful combinations, while my own studies have not led me to believe in any such effect, as a factor contributing to organic evolution.' This view Fisher had expressed repeatedly since he first wrote to Wright about this question on 19 January 1931. This point and the issues involved have not always received the attention they deserve—to judge from Provine's[47] recent summary statement that Fisher 'began to realize that Wright was correct in arguing that evolution would proceed more rapidly in a population subdivided into partially isolated subpopulations'. Fisher and Ford (*CP* 219) gave a useful summary of their reasons for not agreeing with Wright on this question.

> Those evolutionists who find it difficult to attach any great evolutionary significance to such chance effects have urged that the normal segregation of all factors in each generation continually supplies new genotypes selected at random from a number usually much greater than the number in a single generation of even a numerous population, and that the selective increase or decrease of any gene is determined by the totality of the life experience of all these ... combinations: that the number of genotypes tried will generally be larger in more numerous than in less numerous populations; and that the existence of very small and completely isolated populations, such as Wright seems to postulate, will generally be terminated by extinction in a period which must be thought of as short on an evolutionary scale of time.

Fisher never accepted Wright's view that inbreeding is an essential factor in adaptive evolutionary modification and that intergroup selection acting on random non-adaptive changes in local groups is a more effective process than intragroup selection in the adaptive modification of species.

Wright[48] has suggested that he saw intergroup selection as the only process by which the selection of interaction systems could occur. He evidently saw Fisher's Fundamental Theorem as 'a refutation of the possibility of any selection among interaction systems'; his suggestion that interaction systems had been neglected by Fisher apparently stemmed from that view. Fisher expressed his view of intergroup selection when he wrote to J.F. Crow in 1955 that the conditions needed for isolation to be worth anything genetically must be taken to preclude real competition between the imagined groups.

It is interesting, and perhaps needs emphasizing, that both Fisher and Wright considered systems of interacting genes to be of critical importance in evolution. A fundamental difference in their views of the evolutionary process concerned the *means* by which interaction systems could be exploited.

As we have already seen, Fisher, from quite early on, attached importance to the role of individual selection in the evolution of systems of interacting genes. He wrote to Darwin on 7 August 1928,

> I am inclining to the idea that the main work of evolution lies in the discovery by trial of perhaps rare combinations of its existing variants, which work better than the commoner combinations. A slight increase in the number of individuals bearing such a favourable combination will then set up selection in favour of all the genes in the combination, with marked evolutionary results. Many of these genes would have been previously rare mutant types (not necessarily rare mutations) unfavourable to survival. I think of the species not as dragged along laboriously by selection like a barge in treacle, but as responding extremely sensitively whenever a perceptible selective difference is established.

In *CP* 147 and elsewhere, Fisher recorded his belief that the selective intensities effective in evolutionary change were generally very small—of the order of 0.1 to 1 per cent per generation.

Considering what is now known about genetic variation in natural populations, it is interesting to see Fisher's early recognition of the large amount of latent variability and that he believed much of it was due to effectively neutral mutations whose ultimate fate would be governed largely by changes in the environment, including the genic environment. In *CP* 87 (1930) he wrote,

> It is indeed certain that many species contain a large amount of latent variability by the selection of which their instantaneous rates of evolutionary improvement are maintained. There is no need, however, to suppose that the whole of this is due to a stream of mutations beneficial from their first appearance in process of spreading over the species rather than that much of it may be due to effectively neutral mutations which have occurred in the past and the ultimate fate of which is at present in process of decision.

Writing to Regan in February 1927, Fisher had considered the case of a 'tolerably good' mutant which 'in certain circumstances, or in certain gene combinations, may be advantageous but on the whole is neutral'. In *CP* 81 (1929), he wrote that 'factors suffering the feeblest selective action will at any one time be the most numerous ... It is the idlers that make the crowd and very slight attractions may determine their drift.'

Near the end of the Preface to *GTNS*, and after a warning that the book was not easy reading, Fisher wrote, 'I believe no one will be surprised that a large number of the points considered demand a far fuller, more rigorous, and more comprehensive treatment.' Nowadays there is, of course, a fine tradition of quantitative research in theoretical and applied population genetics. The indispensable contribution of such studies to evolutionary biology is now widely recognized. This certainly represents a marked change of view since 1930. Whilst *GTNS* did much to help bring about this change, the book was, as Fisher said, not easy reading. For some readers this added to its fascination but for others it undoubtedly limited their understanding of Fisher's contributions.[49] As A.L. Bowley[50] remarked about some of Fisher's statistical work, not all of the goods are in the window. It was perhaps with some such thoughts in mind that Darwin wrote to Fisher in June 1930, as he began to reread *GTNS*.

> my impression is confirmed that it will be slowly recognized as a very important contribution ... but I am afraid it will be slow, because so few will really grasp all that it means. You must ... trust to ultimate results.

Notes

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4. See Bennett, J.H. (Ed.) (1965). *Gregor Mendel. Experiments in plant hybridisation. With introduction by R.A. Fisher.* Oliver and Boyd, Edinburgh.
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    > Fisher [...] for the sake of manageable mathematics made all sorts of simplifying assumptions, such as: population size large, epistatic effects and linkage negligible, accidents of sampling unimportant, effects of individual genes usually slight. As necessary as all of these assumptions were during the infancy of population genetics, they contained the germ of much of the trouble that plagued the field during the ensuing forty years.

50. See *FLS*, p. 85.

2 R. A. FISHER ON (1) MENDELISM AND BIOMETRY (1911) AND (2) SOCIAL SELECTION (1912)

1. Mendelism and biometry[1]

Paper on 'Heredity' (comparing methods of Biometry and Mendelism) read by Mr. R.A. Fisher, Caius College, (Chairman of Committee), at second undergraduate meeting of the Cambridge University Eugenics Society in Mr. C.E. Shelley's rooms, C. New Court, Trinity College, on Friday, 10 November 1911, at 8.30 p.m.

In compiling this short paper I have not, needless to say, attempted to touch the whole subject; the inherited character controversy I have omitted altogether, as it may be considered as settled, from the practical point of view, in favour of Weismann; the further controversies which raged over Weismann's germ plasm theory may fairly be left to physiologists, if they think that the discussion was profitable.

I rather regret having made no mention of de Vries' mutation theory, or of Johannsen's remarkable work on pure lines; the latter I should certainly have included if I could have got at the original papers.

I have almost entirely devoted myself to the two lines of modern research which are of particular interest in Eugenics, that is to Biometrics and Mendelism; and perhaps experts and professionals will forgive the absence of more complicated details in both branches, if I explain that my object has been to give a fair view of the merits of the two methods, whose advocates have shown so little appreciation of the other school.

In speaking of heredity it has become usual to commence by pointing out that we can only speak of heredity in respect of variations, while variation itself is only a partial failure of heredity; but we are not now concerned with this apparent paradox; our problem is merely—given the parents, predict the children—and we are not even specially concerned with the physiological mechanism by which the latter are determined.

Prediction is a matter of probability; in the case of Mendelian heredity we can with certainty predict the possible types of children of given parents, and say that these will occur in the familiar Mendelian proportions; and if enough offspring can be obtained the numbers actually approximate to the ratios required by theory. The results of biometric research are much more vague, but are capable of a much wider application; the probable measurements of particular organs of the offspring can be calculated from those of the parents, and those of the general population, and we have to take a large number of families of similar parents from the same population before the accuracy of the prediction becomes apparent. A single family may differ as widely from the result predicted, as a single offspring in Mendelian inheritance may differ from the rest of its family. Mendelism concerns itself with natural pairs of unit characters, each of which may affect a number of organs and measurements which are inherited in the simple manner discovered by Mendel; biometry deals with artificial measurements, and applies to them statistical methods which are equally applicable to meteorological or economic data; the only assumption is that a large number of independent causes are acting at random; this explains why their results are only true of populations; in single instances there may be only a small number of independent variables.

I had better begin by outlining the view of inheritance which I have taken up, since I shall be continually using the ideas involved. On this theory the inherited nature of any living creature consists of a large number of Mendelian characters; from the moment the ovum is fertilized the creature is affected by its nurture or environment, so that different creatures with the same inherited nature will manifest every kind of variation from their true type; the independent causes are quite indistinguishable, and will affect the organism in innumerable ways. This variation due to nurture can only be treated by statistical methods; luckily in most cases it appears to be small, and still more luckily it is not inherited.

In case it is not superfluous I shall try to give a sketch of Mendelism. The simplest case is that of the blue Andalusian hen; for years breeders have known that these birds would not breed true; there were always black and speckled white chicks in the brood; if they had taken the trouble to count the number of each they would have found that half the brood was blue each time, a quarter were black and a quarter white. This is a simple case of segregation; the black and speckled white are pure breeds, homozygotes as they are called; when crossed all their offspring are heterozygous blue. Blue crossed with black gives a half blue and a half black; with speckled white a half are blue and a half speckled white. It does not matter what the ancestry of the birds was; the offspring can be predicted simply from the parents.

In most cases the heterozygote is indistinguishable in appearance from one of the pure types; this is then called the dominant, from the old notion that its inheritance was stronger and dominated the weaker or recessive type. A case of this occurs in Mendel's original work on garden peas; starting with short and tall varieties, Mendel found that the cross was tall, tallness being dominant, and was astonished to find that these tall heterozygotes gave one offspring in four of the short recessive type.

Perhaps the greatest simplification introduced by Mendel's discoveries is the fact that different pairs of characters or allelomorphs are inherited independently of one another. For instance, maize grains may be either white or yellow, yellow being dominant; they may also be either smooth or wrinkled; if a plant heterozygous in both characters be self-fertilized, all four types will appear, and the proportion of yellow grains to white will be the same, that is three to one among the smooth grains as among the

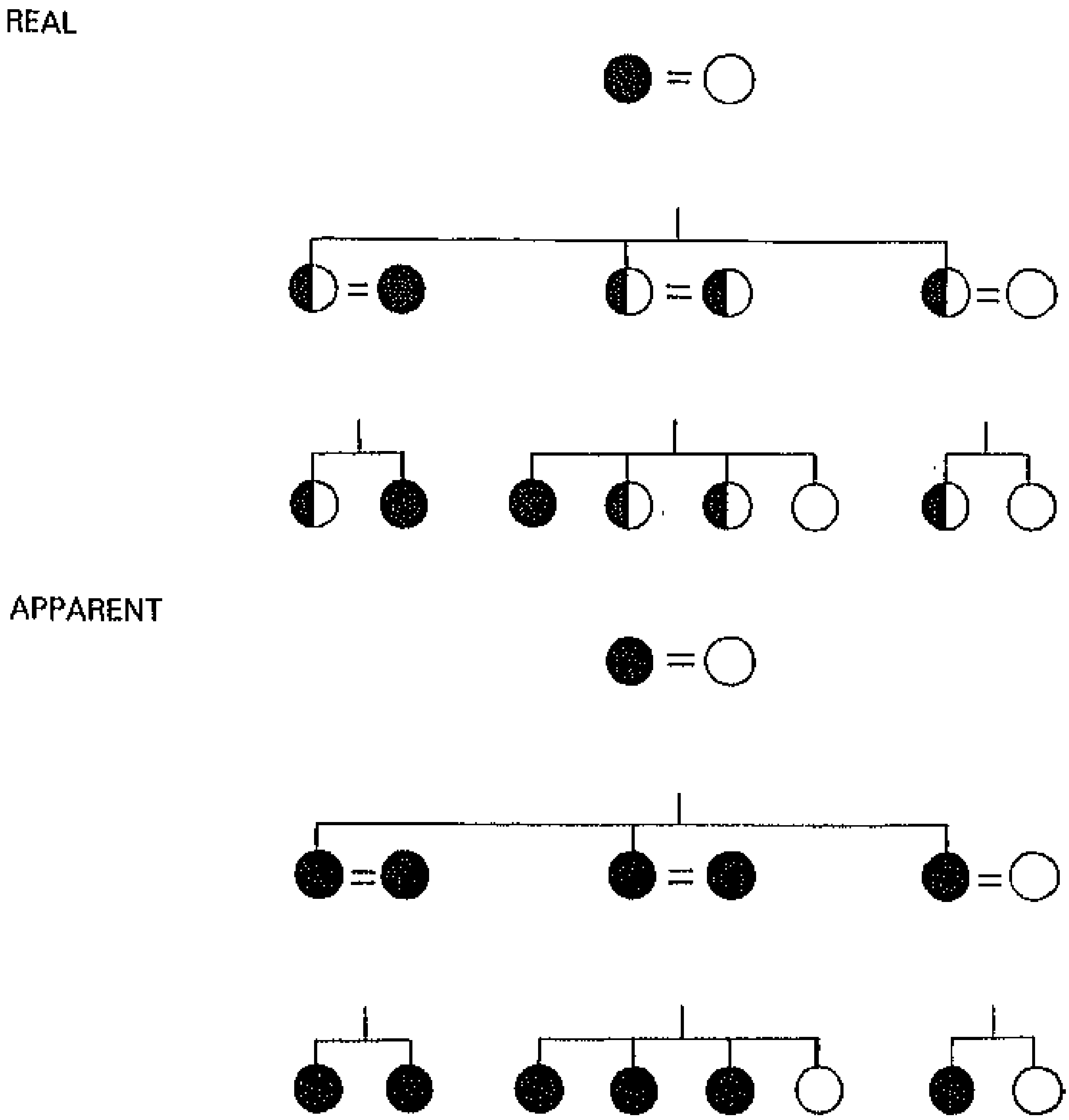


Fig. 1. Fisher's chart, showing 'real' and 'apparent' differences (corresponding to genotype and phenotype) for a pair of allelic genes with dominance.

wrinkled. Besides its admirable simplicity this segregation enables a breeder to create new pure strains; for instance, starting with a couple of grains, one white wrinkled and the other yellow smooth, you could in a few generations produce white smooth and yellow wrinkled grains which would breed true as long as they were wanted.

A number of Mendelian pairs have already been worked out in the case of men; among animals and plants new and valuable races have been created by combining different qualities. For instance, a valuable rust-proof wheat has been obtained by crossing the old rust-proof wheat which gave a poor yield with a wheat which yielded a good crop but was subject to rust. The first cross was heterozygous in both factors, but one-sixteenth of its offspring was pure-bred in both desirable qualities. Suppose we knew, for instance, 20 pairs of mental characters. These would combine in over a million pure mental types; each of these would naturally occur rather less frequently than once in a billion; or in a country like England about once in 20 000 generations;[2] it will give some idea of the excellence of the best of these types when we consider that the Englishmen from Shakespeare to

Darwin (or choose who you will) have occurred within ten generations; the thought of a race of men combining the illustrious qualities of these giants, and breeding true to them, is almost too overwhelming, but such a race will inevitably arise in whatever country first sees the inheritance of mental characters elucidated.

A large number of rare defects among men are now known to be Mendelian dominants; colour blindness, brachydactyly and the form of insanity known as chorea are among these; the inheritance of these is easily traced, since half the offspring of any affected person will be affected; the case of colour blindness is peculiar in being recessive in women.[3] These would all be stamped out in one generation by prohibiting affected persons from pairing. I venture to propound the hypothesis that there is a still larger number of recessive defects, by one or more of which almost everyone is affected; I suggest this first to explain the sporadic occurrence of defects in the children of healthy parents. Thus, if a recessive defect existed in one person in a thousand,[4] it would not become apparent unless two such persons were to mate, and then a quarter of their children would be affected; so that we should notice a sporadic defect affecting one in four millions.[5] Secondly, to explain the defects, which are well known to follow inbreeding; if there were a thousand such rare recessive defects in a mixed population, each member would on the average have one. A brother and sister each have a half chance of inheriting each of the defects of their parents; if they are mated the chance that they both have it is one-quarter, and the chance of each of their children showing the defect is one-sixteenth. If we knew the proportion of such children, who are in any way defective, we could calculate the average number of recessive defects in each healthy member of the popu-

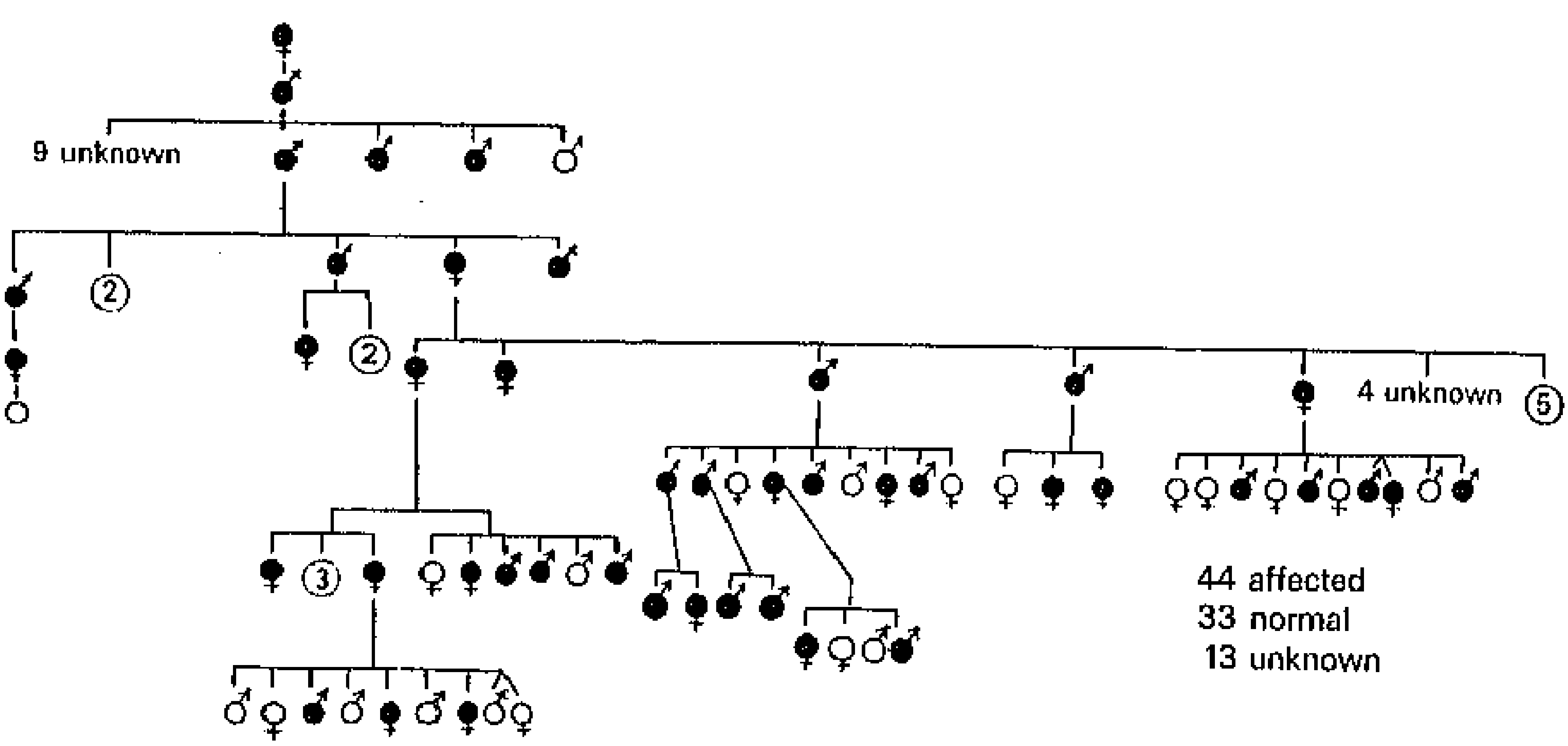


Fig. 2. Pedigree showing segregation for the autosomal dominant trait brachydactyly. (Condensed from Fig. 28 in W. Bateson (1909) *Mendel's principles of heredity.*)

lation. With cousin marriage the danger is divided by four; each of the two common grandparents contributes its defects, but the chances of each occurring is only one in 64. For uncle and niece the danger is the same as for cousin marriages, having four common grandparents, being one-sixteenth for each of the recessive defects which we are supposed, on the average, to possess.*

Among animals and plants the number of allelomorphs known to scientists is rapidly increasing; they have been especially successful in solving problems of the inheritance of colour. The case of mulattos used formerly to be urged against the universal applicability of Mendel's method, but it is now known that crosses of black races with white do not result in a uniform blending of the colours, but that some half-breeds are quite black and others nearly white; it is probable that there are several factors involved, but as with other human characters it is unlikely that any difficult problems can be quickly cleared up, owing to the racial and economic difficulties of experimental breeding.

The theory of inheritance on which the biometricians based their researches was framed before the rediscovery of Mendel's laws; the spontaneous variations which are at any rate partially inherited are supposed to be capable of taking up any of an indefinite range of values for each organ; by taking a sufficient number of measurements, say of human stature, we can construct a frequency curve,† showing the number of individuals per million of population, whose heights lie within successive inches on the scale. If, as is the case with human stature, the measure is determined by a large number of small independent factors, the frequency curve will be of the important normal type, and can be completely specified by knowing the mean value, and the standard deviation, which is a most convenient measure of variability.

Among the beautiful and ingenious contrivances which biometricians have devised, perhaps next in importance comes the correlation table; and here we have a measure of inheritance itself. Suppose the million men, which we measured for the frequency curve, eventually become fathers. Consider the sons of all the men who occupy a given range, say from six feet to six feet one; they also will form a frequency curve; their mean is found to be taller than the general population, showing that there is a positive correlation; it will be shorter than their fathers were, showing a regression toward the mean of the population; actually their mean will be about halfway between these two values, and this is found to be true whichever group

*The theory I have here suggested requires that a strain free from defects may intermarry to any extent without harm; the successive dynasties of the Pharoahs, who habitually married their sisters, must have been such strains; marriage with half-sisters would in their case have been the more dangerous course.

†See Normal Curve

of fathers is chosen. The coefficient of correlation is then said to be about one-half. Coefficients of correlation have been worked out in a large number of cases, between all sorts of characters; the method may of course be applied to different organs of the same individual, and as such, will ascertain the numerical measure of the 'correlation' to which Darwin attached so much importance.

The value of biometrical work is largely due to the fact that the actual evolution of new species in the past is a question of populations, and must have taken place in the way indicated by statistical methods. The synthetic breeding required by Mendelism could never have taken place in a state of nature; the strains would never have become pure, until a slow and continuous selection had long acted on the whole population. Gradually the breed would improve in those qualities which were of importance; the work which a breeder could now do in three generations might take a hundred years for the slow haphazard elimination of nature to accomplish.

It has been shown by Karl Pearson, on whose mathematical work the whole science of biometrics has been based, that a number of pairs of Mendelian allelomorphs scattered at random in a population would serve as the independent arbitrary causes which biometricians require. On this basis he has worked out the coefficient of correlation between parent and child, and finds that it should be one-third if dominance is complete, and one-half if there is no dominance, i.e. if the heterozygote lies mid-way between the pure races. The coefficient found experimentally is usually about one-half, which seems to indicate that the factors which determine the principal measurable quantities are to be regarded as exhibiting no dominance. At first sight this may seem a curious discrepancy from the ordinary Mendelian results, in which dominance is an almost universal phenomenon; but it must be remembered that the majority of these results refer to colour inheritance, which is apparently determined by the presence or absence of some enzyme or ferment, capable of producing the colour; the heterozygote also contains the enzyme, possibly only as a half dose, but this is sufficient to determine that the pigment is produced. It would not be at all surprising if allelomorphs relating to structure showed imperfect dominance, or no dominance at all.[6]

One of the great beauties of biometrical work is the certainty of the results obtained; biometricians avoid all the difficulties of abstract theories, they deal only with observations; and even if their observations are full of small errors, and they probably are, they appear to be able to squeeze the truth out of the most inferior data. The probable error can in every case be calculated, and though possible error is unlimited, the probability of large errors can be shown to be very small. I was recently impressed by the potency of the theory of probabilities in this respect; if you put a kettle over a fire it will probably boil, but it is not a certainty; it may freeze; it is true that the odds against such an event are very large; but it remains a possibility, or so my 'theory of gases' tells me.

It is interesting that Mendel's original results all fell within the limits of probable error; if his experiments were repeated the odds against getting such good results is about 16 to one. It may have been just luck; or it may be that the worthy German abbot, in his ignorance of probable error, unconsciously placed doubtful plants on the side which favoured his hypothesis.[7]

The interest of biometrical work for eugenists lies in the fact that Francis Galton employed this method, the only one then open to him, to show that human characters are as strongly inherited as those of animals, and mental characters as much as physical. Karl Pearson has collected data of school-children and has established the fact that all the mental characters for which he has data are as strongly inherited as are physical measurements. In his *Hereditary genius* Galton treats of mental and moral characters on the assumption, now seen to be fully justified, that intellectual and moral excellence follow the normal curve, or what is known as Quetelet's law; he arranges men in 14 classes, seven above and seven below the average, lettering them from the centre from A to G. Little 'f' and little 'g' are insane or idiotic, little 'd' and 'e' are stupid and often feeble-minded; thence we rise to the bulk of the population lying from c,b,a,A,B, to C, which is the level of the ordinary foreman of a jury. D and E are able, resourceful men to whom most of the prizes in life fall. F and G, Galton described as eminent; they contain about 1 in 4000 of the population. They are the men to whom all advances in thought are due, they produce all the best literature, give us leading scientists, doctors, lawyers, and administrators: in *Hereditary genius* Galton shows how strongly such talents are inherited; and it is of the utmost importance to select such men from whatever class they may be born in, to enable them to rise in the world, to encourage them to marry women of their own intellectual class, and above all to see that their birth-rate is higher than that of the general population. Most of them rise inevitably to a comfortable position; it is natural that they should marry into families of high if not conspicuous ability; but at present, there is no doubt that the birth-rate of the most valuable classes is considerably lower than that of the population in general, and conspicuously lower than that of the lowest mental and moral class of the population.

Biometrics then can effect a slow but sure improvement in the mental and physical status of the population; it can ensure a constant supply to meet the growing demand for men of high ability. The work will be slower and less complete than the almost miraculous effects of Mendelian synthesis; but, on the other hand, it can dispense with experimental breeding, and only requires that the mental powers should be closely examined in a uniform environment, for instance, of the elementary schools, and that special facilities should be given to children of marked ability. Much has been done of late years to enable able children to rise in their social position. Still we may as well remember that such work is worse than useless while the birth-rate is lower in the classes to which they rise, than in those from which they spring.

2. Social selection

Paper on 'Evolution and Society' read by Mr R.A. Fisher, Caius College, (Chairman of Committee), at sixth undergraduate meeting of the Cambridge University Eugenics Society in Mr W.B.G. Batten's rooms, S. Tree Court, Caius College, on Wednesday, 13 March 1912, at 8.30 p.m.

One of the most interesting things about Darwin's explanation of the origin of species is that scarcely anything need be assumed about the actual nature of species, as evidence that natural selection occurs; the same process is in progress with respect to languages, religions, habits, and customs, rocks, beliefs, chemical elements, nations, and everything else to which the terms stable and unstable can be applied. The only things required of a species are the capacities of variation and inheritance and although in examining and analysing these two capacities we may come across the most complicated properties in fact, and the most delicate distinctions in theory, yet the only thing necessary for natural selection is that those which are suitable to survive shall survive, and those which are unsuitable, unstable we may call them, shall cease.

Instances are familiar enough; there is a parasitic worm which infests the gullets of parrots; the worm tickles the parrot's throat, the parrot coughs over its food, and other parrots become infected; the worm, I imagine, had no intention of making the parrot cough, but the fact that it does so is a vital point gained in its struggle for existence. The habit of playing bridge survives in a very similar way; the habitual player finds himself driven quite involuntarily to infect others with a similar passion. The game of bridge cannot be said to have any desire to recruit fresh adherents, but I have no doubt that cards would never have come into use at all, if they could only have been used for solitary games of patience.

When dealing with the matter in such a very general manner as is illustrated above, we may use the idea of an organism in a very wide sense; a habit like smoking may be said to be parasitic on an individual, or on a class, or on a nation in which it has become habitual; on the other hand, the hosts which support an institution like family prayers are the household, the family, or the religious sect which encourages the institution. In speaking of parasites too, it is clear that these parasitic institutions are not necessarily evil; this is true even of animals; for instance, I believe the human stomach could not digest cellulose were it not for the action of a colony of bacteria, which performs the necessary katabolism. Besides this, parasitism is not a sufficient term to apply to the general relations of organisms; indeed we may say that every form of symbiosis found in the animal kingdom, is paralleled, usually with greater complexity, and more perfect development, in human society. The terminology too in the latter case is so much more varied and complete that it is at first difficult to see that all the modern social problems, for instance of centralization or decentralization, of personal freedom or regimentation, of differentiation of the sexes and specialization of the classes, have been faced under other conditions in the animal kingdom, and solved in Nature's provisional, tentative way by the simple, pragmatic method of trial and error. And it is worth noting that the solution which commends itself to Nature, and which is of interest to us, as that which will be adopted by the future, is characterized not by the greatest happiness, or by the most magnificant realization of human ideals, of this age or of any other, or by any other such considerations, but solely by its stability and power of survival.

An instinct from the external point of view is a tendency to perform some definite act or series of actions under the stimulus of a suitable train of circumstances; the term is rightly restricted to those acts which have some purpose by which the animal benefits directly, or indirectly in furthering some symbiotic alliance. From the psychological point of view it is a motive or desire depending on the idea that the man's state is more desirable, more pleasant, more happy if the instinct is obeyed than if it is not. Pleasure is Nature's bribe to persuade a conscious mind to obey its instincts. The terms pleasure, happiness, contentment refer to states which differ in their durations, and differ in their activity; it is as well to emphasize the similarity of their origin as due to the need of persuading a free will to conform to the courses which selection has shown to be best.

Now if our object were the greatest human happiness, would we succeed by producing a race whose instincts exactly coincided with their economic needs? It will help us to answer this question if we observe that the more complicated an instinct is, and the more difficult to perform, the greater is the pleasure derived from it. Indeed it is necessary than an animal's interest should be centred on those objects which are hardest to obtain; the greater effort requires the greater reward. Among carnivorous mammals the great problem is to obtain food, and their highest pleasure seems to be in hunting and eating; among men selection seems to have acted most ruthlessly by failure to obtain a woman, especially during the immense periods over which female infanticide, often combined with polygamy, seem to have prevailed, and the result is that half our poets devote their labours to the pleasures of love. This consideration by itself suggests that our pleasures will be of a tepid nature if ever our instincts become easy to obey, but we have another side light on the problem. The very existence, real or apparent, of Free Will implies a multiplicity of possible courses, a conflict of instincts; if ever the instincts become so perfectly adapted to economic needs that the wisest course is inevitably followed, we should have no choice, no need for motives, and rewards, and penalties, nothing but an automatic reflex action.

Although we may agree that this economist's paradise with its utilitarian instincts would be a thoroughly undesirable arrangement, it remains to be considered whether or not it is an inevitable one. A society of amoebae in some dim pre-Laurentian age, might well be imagined as discussing how undesirable it would be if free-swimming protozoa with all their faculties intact, contractile, irritable, capable of absorbing food, and of reproduction by division, should ever bind themselves together to form a many-celled animal, should degrade or lose one or more of their faculties in specialization for some particular function, should lose their free motion, and live out a sterile life cramped in a wall of cells as inert as themselves. They might have argued thus and yet overlooked the fact that if these organized societies were more efficient in the struggle for existence than disorganized units, they would certainly come into existence and increase in organization and perfection by competition with one another, until their cellular structure were barely recognizable. And further, that associated with these societies would arise a mind, not associated with one cell or another but with the whole society, beside which the mind of an amoeba would be, as it is, utterly indiscernible.

This process of co-ordination, of integration of units into societies has been carried a step further among the social insects; here, at any rate, the great problem of reproduction has been solved in precisely the same manner as in the self-fertilizing hermaphrodites of the animal kingdom. Queens and drones are produced which by their union cause an immense increase in the number of insects and finally [lead] to the production of a fresh hive. In these respects an ant hive is very similar to, for instance, a fresh water polyp. The subjection of the ants on the one hand, and the cells on the other, to the needs of the whole, has in both cases been established by intercommunal competition. The complicated and highly perfected instincts of the workers have been produced by the natural selection of those hives in which these instincts were well developed. There is no conflict between the interests of the family and the nation, which in human society constitutes the central problem in eugenics; where those individuals who are of most use to the state, and who will sacrifice themselves most readily for the common good, are often prevented by that very sacrifice from procreating their valuable kind. Among social insects the instinct of self-sacrifice may be completely developed, since the only chance of reproduction lies in the survival of the hive.

Human societies are not so far developed as those of insects, and are very far from the complete cell-socialism of the animal body; still it is obvious that the best organized will survive, those in which every class is well cared for, and correspondingly every class performs its functions regularly and without interruption; the nations in which moreover there exist highly skilled and efficient specialized members will reach a higher degree of organization than those in which the members are unskilled although efficient in a general way. The great problem is how far will the individual come to act as a mere part of the social machine, with his instincts perfectly adapted to his life of social service.

We may admit that efficiency in the petty duties prescribed for him by the state is an economic factor which may determine the usefulness of the ordinary man in times of peace; and it is possible that as armies become more elaborately organized, no higher qualities will be required of him in time of war. Although here history is against our argument in showing several instances of enormous, wealthy, highly organized nations having broken themselves in trying to subdue some small, poor, high-spirited race, to whom such social organization would smack too much of servility, and who valued their personal liberty more than wealth. If, however, this is not so in the specialized armies of the future, we can only look for the qualities which men admire to some small ruling caste who may limit the energies of the great national machine. And here too the question arises, 'Will this great organized nation, so like an animal organism in its mode of origin, acquire a Mind, not residing in this man or in that man, but in the whole community of men?' It is possible that some such instinctive groping after the idea of common obedience constitutes the social value of Theism, and it certainly is related to the Catholic notion of the corporate unity of the Church. If this is the fact, that a Mind will come and take control of an organism as soon as it is sufficiently organized to obey, as one animal, just as minds have taken possession of those colonies of cells which we call men, then there will be no need of a ruling caste, with phenomenal intelligence, but all men will act instinctively as parts of the vital mechanism of a Greater Being.

There is another point of view from which we may follow the same analogy; the original free-swimming cell was composed entirely of different forms of that strange substance called protoplasm, which is, practically speaking, live matter; in the animal and vegetable bodies, although they are made of cells, all sorts of other materials of organic origin come into use in the structure; much dead matter is deposited as carbonate and phosphate of lime in our bones, the wood fibres in trees are principally dead cellulose, and a hundred more cases might be cited, but still the body is built out of cells and their products, and cells have to devote themselves to special purposes, such as nerves, or to secreting the material needed in building. In a hive of insects quite foreign matter is utilized in building the combs for honey, and for other purposes; showing that living matter has extended its dominion to substances outside living organisms. Finally, among men all manner of inorganic material has been added to the dominion of the life-force, so that we have houses of stone instead of cell-walls of cellulose, wires of insulated copper instead of living nerves. Indeed it is the lack of communication which seems the great bar to a communal mind among insects; if their sense impressions could be received at a central exchange, there would be a co-ordination in the movements of the hive which would resemble, at any rate, the working of a single intelligence. But it should be noted that this external material besides aiding co-ordination, to some extent renders degradation unnecessary. As an organic substitute for the telegraph we might have to post men, like the Earl of Queensbury's cricketers, along the route, to throw the message one to another. Men bred and specialized for this purpose might be contented, but they would not be men.

After all we may still hope that the magnificent qualities and capabilities of the best type of man will render specialization unnecessary. And that the small spirited nations were right in believing that liberty was better than regimentation.

Notes

1. An uncorrected copy of this paper was incorporated in Norton, B. and Pearson, E.S. (1976). A note on the background to and refereeing of R.A. Fisher's 1918 paper 'The correlation between relatives on the supposition of Mendelian inheritance'. *Notes Rec. R. Soc. Lond.* **31**, 151-62. Fisher's copy of the paper, given here, includes his original footnotes, diagrams, and corrections of typographical errors.
2. With 20 gene pairs there are $2^{20} = 1\ 048\ 576$ different pure or homozygous genotypes. The frequencies of these genotypes in a population must depend on the gene frequencies and the system of mating, but Fisher does not mention this aspect of the problem. His typescript gives the frequency of each of these genotypes as rather less that 1 in a *million,* but on his copy Fisher has written in *billion* to replace million. Once in a billion (10^{12}) would seem to be roughly equivalent to once in 33 000 generations, if we take 30 years for the length of a generation and about 1 000 000 births per annum. Although the same frequency of 1 in 10^{12} would also be appropriate for an F_2 progeny with 20 independent gene pairs, it scarcely seems possible that Fisher was thinking of this example somewhat loosely as an extension from the synthetic cross involving two factors in wheat which he had just considered. Later on he writes, 'the synthetic breeding required by Mendelism could never have taken place in a state of nature'.
3. The influence of W. Bateson's book, *Mendel's principles of heredity,* is clearly evident. Fisher's reference to colour blindness as 'peculiar in being recessive in women' agrees with Bateson's description—although by 1911 E.B. Wilson had, in fact, suggested that the genes responsible for the common defects of colour vision were on the X chromosome. Like Bateson, Fisher does not mention linkage. Also in conformity with Bateson, he uses *allelomorph* but not *gene,*

genotype, or *phenotype*—terms which were introduced by Johannsen in 1909. However, Fig. 1 shows that Fisher was making the same basic distinction as Johannsen between genotype ('real') and phenotype ('apparent'), a distinction of great importance in understanding the action of selection.

4. i.e. in the heterozygous state.
5. In other words, if the frequency of the recessive gene is $q = 1/2000$, then the frequency of affected persons is $q^2 = (1/2000)^2$ or one in four million. It is perhaps surprising that Fisher does not introduce the concept of gene frequency here. Though he was apparently unaware of G.H. Hardy's 1908 paper giving the relationships between the equilibrium genotypic frequences in a random mating population, one can scarcely doubt that Fisher would have found it easy in 1911 to derive the general law of binomial square genotypic frequencies and also to introduce the concept of gene frequency.
6. Pearson, assuming complete dominance, had argued that Mendelism could not account for the observed correlations between relatives for measurable quantities, whereas Yule had suggested that it could—if incomplete dominance were taken into account. Fisher is here concerned to offer some reasons why dominance might be complete for colour inheritance but incomplete for genes affecting structural characters. The interesting suggestion that dominance in colour inheritance is 'apparently determined by the presence or absence of some enzyme or pigment capable of producing the colour' perhaps arose from Fisher reading in *Mendel's principles of heredity* about Garrod's work with alcaptonuria which, Bateson says (p. 233), 'must be regarded as due to the absence of a certain ferment'. Fisher later showed (*CP* 9) how assortative mating would increase the correlations, which Pearson had found to be too low with complete dominance, and that for a quantitative character such as height, dominance made an important contribution.
7. Fisher (*CP* 144, 1936), after a detailed study of Mendel's work, concluded, 'the data of most, if not all of the experiments, have been falsified so as to agree closely with Mendel's expectations'. Clearly, by 1911, Fisher was already aware of the exceptionally close agreement of Mendel's data and expectations.

3 DARWIN-FISHER CORRESPONDENCE 1915-1929

Darwin to Fisher: [*August 1915 or earlier?*][1](*a*)

Problem Imagine a species composed of a group of genotypes, all of which breed perfectly true as regards their average descendants, or the parental correlation coefficient being 1.0. Imagine these genotypes as regards any one character to be distributed about a central form according to the normal law of error. Then imagine these forms to begin to fluctuate, the fluctuations not being inherited.

What is the law of ancestral descent?[2]

Does not the parental correlation coefficient merely indicate a relationship between the standard deviation of the genotypes before they began to fluctuate and the standard deviation of the fluctuations? ...

How does such an ancestral law of descent differ from what is found to exist?

2nd Problem If there are mutations and fluctuations, in what conditions if any do the fluctuations help in the action of natural selection? ...

Darwin to Fisher: [*August 1915 or earlier?*] (*b*)

Thinking over your sexual selection point again, I see how *an* aesthetic taste is aroused through the desire to select the healthy; and I am not sure if this has been remarked on elsewhere. But further than that I as yet fail to follow. Take butterflies. The male beauty would on an average be more prolific than the non-beauty. But this would be because he *is* sought after by the female. But take a female who cares for male beauty *less* than the average. Would she not get a mate all the more easily, having the ugly to pick from? Would she not be more prolific on the average? This would only be harmful to her stock if it led her to prefer the unhealthy. If it made her take the male less exposed to danger, it would benefit her stock. But possibly I don't quite see your point. Don't write on this. I am only writing because it comes into my head.

One more word about my problems. I am, as you see, building up ideal conditions and seeing how far they work like nature does work. You say the parental correlation = grandparental = $\sigma^2./\sigma^2$, on my suppositions. This is, I presume, *ex hypothesi*. ... Take such a relationship between the σ of the fluctuations, and the σ of the immutable characters of the factors as will make the correlation coefficient between father and son = 0.5. Problem: what will be the c.c. between grandfather and grandchildren? If it works out at 0.3, we have, as it were, imitated nature. I have no doubt that if I was not stupid at mathematics I could answer this from what you have said. Don't trouble to write. I am only suggesting points that I should like to talk about. ...

Darwin to Fisher: 3 September 1915

Thank you for your letter. I will answer your points in the order you raise them.

As to my 'first problem', I gather that you think by a scheme of genotypes and fluctuations you can, as it were, imitate the facts of nature. I do want to 'explain' the regression we know to exist. We will have another talk on this subject, as it interests me *much*.

As to sexual selection, I hope you will get a paper written for the October journal.[3] I expect you can make an interesting point. I won't say in advance how much I shall agree with you. But I do want discussion with differences of views, as it is only in that way that the truth emerges.

Then as to the blunder, Pearson's or mine as the case may be. *I* shall not move in the matter, but naturally I should like to see myself proved to be right.[4] I want to think mainly of what will do Eugenics good, and at home I was brought up to believe that controversy with individuals was a great waste of time. Supposing Yule[5] said you were right, should you write something on the point? Where for? It would make Pearson your enemy, I fear, and that should not be forgotten. If for our journal you should write, then I must have some responsibility, as President of the Society. It would be easy to write a note saying that I had in the July 1913 journal in effect expressed a wish that my views should be criticized. Then quote offending passage. Then say that I had said in the Oct. 1913 journal it had been pointed out to me I had made a blunder. This, you could say you presumed from *Biometrika*, was from Prof. Pearson, and it was little wonder that I accepted his Correction, as he is the leading authority. But you hold I was right. Then give your reasons, and show why question is of some importance. Now in all this I am thinking on paper rather than in the least dictating to you. I am wondering whether if you are confident you are right, and if you did intend to write something, whether it would not be best to write out your remarks in their final form, and submit them to Yule, or get us to do so. I should be bound to get assurances you were on the right tack before publishing in our journal. For I cannot profess to judge myself, and Schuster[6] agreed I had come a howler.

It would be tempting to bring in Galton's name and say one wonders what he would really have thought! But this would only embitter the controversy, which may be bitter enough anyhow. I doubt if P. is honest enough to confess an error.

Darwin to Fisher: 5 October 1915

I want to bother you once more about my inheritance hobbies, as I may now find time to work at them a bit.

To remind you of what I said before, first imagine a number of genotypes of pure lines, the genotypes as regards each character being normally grouped about a centre. Then imagine each genotype to begin to fluctuate. Then we shall have a state of things in which we can account for the regression of the son as compared with the father. ... Now according to Pearson the correlation coefficient of father to son is about 0.5, and ... the correlation between grandparents and children is often about 0.3, and it seems to me the problem is: how nearly can this comparison between the parental and grandparental correlation coefficient be accounted for almost entirely as a case of random mating regression? If there is any selective mating, this will lessen the regression. If the regression cannot be at all nearly thus accounted for, there is something wrong in my views. This is the main point on which I should like your help. I have looked through your old letters, and I think I ought to be able to answer this question myself. But I cannot.

One other less important point: I gather that you came to the conclusion that fluctuations would not assist the action of natural selection. In thinking it over, I wonder if you have assumed that the death-rate is some function (it does not matter what) of the difference of the measure of the character from the median. If so, I agree that fluctuation will not help natural selection. But this is, I suspect, a law which is seldom even an approximation to the truth. Take an extreme case. In certain circumstances it is conceivable that all giraffes would die from want of long enough necks, whilst some would live if the fluctuations of neck length were great enough. Or again, all giraffes below the average in neck length might have equally bad chances of life, whilst the fluctuations of the tall-necked ones might materially affect the distribution of the death-rate in this long-necked half of the species. In short, it seems to me that whenever selection is lop-sided, fluctuations will increase selection, and that selection is generally lop-sided. Where the selection, as it were, centres about the median, does it not mean that the median is the best position, from which no progress can be made? And this is seldom the case. ...

Darwin to Fisher: 11 October 1915

It is good of you to take so much trouble. I am I fear rather stupid at these mathematical ideas, and I do not myself readily draw broad conclusions from what you write. I gather from what you say that your conclusions do not negative the idea that the system of hereditary correlation coefficients, which we find to exist, may be accounted for by scattered genotypes with fluctuations of the individuals composing them, though it does not go far to confirm it. I was surprised at your results before you took the fluctuations into account, and I wonder if you are breaking quite new ground here. You seem to get far nearer to an explanation of the facts than I had expected, but it still seems to me that fluctuations must be added, and here I do not know if you agree. Anyhow, all this seems to open up an interesting field for research for you Mathematicians.

I am only thinking of these questions in their broad and general aspects. I shall put down my ideas as clearly as I can on paper, and later we might have a talk to see if they seem to be leading in the direction of anything useful.

Did I tell you that I am a convert to your views on Sexual Selection?

Darwin to Fisher: [mid-October 1915?]

I also keep thinking over your problems. It seems to me, if I understand you right, that you are breaking up new and very interesting ground. ...

I am going on writing out my hypothetical views. If you can show that the figures can be explained without any reference to fluctuations, then things will become more simple. But I am provisionally assuming both fluctuations and mutations. ...

Darwin to Fisher: 23 October 1915

Herewith my notes. I suppose all about fluctuations,[7] or nearly all, will come out. In fact, a good bit of the first eight pages won't hold water. But that illustrates how your conclusions will simplify matters.

I have dealt with certain quasi-mathematical matters in this paper, and as it is by the impressionist method, I am here especially likely to come to grief.

I do not like my suggested definitions on second thoughts. We want the ordinary words to be used for the ideas in most common use. Large mutations will, I believe, figure but little in the future, and I don't therefore want 'mutation' only to mean a large change. How will the following do?

Modifications are differences between individuals which would not have existed if they had been exposed to similar environments.

Mutations are differences between parents and offspring which are due to changes in the germ plasm (Mendelian factors), generally of a permanent nature.

Fluctuations are differences in the members of a sibship due to different arrangements in the Mendelian factors.

Variations comprise all differences between the individuals of the same species.

I don't know that you will agree that you are dealing with fluctuations! It is difficult to get these definitions to run nicely.

[P.S.] ... Do you see Pearson has republished by Cambridge Press that article in *Biometrika*—the one in question?[8] He is a strange being. Whether correlation coefficients are a measure of the relative amount of attention to be paid to different questions is an important matter, about which statisticians seem extraordinarily uncertain!

Darwin to Fisher: [late 1915?]

I saw Udny Yule yesterday. He had asked me to write a paper for the Statistical. I have agreed—'On the statistical Enquiries needed after the War in connection with Eugenics'[9]—Heaven knows what I am going to say! But I now write because he told me that both Pearson and Snow have written on the lines you are now working on. Snow's was, I think he said, a paper for the Royal Soc.[10] He himself had written something short for (?) a congress of hybridization some five years ago in London (?).[11] I am not sure if you know this. It is a constant story in Science now to find oneself worked on ground already covered. But it is annoying. I thought I would let you know.

Darwin to Fisher: 18 January 1918[12]

The enclosed correspondence is very disappointing. There seems no end to the trouble. I think the Eugenics Society could run to £30. Do you see your way to putting up the balance?

Castleton House,
Old Aberdeen.

16 January 1918

Dear Major Darwin,

I have today the enclosed rather disappointing letter from Prof. Cargill Knott. It seems a pity that so rough an estimate was given before, for it led to the expectation that a subscription of £25 to £30 would make publication practicable. I suppose that the question now is whether Mr. Fisher's friends can rise to £43. I dislike the phrase 'or whatever the sum might be'. It is not for a well-to-do society to haggle surely.

Yours very sincerely,

J. Arthur Thomson

Prof. J. Arthur Thomson,
Natural History Department,
University,
ABERDEEN.

Royal Society of Edinburgh,
22 George Street.

14 January 1918

My dear Thomson,

The Council has considered the offer made by Mr. Fisher's friends to advance £25 towards the expense of printing his statistical paper. Mr. Fisher kindly sent the MS. back to me, and I got from our printers an estimate of the cost. ...

As the Council could not see its way in the present financial stress to give more than 10 pages for an abstract of the paper, i.e. about one-fifth of the whole, they are prepared to pay £12 towards the cost of printing this paper, i.e. fully one-fifth of the estimated cost. If Mr. Fisher and his friends could see their way to meeting the difference amounting to £43, or whatever the sum might be, then the paper would be printed *in extenso*. This is the position which the Council with great reluctance are compelled to take. ...

I shall keep the MS. by me until this matter is finally settled.

Yours very truly,
C.G. Knott
Gen. Sec., R.S.E.

Darwin to Fisher: 6 May 1918

I wrote to Professor Thomson about your paper in the *Eugenics Review*; he tried to square the Royal Society of Edinburgh, but failed. Then I found he was getting rather fussy and so possibly was Professor Knott of the Royal Society of Edinburgh. So I thought it advisable to clench the matter by sending Professor Knott £30, which I described as a practical guarantee that our share in the expense would be forthcoming. Do not trouble to send me your £15 till the matter is quite concluded. I may try to get them to go on with the printing now if I can, though this is doubtful. Why I write is this; I fear we must now break up the type of your article without our putting it in the *Review*. This is the fortune of war and cannot be helped. Shall we get two dozen pulled before it is broken up? It would not cost much and might be useful. For example, I don't know where to lay my hands on a corrected copy, by which to reset up the type in future.

Darwin to Fisher: 20 February 1919

... I have been doing a little work lately—rewriting a paper which you once read on the Postulates of Evolution. I think I shall be sending you one or two mathematical conundrums on this subject in the hope that you will kindly solve them for me.

Darwin to Fisher: 5 April 1919

Here is my paper on postulates. I have found it difficult to write, as it is in parts trying to put mathematical ideas into ordinary words, and it is in these parts I am most likely to have blundered. I should be very glad of your help in detecting howlers, and should also like a frank opinion as to how it strikes you in the broad. You will not like the multiple allelmorphs, but you must bear them as well as you can! ...

Darwin to Fisher: 13 April 1919

Thanks for reading and returning my paper. I have not yet fully digested your remarks, but we evidently don't see eye to eye. This may be want of clearness on my part, or muddling, or both.

I think we are using the words in the same sense, but am not quite sure. By a mutation I mean a change in the gametes from one generation to the next. You say, 'are not mutations essentially centrifugal?' Certainly not in my sense. But here my words may not be happily chosen. ... I do not see why a random mutation adds to the variance necessarily. ...

The heaping up of species, or the disappearance of intermediate forms, and the creation of new genotypes in the direction in which selection is acting seem to me primary puzzles not yet faced, and what I have been trying to do is to face them. ...

Darwin to Fisher: 13 May 1919

I have now had time to consider your letter of the 21st April, with which I find myself in general agreement. I think that to look at experimental work always tends to focus the mind too much on sudden changes as compared with slow effects. ...

I am sending you a letter which will serve as a testimonial. I believe it is more effective to write it in this friendly way than as a formal document, but I could easily adopt the more formal tone if you prefer it.

Darwin to Fisher: 7 August 1919

I was so sorry that I let you slip away from Cambridge without having a good talk. This arose through a misunderstanding as to the length of your visit. I especially regret it now—I hear through my wife that Pearson has made you an offer,[13] as I understand. I am astonished at it, as I should think you were too tarred with the Eugenics Society Brush. If you are refusing, I quite understand your feelings, and I would say nothing to dissuade you. But I cannot but be sorry in a way, for I know you are truly Eugenic, and it is very hard to find those that are. You could not be certain to succeed Pearson. I say this because I know something of that strange body, the University of London.[14] One cannot rely on their actions. But it would give a good chance. ...

Darwin to Fisher: [*22 August 1919*]

I am reading your manuscript,[15] and write as I read. After reading the first chapter I feel that you may make an exceedingly useful and interesting book. I think I did tell you of Brentano's paper[16] ... quoted in Pigou's *Wealth and welfare.* I believe that the Registrar General's office is now at work on the statistics of this question, from the last census, and getting confirmatory results.

Chapt. II does not please me so much; but this may merely be that we don't see quite eye to eye. But I do feel also it wants more orderliness. It is worth taking great pains with your first book, even though a book is an awful grind. I generally write a thing out, make a careful precis or analysis of what I have written so as to get the whole argument clear, and then write it all again. Huxley said he, often I think he said, wrote a thing out six times before he was satisfied.

Chap. II gives me a feeling—if I may speak frankly—that you are making a case to fit you preconceived conclusions. Limitation ought to, on your hypothesis, increase not only the objections to limitation but also sexual desire, and carelessness about the future, including the future welfare of progeny. Natural selection ought to have lessened such forethought, and to have made us more reckless in certain matters than primitive man. You must not take your facts only when they fit your theories and neglect theoretical conclusions when facts are not available. Civilization has increased our power of looking to the future, and added to the desire to limit offspring. In this respect, though it has not altered the instinct, it may have weakened the effect of the reproductive instincts ...

I do not think you make enough of the existing environmental causes of limitation, such as those I sketched in my statistical paper. It is for this reason I should like you to read Brentano if you have not done so. ... I like Chap. III ...

These notes are hastily written, and will be mainly useful, I hope, to show how much I want you to make a thorough good job of this work.

Darwin to Fisher: 23 August 1919

I am *very glad* indeed for your sake you have got the job.[17] It will, I think, suit you well. I am only a little sad that you may not have much time for Eugenics.

I sent your manuscript back yesterday with what I fear were rather inadequate remarks. ...

Darwin to Fisher: 31 August 1919

Thanks for your last letter, with analysis of Chap. II, which does make the matter clearer to me. With almost all you say, I am in agreement, and I am inclined to accept the importance of this factor[18] in racial decline. Therefore I am most anxious you should go on and make a good job of it. I doubt if I have any further useful criticisms to make at present, but will keep your letter and write if anything turns up. Where I am doubtful is as to your views as to the growth of conscience. ... The care of offspring is the most ancient and most highly developed of all the instincts. The religious ban on infanticide seems to me nothing but an expression of this fundamental instinct. Religion is always backing up the social instincts against the individual instincts, as in regard to murder. A pronouncement about infanticide might indicate nothing new as regards instinct. As to abortion, reason might have made it apparent that it was equivalent to infanticide, and therefore added a new force to the religious support to the very ancient social instinct. If you are right in thinking a great change in innate instincts can be so quickly developed, why do not celibacy and late marriages come under the religious ban? I believe fundamental instincts take *far* longer to develop, and that historical proofs of a change of innate feeling in such fundamental instincts must be accepted with great reserve. It would only be small changes of mentality I should expect to find. But I confess I am writing this rapidly with insufficient thought, and even if I am right, it affects your final position but little. ... *Don't* take much notice of this, as it is all so crude. But do go ahead. ...

Darwin to Fisher: 25 September 1919

I have no doubt you remember reading a paper of mine,[19] when you fell foul of my ideas of multiple allelmorphs. I should not care for your opinion a straw if you did not express it frankly, and I am grateful for that frankness. I have been going over the whole paper again, rewriting 9/10ths of it, but finding that my opinion on all essential matters remained unchanged. This has made me wonder whether you did fully grasp what I was driving at. You gave me the impression in your letter, if I also may be frank, that you had not fully realized the criticisms of Bateson and others against 'Darwinism'. I have in my paper given a brief account of the criticisms that seem to me valid. Then as to multiple allelomorphs, I have tried to get over the difficulty by dropping the name!! Now I wonder if you could find time to read it once again, with the pledge to be as frank as before if you don't like it. I don't know who would give me a good biological opinion on its merits. I don't want to write anything on evolution over the name of Darwin which can be described as nonsense. Don't scruple to say you are too busy, but if you have a little time to spare, where shall I send the paper? When do you take up your new work? ...

Darwin to Fisher: 14 December 1919

... You quote the *Origin* about each part of an organism being so beautifully related to its conditions that it could not have been suddenly created. But in Chap. II of the *Descent of Man,* my Father says he did not sufficiently consider structures neither beneficial nor injurious, and that this was 'one of the greatest oversights as yet detected' in his work. He then goes on to argue that uniformity of character would nevertheless arise from 2 causes. First, from uniformity of exciting causes. ... Secondly, he speaks of the effects of free intercrossing. But Mendelism has killed that argument.

You ask in your letter in what way specific differences differ from differences between varieties or orders. I don't know what answer men like Bateson would make. I myself think they are only differences of degree, not of kind. But I don't see how the variety heap is formed any more than the species heap, as regards useless characters. And even as to useful characters, where the change seems to have been brought about by changes of environment and where the different environments still exist, there is no reason why natural selection as ordinarily described should kill out the intermediates. ...

Darwin to Fisher: 20 August 1920

As someone said, one must not treat Pearson like anybody else. I think he means to be civil. But it is an astounding attitude to take up. To allow nothing to be published which does not back him up, or which he personally does not have time to read? & pitch into—it is going far.[20]

Now as to publication elsewhere; of course I am quite incapable of estimating the merits of your work. Nor do I know anything about the international journal you mention. ... Then how about the *Journal of the R. Statistical Soc.*? I am on the Council, and I could speak to the secretaries, and find out what they think semi-officially, if you like. But I forget who they are, and I feel it had best be done verbally. This I could do in October probably but not before. I think Greenwood is one. Let me know what you think about this, and whether you would like me to do this in spite of the delay it would cause. If so, may I show Pearson's letter confidentially? ...

Darwin to Fisher: 14 October 1920

I saw Dr. Greenwood[21] yesterday, and had a talk with him about your paper. He says that he fears that the Statistical Society could not take it, because they have to cater for an audience many of whom could not understand it, and they therefore have to limit the number of highly technical articles.

He would, however, be glad to send it on to Professor Gini for insertion in *Metron*, if you would care to modify it in certain respects.

In the first place, there must be some introduction, which I know you have had in view. In the second place, he would like certain phrases modified. He says that a great deal of friction arises between statisticians in consequence of the way they state things rather than because of the substance of what they state. He thinks you might put several sentences in a less provocative way. For instance, you speak of someone's interpretation of your remarks being 'so erroneous etc., etc.' Could not you say that 'this was certainly not the meaning I intended to convey', or something like that? Again, you imply that your opponents have criticized you without reading your paper, and Dr. Greenwood thinks that such implications merely irritate without doing good. In fact, he will recommend publication if all that is provocative is taken out, whilst everything that is mathematical remains in.

If I have expressed this rather clumsily please put it down to me and not to Dr. Greenwood, who spoke very nicely. ...

Darwin to Fisher: 2 April 1921

... As to the uniformity of useless characters, and the need for explaining the disappearance of intermediate types, it is my Father's very strong views on these points that affect me. The shape of a leaf is the type of a useless quality. The leaves of trees are so characteristic, but so unimportant apparently.

Darwin to Fisher: 10 June 1921

Many thanks for your two letters, although as regards some of the symbols it was putting mathematical pearls before unmathematical swine. I am sorry I cannot tell you anything in the way of statistics about the nature of wide ranging species.[22] ...

Darwin to Fisher: June 1921

I took away [the] Hagedoorns' book[23] to read and review, when I did not know what it contained. I have written out a few notes[24] which may or may not serve as part of a review, and a carbon of these I will send you before long. I think you will want to read the book, and, if you do, you could make a really useful criticism of the 'Hagedoorn' argument. Will you do so for the *Review*?[25] If so, I will send you the book by post. They would like the review before the end of July. You could incorporate all or none of my notes. I have hardly touched the Hagedoorn argument. ...

Darwin to Fisher: 14 June 1921

This is how it stands with regard to my blessed old centripetal and centrifugal mutation paper. I got it set up in type. Then I was tempted to send it you to read, but I thought it would be hard luck on you, especially as I know you could only repeat the statement that you did not like the idea. ... I know I shall not convert you, but you might keep me out of quasi-mathematical howlers. I wonder if you could find time to read it. It is about 60 pages of big print, with several pages of typewritten additions. You must not scruple to say you are too busy if that is the case, for I know I am making a serious demand. But I think it will be my last regular scientific paper, and I should never trouble you exactly in this way again.[26] ...

Darwin to Fisher: 28 June 1921

Now for your letter about my paper for which many thanks.

As to the inheritance of acquired characters, I was in truth arguing in my mind with those who (like my Father and brother) believe in it without believing in vitalism. ...

Now as to your second point. It is that interbreeding between 2 varieties, when the cross is not so good as the 2 types, will make for the appearance of infertility of some kind appearing. This is a point I had not thought of. But it is *your* point, not *mine*! ... The use of a paper like mine—if of any use—is to stimulate thought, and create rival suggestions like yours. Your suggestion shows how infertility may tend to arise between divergent types belonging to the same species when the mediocre type is less well adapted to the environment. It seems to me, on first thoughts, to be a very useful suggestion. Is it purely your own?

To put it bluntly, I think the choice before me is to publish, cutting out any regular howlers, or to scrap-heap the whole. I am quite ready to bag some of your ideas, but that must not go too far! That might result in complete disintegration.

Anyhow, can we have a talk, which might to me be very useful?

Darwin to Fisher: [July 1921?]

... Your other point is more difficult. Who but yourself has collected this evidence? And you have not yet published. I think you are very wise not to be in a hurry. The *Origin of Species* was brewing for 20 years. Lots of people have pointed out the decay of ancient civilizations, to which I allude as an incontrovertible fact. Also we have a great deal to show that wealth and infertility are correlated. I cannot allude to you till you have published; for, amongst other things, I must study that evidence before endorsing it. I did read some of it in manuscript, and frankly I felt in some particulars you were a little inclined to jump to conclusions.[27] This feeling may all disappear with your more mature work. ...

Darwin to Fisher: [August 1921]

... My present idea is to boil down all my papers into a book during the next three or four years. But I rather funk the task as my memory is, I think, not so good as it was. But I am much impressed with the fact that papers as permanently affecting opinion are of comparatively little use. Thus I hope when you are fully ready—not before—you will put your ideas into a book. But a book is an awful grind. ...

Darwin to Fisher: 5 November 1922

I do not think I ought to trouble you any more on the evolution problem, as I know I shall write no more about it. I hope to stir you up to write a great work on the mathematics of evolution. ...

It is true that Bateson set me thinking about useless characters; but my father's words affected me much more. In the *Origin* he speaks of species where they mingle being 'absolutely distinct from each other in every detail of structure'. In the *Descent of Man* he states that not sufficiently considering useless structures was one of the 'greatest oversights' in the *Origin*. He adds that 'it is, as I can now see, probable that all organic beings, including

Man, possess peculiarities of structure, which neither are now nor were formerly of any service to them.' He gives explanations which do not seem to me to be satisfactory. ...

Darwin to Fisher: 29 January 1923

... If genius had been due to a single factor, it would have been worth millions to try to pick out a male and female homozygous and mate them. But such a thing never occurs. I suppose ... bad single factor qualities are due to something dropping out of the genes. This would naturally lead to recessive qualities as a rule, but I don't see that it would inevitably follow. But why should not there be useful single factor qualities created in equal numbers and therefore often found in nature? I explain this partly by the adaptation of an organ being such an extremely complex and slow business that a number of genes are always, or nearly so, involved in the affair. ... Must pattern be quite as complex an affair as it seems at first? Can there be any lines of growth which help in the distribution of colour, and which remain anyhow? I can only conceive that the genes in these cases have been slowly evolved, and I do not now see how this is to be done without assuming the presence of slightly differing allelomorphs between which selection is possible. ...

P.S. ... I think the Stats. have treated you badly.[28] But I hope you will think twice before resigning. The fault lies with at most 2 or 3 individuals, even if more nominally consent. These men go in time and the affair is quite forgotten. If you now protest to the Council or resign, you will get the reputation, justly or unjustly, of being very touchy and easily put out. That reputation will not die out easily. Therefore you will lose by any action. The dignified course is that which makes you appear to say, 'I don't care a damn what you do or say.' Forgive me writing thus plainly.

Darwin to Fisher: 12 March 1923

Thanks for yours. My impression is that it would be useless sending your note again for publication—but it is but an impression.

I forgot exactly what I said in my last letter, and only to make it clear, if it was not so before, my opinion is that resignation is not your wisest course, though I am under the impression that you have been badly treated. ...

Excuse a scrawl, as I am not too fit today.

Darwin to Fisher: 15 March 1923

I feel sure Flux[29] is the senior editor, or at all events the man chiefly concerned.

This answers all you ask me, but I do not like to leave the matter there. You may well feel that I preach to you unwarrantably, but it is friendship to you which makes me risk annoying you. Please remember this in what I now say.

When there is a difference of opinion, both sides in very many cases have, or imagine they have, a grievance. And I am sorry to say Flux considers that your letters to the Society, or your action in some way, has not been courteous. I can't say more, because I only know it from Flux's letter to Mallet.[30] Now if you go to Flux, and if you give the impression—an impression he would adopt on entirely inadequate foundations—that all you want to show is how foolish the Society has been to refuse a very important paper by you, the only result of the interview will be a useless and unpleasant row. If, on the other hand, you cared to say that you were much perturbed to find that Flux felt you had been uncourteous, which was the very last thing you intended, and that you would like at a personal interview to put things right, then the interview might do good. And it would do most good if you took up the attitude that you do not care whether the Society does or does not publish your paper; that that is a matter of minor importance.

So many scientific men have destroyed a great deal of their contentment by heart-burnings about the reception that their works receive that I dread anyone starting on that path. I am certain the wise and the pleasant path is to do the work, let the reception of it take care of itself, and push on quietly avoiding as far as possible all controversy.

Thanks for what you say about my health. It was only a passing headache such as you often have.

Darwin to Fisher: 20 March 1923

I am glad you have taken my letter in the spirit in which it was written: that is all that I care about. I fear I can give you no more help. I do not understand Flux's attitude any more than you do. I expect he has got very much the mind of a government official, and looks on contributors to his review very much like subordinates in his office. I suppose a man cannot help being influenced by the life he leads. ...

Darwin to Fisher: [*April 1923?*]

I have been reading your paper on evolution [*CP* 26?] with care. It makes me see that mutations may not need to be as frequent as I thought. ...

Darwin to Fisher: 21 October 1925

I have been thinking at odd moments about the problem you told me you were writing about, and I want to put down a few ideas mainly to get them out of my own mind.

As to big mutations, I have no doubt they are generally harmful. But are not they rare and soon stamped out? If so, they are of no great importance in evolution.

As to small mutations, these are what I believe evolution mainly relies on, and it seems to me difficult to prove that they are more often harmful than not. The geological man who spoke about evolution at the British Ass. spoke of perfectly adapted organisms.[31] ... Perhaps there may be such a thing as an organism which is as perfectly adapted to its environment as selection can make it. In that case, *ex hypothesi*, every mutation must be harmful. ...

Darwin to Fisher: 19 November 1925

You very kindly said something to me a few days ago about reading my proofs,[32] and, if the truth be told, I had previously been considering whether I could ask you to do so. But do you know what it would involve? I estimate the number of words as somewhere about 200,000; and if I have made no serious blunder, it would mean reading about 7,000 words a night for a month. Before you decide to renew your kind offer, may I say very plainly what is the part which I should feel it very valuable if you would play? It is no use trying to improve my style. A man's style is himself, and it had better be left to show itself, good or bad. What I want is help in avoiding howlers, such as I am not unlikely to make. These may take many forms, from illogical arguments, statistical mis-statements, etc., down to wrong use of words, bad grammar, etc. ... May I also say that I know that when looking over proofs for another person, one is apt to think one ought to suggest corrections. I remember reading the proofs of one of my father's books, and that I pleased him by making very few observations. The fewer they are, the more the author rejoices. Of course you will disagree with me on some points, and I should be much interested to know where you differ in regard to the arguments I set forth. What I have tried to do is to show the general way in which I hold that racial questions should be approached; for I think that a few mistaken applications of sound principles do little harm. If you will kindly show me where you disagree in principles or arguments, I should be much obliged, but I am sure you will forgive me for not arguing the points, if any, which may arise, and for my sticking to my guns when I do so. These are the chief points to hold in view when deciding whether you will really undertake this tedious task of reading proofs.

One more question I must ask, and that is if you do undertake this job, whether you will allow me to celebrate the publication of my work by subscribing thirty guineas or so to your twin investigations. I should feel it anyhow a privilege to do so. The money must be needed by you in travelling expenses, clerical assistance, etc., and I should much like to push forward your work under the excuse of your assistance to me. Please do let me.

Possibly you will get a chance of reviewing my book somewhere. If so, don't scruple to make it a bit spicy by pitching in to me. ...

Darwin to Fisher: 30 November 1925

I found your kind letter about reading my proofs the next morning after I had seen you. I am very glad that you consent to do so. It was tactless of me to hang the two questions together, the triplets and my proofs; for it is really true that I want to promote your enquiries because of their value, and without reference to any other consideration whatever. I am very sorry that the finances thereof are in a bad way, and that makes it all the more pleasant to send you the enclosed cheque.

As to my book, it will interest me to know how much you differ as to birth control. What I have tried to do is to make it a storehouse of arguments rather than of facts, in the hope that this will make it useful for a longer time. I don't think that we shall differ as much as you expect in regard to what I say in my book. ...

Darwin to Fisher: 6 March [1926]

I understand you have left it to me whether to post the enclosed to the *Morning Post.* This places me in an awkward position. I think your letter is a very good one and temperately expressed. On the other hand I have been brought up with a very strong distaste for controversy and I would do a great deal to do anything to avoid such controversy within the limits of the Society. The balance seems to me to tell against sending the letter and therefore I have not sent it. I fully admit that in this decision I may be quite wrong.

[P.S.] The Dean,[33] who dislikes what we do, blows off steam in the *Morning Post*. I, with the authority of the Council, let fly in the *Spectator*. May it not be quits?

Rothamsted Experimental School,
Harpenden.
5 March 1926

Sir,

It cannot fail to be a matter of grave concern to all who are interested in the future of our race that the Dean of St Paul's should find himself opposed, on humanitarian grounds, to the policy of eugenical sterilization; more especially since in the opinion of many of us who have long studied the subject, this means affords the only *practicable* remedy for some of the saddest afflictions to which mankind is subject.

'Mutilation' is a hard word, and in certain cases may be a hysterical word. The dentist who pulls out a tooth may be said to mutilate the patient, and certainly this is a more severe operation than the simple section of the duct which is sufficient to render a man sterile. The horrible associations of the word mutilation are inappropriate because the patient voluntarily undergoes the operation and we do not urge the legalization of eugenical sterilization save with the consent of the patient. To this vital fact the Dean makes no allusion, and it has evidently entirely escaped his attention.

Drawing a tooth is a nasty business, but if it causes us suffering we do not hesitate to submit to its loss without a feeling of degradation. Much less should such be felt if the suffering is spared not to us but to our innocent posterity.

R.A. Fisher,
Secretary, Eugenics Education Society.

Darwin to Fisher: 1 April 1926

My dear Elisha,

Next time you see old Elijah,[34] give him my kindest regards, poke him in the ribs on my behalf, and say I know how glad he must be to see how much better his mathematical mantle fits you than his χ^2 test fits ... —you will know how to put it to make him laugh heartily. By the by, I hope he won't read my book, or get it, just after he reads this review. If so, I, like you, had better avoid meeting him in a dark lane. But I think you imply your wicked document [*CP* 49?] has not yet seen the light.

I hope we meet Wednesday.

Yours sincerely,

Leonard Darwin.

Darwin to Fisher: 14 June [1926]

I have just been reading your Essay Review[35] with very great satisfaction. I will not pause to enquire whether it is too flattering to my efforts, but I will say without doubt that as a brief general essay on Eugenics it seems to me quite admirable. ...

There is only one line to which I want to call attention, tho' only with reference to the rating of our premises!! You say 'not a science'.[36] Possibly you would reconsider this phrase with a view to possibly substituting words somewhat like the following—'not all Science but all its inspiration drawn from...'

Now if you have the slightest objection on the grounds of morals, style, or science to such an alteration please put it entirely out of your thoughts. ...

Darwin to Fisher: 15 September 1926

I wonder what you have been doing this holiday time, if so it is with you. ... I have *written* a 4000 word essay review on a book by one Berg, a Russian, called *Nomogenesis*,[37] with a preface of a laudatory character, by D'Arcy Thompson. It is the most definite and completely worked-out attack on Darwinism that I have seen, giving one plenty to answer; indeed too much, for it seems to me to be very illogical. Now I don't know what to do with my Essay. ... I should much like your frank opinion on it some day, if you should at any time not be too busy to read it. Should it be burnt, is the question.

When last we met, you were saying you might write a paper on the mathematics of evolution and Mendelism—that is badly expressed, but you know what I mean. I do hope this idea will continue to hold good. I have had a few thoughts as to points which ought to be cleared up, and if the spirit moves me, I shall write them down and send them to you.

Darwin to Fisher: [*late-September 1926*?]

I have read your paper [*CP* 59] with great interest. ... All I will now say is that it increases my wish that you should deal with the whole problem of selection mathematically. You will have a small audience, but it will gradually be realized that many of these problems can be attacked in no other way.

I don't know why you expect me to disagree with you about men of science and their critics. It is an odd fact that only a week ago I was asking my sister if she did not agree with me that it would be worth republishing the *first* edition of the *Origin of Species* (you can't now easily get it to read, and I have never read it, I believe) *because* it was written before my father had been subject to *any criticism whatever.* His extraordinarily modest nature made him especially liable to pay too much attention to what others said. Somewhere he declared that he had made the mistake at first of paying too little attention to the effects of environment—the direct effects; and it is tacitly assumed that his second opinion must have more weight than his first. I should like the first edition republished with a *few* notes as to where it would be very generally allowed that the last edition was better, and what the changes implied.[38] ...

As to what you say in your letter about the evolution of unpalatableness, I had not thought of the point till you mentioned it. Suppose a bird is in doubt, when food is plentiful, which would be the choicest morsel, a butterfly or a fly. Let him select to go for the butterfly, and to find it a regular tit-bit. Will he not *immediately* repeat his attempt? On the other hand, let him be slightly disappointed in the taste, and will he not go for a fly next time, possibly returning later to the butterfly hunt? May one not assume that the more quickly the one attack follows the other, the greater the probability that the two victims will be close blood-relations? If so, does not this open the road to selection. ...

[P.S.] ... I will send you *Nomogenesis* by post.

Darwin to Fisher: 5 October 1926

Thanks for all the trouble you have taken over Prof. Berg. I will consider carefully recasting the review into an article of some sort.[39] Some of it won't go easily into a general evolutionary talk, I fear. As to your proposal to give *Nomogenesis* to MacBride as a kind of emetic, possibly you might consider ... what are the chances of the poison being assimilated and not ejected, thus rendering the patient's condition quite hopeless[40]. ... It is a bold proposal. ...

Darwin to Fisher: 6 January 1927

... I thought of getting MacBride to propose a vote of thanks [after the Galton lecture].[41] My question is: who would be the best man to second the vote of thanks and to say with authority that we are still almost entirely ignorant of the causes of mental defect and that our knowledge is entirely insufficient to enable us to found a policy thereon? I can say a word or two, but it is harder when in the chair. It must be all very civil. ...

Darwin to Fisher: 29 July 1927

... I have just been looking at a book by Moore on Evolution and Religion—I forget its title—which made me rather angry. He is so unfair on my father and his views about Lamarck. He says my father never gave any credit to Lamarck. I know of nothing *published* by my father which is not expressive of appreciation of Lamarck as a naturalist. If you ever come across a *published* sneer, let me know. I mean not in letters never meant for publication. These were in truth merely letting off steam to a few intimate friends, who knew well how to discount them. I don't know why I write all this, except to blow off steam myself.

Darwin to Fisher: 1 November 1927

... I look on my letters to you in the light of pins, the pin pricks to urge you on with your great work on the mathematical theory of inheritance!

Darwin to Fisher: 22 January 1928

... We were talking of fecundity when last we met. I want to amuse myself by jotting down certain ideas, though I have a suspicion that they are really your ideas.

When the cuckoo began her nefarious practices, did she lay her eggs in other cuckoos' nests—which must then have existed? Do birds do this trick even now? It would seem the wisest plan, because the foster mother would then certainly be suitable to the task. Now if all birds allowed other birds to drop eggs in their nests, selection would not be brought into play. This is, I believe, the case with the S. American Ostrich with the *result* that they lay a great number of eggs. If some birds of a species allowed it, and others did not, the race of foster mothers would be exterminated by selection. We should expect a strong instinct to arise against such a practice. Can this partly or entirely account for the territory instinct? A pigeon will go 60 miles there and back for its food every day, so I have seen it said. A bird like that cannot mind another bird nesting within a mile of it because of food supply. Then again, if the male gets an instinct to pick the eyes out of any hen, except his own, who comes near the nest, won't this make for domestic purity? May this also have been the origin of the *very* strict monogamy amongst birds?

Fisher to Darwin: 25 January 1928

... Now for the *really* important part of your letter; of course the cuckoo must have started parasitizing mainly cuckoos, but this is certainly not my idea, and I have never heard it before. A certain amount of such communism once established would bring in some selective effects, I fancy. Consider the equilibrium which must exist between instincts making for perfect workmanship in the nest, or a warm, or a well-nourished brood, and the instinct to avoid danger with which the former must occasionally come into conflict, sometimes with self-nutrition also perhaps, certainly also, as you say, with fecundity. Start with these in equilibrium in a non-parasitic group, and introduce the communal habit of sharing eggs. You must at once begin to lower the standards of parental diligence, and to increase timidity, perhaps greed, and certainly fecundity. Chick mortality increases (which tends to raise again to some extent the standard of diligence) but it is only when the average cuckoo becomes a materially worse patient than neighbouring birds that an instinctive preference for foreign nests would be an advantage. Parasitism depends, in fact, on the co-existence of two different standards of parental care! At first, the young cuckoo in the foreign nest would do only slightly better than in his own, or some other cuckoo's and presumably would do worse than his foster brothers; but he is in a position to profit by fratricidal powers which would be merely harmful in the host, and can go ahead. The Rhea is excellent in showing that higher fecundity came before true parasitism.

I wonder what means of protection have been evolved. Some birds are particular enough to throw out objects which are not very like their eggs; others will sit on marbles. I understand that both groups are victimized, but the former more skilfully than the latter. This suggests that the method has paid in some cases, but is not a sovereign remedy. Now for a given population of cuckoos, would not the rarer hosts suffer most severely unless specifically protected? Are the rare hosts the more particular? Perhaps you have a fairly recent paper, I forget who by, who contrasts the cuckoos' eggs foisted on these two types of host. If not, I must get the reference from Huxley.

The effect on territory instinct would only work at laying time, though it might have been developed for this time and merely extended, as still useful, earlier and later.

Polygamy would certainly require greater powers of discrimination in the male; it would also give the young a smaller share of his labour. Is the inference that this labour is unimportant in polygamous birds justified? Except as a guard, or a sentinel. I suppose *Gallus* is chiefly useful as a sentinel, or a lightning-conductor, perhaps, if his conspicuousness draws the danger on himself. Are not pigeons strictly monogamous, and at the same time gregarious in nesting? I suppose the nests are always distinct, and the right squabs always fed by the right parents.

Do you know if the non-parasitic relatives of the cuckoo are gregarious, like rooks? A communal territory might easily be a first step in their degeneracy.

Darwin to Fisher: 26 January 1928

Thanks for yours about cuckoos. ...

Do not ants give rise to some nice selective problems as regards fecundity? The ordinary ideas do not apply to sterile offspring. If the young females originally had their natural instincts developed abnormally young, and began to look after their young brothers and sisters, we see how a beginning might have been made. Then, if some were sterile, so much the better. And does not such a state of things put a stop to the ordinary check on fecundity? Here is a nice thing to think about. ...

Darwin to Fisher: 27 April 1928

Herewith correspondence,[42] which I have found very interesting. I will *hastily* jot down my thoughts for what they are worth.

Galton said to me that Pearson can understand Bateson, but Bateson *cannot* understand Pearson. This seems to me somewhat the same case.

You say that abnormalities in vertebra number are correlated with other abnormalities. (It might be with advantageous differences.) He seems to reply that this indicates that when the vertebra number is normal, these other abnormalities cannot, therefore, exist, and natural selection cannot apply. Of course your argument does not imply this at all. The harmful or beneficial differentiation might be insufficient to bring about the correlated change in vertebra number. That is how I understand you. ...

I did not know my father used the word 'particulate'.[43] I thought that was Galton's origination. I guess he would have said that his knowledge only enabled him to look at things more vaguely. It is difficult to get back to that frame of mind. I believe Huxley once said to me that use might produce effects of a hereditary kind only after it had been in operation for many generations, though we could not see how. My father saw contradictions and could only build his theories on generalities. I doubt if he saw distinctions quite as clearly as we can now see them. That is all very hastily written. ...

Darwin to Fisher: 7 May 1928

I think you asked me as to the difficulties I saw in regard to natural selection connected with useless characters. I have little new to say, as I blew off steam on that subject in my Cambridge pamphlet on Organic Evolution. There I think I showed how my father, in *Descent of Man*, Vol. 1, Chap. II, 6th para. from end, said that many useless structures, as now supposed, would be proved to be useful; but that his omission of the consideration of such structures was 'one of the greatest oversights' of the *Origin*. It is probable, he said, that many peculiarities are of no service to the organism. He goes on to suggest an explanation, which does not seem to me to hold water. In the *Origin*, Chap. VI, he speaks of interlocking species being absolutely distinct in every detail of structure.

I agree it is extraordinarily difficult to point to any quality and say that it is certainly not correlated with any useful character. But there are so many where no such correlation appears to exist. Specific characters are, I believe, generally not correlated physiologically with other characters, and we should look to them for most variation. This we find, but why the remaining uniformity, which is often very great? ...

Darwin to Fisher: 14 May 1928

I am not sure that we have caught each other's meaning about useless characters. If not, it does not much matter. You say that the length of the 7th joint of your midge is a by-product of the developmental changes which *have been selected*. If I could believe that all these unimportant specific characters were necessarily co-ordinated with some other character under the sway of natural selection, I should feel that all my difficulty had vanished. I think I mentioned how my father, in the *Descent*, said he had made a mistake in not considering these useless characters, and how he strove to account for their uniformity. In the *Origin*—I quote from memory—he speaks of the uniformity in the same species of two interlocking species, of every detail of structure. Can this uniformity in every detail be correlated to some useful structure? In Chap. II, 2nd para. of 'individual differences', he suspects that we see in some polymorphic genera, 'variations which are of no service or disservice to the species, and which consequently have not been seized on and rendered definite by natural selection.' But how then have they become sufficiently definite to separate even varieties? In Chap. V, 'Correlated Variation', para. 5, he speaks of modifications viewed as of high value being possibly due 'to the laws of variation and correlation, without being' of the slightest service. Here, I presume, he meant correlated with some useful structure. But this should be read in conjunction with what he said in the *Descent*. What is an 'important structure'? Is it not one generally which is bound up with the whole method of functioning of the organism? If so, it is one tied by ties to other structures, and in such circumstances it cannot vary much. The systematist is, so I think, on the horns of a dilemma. He must take qualities which do not vary so much as to overlap the two groups he is comparing. But, if descent is the real basis, he must take the more rapidly changing characters, which are the most variable. The colours of butterflies vary very greatly, but are a useful specific character.

I have written out my correction[44] of my error, as I now think it, in my Natural Selection paper, and I will send you a copy before long. I should like *your considered* judgement some day. ...

Darwin to Fisher: 5 July 1928

Mark Twain tells somewhere how he could only get some lines, which were running in his head, out of his mind by telling them to a friend. I have been thinking over your dominance theories, and I want to blow off steam, and get rid of my thoughts. Mark Twain did not make nonsense of the poetry, and did not get rid of them on to the poet. So the cases are not quite parallel.

You bring in the idea of modifying factors. If these are separate entities, must we not suppose that a species has now modifying factors for every past mutation, if now recessive, which ever occurred? Moreover, why should not there be modifying factors in the mutant also?

Can we get a simpler way of putting your theory by assuming that the original species, **O**, has some individuals (**O**$^+$) which are more dominant, and some (**O**$^-$) which are less dominant to the mutant **M**. Also that the same is true of **M**, some (**M**$^+$) being less recessive to **O**, and some (**M**$^-$) being more recessive to **O**. ...

I daresay there is nothing in all this. So don't answer. ...

Fisher to Darwin: 7 July 1928

I will answer your letter in spite of your protest, because you are one of the very few people who will ever appreciate the consequences of my suggestion,[45] so I shall be especially particular that you shall understand me clearly about its framework.

I take **O** and **M** to be physical organic structures (genes) handed on from generation to generation. For some millions of generations selection has always favoured **O** and we should have long ago seen the last of **M** if **O** had not regularly mutated or changed into **M**, sufficiently often for about one in a million **O** genes to turn to **M** in each generation. This keeps a certain supply of **M** in being, a number proportional to the mutation rate, though also influenced by the intensity of the counterselection.

If **M** possessed an advantage over **O**, no such situation would have occurred, for **M** would replace **O**, apart from back mutation, in a few thousand generations. (I need to think about the case in which **M** is sometimes, in certain places, advantageous.) The case I deal with, and to which I believe the mutations of our little genetical samples nearly always belong, are the importunate failures.

If the mutations of **O** were of several different kinds, producing **M**, **M**′, **M**″, etc., (as is known in some cases to be the case) from the same kind of **O**, this will not help any progressive change, for the mutants we deal with are those which actually arise in the cultures and are brand new; in any case, the old mutant genes must all fairly soon be extinct, the supply depending upon fresh mutations occurring. However, something does seem to have happened to **O**, supposing it to have been originally a mutant of a proto-original gene **W**, for, whereas the heterozygotes **OM**, **OM**′, **OM**″, all look like **O**, the heterozygotes which we build up by artificial matings **MM**′, etc., are intermediate between **MM** and **M**′**M**′. This is my first fact; the original puzzle which set me thinking. For even when **M**′ arises as a mutation from **M**, **MM**′ is still intermediate.

Your more dominant form $\mathbf{O}^+$, I represent by $\mathbf{Oa}_1$, and the less dominant form $\mathbf{O}^-$ by $\mathbf{Oa}_2$; here $\mathbf{a}_1$ and $\mathbf{a}_2$ are alternative genes, one of which doubtless arose from the other by mutation. There may be any number of such so called modifiers (all Mendelian factors are modifiers if we choose to think of them as such, though doubtless some only affect the degree of dominance shown in **OM**); thus $\mathbf{Oa}_1\mathbf{b}_1$ may be $\mathbf{O}^{++}$, $\mathbf{Oa}_1\mathbf{b}_2$ may be $\mathbf{O}^+$, $\mathbf{Oa}_2\mathbf{b}_1$ may be $\mathbf{O}^-$, $\mathbf{Oa}_2\mathbf{b}_2$ may be $\mathbf{O}^{--}$. All that this means is that $\mathbf{OMa}_1\mathbf{b}_1$ is most like **O**, $\mathbf{OMa}_2\mathbf{b}_2$ most like **M**, least like **O**, and the other two intermediate.

Quantitatively, the effect of the modifying factors on **MM**, if any, is of no consequence, so long as dominance is incomplete, for **MM** will be then so exceedingly rare that no appreciable part of the ancestry of existing individuals will have been **MM**. But I show that an appreciable part will often be heterozygous, **OM**, and in this part the + modifying genes will have been selected, thus tending constantly to produce complete dominance.

It is interesting that such a selective influence acting on a thousandth part of our ancestry should have made us completely dominant to the many importunate mutants which have been shot at our race, and this accords with the view that they have been clamouring at the gates for more like millions than thousands of generations.

Since we distinguish the effects of the factors **a**, **b**, etc., only in the combination **OM**, they cover both the distinctions of your letter $\mathbf{O}^+$ or $\mathbf{O}^-$ and $\mathbf{M}^+$ and $\mathbf{M}^-$.

About the supply of modifiers there is a very satisfactory answer. If I wanted to increase human stature I should select from the mass of modifiers in the existing population, and quickly enough build up a type exceeding the tallest normal variants. At this stage I should expect physiological disharmonies to appear (control of growth, blood pressure, etc.) and selection would be chiefly concerned in remedying these, and if the process had only taken 10 generations or so, I might be held up and have to wait for favourable mutants; but if I were content to produce the same change by a mild selection in 10 000 generations, I could never deplete the supply of modificatory variance, and it would always be available well in advance, as it is now in stature. In modifying dominance, natural selection only examines one individual in 1000 or 10 000, and consequently the supply of modifiers is never depleted, and the minute selection at work produces always its full effect.

But what a striking effect for such a minute selection! ...

Fisher to Darwin: 7 August 1928

... I think, in fact I am sure, that we have very much the same picture of evolution in our minds, but the picture in my mind has been changing of late, not in any way in principle, but, by groping after approximate magnitudes, in the proportion of the different parts. ...

My suggestion about dominance makes me think of mutation rates as changing rather slowly, since the mutations which have become recessive in this way must have been very persistent. If, then, there is a possible but exceedingly rare mutation which is slowly increasing in frequency, then it may 'take' if it happens to occur and happens also to get a good start, at an evolutionary stage at which it happens to be beneficent. But I suspect now that its usefulness to the species will change just as rapidly as its mutation rate can be expected to do. That is why I feel that the situation of the species waiting for the lucky mutation to occur may be quite an unreal one. I am inclining to the idea that the main work of evolution lies in the discovery by trial of perhaps rare combinations of its existing variants, which work better than the commoner combinations. A slight increase in the number of individuals bearing such a favourable combination will then set up selection in favour of all the genes in the combination, with marked evolutionary results. Many of these genes would have been previously rare mutant types (not necessarily rare mutations) unfavourable to survival.

I think of the species not as dragged along laboriously by selection like a barge in treacle, but as responding extremely sensitively whenever a perceptible selective difference is established. All simple characters, like body size, must be always very near the optimum, so much so that the average body sizes of two alternative genes must be balanced on either side of the optimum, selection always tending to eliminate the rarer because it is further from the optimum. The selection in this case is proportional to the square of the magnitude of the effect of the gene, and a species affected by mutations making it larger and mutations making it smaller will select persistently against both lots and make both recessive. If now an increase in size becomes desirable, a number of the recessive enlargers will triumph, and the recessive diminishers will remain as rare recessives. So that the prevailing bias of dominance (enlargers being more often dominant than diminishers) will reveal the direction of the prevailing selection of the recent past. I should like to know if intelligence is less dominant to stupidity among Englishmen than among (say) Afghans.

Is not the case of poultry queer? There must be 8 or 10 factors in domestic breeds, non-lethal and dominant to the apparently wild-like characters. I do not feel it personally as a difficulty to my theory of dominance, because on any view one would want to know why poultry should behave differently from other beasts and birds, to say nothing of plants; and to this we have no clue. That species crosses have occurred is likely, and though all possible species have, I believe, single combs, they may, as you suggest, [be] genetically unlike single combs, which on combination might give Rose and Pea. Is any form of unintentional human selection possible? Were hens only kept at one stage, constantly outcrossed with wild cocks, and so only dominant novelties selected?* (probably some cocks also).

* P.S. I believe this *works*. The primitive fancier would have to be always selecting heterozygotes from wild-type birds in the same brood, and would therefore be constantly increasing the contrast. Dominance of several of these fowl dominants is very variable in its completeness in different breeds. How is that!

Darwin to Fisher: 12 October 1928

... I am glad you are at work on your evolution book. I shall be delighted to be of any use, and could read your chapter any time—not that I expect to be of use. How about your new statistical work? I hope they can go on simultaneously. *Don't* hurry evolution, but *do* go on with it. ...

Darwin to Fisher: 5 November 1928

... I hope now to tackle your chapter in earnest. I have only seen so far as to convince me that it will be a very important book, well worth labouring over. ...

Fisher to Darwin: 13 November 1928

Very many thanks for the care you have given to reading my Chapter [I]. I wish I could believe it was worth the trouble. I have decided to write on, sometimes ahead of my convictions, with a view to subsequent careful revision, which I hope may be less difficult than making a fresh start. I should like first to thank you generally for many smaller hints which I probably shall not mention separately.

I had expected you to demur to my version of your father's reasoning, because I am concerned to reconstruct the earlier and possibly subconscious elements of an argument, which possibly he himself might repudiate in later years, yet the effects of which can, I believe, be traced in quite late opinions.

My belief is that your father was more capable than most men of relatively long logical trains of theoretical reasoning, but that he utterly distrusted his power of giving them expression, and later tended more and more to delete his reasons in favour of his evidence. Myself, I most admire the reasoning (hence quotation (2)).[46] Ultimately I should like, if you would permit it, to incorporate your testimony as to your father's views in footnotes or otherwise, in cases you consider important.

Instead of saying that your father accepted the theory of blending inheritance, I might have said that he accepted its logical consequences, which no one else seems to have perceived. I take the phrase 'our ignorance of the laws of variation is profound' to mean our ignorance of the nature and particular causes of the mutations induced by the environment, though perhaps he also felt the same about inheritance. I should be very glad of any reference to supplement the letter to Huxley,[47] which reads to me as though the idea of mixture v. fusion seemed then new and conjectural. I had noticed the term 'unequal blending' and it well shows the kind of way in which he was trying to reconcile the blending theory with the difficulties he felt in connection with it.

Did he go by facts *rather than* theories? May I suggest that he, later in life especially, felt it his duty to, but was far too great a man not to anticipate many facts before they were observed.

You have taken my point about the last quotation. The principle of exclusion is a very great principle. A man is more right in drawing the best conclusion from the facts available than in drawing the right conclusion, if it is not the best on the facts. ...

Did he say the nature of [the] organism is far more important than the surroundings in *causing variation*? I should have expected him to say 'in determining what variations are caused'.

As to any erroneous views your father held, my point is that they all sprang from an assumption for which he was not responsible, and that he was more right in drawing the logical consequences of that assumption than were those who failed to see them.

I must restate one point. I do not argue that mechanisms for causing mutations, by volition, use, etc., do not exist, but that if they do exist they are ineffective in causing evolutionary change. On this view I can afford to deal very slightly with the arguments for and against such mechanisms. I agree that the power of transmitting acquirements might have been attained by Natural Selection, in which case it would not be primordial. I do not need even to exclude blending entirely, only that variance due to such causes is trifling in amount. ...

You will groan to hear that I am going the whole hog about dominance;[48] any example to the contrary is therefore badly needed. ...

I have finished drafts of Chapters II and III, but not yet started IV. They

are at your disposal but I do not want to press a lot of heavy reading on you. Chapter II is heavy. I want you to read III when you form an opinion on whole-hoggism.
[P.S.] Thank you ever so much for real encouragement.

Darwin to Fisher: 17 November 1928

... Your letter brings us much nearer together. If you say as to blending that he accepted its logical consequences, all right. I do not mean that I had myself thought it out thus, but that I agree. Remember that if you say 'universally', it includes yourself. Also ... [in Chapter I] of *Origin*, VI[th] [edition], my father wrote that 'the laws governing inheritance are for the most part unknown' [and] in the II[nd] [edition] 'quite unknown'. I suppose that he saw the difficulty of blending, and until he could see the way out, he must hold that the laws were unknown. I have not now studied the passage and don't know quite what he included in these laws; but, anyhow, you have to reckon with these words. I took the words about ignorance of laws of variation being profound from Chap. V, beginning of Summary. That may help you to judge what he meant. As to supplementing what he said to Huxley, it may be worth noting that ... [in the] summary of Chap. IX, he says sterility depends on the organism of the hybrid being 'disturbed by being compounded from two distinct forms'; wherein he was, I suppose, nearly right; though he goes wrong in the next sentence.

Under the heading of Causes of Variability [in Chapter I], he says that the nature of the organism seems to be much more important, 'for nearly similar variations sometimes arise ... under dissimilar conditions'. I think this supports your view. ... [At the end of this section] he speaks of 'determining each particular form of variation'. ...

I should like to read your other Chaps., and shall be ready for them a week hence. But I shall not understand them! And I shall anyhow do no harm.

Darwin to Fisher: 17 December 1928

I should have written before this to thank you for Chap. III had I not been rather seedy. Nothing much amiss, but it seems to addle my brains. You must not pay too much attention at any time to any of my criticisms, because they are just written straight away, and may easily be erroneous. It may suggest thoughts, that is all.

What I had mainly in my mind about Chap. II was probably the point I tried to make in my article on N.S. in the *Review*, and the letter subsequently correcting it.[49] It was that the necessity of co-ordinating the different parts of the same organism is the main check on the pace of N.S., and consequently that, with complex organisms, the pace is very slow when co-ordinated changes have to be effected. If the colour of a butterfly can change without any change in any other quality, it can be quickly made to fit its surroundings. The point which I did not see, and your chapter has made me see, is that the more complex the surroundings, the slower will be the adaptation. If there is only one other butterfly to mimic, N.S. will do the job quickly. But if there are 2 or 3 different butterflies, to imitate each of which would be advantageous, the benefit from imitating any one of them is likely to be diminished, and N.S. made proportionately slower. It seems to me therefore probable that it is generally true that the simpler the organism *and the simpler the surroundings,* the quicker will adaptation take place. Lowly organisms at the bottom of the sea will become almost perfectly adapted to their surroundings, and will, therefore, not alter for vast periods of time. On the other hand a highly complex organism in a highly complex environment will move so slowly, and will have such vast possibilities before it, that it would take a practically unlimited time to reach the stage when no further improvement would take place. I may have been making the assumption that the possible range of mutations is more limited in the simple than in the complex organism. But I want to establish the view that evolution of complex organisms will go on quite indefinitely in an unchanging environment. But please remember my brain is yet a bit addled. ...

Darwin to Fisher: 23 December 1928

... If I have stimulated you to rethink over these problems, that is as much as I hope for. I do *not* mean this to imply doubt, but in these new and difficult regions, reconsideration is nearly always useful.

I will only make a few general remarks. One of your points I could only deal with at all properly if I had your chapter again before me. I agree as to there being an ideal organism, developed from a lion, which would probably be unlike any existing animal; this, I presume, in an unchanging environment. In other cases, with simple organisms, the real and ideal might be much alike. Natural Selection, having a limited scope for action, must concentrate chiefly on the qualities, which, in their range of variations, have the most clearly marked peaks of advantage. These peaks will be most likely to occur where the conditions are most simple, conditions in the organism and in the surroundings; and these conditions seem to us petty. It is here that we get the quickest action, and therefore specific differences. May we not say that 'fundamental' differences, such as those between the qualities of orders, are such as affect the co-ordination of many parts of the organism? I am here putting your ideas, as I apprehend them, into my words. It is going over the same ground again. But it won't take you long to read.

I have not begun Chap. III yet. ...

P.S. The ideal lion can be no further evolved by N.S. What is then to set evolution again working? It can only be a change of environment. If organisms often reached the ideal stage, changes of environment would be of great importance. Organisms living in the sea ought then to be much less evolved than organisms living on land. This is not markedly the case. They are less differentiated rather than less evolved. There is no land animal which has a lantern on its snout to light up its prey. Hence I think changes of environment are probably not of supreme importance. ...

Fisher to Darwin: 28 December 1928

I had not answered your last letter when Chapter III arrived with your comments.[50] I am glad you think it is not out of place.

Let me take your numbered points.

(1) and (2) adopted with gratitude.

(3) New loci must appear, I suppose chiefly by doubling whole chromosomes and later gradually specializing the functions of the duplicates, [and] sometimes by attachments of bits of chromosomes to the ends of others. I do [not?] think I can do anything with this though.[51]

(4) I of course agree strongly about recessive mental defect. Those who do not must put up a case. What an achievement for a mutation to raise a feeble-minded race up to normal mentality!

(5) I think if you listed the human defects for which there is strong evidence of single-factor inheritance most of them would be dominants, for the evidence in the case of recessives is seldom very strong; hence my remark that albinism, which by analogy everyone would expect to be a simple recessive in man, is still a disputed case on the human evidence. If this seems clear, send it back and I will rewrite the sentence.[52]

(6) is a subtle point. I do not think it is so much the fault of the wording as of the idea; we have much experience of the relation (Common, Wild, Mother) gene dominant to (Exceptional, Mutant, Daughter) gene. Is the dominance to be ascribed to the relation Mother-Daughter or to the relation Common-Exceptional? The cases which settle this are (Exceptional, Mother) not dominant to (Exceptional, Daughter), (Exceptional, Sister) not dominant to (Exceptional, Sister), [and] (Exceptional, Mother) recessive to (Wild, Daughter). I have called the 'mother' gene the predecessor, and the 'daughter' gene the successor.

(7) About species v. orders, my point is simple, but I cannot say that it is exactly the same idea as Wallace, Bateson, [and] Robson have had in mind on the same theme. I can understand that the dentition of a lion, which is characteristic of his order, is suitable for tearing flesh, as contrasted with that of a goat. But as to the mouths of lions and tigers, which I suppose are somewhat different, as doubtless are their prey, I do not think we know enough to understand the association of the two sets of differences, or other

relevant explanations of the specific distinctions, except in colour, where we have a glimmer, only because we are better placed to appreciate it.

(8) I do mean that a mutation might have an effect if the pupa were kept at 20° but none if it were kept at 30°.

(9) I must write more (probably in Chap. II) on intensity of adaptation.

(10) I do assume the maladaptation to be capable of repair; is this all?

(11) I think this is much to the point, but it is a very elusive question. The leaves of trees are the best example you have given me,[53] but do we know enough even now to think about plants? An engineer finds among mammals and birds really marvellous achievements in his craft, but the vascular system of the higher plants, which we do not understand, has apparently made no considerable progress. Is it like a First Law, not a great engineering achievement, but better than anything else *for the price*? Are the plants not perhaps the real adherents of the doctrine of marginal utility, which seems to be too subtle for man to live up to? We can understand that a leaf must catch a lot of light, must not snap out quickly, should be distasteful to parasites, but we understand nothing of the *workings* of each of these desiderata. Can we judge well without this knowledge?

I am sending back [Chapter] III so you shall have it in reading this, not to worry you with it again; also V[54] which I hope will interest you, even if it does not please, which latter must always take its chance, though I am more confident some times than at others. IV is unwritten, and I am labouring almost vainly at making it clear.

Darwin to Fisher: 2 January 1929

Thanks for letting me see III again, with your counter-notes. ... I feel a little alarmed that you take my remarks so seriously. If *you* think the matter over again, and stick to your point, then *I* shall be satisfied.

I made, before getting your last, some rough notes, partly for my own edification on some of these points, and I send you a copy which my wife has written out for me by dictation. Now *don't* bother to comment on them, nor return them.

I have not attacked V yet.

Darwin to Fisher: [early-1929?]

... The question of overlapping species gives rise to some nice problems. See *Origin*, ... beginning of Chapter VI. If two species in the same area are equally well adapted to their surroundings, then the contest between them depends solely on their relative rate of multiplication. Does not this tend to make each species take a definite area for itself? My Father seemed to see this, but not with mathematical exactitude, and I am not quite sure that I see it either. ...

Fisher to Darwin: 15 January 1929

I am answering your last letter piecemeal, so do not answer unless you feel so inclined. I now return the Galton letter, which I thought so interesting that I had it copied, so now I ask your permission to keep a copy.[55]

It is perfectly true that village communities may be much isolated, but I wonder if Galton ever considered (or people like Fleure, who find 'neolithic' villages all over the place) how complete the isolation must be to be worth anything genetically.

If only one in 10 filter in from outside in each *generation*, in seven generations half the population comes from outside and in 70 generations all but 1 in 1000. Isolation would be very extreme at this level, in the ordinary course of events, and catastrophic events, war raids, famine, plague, are not so uncommon as to be ignored in the case of such habitual isolation.

King Solomon lived 100 generations ago, and his line *may* be extinct; if not, I wager he is in the ancestry of all of us, and in nearly equal proportions, however unequally his wisdom may be distributed.

You see I shirked the problem of optimum mutability for asexual organisms [in Chap. VI], merely proving that there must be an optimum. The problem has a very beautiful general solution in operative form, but I cannot make it manageable for any simple case. I will try again owing to its importance for single loci, where I believe (at the optimum) most would be absolutely uniform (at least apart from the rare defects always being eliminated); perhaps all loci have a few lethals going.

Darwin to Fisher: 16 January 1929

I thought you would like Galton's letter, and am glad you have a copy.

As to Bateson, if I had to write, I should write something like the following. But I am not well up in what he did do, and may well blunder. ...

> In the future the great merit of Mendelism will be seen to rest on the proof that the ingredients of the germ plasm on which heredity depends are located in pairs in each organism, one of each pair selected by chance disappearing at each sexual union. On this fact a rational system of evolution can be based, and it is, therefore, of enormous importance. The merit for this discovery must mainly rest with Mendel, whilst amongst our contrymen, Bateson played the leading part in its rediscovery. Unfortunately he was unable to grasp the mathematical or statistical aspects of biology, and from this and other causes, he was not only incapable of framing an evolutionary theory himself, but entirely failed to see how Mendelism supplied the missing parts of the structure first erected by Darwin. Nothing but harm can come from following Bateson in regard to evolutionary theory, though his name will come to be honoured for his pioneer work in Mendelism when what he failed to do as regards theory has been accomplished.[56]

Having written it, I daresay I should tear it up, and advise you to do ditto. ...

Fisher to Darwin: 21 January 1929

Many thanks for the note on Bateson; it puts the point admirably, and though I have already altered the wording somewhat, it seems to me just what was wanted.

The only thing to do is to commend Bateson's enthusiasm for genetics, without saying, which would rather comfort my conscience, 'while greatly retarding its progress in his own country'. But it is difficult to be sure. How far did he alienate the better biologists, e.g. Poulton, Goodrich, from Genetics, and how much did it matter? I wish one could deal frankly with peoples' ideas without seeming to asperse their august persons, but then a man's value *as a man of Science* lies in his contribution to Science.

I have just been reading Samuel Butler's *Luck or Cunning;* what a malignant knave he must have been, yet Bateson borrowed his sneers and quoted his opinions.

Fisher to Darwin: 18 February 1929

... I am sending you a copy of Chapter IV, which will have to be Chapters IV and V, as it has grown so confoundedly long. Do not try to read it, except the summary and any points which the summary makes you want to look up in more detail. I have made an abominable mess of the whole thing and failed to get out an adequate solution of nearly all the problems, but I hope it may at least show what further work is needed.

I have made a start with Mimicry (Chapter VII), which will contain little more than a paper on the subject [*CP* 59] which I think you have. The rest of the book will be essentially Man, and I hope about four Chapters may do it. Do not tell me that this is unintelligible and, when examined, so incomplete as to be scarcely worth understanding, for I know that already.

Darwin to Fisher: 23 February 1929

I was delighted to see the R.S. [Royal Society] list[57] in *The Times*. You have won a well-deserved honour, and you may justly be proud and pleased. I am so glad that the R.S. is beginning to realize the place that statistical investigations must play in science. ...

Fisher to Darwin: 25 February 1929

I knew you would be glad, and your pleasure is as good to me almost as though my own father were still living. He lived long enough to see me fail in two occupations,[58] and to hear me *say* that I was on my feet in research. That is nine years ago, and it has gone well.

I wonder if you have any words of wisdom on a contingency which I suppose is not now too improbable to be considered. If I were offered Pearson's Chair,[59] what in your opinion should I aim at making of that place. It would be easy to continue mathematical researches, and possibly in time to build up a reasonable biological outlook. Is that the whole programme?

Do you remember the help you gave in getting my first Edinburgh paper [*CP* 9] accepted, and introducing me to Horace Brown?[60]

[P.S.] I enclose a good one from MacBride; he has just refrained from underlining *Mathematics*.

Darwin to Fisher: 1 March 1929

You give me rather a difficult conundrum to solve about the professorship. I told you that you were unlikely to get into the R.S., especially first shot, and if I now strongly advise you not to begin to count your chickens, I really hope that I am equally at fault. Even if you are to get it, I am inclined to think that the first effort should be to keep on on the old lines to a considerable extent, whilst making the value of the results bear some relationship to the labour involved. From this and other points of view, it is well to realize that those of the staff who hold regular University appointments—I do not know how many do—cannot be got rid of, even if you should desire to do so. ... Nothing short of murder is now a sufficient excuse for sacking a reader or other high official. This will make them more independent, and difficult to turn on to new lines. They will, moreover, all be more or less prejudiced, I suppose, against anyone who is connected with the Eugenics Society, and taking over such a staff may make the job rather far from a bed of roses. Those who could stay with Pearson became, as far as I could see, his willing slaves, and that spirit won't wear off quickly. It will also probably affect the chances of your appointment. The Board consists of (1) outsiders of highest standing, (2) members of the University, (3) members of the College. If Pearson is alive, he will pull his hardest to get the last two lots appointed so as to back his nominee. And you must admit that you have not always dealt with him in the gentlest way. And as to the outsiders, they must and are right to be a good deal influenced by what the University people say as to the probabilities of smooth running. I am writing exactly what I think, even at the risk of saying what is disagreeable, and showing myself a false prophet. But that is, I am sure you will recognize, what should be done by a true friend.

Darwin to Fisher: 4 March 1929

Perhaps I did not express myself clearly also. If I knew I was going to get the job I should look on it to a large extent as a running machine, with a good deal of momentum. I should consider that it could not be stopped and directed in any new direction quite at pleasure. I should feel that my task would be rather to guide it gradually into better paths. And that I could hardly form any sound idea of what these lines should be in detail till I was in the saddle. Fixed ideas would be little use. This would be my idea of what

I should do myself, and it may have made me lazy in not thinking out the lines I should adopt if I had to decide in advance. I have no fear of your not having sound ideas enough. If you got the job tomorrow, I should hope that the finishing up of your book would be a main task, together with some new investigations to confirm your theories. For instance, get land shells from an island, sufficiently different from the mainland form to prove long separation, and sufficiently alike to be comparable; and then measure their variance. Your work on natural selection will confirm the theories on heredity which you hold, and I am sure that Galton would have felt that anything which made hereditary theory stand on more sure foundations would be a valuable help to eugenics. Broadly to bring about that result by statistical enquiry would, I hope, be your broad aim.

I have dipped into a few pages of Chap. IV-V, not more as I have had a job on hand. I wonder if I understand rightly the increase of variance with numbers. With a 'population' of a single couple, the result would be a pure line, and no variance. That I see fairly well. But it never occurred to me that the more you depart from 2 as a population, the greater must become the variance. I wonder if this is thinking on right lines. It seems to me very important from the species-making point of view. A species in a big area will be divided into groups of different sizes, and not breeding quite freely together; and they will come to have different variances, and different rates of progress. They will also advance on different lines somewhat, and the bigger will kill out the smaller, and so a split will take place. I wonder if you will touch on these problems.

Darwin to Fisher: 8 March 1929

The impression I get from this chapter [IV] is that you have been digging in virgin soil, and that if you have not covered the whole surface, it is because the ground is very very stiff. In pioneer work of this kind, no one can be expected to solve all the problems.

I have the satisfaction—perhaps not wholly unalloyed—of finding that my father's view as to big species ...[*Origin*, Chap. VI] are right and that my criticisms on p. 19 of my *Organic Evolution* are wrong![61] At least, that is how I read your conclusions. ...

I give on separate pages a few notes. They are of little value, but I wrote them down as I thought about it.

Don't bother to discuss any point.

It is a big work, but you will win through.

Fisher to Darwin: 19 March 1929

Many thanks for the little copy of the *Origin*. I hope some time to compare it carefully with the 6th Edition, though it is not easy always to appreciate whether the changes are intended only to improve the form of the sentence, or to modify its sense.

I forgot whether I have ever broached to you quite an old intention of mine to dedicate my book to you, with some such remark as that I have discussed with you some of the problems during 15 years. I cannot help it that this will be read as an overstatement and as implying that you agree with more than you do. I imagine that such as implication in so far as it is misleading will apply chiefly to the human chapters.

I enclose the introductory chapter on Man, which is necessarily rather diffuse, but is aimed at preparing the reader for what follows. Also Chapter VII in case you care to look at it. I do not expect you to agree that I am necessarily right about Man, but only that I am approaching the subject in a rational spirit.

Darwin to Fisher: 20 March 1929

Thank you for the two chapters safely come to hand. I hope to tackle them before long. ...

I shall be proud to have your book dedicated to me, and it will greatly enhance the pleasure with which I shall see it in print. I am not the least afraid of being tarred with the same brush as yourself, especially as a dedication never implies complete agreement. I am only afraid that you will imply that I have been of more use to you than has really been the case. ...

Darwin to Fisher: 26 March 1929

I was glad to see Mimicry again. It seems to me a good bit of work, and we hope it may make wiser biologists see that some of their problems can only be attacked mathematically or numerically.

Your Chap. VIII seems to me to be one of the most interesting in the book, and very well written. I have made a few notes in the margin where it seems to me improvements might be made. One idea one sentence is, I think, a good rule. All about ants interested me *much*.

In all essentials I see no reason to differ from you. A few minor points we don't see eye to eye. I cannot agree with what you say ... [*GTNS*, p. 190] about the elephant's trunk. The brain seems to me a *far* more complicated affair. All that I could say would be that the trunk is, like the brain, such a complicated affair that we are quite incapable of fully understanding its action.

I don't agree with what you say as to my father's views—see the first pages of my *Organic Evolution*.[62] He thought evolution, I believe, of enormous importance in itself as helping to co-ordinate many facts—in geology, embryology, etc. He felt that Lamarck had not opened his eyes, and without a real cause he could not open the eyes of others. Then ...

[*GTNS* p. 192] you seem to me to ride far too easily over the greatest difficulty in human thought—uniformity and free will. ...

I find myself bound to believe I have free will, and also bound to believe I have inherited conscience—and the two ideas seem to me contradictory. It is the mystery of mysteries, which I do not happen to have solved! ...

Fisher to Darwin: 28 March 1929

Many thanks for your letter on Chapters VII and VIII.

About free will, modern physical views do seem to be beginning to make a little difference to the problem. If you consider the two alternative dogmas—(i) the exact laws of physics can be expressed as differential equations, (ii) the exact laws of physics are statements of probability, I doubt if any of the wave mechanics people would say now that (i) is more probably true than (ii).

If (ii) were true, interest centres on the ultimate independent units, independent being now defined purely by the law of compounding independent probabilities. Such units are like monads, there is no going behind them, and though the behaviour of a large aggregate can be predicted, that of an individual cannot be. Monads need not be permanent entities in time.

The question arises 'What determines which possible course a monad will take?' and the answer on this system is definitely *NOTHING* external to the monad. We may, if we like, say the monad chooses, but not that its choice, like that of man, in my use of the term, is influenced by outward circumstances.

There is no contradiction to rational thought in all this, though it certainly leaves unsolved the question of undetermined choice in the animal brain. It is not easy to imagine a system of considerable physical size the behaviour of which is appreciably arbitrary, but, though not easy, it is not impossible.

I doubt if all this affects my actual argument, which only requires that different men should behave differently, and would, I think, apply quite well to automata if they had an illusion of free choice.

I am particularly anxious to avoid misrepresenting your father's views; though I do not agree in emphasis with the earlier pages of *Organic Evolution. If* Lamarckism had seemed acceptable I think it would have done all that your father said about Natural Selection and would therefore have been as important as Natural Selection really is. To me it all hangs on the if. I believe your father jibbed before 1837 at putting forward the historical evidence without an effective working cause, and that this attitude he would feel to be his duty as a follower of Lyell in geology.

In order to give a better form to the sentence, I have amended [it] to:

With a clear grasp of scientific principle which is not always sufficiently appreciated, it is evident that they felt that the mere historical fact of descent with modification, however great is popular interest, could not be usefully discussed prior to [or] (was of minor importance compared with) the establishment of the means by which such modification is being brought about.[63]

Let me know if this seems to you a true statement of the state of opinion which made the reading of Malthus the turning point in the development of Evolutionary theory. This is not quite the same as asking you to agree with me in the matter of emphasis, which I do not altogether expect.

There is a sense in which an elephant's trunk is more different from a pig's snout than a man's brain from a dog's. I will even claim than a man's mind than a dog's, which is more than I can say. However, the example is not the best I could have chosen and perhaps I ought to suppress it.
[P.S.] *I have just received a third daughter.* All well.

Fisher to Darwin: 2 April 1929

I have the chapters back and wrote a reply which I find is still waiting to be typed, so this will go with it. ...

I have considered but not written about selection of mutation rates, and I am convinced that they are too small to make any difference. The only exception I should make is that deleterious mutations which have perhaps been occurring for millions of generations might in the course of time become very frequent, and this could be checked by Natural Selection. It is interesting that actually they do not seem to get beyond about 1 in 10^5, which seems to me a marvellously high level for Natural Selection to check them at. This is in *Drosophila*; plants are certainly different and we need to know more about them.

If I am right, beneficial mutations when they are being selected must have rates of about 10^{-9} or 10^{-12}, and a strain with double the average mutation rate would have no time to increase before the whole population has adopted the new mutation. ...

Darwin to Fisher: 5 April 1929

I am a bit hunted, as I am going away for a few days, and want to wipe things up first. Hence I do not expect to answer your letters for a week or more, except to thank you for telling me your news. I hope that mother and daughter both go well. You are answering, 'What is Eugenics?' in the most practical manner.

Darwin to Fisher: 12 April 1929

I can now answer your two letters ...

[As] to my old friend free will, I am afraid you don't help me. Eddington says we can foretell an average because it is an average. I don't agree. ... You do not seem to me to get over the fact that determinism is a necessary postulate of science, or to help me in believing this at the same time as free will. ...

Then as to my father's views, I daresay I did overstress what I said in *Organic Evolution*, for I did not then realize the effect of the pressure to make him minimize natural selection. What you propose now to say seems to me quite correct, i.e. 'could not be usefully discussed ...'. You leave out the word 'importance', which I believe constantly leads us into trouble, not being defined. Looking to the future we might say that the discovery of the methods of evolution are of far greater importance now than the fact of evolution. But it would be hard to say exactly what was meant. Anyhow it would imply that the fact of evolution was firmly established. If that is *not* admitted, then we should say that the loss of a belief in evolution would be a more important catastrophe than the loss of a belief in natural selection, the whole being greater than the part. ...

Fisher to Darwin: 18 April 1929

I think you have answered Eddington rather than myself, about free will. What I mean will be clearer from a related point. On a purely deterministic scheme, causation itself would be an illusion, [since] all things being already assigned their appropriate places in space-time, it would be very arbitrary to take two items of the *nexus* and call one cause and the other effect. This would be so even if subsequent and antecedent in time were unambiguous terms, for, as Eddington emphasizes, one might reverse these terms. Introduce arbitrary elements and causation takes quite a definite meaning, that if A had happened otherwise (as it might at that instant quite well have done), then B would have been modified. Now I feel that the reality of causation originating in self is all we have a right intuitively to claim; put in this way, one abstracts the essential element in the psychology of choice from all its less relevant connections. I admit that one ought still to hesitate about saying 'it is I that choose', because it is not clear that the 'I' can be identified with any particular element of the activity with which we identify ourselves. But physical arbitrariness does seem to have the great merit of reinstating causation.

Fisher to Darwin: 11 May 1929

On paying my sub. to the Royal [Society], I received a number of forms to fill in, among them a very meagre one designed for statistical information, asking I think nothing but my age.

It struck me that the body of Fellows is itself an interesting body Eugenically, and that whatever the scientific value of the data ultimately accumulated, it would be a good thing if the Secretaries could be induced to authorize a much fuller form, especially about reproduction, if only to call the attention of new Fellows to an important question.

I tried to draw out a form, but it is shockingly difficult to frame anything useful but not inquisitive. Would you care to help me frame a questionnaire, which I shall send in? ...

Darwin to Fisher: 15 May 1929

I, like you, do not see my way clearly to frame a good set of questions. ... My experience is that scientific men are, outside their own narrow sphere of work, just as narrow, conservative, and touchy as any other class. How would it be, first of all, to discuss with the biological secretary [of the Royal Society] your idea in the vague, and see what he says? If nothing would come of it, it would only be a regrettable waste of your time. ...

Darwin to Fisher: 15 May 1929

... Do not you think you ought to rejoin the Stats.?[64] May I set the ball rolling? Mallet, I, and who else for sponsors? Udny Yule? If the latter, give me his address. I am sure now you are F.R.S. you should be F.R.S.S.

Darwin to Fisher: 25 June 1929

You remember no doubt that I spoke to you about rejoining the R.S.S. After doing so, I wrote to both Yule and Mallet, and the enclosed signed forms are their practical replies, willingly sent. I should add, however, that they both sign of the supposition that you really *wish* to rejoin, Yule considering that it would be doubly unfortunate if anything, even financial considerations, were to lead you to resign for a second time. You know that it was I who suggested to you that it would be well that you should rejoin, and that being the case, perhaps I may be allowed to explain very clearly what was in my mind in so doing. To take what was really a secondary consideration first, I knew that there had been some friction before your resignation, and I wanted to see that episode entirely forgotten by all, which would best be brought about by your quietly rejoining the Society. What was more in my mind was that it would be useful to you to be a member, and that you would be useful as a member. On that last point, it was not your taking part in the management of the Society I had in mind. That might come, but I myself think that the leading men of science are apt to take up too much of their valuable time in routine work needing only patience and perseverance. My father could not have done the work he did, but for his ill health keeping him free of routine work. You have one troublesome society[65] on hand, and there more is needed, because it necessitates decisions in regard to policy. I don't want to be the cause of more of your time being frittered away, though I feel you could play a useful part in discussions or on committees in regard to questions especially interesting to you.

Now if you do decide that you yourself do really wish to rejoin the Society, I want you to *do me* a favour, and accept a life membership as a birthday present from me; then each time the journal reaches you after I have departed, you will look on it as a little gift from me, and that thought would now give me real pleasure. I look on my money to some extent as a trust, and this is, I believe, a good way of fulfilling my trust. If you will do me this favour, send the enclosed *at once* to *your* bank, and also the enclosed letter and form (filling in your name) to the R.S.S. When the election is completed—which I gather will not be for some months, because there will be no meetings—send them a cheque for £21 *drawn* by *yourself*. No one but you, I, and your wife should know of this. Mallet and Yule neither have, nor will have, any idea of what I am suggesting. Now *do* accept this gift in the spirit in which it is made.

Fisher to Darwin: 27 June 1929

Let me thank you at once for the very great kindness of your idea respecting the R.S.S., and the thoughtfulness with which you have carried it out. I can have no hesitation in accepting your offer, put as you put it, and will do my very best to see that the result is all that you desire. The journal as it comes out will be a perpetual reminder of your kindness and goodwill.

For the moment I have mislaid your letter on longevity, which I had meant to return with this. I certainly hope to find it soon. Only one or two points which might interest you have occurred to me.

In man, the death-rate increases and the expectation of life decreases with increasing age. Death might be just as inevitable without this being so. For example, if the expectation of life were 20 years at all ages, we should have a half chance of dying within about 14 years, only one in a thousand would live to be 140, and one in a million to 280. We should all die sooner or later as we do now, only—if fertility continued—even the oldest would have the same expectation of further posterity as the youngest, and would be as much affected by selection, and consequently there would be no tendency for their death-rate to become higher than at early maturity, where in man it is least. In fact, the incidence of death or cessation of reproduction (or at least of reproductive usefulness) determines the action of natural selection, which in turn reacts on the death-rate. In an oak in a forest, I suppose an old tree has a greater expectation of posterity than a young one, so that it would be a bad bargain for the father oak to benefit his offspring unless he could do so by losing considerably less than the offspring gains.

The reproductive value at different ages must determine the extent to which parental care pays. If all ages were of equal reproductive value, a species would tend to benefit its offspring up to the point at which the offspring gains double the advantage which the parent loses, but no further. Of course immature offspring are usually worth much less, and so should be cared for only at a cheaper rate still. But if crocodiles were able to recognize their mature offspring, I suppose they would co-operate with them not only on terms of mutual advantage, but on terms of joint advantage so long as the loss of either did not exceed half the gain of the other. Hence society starts with the family.

Fisher to Darwin: 29 June 1929

I have just finished correcting duplicate copies up to the last Chapter, and enclose five! chapters [VIII-XII] on man, including the one you had before, so that you can see what I was driving at in writing in it what I did. The other copy is going straight to the publisher who has been hurrying me a little. I am afraid he will have a shock when he reads the human chapters and I only hope you won't. I feel on a knife-edge between timidity and audacity and need all the wisdom I can collect if I am to keep my balance.

Darwin to Fisher: 2 July 1929

I like your dedication, & I still more like the thought that you want to insert it. *Whatever* wording you select I shall be pleased with. If it is to indicate what I have *wished* to do, it is certainly true to speak of the 'encouragement given to the author during the last fifteen years by discussing many of the problems dealt with in this book'.

The big pile of MS. has come to hand, and what a pile! If you want it back by any particular date, let me know. ...

Darwin to Fisher: 18 July 1929

I have begun by again reading Chap. VIII with great interest. ...

Chap. IX ..., Chap. XI. These chapters are so interesting that I wish they could have come earlier in the book. It takes a lot of thinking, and I feel I am no longer able in one reading—if at all—to criticize effectively. It seems all sound, as far as I can judge. But it is stiff.

Chap. XII. My feeling on reading these chapters is that you have written a very important book, and one which will slowly—though slowly—influence public opinion. I am so much inclined to agree with your views that I don't feel it startling or alarming. I think you should look forward to the issue of a second edition, say ten years hence, and with that in view keep keeping it up to date. ...

You must be glad that your last [chapter] is finishing, and you have my congratulations.

[P.S.] You must not be disappointed at a small sale. It is the kind of book to work through others. I shall read it all again when published, more slowly, and shall take more in.

Darwin to Fisher: 2 October 1929

I have not yet read your food paper [*CP* 82], but intend to do so when I can give it quiet thought, which I see it will need. Now I want to *amuse* myself with another evolution letter, this time to consider when evolution may, not must, be slow. But I want to begin irrelevantly about butterflies.

The Meadow Brown, and two closely allied species, have black spots—eyes—on the *undersides* of their wings, with little white marks on them. Look at any picture of an eye, and you will generally see it as a black disk with a white splash on it, the reflection of some light. Is it fanciful to think the white spot on the Meadow Brown's eye is to make it more protective? It may be. My point, however, is that being found in 3 allied species, it is probable, but not certain, that it was evolved before these 3 bifurcated; and this may have been a very long time ago, considering the place in evolution occupied by insects. Being so long in existence, it hardly can be at all harmful. Here then is a case where, I suggest, evolution can have acted with extraordinary slowness. If two butterflies were on the same flower, and some insect went to eat them, and ate the one without white marks in his eyes, because they were less like eyes, that might cause a permanent change of minute proportions in the proportion of genes in the species. In fact, when a selective process does a very little good and no harm whatever, it may proceed with any degree of slowness. ...

What puzzles me about butterflies is this—there is no mimicry in England, I think, and to say that birds don't eat butterflies here often is not to the point. But nearly all are duller coloured on the underside, surely for protection. This, I guess, must be some disadvantage, as making them less conspicuous in the mating season. ... Hence there must be active selection still going on to preserve the dull colours on the underside. Butterflies do not seem to mind showing off, as it were, on the ground or on flowers in the day time. They show little sign of fear, and I have never heard of a bird going at them when sitting. From all this I guess that this underside protection is entirely for night use. I have seen an account of a white butterfly carefully selecting a white flower for its perch for the night. But what creatures attack sitting butterflies *at night*? I cannot think, unless it is bats. Has anyone examined the insides of bats to settle the question? If you ever come across a wise bugologist, ask him the question. ...

Fisher to Darwin: 4 October 1929

... I know the circular spots on the undersides of the Ringlet, Meadow Brown, Gatekeeper and Scotch Argus, but are they eyes? There are two points which might give a clue to their interpretation, one that they occur in series, about 7 in the Ringlet, and secondly, that the Meadow Brown and, I think, the Scotch Argus, have one of them doubled. Is it possible that in twilight they look like dewdrops, a dark disc with a bright point? All these species haunt grasses, but I do not know if they roost on them. If so, perhaps amphibia and reptiles are the enemies. I wish I were a naturalist. ...

Darwin to Fisher: 4 October 1929

I have just been reading Haldane in *Nature*.[66] I am glad to see that he mentions your work, and appears to see its importance. I do not see anything in the whole article which necessarily runs counter to your arguments. Things would work out more neatly from a mathematical point of view if all heredity was dependent on genes and small mutations. But we do know that sudden changes in chromosome number do take place, and that must be allowed for. ...

Fisher to Darwin: 7 October 1929

Yes, I agree with Haldane, on selection in general; it is only on my dominance theory that at first sight he was inclined to attack me. Perhaps he will.

I regard the grosser types of mutations as chiefly of use in producing physiological isolation, and for this reason as frequently found as between nearly related species [*sic*].

I am rewriting most of Chapter IV; it is a burden.

Darwin to Fisher: 20 October 1929

I read your *Realist* article [*CP* 82] yesterday with some care, though I have not yet fully absorbed it. You know that I agree heartily with all the family allowances part, and the whole of it made me think hard. At first I decided not to write to you because I feel my views are *not fixed*, but on second thoughts I decided to do so, as it is probably now or never.

I have been in the habit of regarding things as follows. The use of machinery, etc., has enabled one man to produce more food. Hence men had to leave the country, this movement being increased by the manufacture of agricultural tools in towns. Conservatism resulted in wages being lower in the country, a difference compared to town wages being produced, which is slowly lessening. Everything became cheaper in like manner, but all men sought and generally got employment. The number of men employed in agriculture as compared with the numbers in other callings is an index of the expenditure on other things besides food, and therefore of the standard of living. If you turn your diagram on p. 48 upside down, it seems to me to give a rough measure of the rise in the standard of living. Looked at thus, it does not seem as 'serious' as you make it out to be. Looking to the future, it will go on. The advantage of cheap nitrogen will be, besides more production, less labour for what is produced. I forgot to say above that I see *far more* desire to go from country to town than vice versa.

On p. 54, you say that it might be wise, in the interests of existing cultivators, to restrict the area of growth—as was attempted with india rubber. This may be true, but it is protection, and like all protection, it injures others. It may not be true as regards *labour,* which I think becomes apparent if *rent* is taken into account. The men thrown out of work by the restriction of area, or not getting work, would tend to keep down wages. The rise in prices would raise rents. The net result *might* be no rise in the standard of living of labour and a greater differentiation of wealth. I don't know what it *would* be.

We have to face the fact that town life is going to predominate, and to try to make it everywhere as healthy and cheerful as it is in our best towns.

I have been trying to think what meaning I should attach to certain expressions. The over-production of goods would generally mean, I think, the production of goods which had to be sold at a loss. This would always be due to a mistake in estimates. It would never be a permanent situation. It would be the same in regard to food, if over-production is used in this sense. If the phrase means production such as tends to lower prices, I see nothing to say where it begins or ends.

To over-population I can give a certain not too definite meaning. If we imagine a population increasing from zero, I suppose at first, on the principle of increasing returns as explained in text books, prices would fall. They would go on falling up to a point, and then begin to rise; and the standard of living would rise and fall similarly. Where the change took place would be the optimum population. I assume knowledge not to change. But with a change in knowledge it is probable that the optimum for today would not tend to produce the optimum in the future. How to take the future into account theoretically, I do not see.

You speak of the development of the British Empire, and I think some of my father's words in (?) *The Descent of Man* could be quoted in support of this view. I cannot make up my mind how much I would sacrifice our present standard of living for this object. I would go some way. But, if we do so, let us be open, and declare plainly that *over-population* is what we want, so as to have numbers ready to go abroad.

On a few minor points. White men have known and inhabited tropical West Africa for ? 400 years. Why has not this potential food-supply area been developed? I think there must be some solid reason. Chinese and Indian civilizations have, for far longer, been close to undeveloped tropical areas. Do coffee, cotton and tobacco flourish where tropical forest is thickest? I thought not.

My manufacturing firm did not speculate beyond what was well in sight when considering capital expenditure. I think few firms are built up on longer expectations.

As to p. 56, I regard the fall in the death-rate as the most potent cause of the fall in the birth-rate, contraception having made the coincidence take place much more rapidly, and done a little more in addition. I guess you would agree.

With regard to over-population, it seems to me that, accepting my definition, all Europe is probably much over-populated. By cutting off the industries producing lowest returns and throwing the worst land out of cultivation, would not the standard of living rise?

When the coal gives out, then we shall certainly be over-populated. How will this begin to show itself? Will it not be by unemployment? That seems to me the best rough test we can get for over-population, and I am sorry to see it discredited. Waves of unemployment will occur always, but how can we tell it is only a wave? Is it not best to keep this practical test well before our eyes?

No more boring you today. This at all events shows that what you say has set me thinking very hard.

[P.S.] *No answer needed.*

Fisher to Darwin: 25 October 1929

Supposed a fixed population with two needs only, Food and Bricks, say. They work at these two industries until an extra expenditure of a unit of labour upon either is just balanced by the additional satisfaction due to greater quantity or better quality of the product. Let them make an invention which enables them to produce more or better bricks with the same labour. Bricks will become cheaper relative to food, and they will direct some of the labour previously given to brick-making towards food production, the standard of living in both respects being raised, and maintained equal as between brick-makers and food-producers. If the invention applies only to food production, the reverse should take place, and if the progress of knowledge applies equally successfully to the two industries, the standard of living will rise, without diversion of labour.

I do not think that we can argue that mechanical improvements have aided food production more than industry, but rather far less, except in the important item of opening out new lands. The facts that such lands are available, that it is politically important to civilize them, and that there is little else other than agriculture that we can do with them, are those which I am inclined to emphasize as the causes of the lowering prices of foods, and the diversion of labour to other occupations. I think this is only another way of saying *World under-population.*

As to local over or under-population, I have had great difficulty in understanding how the state of employment is in any sense an index of it. No one believes that the number of jobs is fixed, without reference to the demand for services, and this demand turns everywhere on the population to be served. Of course certain jobs, such as police supervision, will not increase proportionately to the population, but this only shows that a denser population can devote a large proportion of its man-power to productive work. If I wanted over-population I should be open enough in saying so, but I cannot see the evidence that 40 millions, or 90 millions, *is* over-population for this country.

Unemployment means, I think, supporting a number of men capable of doing useful work, without giving them an opportunity of doing it. Why should this maladjustment be associated with the condition in which an increase of population lowers the general standard of living (over-population) rather than one in which an increase of population raises the general standard of living? I cannot find any logical connection.

It is probable that I differ from you essentially about Free Trade and Protection, for I have never understood why Free Traders, however right they may be as to the advantages of Free Trade when full employment is available, do not accept Protection at least as a means of guaranteeing full employment for the available man-power. Any useful work seems better than none. I leave aside the advantage which I believe Protection gives of choosing among different industries which shall be fostered.

I am rather surprised that you do not think the confident expectation of world settlement has influenced our commercial as well as our political development. The unquestioned confidence with which men speak, even in Australia, of 'when the interior is opened up', has certainly led many men to make their homes in the wilderness to their ultimate ruin. Has the financial loss been borne only by a few wild enthusiasts, or is it shared in less proportion by others who use the same phrases?

I have simply picked out the points in your letter I disagree with, or on which I think your opinion might be modified by what could be said on the other side. So I am very argumentative. About tropical forest, do you know any physiographical reason why the valleys of the Ganges and the Yangtse should not revert to dense forest, if the cultivators were removed?

Darwin to Fisher: 1 November 1929

I did not answer your 'argumentative' letter, as time did not permit—or I was lazy. I wish we could have a real good jaw over some of these points. I don't hold out strongly about tropical forests, and would only make two points. Do not both the Ganges and Yangtse valleys have cool seasons? Then it seems to me that the very luxuriance of growth in the all round hot and damp climates seems to increase the difficulty of cultivation, and would make it only possible at a low standard of living. But I don't feel sure. As to your bricks and food, the difference seems to me to lie in the fact that the amount of food wanted per head is strictly limited, whilst the amount of goods which might help to raise the standard of living, including leisure, is quite unlimited. Calculate the percentage of exertion a naked savage expends on his food and on other things, and the same with civilized persons, and my point would stand out. Each item of food may not have been helped more than separate items of other things. I am looking at food as a whole versus other things as a whole. The question seems to me to be to what extent the population can be increased whilst maintaining our standard of living. The land at the margin of cultivation must be one important factor. I have no doubt a considerable increase can *slowly* be made by more colonial land being made available, but am inclined to think that the possibilities have been much exaggerated. As to unemployment, as far as I can see no one would be unemployed if all would take the best pay they could get. It is all a question of keeping up the standard of living. Surely, if bad land is cultivated and bad trades carried on, it absorbs the unemployed in a useful manner, but it does not allow unemployment to act as a regulator to prevent a fall in the standard. Now I had intended to have said nothing, and now I have jotted down some half-baked thoughts. As to free trade, we should have a fine fight, for some of your reasons for are my reasons against! There I admit, however, that free traders generally over-state their case. Some of the indirect results would be the worst, e.g. political corruption. Better burn this letter!

Fisher to Darwin: 12 November 1929

I have left yours of the 1st inst., unanswered unduly long, and I doubt if I know enough of economics to answer it properly.

My feeling about the valley lands of the equatorial rain belt is that the vigour of native vegetation has imposed a serious obstacle to cultivation by tribes at a low level of social organization, and that they have never been subjugated by natives for this reason, but that they possess immense natural resources not only for timber but for food production, if reclaimed on a large scale with great resources and determination. Whether the Asiatic valleys were easier to control, or have happened to be attacked by better organized or more persevering peoples, I cannot easily guess.

I quite agree that the increased real value consumed will be greater (when the standard of living rises) in goods other than in food, the demand for which is relatively inelastic, but this will not explain an increase in the price of any one particular item, such as pig-iron, as compared with a bushel of wheat. Our daily budget ought in fact to comprise more pig-iron in various forms, and not so much more wheat, but not dearer pig-iron relative to wheat.

If a population were too great for its natural resources, would it not tend (if well organized) to lower its standard of living by putting in more work, at the expense of longer hours, later pensioning, shorter, more intensive industrial schooling, etc., in fact more employment and less leisure? If this were becoming burdensome, there would be a case for diminishing population, supposing there were really a decreasing return from the natural resources for the labour being expended. But unemployment, as we know it, is a kind of wasted leisure. Men, women, and children are supported without adequate economic contribution, but also without being able to make the indirect cultural contribution of a leisure class. I doubt altogether if the standard of living in the working class (or the country) generally would fall, if the unemployed were taken at lower wages, provided there were adequate wage differentiation for skill and output, which should not be beyond intelligent social organization, however difficult in the prevailing state of opinion.

How would a small compulsory automatic wage increase with length of service work in practice, in conjunction with unrestrictedly low initial pay? It is not obvious to me that frequent dismissals would be profitable to the employer in most industries.

Darwin to Fisher: 16 November 1929

I always like getting yours, because they make me think. I guess inventions have lowered the difficulty of production of both iron and wheat, though iron more than wheat. A man does not now get or want much more bread, but he gets a totality of other things than food much greater than before, and that means a rise in his standard. Then you mean that if there is now increasing over-population, it ought to show itself in a decrease in the standard. There would be that tendency; but if increasing knowledge is making a rise in the standard a possibility, then the standard may be rising, and yet the increase in the population may be lowering the *possible* but not the actual standard; and it is the possible that I am inclined to look to. I believe with you that the standard of living would rise with the employment of the unemployed. The difficulty is a practical one of employing them, about which I don't see my way clearly in this imperfect world. I think I am rather more accepting human imperfection and folly as a necessary ingredient, whilst you are considering more ideal pictures. A compulsory rise of pay is a plan I have never thought of, and now do not, probably, see its full merits, though I see some. But it seems too far outside practical politics to me. But I won't write more, because I am wandering and must keep my brains for my next job. ...

Fisher to Darwin: 28 November 1929

Mrs. Hodson called my attention to the advertisement of this Chair[67] and the subjects in view, in the marked paragraph, do seem rather attractive.

Would you advise me putting in for it? ...

Darwin to Fisher: 29 November 1929

I am certainly of opinion that you should have a shot at the enclosed. I see no argument against it. You must not mind failure. They are, I think, a cranky body, and one cannot guess what line they will take. ...

Fisher to Darwin: 3 December 1929

... I suppose I ought to raise the question of subordinate appointments if things go any further. I should like to get a geneticist, and an experimental psychologist, if they will go so far. ...

Darwin to Fisher: [4 December 1929?]

... As to the staff under you, would it not be wise to catch your hare before trying to fatten it? ... Seriously, I advise beginning slowly. And I am not so sorry as you will be. I believe you still have a lot in your head which merely needs leisure and opportunity to bring it out. It is in such lines that you will continue to enhance your reputation. My father only had one old and inefficient gardener for his 'staff' for many years, and I believe his work was in some ways all the better in consequence. It made it more original. And I want to get emptied out of your head all that is original in it, and I believe that means a lot. ...

Fisher to Darwin: 6 December 1929

I take your letter as a salutary dose of medicine, and by way of giving their proper weight to your points should like to discuss them.

The value to me of the hare—unfattened—consists of two items; (i) £170 per annum increased salary, with a prospect of £250 more in 5 years' time (both less tax), (ii) the possibility that my work in mathematical statistics will be more valuable if applied to researches on Man. I do not really now lack opportunity to say anything I have to say about Man, but could perhaps reduce our present ignorance somewhat by designing and directing specific enquiries and studies in the subject.

My department here[68] now has two research assistants of the status and pay of University lecturers, four laboratory assistants for routine computations and clerical work, and a variable number (at the moment four) [of] voluntary workers, three of whom from Australia, Denmark and India, correspond to advanced students doing research, while the fourth is an American Professor writing a text book on Statistics. I have to consider whether a smaller organization would make any useful headway in the problems proposed for the new research Professor. Do you not think this should be considered early, if not before applying for, at least before accepting such an appointment?

Would you agree with me that, at about 50, your father had decided that there was little more to be done for the subject out of his own head, but that as a good theorist makes a good observer, so still more in experimentation, that there was a great need for well directed experimentation which should answer the problems, and consolidate the conclusions, at which he had arrived?

If this is so, he was several generations in advance of his time, and in the absence of a ready supply of trained assistants, and under the restriction of working at his private expense, he was unable, without being unwilling, to set a much needed example of what a director of research should be. Were his experiments really any better, I mean more useful to himself and others thinking of the subject, than they would have been had he been in Sir Daniel Hall's place at Merton?[69] I doubt it. The contribution of the inefficient gardener must chiefly be to destroy or mix batches of experimental plants, and if one picks up scraps of observational information from his mistakes, are not the experiments of others, usually carefully published and open to inspection, a sufficient source of enlightenment of this sort? ...

Darwin to Fisher: 7 December 1929

... I have had little experience myself of team work, and my judgement is of no value on its merits as a whole. My father wrote *Domesticated Animals*[70] when he was 59 years of age. He had half prepared a manuscript on Variation under Nature (no one seems to know what has become of it!!) and we hoped he would go on with it. But he said he was physically incapable of attacking another big job, and he took to his botanical work as being much easier. Certainly, team work does a lot, and it wants a good man to shove it along. But I still think that the highest and most original work is done by the nearly unaided individual. Here I am no doubt getting into very debatable ground. Directing a lot of underlings must take a lot of time, and the question is whether, with each individual, that time could be better spent in some other way. Anyhow, I want you to have time enough to empty your head of all that is original in it.

Darwin to Fisher: 16 December 1929

I have been pouring some cold water on your back lately, and I want you, if need be, to pour some on mine—though it is a disagreeable job. I wrote enclosed as a possible letter to *Nature.*[71] It has turned out longer than I expected. My question is, should it go to *Nature* or the waste paper basket? Or elsewhere? ...

I have been turning over the pages of a big book, Wheeler's *Social Insects*, 1928. For me it is an aggravating book. He simply loves new scientific terms, and as I find them difficult now to remember, especially as I have no classics to help me, I was constantly swearing at him. My father used to say that everyone inventing a new term should be fined. ... We see the usual phrase—'natural selection has lost its value as an explanation of the origin of adaptive variations'—though I did not see why he thought so. He advocates instead of 'forever croaking "natural selection"', to say nothing but ignoramus. That seems very sound advice to himself! But the book contains a lot of facts.

This is a muddled letter, but I guess you will see its drift.

Now don't be afraid of applying the cold water cure. ...

Fisher to Darwin: 17 December 1929

I am all for publishing the letter, except the last sentence, which does not, I fancy, add to what you have said, and might be taken to mean more than you do.

I have added a few trifling suggestions, all mistypings I think, save one, where the sentence is twice reversed by 'against'. You know what I mean, like: 'We cannot avoid repudiating the opinion that there is no substantial evidence against the view that countersuggestion has in no case inhibited the negative attitude of the subject.' I am not sure now whether this is nonsense or not.

Notes

1. The earliest dated letter from Darwin to Fisher which we have is that of 3 September 1915. As that letter shows, Darwin had, before this, been sending various problems to Fisher for him to solve. The first two letters represented in this collection, though undated, were evidently written before September 1915. They are of interest in revealing not only the problems Darwin was submitting to Fisher but also the manner in which he expressed them.
2. Though his model was a simple one, Darwin was asking, in effect, if the law of ancestral heredity could be explained in Mendelian terms. See *CP* 9, p. 421.
3. See Fisher, R.A. (1915). The evolution of sexual preference. *Eugenics Rev.* 7, 184-92 (*CP* 6).
4. See Darwin, L. (1913). Heredity and environment. *Eugenics Rev.* 5, 152-3. Darwin questioned the use of the phrase, 'the relative influence of heredity and environment', and suggested that it should be avoided because of the difficulty in giving a general meaning to environmental variation. He illustrated his argument by referring to an 'ideal republic', where 'not only were all the children removed from their parents, but where they were all treated exactly alike'. He wrote that, 'in these circumstances none of the differences between the adults could have anything to do with the differences of environments and all must be due to some differences in inherent factors. In fact the environment correlation coefficient would be nil, whilst the heredity correlation coefficient might be high.' Shortly afterwards, Karl Pearson published a paper criticizing Darwin's argument (see Pearson, K. (1914). On certain errors with regard to multiple correlation occasionally made by those who have not adequately studied this subject. *Biometrika* 10, 181-7). Pearson wrote, 'The coefficient of correlation for the environment might be anything from -1 to $+1$; the only obvious fact would be that you could not find its value, except in the form 0/0, from an environment which precluded any measure of variation. How again Sir Francis [Galton] would have smiled at the notion that the

coefficient of correlation for a constant environment must be nil. Why should we follow such advice as that given by the President of the [Eugenics Education] Society to avoid as far as possible 'such phrases as the relative influence of heredity and environment' when on his own showing he does not in the least appreciate the methods by which this relative influence is measured?' Pearson had earlier written to Darwin pointing out his 'error' and in October 1913 in the *Eugenics Review*, Darwin had published a note saying that it had been pointed out to him that he had made a blunder.

Darwin's letter of 3 September 1915 shows that Fisher must have written supporting Darwin's position and urging that Pearson's judgement should be challenged. Referring to this correspondence, Joan Fisher Box has written in *FLS* (p. 52) that it 'showed each the quality of the other: Fisher appreciated Darwin's scientific perception and his lack of self-seeking, and Darwin appreciated Fisher's scientific understanding and his immediate impulse to correct what he felt to be an abuse of science and of justice.'

At about this time, Fisher began detailed work on his analysis of the correlations between relatives. In his major paper on the subject (*CP* 9), completed by mid-1916, he showed how the variance of biological measurements could be partitioned into environmental and genetical components. This analysis was later used by others to define a coefficient of heritability measuring the relative influence of heredity and environment. Fisher never used this coefficient which he regarded as 'one of those unfortunate short cuts, which have often emerged in biometry for lack of a more thorough analysis of the data' (*CP* 245).

5. Mr G.U. Yule, Lecturer (late Reader) in Statistics, University of Cambridge.
6. Schuster, E. (1913). Heredity and environment. *Eugenics Rev.* **5**, 260-1.
7. This letter shows one of Darwin's attempts to clarify the usage of different terms for describing biological variation. The definition which he gives here for fluctuations is unusual, even for Darwin. Elsewhere, he uses fluctuations to describe variation due to differences in the environment.
8. Presumably Pearson's article cited in Note 4.
9. Darwin's paper was published in 1916 in *J. R. Stat. Soc.* 79, 159-75.
10. Snow, E.C. (1912). The influence of selection and assortative mating on the ancestral and fraternal correlations of a Mendelian population. *Proc. R. Soc.* **B 85**, 195-6.
11. Yule, G.U. (1906). On the theory of inheritance of quantitative compound characters on the basis of Mendel's laws. A preliminary note. *Rep. 3rd Int. Con. Genetics*, pp. 140-2.
12. These letters throw light on some of the problems concerning publication of Fisher's paper on the correlation between relatives on the supposition of Mendelian inheritance (*CP* 9). This was submitted originally to the Royal Society of London in mid-1916. The reports of the Society's referees, K. Pearson and R.C. Punnett, have been published in full in *Notes and Records of the Royal Society of London*, **31**, 153-5, (1976). Pearson emphasized that the author had adopted 'a special hypothesis for determining the somatic characters of an individual dropping the Mendelian phenomenon of dominance'. He reported that the paper was not of much interest from the biometric standpoint and said that whether it be published or not should depend on Mendelian opinion. Punnett for his part, said that whatever the paper's value from a biometric standpoint it was not of much interest to biologists, though he did add, 'frankly I do not follow it owing to my ignorance of mathematics'.

In 1917 the paper was submitted to the Royal Society of Edinburgh through J. Arthur Thomson. The Secretary of the Royal Society of Edinburgh has kindly informed me that the Society's records show that Fisher's paper was examined by three referees, J. Brownlee, J.F. Tocher, and E. Whittaker; on the basis of their reports, the Society's Council decided on 5 November 1917 that the paper could not be accepted as it was on account of its great length. The author was advised that an abstract of 10 pages could be published in the Society's *Proceedings*.

The letters reproduced here reveal Leonard Darwin's central role in making it possible for Fisher's paper to be published in full. Having sought and obtained advice from Edinburgh that a donation of between £25 and £30 would allow publication of the entire paper, Darwin promptly said that the Eugenics Education Society would provide this. When the Council of the Royal Society of Edinburgh was told about an offer of financial support at its meeting on 11 January 1918, it agreed that the paper could be published in full in the *Transactions*—but only if £43 were donated to supplement the £12 which was all that the Society could provide. This increase in the estimated cost led to further difficulties, but again Leonard Darwin was ready to assist; the Society's Council, meeting on 3 June 1918, was advised that Darwin had offered to underwrite the balance required for publication of the paper in full. Darwin's letter to Fisher of 6 May 1918 suggests, perhaps, that as difficulties developed over publication in Edinburgh, arrangements were being made to publish the paper in the *Eugenics Review*. When publication went ahead in Edinburgh, Fisher published a short general article on the causes of human variability in the *Eugenics Review* (*CP* 10), with a reference to the big paper.

13. Professor K. Pearson of the Galton Laboratory, University College, London, had written to Fisher in rather guarded terms about a post in the Laboratory.

Old Schoolhouse,
Coldharbour,
Near Dorking.

Dear Mr. Fisher, August 2, 1919

Your name has been mentioned to me as a possible man for a post I have to fill at the Galton Laboratory, namely that of a senior assistant at £350 per annum. I do not know whether the post would have inducements for you, and I fully realize that there would be difficulties in the way. I want a man who will throw himself wholeheartedly into the work at the Laboratory as it is at present organized, not a research worker who would follow his own individual lines regardless of the general scheme of work. A real taste for and patience in the somewhat laborious work of computing tabulating and reduction is essential. Mathematical knowledge is very essential, but it is in a sense secondary, i.e. we do not seek mathematical problems, we have quite enough as they arise in the ordinary course of our work. At the same time I, of course, endeavour to encourage all research tending to extend theory so far as it is of importance to our own subject. At the same time I like also primarily a man who has had experience of observations or measurements, and if possible has been through our special training in computing and statistics. I find as a rule that a high Cambridge wrangler usually takes two years to become an efficient practical statistician and computer, and that by this time or before he wants a more highly paid post than we can give. I want somebody who will stick loyally by the Laboratory for a number of years especially during the present critical time, when we are going into a new building with very considerable extension of our work and possibilities, but with inadequate funds owing to the war-conditions. I have one or two men in view, but as you have been specially mentioned from *Cambridge*

I feel I must write to you among them and find out what your views may be. I may be in London for a day during August, if you cared for a talk, or this is not inaccessible via Reading and Dorking.

I am,
Yours very sincerely,
Karl Pearson

14. Darwin was Chairman of Bedford College, 1913-20.
15. This was Fisher's draft manuscript of three chapters for a book (never published) dealing with 1. variation in human family size, 2. the effects of birth limitation, and 3. the role of selection in human society.
16. Brentano, L. (1910). The doctrine of Malthus and the increase of population during the last decades. *Econ. J.* **20**, 371-93. A.C. Pigou (1912), in his book *Wealth and welfare*, wrote that Brentano's investigations 'suggest that, at the present time, increased prosperity in any class in the modern world is likely to work, not for *any* increase, but actually for a contraction in the number of births.'
17. Fisher had been appointed as statistician at Rothamsted Experimental Station.
18. i.e. birth limitation.
19. Darwin's paper on the postulates needed for evolution—see his letter of 5 April 1919.
20. Fisher had sent Pearson his paper on the probable error of the correlation coefficient for publication in *Biometrika*. Pearson replied that he could not give it his full attention and asked Fisher to publish it elsewhere, saying he was 'compelled to exclude all that I think is erroneous on my own judgement, because I cannot afford controversy'. The paper (*CP* 14) was later published in the new journal *Metron*. See *FLS*, p. 83.
21. Dr M. Greenwood, an Honorary Secretary of the Royal Statistical Society.
22. Fisher had perhaps enquired about the studies which had led Charles Darwin to conclude in Chapter II of the *Origin* that 'wide-ranging, much diffused and common species vary most'. See *CP* 24 (p. 324) and *CP* 52.
23. Hagedoorn, A.L. and Hagedoorn, A.C. (1921). *The relative value of the processes causing evolution.* Martinus Nijhoff, The Hague.
24. Darwin's notes conclude with the following passage.

    The most novel and interesting arguments in the book relate to a unifying process which has without doubt been inadequately explored hitherto. This process depends on the fact that chance is continually weeding out some of the rarer types, with the inevitable result that as time goes on a freely interbreeding group must become more and more uniform in character. This theme is developed in many directions with great ability; but we feel that it tends to run away with the author. When a horse runs away with a rider it proves that the horse is not lame and that the rider at all events has courage enough to attempt to ride such a horse. Unquestionably this influence must be taken into account, but we feel that it will have far less effect than is here depicted.

25. Fisher's review of the Hagedoorns' book (*CP* 17) is his first published discussion of the roles of selection, mutation, and drift in evolutionary change and points the way to several of his later papers.
26. Darwin's pamphlet was published in 1921 under the title *Organic evolution : outstanding difficulties and possible explanations.* Cambridge University Press.
27. See Darwin's letter of 22 August 1919.
28. The Royal Statistical Society had refused, without explanation, to publish an article by Fisher on χ^2. See *FLS*, p. 87.

29. Mr A.W. (later Sir Alfred) Flux, an Honorary Secretary of the Royal Statistical Society.
30. Sir Bernard Mallet, an Honorary Vice-President of the Royal Statistical Society.
31. Probably C. Tate Regan who gave the Presidential Address on Organic Evolution to Section D (Zoology) of the British Association for the Advancement of Science in 1925.
32. The proofs of Darwin's book, *The need for eugenic reform.*
33. Following the Galton Lecture by the Bishop of Birmingham, the Dean of St Paul's Cathedral, London, the Very Rev. W.R. Inge, wrote an article on Eugenics and Religion which was published in the *Morning Post* on 5 March 1926. In this article the Dean expressed his opposition to eugenical sterilization which he described as 'mutilation'.
34. 'Old Elijah' presumably refers to K. Pearson.
35. Fisher's review of *The need for eugenic reform* (L. Darwin). See *CP* 54.
36. This quotation presumably comes from an early draft of Fisher's review. In the printed version, 'not' has been replaced by 'much more than'.
37. Berg, L.S. (1926). *Nomogenesis or evolution determined by law.* Constable and Co., London.
38. A reprint of the first edition of *The origin of species* was published by Watts, London in 1950. In 1959, *The origin of species—a variorum text*, edited by Morse Peckham, was published by the University of Pennsylvania Press. This contains a record of every change, addition, or omission that Charles Darwin made in the five revisions of the *Origin.*
39. See Darwin, L. (1927). Natural selection. *Eugenics Rev.* **18**, 285-93.
40. Fisher's proposal was evidently accepted for a review article on Berg's *Nomogenesis* by Professor E.W. MacBride appeared in *Eugenics Rev.* **19**, 32-7, (1927). According to MacBride, 'Berg's destructive criticism of the theory that the natural selection of fortuitous variations is the cause of evolution is excellent and convincing, but his attempt to institute in its place a constructive idea of orthogenesis is exceedingly weak.'
41. Tredgold, A.F. (1927). Mental disease in relation to eugenics. The Galton Lecture. *Eugenics Rev.* **19**, 1-11.
42. This presumably refers to Fisher's correspondence with C. Tate Regan (p. 252).
43. See Fisher's letter of 7 February 1927 to Regan.
44. See Darwin, L. (1928). Natural selection—a correction. *Eugenics Rev.* **20**, 142-3.
45. i.e. Fisher's suggested theory of the evolution of dominance.
46. This is presumably the quotation from Charles Darwin included on page 3 of *GTNS.*
47. See *GTNS*, p. 1.
48. i.e. the evolution of dominance. See *GTNS*, Chap. III.
49. See Notes 39 and 44.
50. Darwin's letter with his numbered comments on Fisher's Chapter III on the evolution of dominance has not been preserved.
51. Presumably Darwin had suggested that Fisher should include something on the creation of new loci in Chapter III and Fisher, apparently, meant to suggest that he saw no way of including this in his theory.
52. See *GTNS*, p. 55.
53. See Darwin's letter of 2 April 1921.
54. i.e. Chapter VI of *GTNS.* See Fisher's letter of 18 February 1929.

55. The copy of Galton's letter to Darwin dated 5 October 1910, begins as follows.

> I can't help in solving your question. The answer must greatly depend on *where* the people live and *how*. In many villages, notably Scotch sea-shore ones, the Fisher folk never marry outside their immediate neighbourhood. In such an extreme case the number of their forefathers, any number of generations back, would hardly exceed that of the present villagers. On the other hand, a migratory population might have greatly intermarried with outsiders.

56. See the fifth paragraph of the Preface to *GTNS*.
57. i.e. the list of new Fellows of the Royal Society.
58. On leaving Cambridge in 1913, Fisher had worked first as a statistician with the Mercantile and General Investment Company in London, and then as a schoolmaster, teaching mathematics and physics for five years until 1919, when he was appointed as statistician at Rothamsted Experimental Station.
59. i.e. the Galton Professorship of Eugenics, University College, London.
60. See *FLS*, p. 61.
61. In Chapter VI of the *Origin*, Charles Darwin wrote, 'forms existing in larger numbers will have a better chance, within a given period, of presenting further favourable variations for natural selection to seize on, than will the rarer forms which exist in lesser numbers' and 'the most common forms, in the race for life, will tend to beat and supplant the less common forms, for these will be more slowly modified and improved.'

    On the other hand, in *Organic evolution* Leonard Darwin wrote (p. 19), 'Once a beneficial mutation has survived for a few generations, the chances of its extinction become very small; and when this is the case, it matters little whether the surrounding population be large or small.'
62. In the first pages of *Organic evolution*, Leonard Darwin suggested that his father regarded 'the establishment of a belief in descent with modification' as his primary object and that the question of the method by which evolution occurred had been seen as less important.
63. See *GTNS*, p. 198.
64. i.e. the Royal Statistical Socie4ty. See Darwin's letter of 12 March 1923 (p. 76).
65. i.e. the Eugenics Society.
66. Haldane, J.B.S. (1929). The species problem in the light of genetics. *Nature* **124**, 514-16.
67. The Chair of Social Biology, London School of Economics—to which Lancelot Hogben was ultimately appointed.
68. The Statistical Department, Rothamsted Experimental Station.
69. Sir Daniel Hall was Director of the John Innes Horticultural Institution, 1926-39.
70. Darwin, C. (1868). *The variation of animals and plants under domestication*. J. Murray, London.
71. Darwin, L. (1930). Evolution and evidence. *Nature* **125**, 126-7.

4 DARWIN-FISHER CORRESPONDENCE 1930-1942

Fisher to Darwin: [late-March 1930]

I am sending herewith a copy of my book, which I hope will not be injured in the post, as seems to happen too frequently.

I know you will be as eager as I am to know whether it is going to exert any real influence, but of course we can scarcely hope to form *any* opinion about that for a year, and no very confident opinion, I suppose, under five years. ...

Fisher to Darwin: 29 March 1930

Many thanks for the new edition of the *Descent*. It is a nice little volume, and I agree that it is wise to separate Part I and the general summary from Parts II and III; albeit I value the fact that your father felt sexual selection of such special importance for Man that he chose to treat them in one volume.

Darwin to Fisher: 9 June 1930

I have been rather busy of late *for me*, with the Twitchin bequest,[1] and other minor worries. I have not had time or brains, therefore, to tackle your book in earnest. I have read the first chapter, and turned over some of the papers, with the result that my impression is confirmed that it will be slowly recognized as a very important contribution to the subject. But I am afraid it will be slow, because so few will really grasp all that it means. You must not, therefore, be disappointed at the reception which it receives, but trust to ultimate results. I remember that I criticized to some extent what you said about my father's views, and I think you did make some changes. It rather depends on what is meant by the word 'theory'. I can imagine my father saying, if reading your first sentence about what he accepted, 'but, hang it all, I have not got a theory of inheritance. I wish to goodness I had. Cases like the mulatto show that blending does take place, and other cases show that individual characters are inherited. How and why this is, I do not know. But I have come to see that in 1842 I stressed blending too much.' But this is a minor point, as I say depending largely on one word. I have noted two letters, which I enclose as reminders, showing how fogged people are about evolution, and how a thorough knowledge of the particulate theory would help them. Salisbury's letter[2] is interesting and stimulating. ... Is not the death rate at different periods of growth an entirely erroneous basis for comparison? ... Cunningham[3] is too weak for words. He cannot have ever thought it out carefully. ... The whole theory of growth depends, I believe, on genes acting differently in different circumstances. ...

Fisher to Darwin: 12 June 1930

Many thanks for your letter. As a matter of fact Salisbury's letter had stirred me to a criticism, a copy of which I enclose; it is very much on the lines of your letter, but sticking closely to one central point, in the hope of making it at least clear.

I like immensely your point that the theory of individual development depends upon genes acting differently in different circumstances. I was surprised, too, at the calmness with which Cunningham assumes that all the structure and instincts of worker bees could be ascribed to their solitary ancestor. There is a whole series of reactions connected with swarming, the location by scouts of a new site, the instinct to follow the scouts, and to guide the queen's flight, the swarming itself, the preliminary gorging with honey, which seems to be unknown in existing solitary bees, and very improbable in ancestral ones. Then there is the whole set of behaviour mechanisms, which Frisch has found, by which news of new food sources is conveyed and acted upon always by workers. The only loophole for the Lamarckian here is the possibility of social organization prior to the development of a neuter caste. However, the objection is so obvious that Cunningham ought to have discussed it. ...

I am wondering if *any* biologist will follow the argument of the first chapter [of *GTNS*]. First, because a first chapter is always expected to be not only elementary but trite, and secondly, because we have all grown up in the greatest confidence that we know all about what Darwin meant. I am very tired of having some excessively loosely expressed truism, such that 'all defective deer must be devoured by tigers', put forward as 'the ordinary Darwinian argument', and I believe now I ought in the preface to have hammered in the statement that in biological circles Darwin's views are usually grossly misconceived—though this would annoy many people.

Darwin to Fisher: 16 June [1930]

... I am glad you like my remarks that individual development depends on genes acting differently in different circumstances—but I am not much surprised because I am nearly certain that I bagged the idea from you. I am glad also that you have replied to Salisbury's letter. I feel rather muddle-headed to-day and can only say that I think I understand the situation. The elimination of an individual increases in importance in your three stages A, B, and C.[4] This is also true of the survival of individuals. Hence the proportion of elimination in each stage is of importance. A very high proportion of seedlings is eliminated but then the causes of their elimination have very little to do with inborn qualities. ...

Fisher to Darwin: 21 June 1930

The point of my letter to *Nature* [*CP* 88] is quite a negative one, that one cannot gain any guidance from the mere fact that only one egg in 10 hatches to a larva, and only one larva in 100 pupates and emerges successfully. The fact that of the eggs laid, 90% die unhatched, 9.9% die as larva or pupa, while only 0.1% die as adult insects, cannot be taken to imply that Natural Selection is more potent on eggs than on larvae or on larvae than on adults. You are wanting a much more positive contribution, but I was only trying to show the fallacy in the simple argument stated above, by saying that a freshly emerged adult is, on the premises, worth 1000 newly laid eggs, which serves to counterbalance the apparent disproportion.

Your point about how much of the mortality is selective is of course a much more subtle one, and could not be dealt with by a mere enumeration of the number surviving to different ages. One fairly simple step towards a more positive statement is that if **A** and **B** are two groups of genotypes into which the species is divided, then if I kill one in 100 of group **A**, and none of group **B**, I exert the same selective influence at whatever stage I operate up to the commencement of reproduction; thereafter I exert a diminishing effect, and none after reproduction has completely ceased. To do this I should have to kill (supposing the groups are equal as regards other selective agencies) 1000 times as many new eggs, or 100 times as many newly hatched larvae, as if I killed them off at emergence. That is, I must destroy equivalent amounts of reproductive value, but this statement holds even after reproduction has commenced and up to the end of life, or at least as long as there remains 1% of the reproductive value of genotype **A** for me to destroy. ...

Darwin to Fisher: 24 June 1930

I have been reading your book in a somewhat desultory manner, not carefully enough to make it the basis for writing anything on the subject. I have had some little jobs to do which have taken up my rather small available energy. I should like to try to put in as plain language as I can what I feel as to the value of your work in showing how Mendelism is capable of putting the lid on to the theory of natural selection. I don't want to write about any minor criticisms, and if such occur to me I shall write straight to you. Some day you will have a second edition, and the notes you now make will then be very useful. But you are *not* to trouble to say whether *my* remarks are helpful.

Here is one criticism—page 138, line 15, [*GTNS*, p. 153] '... the dates of the breeding ... could only be stabilized if ...'; my ending would be, 'if there was a period of the year at which breeding would produce a *maximum* number of offspring who would survive till the next breeding season.' The effect of the seasons on births and deaths would, I believe, produce such a result, more especially if selection had resulted in a definite limited number of offspring being normally produced. It would at first sight appear that the beauty of males would be harmful up to the period of the optimum date, because it would tend to make them have first choice and thus breed too early. After the optimum date, beauty would be helpful in making them breed as soon as possible. And it might seem that these two influences would cancel each other. But selection would result in both sexes not wishing to breed before the optimum date, and in such circumstances the beauty of the male would do no harm before the date; whilst after the optimum date, when the desire for breeding had commenced, the beauty of the male would be beneficial by hastening breeding. It seems to me that beauty can be explained thus more or less in the way in which my father suggested. Monogamous drakes, which have no period of eclipse, must not be tempted to mate before the proper time, in spite of their fine clothing. What you say in the next para. is, I think, certainly true, but might make the optimum date a little earlier, I think. I wonder if this is all to the point!! ...

I have just got yours of 21st in answer to my last. ... you must *not* take so much trouble in answering me.

Fisher to Darwin: 27 June 1930

I must write more clearly about the non-genetic early nesting theory, especially as I am sure I got it from you.

Supposing the date at which breeding phenomena are initiated, e.g. by migration etc., to depend on the female only, there must be an optimum date, appropriate to the average bird, for these phenomena to start. The date of starting is partly determined by a heritable variate x, partly by other circumstances. We must suppose x to vary among different females and, to make it more concrete, we might imagine x to be determined experimentally by giving a number of young females exactly the same nutrition and climatic experience and noting the date at which they show the first sign of the reproductive sequence.

Now my first point is that the average value of x must be the same, generation after generation, so that the average number of offspring left by females with a high x, and therefore congenitally prone to start breeding early, must be the same as that of females with low x, congenitally prone to start breeding late. Of course I don't doubt that the medium values are favoured over the extremes, but the net effect of selection on the mean value of x must be zero, if the distinction between a winter feeding period and a spring breeding period is maintained at all. How then can it be that the males who breed early[5] gain an advantage? Partly because more of them breed (this is my suggestion in respect of death-rates), and partly, and this, I think, was your father's theory, because those that do actually breed early (as contrasted with those who are only congenitally prone so to breed) really do leave more offspring than those breeding later. This is possible if we imagine the actual breeding date to be modified by environmental factors which are also influential in favouring reproduction so that a group of females having identically the same values of x might start migrating at dates from 15th to 30th March, those moving earliest being destined on the average, by reason of their better nutritional condition, to rear the largest families; but no larger, perhaps, than are reared by birds with a lower value of x who start on March 30th.

Here is a chart; 6^4 means 4 pairs of birds each rearing 6 young. If on consideration you think this is a fair representation of your father's theory, I should like to put it in any further editions [of *GTNS*] so as to make it explicit.

You will see that the selection for increasing x due to the larger families of those mated early is exactly counterbalanced by the selection for small x among those breeding at a given date. ...

[Enclosed chart][6]

	Actual Starting Date →									Average
					7^{1}	6^{4}	5^{6}	4^{4}	3^{1}	5
				7^{4}	6^{16}	5^{24}	4^{16}	3^{4}		5
Increasing x ↑			7^{6}	6^{24}	5^{36}	4^{24}	3^{6}			5
		7^{4}	6^{16}	5^{24}	4^{16}	3^{4}				5
	7^{1}	6^{4}	5^{6}	4^{4}	3^{1}					5
Average	7	6½	6	5½	5	4½	4	3½	3	

Fisher to Darwin: 23 July 1930

... I have noted one point where I think you have misunderstood my letter.[7] I am glad you think the table rightly expresses your father's theory. I have made all values of x equal in average fertility, though I should be doubtless nearer the facts if I made the middle values somewhat more successful than the extremes. This would complicate the table by introducing fractions, and I should like to know if you thought it was worth doing to avoid the misapprehension that I am denying the existence of an optimum x.

On the enclosed page I have drafted an argument on which I have long wanted to have your opinion, though I never feel I can express it cogently enough.

[Enclosure]

Suppose you have two groups of men placed in very different circumstances, differing not in the kinds of actions which conduce to prosperity, or in the average prosperity attainable by such actions, but wholly in the certainty with which it is attained.

(A) Every exercise of energy, intelligence or prudence produces with certainty a corresponding increment in prosperity.

(B) The effect of such actions is obscured by chance effects incapable of prediction which, while balancing in the long run, and having no average effect one way or the other, are individually large compared to the average return from the actions concerned.

The contrast is similar to that between an orderly and well-governed country on the one hand, and a lawless or savage condition on the other; it is also similar to the difference between immediate recompense and postponed recompense, for in the latter case intervening events introduce a chance element, e.g. 'Shall I live to reap the harvest?'

Now I am inclined to claim that similar populations exposed to these two environmental systems would react very differently, that a population which in (A) would show itself industrially competent, careful, and prudent, might in (B) show none of these qualities, because the average effects of competent action would be so much obscured by unforeseen chances. Moreover, the psychological differences in the two cases would be much enhanced by example and tradition.

If you agree with this, as I am confident you will, I want to know how far you would think it rational to apply it to the effects of family allowances, and in particular to the inference that such allowances would increase the fertility of the poorest self-supporting class.

To some extent, of course, the economic burden of children must be regarded as distributed from rational considerations. In such cases the parents presumably decide that the satisfaction afforded by the society of the child, or that of doing what they regard to be their duty, is the economic equivalent of the money spent in its upbringing. To a far greater extent, it seems to me that their incidence, or at least its economic effects, is subjectively accidental, and acts just as any other unpredicted cause of fluctuating prosperity. Among the poorest self-supporting class and, indeed, among wage-earners generally, the loss in standard of living occasioned by a single extra child is certainly large compared to any compensating gain which is open to the parents by increased efforts. I infer, therefore, that without family allowances, the incidence of reproduction, whether or not this is excessive, will induce in some degree the consequences of B, and that the introduction of family allowances will change the social reactions of individuals and the social tradition of the group in the same direction as A.

Now with full family allowances equivalent to the actual average cost of children, there will be quite numerous occasions in which prudence would favour family limitation; such things as the health of the mother, or the restricted accommodation of the house will often act in this way; and an unskilled-worker class in which this major chance element in prosperity was eliminated would naturally possess a much more strictly defined idea of what standard of living they could expect, and would be expected of them; if they are therefore more readily influenced by prudential considerations under (A) than under (B), it seems to me far from obvious that we ought to assume any increase in reproduction in this class as the result of family allowances.

Darwin to Fisher: 25 July 1930

It always interests me *much* to puzzle over your conundrums, but I must put this lot aside for a bit. I have been—for me—a bit snowed under with Twitchin correspondence; for there are financial troubles in several directions. Also a French translation of my little book has been going astray, and I fear time is making my brain no clearer. But I shall have a try before long.

Darwin to Fisher: 31 July 1930

... I am inclined to think that you ought to show the mean values of x in your table more fertile than the extremes. ...

Fisher to Darwin: 7 August 1930

I enclose the sort of thing I had in mind, if ever it seems desirable to elaborate the interpretation I put on your father's theory.

The principal questions are: does it omit any considerations which he would have regarded as essential, and does it introduce any conception which he would have regarded as alien to his views?

For myself I do not judge that he would have objected to the non-inheritance of readiness to breed early, induced by abundant nutrition, even if he were inclined to insist that other efforts [effects?] such as increased size must be inherited.

For your consideration *AT LEISURE.*

[Enclosure][8]

Schematic representation of Darwin's theory of sexual selection in monogamous birds, as interpreted by the author; showing the possibility of a selective advantage of males chosen by reason of superior adornment by early breeding females, without any selective advantage of females congenitally prone to breed early.

									Average brood for given innate proclivity in respect of breeding date
				$(7.40)^{1}$	$(6.34)^{4}$	$(5.16)^{6}$	$(3.86)^{4}$	$(2.44)^{1}$	5.10
			$(7.34)^{4}$	$(6.40)^{16}$	$(5.34)^{24}$	$(4.16)^{16}$	$(2.86)^{4}$		5.28
		$(7.16)^{6}$	$(6.34)^{24}$	$(5.40)^{36}$	$(4.34)^{24}$	$(3.16)^{6}$			5.34
	$(6.86)^{4}$	$(6.16)^{16}$	$(5.34)^{24}$	$(4.40)^{16}$	$(3.34)^{4}$				5.28
$(6.44)^{1}$	$(5.86)^{4}$	$(5.16)^{6}$	$(4.34)^{4}$	$(3.40)^{1}$					5.10
6.44	6.36	6.16	5.84	5.40	4.84	4.16	3.36	2.44	5.28

Average brood for given breeding date

The table shows hypothetical average numbers of offspring reared by females differing in two respects, (a) congenital tendency to breed early, (b) nutritional condition, which favours both early breeding and number of offspring. The indices represent the relative numbers of females in each class, out of a total of 256. Each row refers to a group of females with the same congenital response to the stimuli initiating the breeding sequence, the latest breeders being in the top row, and shows the frequencies of five different nutritional conditions, with the average numbers of offspring reared. Each column refers to birds actually breeding at the same time. The numbers of offspring are adjusted to increase with the nutritional condition of the female in each row, and at the same time to give a small further advantage to those breeding at or near the mean or optimal breeding date as opposed to those breeding late or early in the season. The selective effect upon the cocks is shown in the lower margin of average offspring according to breeding date, those chosen by the hens actually ready to breed early rearing the larger families. The selective effect upon the hens is shown in the right hand margin, there being a slight elimination of hens congenitally prone to breed too early or too late but no tendency to accelerate or retard the breeding date of the whole species.

Darwin to Fisher: 20 August 1930

I have looked at the enclosed again and I really have no criticism to make on it as a representation of my father's views. I guess he would have been a bit surprised that such a complicated explanation was needed. ...

Fisher to Darwin: 11 October 1930

It must be nearly a year ago that I wrote to you that Haldane had attacked Dominance theory on the strength of the dominance exhibited in grouse locusts and the fish *Lebistes.* I thought at the time that his allies might betray him, and give an unexpected support to the theory, as apparent exceptions are wont to do.

So far they have come up to expectations nobly. Of course I need more data to make a complete case, but I think this paper [*CP* 87] may serve to make sure that the necessary observations will be made. I am still quite nervous about my tentative and conjectural last section, because however often one says that he is guessing, there are many people who will take no notice of the difference between a guess and a decided opinion. Personally, I am *sure* that we ought to go on guessing, as intelligently as may be, and if it is an error it seems one on the generous side to do some of it in public.

I feel rather depressed about the Eugenics Society. But I know by experience that I am capable of making a fool of myself, and I suppose I am as liable as anyone else to ascribe that fault to others. This, I believe, ought to comfort me.

Darwin to Fisher: 13 October 1930

Thanks for Dominance theory, which I shall read with interest.

As to the rather dismal last sentence in your letter, I thought you gave the right lead in the right tone at the meeting. As to the Society generally, I am afraid any propaganda is always a difficult and generally an unpleasant job, if any moral questions are involved. That is why it is so generally shirked. We must do our best, and hope for the best, without expecting much comfort out of the job. You will say that my last sentence is even more dismal than yours!

[P.S.] ...

Fisher to Darwin: 15 October 1930

... You have always advocated the claims of propaganda v. research; partly because you think research can look after itself, partly perhaps because our society is worse organized to undertake research than for propaganda. Here is a test case.

A man has developed, by serological methods of admitted excellence, a method of discriminating between samples of blood, even from closely related animals (brothers and sisters, parents and offspring).[9] He is not a geneticist, nor much interested in genetics. I believe, and am willing to put forward at length the case for believing, that his method may lead to a method of discriminating carriers of recessive genes. A good deal of preliminary exploration is necessary, but this will be a direct and progressive approach to the main object, if such an object is in view. He has now undertaken the first step at my suggestion. Now if, as is far from certain, his ability to go on with the work (he is old enough to retire) or to extend it in directions interesting to us, depended on his having an assistant, would you consider it a proper course for the Eugenics Society to provide one?

From the propaganda side you may regard such expenditure as aimed at removing an obstacle to our propaganda or again, making manifestly false the damaging assumption ... that the Eugenics Society is ignorant of the possibilities of genetic research. Obviously, as in all decent research, the object of the grant should be stated in terms of pure science; its success should certainly not be mortgaged.

That is as well as I can state the problem, without details, which I think you will agree do not affect the principle.

Darwin to Fisher: 16 October 1930

... I intended to champion propaganda as against research for our Society only. ... It is because we are the *only* propaganda body, and because I know that that was what Twitchin wanted, that I am inclined to press this view rather heavily. Anyhow, the Twitchin money is coming in badly, and for 2 years we shall have little to spare. Your proposed enquiry seems to me very interesting and valuable, and if money intended for such work was available, I should most certainly like to see the line you suggest pursued.

Fisher to Darwin: 17 October 1930

I think you feel very much as I do that policy should be based as far as possible on a reasoned statement of intelligible considerations, so if I seem troublesomely argumentative put it down to that, but do not trouble to answer me.

... What I am concerned to ascertain is your own feeling, and that only in respect of the Society, and your last sentence suggests that nothing short of compulsion from the testator would make you approve of assistance being given to research, out of the Twitchin bequest or other general funds of the Society. I should regret it greatly if this were your view, but I should be glad to know it, as I am concerned to answer the question, 'Are there any ways in which I can do good through my connection with the Society?'

The claim that research is so much more attractive than propaganda that it can take care of itself would be stronger if one could point to the Galton Laboratory and the Cambridge Scholarship as successfully meeting our requirements in respect of fundamental knowledge. As far as I can see, it is an equally valid objection against research being undertaken by any State or Corporation having material aims (as well as for underpaying such work of this sort as has to be employed).

The fact that abroad and at home this argument has been increasingly disregarded suggests that it does not cover the whole ground. Among other things that it seems to disregard are (i) that there is no sign of diminishing returns or exhaustion of natural resources in quarrying natural knowledge, (ii) even if a fact were bound ultimately to be discovered free of charge, it is often worth much to know it now, (iii) the moral attraction of research to truthful and public-spirited people, which makes it seem possible to get it done at non-economic rates, is also felt by the general public, who even in the most depraved times must in self-defence prefer truth to falsehood, and are not uncertain in preferring to draw their information from the least contaminated sources. These reasons seem at least as cogent for the Eugenics Society as for a business firm.

Of course I confess at once that to reject this claim is not to say that we know how to expend research funds to the best advantage. To the worker it is very often obvious that we do not. I should say that if we make the best use of our experience we could, by examining each scheme on its merits, find some worth acting upon; but it would be preposterous to set out the advantages of a particular scheme before a body which had already decided against it on principle.

Darwin to Fisher: 19 October 1930

Thanks for your long letter about research. I expect that we differ somewhat in views, but not as much as you seem to think. What I now write is only a few first impressions. I shall put your letter aside, and possibly write later. Knowing Twitchin's views, as I believe I do, that we certainly know enough now to move effectively in many directions, and that persuasion is what is most wanted, I do feel strongly about the use of *his* money. As to other money I should feel very differently. If we had a lot of free money, and decided quite legitimately to go in for research to a considerable extent, I should like somehow to divide the organization more or less into two branches, research and propaganda, and in this way to avoid the danger I see of the propaganda being swamped. ... our Review would be a very good place to advocate new lines of research, even if the Society is too poor or itself unwilling or incapable of directing the work. ...

I am rather sorry they picked out an old discontinuous stick-in-the-mud like Punnett to review you in *Nature*.[10] But to get 5 columns is an excellent advertisement. My father would have been much pleased with such a review of the *Origin*, and merely carefully noted the points to answer in his next edition. I think you may be well pleased. *I* never had so long a review.

Fisher to Darwin: 20 October 1930

I ought to have known that my letter would worry you, as indeed I might have foreseen. It was very ill-expressed. I suppose it is useless now to ask you to put the matter out of your mind, so may I suggest that when you do return to consider it, about which I hope you will on no account hurry, you might tell me, what I think would clear the matter up for me, whether you draw any distinction between using the Twitchin money for research, and using it to release other income for that purpose. You will understand that those of us who believe that at least occasional and exceptionally favourable opportunities of furthering research should be seized, might have regarded it as beyond our reach so long as propaganda work was not otherwise provided for, though thinking that when that condition was fulfilled, it became our clear duty.

Thanks for your kind comment on Punnett's review. I think you suggest that a rejoinder would in all probability be unwise. That was my own view before I looked at his statements in detail. I am now doubtful. I enclose a possible letter to *Nature*, which I am inclined not to send in if you so advise.[11]

The distinction I have in mind is between tidying up troublesome trifles now, and leaving serious scientific criticisms to be dealt with later as further facts become known.

Darwin to Fisher: 21 October [*1930*]

It is true that I am generally opposed to anything in the nature of a controvery in any papers on scientific subjects. My Father always used to rejoice that Lyell had given him the advice to avoid such controversies and that he had always followed it. Your letter, however, seems hardly to come within this description and I have no very strong opinion whether it should go or not. I am in fact not prepared to advise against it. If you send it, it might be worth considering whether it might not be cut down a little and perhaps touched up in a few places. As drafted, you accuse him of misstatements, whereas I think you really mean his errors to come under the heading of 'slighter misrepresentations'. It is so courteous that I do not think he could mind.

When I wrote to you about the expenditure of the Society I think I was rather worried about one or two other things and it was that to a large extent which showed itself in my letter I expect. I should now be inclined to say that if the Twitchin money goes to propaganda and to a fair proportion only of the administrative expenses, I should have no objection to any other available funds being used for research if the Council thought fit. This is written straight away but I don't think I shall alter my mind.

Darwin to Fisher: [*late*] *October 1930*[12]

Here are my first *indecisive* thoughts on the very difficult psychological problem which you set me. I agree that everything which makes the future more clearly foreseen also makes for rational conduct; and that family allowances (f.a.) will have some effect in this direction. This is an *immediate* beneficial result which I had not thought of. ...

I see no reason whatever why the sudden introduction of f.a. should reduce the size of families, and good reasons for anticipating some increases. ...

Fisher to Darwin: 30 October 1930

Thanks for your letter and enclosures; I will only answer now some points of your letter.

I think I agree with your view entirely that family allowances will tend ultimately though perhaps very slowly to exert a direct effect towards increasing fertility in all classes. As you know, I also believe that ultimately, though slowly, it will increase the innate fertility of the well-to-do, and diminish that of the poorer classes. At what point these ultimate effects would balance, if at any point, must depend on a host of different circumstances. What I want to say now is that the effect I am inclined to stress about prudence is a much more immediate one, though a permanent one, to be considered in relation to the initial changes introduced by family allowances.

The general economic prudential motive for birth limitation is, I believe, wholly dysgenic in its effects, but there are prudential motives which I think are eugenic—most notably concern for the health of the potential mother. These motives are, I believe, at present much more active and effective among the well-to-do than among the poor. This contrast is dysgenic, although within each class the action is beneficial. I submit that family allowances would greatly affect the poor, not perhaps much in prudence as you use the term, but in a greater sensitiveness to small differences in comfort and standard of living, and thus introduce a definitely eugenic motive for birth limitation among the poor, and abolish largely or wholly the dysgenic contrast between the effectiveness of these motives among the poor as contrasted with the well-to-do. This is all quite distinct from any general and, I believe, much slower effect upon the general fertility of different classes.

The important contrast in this respect is between the more and the less healthy; but I believe a beneficial effect would also supervene as between the more or less competent. No one doubts that the management of a family makes calls on general competence, and I cannot doubt personally that the difference in standard of living between couples at different levels of competence is much greater when there is a family than when there is none. If that is so, and family allowances were paid at a rate which on the average allowed an equal standard of living to parents and non-parents, it follows that the standard of living of the competent will rise, and that of the incompetent will fall, with increasing size of family; this supplies a generally eugenic motive which would become effective among the great mass of the population, if they were at all keenly sensitive to differences in standard of living.

I do not object in theory to discussing such proposals as that before the Trades Union Congress,[13] although I am opposed to them. What I do feel is that if the idea of family allowances is introduced to the English public as a political means of catching votes by relieving poverty out of taxation, then we have lost the first round. Perhaps it is inevitable that we should lose this round, but you must excuse me for fighting against it. What I fear is that both its supporters and its opponents will be prejudiced against its proper uses. If, on the contrary, a non-class scheme could be made familiar to the public in the first instance, it would have done much to prevent the adoption, or even the advocacy, of the more ignorant and ineffective variants. ...

Darwin to Fisher: [*early*] *November 1930*

Many thanks for your letter about family allowances. It is all very puzzling, and I feel that you may be right on all points. In short, these psychological problems are so difficult that I must be content to leave the solution to those who will come after me. Anyhow I shall be very ready to back you up in any movement to get contributory f.a. adopted, as the only satisfactory financial method of aiding parenthood. I shall make no complaint however hardly you fight against state systems; but shall continue to believe that to point out the best safeguards in advance might be useful.

I have been reading your Dominance paper, and though it is rather too technical for me, yet I gather that is an admirable example of a theoretical forecast being verified. I think I shall send it to my nephew Charles,[14] in the hope of maintaining his interest in these problems. I said in a paper in our Review that 'the normal aim of natural selection would be to produce' a stable differentiated series. You here prove, I take it, that considerably differing forms can remain in equilibrium as regards survival value; and, if so, is it not probable that this is a very common phenomenon with slightly divergent forms? ...

Fisher to Darwin: 25 November 1930

... What do you think of this? If insanity of a heritable type appears in a family of otherwise good stock, some members will abstain from parenthood from fear they might be tainted, although really free, and others will take the chance of being free although really tainted. Both processes, arising from ignorance, are dysgenic, and could be stopped if it were possible to test the blood of a patient for the defective gene, without its manifesting its defects somatically, either because it is recessive, or because the patient has not yet broken down.[15]

Todd finds he can prepare a serum to which the corpuscles of every chicken, except one for which it has been specially exhausted, will react[16]. If he exhausts for both parents, he finds he has also exhausted for all their joint offspring.[17] I infer that he is detecting primary gene products, for many secondary substances occur in offspring which are not in the parents.

Darwin to Fisher: 27 November 1930

Thanks for yours. It would indeed be grand if a test for a recessive gene could be found, and blood does seem to offer a possibility. But, from the facts you give, I do not see how to get a serum which only reacts to the proper gene. Of course, at first in such cases the answer is not to be expected. But it is a clue. ...

Fisher to Darwin: 28 November 1930

If Todd had exhausted the possibilities of his method there would be nothing left for us to do. But he has not, and I doubt if he ever will. He is not specially interested in genetics, and talks of retiring. He would like some geneticist to take on this aspect of his work, but apart from Haldane, who is doing two jobs and a lot of journalism already, there is no one who could be interested.

Early this year I suggested an experiment to obtain a serum diagnostic of sex, as that is the only visible thing in which his chicks are segregating. In birds the hens are heterogametic, so the thing is to take blood from a number of hens, inject into cocks, draw active serum from the cocks, and exhaust it with the corpuscles of several birds, all cocks, until it reacts to no cocks. If it still reacts to hens, there is a serum for a single factor (or possibly chromosome). Unfortunately, something Haldane had said had discouraged him from looking for a sex discriminant, so though he was, I think, interested, he was not interested enough to fit in a biggish extra job in his programme.

This autumn he sent me a proof of a new paper in which he reported tests of sera exhausted for different chicks in others of the same broods, and asserted that there was no sex effect. I was so concerned that I tabulated all the cases of positive and negative reactions for the corpuscles of males and females, to serum exhausted for males and females, and was able to show Todd that there was an apparent sex effect in the right direction in all three of his broods, and that in one case it was big enough to be judged significant. This time he was interested enough to cut out the references to sex, and to say that he would do the experiment I had suggested.

Beyond sex, one wants to know, 'Do most genes give an appreciable reaction?' For this, one needs material segregating in single factors, just as any flock does in sex. It so happens that my test flocks for dominance in the wild *Gallus* are just of this kind for, from next year onwards, I shall have lines segregating each in one of 9 different factors. The birds will be smaller than Todd's big Plymouth Rocks, and will therefore yield less serum, but I think this can be got over.

It is quite likely the sex experiment will fail, either because the reaction is too faint to show up with his standard quantities and times, or because there is nothing specific in the female to react to, sex determination being perhaps merely quantitative. In this case, probably, Todd will be disinclined to go any further with this aspect of his work. What in my view is wanted is to offer him a voluntary worker, paid by an outside body, whose programme should be to explore the possibility of detecting single genes.

Darwin to Fisher: 4 December 1930

... I have no very useful—probably useless—suggestion to make about your last point. ... it occurs to me that if you wrote a careful letter and got the Society to send it to the Medical Research Council, it might educate and wake them up, even if it did nothing else. It is, in my opinion, just the job they should tackle. ...

Fisher to Darwin: 5 December 1930

I do not quite know if you will see my point, but I think it would be entirely useless, even if the facilities were offered, to commence research on Man, until (i) the possibility of demonstrating a single gene had been demonstrated in some other species, and (ii) considerable experience had been gained as to the different reactions of different genes.

Only on this basis would it be worth while to set out to build up a test for a specific gene in Man. In Man, too, it may be that a special technique will be needed to circumvent the known isoagglutinin factor, which has a relatively enormous effect, and may not be easy to cut out by 'exhaustion'. I hope, if you happen to discuss it, you will not mention human applications except as a remote possibility.

Half-pay, say £150-£200 a year, would probably suffice to give Todd an assistant with a programme that would suit us, that is, if Todd would take him on. A lot would depend on his getting a sufficient mastery of the technique to prevent a set-back, if Todd should retire. ...

Darwin to Fisher: 6 December 1930

Without having very clear ideas on the subject, I expect that you are perfectly right in thinking that long work on animals would first be needed. I gather you think it would be hopeless to interest the Medical Research Council or the Lister Institute on these lines. One never knows where one strikes oil. They both, I imagine, do work on animals. ...

This is a little problem I have had in my head. Suppose 8 per 1000 are y inches in height above the average. Can you say what percentage of the children of persons y inches above the average will themselves be y inches above the average? If so, does this give some theoretical indication as to the percentage [of children] of mental defectives who would themselves be mental defective? Don't answer if this is a useless idea, which it probably is!!

[P.S.] I suppose the answer depends largely on the amount of assortative mating.

Fisher to Darwin: 9 December 1930

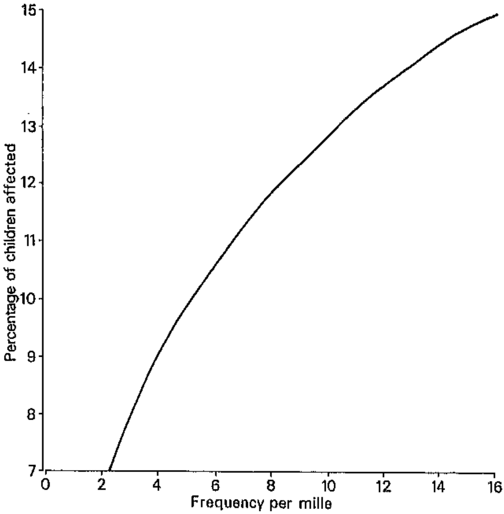
Many thanks for your letter. I must have been writing hurriedly and expressed myself badly. I had only meant that I should not like to try to interest the Medical Research Council in the *eugenic* possibilities opened out by Todd's work. I imagine they are quite satisfied with the value of his work as a serological expert, and are quite prepared to give him facilities for prosecuting the studies he is engaged on in pure (as opposed to medically applied) serology. I believe his discovery arose in Egypt from his work on immunizing cattle to disease; and I suppose the Medical Research Council feels itself justified in expending money on pure research which may make applied serology more efficient. They would presumably give facilities and possibly half pay, if Todd found he could get an assistant to follow up an interesting side line.

Personally I think it is an opportunity of forwarding work of eugenic importance; but I see I have not wholly convinced you, and I am anxious not to be troublesome. So I will not write further on it, unless you decide that you would like to raise the question again.

P.S. Your way of looking at the inheritance of mental deficiency is an extremely attractive one. I wonder why it has not been discussed on these lines before. Perhaps because it leads to rather difficult mathematics.

On the enclosed sheet I have charted the percentage among the children for frequencies of about 5 to 13 per mille, for parental correlation 0.5. I

[Enclosed chart]



calculated the value for 8 per mille independently by another method, and ... it checks well. These percentages give also the diminution of mental defect in one generation, due to sterilization of mentally defective men *or* women. The effect of sterilizing both will be nearly, but not quite double, say 20 per cent at 8 per mille, or 22 per cent at 10 per mille.

A full calculation, involving both parents, would involve frequency tables for 3 variates which have not been constructed. One would need also one further observational fact, namely, correlation between husband and wife.

Darwin to Fisher: 11 March 1931

... Did Huxley ... suggest that to work against individualism was eugenic? I guess not. ...

Fisher to Darwin: 16 March 1931

Yes, Huxley did say that about individualism, but quite tentatively, as an inference from my book. I expected that reaction from Haldane, who has made the same inference, but not from Huxley. I felt, in writing the Chapters on Man, that the great difficulty was to frustrate the people who want to use everything as a handy bludgeon in political controversy, and I re-read everything I wrote in that light. It is not only Haldane, but I think also Hogben, who is influencing Huxley in this direction. What a curse it is that some of the few really good brains should be fascinated by sensationalism, but perhaps it would be worse if they all allowed themselves to be quietly ignored.

Naturally, finding class differences to be an essential feature of the dysgenic process in civilized life, I have tried to conceive the possibility of biologically progressive societies in which class distinctions were unknown. At every point this seems to lead to an *impasse*. Man's only light seems to be his power to recognize human excellence, in some of its various forms. From this it follows that actions, powers, and functions cannot be of equal value. Promotion must be a reality, and the power of promotion a real wealth, whether we call our potentates kings or commissars. I do not believe that political capital of any sort can *fairly* be made out of my book; politically biased people will, I think, merely find it inconsistent, and these must be the great majority of readers. ...

Darwin to Fisher: 20 March 1931

Thank you for yours about Huxley's remarks. It seems to me quite illogical, but what you say shows me that you have pursued this line of thought further than I have. I shall keep your letter to re-read if, as I hope, I carry out my plan of re-reading your whole book. It takes not much to fill my days now, but I am always expecting a time of complete leisure. I guess Plato was right in thinking that all babies must be taken away from commissars, or they would pass on their 'wealth' to their children, and the system would break down. I was reminded of my father's words—though not quite to the point—that if a man 'is to advance still higher, it is to be feared that he must remain subject to a severe struggle'. I *think* he put in the word 'fear' in the second edition of the *Descent*, which indicates the kind of criticism he received. ...

Darwin to Fisher: 30 April 1931

I have read the enclosed,[18] and like it very much. It seems to me most valuable at the present time. ...

I wish Smuts could have read it and your book before the autumn. He made the Berg criticism in a very crude form.[19]

I like what you say here better in some ways than as put in pages 1 and 2 of your book. You here divide it into periods. The reader of your book might be led to think that my father held firmly all your (a) to (f) points *simultaneously*, which I doubt. If he were asked in 1881 or so if he believed in the blending *theory* of inheritance, I *imagine* he would have replied as follows:-

I really do not know exactly what you mean by your question. In '42 when considering the indisputable fact that there is normally a good deal of blending when crossing takes place, I was much puzzled because of the apparently obvious tendency thus to wipe out the effects of selection. Now I have to content myself with the *fact* that great changes obviously can be produced by selection, as is proved by domestication. I have *no* theory to account for blending not operating as would seem probable. I wish to goodness I had.

If you were asked to state what exactly was my father's blending theory, which must have fitted in with the reappearance of ancestral qualities and the differences between sibs, would you not find it hard to reply?

I have sometimes felt that one of the difficulties unconsciously felt by critics is due to the half-formed belief that the 'lower' animals have given rise to the 'higher' in an evolutionary process of 'improvement'. All organisms have probably been subject to an equally long period of selective action, and no surprise should be felt at any perfection of adaptation amongst the 'lower' animals and plants.

But all I really want to say is that I hope this will be published somewhere. ...

Fisher to Darwin: 2 May 1931

I wouldn't be sorry to publish something of the kind you suggest, and *Science Progress* would be a distinctly good place, but I did start writing with a view to repairing what is something like an omission from my book. The trouble is, as you see, that while I look, earnestly and diligently enough, for objections to the theory of Natural Selection, the opponents of that theory always fob me off with objections to Lamarckism or to evolution in general, so that I can really find scarcely anything that has any logical place in my book, in spite of the mass of anti-selectionist literature.

I do think, by the way, that you must be reading too much into my first chapter. Your letter reminded me of something C.G. [Darwin] said in his review,[20] to the effect that my argument, had it been brought forward before Mendelism was known, would have disproved selection theory. Now I don't think this is true at all, and as I must have been responsible for the misapprehension, it is up to me to track it to its lair. Tell me if you think I am wrong, but I do not imagine that your father would have found anything new or interesting in my argument, except where I bring in facts which he did not know and had not guessed, and their consequences to an argument with which, without these facts, he would have felt perfectly familiar. The consequences of blending, which I emphasize, do not stop natural selection from working, for, with sufficiently high mutation rates, a supply of heritable variation can be maintained, and I think I could answer your challenge on this point sufficiently to show that your father did believe in these enormously high mutation rates (almost every individual a multiple mutant) in man, and in the domesticated animals and plants; but that, in the case of wild animals, he long kept his mind open to the possibility that they might be for long periods practically invariable and only be made to vary occasionally by changes in their environment. What his final view was on this I do not know, but I have no doubt that after 1860 Wallace did something to persuade him that wild populations were not so constant as he would have been ready, formerly, to admit. Wallace could have produced evidence only of somatic variability and could not have proved that it was heritable.

There seems to me nothing whatever illogical in the theory that heritable variability is maintained by such very frequent mutation, and so the material provided for Natural Selection to work upon, but this theory does open the door to the view that the particular causes to which each mutation must be done (as your father frequently insists) *might* be also important causes of evolutionary change. And though your father could find, I think, very little observational evidence that this was so, against much in favour of the efficacy of selection, yet this possibility he steadfastly kept open. This strengthens my confidence that he had a perfectly clear grasp of the argument I have set out in its esentials, though he might well have preferred other words, and that he was not merely the patient plodding accumulator of observations which one legend makes him out to be.

The case strikes me as remarkably similar to that of Carnot's principle which is the basis of all thermodynamic reasoning. For Carnot developed his theory in terms of the view that the quantity of heat remains unchanged, not knowing that it was quantitatively convertible with work. In bringing in the conservation of energy instead of the conservation of heat Clausius wisely saw that the principle of Carnot's reasoning was untouched, though it led to somewhat different consequences; for Carnot's reasoning was right on the observational facts known to him; and I am sorry that I should have let the point be missed that your father's reasoning seems to me to have been right, even where his premises were wrong.

On the second point you raise as to your father's theory of heredity, would you agree with me if I said that he would have welcomed a view of heredity which could have included reversion, but that, in the absence of such a view, he was willing to accept the fact of reversion, provisionally perhaps, as a principle independent of heredity and possibly due to some entirely distinct mechanism?

Thanks for your point about the lower animals; I must bear it in mind. Certainly Berg seems to think it rather impudence for such a wretched creature as a free-swimming Tunicate to have such a fine 'test'.[21]

To revert to my original purpose, if I can ever produce anything good enough to stand as a review of the difficulties and criticisms raised against selection theory, how do you think such a chapter would go in a German translation? It would be, in its nature, much more provocative, at least to reviewers in a hurry, than the rest of the book, and my wife has just made the scandalous suggestion of using it as a preface, as this is the only part they are likely to read. I have just had a letter from a German anthropologist, working in America, who wants to translate the book into German; quite probably he will fail to find a publisher, but, while the project is under discussion, I should like to know how you felt as to adding something of the kind I have sent you, with perhaps some boldish speculations on the rapidity of adaptive variation in the formation of the great classes.

Darwin to Fisher: 4 May 1931 (*a*)

... In our Outline,[22] I think *you* put in that 'the Society is strongly opposed to redistribution by means of taxation ...'. Now I have been slowly drifting more and more to tolerate or even approve of such a method of improving the lot of the poor—though my ideas are still very shaky. Now in this *Quarterly* there is an article by Keynes[23] on high wages, which I thought might irritate you nicely. It is true that I neither like him nor trust him, in spite of his being my niece's brother-in-law. But he is very clever, and won't go *far* off the line for any reason. Hence it occurred to me it might do you good to read it. Then read my cousin J. Wedgwood's article, if you have not previously thrown this production into the fire in disgust. Please finally deal with it in that way, for I don't want to see its face again and do *not* write—for I am, I think, going to bore you with another letter tomorrow, on a subject as to which we may possibly agree!

Darwin to Fisher: 4 May 1931 (*b*)

Thanks for your interesting letter. I am glad to hear of your German edition. I do not see why this new part should not form a preface. It is, I think, very important. Let me know if financial or other difficulties stand in the way of the German edition.

I agree that blending won't stop selection if the mutation rates are high enough. You may be right about my father's views. I incline to think, however, that you have a clear idea of *mutation*, which he could not have had if, as I suppose, the idea of the transmission from generation to generation of quite unaltering hereditary elements had never even occurred to his mind. I remember when, about 1890, I was thinking over Galton's ancestral law, I used to puzzle myself as to how it was conceivable that the average quality of the race could be transmitted from generation to generation as well as particular individual qualities, this being necessary if reversion to the mean takes place. The broad view of the transmission of unaltering genes would, I conceive, have interested my father enormously, as well as all the deductions you draw from it. But you *may* be right in thinking that he saw matters more clearly than I suppose. I shall keep your letter and think over it. It may merely be that *I* did not see it in those days. I think I agree with what you say about reversion to the mean.[24] No more today.

Fisher to Darwin: 6 May 1931

Your two letters arrived together this morning. Thank you for asking me to let you know if financial or other difficulties stand in the way of a German edition. I have not yet heard from my publishers, to whom I sent the offer. ...

I am impressed by the way your father insisted that each variation must have had its particular cause. In saying this I think it is clear he meant by variation, not an ordinary difference due to different heredity, but something new and destined to be inherited, and therefore, to use the modern word, in a broad sense, a mutation. I should guess that he did not think of a mutation as a discrete step, but as quantitatively variable, its magnitude being determined by the intensity of the cause which brought it about, and in this his notion would have been more general, but not less definite, than the modern notion of mutation. One is inclined to wish that he had used some more distinctive term than variation to distinguish the heritable novelty just induced by its particular cause, from the inherited differences between individuals. But I think I see why he did not feel any need for this, for, with blending inheritance and high mutation rates, all differences within intrabreeding groups, such as a single breed of dogs, would be due to quite recent causation, i.e. only a very small fraction could be more than ten generations old. I should be *very much* interested if you are inclined to think over this point of view, for it seems to me an entirely logical position, and fits very well with many of the phrases your father used in writing; I gather, however, that he felt he expressed himself with difficulty, but this was perhaps only because he felt the need of guarding himself against the unintentional misinterpretations which people would put on his words. His spoken words, especially when explaining his dissent from some view, which he felt, rather than saw, to be unsound, might be very illuminating.

Thanks for sending my the Keynes' article. I think I feel as you do about *him*, and heartily condemn his one incursion into theoretical statistics.[25] But he does write well, and is wonderfully clever at characterizing different points of view. As far as I can see, what he says is that as we have got to pay non-economic rates of wages, then we must subsidize industry out of general taxation, and he would like to do this by lowering wages, and giving the wage-earner additional benefit through social services. I don't see any particular advantage in this course as compared to, say, subsidizing the employer to the tune of ten per cent of his wage bill, a process which I, being as you know 'in African darkness',[26] think could be done relatively economically and sufficiently selectively by means of a tariff. This assumes, of course, that an honest tariff is still a possibility.

As to family allowances I do still feel that a state-paid scheme financed out of general taxation would be deadly to the principle of proportionate benefit, unless it were introduced after that principle had become established in separate occupational associations.

In the context of our Outline, I take redistribution by means of taxation to refer only to redistribution as between those with and those without children, and not to taxing the rich for the benefit of the poor. I have just noticed that you say do not write, so now I am done for. Is it too late to say do *not* read?

Darwin to Fisher: 18 May 1931

This is mainly to wish you every good luck on your journey. ...

I am going to write you a long letter about my father's views. I guess you won't want it in America. If I do send it after you, perhaps to read on the voyage home, it will be a *copy*, which if lost will do no harm. ...

[P.S.] Do not overwork yourself *in America*. It is, *there especially*, a *real danger*. Do not mind indulging in many platitudes with your audiences!!

Darwin to Fisher: 24 May 1931

In answer to your letter concerning my father's views on the laws of inheritance, it seems to me that we should first of all look to his theory of pangenesis; for that was his theoretical way of accounting for what he believed to be the facts. We may be disinclined to tread this path once more; for we know in advance that we shall again reject his theory as a whole. Nevertheless, it is the best way, I think, of ascertaining what were his underlying thoughts. If I quote numbers, they will be the pages in *Animals and Plants under Domestication* II, second edition.

According to his theory, each cell gives off gemmules, and 'several gemmules are requisite for the development of each (new) cell or unit' (381), presumably some of them coming from each parent. Though not, I think, clearly stated, I gather that he held that these *necessary* gemmules blended completely, so that the parts, when fully developed on such a basis, in their turn, gave off gemmules which 'ultimately developed into units like those' (370) formed by this process of blending. This blending of the gemmules, though complete, was not uniform; for at all events the gemmules 'derived from one parent may have some advantage in number, affinity or vigour over those derived from the other' (382). These gemmules are also held to be 'capable of transmission in a dormant state to future generations and may then be developed' (370). For both these reasons, organisms will only be 'generally nearly intermediate in character between their two parents' (395).

Now the more unequal the blending of the formative gemmules, the greater the 'host of long-lost characters (which) lie ready to be evolved under proper conditions' (369), the more 'incessantly' (394) reversion acts, the longer would it take for complete uniformity to be created in any interbreeding group. 'After a longer or shorter period, the species will tend to become nearly uniform in character from the incessant crossing of [the varying] individuals' (262); but the time might be fairly long. And all this time selection would go on whether or not any other changes were taking place. Moreover, 'the dissimilarity of' sibs and the greater variety of sexually-produced organisms would be accounted for by the 'unequal blending of the characters of the two parents' and by the 'reversion to ancestral characters' (239); but all this nevertheless points to a slow but complete process of blending.

In order to account for progressive evolution, he held that the surroundings of an organism affected its development and that, normally, the gemmules subsequently thrown off represented the form thus produced. The transmission of latent gemmules for many generations merely threw back the environmental cause into the past. With 'absolutely uniform conditions of life, there would be no variability' (242) nor any progress.

In passing, may not all mutations be due to some environmental cause? The regularity with which they appear in *Drosophila* no doubt tempts us to look on it as an inevitable natural process. But the more uniform the surrounding, the more regularly will exceptions appear, as a rule. If the mutations in that fly are due to thunderstorms, they would come in one year about as much as in another. And our knowledge of the effects of X-rays on organisms and lightning on our wireless sets makes this illustrative supposition less ridiculous.

My belief is that my father had no clear distinction in his mind such as we have between mutations and Mendelian differences. All variations were much the same to him though I think he says somewhere, I cannot say where, that some are not inherited. Otherwise, in identical surroundings, variations identical in form differ in hereditary effects solely because of differences in the latent gemmules which they carry. The amount of variation depends in the long run on the amount of exceptional environmental effects; this being, he held, proved by the effects of domestication. I think there is more truth in this last contention than you apparently do. But his system allowed for nothing like the accumulated effects of mutations.

In pangenesis an effort was being made by my father in the direction indicated by his letter[27] of 1857, so it seems to me. Fertilization, he then said, is 'a sort of mixture and not true fusion'; and, according to pangenesis, the ancestral gemmules whilst latent do not fuse. This was a step in the direction of Mendelism. He held that 'each minute element of the body' had an 'independent life' (365), and if he had not come under the influence of a few Lamarckians whom he admired so much, he might have hit on a different idea of pangenesis. He might have seen that each cell contained a basis more or less capable of causing the development of the whole organism. He did realize that hybrids, when united, led to reversions to either parental type (395), his explanation being much the same as ours. 'Reversion depends on the transmission from the forefather to his descendants of dormant gemmules' (399). Replace 'dormant gemmules' by 'recessive genes' and we have pure Mendelism. He felt bound, and he was bound from his point of view, to make his theory cover the inheritance of acquired characters and telegony. Pangenesis is, I hold, a logical system, and being 'provisional' it should only serve to indicate his general beliefs. It is hardly more difficult to believe than Mendelism, when we realize what marvellous powers we attribute to the genes of a single cell, enabling them to control the whole growth of an organism through all its many phases. But pangenesis fails to account for the numerical effects discovered in connection with Mendelism, for correlation coefficients, and for the accumulated effects of variation, and it must, therefore, be rejected. ...

All this, however, if accepted, does not seem to me to necessarily alter your views materially. The blending which my father believed in was, I think, less rapid than you seem to suppose; and I do believe that the great variability of domestic animals is partly due to mutations having been exceptionally frequent under domestication.

Possibly we should take a leaf out of my father's book and be sure that our theory accounts for all that we hold to be true. A graft of a plum, which seeds truly, if placed on another stock, loses this power and becomes variable (247). Sometimes 'more than one spermatozoon is requisite to fertilize an ovum' (356). Tubers of a potato 'produced from a bud of one kind inserted into another are intermediate' in their qualities (360). We may yet have something to learn.

P.S. I am inclined to think that 'definite variations' are best translated by 'acquired characters' and 'indefinite variations' by 'mutations'—only no one then suspected the possibility of the segregation of 'genes' unaltered.

Darwin to Fisher: 10 September 1931

I am very glad to hear that your American tour has been so *very* successful—as I call it compared to what I had expected—for I have known of considerable failures. But I am sorry for the fly in the ointment.[28] I forget if you have ever had an operation. If so, you will know that the operation in itself is *nothing* at all. You know that mine was a big one, but I had *no* local pain, only want of sleep, headache, and discomfort. I hope you will be in good hands. ... I wish I could be of any use to you. *Do* let me know if I can be.

I send you a letter written to you in May, which I did not post, as I did not want to bother you then. ...

Well, no more today, except to wish you good luck.

Fisher to Darwin: 15 September 1931

Many thanks for the letter you wrote to cheer me up before my operation. I had not had one before and was quite three parts anxious. What you said encouraged me greatly. I believed it about half, but it seems to have been quite true. ...

Your letter of May 26th I shall postpone until I can read Pangenesis again and get the context of your citations. I can see that I shall value it greatly.

Do not lose any good opportunity of letting me hear your ideas old or new. I have been learning bit by bit that there is generally the germ of something uncommonly well worth thinking about, in what you say. And from my end this is a good opportunity. ...

Darwin to Fisher: 26 September 1931

... I have had a niece here, who is somewhat interested in science. She said, I understood, that there are some distinctions between the *species* of plants, inland and seaside, which are paralleled by the differences in the individuals of the *same species* when grown in the two situations. It seems to me that this latter power of adaptation to different environments by the same species must have arisen much as you account for the origin of dominance. ...

Fisher to Darwin: 29 September 1931

... I had never thought of the plants in quite that way, though I think I know the phenomenon your niece referred to. So the analogy of dominance struck me as new and illuminating. If I have the point right, you may have plants growing in a salt marsh with fleshy leaves and stunted growth, while others of the same species, growing in soil or fresh water, are tall and thin-leaved. The succulent habit of growth is characteristic also of whole species confined to salt situations, but when the succulent plants are transplanted and grown alongside fresh-water forms they revert to the fresh-water habit. Even closer still, Turesson has shown, with I forget what species, that some of the succulent plants are merely modified, while others, growing in the same site, are genetically succulent in that they and their offspring maintain the habit in culture. In this case the plants with halophytic genotypes serve to show that the habit really is adaptive, and enjoys a selected advantage, which is, however, gained by other members of the same species, by an adaptive modifiability. I take your point to be that the adaptive modifiability must have been acquired by the selection of modifying factors, which alter the differential reaction of the plant to its environment, without affecting its habit in fresh water, just as the dominance modifiers alter its reaction to a particular mutant gene, and that the selection in favour of these modifying factors is only effective in individuals containing the mutant gene, or growing in the salt situations. This method of adaptation favours the cohesion of the species, whereas the alternative method adopted by plants which are thick-leaved *wherever* they are grown, would tend to favour its fission; and if the salt marshes were very extensive, and largely isolated, might ultimately produce a distinct halophytic species. Let me know if I've got the point right as you only give me a hint in your letter. ...

I had a letter from Ford by the same post as yours, in which he gives me an amusing account, though at second hand, of the population discussion in Section D.[29] Huxley was good enough to speak in my place, giving an account of my views, and this seems to have stung MacBride into some wrathful allusions to the valuelessness of the opinions of mathematicians *vis-à-vis* biologists. At this there was applause, Baker loudly shouted 'Shame!' and there was applause from another section. Ford expresses great indignation against MacBride, the more so I think, because MacBride evidently has some support, at least for this part of his views. I feel myself that it is very well worth while to be abused if it gets my book read and criticized.

By the way, I was very much surprised to hear from the Oxford Press that the Natural Selection book has sold even better than my one on Statistical Methods did. It was so long before I heard from them that I had quite made up my mind that it was one of those books which everybody praised and nobody read, and would have no influence on biological opinion. I think this is still its danger, but the sales must mean something. ...

Darwin to Fisher: 30 September [1931]

... You have understood what I meant about the seaside plants. But you must not trust to me for facts.

I was much interested and amused at Ford's account of the British Ass. meeting. You need mind it no more than my father need have minded the Bishop's attack at the celebrated meeting at Oxford. ...

Darwin to Fisher: 2 October 1931

... I am inclined to hold that Lamarckism is doing more harm than you seem to think. But I may well be wrong. It is more or less backed up by many men of science, and, so long as this is true, the public will consider it a main factor in evolutionary changes, and will not realize the importance of selection. I can do little these days, but I shall write a letter saying what I want, to an imaginary correspondent, and then consider what to do. I want a book to show how little Lamarckism could do in evolution, even if it is a real factor, and therefore how in any case we must rely on selection for progress. It is the moral of your book, but I want it more definitely brought against Lamarck. ...

If you ever again consider seaside plants, see *Origin,* Chap. V, end of second para. It is quoted as a case where 'conditions seem to have produced' a slight definite effect. ...

Darwin to Fisher: 1 February 1932

As I think I mentioned before, I have been writing some notes on evolution, etc., and I am going to ask you not only to read them, but, what is more difficult, pick them to pieces as much as you can. I have been doing this mainly to interest myself, as I now find writing difficult, and in consequence the results generally unsatisfactory. ... I am also sending you a few separate notes in my own handwriting. Will you also kindly scribble your remarks in pencil opposite them also, and return. As to the typewritten stuff, I may add something as to the way in which the way I have presented the evolution problem reacts on eugenic propaganda. I feel nearly sure that you, and possibly a couple more, will be the only audience for these two efforts. ...

Fisher to Darwin: 5 February 1932[30]

... Regression, as the word was used by Galton and the Biometers, i.e. regression to the mean, must have at least three contributory causes:-

(a) If the relation of the child to only one parent is considered, regression is due to the contribution of the other parent, for the reason that tall men will on the average have not so tall wives, reckoning tallness in each sex from the mean of that sex, and in the same sense a selected group of short men will have wives who may be below the average, but will be not so short as their husbands. To avoid this obvious cause of regression Galton was led to use the 'mid-parent'.

(b) Non-inherited fluctuations due to environment will cause a group of parents selected for height above the average to have more than their share of those whose stature has been enhanced, and less than their share of those whose stature has been stunted by environmental circumstances. Their children, therefore, if reared on the average in an average environment, will be shorter than their parents for this reason. As far as I can judge, this makes a very unimportant contribution to the regression observed.

(c) The main regression from the 'mid-parent' in man seems to be due to dominance, which may be regarded as similar in its effects to environmental fluctuations, seeing that it, like them, disguises to some extent the genetic nature, so that we select a little amiss, and do not find the whole of what we saw in the parents reproduced in the children. ...

I don't feel that we can reject the notion that some qualities making for genius have been harmful. Some geniuses have had so much common sense that one can feel pretty sure that had they been born a medieval serf or a primitive hunter they would have made a very good job of it. But, without a lot of ballast, I should certainly guess that there are qualities, such as introspection, or an excessive concentration on apparent logical contradictions, which may make for greatness in a musician or a mathematician, but which at the same time may have been harmful during the greater part of human evolution. But I do feel these weigh rather light in the balance against the great qualities which make a mind energetic, persevering, and penetrating, and I should guess that these had only been disadvantageous in very exceptional circumstances. I suppose the great difficulty is to allow for the enormously greater facilities which civilization offers for utilizing special and limited gifts, so that if they hit off the temper of the age they are appreciated, like those of Praxiteles or Nelson.

... [Have] we any right to say that the geniuses stray further from the pile than they ought to do by chance? In the Stone Age, I suppose your father might have been a great trapper; perhaps no one would have selected his flints for chipping more carefully, but if carving goddesses in ivory had been all the rage, would he have been able to do much more for his tribe than to leave a few level-headed aphorisms for them to ponder over? ...

Fisher to Darwin: 18 February 1932

I am sorry that I have delayed in returning your typescript on Evolution and Eugenics. I have written in a few verbal suggestions, none being of any importance; in fact I should have written before if I had not found myself is such full agreement with almost everything you say.

The whole contrast you open up between the rapid changes which can be postulated when one or more gene substitutions offer a definite and universal advantage, and the much slower process which you suggest, if I have taken you right, when the advantage is fluctuating and contingent upon a considerable complexity of other conditions, genetic or environmental, is one which I much want to get my own head clearer about. I think you may have formulated it as well as is possible, but there may be other ideas unexpressed which I could take hold of as a stronger clue.

I am not quite sure if it is safe to class the great differences between orders and classes entirely in the group of differences which have arisen very slowly. Of course I agree in the sense that the bats have been so long differentiated from terrestrial mammals that whatever very slow changes are at work in their organization have had time to modify them considerably, and that these changes, being principally or wholly adaptations to their peculiar way of life, will characterize all or nearly all the order, and so be among those characteristics of the order to which a systematist might attach importance. But I should like to keep a mind open to the possibility that what might be called the primary features of the differentiation of the group, the development of the wings and the habit of preying on insects in flight, might have been developed quite rapidly, if we take an evolutionary scale of time.

Existing differences between species of the same genus must often have taken a million generations in their evolution, so that any great change taking place in, say, 100 000 generations would be from an evolutionary or from a geological standpoint extremely sudden, and I much hesitate to say what could not happen in this time, if the environmental conditions imposed a powerful selection in any one direction.

I do not know what are the morphological relationships of hair, but I suppose it is homologous either with scales, or with some structure of the skin between the scales, either in existing reptiles, or at least in those from which the mammals descended. Supposing such rudiments to have existed in an animal in which it was occasionally of great importance not to lose heat rapidly, I cannot convince myself that it would not have a very good pelt inside a hundred thousand generations, or that during this same time, if activity during chilly times of the day or year continued to be important, it would not have gone a long way in reorganizing its circulatory system, and worked in a number of mechanisms for regulating its temperature. But even if you say that a hundred times longer would be needed for developing the primary distinctions of mammals, the paleontologists would still find that the group arose with great suddenness in the history of the rocks.

I think this must be partly because the evidence is based solely on bones, so that it is after all only a guess if we decide to think that the dinosaurs were cold-blooded, and not protected by something like hair. With this limitation of material one is forced to attach inordinate importance to any osteological feature which is exceptionally constant in a whole range of species. But that constancy, I suspect, is most often due to its being ordinarily so unimportant, or so equally suitable to a great diversity of associated structure, that it has never been materially modified, not to its being at all remarkably difficult to modify. I may be wrong, but I should be inclined to guess that it would take no longer to breed a marsupial without the characteristic inflexion of its lower jaw-bone that it has taken to produce a bulldog.

Now if osteologists are forced to base their principal conclusions chiefly on features of this kind, which happen to have characterized from the first the parents of great radiating groups, they must often be stressing features which have arisen quite rapidly, and in a sense casually, in the sense of being slightly useful to the parent species at a time when its food happened to have some peculiarity, not in the least representative of the types of food prevailing among its descendants. In fact, if a fragment of an animal were discovered in the ancestry of the mammals, which in its major physiological adaptations was really a reptile, I imagine it might be described as unquestionably a mammal from osteological features of exclusively taxonomic importance.

So you see that, from being so far a heretic on the fossil evidence, I am debarred from relying on it in support of what I certainly think may be true, i.e. the rapid origination of the primary distinctions of great classes.

I believe there is a fly whose larvae burrow in human skin, which lays its eggs not on its victims, but along the long legs of a gnat, which it catches for the purpose, with the result that the gnat runs the risk of being swatted, and the larvae, stimulated perhaps by the warmth and moisture of the human victim, rapidly hatch out and burrow into his skin.[31] I suppose this group of instinctive and physiological modifications may have been elaborated in the last half million years. Whatever brought that about should find no great difficulty in a little problem like adapting a small mammal for flight! However, one's judgement is weak about immensities, and rhetoric is no substitute.

Darwin to Fisher: 22 February 1932

I have not yet sucked the whole juice out of your two letters, so I shall keep them by me for another suck. It is good of you to take so much trouble. If what I wrote stirred you up to reconsider these problems, why it has done something, and may rest content for a bit or for ever in its drawer. ...

Darwin to Fisher: 5 March 1932

I see in today's *Nature* a review of Hogben by Haldane.[32] It reminds me that I have not yet read that book. I have rather definitely avoided doing so, because I hear that he attacks me unfairly. I don't want to be tempted into controversy which, you know, I hold generally does more harm than good. But I think I must anyhow read it soon. At the end of the review in *Nature*, Haldane speaks of the 'unfortunate breach between genetic research and eugenic propaganda'. To what does he allude? Pearson? If not him, what? Haldane has, I think, misrepresented my views, and he may have a down on the Dean[33] and me. But I can't see how we are opposed to the conclusions of genetic research. I see that Haldane is publishing a book on The Causes of Evolution which ought to be interesting. He is, I am glad, generally civil to you.

Do *not* answer this unless the spirit moves you. I am an idle man now. But I may bore you with another letter on evolution some day.

Fisher to Darwin: 7 March 1932

I was quite puzzled as to what Haldane could mean, but after the general anathema of his opening I took it to mean, 'all these old boobies have done nothing but confuse the subject, but now that Hogben and myself are interested there will be some progress.'

I am on quite civil terms at present; he is Chairman of a Committee on Human Genetics of the Medical Research Council, of which Hogben and self are other members. I think I can do something there to forward Todd's work, of which I remember writing to you some time ago[34] (blood tests). I have had to slang him (Haldane) to some extent recently in the *Proc. Camb. Phil Soc.* [*CP* 95] where he has written rather foolishly on some points in theoretical statistics, but I do not think he will take offence.

I am heartily glad of his election to the Royal, for he is shoulder above most geneticists in this country; but he is oddly unreliable, chiefly, I think, because he never knows where he is an amateur and where an expert.

As to Hogben's book I think you would find it cleverly derivative, but superficial, especially in its appearance of originality. But I have only glanced at it.

Darwin to Fisher: 29 March 1932

... I have had to, or did refuse two invitations lately which I was sorry for. One was to take the chair when you discuss Family Allowances [*CP* 100], a discourse I should particularly have liked to have heard. For a few days I have been a bit below par, which confirmed the impression that these things are not for me any longer. The moral is not to take up a new subject when about 60 years of age; for there is then not time to do all one would have liked. I only *thought* about eugenics before I was 59. Up to 55 I regarded my life as more or less of a failure, whatever it has been since.

I forgot to say how glad I am that you are on the Committee with Haldane, Hogben, & Co. It will give you some practice in wheedling to get that lot to move in the right direction. I have just finished Hogben's book, without getting much out of it. ...

He follows you about Darwinian blending inheritance, a subject which I discussed in a letter to you about Pangenesis. I was interested in noticing in Chap. II of Galton's *Natural Inheritance* that he himself seems to have *originated* the phrase 'particulate inheritance'. Again in Chap. XII, 3rd para., he writes as follows: 'I need hardly say that the idea, though not the phrase of particulate inheritance, is borrowed from Darwin's provisional theory of Pangenesis ...' Now if the idea underlying particulate inheritance in the mind of the coiner of that phrase was borrowed from a Darwinian theory, it seems hardly historically accurate to use that phrase to imply what is *not* Darwinian. I suggest that segregating and non-segregating inheritance would be the most useful contrast. My father believed the gemmules could be transferred for innumerable generations unaltered, but I gather that he believed that when once actually married to other gemmules in order to form a cell, some blending took place, and at all events their individuality was lost. He used to point to a scratch on the back of his little *white* dog Polly, and point to the *brown* hairs there as the ancestral gemmules being called into action. But no one, as far as I know, before Mendel ever gave the slightest hint that the hereditary elements could unite in marriage and then separate out quite unaffected. That seems to be the distinction of Mendelian from all previous theories.

Hogben certainly quotes me most unfairly. But Huxley mentioned it in his review of the book;[35] I shall take no notice of it; I am fully content to leave it at that; and I hope my friends will do the same. You will have plenty

of chances of saying a word or two about any *theoretical* points where you find you differ from Hogben; and I am convinced that any such quiet hint does more good than all the published controversy *in ephemeral* literature. *All* that is *remembered* is that there was a row of some sort. My father's view was *only* to answer in a book when an answer was worth while. I say this because I own I was much inclined to have a dig at Hogben myself for some weeks after I read what he says of me. And I still should *enjoy* giving him one in the eye!!
[P.S.] Don't answer till and if the spirit moves you.

Fisher to Darwin: 23 April 1932

I see that I have been actually a month in answering your letter, which I am beginning to do this evening. After first reading it I set it aside until I could get hold of a copy of Hogben's book, which I expected to be able to do at once, though in fact, it has only arrived to-day.[36] You must have been tempted to think me intolerably inconsiderate in sending no acknowledgement in the meanwhile, but it always seemed that the acknowledgement would be followed at once by a proper reply, and would have been a mere nuisance. ...

I had adopted the term 'particulate inheritance' partly because I wanted something wider than the ordinary epithet Mendelian, and partly because I knew Galton had introduced it, and had memories of a passage of his, exactly where I cannot now say, in which, in explaining its use, he gave the best early statement that I knew of, of the contrast between these two possible theories. I did not realize that he associated the idea with the theory of pangenesis. I could, as you say, equally have used the term 'segregating', with an added explanation that I should like to include in the meaning the transmission of extra-nuclear elements, such as the plastids in plants, if they showed particulate continuity, whether or not they segregated in fixed ratios like the nuclear elements. I do feel, however, that even if your father had come to know of, and to accept, Mendel's work, and the generality of its application, it would still be proper to point to an important strand in the argument of the *Origin,* a strand, the logical cogency of which has not, I believe, been properly appreciated, as evidence that the blending or fusion theory had greatly influenced the form in which he presented the theory of Natural Selection; and, in particular, had led him to give far more weight, than, as far as one can judge, he would otherwise have done, to the possible effects of non-selective agencies in evolution. ...

Fisher to Darwin: 22 September 1932

... I hear, by the way, that Pearson is retiring, though I have seen nothing officially. I think you rather doubt if I would do any good with that place,[37] if it were offered me, which naturally Pearson is much interested in avoiding. I think I can see possibilities of getting some real work done, but I am not very confident.

Darwin to Fisher: 23 September 1932

... As to the Pearson affair, I have heard nothing. I certainly had no intention of giving you the idea that I thought you would not do good work there. But I did not think you would get the job, and I wanted to discount your disappointment. ... I have always wanted you to get a professorship, though I don't see where. You ought to have got Hogben's job.[38] I *now* wish you had put it regularly, so that some of us could have had our say. I don't remember what I said then. Anyhow, you can go on writing without such a position, and I feel certain you will continue to add to your reputation. No more today.

Darwin to Fisher: 10 October 1932

... I have been writing some notes on my old theme, the similarity of useless characters, which I shall send you some day, so as to have an audience of one. The point that has come home to me with force, and which I had hardly perceived, is that in nature mediocrity in all characters and fitness are closely correlated. ...

Darwin to Fisher: 12 October 1932

Thanks for your address [*CP* 98]. I cannot remember reading it before, though I may have done so—I think the style very good, and, as [T.H.] Huxley used to insist, that does tell even in science. I like it all. I am glad that you speak of my father's 'early thought', possibly in deference to what I have urged. He certainly conceived a particulate form of inheritance, but one that did no more than mitigate blending. Haldane and MacBride—an odd combination—both say that my father thought that variation takes place 'in every direction' (H. p. 139).[39] I wonder if they have any authority for this. I see Haldane (p. 59) agrees that mutation rate varies with external conditions. There was, I believe, that amount of truth in my father's views about the effects of domestication. These are, however, but idle thoughts.

Fisher to Darwin: 14 October 1932

I am glad you liked the lecture. I think the audience enjoyed it, though I do not know if any mathematicians were present to react to what was intended as a stimulus.

Thanks for rousing me about 'in every direction'; it is just the kind of statement I might make myself, though I do not suppose your father ever used the phrase except to say that he did not assume this. But, what does it mean, and (that answered) is it a plausible guess?

One thing it might mean is that an engineer having a full knowledge of the working of the organism and of the process by which it grows, might suggest some physically possible modification, such as that a mouse should have spiral whiskers. Should we say (a) that we should permit this suggestion only provided that he has assured himself that the modification he has in mind could be brought about solely by a redesigning of the collection of genes, or, imposing a more severe restriction, (b) that it must be brought about by a physically possible substitution of a single gene, or (c) that the transformation of the old gene **A** into the required new gene **A**′ must itself be a physically possible process? On the third restriction it might I think be argued that, since all physically possible processes must have a finite probability of occurrence, there is a non-zero mutation rate in all possible directions. Some changes satisfying (b) could I suppose be brought about by a succession of changes satisfying (c), but if some could not, it would be reasonable to say that these are directions in which variation does not take place. Can your father's view be fitted somewhere into this framework?

A priori, I can see no escape from the view that mutation rates must to some extent be affected by environment, since I suppose all organic activities are. Nevertheless, I do not believe that your father would ever have ascribed the great variability of domesticated races to the effect of their environment on their mutation rates, had he not thought that variations were continually dissipated by blending. His deduction was, I think, the right one from the wrong premise, though wrong in itself.

Darwin to Fisher: 15 October 1932

Thanks for yours; but don't answer this. To make *my* meaning more clear—though that is of little consequence—you *have* convinced me that my father was influenced by the idea of blending. Where I am inclined to think you wrong is in not, as far as I see, admitting the *amount* of mutation caused by domestication. ... Then I think you believe that my father had a clearer idea of a mutation than he really had. I see no signs of his believing that his gemmules ever changed. His mind was often expressed by the words of his quoted by Haldane—'what the devil am I to think'—though not quite in this connection.

Darwin to Fisher: 24 October 1932

I am writing this for my own amusement, so take no more notice of it than you feel disposed. ... My father's theory of heredity was definitely particulate. I should like to ascertain if Johannsen ... when he invented the name 'gene', had pangenesis in his mind at all[40]. ...

Darwin to Fisher: 28 October 1932

This letter will make you swear all Sunday. So much the better, for then you will be in the mood to write 'bosh', 'silly', and other suitable comments in the margin of the enclosed draft of a letter to *Nature.* Seriously I should like your views as to whether it is wise or foolish to send it. I care but little what happens, for I have had the amusement of writing it. I suppose I ought to get it typed if it goes.

I have looked at Hogben[41] on Haldane again and am still puzzled. But I must confess that it gives me the uncomfortable feeling that I do not understand it well myself—I mean the action of natural selection. I shall have to reconsider my views on the uniformity of useless structures, so you are saved from that infliction for the present.

[P.S.] It is rather a shame to make you my confessor on all these matters.

Fisher to Darwin: 29 October 1932

I am sorry you have bothered to read again that long screed of Hogben's as in my opinion it wanders constantly from the point nor is it in any sense a good criticism of Haldane's book, even when it happens to be talking about it. The lectures which Haldane gave to the Welsh agricultural students must have been good and stimulating lectures, though, even in lectures, fewer personal opinions or more reasons for them might have been worth while. But the book they make is structureless and loosely written so that almost every statement made in one place may be found contradicted in another, or is so ill defined that one scarcely knows what there is to contradict.[42] Altogether it was an utter disappointment to me and I understand also to a number of geneticists both in this country and America.

I didn't know Hogben had yet written a book on Natural Selection, but I suppose he inevitably will, and then Haldane, if the spirit of gratitude is in him, had better do his best to puff it.

As regard the word 'particulate', I took Galton's term, in the sense in which he used it, to contrast hereditary carriers which maintain their identity, whatever company they keep, with the other sort of hypothetical carrier. I had noticed the term 'unequal blending' and suppose it to mean that a greater mass of Type A blends with a lesser mass of Type B, but I never could see that there was a clear conception behind it, else, if there were such an idea capable of resolving the contradictions to which the blending theory seems to lead, it ought to have been developed very fully and explicitly. ...

For my part I should not have chosen to use the term, which I wanted solely for the purpose of developing the argument on mutation rates, if I had thought that in Galton's mind it connoted something like pangenesis, in which, if I understand it rightly, the gemmules have no continued identity beyond a single generation.

So you see I see very little point in your sending your letter to *Nature*, but this may be partly because I am writing after a bad night, with a heavy cold in my head, and should not be very easily pleased with anything.

Darwin to Fisher: 1 November 1932

Thanks for taking the trouble of reading my draft letter and writing about it. I daresay you are quite right in all you say. There was one sentence I boggled at, however, You say that you understand in pangenesis that the 'gemmules have no continued identity beyond a single generation'. I believe that he[43] held that they might be 'dormant' for a great many generations. So either I or you have misunderstood the theory. If I have, it is of no consequence whatever. ...

Fisher to Darwin: 2 November 1932

I surrender unconditionally about dormant gemmules, and they are essential to the theory. In view of the considerable supply of fresh gemmules brought in from every organ in each generation, I suppose you would take it that the elimination of functionless gemmules would be rather rapid, I mean a goodly percentage, 5 or 10 per cent at least in each generation. Or is this not intended?

Darwin to Fisher: 3 November 1932

Thanks for yours. It would be mere guess-work on my part to say how rapidly he—my father—thought the dormant gemmules disappeared. In *A* and *P* [*The variation in animals and plants under domestication*] II, 2nd Edition p. 369, he speaks of a 'host of long lost characters lie ready to be evolved under proper conditions'. I think he would have said he was merely groping his way towards the light in his *provisional* hypothesis; and I think he was groping in some respects in the right direction to get out of the difficulties which you correctly show that he had felt. But he could not escape as long as he had to account for his beliefs in regard to use and disuse; and it is segregation which has done most to clear the situation.

Fisher to Darwin: 4 November 1932

Thanks for your letter. With regard to the arguments in your father's mind prior to the *Origin*, I found rather an amusing thing recently, namely [T.H.] Huxley putting forward as one of his main criticisms, on first reading the *Origin,* a problem which your father must continually have considered and resolved in his own mind during the previous fifteen years. You will remember that I am inclined to reverse the common conception of your father's attitude towards use and disuse, and other supposed environmentally induced modifications. It is, I think, usually supposed that he accepted these either as probable *per se*, or on the strength of such evidence as the relative weights of the wings and legs of wild and domesticated ducks, as he subsequently adduced as possible examples of such effects. On the contrary, I believe he felt forced to admit that *theoretically* the environment must be capable of producing evolutionary modifications *because* it must be immediately responsible for the large amount of variation which can be readily observed, while, practically, he was continually impressed with the conclusion that such direct effects have in fact only been of slight or occasional importance; and, therefore, that the great mass of mutation produced by environmental causes must be unbiased in direction, *'mere variability'* as he sometimes says, such as might well arise from the irregularity of disturbance of the working of the reproductive system. Huxley is therefore only raising a very familiar point, reflecting, one might say, fragments gleaned from Darwin's own argument, when he writes, 'And second, it is not clear to me why, if continual physical conditions are of so little moment as you suppose, variation should occur at all.' This is in Huxley's *Life and Letters,*[44] vol. 1, p. 254, but it is almost the only point of scientific interest that I have found in the whole volume. I suppose his son[45] thought the public would not be interested in scientific ideas. ...

Darwin to Fisher: 6 November [*1932*]

... I should like to see a question set at a Cambridge Science tripos asking what [T.H.] Huxley had done for science. I wonder what the answers would be like. He threw stones at religion and talked philosophy, the latter being in my humble opinion not at all sound. On the other hand we found him very delightful company and most amusing. My father must have read his grandfather's views on Lamarckism but they seem to have left no impression on his mind. Does not this fact fit in to some extent with your views as to the development of my father's mind? ...

Fisher to Darwin: 9 November 1932

Thanks for your note on Huxley. I had not before understood what you thought of him. So the son may not be to blame. Thanks, too, for the point about Lamarckism or rather Erasmism, as I suppose your great grandfather antedated Lamarck. It would seem inexplicable if your father had attached the importance to use and disuse (though never to 'slow willing') which he is sometimes represented as having done, that he should not have been impressed by Erasmus. I suppose he (Erasmus) developed the argument from structural affinity quite largely, and perhaps touched on rudimentary organs; and that kind of argument unless associated with something (though perhaps only a too speculative attitude) which your father strongly disagreed with, must have made some appeal. Yet had he felt any strength in use and disuse, as a general principle of modification, it is not easy to see why he should have been put off. But I am only repeating your point; a bad habit, only better than repeating one's own. ...

Darwin to Fisher: 13 November 1932

The next time you happen to write, but not before, [say] if *The Scientific Basis of Evolution*—[T. H.] Morgan (Faber) is a good book and one I ought to read.

Fisher to Darwin: 15 November 1932

I should only read Morgan's new book if you are tempted by curiosity. It seems to me a most interesting example of the way in which a man directly responsible for real scientific advances should retain old concepts and arguments which these advances have really made obsolete. This shows up in the way he speaks of the 'Mutation Theory' of de Vries, as though it were a theory of evolution to be considered as an alternative to Natural Selection. de Vries speculated upon the origin *per saltum* of specific forms, and the Drosophilists have shown that a single species shows many hundreds of mutational variants. But Morgan seems to argue that the occurrence of mutations supports de Vries' theory, as though all evolutionists from Lamarck and Erasmus had not postulated mutations, i.e. heritable changes, to have taken place. In fact, much of Morgan's book, though avowedly based on the Drosophila work, might have been written (and, in effect probably was) in 1905.[46]

Fisher to Darwin: 3 January 1933

I am enclosing a screed which I was induced to write for a composite book having, I fear, some such dreadful title as *Mind Behind It All,* though the Editress has not confessed it to me as yet. Quite possibly she will find it so much against the grain of her other contributions that she will turn it down, or, what will come to the same thing, propose a few tactful modifications. As a title, I think 'A Modern View of Darwinism' might do, as leading no one to suppose that it is genuine Darwinism, as I feel rather guilty anyhow of taking liberties with what your father thought or said. On this point, as you know, I should be guided by your comments.

There does not seem to be much metaphysics in it after all, at least not what a metaphysician would call metaphysics, and I hope it does not open the door to the flood of wishful sloppiness which seems to be called philosophy. However, you will judge best if I am showing signs of drivelling.

Darwin to Fisher: 8 January 1933

... As to our old friend, free will, we have never seen eye to eye, and if I say anything, I shall expect it to be ignored. Modern research appears to me only to show that we have not yet dug down to the foundations and not therefore found where determinism seems to come in.

If men had perfect reasoning powers and knew what they wanted, they would always do the same thing in the same circumstances. If *choice* means the possibility of doing two things at any one moment, then there would be no choice, or free will in that sense, in these circumstances. On such a supposition, you have pushed out determinism from the front door, and find it entering at the back. If choice comes in only because of imperfection of reasoning powers, an element of pure uncertainty in the nexus between environment and action is introduced. This leaves determinism in its original commanding position, and only introduces a variation about the mean in the results. If choice is to be creative, it must not be fortuitous; but the less fortuitously it acts, the less choice there can be. If there is free will in marriage, for example, and if choice is not tied to circumstances, the statistics of marriage would not necessarily be uniform. If choice is tied to circumstances, it is not free. The only way in which indeterminism can come in would be by human beings having a limited power of altering what we call previous events, as we now see we can alter subsequent events. Rather a bold supposition! But still I can [not?] help believing in free will. What you say is interesting and not too long. And I liked it all.

Fisher to Darwin: 16 January 1933

... I am much more likely to combat than to ignore what you say about free will, because I find it interesting and relevant, but, where conclusive, capable of a fundamentally different re-statement. Of course, if determinism were axiomatic we must take the view that scientific research has not *yet* discovered the formulae for exact prediction. But this view, though at present possible, does certainly beg the question.

Next you say, 'If men had perfect reasoning powers and knew what they wanted, they would always do the same thing in the same circumstances'. Equally, if all marksmen aimed at exactly the same point, and shot perfectly, all the shots would pass through the same hole. The variation in behaviour can be regarded as compounded of two distinguishable sets of causes, (i) variation in what is aimed at, and (ii) variations due to imperfect knowledge of, or imperfect control over, the environment. On the moral plane you may say that in given circumstances there is usually one course of action which is better than any other, and that any perfectly wise and perfectly good man *must* choose this course. But this is not the same as saying that he is constrained to do so, otherwise the stipulation of perfect goodness could be eliminated. He can say 'I feel I have no choice', but in saying this the 'I' in his sentence is identified with only part of his personality. It does not include his conscience, which he is speaking of metaphorically as constraining it (the 'I'). Equally, a man can say 'I have a good mind to—' when everybody knows that he won't, meaning assuredly that, apart from his own consideration, loyalty, good-nature, or what not, he feels perfectly free to take and justified in taking such a course. Intricate as such phrases are, I suggest that they emphasize the sense of personal choice rather than tend to eliminate it.

Perhaps you may say that, whatever he feels like inside, the choice of a good man is in fact determined by outside circumstances, and predictable by an outside observer from the stipulation that he must act for the best. So that the outside observer is justified in regarding him as an automaton. There are within this view at least three possibilities all perfectly consistent with human free will. (i) The saints and angels may be automata, without men being so equally. (ii) The saints and angels may each have something of their own to contribute, as to what is good; that is, they may invent new sorts of goodness, like musicians composing different melodies. (iii) Even if goodness can be defined objectively, and equally for all, they may yet be perfectly good only because they choose or have chosen to be so, the phrase to 'choose to be good' merely comprehending in a single clause innumerable particular good choices.

On the intellectual side, you say, 'If choice comes in only because of the imperfection of reasoning powers, an element of pure uncertainty in the nexus between environment and action is introduced. This leaves determinism in its original commanding position, and only introduces a variation about the mean in the results.' What I understand by determinism does not allow a variation about the mean, and if the original commanding position of determinism implies merely that the mean can be calculated *ab exteriori*, then I think determinism is left in this position, on the analogy of marriage-rates, and prediction in mechanics. A good deal seems to turn on your phrase 'pure uncertainty' and on the word 'fortuitous' in your sentence, 'If choice is to be creative it must not be fortuitous.' If, in a long calculation, I introduce mistakes, I do not, of course, choose to do the calculation wrong, but I did at some stage choose to put down a 5 where I ought to have put down a 3, not realizing that it was wrong. In this sense the calculation is wrong because there was something wrong about me; and there is in this case little chance of the accident being a happy one. The neuron system which blundered has probably not such a good idea of mathematics as some other neuron system, which is in charge of and designs the whole operation. But in designing an experiment it might be otherwise. A modification which, at one stage, looked like a mistake, might at another stage look a stroke of genius. The joint process of making the modification and recognizing its merits would be creative, in very much the same way as the joint process of mutation and selection has been in biology. Choice to the mind that chooses, is, of course, never fortuitous, though what presents itself for choice may be. But to an exterior mind an aggregate of choices is a typically fortuitous system. If the probabilities of different kinds of choice were not determined by exterior circumstances I suppose the statistics of marriage would not be in the least predictable, but if circumstances only determine these probabilities there is room for individual choice. And if they determine these probabilities only through the constitution of the human mind, or, strictly, if the only non-empirical method of calculation consisted in the enumeration of the different kinds of mind present, and the probabilities in different circumstances with which they would marry, then there is no reason to speak of the choice as other than absolutely free.

I am afraid my paper was a nasty shock to the good lady, and I don't suppose it will suit her book at all. ...

Fisher to Darwin: 20 February 1933

... A new American or International Journal of Philosophy, Mathematics, and Science has asked me for a contribution to an early number, and I shall offer them something of the kind, though not quite as written.[47]

I do not think really that you *need* disagree with me. Indeterminism is a wider hypothesis than Determinism, and should have precedence, until facts can be found which exclude it. If it did contradict any intuition, which I am not convinced about, that would only make things fair, for Determinism certainly does.

I happened to be at the Linnean at a meeting last year to hear a paper about some plants on African mountains; the main paper given, however, was by Hinton on rodent control, and as he very contemptuously dismissed the plan of killing the feamles, and releasing the bucks, without apparently being aware of their infanticidal instinct, I was led to put on record a few facts, which interested me very greatly when I observed them, and which I think you may find interesting.[48]

Darwin to Fisher: 22 February 1933

... As to free will, my difficulty is to reconcile it with the uniformity of vital statistics. I am trying to put it on paper, but find myself very muddle-headed. I do believe in free will, whatever my reason may say!

I like enclosed. You must some day put *all* such thoughts in a *book*. It seems to me that a male will gain racially by killing the offspring he finds for two reasons. (1) It will shorten lactation; and therefore make the female sooner ready to breed *with him*. (2) Granted that the number best looked after by the parents is limited, *his* surviving offspring will thus be increased, in certain circumstances. I guess this is your idea—unless again I am muddle-headed.

Will not a man in like manner gain racially by killing his father, if he, the son, lives at home? Can we thus account for the Oedipus complex?

I see no reason why a mother should ever gain by killing her *own* children. ...

Fisher to Darwin: 23 February 1933

I think the main factor in infanticide in rodents is that the expectation of life is short, perhaps only about a fortnight for a male. Consequently, the prospect of the doe being ready in 2 days instead of 12 is very important. Against this great gain is the danger, confined to older mice, of slaughtering his own litter; so I suppose the instinct is inhibited by the feeling, experienced only by fully mature mice, of being at home in his own territory. I fancy the means of dispersal are so great that the surrounding population with which there is effective competition is large, some thousand perhaps, so that it is competition for the use of a particular doe rather than for the general means of subsistence which is effective.

I do not think I believe in the Oedipus complex, never having felt any inclination to patricide, or even its possibility as a 'Bad dream'. I doubt, too, if in Sophocles, the tragedy is other than an incredibly awful possibility which might be sprung on a mortal by malignant fate.

Returning to mice, a mother might with advantage kill her own young if it was certain that they would later be killed; she would then save herself some time and expense. Whether the mothers do join in the killing I have never been able to make out.

Darwin to Fisher: 16 March 1933

... I have written something on free will and on the uniformity of useless characters. I want them to be read by at least two persons! And I shall I expect sacrifice you on the altar as one of them! ...

Darwin to Fisher: 23 March 1933

Here is Free Will, to be returned at your leisure—you have brought it on yourself! I never found anything harder to write, and I do not like it now it is written. ...

Fisher to Darwin: 31 March 1933

Wilful modification of the past is a magnificent notion, but in the name of Occam is it necessary? From several passages I believe you are putting on 'the regularity of vital statistics' a burden which it will not bear. There are irregularities, small perhaps in the mass, unimportant to the official, if there is one, who decides how many beds shall be set apart for maternity cases, but quite big enough to the individual to accommodate his freedom of choice. Your argument, as far as I have grasped it, would have weight if the regularity were so austere that one could say 'The number of suicides this year in London *cannot possibly* exceed 150.' For, if that could be said, and the quotum was filled by the end of November, we should really none of us be able to commit suicide before January 1st, which would not be freedom. But in reality the regularities that can be observed do not imply any such individual restraint at all. What is sometimes forgotten about statistics is that, from a vast number of independent facts, after some restatement, we select one or two as relevant to our purpose and reject all the rest as irrelevant. The ones which we choose as relevant are those which depend on general causes, or, in other words, the ones which are useful for predicting future experience. What we reject (if the statistical processes are successful) are the facts which arise from particular causes, and which are useless for the prediction of future events.

You feel that the individual is constrained by the total to which he belongs and so he would be if the total were rigidly fixed. But to give the total a little latitude is to give him a lot; and to give the total what we do give our totals is to give him full liberty.

Even if you admit this, I believe you will still feel that the individual must be constrained in order that the aggregate he belongs to may conform satisfactorily to other aggregates. Suppose we offer 10 000 schoolgirls a choice between pink and yellow sweets and about 7 000 choose pink sweets. In doing this we have our eye on another 10 000 schoolgirls not yet tested. You say, 'they cannot really be free to choose, because you know as well as I that the number choosing pink will be within 100 of what it was last time.' As a libertarian I can be more sceptical, but I admit freely that if there *is* more than 100 difference there must be some cause for it, meaning by that, that with sufficient patience and observation of relevant details some genetic or environmental difference between the two groups could really be found that could account for their difference in behaviour. But I admit that for this back-handed reason, which shows how very far I am from admitting any lack of free choice. The argument goes like this. In the total 20 000 there must be some number who will choose pink, say 14 022 to be exact. It is possible to divide the 20 000 into two lots of 10 000 each in a very large number of ways, which can be enumerated. And each way of dividing the total will correspond to a particular discrepancy between the numbers choosing pink in the two lots. In 99 ways out of 100, or some such calculable fraction, this discrepancy will not exceed 100. If it were to exceed 100, therefore, we must choose between two conclusions. Either something has occurred by chance which we know would only happen once in 100 trials, or the children have been divided into lots by some process which is not quite independent of choosing pink or yellow. To trace the nature of this dependence, if it exists, is what we call finding the reason why one lot behaved differently from the other; and it is clear, whatever view you hold about free will, that to search for such a case would be a hopeless undertaking only in the one case in 100 in which the disparity has occurred by chance.

Consequently if we have reason to know that the second lot of girls is homogeneous with the first, we can predict fairly nearly what their aggregate choice will be simply from experience with the first lot; for by homogeneous we mean in practice either that they have been chosen at random out of the same total, or that they are as much alike as if they had been. In these circumstances our prediction is an example of purely inductive reasoning and is independent of all theories of the causes behind our observations.

I feel I am labouring the point, but it usually happens that one labours the wrong point.

Darwin to Fisher: 3 April 1933

It is very good of you to trouble yourself so much about my free will. I fear we must conclude that we cannot cross over our thoughts, one to the other, and this makes me suspect I must have a blind spot in my mental eye. But it does not much matter, as I have no thought of publishing. I came across this sentence in Bohr's writing in *Nature* yesterday.[49] 'I think we all agree with Newton that the real basis of science is the conviction that nature under the same conditions will always exhibit the same regularities': the reason why, *I* think, that present events are rigidly connected with past events. Some great swells think that nature is indeterminate, but there I cannot agree, and am glad to find some on my side; ...

I guess I shall send you what I have written about the uniformity of useless characters before long. After that I hope I shall not trouble you much more!

Fisher to Darwin: 5 April 1933

I hope you will send me your paper on the uniformity of useless characters when that is ready, and not altogether despair of me as a rational mortal even in the matter of determinism. I know that if I start talking about creative causation I shall shock many of my friends much more than if my wife divorced me; but, like Omar, and I think here you may agree with me, if I thought the whole show had been pre-arranged unalterably I should not be so silly as to bother myself about exactly how it worked, but should rather consider the drama aesthetically as a well- or badly-constructed performance.

On the first point, I have recently been reading a chapter by Ford written for a forthcoming book by Hale Carpenter on mimicry.[50] He gives several examples of non-mimetic forms being distinctly less uniform than mimetic forms of the same species. In these cases, at least, variability seems to go with less intense adaptation, more so, I think, than I should have guessed.

Darwin to Fisher: 18 May 1933

... Thanks for your notes on my production. I wrote it for my own interest, not intending to publish. So many old men write when they had better not, that I feel alarmed, and I have lost confidence in myself. Moreover, I do not know who would consider such a publication. But as you pat it on the back, I will reconsider the matter some day.

Another problem I am turning over in my mind in the same way is death as the result of natural selection. Immortality would put an end to selection, and death is thus favoured. But experience in animals and depth of roots in plants makes the aged, as long as fertile, of increased biological value. Hence the higher animals and trees ought to have the longest lives—as they have. But why are fish such long livers—if it be true?

I wish we could have a talk some day on these things. I am really away from home for a few days at the sea, my first absence for ? 18 months.

Fisher to Darwin: 20 May 1933

I, too, have a good many things that I should like to talk over with you, though some of them are not worth bothering you with. But for the prospect of giving more trouble than it was worth, I could run down to Bognor for a night, so give me a word if you think it a good idea, treating my suggestion as you would have one of your own treated by an old friend.

One thing you will be glad to hear. I had a letter the other day from the Provost of University College [London], telling me that at the suggestion of the College, the official committee unanimously invited me to stand for the Galton Professorship. I hope to discuss the situation with him quite soon. I am not yet quite clear what opportunities the post will provide, as they have first, rather comically, divided off the department of Statistics, in order, I presume, to give Egon Pearson a readership. I think I could work tolerably amicably alongside of Egon, but can foresee the embarrassment that many voluntary workers now come to me, and would come as advanced students to University College if I were there, just because they regard my statistical methods as having superseded Pearson's.

The chair includes a curatorship of a museum of Galtoniana which will interest me (though I am a bad curator of my own possessions). It must have one or two assistants, though I imagine at present no provision for biometrical work on living material, and I do not believe that students could fit themselves for research on man without quite extensive training on biometric-genetic lines on some more manageable animal or plant. I do not know that you will agree with me at once about this; but what other hope is there, to take the best case, for an able graduate in mathematics who has but two years to spend at the place? His mathematical training will, from what I know of mathematical departments, have kept him abominably isolated, not only from biological facts, but from the whole mode of thought of an experimental science. He may be eager and clever as can be at acquiring the algebraic development of the probability integral of my z distribution and never have a notion of what facts in experimental procedure to make sure of before it is worth applying a test of significance at all. Besides, I want to attract another class of advanced students that I have seen something of, i.e. people who are already biologists, geneticists, and the like, but sufficiently mathematical to want to use the best available statistical methods and biometrical ideas in their own work, and I shall never get the best of these without facilities for handling living material.

And then I won't give up my own chickens, and snails, and mice without a struggle; even if they aren't Eugenics they should do something to get sound Genetics into the heads of students who will certainly need them, and perhaps make a few sound biologists feel that a Eugenics Laboratory is not such a nest of cranks as they had been led to fear. ...

Darwin to Fisher: 22 May [1933]

I am really delighted at your news, which you know is not what I expected. ...

As to coming to see me, I should really enjoy a talk very greatly, and my only doubt is whether it will be worth while for you thus to spend your time. ...

I think I agree with you about animals, etc. I am sure that you are wise to begin at once to make plans in outline but I should strongly advise waiting till a little after you are in the saddle before making definite moves. I hope you will be able to let Egon Pearson know of your friendly sentiments if you can. It might mollify his papa. I write this all in haste to say how grand I feel it will be if you get the job and how warm will be my congratulations.

Darwin to Fisher: 26 May 1933

It will be nice to see you for as long as you can stay. Sat. June 3 suits us perfectly; but do you remember it is Whitsuntide? ...

You will have some hard nuts to crack. As far as I know, no professors as such have personal assistants, which, it has always struck me, must lead to a great loss of valuable time. When will the news be confirmed and *public*? Let me know next time if and when I may say that you have got the job.

Though there are difficulties, I am really delighted—for I suppose, from what you say, it is a certainty. ...

Darwin to Fisher: 31 May 1933

Thanks for yours in which you say you will come on June 17, ... to Forest Row, when we shall be very glad to see you. ... As to what you say about refusing to bind yourself in certain respects, I do not yet understand whether you have definitely got the job. If not, is it not of immense import-

ance to your children that you should get it? Suppose you missed it by making certain stipulations, might not you repent it bitterly? There may be something very foolish in what they ask, but it is not morally wrong, and it cannot be morally wrong for you to agree. You might always hope to reverse any decisions. My point [is] that it is of great importance to your family, to you, and, I think, to Eugenics that you should be selected, and that you will do *wrong* to throw any difficulties in the way. It will be over-conscientiousness on your part, which is an error I can conceive your making. Please forgive me for speaking frankly.
[P.S.] To save time when we meet, I want to put one *un*important matter in writing. You seemed to think that I should differ from you in regard to your programme of work for the professorship. Possibly you were thinking of my views with regard to the functions of the Eugenics Society. I hold that it should confine itself to propaganda for the following reasons. (1) It was originally the Eugenics *Education* Society, which indicates the basis on which members were first asked to join. (2) Twitchin, who helped us so much, wanted his money to go in widespread propaganda, believing that we know quite enough to justify practical action. And (3) research is so much more interesting and advantageous to the individual that it would drive out all propaganda, because of its cost. On the other hand, though I have not Galton's will before me as I write, I am certain that his aim was research together with *advanced* instruction. Hence I think these are the lines on which his money should be spent. How these ends can best be obtained, it is for the Galton Professor to decide, and I see no reason whatever to think that you will come to unsound conclusions.

Darwin to Fisher: 14 June 1933

... Congrats. from an old pessimist like me might bring bad luck, so I shall not send them till you are bang certain. Then they will come quite hot.

Darwin to Fisher: 22 June 1933

Three cheers for the good news. Now I feel that I must celebrate the event, and I am writing to beg you to allow me to do so in the following way.

Only one of my nine brothers and sisters has lived for longer than I now have, and that only for a few months. Hence I had every right to believe that I should have gone away before this. With such thoughts in my mind, I left such instructions as would have had the effect of a codicil to my will passing on at my death a small sum of money to you for the benefit of my godson.[51] I begin to feel, however, that it is rash to count on the money being available when most likely to be useful, and moreover, if I survive for three years, I shall defraud the government of an appreciable amount of death duties if I now pass on the money. Does not that appeal to you? Seriously, will you give me the great satisfaction of helping Harry by now accepting the enclosed cheque to aid in his education? I am sure that you will. You must use it as you think best, and I will only make some tentative remarks. ...

I have only accounted thus for part of the full sum. Now I should much like, if you will permit it, to celebrate your becoming the Galton professor by helping you to join the Linnean Society, which I presume can be done for some £20. No one will ever know that I have had a finger in the pie, but it would not only be a great satisfaction to me to feel that I have been permanently helpful to you, but also, I believe, of some use to science in this way.

Now if you will agree to all this I shall again throw up my hat with joy.

Darwin to Fisher: 27 June 1933

I was very glad indeed to get your letter. It pleased me very much. ...

Fisher to Darwin: 27 June 1933

I am just writing a note on a small technical point, connected with graded or flat-rate family allowances, because I fancied ... you were taking for granted that the only difference between such schemes lay in how much the wealthier members subscribed towards the support of the poorer. I want to make it clear that this is not so ... Now the economic purpose of family allowances, as I understand it, is to equalize the standard of living between parents and non-parents doing equivalent work. That is to say, that provided the services they actually perform are equivalent, to make sure that parents and non-parents shall, on the average, equally be able to afford the material advantages which constitute the reward society has to offer for these services. It is not essential, at the moment, to my argument that this object is worth pursuing, the only point needed being that it is attainable by a system of graded allowances, but quite unattainable by any flat-rate system within the profession, with or without the addition of a tax on the wealthier for the benefit of the poorer members. ...

Fisher to Darwin: 23 October 1933

You played a nice surprise on me today. I had hurried into my room, after running myself rather late going over some of my snails, and saw with falling heart that there was some more correspondence not yet dealt with. Still, it was only a book parcel; so I put it in my bag to look at in the train, where I found as you will guess that it was Mrs. Barlow's edition of the *Diary*,[52] which has such a big review in this week's *Literary Supplement.*

We had read the review eagerly at home and thought it very good, so your present, which is a very charming one, comes just in answer to our curiosity. I have scarcely looked at it yet, just enough to make me wonder if your caution about reading too definite a meaning into phrases meant to contain some suspense of judgement ought not to be applied to your father's use of the word creation and 'centres of creation' during the 'Beagle' period. The notion that the origination of new species, even though not by generative descent from pre-existing ones, might none the less take place in accordance with natural laws, not yet discovered, must have been familiar to your father from the second volume of Lyell's *Principles*, and I should guess it must have been in this sense that he used the phrases. That is a little less dogmatically, perhaps, than Mrs. Barlow takes them to be. But I must now start my treasure hunting in earnest.

Fisher to Darwin: 10 November 1933

Many thanks for your letter. ... I am exceedingly sorry to hear that the two departments are to be separated,[53] as I believe this will be very injurious to the Scientific reputation of Eugenics in the States, which is already by no means all that could be wished. ... I am more than ever convinced that Eugenics will make no progress either in Academic circles, or [with] Public Officials, or with the Public at large, unless it has widespread sympathy and some active support from Professional men of Science.

Since you resigned the Presidency, in fact, I have been increasingly conscious of the same danger on this side.

Darwin to Fisher: 12 November 1933

... the part played by biologists in the field of Eugenics has been most disappointing. Few have given the movement a real shove forward, and I fear that jealousy has been one cause of their standing aloof. I do not believe in psycho-analysis, but I do think that people are very often influenced by low motives without being aware of the fact. ...

Not many can seek to promote truth without some thoughts of self affecting them. ...

Fisher to Darwin: 13 November 1933

I think I agree with every word of your letter, except your inference in respect of practical policy. The attitude of Biologists to Eugenics has been disappointing, and will continue to be so, I am afraid, so long as they are treated in such a way as to arouse the subconscious motives which you suspect.

Some, of course, are incapable of disinterested action anyhow, and they are no loss to the movement, but there are a great many who could be disinterestedly keen had they not felt on some occasion or other, that they were being lectured on a Biological subject by persons very little qualified to speak upon it.

It is meaner, easier, and generally more consonant with human nature to react as an adverse critic, than to offer hard-won technical knowledge in the service of some ass, who will not appreciate its merits.

Darwin to Fisher: 15 November 1933

I am glad you have taken my letter in the way I intended it. It matters little if I am wrong in my practical policy, as I shall make no move. Something I heard *after* I had written my last letter to you made me fear that you would think I was hinting at things which were not and could not have been in my mind. I shall never *hint* to you, but speak out. The action of some of the biologists has always been a puzzle to me. ... I wish we could pull together better. Of course eugenists make mistakes—I know I do.

Fisher to Darwin: 16 November 1933

I realized that it was just a coincidence that yours about the American Society came just as I was rather bothered about the analogous situation in the English Society, but as it happened my views on the first question are largely influenced by what I heard during my two recent visits to the States. The proposal to abolish Honorary Secretaries, apart from other questions, puts the [English] Society for the first time, I think for at least twenty years, in the position of having no active officer who is a professional Biologist. ... I proposed at the last Council, speaking of what I had seen in America, that the Society had everything to gain by putting a number of Biologists on its General Purposes Committee, which in fact handles all detail matters of policy for the Council. To my surprise and regret, great reluctance was shown from the chair (Bramwell), an attitude which I fear impressed all the Biologists present, which included Poulton, very unfavourably. ... I feel that the attitude of the small group of non-Scientific's which control the Society much more than undid the good feeling I was aiming at. ...

I do hope you will not bother yourself at all about this. If the Society goes to pieces or reduces itself to the status of the American Association, it will not be the end of Eugenics. ...

Darwin to Fisher: 9 March [*1934*]

Many thanks for looking over the extract from my article on The Brock Report, [54] and for your suggestions, all of which I have incorporated.

Fisher to Darwin: 12 March 1934

It was good to get your letter. ...

Did you notice that we carried out a suggestion which I remember your making years ago by ascertaining the mental condition of a large group of children of mental defectives. I put in some work on the results [*CP* 120], though they came to me very late in our deliberations, and they struck me as really remarkable. I was especially struck by the proportion of children from defective fathers and normal mothers being the same as that from defective mothers and normal fathers, since the environmental conditions in the home, especially for infants and young children, must be materially different in these two groups. But perhaps the most remarkable result of all was the actual incidence of defect in these families, which is more, I think, than could be anticipated on any theory of inheritance without strongly assortative mating. I should judge, in fact, that though carriers may well be more numerous than defectives, they must bear to them a much lower ratio than we have all been inclined to suppose. ...

Fisher to Darwin: [*July 1934*]

At the meeting of the Genetical Society recently at Down House, I was delighted, as indeed we all were, to hear your letter read by the President [J.B.S. Haldane]. You will be interested, I think, by Haldane's remarks at the end of the meeting, to the effect that your father knew so many more facts relevant to evolutionary theory than any of us did, that we should hesitate to think that anything we knew disposed of his views.

The day was very hot, and fine, and the meeting well attended. I think we all enjoyed the opportunity of visiting the historic spot.

Darwin to Fisher: 14 July 1934

Thank you for your letter. I was glad to notice what a glorious day you had for your Down expedition, and I wish much that I had been there to wander round some of the old familiar places with you. ...

Darwin to Fisher: 10 October 1934

An uncle of mine, who belonged to a large sibship, wrote the following lines, when young, at some period of family commotion:—

> Write, write, write a letter,
> Good advice will make us better,
> Father, mother, sister, brother,
> Let us all advise each other.

He was evidently thinking that too much advice was flying about; and that may well be the case if I give my views about your public lectures. Advice should be readily asked and readily neglected.

I have never, I think, heard you give a regular lecture; but as you can write well, you ought with forethought be able to lecture well. I always wrote out my lectures and had the text before me; but I did not try necessarily to follow what I had written word for word. This is not a good plan, I expect, for most *ready* speakers; though I believe nearly all gain by *writing* it out in advance. ... The spoken word should be decidedly more diffuse and easier to understand than the written.

I decidedly like the idea of your public lectures. You may have to face disappointment in the size of your audiences. ...

Darwin to Fisher: 17 January 1935

I think it is no use searching for the Wedderburn letter.[55] My father used to put a letter, after being noted and read, on a hooked spike. The note was put in some labelled shelf. The spit when full was put in a cupboard under the stairs, and when that got too full, the letters were burnt to make room for more! We protested, but my father could not conceive that his correspondence would be of value! This anyhow is my memory. I return the notes[56] in case of their being of any use to you. And I shall remember the name of Wedderburn in case of a miracle occurring.

Congratulations on the *Annals of Eugenics.* You are right to keep it up to a high standard, though in truth it is so high as to be clear over the top of my head! ...

Darwin to Fisher: 4 May 1935

I have not troubled you with a letter for a long time, though I feel there is a subject on which I should have expressed my feelings long ago. I know that it was you that originated the idea that certain research studentships[57] should be called after me, a fact from which I have derived much pleasure. I did write to the Council to express my gratitude, twice I think; but I felt I was doing it very clumsily. And I think the difficulty of putting my thoughts adequately into words has been the underlying reason why I have not written to you. I think you know that I have always urged that propaganda should be the main aim of our Society, because research is both more entertaining and profitable, and might drive its rival out of the field. Moreover, research is better done by a University than by a Society. But, though these are still my views, I think they need not militate against what has been done; both because it does not go too far, and because of the precautions taken in connection with these scholarships. I think I may, therefore, enjoy my scholarships and stick to my views. ...

Darwin to Fisher: 20 May 1935

... If the research studentships have the effects you hope for, my ghost will be seen wandering about your Lab. at night with a broad smile on its face. ... I do not gather if your Lab. is to be the home of the new serological show based on American money. Anyhow, it is an admirable move. ...

Fisher to Darwin: 21 May 1935

... Yes, the serological work is to start here next October. ... The grant is good for five years, but I presume the Medical Research Council would weigh in to continue it, if there is half as much in it as I hope. I do not at all see why the hidden inheritance of a recessive defect should not be directly detectable in a blood sample; but I ought to say that no one has done this yet, even with animals.

Darwin to Fisher: 11 January 1937

I have heard little of eugenics lately, and what little I have heard is not very encouraging. Judging by the title, M. Keynes's Galton lecture[58] will have no bearing on eugenics proper. I remember rather vaguely a story about an official at the church in Cambridge where they had broad church sermons at intervals. I can paraphrase it by saying that I have heard or read every Galton lecture, but I thank heaven I am still a eugenist. ...

Darwin to Fisher: 26 March 1937

Just a line to thank you for several reprints received at various times. I was glad to see that you confirm my father's generalization about variability and abundance [*CP* 153]. ... As to some of your papers, I can only admire them from a safe distance, whilst making me see how busy you are. ...

Fisher to Darwin: 30 October 1942

I think you will be interested to see from the enclosed offprint [*CP* 192] that the problem in *Lythrum salicaria* to which your niece, Lady Barlow, first called attention, has at last been solved. ...

It has been a great pleasure to me during the last seven years to take some steps in clearing up at last the genetics of the polymorphic situation which so much interested your father. Although the genetics constitute only a small part of the problem, it is, I think, essential to get them right before one can speculate usefully on the manner in which the present situation in *Lythrum* has come into existence.

Darwin to Fisher: 2 November 1942

I was glad to hear from you again, especially as it was to vindicate my niece. But I cannot pretend to make any intelligent remarks on the subject. I shall be 93 next Jan.; my sight, and probably my brains have gone slightly down the hill, and technical Mendelian terms constitute now a considerable difficulty. You seem to be carrying on as hard as ever, on which I congratulate you. I am sure my father would have been very much pleased to know that the *Lythrum* puzzle had been solved.

I wonder if you heard Huxley broadcast.[59] I thought *his* part very good. But such a performance should be either a lecture or a play. I disliked the other performer breaking in. I am trying to read Huxley's new big book but it is so full of technical terms that I don't understand a lot of it. However, I am naturally pleased that he backs up my father's views on some big questions.

I live here very quietly, with my old staff taking great care of me, and occasional visits from nephews and nieces. ...

Notes

1. Darwin was an executor of the estate of Henry Twitchin, a major benefactor of the Eugenics Society. See p. 16.
2. Salisbury, E.J. (1930). Mortality amongst plants and its bearing on natural selection. *Nature* **125**, 817.
3. Cunningham, J.T. (1930). Evolution of the hive-bee. *Nature* **125**, 857.
4. A, B, and C: three stages of development to which 1 in 10, 1 in 100, and 1 in 1000 seeds attain. See *CP* 88.
5. Darwin returned this letter to Fisher with 'early' crossed out and replaced by 'as soon as possible after the optimum breeding date' and the word 'early' in the following sentence replaced by 'thus'. However, Fisher has written in the margin: 'No, I really mean early, before the optimum date for the average bird.'
6. Below this chart, Darwin has written, 'quite right, I think. L.D.'
7. See Note 5.
8. The text of this passage was inserted in *GTNS* in 1958 (pp. 153-4) but unfortunately a modified tabular arrangement was used which does not agree exactly with the given description.
9. See Fisher's letter of 25 November 1930 to Darwin (p. 134) and also his letters to C. Todd (p. 267).
10. Punnett, R.C. (1930). Review of *The genetical theory of natural selection.* (R.A. Fisher) *Nature* **126**, 595-7.
11. See Fisher, R.A. (1930). Genetics, mathematics and natural selection. *Nature* **126**, 805-6.
12. This letter, in which Darwin comments upon the argument Fisher presented in his letter of 23 July, bears the dates 4 August and October 1930. It was evidently returned to Darwin by Fisher after 4 August and then sent again to Fisher, with some changes, in late-October.
13. i.e. flat-rate systems of family allowances payable out of public funds, for children of low-income parents not liable for income tax.
14. The physicist C.G. (afterwards Sir Charles) Darwin, who later discussed various population and eugenic questions in his book, *The next million years* (1952).
15. e.g. with late age of onset for the given defect.
16. See Fisher's letter of 15 October 1930 (p. 129).
17. See Fisher's letter of 23 April 1930 to C. Todd (p. 267).
18. Presumably Fisher, R.A. (1954). Retrospect of the criticisms of the theory of natural selection (*CP* 258). See Fisher's letter of 23 October 1951 to E.B. Ford (p. 202).
19. J.C. Smuts, South African statesman, author of *Holism and evolution* (1926). See also Darwin's letter of 15 September 1926 (p. 80).
20. Darwin, C.G. (1930). Review of *The genetical theory of natural selection.* (R.A. Fisher) *Eugenics Rev.* **22**, 127-30.
21. See *CP* 258, p. 92.
22. A pamphlet entitled, *An outline of a practical eugenics policy,* prepared and published by the Eugenics Society.
23. Keynes, J. Maynard (1930). The question of high wages. *Political quart.* **1**, 110-24.
24. Darwin seems to have taken Fisher's reference to reversion in his letter of 2 May 1931 as equivalent to Galton's early use of this word for regression to the mean.

25. See Fisher, R.A. (1922). Review of *A treatise on probability.* (J.M. Keynes) *Eugenics Rev.* **14**, 46-50.
26. Whereas Darwin believed in free trade, Fisher favoured protection.
27. Darwin's letter to T.H. Huxley, referred to in *GTNS*, p. 1.
28. Fisher had found that he required an operation for a fistula.
29. i.e. the Zoology Section of the British Association for the Advancement of Science. See p. 224.
30. This letter was presumably Fisher's reply to the hand-written notes mentioned by Darwin in his letter of 1 February 1932. Darwin's notes have not been preserved.
31. I am obliged to Dr R.I. Sommerville for the following comment.

    Fisher was probably referring to *Dermatobia hominis,* the human botfly of South and Central America. The botfly catches female mosquitoes and sometimes other flies and glues a batch of eggs, from 10 to 100, on the ventral surface of the abdomen. I cannot find any record of eggs glued to the legs, as Fisher suggests, but it could happen. When the mosquito feeds on its host, the eggs, stimulated by warmth, hatch. The larvae penetrate the skin of the host probably through the lesion made by the feeding mosquito or through hair follicles. They then develop in cysts under the skin.

32. Haldane, J.B.S. (1932). Review of *Genetic principles in medicine and social science* (L.T. Hogben) *Nature* **129**, 345-6.
33. Presumably Dr W.R. Inge, Dean of St. Paul's, London, 1911-34.
34. See Fisher's letter of 28 November 1930 (p. 134).
35. Huxley, J.S. (1932). Review of *Genetic principles in medicine and social science.* (L.T. Hogben) *Eugenics Rev.* **23**, 341-4.
36. A review by Fisher of Hogben's book was published in *Health and Empire,* 7, 147-50 (1932).
37. The Galton Laboratory, University College, London.
38. The Chair of Social Biology, London School of Economics.
39. Haldane, J.B.S. (1932). *The causes of evolution.* Longmans Green, London.
40. When W. Johannsen introduced the word 'gene' in 1909 in his book, *Elemente der exakten Erblichkeitslehre* (G. Fischer, Jena), he referred to Darwin's theory of pangenesis and de Vries' subsequent use of the term 'pangene' and then suggested that as only the syllable 'gene' was of interest, the simplest thing was to use this for the hypothetical unit of heredity, without any assumption as to its nature.
41. Hogben, L.T. (1932). Review of *The causes of evolution.* (J.B.S. Haldane) *Eugenics Rev.* **24**, 222-5.
42. Fisher wrote a review of Haldane's book and sent it to the editor of the *Eugenics Review* in June 1932 but it was not published—possibly because Hogben's review had already been accepted. See Appendix B (p. 289).
43. Charles Darwin.
44. Huxley L. (1903). *Life and letters of Thomas Henry Huxley,* (2nd edn.) (3 vols.). Macmillian and Co, London.
45. Leonard Huxley.
46. See Fisher's letter of 11 October 1932 to T.H. Morgan (p. 239).
47. See Fisher, R.A. (1934). Indeterminism and natural selection. *Philosophy Sci.* **1**, 99-117 (*CP* 121).
48. See *Proc. Linn. Soc. Lond.* **144**, 124-5 (1932) for Fisher's observations on the infanticidal instincts of male mice when confronted with litters fathered by other males.
49. Bohr, N. (1933). Light and life. *Nature* **131**, 421-3, 457-9.

50. Carpenter, G. D. H. and Ford, E.B. (1933). *Mimicry.* Methuen, London.
51. Darwin was godfather of Fisher's younger son, Harry Leonard.
52. Barlow, Nora (Ed.) (1933). *Charles Darwin's diary of the voyage of H.M.S. Beagle.* Cambridge University Press.
53. Darwin had referred to a suggestion that with the approaching retirement of C.B. Davenport as Head of the Department of Research in Evolution and the Eugenics Record Office in Washington, these two departments were to be separated.
54. Darwin, L. (1934). Analysis of the Brock Report. *Eugenics Rev.* **26**, 9-13. See also *FLS*, p. 199.
55. See Darwin, C. (1875). *The variation of animals and plants under domestication* (2nd edn), Vol. II, p. 319. J. Murray, London.
56. A typescript of Hutt, F.B. (1935). An earlier record of the toothless men of Sind. *J. Heredity* **26**, 65-6.
57. See Fisher, R.A. (1935). Eugenics, academic and practical. *Eugenics Rev.* **27**, 95-100 (*CP* 136).
58. Keynes, J.M. (1937). Some economic consequences of a declining population. *Eugenics Rev.* **29**, 13-17.
59. Huxley, J.S. (1942). Message from another age, an imaginary interview between Julian Huxley and Thomas Henry Huxley. *Listener* **28**, 501.

5 FISHER'S OTHER CORRESPONDENCE ON NATURAL SELECTION AND HEREDITY

Fisher to J.R. Baker: 24 April 1931

As far as I can see you state the matter quite exactly in the three sentences variously underlined.[1] The main difference in the printed statements is, however, less in what we say than in what we imply. I.e. Elton was certainly trying to make statistical sense of the 'mutationist' view of non-adaptive chance modification, and suggested that density fluctuations would give such a process a chance to work; while I have always felt that the probability of a whole species changing non-adaptively is the probability of a miracle, and saw in the phase of increasing numbers only the chance for a conditionally beneficial change, exposed in stationary conditions to slight counter-selection, finding the genetic and ecological environment in which it can increase.

Ford agrees with me on the adaptive question, and in discussing the contribution of Elton and self, I think we should not ignore his, since it was he who put forward the logical connectedness of the three statements you mention.

Fisher to Nora Barlow[2]: 26 July 1948

On the boat from Sweden I happened to pick up in the library your interesting book on Darwin[3]. May I congratulate you.

There is one point which incites me to write to you, which at first may seem trivial, even if it is not altogether so in reality, namely that concerning Darwin's attitude to Paley. I think it is in his autobiography that he expresses admiration for the clarity of this author's method of reasoning, and on page 23 of your book you advert to this, namely Paley's *Evidences of Christianity* only. I wonder if you have considered it possible that the more influential work may have been rather his *Natural Theology*.

The *Natural Theology* is full of material of interest to naturalists and displays Paley's wide interests in biological phenomena. It is not altogether without special pleading, but that element does not obtrude itself in the way in which it does to my mind in the *Evidences*. It just might be worth your while to look at the *Natural Theology*, if you do not know it, as an aid to forming an opinion on this element of Darwin's traditional background of ideas. For my own guess is that he was quite considerably influenced by the *Natural Theology*, while the *Evidences* had to be mugged up for examination purposes.

Nora Barlow to Fisher: 30 July 1948

I was glad to hear that you had enjoyed reading *C.D. and the Beagle*—an editing job that gave me great satisfaction. The point you make about Paley's *Natural Theology* is a good one, and one which reaches straight to my conscience for I have to confess that I have never carried out my intention of reading either the *Evidences* or *Natural Theology*. It is scandalous to go on citing influences and admirations without going back to the sources, especially when seeking for the current values and opinions on cognate matters as I have been doing. Perhaps your timely note will bring me to the point of reading Paley. Another curious case of a pre-evolutionist who had believed in some sort of a world system of a mutable kind was Grant, whose intimacy meant so much in the Edinburgh days, and yet who seems to have dropped out of C.D.'s orbit completely after he became Professor in London in 1827. Certainly the time was ripe for a revaluation.

Many thanks for drawing my attention to this point and for your kind letter.

Fisher to Nora Barlow: 2 August 1948

Thanks for your note. I believe you will enjoy dipping into the *Natural Theology*, if you have time, though I have not so much hope of the *Evidences*.

Fisher to Nora Barlow: 3 June 1958

Some time ago *Nature* sent me your re-edited grandfather's autobiography[4], of which I had already secured a copy, asking me to review it. This I have indeed done and should like to know, if you can spare the time for a glance, that you do not too much dislike what I have said about Erasmus, for amid all that might be said or left unsaid I felt I wanted a different emphasis from that of your own discussion. Please send it back as it is my only copy.[5] ...

Nora Barlow to Fisher: 5 June 1958

Thank you so much for your letter of June 3rd, enclosing your draft Review of the *Autobiography*. It was so kind of you to send it to me to see; and I was interested in your views on Erasmus' poetry.

You will not expect me to agree with all you say; I do, however, agree that there is a vast amount more that 'might be said or left unsaid' of the relationship between grandfather and grandson, but I did not feel that I could stress the point further in this volume. After all it is C.D.'s Autobiography. ...

I had hoped that I had done justice to E.D., who was a pioneer of his own generation. The whole historic set-up was different, and accentuated their differences. Coleridge's criticism was nearly contemporary with E.D., and not 80 years later; and he was so good a critic that now, 160 years after publication of *The Botanic Garden,* no one remains who would claim that E.D. was amongst the greatest of poets. I do not think it was spite—but good judgement. ... I think E.D. was trying to do what his grandson did later; for he tried to put into contemporary poetic form a mass of factual evidence. See the voluminous notes in his *Botanic Garden.* ... But C.D. also wanted quite early on to grasp the 'grand scheme of things'; this is from an early letter of C.D.'s to Henslow, and I am convinced that he was marshalling the evidence from near the beginning of the Beagle Voyage, and that his genius lay in biding his time till he found his 'naturalistic explanation', as you call it.

I certainly don't attach the slightest blame to E.D. for not doing what C.D. did; nor the slightest hint of plagiarism to C.D. But I think their parallel interests two generations apart deeply interesting.

Please don't think I take any exception to what you say; it is your review, and what you have written has interested me.

[P.S.] Copy of draft review enclosed.

Fisher to Nora Barlow: 7 June 1958

Just two words in reply to your nice letter of June 5th.

(a) I do not imply that Coleridge was 80 years later than Erasmus, but that during the following 80 years the function of poetry, and therefore what poets were aiming at, changed a great deal. (b) To say that the verse of a rival poet makes one sick, does seem to me spiteful.

Frankly, I do not think that your judgement or mine, if we have any, of the intrinsic merits of the verse, are the least bit to do with the matter.

[P.S.] I had looked at *The Botanic Garden* again before I wrote. In what ways to you find E.D.'s *ideas on scientific inference* defective? I am not asking on what points you think his opinions incorrect.

Didactic poetry has in the past had an educational function. Coleridge did not appreciate it, and if he had written better himself one might give some weight to his opinions, and ignore his spleen. Does 'good taste' compel you also not to appreciate it?

Nora Barlow to Fisher: 12 June 1958

It was good of you to answer my letter, and here am I answering back once more. Indeed, you ask for it, for you pose two questions at the end of yours.

I agree entirely that our opinions of the merits or demerits of E.D.'s or Coleridge's verse have nothing to do with the *Autobiography*—or a review of it. But there are points raised typified by the E.D.-Coleridge disagreement which do touch on C.D.'s odd denials of earlier influences—which was the reason for my intruding the subject at possibly undue length in the Appendix.

You ask two questions:—A) In what ways do I find E.D.'s *ideas on scientific inference* defective? and B) Does my 'good taste' (i.e. bad taste in following Coleridge?) compel me also not to appreciate it? A) E.D.'s ideas of scientific inference were still partly in the trammels of an earlier set of concepts. Raven says of Ray's time, 'The scriptural tradition was the primary datum for philosophic thought', and this attitude was slowly being transformed by the Natural Philosophers. But even well into the 19th century, the clergy were the Natural Philosophers, with the 'Ens entium' (E.D.'s phrase) as the unknowable law behind all nature. Don't forget that even C.D. never altered the phrase 'centres of creation' even in late editions of *Journal of Researches*. There was no self regulating law or process; and in both Advertisement (*Bot. Garden*) (Vol. 1) and in the notes, it is obvious that his attitude was essentially different from C.D.'s. Someone has used the phrase 'the changing degree of empiricism'—a useful idea. E.D. was using poetry for didactic ends, and was turning towards the stricter analogies 'which form the ratiocination of philosophy'. But though E.D. certainly was an observer, he had a bias in his 'degree of empiricism'. There were laws that were not generalizations based on observation, but generalizations based on the unobservable, i.e. the power within as a beneficent gift of the creator. This is very obvious in his discussions on the 'will' of the plant to fertilize itself.

It is an essential difference of the thought of the two centuries; I should not put it as you do that 'I find *E.D.s' ideas on sc. inference* defective.' B) I can't appreciate E.D. as a poet—but I deny that I am merely following Coleridge. And I think Coleridge entirely justified in giving an artistic judgement! But don't mistake me. I have an enormous opinion of E.D. as a man and as a thinker of his own time. I'm sorry I have run on at such length. Don't answer.

Fisher to Nora Barlow: 13 June 1958

You may not agree with this all at once, but it will let you know why I was so surprised that you did not like my review.

Enc.

Erasmus Darwin knew well what he was composing—a paean or hymn of praise and gratitude addressed to that *Nature* which is the object, or subject-matter, of scientific study.

Perhaps he thought that this study would not be made less attractive by such preliminary admiration.

He rather enjoyed his notes. They are intended to clarify allusions in the verse, which might be obscure to the less instructed readers—mostly teen-age girls of good family for whose education he was solicitous. What *he* thought important he put in the text.

How Coleridge must have hated his eupeptic serenity!—And his cheerful nymphs.

'Her lips were red, her looks were free,
Her locks were yellow as gold:
Her skin was as white as leprosy,
The Nightmare LIFE-IN-DEATH was she,
Who thicks man's blood with cold.'[6]

Horror, disgust, superstitious terror are emotions familiar enough to the human race. Are they *worth* all this screaming emphasis? The honours seem to be divided between dyspepsia and hashish! (Should I say laudanum?)

And this is admittedly his *best* poem;

'The Father of the Horror Comics'.

Both Butler and Coleridge had odd addictions. I suggest that in both cases INVIDIA was their most poisonous indulgence.

Envy of celebrity, which each would so dearly have wished for himself, made Coleridge eager to show that Erasmus was a bad poet, as it made Butler eager to show that Charles was both stupid and dishonest as a scientist.

Fisher to E.W. Barnes: 4 October 1930

Many thanks for your exceedingly kind and encouraging letter. I should be very glad indeed to discuss with you any points you think worth raising on the mathematics of my book[7]. I ought to say, though, that I think Prof. C.G. Darwin[8] was wrong in suggesting that Chapter IV is the kernel of the book. It is the most difficult mathematically, though not so difficult as some of what I have left undone in connection with other chapters, notably the opening of Chapter VI; but, in any case, mathematical difficulty is no criterion of importance. To predict the path of the earth is much easier than to predict the result of the next election, and would be even if we had full data in both cases. ...

Fisher to E.W. Barnes: 12 January 1952

Thank you for writing so kindly on my very amateur attempt at a sermon. It was, of course, not meant to be very ambitious or comprehensive, but particularly to show that one can give one's thoughts consistently to a scientific discipline without being completely alienated from the Christian tradition.

... On the question you raise[9], I wonder if the following seems to you at all like sense?

Man is in process of creation, and the process involves something we can call improvement, in which Man's own co-operation is necessary. Hence the need to become acutely conscious of evil or quasi-evil in ourselves and in the world, just as the increase of natural knowledge requires a corresponding consciousness of ignorance. Complacency in either respect would seem quite deadly to progress. ...

Fisher to Julia Bell: 24 February 1941

Thank you for your letter, and for what you are doing[10]. ...

I do hope you will look after yourself and not allow other people's anxieties either to wear you out with extra work, or to frustrate your own programme. Work of the kinds for which one has fitted oneself to do well seems to me not only a kind of prayer, but just as much an answer to prayer.

London looks frightfully depressing, as it has often done before, but I think you have enough of *Epictetus'* mood in you to regard that as a light challenge.

Fisher to C.I. Bliss: 15 February 1937

... I am amused by your speaking of the anti-Marxian character of the sociological portion of the *Genetical Theory,*[11] since, though the remedies proposed were not developed by Marx, the conclusion that all societies hitherto have degenerated by reason of their organization into classes characterized by different levels of wealth, and the conclusion that the only possible remedy involves pooling the cost of raising the next generation, have struck others as ultra-communistic. I presume, however, that the work is judged on Galton's political views, which, if you come to think of it, is an entirely aristocratic method of judgement, namely to put a price on the child by evaluating the parent.

Fisher to W.C. Boyd: 18 October 1934

Thanks for your letter of October 7th, which interested me greatly. I am, as a matter of fact, very strongly interested in the human blood groups and ought probably at least to have mentioned them [in *GTNS*][12]. At first sight the **A, B, O** series seemed to show some analogy with what is found in several polymorphic species, namely a relatively common and widespread recessive with a number of dominant allelomorphic variants. The evidence for dominance in blood group work is, however, rather exceptional, and I think it would, at present, be premature to conclude that no antibody reacting with **O** can be produced in immune sera. If this were done, the heterozygotes could be detected, as with **M** and **N**. Judging from Todd's work[13] with poultry, I am tempted to think that many, if not most genes, are capable of stimulating the production of specific antibodies. ...

I was thinking of the blood groups in emphasizing that a gene would not be found disseminated among many millions of people without the positive aid of selection, if it had arisen within ten thousand generations or so in only a single mutation,[14] as I think the first speculations about the ethnographic distribution of the blood groups were inclined to assume. If, moreover, not a single mutation, but a definite rate of mutation is postulated, the question arises why the mutation rate should be different in different races. Consequently, I cannot see any escape from the view that the frequencies have been determined by more or less favourable selection in different regions, governed not improbably by the varying incidence of different endemic diseases in which the reaction of the blood may well be of slight but appreciable importance.

You will see, therefore, that I cannot accept the postulate that selection must be excluded in speculating on the racial distribution. I would not like yet to claim that the evidence for dominance confirms my view because I feel that the evidence for dominance is still somewhat equivocal in this particular group of factors.

I am delighted to hear that you liked my book. My wiser friends warned me not to expect that it would have any great effect at once, but that those rare souls who think for themselves would, after a time, begin to make use of what good there is in it, and I think now that this prediction showed some foresight.

Fisher to W.C. Boyd: 9 November 1934

Many thanks for your offprint and letter. It may well be that serology will not prove as fruitful as I had hoped in discriminating genetic differences. Yet, if this is so, the cattle and fowls which Todd happened to utilize must be somewhat exceptional species. Is it possible on the other hand that it is the rodents which are exceptional?[15] I suppose only future work can show, and we must go on and follow up every hopeful path that opens out. ...

I am quite sure with you that small isolated groups have played a great part in human dispersal, but when we consider long periods and wide areas, is it not probable that colonization must always have been repeated by other isolated groups? And if this is admitted, it greatly diminishes the probability of wide differences in gene ratio having been produced by chance selection, and even a small group need not be genetically homogeneous, and would not often have been unless close inbreeding had ever been the rule in man.

Fisher to W.C. Boyd: 31 August 1946

Many thanks for your letter of August 21st. ...

I think my only point about your book, which I am looking forward greatly to seeing, is that in my opinion Wright has left his own exposition of the subject in great confusion. There is, of course, no controversy as to the reality of the occasional extinction of genes by chance in small populations. There is room for disagreement as to the possible evolutionary significance of the fact. From Darwin's time no one has doubted that the division of a species into a number of small separated populations is favourable to their evolutionary divergence and to the evolution of new species, but there is, I think, no reason whatever to think that this process depends upon the absolute numbers of the isolated portions, still less to imagine, as Wright undoubtedly does, that such a subdivision is favourable to the evolution of the species as a whole, when separate species are not formed.

I have been disappointed too by Wright's reiteration of theoretical formulae for the distribution of gene ratios in which, for the sake of simplicity, factors of undoubted importance are ignored, especially as the general nature, so far as it bears upon evolutionary theory, of the distribution of gene ratios was early established and is not in question. ...

Fisher to B.S. Bramwell: 16 August 1934

Thanks for your notes. I very much agree that the tendency towards increment salaries terminable at a fixed age is of much greater eugenic value than the older commercial tradition of working at a miserable wage for many years on the chance of stepping into a fat job in a crisis.

I don't think the question of ability really comes into it. There is no body in this country whose decision as to the eugenic merit of different individuals would be tolerated, and I think we should be careful not to give the impression that family allowance schemes would in any sense be saddled with this invidious duty. ...

With regard to the rules you suggest ... I do not object to them in the sense that I do not think they would do any appreciable harm. I should not myself, however, propose anything which looked like interference with the choice of the individual in marrying and reproducing at what age he pleases. ... I much doubt if there was any period in the 18th and early 19th centuries when the birth of children was not artificially restricted in a large number of families. The heiresses in Galton's lists were no doubt on the whole to some extent physiologically infertile and also to a considerable extent temperamentally ill adapted for early marriage. It would not be surprising if they were also psychologically disinclined towards reproduction. I don't think we can separate these several causes, though it is easy to show that the net effect is large and occurs in other data besides Galton's. ...

In general, I do not think that families of two are common compared with families of one or three and other numbers, in this country or elsewhere. The greatest effect of birth control has certainly been to increase the number of families of nought. A point which I think could be usefully investigated is whether there has been a decrease or an increase in the relative variance of the size of family. To speak of any people as having adopted 'the two-child system' is the kind of nonsense with which we are all too familiar.

Fisher to B.S. Bramwell: 23 June 1938

Thanks for sending your paper, which interested me very much, and which I am returning herewith. I think the genealogists ought to like it. Sometime I should like a short note from you for the *Annals*, as cousin marriages are quite important genetically, though a large sample of patients in London hospitals gave only about 0.65% admitting first cousin parentage.

As regards allowances for unrelated marriages of the same name, I wonder if this would help. From the whole group of marriages concerned, one tabulates the frequencies of all names, though it is only the more frequent ones that will matter. Suppose their frequencies relative to the whole are p_1, p_2, p_3, etc., as many as there are surnames; then one would expect the frequency of like-name marriages, if marriage were completely uninfluenced by the names, to be $p_1^2+p_2^2+p_3^2$, etc. This allows correctly not only for the total number of names, but also for their relative frequencies. Its value is in allowing correctly for the chance factor, though there may well be other factors producing unrelated marriages between persons of the same name.

Psychologically, a namesake starts by arousing some interest and curiosity. Again, if all the Davies in London were engaged in selling milk, as so many of them are, they would see more of each other than pure chance would allow.

On another point, one might guess that less than one-quarter of first cousin marriages are between children of brothers, on the ground that men are more readily dispersed than women, though there may not really be much in this.

However, the whole subject interests me, and I hope I shall hear more from you later.

Fisher to L.P. Brower: 29 November 1955

During the few years following the publication of my book *The Genetical Theory of Natural Selection* in 1930, various friends suggested additional cases that might be mentioned, and among them I find a note on the butterfly of the genus *Limenitis* in the Eastern United States of which, so Dr. E.B. Ford tells me, you will know all there is to be known.[16]

As I had not kept abreast of the literature of entomological genetics in the long interim period I consulted Ford about the following statement:

> 'The interpretation of the data is facilitated by the circumstance that the conspicuous white band in *L. arthemis* is due to a single Mendelian factor, in which that form differs from *astyanax*, although this is evidently not the only factor in which the forms differ.'

He does not know whether there is good evidence that the white band is due to a single factor or not. If this statement appears to you to be well founded I am inclined to include the note, if only in memory of my esteemed friend the late Professor Poulton of Oxford.

If, however, the case is obscure, I could perfectly well leave this item out, as my book would have to be totally rewritten if it were to be comprehensive in this field of work. Please give no particular trouble to this matter, but let me have a line as soon as you can, as my other material is waiting for this decision.

Fisher to L.P. Brower: 23 December 1955

Very many thanks for your kindness in looking into the matter of *Limenitis*. I was anxious lest in the long interval of time which has elapsed since my note was originally written, the facts on which it was based had been superseded. It is good of you to reassure me.

Of course, the attitude of zoologists generally has changed so greatly, the importance of natural selection has become so acceptable, and the various alternative proposals once so strongly canvassed have fallen so much into the background, that in the choice of subjects which need exemplification and emphasis I can scarcely hope to bring the book up to date. Indeed, I should prefer that it should stand as the first attempt in strictly genetical terms to appraise the weight of evolutionary theories going back for nearly a century.

Since the book has had its effect, it is indeed inevitable that much of what it contains should now be less fresh and interesting than it was in 1930.

Many thanks again. May I wish you enjoyable Christmas and New Year celebrations.

G.D.H. Carpenter[17] *to Fisher: 7 August* [*1934*]

At the debate on the egregious McAtee last winter you said that recent studies had convinced you that if elimination had been even at the rate of 1%, species would have become unrecognizable since Pleistocene.[18]

Have you said this in any paper from which I could quote—or would you mind my giving it as your opinion in a paper I am contributing to the publication of the recent International Ornithological Congress here in Oxford?

I am directing the attention of ornithologists to the subject of birds being the selective agents causing mimicry in Butterflies and quoting published records probably not known to *them*.

But it would much help my argument if I might draw support from your pithy statement (which I noted down verbatim at the time) which, so to speak, excuses what *some* folk consider to be the very inadequate evidence, from observation, that birds *do* attack butterflies.

Your statement means that people expect far more evidence than could be provided by actual observation. ...

Fisher to G.D.H. Carpenter: 9 August 1934

Thanks for your letter. Looked at critically my statement rests on two really different points.

One, that I have given a fairly adequate discussion of in Chapter IV in my *Genetical Theory of Natural Selection,* is that selective intensities much smaller than 1% do in reasonably numerous species exert entirely regular and calculable evolutionary effects. In fact, if n is the number of individuals living to reproduce in each generation, this is shown to be true for selective intensities greater than about $1/n$. Next, it appears that if the majority of selections were of the order of one in a million a considerable number of genes would be changed in a million generations or more, but not much change would have taken place, in say, ten thousand generations. Now in the last hundred thousand years, each representing a generation for quite a lot of the higher animals, the changes in rodents, etc., seem to have been phylogenetically unimportant, though I think it would be rash to say that a number, perhaps as many as a hundred, of gene replacements had not taken place.

On the other hand, it would seem to be stretching the probabilities extremely to suppose that many gene changes had swept over these species during the course of each hundred generations in this period, as would be the case if many of the concurrent selective intensities had been as high as 1%. My basis for argument is, however, lamentably vague, and I certainly think that the number of genic differences between local varieties is often much greater than geneticists are willing to assume, but then that would be so even if selective intensities rarely exceeded one in a thousand.

Of course, all this refers to net or unbalanced selective intensities. A selection acting at one stage of the life history might often be quite large, if counterbalanced by another equal selection at another stage, and in the polymorphic species I am now getting evidence of really enormous intensities, the equilibrium of which determines the frequency of the different forms in the wild populations; but only some of them are enormous, and these are naturally the ones which show up. In some cases one can detect them well below the 1% level, and these are much more numerous.

I imagine that on the general evidence evolution in protective and warning colours has been relatively very rapid, so that perhaps it would not be too incredible to find a noticeable change, involving perhaps a dozen gene substitutions, having taken place in a thousand generations, and this would mean that some of the most strongly selected genes gave an advantage of the order of 1%.

Fisher to R.B. Cattell: 1 August 1935

... It is probable in most English communities that parents of a lower social status have, on the average, more children than more prosperous parents, [and] also, from the enquiries to which you refer, that the latter have the more intelligent children. The question whether, among parents of a given status, the more intelligent have more or fewer children appears to be an open one, and one needing rather special care in its elucidation. In the same social class it is certain that parents of many children can give them less ample educational opportunities than parents of fewer children. In consequence, if in an enquiry it were possible to choose children having closely equalized educational opportunities, it is possible that, from this cause alone, the more intelligent would come from the larger families.

It seems that a large part of the social promotion by which children of the less affluent parents are promoted into the better-paid occupations takes place through the medium of educational opportunities. The extent to which such promotion is conditioned, respectively, by the inherent ability of the child, and by the size of the family to which he belongs, is a problem of the greatest sociological importance, on which we have, so far, but little direct data. I hope you may find it possible to orient your enquiry so as to throw as direct light as possible on this problem.[19]

Fisher to J.L. Crosby: 5 July 1940

... The case you have found[20] seems to me particularly interesting, as its investigation may throw light on the much wider problem of why plants generally are not forced into a condition of self-fertilization by the immediate selective advantage which this gives. It may be that the population you have found is trying an experiment which has been tried before and failed for reasons which would be very well worth knowing. I ought to say that I see no reason for expecting the homozygote to be lethal, and, if it were, I should certainly expect partial or complete compensation in the seed output of the homostyle plants. It is very interesting that some of the samples fall near or between the evolutionary paths appropriate to viabilities somewhat less than unity, and this may really be the situation, though it certainly needs confirmation from direct tests in culture. ...

Fisher to J. F. Crow: 1 November 1955

Thanks for your letter with the interesting discussion of intercommunal selection.[21] In thinking about this subject in the past I have been impressed by the relatively long life ascribable to such 'perfectly insulated' communities, and, therefore, with the implausibility of ascribing insulation which shall be perfect relative to their long existence. In fact, I think that complete insulation of the degree required, such as could of course occur through geological changes, must be taken to preclude real competition between the imagined groups. ...

Fisher to C.D. Darlington: 9 January 1936

I am surprised, and rather shocked, to hear that you should have experienced any difficulty in placing scientific papers. Although most of my stuff has been on subjects very different from yours, my own experience on this point may not be altogether irrelevant.

When I started writing on mathematical statistics I supposed that a specialist journal was the most suitable place in which to publish. *Biometrika* was then the only journal available. I published one paper there, which appeared in 1915. This was followed, in that and the following year, by two long editorial articles, under the names of a group of contributors, developing the solution I had given. The editor had not informed me that he thought any further development desirable, or invited me to co-operate, or, indeed, told me that he was doing anything about it. Next, he refused to publish a further paper giving new results and answering certain criticisms which he had embodied in the co-operative study. I was, therefore, forced to look elsewhere for the future, and published my answer in the Italian, or international, journal, *Metron,* sending it direct to the editor to prevent its suppression by the nominated editorial agent of that journal in this country. Since then I have not offered any paper to *Biometrika*, and have published very little at all in journals specializing in mathematical statistics. In consequence, the methods I was developing appeared, usually apropos of some particular application, in something like 30 different journals.

The only inconvenience I have felt in consequence of this is that, rather frequently, some mathematical writer, in search of proofs and of a more comprehensive and coherent theoretical disquisition than he has come across, has published as new some result I have previously given, or, what is slightly more annoying, has asserted that I had given no proof of some important point, when he has merely overlooked it.

Apart from this merely academic drawback, I am convinced that publication in non-specialist journals has been very much to my personal advantage, both in forcing me to think out problems from the point of view of those likely to need their solutions, and in bringing my methods to the notice of a far wider group of workers likely to use them.

The moral I am inclined to draw is that our scientific journals are, on the whole, too specialized for real utility; that genetics, for example, has become quite unnecessarily isolated from, and unknown to, the larger body of zoologists, botanists, and physicists, just because it was early provided with good specialist journals, so that the genetical discoveries, as they were made, only came to the knowledge of the small group already interested in the subject. Consequently I say, on no account found a journal devoted to cytological genetics as many will, perhaps, be inclined to advise.[22] ...

Fisher to J. Davidson:[23] [*17 April 1930*]

I am sending with this a copy of a book on Natural Selection which I had the impudence to write a year or two ago. It is now just out. I hope you will like it, both in itself and as a reminder of our very pleasant association at Rothamsted.

Do you remember at the British Association Southampton meeting, nearly six years ago, urging me to talk in Section D on Tate Regan's address?[24] I had come in unprepared to speak and funked it quite shamelessly. However, I took up the matter with him in correspondence[25] a year or two later, when I began to think I had a glimmer of what interpretation to put on the facts he relied on and, though I doubt if I made the least impression upon him, it did set me looking for just such evidence as I quote from Ford and Bull, in Chapter V.

I think some of the arguments in Chapter VI will interest you, especially in connection with the abandonment of sexual reproduction by some of your Aphids. You will see that I am led to think that while, in a wholly parthenogenetic form evolutionary progress would not absolutely cease, yet that it would be enormously retarded. I wonder how this fits the phylogenetic facts in your group—has every *genus* a core of sexually producing species from which any wholly parthogenetic forms may have been derived, or are there any wholly parthogenetic genera?

You will be amused to hear that my genetic work has been extending and I have added a chicken experiment on the farm to my mice at home. The chicks are destined to test the queer theory of the origin of dominance in *Gallus* which I put forward in 'Two further notes' [*CP* 69]. I should dearly like to try the genetic possibilities of marsupials since all work on mammals hitherto has as far as I know been done with eutherian mammals, and, indeed, practically all with four closely related species of rodents. The thing is to find a marsupial as easy to keep, as quick breeding, and as prolific as mice, and I seriously want you to tell me, if you can, what is known about rearing and breeding 'pouched mice' in captivity, and whether, if they seem to be suitable material, it would be possible for me to obtain some from Australia[26]. ...

My wife sends greetings to Mrs Davidson and inquiries after her health. How are the kids? I have five at the moment—what is your score?

Fisher to P. de Hevesy: 28 September 1945

I am returning herewith your interesting chapter on the Human family.

Of course, I agree and agree strongly that one of the great problems before mankind is to live in amity with other somewhat different inhabitants of the same planet. Mankind as a whole certainly constitutes a single family, and it is an old ideal and certainly not a dead one to treat all mankind as our brethren. I do think, however, that it is an essential part of the problem which, if ignored, will prevent us from solving it, if we do not recognize profoundly important differences between races, or if we imagine erroneously as to believe that such differences are rapidly disappearing through race mixture. By profoundly important differences, I mean, of course, not the superficial indications provided by skin and hair, but temperamental differences affecting the moral nature.

I have annotated the margin at a few points ... I should like you to recognize, if you agree, that it will be for us to regard other men with brotherly affection, and as in some senses, equal inhabitants of the world, without fostering what may be a dangerous illusion that we are equal in all respects, or discourage earliest enquiry as to the nature of racial differences, and without assuming that racial intermixture is necessarily a step in the right direction, however much, assuming it could be accomplished in, say, ten thousand years, its accomplishment might seem to simplify world problems.

Fisher to P. de Hevesy: 16 November 1945

Many thanks for your letter with enclosed section of your book ... [which] I am returning herewith.

You will see I have made a marginal note on the 'good' selection, perhaps not really relevant to your purpose, but it is important that the Darwinian process of natural selection is yet capable of acting in ways which generally speaking are not progressive, so that we may, in a sense, regard mankind, unless it rises to the task of helping itself and guiding its own evolution, as being at the mercy of non-moral forces which might mould or hammer it into most undesirable shapes.

I think, for my part, that we must regard the human race as now becoming responsible for the guidance of the evolutionary process acting upon itself.

Fisher to C.V. Drysdale: 4 October 1929

... We have certainly not reached the limit of the process of lowering upper class fertility, and the opinion, fallacious as I believe, that the welfare of the country is favoured by further restriction seems to be a real factor in those classes. Actually, the economic advantage to the individual and his heirs of birth limitation must, in all classes except paupers, be greater than the national advantage, if any, of such limitation, for the potential parent saves in the unproductive period of childhood and adolescence, whereas after this period the average citizen must produce more wealth than he consumes. It is for this reason that I believe that if ever the irrational objections to birth control were wholly in abeyance, the production of children would necessarily fall much below the economic optimum. You think these irrational objections, such as the Catholic view, have been waived much more fully that I do, so that you should give more weight to the economic dangers, though less to the selective dangers, of the very rapid fall in births now in progress, than I do.

In my view, free competition is invaluable in stimulating the production of wealth, but should be excluded on economic and eugenic grounds from the question of the reproduction of children. Unless it is so excluded, you cannot fail to recruit the next generation preferentially from the least prudent, or the most bigoted.

Fisher to L.C. Dunn: 26 October 1928.

Many thanks for your letter, which I was particularly glad to receive, as I was beginning to think that you did not see much in my suggestion anent dominance, and I was rather eager to have your judgement upon it. I very much agree with you that we have to do with dependence of gene expression on the whole hereditary gene background; so much so that I can scarcely find a meaning to put to the phrase 'dominance *per se*'. ...

I wonder how confidently you ought to say that dominance is practically never complete. Nothing is easier than to get some evidence of intermediacy, if the crossed forms differ in more than one factor, as is clearly apparent in my mice, and it is not easy to devise an experiment which excludes such a bias. The best cases available seem to be provided by mutants at their first appearance, and with these is not the heterozygote *very often* indistinguishable from the wild? ...

Fisher to L.C. Dunn: 13 February 1943

... With respect to the main controversy on dominance-theory, I agree with what I think is your final conclusion, that the question of the specificity of modifiers must depend simply on the developmental processes by which different mutant genes bring their effects about. If two different mutations modify the developmental processes alike from an early stage, I should expect as much as Muller should do that the same modifiers would influence them both, but I doubt much if any concrete meaning can be attached to such a phrase as 'modifiers which tend to enhance normal development', for considering a modifier and its allelomorph which affect the visible pigmentation on a heterozygote for Black and Brown, it seems impossible to say which allelomorph of the modifier favours normal development until it has been decided whether Black Agouti or Brown Agouti is to be the prevalent wild form.

In fact it seems to me that you must confront the modifier allelomorphs with the wild population including its rare mutant types, before Natural Selection can choose between the modifying alternatives.

What my experiments [*CP* 199] demonstrate is that in my Galton Laboratory stocks there existed, before **Sd** was introduced, both the allelomorphs which tended to make it recessive and those which tended to make it dominant in a number of the underlying factors available. On Muller's view[27] or Plunkett's,[28] I think that my stocks, and indeed your Bagg albinos and

Danforth's before you, should have contained only the allelomorphs of those factors which favour a long tail in the heterozygote, for these must be those which are meant by 'genes tending to enhance normal development'.

Fisher to A. Ernst: 27 July 1957

It is a pleasure to send you one of my remaining copies of the paper [*CP* 214] I gave at Woods Hole in 1946. I was, indeed, influenced in forming my ideas about the Rhesus complex by the system you had first proposed for the factor in *Primula* determining dimorphism.

Of course, a number of such cases are now known in different species, but I believe yours was by many years the earliest.

Fisher to M.J. Feldstein: 30 December 1929

Many thanks for your kind wishes conveyed to me in your interesting letter of December 18th. May I wish you in return a very profitable new year. I sympathize with you entirely as to the reception of new ideas by all the kind hearted folk who are too lazy to use them. There is one amenity of our age, easy publication, which, however, as it seems to me, can be put to a good as well as to a bad use. I agree that the editors ought to reject much more, and would do so if they had the brains, and the time, to do their job properly, but to be able to set out your work piecemeal as it is done, is a real advantage both to the writer and the reader. It gives valuable opportunities for reconsidering questions of order and emphasis in the presentation of the completed work: and it helps greatly to educate the small group of readers who, at most, will in the end be ready to appreciate it. The history, too, of the development of fundamental ideas has been much obscured by the hesitation of great men to publish incomplete work. I have recently been much struck by this in the comparison of the *Origin of Species* and other later works of Darwin, with the two originally unpublished essays of 1842 and 1844. In my new book, *The Genetical Theory of Natural Selection*, which I hope will soon be out, I have devoted the first chapter to showing that the logical argument upon which Darwin relied, which finds expression only in these essays, in fact governed the opinions expressed in the *Origin*, and later, by Darwin and other biologists resting on his authority. The bearing of Mendelism upon evolutionary theory could scarcely have been so misunderstood as it has been, if these essays had first put Darwin's views incompletely before the world. ...

Fisher to D.J. Finney: 19 November 1948

Very many thanks for your letter. Of course it was an immense satisfaction to me to have the Darwin Medal[29] awarded, as I have worked for a good many years, and indeed saw the need nearly forty years ago, to reverse the trend then prevalent of misrepresenting and minimizing the importance of

Darwin's achievement. The books and articles to be bought in Cambridge in 1909, the year in which the centenary of Darwin's birth was celebrated, make very strange reading today, and it is relevant to anyone really interested in the way science makes progress that the writers of the first ten years of the century, which began with the rediscovery of Mendel's work, were so biased against Darwin and natural selection by the controversies preceding this rediscovery that much that Mendel himself said in his 1865 paper was completely overlooked.

Evolutionary problems were, of course, not the subject of Mendel's paper, but as a side issue he points out that the view of inheritance at which he had arrived does remove one of the principal difficulties which Darwin and others had felt about the theory of selection. Indeed, Mendel was so clear about the theoretical implications of the particulate view of inheritance, that one rather wishes he had written a paper on the theory of evolution. I should guess it would have anticipated a good deal of what later trickled in through Weismann and Galton. However, that is only a guess. ...

Fisher to E.B. Ford: 17 March 1930

You may be interested to see a draft on polymorphic species [*CP* 87], which I have written, but which it seems rather premature to publish, although it will apparently be some years before much further information will be available.

I should be much interested if you care to annotate it in pencil. I have sent a copy to Haldane, but have not yet had time for a reply.

I really want to know a lot more about *Helix* and other snails. Let me have it back soon.

E.B. Ford to Fisher: 21 March 1930

I read your paper with the greatest pleasure and interest. It seems to me a contribution of the first importance to evolutionary genetics. I trust you will publish this far at once, and not wait for additional facts. It may be some time before sufficient data accumulate to carry the matter definitely further.

I have been through it most carefully, and I must say it hangs together extremely well. I have no real criticisms, and indeed very little to add or suggest.

Quite the most fascinating possibility is the opportunity of estimating the magnitude of a bionomic advantage in nature—very good!

On p. 20 is a long sentence which would perhaps gain in value if divided up. It concerns the point that beneficial mutations need not always have been of advantage.[30]

Would not this process of the conversion of a mutation to a more favourable type be hastened by the fact that so many species have periodic fluctuations in numbers (I expect you know the work of Elton and others on this subject)? These may be regular (like the 4-year cycle in mice) or irregular, as in many insects. The difference in numbers between max. and min. is commonly very great.

Now a disadvantageous mutation occurring when the numbers are going up, would have an unusual chance of spreading through the species (for of course increase in numbers = mitigation of selective intensity). Thus at such times recurrent disadvantageous (or neutral) mutations would have an unusual chance of spreading into different gene-complexes, with which they may act in a new and perhaps favourable manner[31]. ...

Fisher to E.B. Ford: 24 March 1930

Thank you for your letter and the further points you raise. ...

I do not know a bit how much importance to attach to large cyclic variations in numbers. I doubt if we can be sure that selective intensities are less in an increasing phase than in a decreasing phase. It is true that in an increasing generation the chance of a mutation surviving is increased, whether the mutation is beneficial or harmful, but is its chance of surviving round a complete cycle any higher if it occurs in an increasing generation than in a decreasing generation? I can see that more mutations will occur in the 'summer' than in the 'winter' of the cycle, because there are more creatures produced, but not that they are worth more in the 'spring' than in the 'autumn'.

There is rather a subtle principle by which any increase in the proportionate numbers of a new gene will certainly increase the rate at which it is becoming more favourable, or decrease the rate at which it is becoming less favourable by altering in its own favour the rates of other gene substitutions favourable or unfavourable to itself;[32] but I do not think this applies to changes only in the absolute numbers.

You will be glad to hear that my book on Natural Selection is at last out. I am sending a copy to Poulton, who helped me much with the Mimicry chapter.

E.B. Ford to Fisher: 28 March 1930

Many thanks for your kind letter. I have today ordered your book, and I look forward most eagerly to reading it.

In regard to cyclic variations in numbers, I should have supposed that the numbers of a species were an equilibrium between its reproductive capacity tending to increase them and selection tending to diminish them. So that increase in numbers would suggest relaxation in selection. If this were so, there should be an outburst of variation as the numbers go up, owing to the spread of disadvantageous variations which would normally be kept in check. Once the optimum had been reached such variations would be weeded out, and *a fortiori* they would not spread when the numbers were decreasing under stricter selection. Thus I should have thought that variation would be worth more during 'spring' than in 'autumn'. For then there would be an unusual opportunity for disadvantageous mutations to get into many combinations, with some of which they might act in a new and more advantageous manner.

Of course I only suggest this. But here is an instance from my own experience.

I have been studying an isolated colony of the butterfly *Melitaea aurinia*, personally for 13 years, and previously to that back to 1894 by means of specimens caught and records kept by a careful observer who worked the locality from then to 1915.

From 1894 to 1900 the species was exceedingly common, thousands flying together. The race was characteristic in appearance and very constant; varieties of all kinds were rare. From 1900 it gradually decreased, and by 1912 one had hard work to capture two or three specimens during the season. In this condition it remained up to and including 1919.

In 1920 the numbers began to increase. They increased rapidly until 1924, when the insects were once more in thousands. Since then the numbers have remained fairly constant, with a slow steady increase until now.

From 1920 to 1924, while the numbers were increasing, there was a most extraordinary outburst of variation, ... in size, colour, and marking. Great numbers of the insects were in various ways crippled and deformed; generally the most extreme variations were the most affected.

When the numbers became nearly constant variation practically disappeared, and so did malformation. For the last four years it has been extremely difficult to obtain any marked variations at all, although the species is now so exceedingly common. It has settled down once more to a constant form *which is recognizably distinct* from that which was found during the former period of abundance. These two distinct forms, and the insects caught during the period of great variability, make quite an interesting comparison.

During the former period of abundance the insect increased beyond its food supply. It feeds on *Scabiosa succissa*, of which there is a limited amount. The larvae were starved into eating honeysuckle, a food which otherwise they have only been known to take under compulsion in captivity.

Perhaps the greatest factor in reducing the numbers was parasitism. About 1902, 80% to 90% of the wild larvae were parasitized (parasitism is always fatal). From 1920 to 1923, though I bred hundreds, I never found one parasitized. Now parasitism is appearing again. Two years ago about 12% were affected, last year about 30%.

I am afraid I have bothered you with a very long letter. But if you are busy (as no doubt you are) do not bother to reply at once—I should quite understand.

Fisher to E.B. Ford: 1 April 1930

What you write about *Melitaea aurinia* seems to me to be extraordinarily interesting, though it is not quite what I thought you had in mind, as it does not involve the survival of mutants round a complete cycle.

If the 5 years' increase amounted to 1 000-fold, it would be 4-fold in each year; I suppose it might be 10-fold. Then a mutation appearing in this period would certainly have a good chance of surviving even if rather harmful. But would you expect the *proportion* of variants to be high? Or were the variants you noted, though surprising in frequency and variety, yet only a small fraction of the population flying about?

Did the proportion of variants increase during this period, or was it as noticeable in 1920 as in 1924? Were the deformed specimens about each year, or only in one season? I am asking more questions I suppose than you can possibly answer, but the whole thing interests me greatly.

E.B. Ford to Fisher: 4 April 1930

I have just got back here from Newcastle, and found your letter waiting for me. I am very pleased that you find the observations on *Melitaea aurinia* of interest.

I should imagine the total increase to be at least a 1 000-fold. Any year since 1924 I suppose it would have been possible to capture several thousand specimens without having any obvious effect on the numbers flying about. During the years of scarcity I do not think we ever saw more than two specimens in a season, working the locality quite carefully at the right time.

The second point can be answered definitely. It was the *proportion* of variation which increased. The insects flying about while the numbers were increasing rapidly were highly variable in size, colour, and marking. It is quite true to say that hardly any two were alike. Now there is scarcely any variation. One can catch dozens and find no detectable difference at all.

Really striking variations (i.e. forms with quite different patterns, etc.) were not rare, say at a very rough guess 5%. In the last four years we have got one such form among many hundreds examined. Nearly all the more striking variations were deformed. Such deformed specimens were about for several seasons, but more commonly during the first two or three years of the increase than in 1923 and 1924.

It it difficult to say, but I think the numbers were increasing faster during the first two years.

Fisher to E.B. Ford: 19 January 1931

Many thanks for sending me the offprint on *Melitaea aurinia,* which makes an extraordinarily interesting short paper.[33] I do hope it will lead others to make similar observations. ... The whole thing should do much to call attention to the evolutionary effects of the subdivision of a species into local groups, a subject which is very obscure to me at present. In this connection I wonder if you have seen Sewall Wright's review of my book in *The Journal of Heredity* for August last? In spite of its date it seems only recently to have reached this country, so in case you have not seen it I send the number herewith. When you have done with it you might post it back to the Eugenics Society, 20 Grosvenor Gardens, S.W.1 whose copy it is.

I am mightily pleased with Wright's review, because he has read and understood the book so well, which is quite a different virtue from agreeing with it. It is the first American review that I know of. I judge that he thinks I have overlooked a major factor in the effect of random survival in small isolated colonies; but though I see that it may be of special importance in some cases, and your *Melitaea* case is especially convincing of this, I do not appreciate how it can generally favour a more rapid progess in *adaptive* modification. Probably he will develop the view more fully later, when it will be possible to judge better how much weight should be given to it. I do not know if you have been able to form any opinion yet. Of course, I have no doubt of the general importance of local isolation, but at present I doubt if the adaptive modification of the species as a whole would in general be at all retarded by a complete mixture of every generation.

Fisher to E.B. Ford: 2 January 1936

It was exceedingly good of you to send me your paper on *Dardanus*. ...

On quite another matter I have had the shocking experience lately of coming to the conclusion that the data given in Mendel's paper must be practically all faked. I cannot conceive that Mendel himself had any hand in it, and quite independently, and this is what I was really studying his paper for, I have come to the conclusion that his experiments were planned and set out exactly as he records. I mean, for example, that his primary crosses really were unifactorial, and that he had carefully selected them to be so. So, if the data were faked, I presume it was by some assistant who knew too well what was expected.

The first thing that struck me was that in testing homozygosity in plant characters Mendel used F_3 progenies of only 10 and did not notice that the chance of a heterozygote being misclassified as a homozygote is not negligible, being between 5% and 6%. None the less, Mendel's data agree with the 2 : 1 ratio, requiring a compensating chance deviation which would only come about once in 30 trials. And then the same thing happens again later, and there is not a sign that Mendel saw the complication and allowed for it.

Now, when data have been faked, I know very well how generally people underestimate the frequency of wide chance deviations, so that the tendency is always to make them agree too well with expectation. So I tested all the larger experiments and, finally, the whole of his recorded data, and in the aggregate the deviations are shockingly too small with χ^2 about 30 for 64 degrees of freedom. I have divided up the data in several different ways to try to get a further clue, e.g. by years and by the absolute sizes of the numbers, but as far as one can judge the subnormality seems to be uniform in these respects. The only subdivision which seems to make any difference is that those 15 degrees of freedom for which bias has also been corrected have been less stringently adjusted to expectation than the remaining 49 where there was no original bias. It may be that when there was bias only the deviations on one side were adjusted, but beyond that possibility I can get no clue to the method of doctoring. As I said, I don't believe this touches Mendel's own *bona fides* or the reality of the experiments he carried out; and I do not think it has any bearing on the way in which his contemporaries in Germany ignored his results. After all, Darwin's more prolonged experiments on cross- and self-fertilization, in spite of his great reputation, led to nothing further at the time, and even a longer period elapsed between 1876, when he published his results, and the American work on inbreeding, than elapsed between 1866 and 1900.

I was engaged on writing a paper under the title, 'Has Mendel's work been rediscovered?' [*CP* 144] when I made my own abominable discovery. I suppose the title must stand with more irony than I had meant.

Fisher to E.B. Ford: 15 January 1936

... Your question as to Mendel's strategy is really most interesting and important.[34] It is difficult to know how much confidence he felt as to the application of his laws to other organisms. I imagine that his confidence wavered greatly from one time to another. He stresses once or twice that his data refer only to a small plant group. Against this, he writes rather confidently of the results with *Phaseolus,* which, later, it seems, he decided not to publish, for he only includes qualitative statements in his paper on *Pisum.* The two indications available as to his preliminary experiments are that attention was, from the first, directed to leguminous plants, and that ornamental garden plants were used ... . If it were not for the mention of ornamental plants, one would suppose that he had ascertained seed character segregation in *Pisum* either before he went to Vienna or after his return, and that, after the first large counts ... the ideas formed from these early observations crystallized rapidly into a factorial scheme being definite. This scheme suggested a number of verifications, which might well lead him to work more extensively with peas, perhaps at the expense of other plants, than he had originally intended.

When he wrote his paper, I should judge that his attitude was that he would refuse to claim that his laws had been demonstrated beyond *Pisum*, but he would be much disappointed if they did not, in fact, extend much further. It is not really improbable that he was theorizing much more confidently before his experimental work than he was afterwards.

Fisher to E.B. Ford: 2 May 1938

Many thanks for having sent me the page proof of your book on *The Study of Heredity*. I have read it with the greatest pleasure and interest, as I think you would expect. There is only one point which I should like to take up argumentatively; that comes on pp. 174-5 where you give a statement of views developed by Sewall Wright,[35] and either the statement of [or?] the original views seems to be confused. If one thinks of the different genotypes possible in a species segregating in some hundreds of factors, it appears that these are discontinuous and may be represented spatially as the points of a lattice. I mean, for example, that, if there are two competing allelomorphs at any one locus, then in respect of this factor every genotype must be one of three types; that is, there will be two other genotypes differing from it, but alike in all other factors. Varying two factors at a time, one gets similarly a 3×3 lattice of 9 possible genotypes, and for n a 3^n lattice. Lethality will cut out certain combinations, and multiple allelomorphism will require a slightly more elaborate representation having a number of dimensions to each factor, which is also adequate to deal with the different types of multiple heterozygotes which can be formed by linked factors. The point is, however, that, so far as individuals are concerned, there is only a discontinuous aggregate of lattice points, each having its own selective value. There is no continuum of possible values in which we might speak of peaks or maxima.

Such a continuous representation in multiple space occurs only when we think of the gene ratios existing in a species as a whole. A point then does not represent an individual, but a possible specification of the gene content of the species. Any such species must contain individuals of greatly differing selective value, which, if favoured by selection, will move the point representing the aggregate of gene ratios to another part of its field. If one is thinking of a spatial representation of possible species compositions, it is not clear on what the distinction between peaks and valleys is based. So far as I can see, natural selection is only definable in terms of the relative selective advantage of the different genotypes possible to individuals. I think Wright must be thinking of altitude as a kind of average selective value of all the individuals of the species, which is quite reasonable if the different genotypes can be assigned fixed values independent of the genetic composition of the other individuals present in the population. If this is so, the fact that a number of different genotypes may be of equal selective value is no reason for anticipating a multiplicity of peaks. The difficulty of imagining such a multiplicity seems to increase with the number of dimensions, that is, with the number of factors the gene ratios of which need to be represented.

In one dimension, as in a road, we pass over an alternate series of hills and dips, so that half of the level points are maxima. In two dimensions, in addition to peaks and bottoms we have cols, which may be regarded as lowest points on ridges or highest points on valleys, the curvature of the ground being positive in one direction and negative in another, and the peaks are only about one quarter of the level spots. In n dimensions only about one in 2^n can be expected to be surrounded by lower ground in all directions.

I make these points because I think your experience with the *Meliteae* colony likely to be of great importance for the problem of species formation, but that its importance may be overlooked if it is thought that it is all plain and easily understood on current views. ...

Fisher to E.B. Ford: 17 September 1951

... About Julian's book,[36] I should most certainly like to do something to express respect and appreciation for his general activity in regard to selection theory over a really very long period. I could wish there might be some opportunity other than one of these compound books which I have grown considerably to dislike, though I suppose they have their special role to fulfil in scientific discussion. It is, however, utterly different from a book from which you can gain a unified point of view due to a single individual and form one's own opinion as to what strands are going astray and what are worthy of further development. In fact, such books do mess up scientific discussion a good deal and often through allusions at second hand, give a very wrong idea as to what each worker has in fact contributed. ...

Fisher to E.B. Ford: 23 October 1951

I am now enclosing something [*CP* 258] which you may think will do for Julian's book. I wrote it a long while ago when the possibility of my bringing out a second edition of the *Genetical Theory* was in my mind, but I do not think now this should ever be done, and the most I should be inclined to attempt would be a book of essays taking up particular topics such as this one.

For this reason, I wish to retain the right without further discussion or negotiation, to reprint it at any later time if it is now printed as part of Julian's Festschrift.

Fisher to E.B. Ford: 25 November 1955

I have recently been induced to look over *The Genetical Theory of Natural Selection* with a view to a reprint. I do not like to call it a new edition, for I feel that I could never now give the amount of work necessary to bring the original up to date in its various aspects, genetical, evolutionary, sociological, etc.

I have dug out, however, some old notes of about 1935 intended for incorporation in a subsequent edition, if ever one were needed, and some of these will make manifest improvements in the earlier chapters.

I wonder if you would be so very good as to look through the one that I enclose herewith, which must certainly have come in essence from Poulton[37]. As I am completely out of my depth in this field, perhaps you will give it a glance and a quick 'yes' or 'no' for inclusion. I would not think it worth your while to put it right if, as is quite likely, there are a number of points now needing correction or change of emphasis. It is indeed something which should scarcely be included as my own, though as a tribute to that very kind old man I should be glad to include it. Anyway, without wasting your time, for you are always busy with more important things, let me have your reaction.

E.B. Ford to Fisher: 28 November 1955

How nice of you to consult me in regard to the notes for possible inclusion in a reprint of *The Genetical Theory of Natural Selection.* I need hardly say how delighted I am that one of the most outstanding text books of biology is to be reprinted. It has been an amazement to me that the original edition did not sell out long before the War but, after all, a book is to be judged not by its sale but by its effect upon science, and no book of the century has has a greater effect upon biology than has this one, the ideas spreading out from it through, apparently, a limited number of readers of the original, but that kind of thing is what both you and I are accustomed to find (people like to be given little summaries).

I think that these notes are quite all right, and that the remarks about hybridization and so forth can be relied upon. There is, however, a statement half way down the first page, which I have marked lightly in pencil in the margin, which I am not at all happy about. It may be that there really exists published data on the genetics of the conspicuous white band in *Limenitis arthemis.* If so, neither I, nor any of the likely people I have been consulting here, know anything of it: and I suspect if it were published in at all a wellknown place we should do. Either (a) this is a personal communication of unpublished work to Poulton, in which case it certainly ought not to be taken for granted, being genetic. (b), Alternatively, data demonstrating this may have appeared in some remote American entomological or biological journal (perhaps even a Collectors' Society) of such a kind that one is almost certain to miss. Now I have a friend in the States who has made close search of this sort of literature, and if he does not know of published evidence in this matter, I think one ought to take it as not established. The name is Lincoln Brower, Osborn Zoological Laboratory, Yale University, New Haven, Connecticut. ... I am sure he would give you a good opinion. ...

Fisher to A.B.D. Fortuyn: 20 April 1931

It was a great pleasure to me to receive your kind letter about my book on Natural Selection. Its publication has been too recent for me to be able to judge with any confidence of its effects on scientific opinion generally, and it is therefore of particular interest to me to receive your personal impression.

I had read Dr Hagedoorn's stimulating book[38] some years ago, at a time, however, when my own views as to the bearing of genetics upon evolutionary theory were quite immature, and my reaction was, therefore, probably less favourable than it ought to have been. Professor Sewall Wright of Chicago, an extremely able geneticist, who on most points has given me extremely valuable support is, however, powerfully advocating the importance of partial isolation as an evolutionary factor, and this, I believe, was one of Dr Hagedoorn's principal contentions.

I think we must distinguish sharply between the processes causing evolutionary modification and those causing fission or subdivision into distinct species. The term 'origin of species' may be used in either sense. As far as I can see at present, isolation, whether geographical or physiological, while of immense importance to the problem of fission, is not a primary factor in adaptive modification, save in the subordinate sense that fission is a necessary condition for divergent adaptation. Sewall Wright, however, at present thinks otherwise, and there are very few men who have a better right to form their own opinion.

I was particularly interested in what you say with respect to the argument in the chapters on Man. This argument had to be developed rather fully, since, unlike the other applications of selection theory, such as sexual selection and mimicry, there is, as yet, no considerable literature on the subject. I would be especially interested to hear if you have formed any opinions, during your stay in China,[39] as to the temperamental contrasts between the anciently civilized Chinese and either Europeans or the less civilized nations of N.E. Asia. Such temperamental contrasts are, I believe, of the highest importance in human evolution, and, though the difficulties of setting one's impressions upon an objective basis are very great, yet I am convinced that a sympathetic observer who faces these difficulties can accumulate results of permanent value, and of very widespread interest.

Fisher to A.B.D. Fortuyn: 13 January 1939

Thanks for your long and interesting letter. I do not know whether what I have to say on your points will be particularly helpful, but at least it should serve to make clear my own point of view. With respect to your citation from *Statistical Methods*,[40] I certainly want you to understand what I am driving at. In England, at all events, and to a fair extent elsewhere, the cleavage in opinion between statistical and genetical studies of inheritance had been drastic and injurious. For twenty years I have laboured, with more or less success, to get statisticians to appreciate the importance of Mendelian inheritance, and to get geneticists to appreciate statistical methods. The phrases you quote are in the latter category. You ask if it is wise to support in this way a rather too simple popular idea. The simple popular idea which I am opposing, however, may be made clear. It is that familial resemblance may easily be ascribed to differences in the social and economic conditions of different families, and that inheritance should only be postulated where genetical factors have been individually analysed and recognized. This attitude seems to be widespread, and is, I believe, profoundly untrue. On the other hand, I know of no work pointing to any measurable factors capable of explaining quantitatively more than a very small fraction of the observed covariance in the resemblance between relatives. I infer that this is predominantly due to similarity of inheritance involving many factors.

I appreciate your point that inheritance is often strikingly demonstrated by the differences, especially in characters which can be appreciated but not measured, observable between brothers and sisters, whose social and economic environment has been certainly very similar.

Of course, the more factors you introduce, the more seldom will genotypic identity occur, even between near relatives. On the other hand, the more frequently will similar, but not identical, genotypes be phenotypically indistinguishable, so that in a multiple factor system you may expect a measurable degree of similarity between parent and offspring, and between other near relatives. ...

Fisher to A.B.D. Fortuyn: 11 December 1944

I was very glad to receive your letter. ...

I hope you were interested in the response to selection of the tail-development with Danforth's mutation [*CP* 199]. It seems to show that the stocks I had in England, though comparatively inbred, were really (though invisibly) highly heterogeneous for factors which, in the presence of the short-tail mutation, are capable of influencing the development of the tail. It is this great pool of latent variability which I think geneticists of the period of the rediscovery of Mendel's work at the beginning of the Century very greatly failed to appreciate. ...

Fisher to P. F. Fyson: 5 September 1938

Thank you for your letter of August 21st, which I have just received on my return from holiday. You have my entire support in the belief that the [Eugenics] Society ought to take a much more active interest in current politics and should throw its weight more strongly in favour of positive measures. For years, indeed, I have felt that the controlling group in the Society were almost without Eugenic knowledge or ideas.

I am not so sure that the decline of civilization should be ascribed to licentiousness, though, obviously, this does a great deal of harm personally, just as does drunkenness, yet my impression is that Gobineau was right when he asserted, in the early paragraphs of his essay on the inequality of man, that the early and virile stages of successive civilizations were not more exempt from licentiousness than were the later and decadent phases. I should say, indeed, that self-control in general tends to increase in the history of all civilized peoples, even while their capacity for spontaneous co-operation and the pursuit of unselfish aims is diminishing. I think, however, you would be right to point to moral laxity as an important symptom of social disintegration.

Fisher to P.F. Fyson: 12 September 1938

Thanks for your letter. I do not see that much can be done with the Eugenics Society, as its present directors of policy are strongly entrenched and appear almost impervious to scientific advice. Indeed, I think they are suspicious and resentful of it. In consequence, I have of recent years not attended the Council, although I have allowed my name to remain as Vice-President.

Fisher to R.R. Gates: 1 July 1930

... With respect to blood groups,[41] I fancy we must give up the two factors in favour of a multiple allelomorph series, **O, A, A′, B.** They seem to resemble *Apotettix* in their dominance, i.e. there is a fairly common universal recessive, and a number of dominants, which however show no mutual dominance, but a combination of the single effects. I cannot think what such a factor is doing in Man.

There are a good many climatically limited blood diseases, such as malaria and yellow fever, so I would not be too sure of the absence of selection. However, if it is absent, a mutation rate of 10^{-6} will establish itself in about 62 per cent of the population in 10^6 generations, which seems too long to allow, or a little less than 10 per cent in 10^5 generations, which is still a long time, and an uncomfortably low percentage. It looks as though you must postulate high mutation rates ethnographically limited, or else local selection.

Fisher to H.D.Goodale: 2 January 1932

I think I can make somewhat clearer that part of my letter which you find questionable, for I have evidently not expressed myself very clearly. I entirely agree with the principles you lay down:—

(1) the rating given to a bull should be based on the information supplied by the performance of his daughters and their dams,

(2) convenience and genetical common sense agree in suggesting that the appropriate type of formula is found by taking some multiple of the

daughter's yield, and deducting some (other) multiple of the dams' yield. Thus our estimate from a single heifer would be:

$$aH - bD$$

where H and D stand for the performance of heifer and dam, and a and b for the constants of the formula.

In an extensive paper for which, I believe, Gowen did the calculations, Pearl tabulated the mean values of

$$H - D \tag{1}$$

for a large group of bulls. Examining the groups of bulls which stand highest and lowest on his list it is obvious that those that stand highest had been mated to exceptionally poor cows, and those that stand lowest to exceptionally good cows. The formula in fact gives too much weight to the dam and too little to the heifer. Since half the germ plasm of the heifer comes from the bull, the formula

$$2H - D \tag{2}$$

suggests itself as more plausible, i.e. free from gross error, though probably capable of improvement. To this it has been objected (by Lush) that if we consider the different daughters as giving different estimates of the rating of the same bull, (2) will be more variable than (1), and consequently must be judged less precise. This criticism overlooks the fact that using (2) the ratings of the different bulls will also be more widely spaced, so that their differences will be as significant as before in relation to their higher standard errors. The inadequacy of considering only the variance of different estimates of the same bull may be easily seen by considering the formula

$$H - \tfrac{1}{2}D \tag{3}$$

which is obviously equivalent to (2), but gives a lower instead of a higher variance for different ratings of the same bull.

It is for this reason that I introduce the condition that the variance of the different ratings of the same bull should be minimized in relation to the variance of the average ratings of different bulls on the same formula. Applied in this way we are only concerned with the ratio b/a, and it is obvious that it is only this ratio which matters in the application of the formula.

To take the variance among different bulls as the denominator of the fraction to be minimized does not imply that a different formula would be obtained if this variance is changed. If the true ratio of b/a is the same, we should obtain estimates of it, agreeing within their sampling errors, from groups of data having very different variabilities of the bulls tested.

We should, I think, however, recognize that the ratio must depend on the particular group of genes segregating in the material examined, and on the degree of inbreeding, so that it may really be different in different lots of material. If this is so, it will be a real advantage to apply to each group, the formula appropriate to its peculiarities, instead of a single formula for all cases. ...

Fisher to J.B.S. Haldane: 15 March 1930

I think you may like to see the enclosed [*CP* 87] which I have written but not yet decided to publish. I should much rather wait a year or two for fuller information; in fact the only case for publishing at once is that it may speed up the further investigations which are needed.

If any points occur to you please annotate the copy freely. It is not, of course, primarily an answer to your note, but a further development of my own theory on lines suggested by your note, and especially by your suggestion of duplication.

Let me have it back soon.

J.B.S. Haldane to Fisher: [*March 1930*]

I have read your typescript with great interest ...; here is my serious criticism. Nabours has since published a big paper (*Bibliographia Genetica*, V). ... I feel that any discussion which does not include these data is premature.

However, the theory, especially as regards *Lebistes*, is most attractive, and I like the idea of an evolving species doing one thing at a time. I am glad my note has stirred up thought on the matter. I agree that my suggested limitation is 'curious', and that your criticism of it is quite cogent. That is a fair tit for my tat as to the, to my mind, 'curious' specificity of your postulated modifiers. I feel, however, that all this back-chat is leading somewhere. I hope you will publish after digesting Nabours' new data. ...

I have not annotated because I feel you may modify in response to Nabours' new stuff. If so, perhaps I can see the paper again. I am just doing the theory of segregation in polyploids, also monstrous calculation on inbreeding with 22 simultaneous difference equations, which admit of a simple solution.

Fisher to J.B.S. Haldane: 25 March 1930

I had looked through the *Bibliographia Genetica* material, but unfortunately it cannot be used for examining the viability of the dominants, since the zygotes are not recorded. For example, you suggest in your letter that the matings showing segregation in ×/+ were all matings ×/+ × +/+, and these I could use readily. But Nabours refers to his 1917 paper for an example showing the segregation of **C/9** and the mating was actually **C/9** × **B/E** giving four types all heterozygous.

Possibly on seeing my paper he will sort out the evidence for other species, and I should be especially pleased if on large numbers there should be no significant deficiency of $+/+$. On this point my paper only raises a question which cannot be answered for the data published so far.

I am glad you like the beneficial mutations all having to 'cue up' (or is it 'queue up'?) when linkage is too tight.[42] Let me have any further comments soon as I am being urged to publish.

J.B.S. Haldane to Fisher: 29 April 1930

Referring to your esteemed favour of 23rd inst.,[43] you suggest two alternatives: (a) that the liability to respond by agglutination to any particular ingredient in the serum is always completely dominant; (b) the liability of recessives so to respond is always shared by the heterozygotes. I do not see that (b) has a definite meaning; to my mind the definition of a recessive is a zygote having a character *not* shared by the heterozygote.

With regard to the suggestions, Todd has not, so far as he knows, got any homozygotes. I have had a look at some of his results, and he is trying to get some, only choosing what would appear to be fairly recessive birds to mate together, as these would seem more likely to give a pure line within a measurable period.

Perhaps I have not got your point, however. I should expect to find both dominance and summation of effects, as with the human blood group genes, where **AO** is indistinguishable from **A** (**A** dominant) and **AB** differs from **AA** or **BB** (no dominance).

With reference to your book, I have finished the first reading, and think the suggestions as to 'inertia' on pp. 111, 137 [*GTNS*, pp. 125, 152], and elsewhere, are even more important than the theorem of p. 35 [*GTNS*, p. 37], as they may serve to explain a good deal of otherwise unintelligible 'orthogenesis'.

I disagree with the statement (p. 119) [*GTNS*, p. 133] that linkage values are eminently susceptible to selective modification. Linkage modification is generally due to cytological change (segmental inversion) and in this case intense linkage is characteristic of cytological heterozygotes, not of pure lines save for the genes concerned. Also I doubt if linkage will be much affected by selection if the COV [cross-over value] is large compared with the coefficient of selection m.

The social part is highly controversial. If you convince me I shall have to become an extreme form of socialist, since the inheritance of property must tend to promote infertile stocks, even with family allowances of 12% on income per child. E.g. if I have one child and an income of £1120, while you have 6 and an income of £1720 you may save more than I, but you are not likely to save 6 times as much. So your children will start with less capital than mine. I suspect your economic views represent a compromise between the conclusions of your probably unorthodox but 'bourgeois' economics, and your non-bourgeois (—non-proletarian either, but shall we say human—) biology.

Correct me if I am wrong. I have not yet begun to digest the book, especially not pp. 106-110 [*GTNS*, pp. 120-4].

Fisher to J.B.S. Haldane: 29 April 1930

Many thanks for your letter; you can scarcely guess what a satisfaction it is that my book has found at least one very intelligent reader. I kept feeling all the time 'This won't be understood unless I expand it to a whole chapter about things I really know nothing about'. It is tremendously good to feel that you are reading it carefully, and I hope you will write again as the spirit moves you on any points you care to discuss.

One thing which makes me think that linkage values would respond readily to selection is the appreciable discrepancies between the linkage values in different lines of *Drosophila*. I do not mean large scale suppressions which, like you, I should put down to segmental inversions, etc., but the general heterogeneity of all extensive data which makes linkage maps always relative to a 'standard stock'.

I do not believe (if I convince you on Man) that you will be attracted by any existing 'ism'. I only fear that you will say that it is so intricate that we must cut the Gordian knot by ectogenesis. I may be wrong about inherited capital, but I do not believe it is important in a sufficiently large class to be a major factor in the problem; though I do think that if family allowances were general among earners it would seem normal and natural (and on racial grounds desirable) to consider national insurance schemes applicable even to millionaires, which would have the effect needed. But, again, I am convinced that it is the body of the population that matters, not the economic extremes. Your point about capital *saved* out of earnings really means, does it not, that somewhat more than 12% would be needed to equalize the standard of living.

I realized in our talk last week about two factors that 'maintain each other mutually in equilibrium' was a misleading phrase in suggesting that pairs of factors could be held in equilibrium by an agency essentially different from the case of one factor. All that I meant was that cases of stable equilibrium in two factors can occur for which the one factor analysis was inadequate and that all such cases must favour close linkage, as the single factor cases favour cross-fertilization. Possibly the case on pp. 110-11 [*GTNS*, pp. 124-5] is the more important agency of this kind, but I do not think there is any agency of the same sort favouring looser linkage, which may give us a gauge ultimately for W.

Wherein are my economics bourgeois? Are you thinking of pp. 182-4 [*GTNS*, pp. 201-3], or is it merely that I do not go out [of] the way to consider a collectivist egalitarianism which has never existed?

As a biochemist, have you any preference as between the diagrams on pp. 63 and 64, [*GTNS*, pp. 70-1]?

About agglutination you are right; (b) means no dominance in that matter, though a dominant genetic factor like Barred might show no dominance in its serological reactions. I take it Todd using Plymouth Rocks has homozygotes for a fair number of factors, though his stuff shows plenty of variation in other factors which do not affect the plumage. I want to know if he could make up particular brews which would discriminate sex, or any other known genetic factor *alone*. When you see my meaning about this I expect you will be able to say how the test could best be made, and I hope you will if Todd is interested.

Fisher to J.B.S. Haldane: 14 May 1930

I have put some notes on the margins of your 'Further note on dominance', but they may be only criticisms of your wording. It would, I think, be a really good point if multiple allelomorph series had a number of recessives on one side and semi-dominants on the other, but the case of the rabbit is not easily reconcilable with any simple response curve. If the 'dominants' are dominant through producing more effect than the normal, all the recessives ought to be incompletely recessive, through the reduction of the effect in the heterozygote, i.e. they ought to appear semi-dominant also. If you build up a response curve to fit the facts of dominance it needs almost as many inflexions as there are allelomorphs. ...

J.B.S. Haldane to Fisher: 6 June 1930

I do not altogether agree on the necessity for inflexions in the (gene stimulus) - response curve. Suppose that x represents amount of gene substance (i.e. something additive as regards genes), and y the effect measured. Then $y = f(x)$. Supposing $y = k \log x$ (Weber's law), then it is a sufficient condition for dominance that the minimum distinguishable change in y should exceed $k \log 2$. Thus a gene of value a will be dominant over one of value b if $a > 3b$

	Gene value x	Phenotypic value y	Difference
Dominant	$2a$	$k(\log a + \log 2)$	
			$k \log 2 - k \log(1 + b/a)$
Heterozygote	$a + b$	$k \log(a + b)$	
			$k \log(1 + a/b) - k \log 2$
Recessive	$2b$	$k(\log b + \log 2)$	

Clearly the first difference $< k \log 2$, the second $> k \log 2$. ...

P.S. I am reviewing you for the *Eugenics Review*.

Fisher to J.B.S. Haldane: 10 June 1930

... The argument involving the 'minimum distinguishable change' is worthy of the High Court of Justice, but is experimentally at the mercy of anyone who, by observing more animals, or under more comparable conditions, takes the trouble to distinguish smaller changes. Of course, its consequences might be verified by such an observer.

'Bourgeois' economics still puzzles me. The word is really rather well defined, so I suppose you did not mean just reactionary, or did you? That would be true if the reaction is taken to be not merely to the progressive party's programme but to the whole interaction of the two antagonistic politico-economic principles. They play into each other's hands in guaranteeing the process of Chapter XI, but by doing so thoroughly frustrate each other's aims. ...

About Todd, he seems to think you have some reason against sex being distinguishable by his method, but if you thought it worth doing I believe he would make the following test for the ♀ chromosome:— Make a compound serum from cocks using hen donors; exhaust with corpuscles from several cocks; try if it reacts to hens. If it worked, it would be a good first step towards detecting a single gene.

I am rather sorry about the *Eugenics Review,* as I had hoped you would be collared for *Nature*, but perhaps you will do both. At any rate, the *Review* will give you all the space you want.

J.B.S. Haldane to Fisher: 9 November 1930

I enclose a draft of a paper on selection as a function of mortality rate.[44] The conclusions are rather odd, but I cannot get away from them. They remain true for small values of mortality even if the viability distribution ceases to be normal for large deviations (as with human stature). If you see any *gross* error, will you let me know as soon as possible ...

Fisher to J.B.S. Haldane: 11 November 1930

I think I see the point of your calculations now. I should take $+ \log (z + 1)$ instead of $\log z$, since $\log (z + 1)$ measures the amount of elimination in the sense that if such a process, e.g. decimation, is repeated, $\log (z + 1)$ is doubled. ...

I do not think one ought to be surprised at the result that small mortalities are much more efficient selective agents, in that they produce a greater effect 'per decimation'. One would find very much the same taking the variate selected as an ordinary heritable variate, and not confining the heritable difference to two groups having different means. Actually, I suspect that selection always acts by a graded series of rates of death or reproduction, rather than by truncating the distribution. ...

Fisher to J.B.S. Haldane: 17 December 1930

Many thanks for your note ....

When I found that, contrary to my anticipation, you were not reviewing my book in the *Eugenics Review,* I feared that there might have been some muddle, but my enquiries from Cutler and Major Darwin both showed that they thought that nothing of the kind had occurred. I have since learnt that you had been willing to write a review, and had possibly even written one, and I am exceedingly sorry that for some reason it has never appeared.

I still think a review from you would be most valuable, and this even apart from my personal interest in how far you are willing to go with me, especially on the human part, which has not in the English reviews been given very much space. I do not think they are wrong scientifically in stressing the purely biological parts for these constitute the scientific foundation of the rest, but the human inferences, if well founded, are of such practical importance that they will certainly be the ultimate centre of interest.

Is it too late for you to consider whether it would not be worth while to allow what you have written, or what you would like to write, to appear in the *Eugenics Review*? I understand that the Editor would be very glad to have it, and I should very much regret it if you of all people contributed not one of the notices of the first edition.

Fisher to J.B.S. Haldane: 6 February 1931

I am sorry that the M.S. has disappeared.[45] I should greatly have liked to read it. What do you think, though, of putting down something on Man in particular, since a great deal of what I have written, believing it to be a single and coherent argument, has never been criticized, and therefore presumably not followed. The diagnosis of the differential birth-rate is central, and a great deal both of theory and of practice must hang on the diagnosis chosen.

J.B.S. Haldane to Fisher: [*March 1931*]

... I think it would be an excellent thing to present your results about eugenics in a more popular form. I hope you will refer to the fact that Berlin, as well as Stockholm, has now got a net differential fertility in favour of the rich. However, I take it the Malthusian parameter for *all* classes is negative.

Fisher to J.B.S. Haldane: 17 March 1931

... Do you believe the Berlin tale? The fallacies of Edin's work on Stockholm[46] are fairly easy to see, but I have not looked at the Berlin stuff.

Fisher to J.B.S. Haldane: 1 May 1931

Many thanks for the M.S. you have turned up at last.[47] I have sent it on to Moore. Naturally I find it extremely interesting, apart from its flattering aspect. I agree with you entirely that the main scientific point is to test very thoroughly the theory that social promotion is the main cause of differential reproduction. But the main practical point is to combat the idea that racial decay, or the differential birth-rate, or any other social phenomenon which we judge undesirable, is to be accepted fatalistically as the 'Will of Allah', rather than tackled scientifically like *rabies*.

Fisher to J.B.S. Haldane: 24 May 1933

As you will already know, I have been invited by the special board and by the Provost to apply for the Galton professorship,[48] and shall do so as soon as I can find the Registrar's letter on the subject. The situation is peculiar, but interesting, and I ought to thank you first for the great part that you have undoubtedly played in putting the invitation in my way. Apart from snails, which I think I can keep anywhere—and poultry, alas! nowhere, unless I can keep them on at Rothamsted, there appears to be an 'Animal house' equipped for the nurture of putrid little dogs, which should do for mice, though the rent and maintenance charge of £345 seems a little extravagant for the purpose. So if you have an overflow of rabbits or kangaroos or anything from your department I should do my very best to make them welcome. I hope you won't hesitate to convenience yourself in this way, especially as some day I might want you to wangle me a little Naboth's vineyard down at Merton.[49] Besides I think that this sort of hospitality is extremely valuable in giving members of different departments a chance of knowing something about what is done elsewhere, provided, of course, that their chiefs are not fighting about tithes of mint and cummin.

The great problem seems to be to get anything like personal assistance. I find that the lecturer in medical statistics in the department (or perhaps now it will have to be Medical Eugenics) has a whole time research assistant at his disposal, whereas the Professor seems to have a secretary up to £150 a year who may not be versatile enough to feed snails and work a calculating machine when she is not typing letters. My best hope seems to lie in the allocations for the wages of the dog-man, and especially for their food; I have great hopes of their food.

Tell me, who knows next to nothing about University organization, supposing mathematically trained lads come to me, hoping to get some sort of a doctorate by working in my department, knowing nothing, and not very willing to know anything of experimentation with living material, can I make them attend lectures in your department on genetical theory as, at any rate, one step towards apprehending the kinds of reasoning used by experimenters? And will they have any reason to believe that the knowledge so acquired will help to make their theses acceptable? Perhaps the right way is to get a geneticist appointed as outside examiner, but does the Professor choose the outside examiner? *Per contra,* will you want me to chat of covariance to babes of yours?

But instead of my writing at random, tell me when I can meet you and hear what you have been thinking about it.

J.B.S. Haldane to Fisher: 30 May [1933]

Please do not thank me in connection with your appointment. When asked my advice I mentioned a number of arguments against you, some of which were new to members of the committee. It was the merest regard for truth, and not any personal regard which I may feel for you, which forced me to add that you were the only possible candidate for the post.

There should be absolutely no difficulty about co-operation between our Departments. ... I shall be very glad to talk any details over with you any time ...

J.B.S. Haldane to Fisher: 23 March 1939

I hope to have the paper leading to the calculations of the value of α ready in about a week. I think the most interesting point in this paper[50] is that it clears up the reason why human recessives are so scarce. I never believed Levit's theory,[51] which is held by various other Marxists, that natural selection is more or less inoperative in man, any more than I believed in yours as to its social determination at the present moment.

I should be genuinely interested to know if you think there is a way round the argument developed in this paper—given that the mean coefficients of inbreeding are substantially correct, of which I have little doubt.

J.B.S. Haldane to Fisher: 25 June 1940

I enclose a note for the *Annals.*[52] ... It is fairly clear that where you have parental or sib correlations of the order of 0.8 for the age of onset of a disease you cannot be dealing with modifiers, but several different genes must be concerned. Almost all the variance is between pedigrees and not within them. It looks as if your views regarding modifiers were correct for Huntington's chorea and optic atrophy, while in Friedreich's ataxia, for example, they play a minor part. ...

Fisher to J.B.S. Haldane: 27 June 1940

Thanks for your note for the *Annals.* ...

I am a little puzzled to know what you mean by 'It looks as if your views regarding modifiers were correct for Huntington's chorea ...', as I do not take any objection to the notion of multiple allelomorphs in rare defects. ...

I think your discussion of the causes of variation in age of incidence in families is really valuable.

J.B.S. Haldane to Fisher: [*September 1940*]

Can you help me on the following question? In a series of estimations of blood constituents, the mice of genotype **A** were compared with those of genotype **B**. The means of the two groups differ nearly significantly ($P \approx 0.07$). But there seems to be a decided correlation between litter mates. If we had only one per litter of each genotype we could simply find the mean of the differences. In the data enclosed I have calculated t from the differences, giving the mice in the order of their occurrence in a table of Grüneberg's. This is illegitimate. I have also averaged each genotype. Finally I have averaged litter mates. This sacrifices some information, but seems the best method.

Is there any simple method of dealing with such a case? If so, is it published? Such cases are likely to occur with increasing frequency. I cannot find them treated in your 7th edition of *Statistical Methods.*

This place[53] has been heavily bombed. The Great Hall and Physical Laboratory are wiped out. The library has been partly burned and partly flooded. We are still carrying on, as we have nowhere to go. Do you know of any possible refuge? We only need electric lights, a wash basin, gas, and a little (very little) artificial heat.

Fisher to J.B.S. Haldane: 26 September 1940

Thanks for your note. As an emergency measure what do you think of coming down here?[54] I am entitled, without more ado, to add one to the number working in the Department, and with some ado it should be possible to get Sir John Russell, the Director here, to consent to arrangements for your assistants. Are there two at the moment?

We get daily warnings here, but no raids so far. Russell takes the reasonable view that we need not obligatorily cease work on a warning, but should place ourselves to avoid flying glass, and take cover when there is actual firing, or near bombing. Conditions for work will not be ideal, but perhaps no worse than any obvious alternative. I should be delighted if you found this possibility one you could utilize.

Your mouse problem is just the beastly sort of thing you would dig up. I mean that it involves two distinct estimates of error, between and within litters, unless you can get both genotypes in the same litter. If you can, which I can't verify from your rough sheets, then a decent test can be worked using only variation within the same litter.

Fisher to S.C. Harland: 11 October 1940

Many thanks for your letter, which I am very glad to get. Nothing could be jollier than a situation in which scientific views were discussed with the exactitude and impartiality appropriate to pure logic, for in that case any new fact is an obvious enrichment of the material available to all thinkers.

and a new argument is as good as a new tool in a workshop. We should perhaps feel grateful and gratified all round; but in fact the situation of research is rather different. Actually, almost anyone who makes a scientific advance of almost any kind is bound to be exposing, as erroneous or obsolete, views and methods formerly taught and trusted. The teacher especially who is accustomed to pontificate is decidedly reluctant to eat his words or to recast his courses. He therefore finds some excuse for not doing so by ignoring or, failing that, belittling and criticizing, with more or less astuteness, views which threaten his current stock of ideas. This temperamental factor is almost always in evidence in the earlier reactions to any new notion, and of course the publication of new findings and the discussion of their relevance is not really carried out in logical terms, much of what is said being read, and I suppose written, in the sense of a vote *Aye* or *No.*

In fact, of course, controversy even with ruffled tempers does not do nearly so much harm as might be expected, but it does enough harm to make me want always to avoid writing severely except in cases where unfair personal attacks have been made on a third person.

On the question of modifying factors selected on their own account, there is a distinction worth making, of which I do not know whether you have ever formulated it to yourself: it is exceedingly difficult for any factor to be mathematically neutral; indeed this is almost impossible, but even to be neutral enough for the incidence of such factors in a large population to be approximately as though they were neutral requires a balance of forces about as accurate as a chemist uses in the finest chemical weighings. Consequently, the factors actually used in dominance modification will necessarily be predominantly those which have some, perhaps slight, selective advantage on their own account. This, however, affords no explanation as to why dominance is modified in the right direction; the explanation lies in the additional selective advantage afforded by improvement in the heterozygotes, i.e. there is no need to postulate that those genes which make changes of dominance in the right direction do *ipso facto* enjoy any selective advantage other than that provided by the improved viability of the heterozygote.

This is presumably true of all selective effects without exception, e.g. those by which the spur of a cock was built up were presumably the most advantageous, or least disadvantageous, of those by which the same morphological change could have been brought about. ...

Fisher to H.W. Heckstall-Smith: 23 January 1957

Thank you for your pamphlet[55] and your letter of the 22nd. So far as I can see, controversy will be confined to matters of proportion, for those are very important in exciting anxieties. My own view is that damage to life, health, and property are far more important effects of atomic weapons than damage to posterity through injuries to the germ plasm, though the latter rouses the most acute anxiety to our instinctive feelings.

With respect to the latter I am inclined to discountenance exaggeration largely because the future germ plasm of the human race seems to me threatened by so much graver danger from other causes, and that stress upon the rather hypothetical damage to be feared from nuclear warfare is likely to obscure, and may even in some cases be intended to obscure, the measures we ought to take to protect future generations from these other sources of injury.

Fisher to L.T. Hogben: 6 May 1932

I am not now working on the problem you mention,[56] so please go ahead without scruples. What originally made me ignore the sex-linked case was the absence of any apparent effect in the old Pearson and Lee Father-son, Father-daughter, Mother-son, Mother-daughter correlations.

The work for these was all done about 30 years ago, and the Biometric Laboratory has never confirmed the results from independent material. This might well be worth doing. The School Medical Officers' height measurements would, after correction for age, give many thousands of the 3 sorts of pairs of sibs, which might well give an idea of the importance of the X chromosomes in human heredity (assuming the Y chromosome is of no importance, which in view of the Hapsburg lip one scarcely likes to do).

I do not think the sex-linked case especially suitable for selection, and think you altogether underestimate the efficiency of the latter. After all, quite moderate selection is known on biometrical grounds to alter the mean stature by 1 inch in a generation, say a foot in 400 years. That [the] human population has not changed at this rate is evidently due to the character not being strongly selected.

Fisher to L.T. Hogben: 25 February 1933

I think I see your point now. You are on the question of non-linear interaction of environment and heredity.[57] The analysis of variance and covariance is only a quadratic analysis and as such only considers additive effects. Academically one could proceed in theory, though in a theory not yet developed, to corresponding analyses of the third and higher degrees. Practically it would be very difficult to find a case for which this would be of the least use, as exceptional types of interaction are best treated on their merits, and many become additive or so nearly so as to cause no trouble when you choose a more appropriate metric. ... However, perhaps the main point is that you are under no obligation to analyse variance into parts if it does not come apart easily, and its unwillingness to do so naturally indicates that one's line of approach is not very fruitful.

Fisher to Aldous Huxley: 23 September 1931

I have collected three excuses for writing to you, (i) that I think you know my name already, (ii) that I have been for some years very good friends with your brother, the biologist, and (iii) that I am at present on my back regenerating discarded tissue and have been reading an old book of essays of yours, *On the Margin*,[58] with very great satisfaction.

What a remarkable series of changes you call attention to in the one on 'Accidie', and what a good example of the change demonstrable from literary sources of the habitual attitude of mind towards the same experience. I had noticed the contrast between the gracious young lady called Ydelnesse in the 'Romaunt of the Rose' and her namesake riding the ass in Spencer, but I had not at all appreciated the 'subtle and complicated' vice you describe. It is really delightful the way this melancholy sulkiness changes from a vice to a disease as the machinery of social co-operation changes from the excitation of common emotions to the pursuit of individual interests. The melancholy man who does not share your hopes and lively intentions must seem as much a traitor to all decency and right thinking as a little brother or sister who unexpectedly expresses a distaste for some gleefully anticipated game. Could one's anger at such a disappointment be other than a *moral* indignation? And I suspect that for the greater part of man's social history he has relied far more on the infectiousness of emotion than on expressed or implied contracts, for getting people to work together.

Of course, the mood only becomes a sin when it is already taken for granted that social co-operation is a binding obligation. It was not a sin in Achilles, though I suppose it would have been in a crusader taking similar umbrage. What makes it specially valuable is that the Middle Ages is just that section of our history which is most difficult to parallel in other civilizations. I suppose Accidie must have been a sin some time between Homer and Solon, but one could scarcely hope for evidence of it, and the 'Middle Ages' of the Islamic civilization were telescoped into a couple of generations under the Ommayads.

Was the later literary affectation principally attractive as an *Aristocratic* contrast to the jauntiness of prosperous mediocrity, or by the fatal allurement of a malady curable, perhaps, by sympathy and feminine graces? You notice that I reject your theory that we have a right to our Accidie.

Has anyone taken you to task for your injustice in Cardinal Maury? (p. 123). Your exclamation recalled a sentence of Gibbon: 'And, since mankind must be either compelled or persuaded to obey, the use and reputation of oratory among the ancient Arabs is the clearest evidence of public freedom.'

See how argumentative it makes one for his chief work to be, like mine, purely vegetative. Don't bother to answer unless I've recalled a vein that amuses you.

Aldous Huxley to Fisher: 26 September 1931

Thank you for your very interesting letter. I think your diagnosis is quite right and that the sinfulness of accidie was stressed at the time when individuality was breaking out of social co-operation in what must have seemed a most dangerous way. Like heresy, it was punished for being anti-social. I shall put your suggestion up to Gerald Heard, who has written so curiously and learnedly on just this question of the rise of individuality in his *Ascent of Humanity* and *Social Substance of Religion*. Once the individual has been completely separated out and is aware of his separateness, accidie, I think, becomes inevitable among those who have too much leisure. Certainly the aristocratic motif entered in at the Byronic period. Being able to afford boredom was—and I suppose still is—very distinguished. Finally there is the type of boredom illustrated by those unhappy South Sea Islanders described by Rivers—dying of ennui because we have killed the old religious purposefulness in their life and substituted mere distractions. This kind of boredom occurs nearer home; the total laicization of modern amusements, the fact that they exist only for their own sake and not with some ulterior aim in view—such as would be the celebration of some event in a communally accepted religion—this robs our 'good times' of much of their efficacity. The moment the distractions cease, boredom is apt to set in. Hence the 'continuous performance' of our movies.

No, perhaps we have no right to boredom. But after reading in your book about the effects on the human stock of a social organization based on economic reward I think we have a right to a good deal of gloom and alarm! The really depressing thing about a situation such as you describe is that, the evil being of slow maturation and coming to no obvious crisis, there will never be anything in the nature of a panic. And as recent events only too clearly show, it is only in moments of panic that anything gets done. Foresight is one thing: but acting on foresight and getting large bodies of men and women to accept such action when they are in cold blood—these are very different matters.

Fisher to Aldous Huxley: 3 October 1931

Thanks for your letter and for your sympathetic reference to the 'gloom and alarm' which, like the Djinn released from the bottle, seem to be the chief reward of my inquisitiveness. The demon is an old friend of mine now, and we are on much better terms than we were fifteen years ago, when he made so many things seem not worth doing, that I might well have thought there was nothing left. But the fact is that the more surely one realizes that the reasons for horror and dismay are not illusory, the more widespread and the more deep-seated they seem to be, the more unmitigated and exempt from natural compensation their destructive effects upon human nature, why, so much the more surely has one the rarest thing is this aimless and disillusioned world, something wholly and lastingly worth doing; and of how many of the little strumpet 'causes' that we dress up to discharge our loyalties upon, can anything like as much as that be said? I mean if we consider them as achieved and try candidly to evaluate the achievement.

I am fairly convinced that this need for something worth one's loyalty is pretty widely felt, (or sub-felt, for I suppose the subconsciousness has sub-feelings) among people naturally critical. The really impressive thing about 1914 was the eagerness with which men jumped to the conclusion that they had found something worth doing whole-heartedly. If there, sanity requires that it should be jealously guarded. And, though panic is certainly the way to move politicians, I am wondering if the mental requirements which drew educated pagans into schools of philosophy are not already operative in our own generation; and the Stoics, had they had a social policy, were certainly powerful enough to have won their way. But they were too defensive of the individual soul.

I appreciate immensely what you write on the laicization of our festivals. I do not in the least believe that merely scientific criticism of religious fables in history or cosmology is responsible for the loss of zest. The decay of interest, both in the religion, and in its festivals, must come from a failure to be moved to admiration or enthusiasm by certain ideals of human excellence. What is dreadful to think of is not the admiration of one type giving way to that of another—which, as loyal conservatives we may well dislike—but the decay of the entire power of recognizing human excellence of any sort; and certainly the later ages in Rome show as great a genius for factious mutual hatred and distrust as the Homeric poems or Chaucer show for admiring wonder.

That looks like one of the ugliest of my pot-full of bogeys.

To return to politics. Is it not a sheer gift that family allowances should happen, as far as one can judge, to be good economics? It is sheer luck, as inconsequent as a miracle; but it does suggest one alternative method to the stampede; that is to get important things done for unimportant reasons. I mean that much less real hardship would have been felt by the teachers and sailors by reason of the cuts, had the pay been simultaneously redistributed, giving each child say 10 per cent of the childless man's pay; and the conditions in French industry in respect of employment, and absence of strikes, since their system was adopted, might well make our industrialists' mouths water. What a horrid thought!

But it does look like a gift.

J.S. Huxley to Fisher: 4 May 1930

I have just finished your new book—all my spare time since Wednesday when I got home has been taken up with it—and must write and congratulate you on it. It does seem to me the most important book on Evolution which has come out this century.

I shall have to have a go at some bits of it again—mathematics is not my strong point, and quite apart from that I found some passages very obscure, if you will allow me to say so!—especially in the chapter on metrical properties.

I wish I had known you were doing this book—I would have liked to have talked over the Sexual Selection business—I have definite ideas as to the value in monogamous territory birds. Also I could give you a beautiful case of isolation creating a gene-gradient, p. 127 [*GTNS*, p. 141], viz. Sumner's Florida Deermouse. ... [*GTNS*, p. 151], E. Selous actually got observational evidence of marked differential success of male Ruffs in getting mates[59]. ... I can't see how you can omit all discussions of Haldane's papers—doesn't it come in to your scheme? You also don't mention Elton's ideas—I'd like to hear you on these. In reference to change of selection in man, I think it was Huntingdon who pointed out the enormous effect it would have to settle down to agriculture from nomadism and hunting—prudence and routine qualities would be encouraged—rashness and quest for excitement would very likely run off and join hunters elsewhere etc.—or go into the army and get killed. (This is in E. Huntingdon, *Human Habitat,* Chapman and Hall, 1927—quite worth reading).

There is also the selective effect of migration—e.g. Pilgrim Fathers weren't a random example of Britons, nor the first Australian colonists. Effect of migration on Ireland, on move to towns on country folks temperament. There are misprints ...

Again congratulations on the book.

Fisher to J.S. Huxley: 6 May 1930

I am extremely glad that you think well of my book, and want to thank you especially for writing so quickly and kindly about it. The importance which you and Haldane attach to it—and there are no two opinions in this country to which I would attach more weight—gives me much pleasure, but not a little embarrassment, for if I had had so large an aim as to write an important book on Evolution, I should have had to attempt an account of very much work about which I am not really qualified to give a useful opinion. As it is there is surprisingly little in the whole book that would not stand if the world had been created in 4004 B.C., and my primary job is to try to give an account of what Natural Selection *must* be doing, even if it had never done anything of much account until now. It struck me there was a great deal untouched in this line of country besides much confusion due to past neglect to be cleared up.

As you have seen I have often been tempted beyond these austere limitations and, judging from your letter, I shall be still more tempted in future. I should love to talk over sexual selection in relation to monogamous territory birds, some time when we can get together. Will you be saying anything about it in your broadcast lectures? You must tell me when we meet if you are with me as to the origin of sexual preference, and as to the very sweeping argument of the first chapter. ...

One thing I much regret is not mentioning Haldane's work in the preface as an example of the mathematical groundwork in biological problems which seems to me so much needed. Perhaps I should have mentioned Bernstein in the same place.

Many thanks for your other points ...

Fisher to J.S. Huxley: 24 September 1931

It has occurred to me that in our present paroxysm of crises the discussion in Section D may drift into economic topics;[60] and, in that case, you might find it worth while to have looked through the enclosed reprint [*CP* 82]. I am really rather proud of it, because it was written early in 1928 during the rising tide of fictitious prosperity and I tried to rub in that the non-rural industries would suffer in their turn, through the failing purchasing power of the agriculturists, which is just what has happened in the last two years. We are in the same position with respect to the failing purchasing power of Australia and the Argentine as New York and Philadelphia are with respect to the failing purchasing power of the Western States. Even Malthus would have recognized that the over-production of primary foodstuffs is a sign not of over- but of under-population. It may be useful to recall this in case MacBride or someone chooses to attack Family Allowances on the ground that we, or the world, are over-populated.

As someone may state or imply that Family Allowances would be an *extra charge* on industry, it may be worth recalling that they were introduced as an economy by the industrialists in the French post-war reconstruction, and the financial position of French industry compared to our own at the moment does not encourage the view that in this matter they were being extravagant and we economical.

I don't know that the subject will come up at all; but I send this brief memo. as I know how much more satisfactory it is to be prepared, even for the most unreasonable lines of attack, and I should not easily forgive myself if, when you were taking my part, some hostile zoologist had reason to think he had an opportunity of scoring off you.

I have now just had your note of the 23rd where you raise the question of introducing Family Allowances into your address. ... *If* you have time I am sure that Family Allowances as a constructive social suggestion would add greatly to the public interest in the discussion and, I am afraid, also to the divergence of biological views. To develop the subject as far as this in the short time would need a greater power of conveying ideas clearly and briefly than I myself possess, but I believe you could do it.

At least, if you try, you have my very best wishes.

J.S. Huxley to Fisher: 28 September 1931

Thanks for your letter and enclosures. I brought in something about family allowances, and I think it went off quite well. The discussion as a whole certainly attracted a very large audience, and a good deal of notice in the papers. MacBride made a long and rambling speech in which he made a bitter attack on you 'butting in', as not being a biologist! and therefore having no business to discuss these matters! ...

Fisher to J.S. Huxley: 29 September 1931

It was exceedingly kind of you to speak for me at the Population Discussion and I am glad you brought in something about Family Allowances. I was much disappointed in the newspaper accounts of the meeting, ...

I have had, however, an amusing account from Ford which he had from Baker telling me of MacBride's attack and of Baker's interruption. Ford writes with great indignation against MacBride but I half suspect he is doing me more good than harm. ...

Fisher to J.S. Huxley: 2 November 1931

I mentioned some time back that I had put together some stuff about objections to selection theory. It is at present quite incomplete and glancing at it some other examples might occur to you of the kind of thing I am combatting.

I have thrown the thing into the form it would take if I used it to replace the present preface to my book, which preface has entirely failed in the purpose for which I wrote it; for it was specially written in the hope that no reviewer could possibly review the book on it, and the majority have done so nevertheless—three sexes seem to be irresistible to them! So when a German edition was proposed I thought I'd have a shot at discussing some of the difficulties. The extraordinary thing, interesting too and half discouraging, is that in the history of each difficulty one can usually find a perfectly rational statement of it right at the beginning, while its later appearances become less and less rational, until it is twisted into some form which is logically almost unrecognizable. However, you will see what I am driving at if you look through the paper. Darwin has seen part of it and wants me to publish the stuff in some journal or review, whether I pitch it into my book ultimately or not.[61] Do you know any Editor that would care for it? ...

Fisher to J.S. Huxley: 23 November 1931

I am enclosing the paper on Dominance and a couple of others ... You will see that the dominance paper deals fairly thoroughly with the many sources of genetical evidence, but does not enter upon the broader subject of dominance as confirmation of the view that evolution has generally taken place in opposition to the direction of mutational changes, thus explaining the separation of the sexes, methods of ensuring cross-fertilization, etc., as means of avoiding undesirable recessives. This would need much more extended treatment, but is clearly the part of the story of wider interest. For the present, however, it seems best to concentrate on proving the case that dominance is an evolved phenomenon.

Fisher to J.S. Huxley: 27 November 1934

I am returning the three papers on Race, which you sent me. I cannot see anything particularly wrong about them. I suppose they should have a soothing influence.

I am glad you mention community of ancestry, which I think is an essential measure of racial similarity and, indeed, of genetic similarlity when applied to groups, rather than to individuals. However, there is room for difference of opinion even there.

I cannot think that in view of their racial tradition, our Hebrew brethren will find any permanent intellectual response in the conclusion that the word 'race' has lost any sharpness of meaning, or that it is hardly definable in scientific terms, ideas which seem attractive, only, I fancy, in the framework of current controversy.

J.S. Huxley to Fisher: 11 December 1940

To my surprise, I am finding great difficulty in getting any information, however rough, on the following point: what proportion of the adults of reproductive age in one generation produce what proportion of the children of the next generation?

I want this in some striking form for a popular article, and should imagine that about one-third produces about two-thirds. I would not mind putting down a guess and saying so, as long as I had assurance that it was not too far out. I can get lots of information as to the proportion of dependent children under 15 who come from, say, families with three or more children, but this is not at all the same thing. ...

It seems to me very curious that this has not been worked out, even approximately, as it obviously has very important selective consequences. There can be no other animal species with such a remarkable degree of differential reproduction among adults which have already reached reproductive age—and especially among adults who are actually reproducing.

You will be interested to hear that I have at last finished my Evolution book and am sending the final slip proofs in to the printers to-morrow—thank goodness!

Fisher to J.S. Huxley: 13 December 1940

I have hunted up one reference, I think the best, to the point you mention: D. Heron (1914). 'Note on Reproductive Selection', *Biometrika* X, p. 419, finds that 'approximately three-fifths of the males born die unmarried, and one-half of one generation comes from one-quarter of the married population, or from one-ninth of all the males born in the preceding generation'. Also, 'nearly half of the females die unmarried, and that half of one generation comes from one-quarter of the married, and from one-seventh of all females born in the preceding generation'. There is quite a useful diagram referring to the males on p. 420. These results are based on Australian data, death registrations 1912.

Naturally our own death registrations are useless, for they do not even require a statement of marital condition or number of children, if any, and this in spite of the relevance of these facts to the granting of probate. However, we can be quite sure that the facts are nearly the same in all civilized peoples.

I agree with you entirely that mankind must be unique in this enormous difference of reproduction among the adult and sexually mature—unless one counts in the adult but sexually imperfect social insects. Its chief importance to me lies in the fact that it supplies a medium in man for higher selective intensities than probably exist in any wild species, or at least to any long stabilized in their environment, whereas it has been constantly assumed and asserted that the reduction of the death-rates has abolished natural selection in man. I allude to Heron's conclusions and similar evidence on p. 190 of *Genetical Theory* [*GTNS*, p. 209].

It is sometimes assumed that the general fall in birth-rate must tend in the direction of equalizing reproduction, but I doubt if it has had any effect in this direction, and it might have the reverse effect.

Good luck to the book.

J.S. Huxley to Fisher: 16 December 1940

Thank you very much for your letter with the reference, which exactly fills the bill.

I entirely agree with what you say about the selective implications for man, but I had not thought out the conclusions to be drawn as regards the fall in the birth-rate, which are very interesting.

Fisher to J.S. Huxley: 5 July 1954

... About the polymorphisms,[62] I should myself stress the effect two gene substitutions may have on each other's selective intensity as the operative cause of close linkage, and it seems natural that such mutual influence is common with genes affecting the same characters, e.g. conspicuous pattern genes in the grouse locusts or *Lebistes*, and rather widely between loci influencing the same quantitative character, if such a character, as must be usual, has an optimal value.

What I felt rather puzzled about in 1930 was how, in spite of such widespread tendency to closer linkage, free recombination had in fact been retained, as is needed if different improvements are to be combined, though I find it difficult to understand how this *effect* is itself effective in promoting recombination.

Fisher to D. Caradog Jones: 12 December 1932

Many thanks for your kind letter. It is a pleasure to hear that what one has written has been enjoyed. I was, I think, very fortunate in my reviewers, but in spite of that it will evidently take a long while to make any impression on biological, or equally on sociological, thought. I should be very glad to hear, now or later, of your impression of the chapters on human selection. While writing them I felt they were growing unduly, as I had originally intended social selection in human fertility, following sexual selection, and mimicry, as a third development or application of natural selection, having, like them, special relevance to special circumstances. Whereas, in the other cases, I could take a groundwork from earlier writers, and could concentrate on critical discussion and amendment, in the human case I felt I had to justify the primary propositions, such as the heritability of fertility, whether consciously or unconsciously conditioned, and this took so much space, that I fear Chapters VIII to XII are not easily grasped as a single argument.

Again thanks for your encouraging letter.

Fisher to O. Kempthorne: 31 January 1955

I have been puzzling over your letter and paper[63] for some time, and maybe I have not got it clear yet.

I do not at all agree with the last sentence of the opening paragraph of your introduction, 'Later in 1941 Fisher showed that this is true only if the quantity Q^2/PR remains constant...'

What I said on the second page of the paper cited [*CP* 185] was, 'The direct mathematical measure of the average effect of a proposed gene substitution is the partial regression, in the population as actually constituted, of the genotypic measurement on the numbers 0, 1 or 2 of the allelomorphic genes in each genotype.' i.e. in that paper I set aside the experimental test of merely introducing more genes of any one kind in an experimental population, and measuring the change in average population value; I do this through recognizing that any gene substitutions do not merely act by substituting new for old genotypes, but that they ought properly to be regarded as also affecting the environment in which a natural population lives. Interactions with the environment are not, however, specified quantitatively in terms of the genotypic constitution of a population, but would require a full specification of the climatic and ecological situations in which a species finds itself.

For example, dominance deviation favouring, over a large number of loci, heterozygotes on the average over homozygotes, would in hermaphrodite plants favour the spread of genes having a variety of effects on flower size, colour, nectar secretion, scent, etc., and also other genes favouring self-sterility, if genes of either of these two kinds existed and were available for selection. If they are available, any improvement in the species, through increase of heterozygotes, may properly be ascribed to these secondary gene substitutions, leaving nothing over to be ascribed to the dominance deviations behind them, for these latter, by themselves, could produce no effect whatsoever on the evolution of the species; but a change in the attractions offered to insect pollinators, or an improvement in a self-sterility mechanism, would constitute such an evolutionary change.

My point here is that there is no quantitative relationship between the dominance deviation of the numerous effects first mentioned and the rate of evolutionary advance; but there is a quantitative relationship recognizable as specified in what I call the 'fundamental theorem', between the genetic variance[64] in fitness to survive due to the genes capable of influencing the frequency of cross-pollination.

Equally it should be noticed that external features of the specific environment, such as an increase in the numbers of particular species of insects, or a meteorological change favourable to wind pollination, is capable of raising the specific average through increasing the proportion of heterozygotes without any evolution being ascribable to the plant species.

Due to all this I am completely puzzled by the statement in your letter that the rate of evolutionary change may be equated to the total variance rather than to the genetic component of variance as I had done. I imagine that by 'total variance' you mean to include the dominance component and the total of epistatic components, but perhaps not the environment components in the actual variance. For my own part I think these are all in the same boat, even the last, for an environmentally induced variance in fitness, i.e. in capacity to leave a remote posterity, may, like the others, induce selection in favour of genes capable of enabling the organism to secure for itself an environment of the desirable type, and this, it seems to me, is exactly what happens as a consequence of the other non-genetic but genotypic component of variance. ...

Fisher to O. Kempthorne: 18 February 1955

I should be entirely satisfied if you cared to use the two quotations from page 56 of the 1941 paper, which seemed to express just what I mean. On your second page you say, 'I can accept the statements in your letter about secondary gene substitutions in that if the dominance deviations favour heterozygotes and hence favour secondary gene substitutions, then the resultant effects should be attributed to the secondary gene substitutions and not to the dominance deviation.'

My point is that the evolutionary improvement is due to the secondary gene substitution, and the evolutionary effects are constituted by such substitutions. It is not at all that the dominance deviations are ascribable to the secondary gene substitutions, as suggested in your following sentence.

... the only evolutionary effect, either in increased fitness or in anything else, that I can recognize as such, is constituted by the changes in gene ratio, and if by the extinction of certain insects a plant were rapidly to become generally self-fertilized and homozygous through lack of means to cross-pollination, I should, so long as the gene ratios remained unchanged, consider that the plant had not evolved but was reacting passively to its changed environment.

Sorry to be so long-winded about all this.

Fisher to M. Kimura:[65] *3 May 1956*

In considering the original statement of what I ventured to call 'the fundamental theorem of natural selection', I had, of course, considered the relation between such a situation and that in which a potential function existed, for my mathematical education lay in the field of mathematical physics. As you realize, I preferred to develop the theory without this assumption, which of course in another aspect is a restriction. Of course, I do not question that the selective intensities acting instantaneously may well be equivalent to those derivable from such a function, but I think it should be emphasized that both changes in time, that is in the environmental *milieu* and in the gene ratios themselves, that is the heritable constitution of the organism, will change this virtual function in a way that cannot be specified in terms of the quantities used in formulating the fundamental theorem.

Of course I realize that Sewall Wright has often argued as though such a potential function must exist, or as though all systems of forces were conservative, and in such systems, the idea of the mean fitness of the population has, I presume, a meaning more absolute or permanent than the mean value of the Malthusian parameter actually in being.

In answer to my question about in what respect you thought the fundamental theorem needed extension, you say that your original purpose was 'to obtain the general expression for the rate of change of population fitness'. Now, of course I purported to give such a general expression, and I should like to know whether your expression differs from mine in substance rather than only in form, and in what respect you think that my expression is erroneous. Of course I had developed the multiple allele case actually before the book was published, and have put it into the Dover Publications edition, which I hope will soon appear. I should like to be clear, however, that the expression I have obtained for the rate of change of population fitness by equating it to the variance in fitness at any instant, does not depend on the existence of any potential function. ...

Fisher to M. Kimura: 14 July 1956

... The possible interactions among different organisms can be specified either in respect of relationship, e.g. the mother yields milk well and her bull calf grows to be big, or specifiable by interaction between different genotypes in the same locality, such as you are considering, or the effects of genotypic differences on the mating system, such as I considered in the paper you refer to [*CP* 185], but I can only think of them in general as parts of the environment in which the advantage, or disadvantage, of any particular gene is determined.

For example, it has probably been widely true among hermaphrodite plants that products of self-fertilization do not themselves bear so many seeds, or have so many offspring, as the plants from the same mothers by cross-fertilizaticn. Whatever this may be due to, and of course I think a rational theory has been put forward, it will certainly have as one of its effects that the heterozygotes of any gene pair are, on the average, at an advantage compared with the two corresponding homozygotes, from a cause quite independent of the developmental sequences induced by these genotypes. This would add a component to the genotypic variance of fitness, which, in the hypothetical case of gene ratio equilibrium, would be without effect on the gene ratio concerned, and therefore on evolution, due to change in this gene ratio.

It has, none the less, manifestly had very important evolutionary effects, and these are due, and in my formula are ascribed to, variants in other factors such as might affect the size of petal, the brilliance of pigmentation, the abundance of nectar, the scent of the flower, or any other characteristic aiding, or encouraging, the process of cross-fertilization. In fact, the non-genetic genotypic component concerned would be without evolutionary effect save for the existence of variants in these other factors. In the meticulous accountancy of biometrical genetics it must be ascribed to these factors, but I cannot think it misleading to say that the widespread advantage of the heterozygote has as its evolutionary effect the development of apparatus, or of a mating system, favouring cross-fertilization, or in animals the development of separate sexes. ...

Fisher to R.S. Koshal: 7 July 1938

I will answer first the genetical part of your letter. If s parent lines had been used with the complete set of $\frac{1}{2}s(s-1)$ first cross progenies, one could pick out $s-1$ comparisons among the $\frac{1}{2}s(s+1)$ sets of samples available, using the form

$$\begin{array}{c} 2\,\mathbf{AA} + \mathbf{AB} + \mathbf{AC} + \ldots\ldots\ldots\ldots\mathbf{AZ} \\ 2\,\mathbf{BB} + \mathbf{AB} + \mathbf{BC} + \ldots\ldots\ldots\ldots\mathbf{BZ} \\ s \text{ items} \end{array}$$

These would compare the effects of the whole sets of genes **A**, **B**, etc, characteristic of the s parent strains. The comparison enables one to say which varieties give generally the best results on crossing.

In addition the material gives $\frac{1}{2}s(s-1)$ comparisons of the form

$$\mathbf{AA} + \mathbf{BB} - 2\mathbf{AB}$$

i.e. the double value of each cross may be compared with the sum of the performance of the two parent lines. The effect known as heterosis is that in some species and in some characters these comparisons would be predominantly negative; consequently their total contributes a single comparison for heterosis, or, as it may be called, for dominance bias.

There remain the $\frac{1}{2}(s-2)(s+1)$ comparisons representing the variation among the last lot of $\frac{1}{2}s(s-1)$. In Calcutta I think I spoke of these as due to epistacy, but this is a wide use of the word, and it is difficult to name the effect, if it exists, in genetic terms. Since in each comparison direct additive effects of the genes are eliminated, it clearly can only depend on the way different genes interact, and this is generally spoken of as epistacy.

I liked your analysis of the three cotton lines, showing in that case that the genetic comparison alone explained the observations, neither heterosis nor epistacy having any appreciable effect. I think this may often turn out to be the case, but the plant breeder will find it useful when departures from such a simple rule are indicated. ...

Fisher to A.G. Lowndes: 23 June 1945

Thanks for your offprints and letter. My point[66] was to stress what is sometimes overlooked, that natural selection will only explain adaptations insofar as they are effective in preserving the germ plasm of the individuals concerned. This does not preclude adaptations which are effectual through the survival of relatives, for these share to a greater or less extent the germ plasm of the individual. So the parental instincts, though altruistic, are accessible to improvement through natural selection, and in my book I do discuss how far we may think of the development of nauseous flavours in insect larvae, at least where these larvae are gregarious and not [living?] singly, without postulating that a larva, once tasted, can survive, which was the point upon which Poulton always relied. I wanted to avoid the assumption that an instinct, such as the avoidance of cannibalism, which might be conceived to be beneficial to the species, could have arisen unless it also furthered the survival of the individuals manifesting it. I think this distinction is needed to avoid the multiplicity of meanings of such phrases as 'beneficial to the species'. Of course, the instincts of carnivorous animals which care for their young must be very sharply inhibited to prevent them regarding these as prey, but natural selection would not explain any gentlemen's agreement among dogs not to eat each other.

There are a number of instances of tendencies which have been developed apparently clean contrary to the general interest of the species, while they have favoured individual survival. I think a good example of this is in the sex-ratio of polygamous animals living naturally in flocks and herds, where the economy of the herd as a whole would seem to suggest (and the stock breeder would prefer) a sex-ratio of about 5% males, but where Nature, through the action of a type of selection which I discuss in the chapter on Sex, insists on producing nearly equal numbers of the two sexes. Another and more widespread example is in the evolution of dominance to deleterious mutations, for the effect of this is merely to allow the deleterious recessive to increase in numbers, so affecting the inheritance of more individuals, while keeping the number of defectives eliminated at the unchanged level required to balance the mutation rate. Mechanisms of cross-fertilization act, at least for short-range purposes, in the same way of avoiding the immediate injury of exposing deleterious recessives to selection at the expense of allowing them to accumulate, until in many plants and animals even slight inbreeding is quite dangerous. ...

Fisher to S.A. McDowall: 19 November 1931

I am very glad you liked my old dominance paper—I think it was the 1928 one [*CP* 68] you referred to. It was quite a revelation to me when I first realized that the failure mutations, which cannot effect direct evolutionary changes, have yet left their marks so extensively on the species in which they occur. One might, in fact, make a chain of effects, (i) deleterious mutations become recessive, (ii) the recessiveness of defects makes homozygosis dangerous and gives an advantage to cross-fertilization over self-fertilization, (iii) separate sexes in motile animals and some plants, separate inflorescences in others, and devices to ensure cross-fertilization. A further development in this line has recently been found among the midges, families of small diptera, where many genera are now known to have unisexual broods, produced by male-producing females and female-producing females, which are genetically different in the sex-chromosome. Thus brother by sister matings, which would otherwise perhaps be habitual, through the short lived flies hatching out at the same time, are precluded in these species. The selection in favour of all these arrangements seems to arise entirely from the individual advantage of avoiding the exposure of the underlying recessives, for the racial advantage would rather lie in the other direction, in bringing them to light and eliminating them. ...

Fisher to A.H. Machino:[67] *9 December 1948*

The point of my contribution to the discussion of the Lysenko speech was that certain inferences could be made from the words used by Lysenko himself, and that to this extent the issue could not honestly be evaded, as it would appear Haldane would like to do, on the grounds that certain contributions made in Russia might not yet have been fully studied in Western countries, and that certain 'scientific' claims have not been exhaustively disproved.

The inference I make from Lysenko's speech, and this inference is justified solely by the excerpts chosen, is first that he is not a scientist, however cranky, in that his object is not to establish the truth, and secondly, that he is not interested in the welfare of Russian peasants, although we can imagine such a benevolent interest to be in fact very ignorant.

He is, as his address shows, an advocate and partisan, concerned to grasp power by successfully 'winning a case' before the court of appeal, represented, I suppose, by one of the political bureaux of the Party.

I do not think I can write all this over again in shorter space than that taken by my British broadcast. I imagine you are entitled to quote the latter for broadcasting to Russia, but I do not think you can leave out the quotations without missing the only point I have to make.

Fisher to J. Marchant: 24 November 1938

Perhaps the discrepancy between National Statistics, showing little or no fall in birth-rate for the last few years, and the experience of doctors lies in a change of attitude, rather than a change of practice.[68] I mean that many ignorant people who, in the past, practised various methods of birth control surreptitiously, now realize that it is proper to ask medical advice.

So far as I can judge, it is a complete, but very widespread fallacy to think of these practices as having spread from the socially upper to the socially lower classes during the last two generations. There is no sign of this, at least, in our rather inadequate data on birth-rates of different classes at different times, and I remember Dr. Brownlee producing extensive data to show that different districts, containing very different proportions of well informed and ignorant people, in fact changed their birth-rate nearly simultaneously. One must remember that the early propaganda by pioneers like John Stuart Mill was particularly directed at the poorest classes, and that the hardships entailed among them by large families have been constantly insisted on by neo-Malthusian advocates. I should say, and Heron's figures support this, that there was a clear differential fertility at least as early as 1851, and that this has increased rather than diminished ever since, but that the main feature has been a simultaneous diminution of birth-rate in all classes, approximately in proportion.

Much publicity has been given to some data from Stockholm[69] purporting to show a higher fertility among the better paid, but in Sweden as a whole it is certain that the poor have the larger families, and it is probable that the data from Stockholm are greatly affected, as in the case of other large cities, by a segregation within and without the city area between wage-earners with children living largely outside, while wage-earners without children live in blocks of city flats.

If you take family allowances in their fullest sense as meaning allowances sufficient in magnitude to give an equal standard of living to parents and non-parents doing equivalent work, then the family allowances offer no bribe for parenthood; they merely annul the existing economic bonus for refraining from parenthood. They would leave the question of procreation to be settled exclusively by considerations other than the immediate economic necessities of the family, e.g. either the health of the mother, the environment of the home, the parents' beliefs in respect of the national interest, of over- and under-population, on the opinion of neighbours, etc. The only change would be that the prudential considerations on the future economic prospects of the offspring would no longer be a motive for family limitation.

These considerations, other than that of economic pressure, seem, on the whole, to be eugenic in their action, especially with respect to health, and a confident optimism with respect to the world's future. In fact, if an effective system of family allowances were in action, I should not think of dissuading parents from limiting their families to zero if they thought that was in their own, or in the public, interest.

Fisher to K. Mather: 18 May 1934

Thank you for your long and interesting letter ...

About Sewall Wright, he has changed his ground so frequently since I first published on Dominance in 1928 that I am not quite sure what his alternative theory is supposed to be. After all, I suppose that a theory must always be an attempt to deduce some admitted phenomenon, which is regarded as requiring explanation, from causes the working of which is supposed to be understood. Wright makes a good many general assertions, many of them quite acceptable, but I cannot disentangle any coherent theory from them. This may be because I am still occasionally trying to work in points of views which he has now abandoned.

It is quite obvious that in a chemical reaction one ingredient may be present in excess, in the sense that small variations in its amount have very little effect on the speed of the reaction, while a large diminution of it would slow the reaction down. That this is probably the case with the products of some genes is shown by Stern's 'bobbed' allelomorphs. It is a relatively obvious way of producing dominance against mutations which partially inactivate the mutant genes. It might, as far as my theory is concerned, be the only mechanism by which dominance is produced, though I do not imagine that this is so. But if this were so, the occurrence of dominance would be just as much in need of explanation as if dominance were produced by some other mechanism. For the fact that one component of a reaction is present in excess implies that its speed is regulated by other components, and that mutations affecting these, if they occurred, would not be recessive, whether the mutation reduced the activity or enhanced it. On the theory of components in excess we should have to say that the organism had been so modified that the speeds of all biochemical processes were regulated only by the products of genes incapable of mutation.

Actually, I think ... much of Wright's argument turns on the very well authenticated fact that the wild type is much less variable than are the mutant types. This seems a good fact of observation which can be understood if modifiers have been worked into a system of checks and counterchecks to stabilize the normal course of development, but which naturally fail when development is in any important degree abnormal.[70] I am not at all unwilling to regard dominance as a particular case of this more general phenomenon, but I am quite unwilling to say that we understand this general fact except as due to an evolutionary process by the selection of modifiers, or that it is available on its own merits as an explanation of the particular case offered by dominance. ...

Fisher to K. Mather: 7 January 1942

... As to the *sheltering* question [*CP* 133], I imagine the disadvantage which accrues to a potential, but not incarnate, homozygote must be due to interaction of other factors with that for heterostyly itself. I do not think there is any ground for expecting in the neighbouring of the S locus an accumulation of genes having unconditionally any deleterious effect; but throughout the whole germ plasm there may well have accrued genes which react less favourably with **SS** than with the other two phases of the heterostyly factor. ...

Fisher to K. Mather: 5 February 1942

I am very glad you have taken up the discussion started by Espinasse[71], for you are one of the few people capable of doing it properly and setting the present position of genetics against its proper background. ...

As a tradition, though of course not as a science, genetics is exposed more indefensibly than you seem to admit to the criticism of being anti-Darwinian, not in the Russian sense of theological heresy, but in the equally damning sense of factiously attacking and trying to discredit the far-reaching and penetrating ideas on the *means* of organic evolution which Darwin had originated. It was not only Bateson and de Vries, but almost the whole sect of geneticists in the first quarter of this century, who discredited themselves in this way. The ideas of this period are permanently embalmed in amber in Morgan's mind. Writer after writer asserted, or implied, as though it were a demonstrable fact, that species arose by single mutations, and that selection of small continuous variations within the species was known to be inoperative pending the arrival of an appropriate mutation. Continuous or normal distributions were identified by de Vries with non-heritable fluctuation. The idea of polygenic Mendelism was frowned upon by both the biometricians and the geneticists when I published the paper you cite [*CP* 9] in 1918. It would not have been published had not the cost of publication been reimbursed to the Royal Society of Edinburgh by my friends.

I am very glad that Dubinin has grasped, as you mention, the fact that particulate inheritance, so far from being antagonistic to Darwin's main theory, actually removed the principal difficulty with which it was encumbered. This assertion was entirely new when I put it forward in 1930. Indeed, before that time I doubt if anyone had taken the trouble to understand why Darwin should have concerned himself so much with Lamarcoid effects of changed conditions and increased food as the causes of variation, although, as he shows in many passages, he was clear that, as regards *evolutionary* effect, such factors were quite subsidiary. The whole distinction between mutation and evolution latent in Darwin's thought was ignored by de Vries and Bateson, and entirely obscured throughout the infancy of genetics. ...

Fisher to K. Mather: 10 February 1942

Thanks for your letter. If you learn anything further of Timiryazev, I should, of course, be glad to hear it, though, as you say, there is nothing to build high hopes on. It is only too common, both in England and abroad, for biological writers, even those capable of meticulous care and self-criticism in matters of factual detail, to be entirely without these restraints in abstract or theoretical statements.

Levit, however, who had, I think, a central laboratory in Moscow on human genetics, was lecturing on the *Genetical Theory* very soon after its publication, and had a panel, I suppose of his students, at work on its translation into Russian. I remember being offered 1000 Roubles, apparently in compensation for the infringement of copyright.[72] I remember it because they were only available at the expense of visiting Russia where they could be expended. Anyway, my book was well known in Russia quite early.

Fisher to K. Mather: 16 February 1942

I have been reading Lewis's very useful paper on the evolution of sex in flowering plants, in *Biological Reviews.*[73] There is part of it that makes me wonder whether I really got my argument across in the section 'Natural selection and the sex ratio', pp. 141-143 in the *Genetical Theory* [*GTNS*, pp. 158-60].

If natural selection were determined by 'the advantage of the species', whatever definition might be given to this, I suppose that, as a stock breeder finds he can do very well with one bull to 20 cows, Natural Selection ought to have been expected to produce such a ratio in large herding ungulates; but it hasn't, and I think the section referred to does supply the reason. The same should, I think, be true of dioecious plants; if there were but one male to 20 females, and even if this ratio were sufficient to ensure adequate pollination of all ripe stigmas, then, on the average, every male plant contributes 20 times as much to future generations as a female plant, and the individual parent would gain great selective advantage if its style mechanism were such as to produce a high proportion of males. Setting aside small factors, such as differential viability of the sexes, this would lead to a stable sex ratio near to 50%, by reason of individuals competing to contribute to future generations, though this might be not at all necessarily advantageous from the point of view of the species as a going concern.

I make this point because, if it is right, species such as the two *Humulus* and two *Rumex* in Lewis's table do present a special evolutionary problem, and are not to be accounted for by saying that one male is quite enough to fertilize a large number of females.

If this argument *were* sufficient, the animal kingdom with its commonly separated sexes would present a very different picture.

Fisher to K. Mather: 21 February 1942

Thanks for your letter. ...

I am glad of what you say about Lewis, that he is writing to me, and to hear also what you say yourself of some of these transitory situations being, perhaps for that reason, imperfectly adjusted. This seems to me a line of thought well worth exploring.

If you were to make a survey of the whole of some extensive genus e.g. Leguminosae, classifying each species as

a) Apogamous, or effectively asexual;
b) Hermaphrodite, and strictly self-fertilizing;
c) Hermaphrodite, and normally outcrossing;

d) Seldom or never self-fertilizing owing to protandry, a self-sterilizing factor, heterostyly, etc., and
e) Dioecious;

would you get evidence that the central condition of hermaphroditism was so wide-spread, i.e. present in every taxonomic branch of the assemblage, and so common as reasonably to be thought present in all phylogenetic stems, and that both extreme conditions occurred sporadically only in isolated species, or groups of species? I do not know that anyone has systematically assembled the evidence from any considerable family or natural order. It seems to me most important for purposes of interpretation that this should be done, for, theoretically, it might be that one of the extreme conditions was more universally present in the ancestry, though continually throwing off side-shoots towards the other extreme.

Fisher to K. Mather: 3 December 1942

Thanks for sending me your article for *Nature,*[74] with which, of course, I find myself very much in agreement.

With respect to my own work, it might be worth while referring to the paper of 1927, 'On some objections to mimicry theory: statistical and genetic' from the *Trans. Ent. Soc.* 75: 269-278, [*CP* 59] where the notion of a gene acting as a switch was first developed ... .I should not like people to come to think that my interest in the modifiability of gene action was confined to, or dated from, the 1928 paper on Dominance [*CP* 68]. It would be truer to say that in 1928 it first occurred to me that *even* in respect of dominance the effect of a factor was conditioned by other factors.

Waddington does not use the phrase, but would it not be clearer if he had spoken of the canalization of the phenotype rather than of the genotype? I imagine that the important effect is always that in certain regions within the range of phenotypic expression, the phenotype is very much more sensitive to genic substitutions than it is in other phenotypically definable regions. These last regions we can speak of as buffered, or stable, while the first are unstable and appear as pathological compromises between two possible consistent policies.

It will be interesting to see how terminology develops to cope with this sort of idea. ...

Fisher to K. Mather: 23 February 1943

I am returning now this fat paper on Australians,[75] and see what you mean about pruning. Whatever may happen ultimately to the paper, I am sure it would be of service to the authors if you could give so much trouble to the matter.

Psychologically, I think—and this of course is nothing to do with the paper's fate—that they have got hold of the wrong end of the stick. I mean that the human race seldom or never notices good results, least of all from innovations, nearly all of which are done with rather a guilty conscience, just as the first inventors of printing doubtless regarded themselves as swindlers for foisting off this cheap substitute as honest-to-God manuscript. On the other hand we *are* capable of noticing anything sufficiently alarming or grotesque in the way of bad results, especially if these can be connected with anything so guilt-provoking as sexual intercourse. Many African peoples regard the appearance of twins as an accusing finger pointed at their own duplicity. Deformities, imbeciles, and albinos must be alarming phenomena to primitive parents, so long as they are unfamiliar and inexplicable, and the long period of dependent childhood in Man gives the parents a chance to fret about their causation and to exaggerate the guilt of their early misconduct. I doubt if a completely albino tribe would recognize normal pigmentation as a 'good result' of anything whatever.

To me it is puzzling that mankind should have passed through what must have been a very long phase of inbred nomadic kindred-groups, with perhaps no more than six to ten fertile women in each, without eliminating completely the animal instincts for the avoidance of incest. However, there is no doubt that they are extremely strong and wide-spread in Man and that a good many rare and alarming recessives are common enough, at least to cause occasional alarm. ...

Fisher to T.H. Morgan: 11 October 1932

I have taken, as you see, some time to consider the big book,[76] of which you were good enough to present me with a copy. I thought, however, that you would prefer this rather than have me form a hurried and therefore an inadequate opinion. I think you will agree with me that one of the chief reasons why, in spite of raising so much dust, we are not making in this generation more rapid progress, is that we do not really give ourselves time to assimilate one another's ideas, so that all the difficult points, the things really worth thinking about, have to be thought out independently, with great variations in efficiency and success, some hundreds of times.

You will not want me to say, what is obviously true, that your book will for many years be a milestone in the progress of genetics, and in its application to evolutionary problems. I should rather say something which perhaps has not been said to you before, namely that in trying to assess the effect of the book as a whole I believe you have erred in underrating the effect of Morganismus upon the interpretation of genetic facts in relation to theories of evolution. Several particular passages suggest this to me, in which you take up discussions originating about the beginning of the century, without stressing to the unobservant reader that almost every term in our vocabulary has been given a sharper definition by the *Drosophila* work, so that a statement which was merely plausibly vague in 1905 is highly precise and scientific in 1932.

This criticism, which I feel sure you will want me to state frankly, seems to me to be well illustrated by your use of the term Mutation Theory, as though the views we owe to *Drosophila*, and her devotees, were at all to be recognized in de Vries and Bateson. It seems to me that it is almost entirely through the work you initiated that we know something about the frequency and nature of mutations, and this knowledge may be regarded not only as completing the basis for a particulate theory of inheritance, but equally as destructive of the crude hypothesis of the early Mendelians, that mutations alone could 'explain' evolution.

I should bore you if I developed this further. Instead, if you really want to be bored, I enclose an offprint which has just come to hand of a lecture I gave last January to the Royal Society of Dublin [*CP* 98]. I do feel about your book, however, that you leave to us Drosophilophils abroad a lot of the explaining of how much we owe to that *genus*.

I hope you duly received $8 from me, through Dunn. Many thanks for the loan.

Fisher to C.S. Myers: 6 December 1932

... I want especially to take up the question you put to me, in your letter of 17 November, as to fertility, as this seems to be vital to the whole sociological aspect of what I was talking about.[77]

I do not want in the least to rule out voluntary infertility, whether it takes the form of celibacy, prudential postponement of marriage, or contraception. In each case the stringency with which it acts must depend, not only on the environing circumstances, but on the individual's reaction to them; indeed, this is part of what we mean by a thing being voluntary. If I want no more children, that is *my* reaction to my environment, just as definitely as though I had never wanted to get married, or as though I had never been conscious of the reaction as a personal choice, and the traits of temperament which influenced my choice must be as heritable as other traits of temperament. Indeed I imagine that by appropriate psychological tests applied, say, to undergraduates, you could pick out the traits which make for early marriage, and get a correlation with subsequent performance, in the same way as with vocational tests, or directly with size of family for that matter, though I suppose the women would be the best subjects for this. So the voluntary causes of the variations in fertility fall into line with the involuntary, and, being at the moment (for all I know, generally) much the more important, they add greatly to the force of the argument.

One may say that the richer classes practice birth control more stringently than the poorer because they are already flooded with types of temperament likely to set a high value on its advantages, and a low value on its disadvantages; whose parents and grandparents have been promoted into these classes partly for this reason. After all, it is not historically true, often as it is asserted, that birth control started in the upper classes and spread downwards. The early propaganda of the Neo-Malthusians in the '60's and '70's of the last century was deliberately aimed at the poorest strata of society, where the economic and moral case for limitation was strongest. What is true is that the practice spread quickly and far among the well-to-do, and slowly and not so far in the poorer groups.

You ask me what is 'proved'. I should say that undoubtedly Galton proved his case as far as the peeresses were concerned, and later peerage statistics show an appreciable positive correlation in the size of a peeress's family, not only with her mother, but with her *paternal* grandmother. There are also a good many other miscellaneous facts which do not square with the notion that the difference in fertility is due, even principally, to the difference of social tradition of different classes. For example, the people in the American *Who's Who* have been classified according to the extent of their education, and those with the best education have larger families than those with a poorer education. If it had been social tradition, one would have expected those with a poorer education to retain some of the characteristics of the class from which they originated, in fertility as in other things. Actually what we seem to have is merely the more rapid promotion of less fertile than of more fertile strains. Again, in mixed schools, such as public elementary schools, drawing pupils from a wide social range, there is usually a negative correlation between intelligence and size of family, whereas it appears from the Yale statistics that the children from families of 6 or more are the most capable, on a variety of tests, and the only children the least capable, that they get. Not, I imagine, because the most capable people have the most children, but because a lower measure of success will send an only child to Yale, than would be needed to send one of six or more. In fact, if you equalize the 'start in life', there should be a positive correlation between fertility and ability; and I do not think any other view makes sense of this. ...

... As far as the British statistics go, it seems that the class difference of reproduction is due to more celibacy, plus later marriage, plus more birth control; and I should be reluctant in any case to postulate three different agencies in the social environment all happening to pull in the same direction.

Fisher to R.K. Nabours:[78] *10 September 1929*

The remarkable genetic situation found by you in several polymorphic species in Tettigidae, will, it now seems likely, throw light upon a whole group of cases of polymorphism, combined with dominant variants, and little recombination of the factors. There is one group of facts of which perhaps you are already in possession, or in a position to obtain, which will have an essential bearing upon the interpretation adopted, namely the frequency of occurrence in nature of the recessive, and of its several dominant variants, including combinations of these, if such occur in nature.

I imagine that counts of 1000 wild specimens from each of a number of suitable localities would be sufficient to determine the gene ratios with sufficient precision, and possibly you have records or preserved specimens on this scale. In any case I should be very much obliged if you could let me know the frequencies observed in such enumerations as are available, and if these are not sufficiently numerous, if you could possibly arrange that collections should be made on a sufficient scale to determine the frequencies. The most important species is *Apotettix eurycephalus* (Hancock) of which the genetic data are I believe much the most abundant.

It is of course essential that the counts should be based on material the collector of which takes all wild specimens which come his way, and is not specially concerned to secure the rarer varieties. I suppose therefore that collections deliberately made for frequency determinations will alone supply satisfactory data.

Fisher to R.K. Nabours: 21 October 1929

Many thanks for your letter. ...

I had scarcely expected that the frequency of Tettigidae types would have been already determined. Perhaps I may explain the connection in which they will be of especial interest.

The species you have investigated show a relatively common recessive type, and a number of rarer dominants, the dominants usually lacking dominance *inter se*, but showing usually complete dominance to their common recessive. At first sight this genetical situation, which may perhaps be paralleled in *Lebistes, Helix*, etc., seems the direct reverse of that found in multiple allelomorph series in Rodents, and *Drosophila*, where we regularly find a prevalent wild type dominant to a number of rare recessive mutants, showing no mutual dominance. I have argued from these cases that the prevalent wild type must in some way become dominant to its rare mutant competitors, else such a rule would not continue to be observed during an evolutionary progress in which numerous gene substitutions have taken place; and I have suggested the selection of modifiers affecting the appearance of the heterozygote as a possible means of this being very slowly brought about. The cases in Orthoptera and in other polymorphic species, showing an apparent reversal of the usual phenomenon, are therefore likely to throw new light on the question.

The most severe possible test of any theory is to draw all its possible consequences in conjunction with observed facts. If any necessary consequence is found to be certainly false, the theory goes. If new consequences, not otherwise to be expected, are found to be true in fact, the theory is strengthened.

To test the theory of the modification of dominance by selection, one might argue thus. A number of colour patterns in *Apotettix* are clear dominants to the standard recessive; therefore these colour patterns are on the average somewhat more favourable to survival than that borne by the recessive. But they have not replaced the recessive in nature and must be regarded as in stable equilibrium with it in respect of numbers. Stable equilibrium is most simply assumed if the heterozygote has some advantage over both homozygous types. This agrees with the inference that the heterozygote pattern is more advantageous than the recessive, but requires in addition that the homozygote must suffer some disadvantage. Since there is no visible difference in pattern this disadvantage must be sought elsewhere, and is possibly constitutional. In testing this I find that in your matings between heterozygotes between two dominants, of generalized type **P/Q**$\times$**P/Q**, there is in fact an excess of heterozygotes and a deficiency of homozygotes, on the average of about 7 per cent. This then is a new inference not otherwise expected, but found to be experimentally verified. A very special interest of such cases of balanced selection is that they afford a unique means of measuring a selective advantage in nature. For if the three types +/+, +/**P**, **P/P** leave descendants in fact in the ratio $a:b:c$, then the gene ratio +:**P** will settle down to a stable equilibrium at the value $(b\text{-}c)/(b\text{-}a)$. If $b\text{-}c$ is due wholly to constitutional causes measurable at least approximately by survival in culture, then $b\text{-}a$ can be inferred from the frequencies in nature. The principle is one which I have often wished to apply, but have never yet come upon so favourable a case.

The full story of these polymorphic species must be exceedingly complex; they all seem to show excessively little recombination, and this I believe may be the reason why modifiers can modify the heterozygotes, but not, as would be thought more directly advantageous, modify the common recessives. This if true would depend on the rate of supply of advantageous mutations generally, and may prove later to be of greater evolutionary importance in supplying some sort of a gauge of the rate of evolutionary progress. However, this would be much too long a subject to go into in a letter which is already too long.

Fisher to R.K. Nabours: 30 December 1929

... I am very glad you raise the question of the viability of +/+. The *eurycephalus* data I worked through had too few matings involving this type to settle the question, but it is one which could be easily settled if, without neglecting the linkage work to which the bulk of your matings are devoted, a series of comparable extent were devoted to the question of viability. To test dominant forms individually to determine whether they are heterozygous or homozygous would be laborious, and probably cut down the numbers so low as to be useless, but this can be avoided by making experiments in pairs.

(a) **P/Q** × **P/Q** giving **P/P**, **P/Q** and **Q/Q**.

(b) +/**P** × +/**Q** " +/+, +/**P**, +/**Q** and **P/Q**.

A sample of 5000 young from each type of mating would then give the viability of **P/P** and **Q/Q** in terms of that of **P/Q** with a standard error about 3½% and that of +/+, +/**P**, +/**Q** in terms of that of **P/Q** with a standard error about 4%. The comparison of heterozygotes with homozygous dominants may be derived with about 5.3% standard error. I dare not suggest much larger numbers, though these would increase the precision of the comparison, but it would be worth while to breed about one-third more of mating (b) than of mating (a).

As regards particular factors, in your published data for *Apotettix*, **Y**, **O**, and **RK** showed individually significant deficits of homozygotes, but **K** alone showed an apparent but not significant excess. It would therefore be especially valuable to include **K** in such a further experiment as I suggest. For the rest I suppose one should be guided by ease of discrimination. I should certainly use single genes rather than complexes in such tests.

I have, as you suggest, material for a paper on the subject, but I feel strongly that the conclusions to be drawn may be too important to be based on gleanings from your published data, rather than on *ad hoc* experiments, in which you can assure yourself that the ratios to be determined have been fairly arrived at. Also the full advantage of the viability determinations will only be reaped in conjunction with determinations of the wild frequencies. I should be most happy to collaborate either in a joint paper or by simultaneous publication, should you find it possible to devote some of the space and time available to these points.

Fisher to R.K. Nabours: 16 August 1930

Many thanks for the two reprints, which arrived with your letter today. I am very glad to hear of your plans for collecting.

As in all observational work it will be difficult to do enough to answer all the questions which present themselves. In this case especially the difficulty will be to reconcile the claims of large local collections (large enough to give a fair idea of the frequency of the rare types), and comparison of different localities, which can only be done if each local collection is fairly large, but which is certainly of too great interest to be ignored.

After some cogitation I should guess that collections of 1000 each from 10 localities would certainly be more informative than a single collection of 10 000, and would certainly be easier to deal with than 100 collections of only 100 each. It is of course conceivable that the last type of programme could be so skilfully planned as to be the best of all, only it would need a great deal of consideration, and more knowledge than will be available before your 1930 collection is made.

I am glad you were interesed by my book. It was unfortunately written too early to include the speculations on polymorphism, which seem at present to constitute a very pretty extension of Dominance theory. ...

Fisher to R.K. Nabours: 8 August 1932

I have received a very interesting letter from your assistant on the proposed collection of grouse locusts. Unfortunately, I have lost his letter and therewith his name, so I am replying through you. I should in any case be glad for you to see my letter.

[Enclosed letter]

I received your considerate letter on the proposed enumeration of the *Paratettix* phenotypes by collections from nature a fortnight ago, immediately before my departure on a short visit to Scotland. On my return I was much disappointed to find that your letter had been mislaid: and I am therefore replying to you via Dr. Nabours and without the advantage of having your letter before me.

I am exceedingly glad to hear of the research you have undertaken, as it appears that polymorphic species, at least those showing polymorphism of the same type as the grouse locusts, offer a unique approach to some of the most fundamental problems of evolutionary modification. You will perhaps have already seen the papers in the *American Naturalist* [*CP* 87] and in *Biological Reviews* [*CP* 93], in which I suggest an interpretation of the genetical situation found by Nabours in this group. For your convenience I enclose copies of both papers. The evolutionary history is likely to be in many ways more intricate than that which I have suggested and your researches may well open up unexpected developments. All that I have attempted is to sketch the broad features in outline.

There are in Nabours' published experiments strong indications that the homozygous dominant is somewhat less viable in the conditions of culture, and presumably also in nature, than the corresponding heterozygote. But this may, I think, be ignored in estimating the gene ratio. Thus, even if a particular dominant phenotype appears in as many as 36% of the sample taken, this leaves 64% as recessives, or 0.8 as the proportion of recessive genes, leaving 0.2 for the dominant genes and only 4% homozygous dominants on the assumption of equal viability and random mating. Even wih this high proportion, then, eight-ninths of the dominant phenotypes captured will be heterozygotes and it would make very little difference to one's estimate if the 4% of homozygotes had really been depleted by about a twelfth, owing to lowered viability. As far as this is concerned I believe the gene ratio could be inferred with confidence from the frequency observed in the sample.

As to the accuracy with which it could be determined, if the sample consisted of 1000 insects a count of 640 recessives (in respect of any one factor) would be affected by a standard error of about 15. The proportion of recessive genes, and therefore also of dominant genes, would have a standard error about 0.01, and the gene ratio, 4:1 in this case, would have a standard error little more than 5% of its own value. This seems a very satisfactory level of precision. The point of determining the gene ratio lies in its being equal in a state of statistical equilibrium to the ratio of the selective disadvantage of the two homozygotes, compared in each case with the heterozygote. Thus, if in any particular case the dominant homozygote is at a selective disadvantage of 8%, owing to inferior viability, and this is the average value I find from Nabours' data on *Apotettix*, then a ratio of four recessive genes to one dominant gene would indicate that the recessive genotype in nature was at a net disadvantage of only 2%, and to determine so small a quantity with a standard error of only about 5% of its value would be beyond the precision even of laboratory experimentation and almost infinitely beyond our very crude powers of detecting selective advantages in nature by direct observation. Obviously a means of detecting in nature selective intensities of this order, and I suspect that the intensity of natural selection is seldom much greater, would be an enormous step towards putting the theory of selective adaptation upon a quantitative basis. It would, for example, be of the very highest interest if you found that the proportion of dominants, and therefore the selective advantage of the colour pattern, varied from place to place, for this would open up a whole new field in the quantitative study of ecological conditions. The subject may, indeed, well prove to be of astonishing intricacy, but it will be a great step to have opened the door to its exploration.

If everything were going to be as simple as the example I have written about above, I do not think difficulties would arise in the interpretation of smaller samples of 200 or 300, if it happened to be difficult to collect the larger number. The main difficulty I can foresee is that the multiple dominants may either be double heterozygotes in repulsion or in coupling, and, owing to high linkage, these latter should be regarded as dominant compounds almost as stable as the single dominants, and existing therefore with a frequency appropriate to the selective advantage of the compound phenotype (and the selective disadvantage of the doubly homozygous dominant) which may not be simply related at all to the selective advantages of the simple phenotypes of which they are compounded. It may be that dominant compounds in coupling are really rare in nature, in which case my anxiety on this head is groundless, but, if not, the situation may need a rather intricate discussion and it might prove very advantageous to preserve multiple dominants alive, or at least a sample of the commoner compounds, with a view to testing their genetic constitution. But this, though it would greatly aid the interpretation of the sample, may prove to be impossible in practice.

I can only wish the best of luck to your hunting and hope perhaps I may meet you and Dr. Nabours at the Genetical Congress at the end of this month.

Fisher to R.K. Nabours: 22 February 1933

I have your interesting letter and enclosures. May I say at once that you put your proposals in such a way as to ensure that I shall co-operate with the greatest pleasure. I hope you will act, as it were as editor, receiving notes from me from time to time, and deciding what to do with them, i.e. inclusion in a joint paper, or leaving over for separate publication. I enclose three notes at once, on the remote chance of being in time for a small modification of your paper for *Genetics*. I fear, however, that even if you agree entirely with me, my notes will be too late.

Fisher to R.K. Nabours: 27 February 1933

I enclose another note, the last probably for some little time, this time on some associations in *Paratettix cucullatus* and some inferences from them. I understand that you have a body of breeding data, hitherto unpublished, which you intend to send me next June. In the meantime I should be glad to have offprints of all your previous publications on the grouse locusts, so far as you can spare them to me, with a bibliography of any that you cannot spare, or perhaps, better still, an inclusive bibliography, so that I shall not miss the point of any new information that becomes available. I should particularly value the offprints as with these I could use what time I have to the best advantage; and the data in them may suggest further inquiries which the original material in your possession may be capable of answering.

I should like, when I have done with them, to present the collection of identified phenotypes which you have sent me, to the Natural History Museum in this country, but before doing so I should be glad to be sure that this step would meet with your approval.

Fisher to R.K. Nabours: 22 March 1933

I was afraid my notes could not be got to you in time for the insertion of any reservations in the *Genetics* paper.[79] I can entirely sympathize with your desire to get an additional note printed in time for circulation with your reprints, for whenever I have seen reason to modify or abandon a scientific opinion, I have been extremely impatient to put myself right in public.

Nevertheless, looking at the thing dispassionately I do not see in this case much need for haste.

I had supposed that, in the event of you and Sabrosky finding my notes convincing on linkage in *Acrydium arenosum*, that we might take up that topic later in a joint paper, perhaps after further experiments had made the evidence more decisive. The fact that you are giving up experimenting with this species, however, is a point in favour of publishing at once, and how we should do this depends, I think, on how fully you and your colleague accept the probable validity of the alternative interpretation of the linkage data which I have based on your experimental observations.

Provided you find yourself in agreement with my general conclusions, that is that there is a single long, and probably linear, linkage group, the physical basis of which *may* be a single chromosome, but may again, possibly, be several chromosomes, more of less frequently associated in transmission (e.g. by occasional attachment) then I believe the best course would be for you to incorporate my arguments and calculations in a supplementary note under our joint names, to be published in *Genetics* if the editors will expedite the supply of offprints to you, or in the *American Naturalist* if they would supply the stuff quicker. This would have the advantage, which separate publication by me would lack, that it would not give the impression that, after considering the evidence, we took different views of its interpretation, when, in fact, as I am now postulating, we agree entirely as to the main inferences. I should, therefore, be perfectly content, if, merely to save time, you were to embody the chief points of my letter in a short note to either of these journals, if necessary without delaying even to let me see the proofs.

With respect to your application to the National Research Council, I shall, if consulted, do most heartily all that I can to forward it. For, confident as I was two years ago that the direct determination of the frequencies in Nature of the forms of polymorphic species which had been subjected to a sufficient genetical analysis would throw a direct light on problems connected with the evolution of dominance, now that I have seen your data for the collections of last year I am more fully convinced of the richness of the biological field opened up by such observations.

Assuming that the long linkage group in *Acrydium arenosum* is homologous with the very short linkage groups of most of the other species it should be possible to throw new light on a very important problem, to which I have found, so far, no satisfying solution. For on this view it is probable that in this species, unlike most of the others, crossing over has become progressively more and more frequent in all parts of the chromosome. Now a selective agency producing progressively closer linkage has attracted my attention for some years, and is very demonstrably present in the species for which you have counted a sample of the wild population. Such a selective action is always at work when two factors in the same linkage group are both in equilibrium in such a way that each greatly affects the selective advantage of the other. Your data supply a great abundance of cases where the frequency of one dominant is largely influenced by the presence or absence of another so that this particular agency, acting constantly towards closer linkage, must be particularly active and widespread in the grouse locusts. Such a supposition accords perfectly with the fact that in most of your species the linkage of the factors governing polymorphism is found to be extremely close. Now I have never satisfied myself as to what agency in Nature usually counterbalances the action of the agency considered above, so as to maintain any recombination at all among linked factors. Some selection in favour of looser linkage must be exerted by progressive evolutionary changes, though I have never been able to see how this could be great enough quantitatively. This linkage loosening effect might, I suppose, be much enhanced in a species which had recently experienced great changes in environment either by spreading into new habitats or by its ecological situation, including its predators, being much affected by human occupation. And some such circumstance may afford a clue to the case of *Acrydium arenosum*.

Perhaps the ideal form of selection for loosening linkage in general would be one in which one set of pattern combinations was highly selected for a few generations and a totally different complementary set were just as highly selected a few generations later. Seasonal selection, e.g. fertility in summer versus viability in winter, might perhaps really work in some such way, but if I am right in supposing that *Acrydium arenosum* is exceptional, and isolated from the others of its group in respect to its linkage, I should be inclined at first to guess that the cause of its exceptional character should be sought rather in some transient and exceptional circumstance of its recent evolutionary history. A good guess here which turned out later to be verifiable might, I think, lead to quite a big step forward.

I am exceedingly glad to hear there is now a prospect of collections from Southern Mexico especially in view of the possibility of bringing them into comparison with the genetical data already in your possession on *Apotettix*. I believe, however, that you have also secured perhaps equally extensive genetical data of some other species which, having been published more summarily, have not yet given an opportunity of verifying the deficiency of homozygous dominants found in the *Apotettix* data. I think it would be very desirable, both for its own sake and for the sake of detailed comparison with the frequencies in Nature, if at least the matings giving information on this point could be sorted out.

Fisher to R.K. Nabours: 20 June 1933

I am exceedingly glad to hear that the plans for the collecting trip in Mexico are now to be fulfilled. I wish you the very best of luck, and hope you will be able to make big collections at a variety of localities. These should be extremely instructive.

I hope before you go you will be able to send me the breeding data on *Acrydium arenosum,* and any other species, in which there are data bearing on the viability of the homozygotes. I much want to compare these with the frequencies in Nature.

Fisher to R.K. Nabours: 20 September 1933

I enclose:

(A) A discussion of the association of Mahogany (**My**) and white (**W**) in *Acrydium arenosum.* The full details of the calculation would be extremely tedious, and even what I have given is perhaps too much; the principle of using inequalities does seem, however, to be worth putting on record. I conclude that +/**My** individuals must have a low viability in Nature to the extent of about 42 per cent elimination, and that the association observed cannot be explained by differential fertility alone. The discussion is incomplete until you can tell me what your breeding experience has been with **W** and **My** in the linkage tests. The questions which need answering are:

(i) Are your experimental progenies consistent with the view that **My** is eliminated in comparison with + to the extent of as much as 42 per cent, and in comparison with **W My** to the extent of nearly 50 per cent?

(ii) If not, the balance must be made up by elimination in Nature due to causes not operative in the genetical material.

(iii) Is there any indication of reduced fertility of **My** individuals? A list of all broods or matings involving **My** would enable me to finish the discussion.

(B) A discussion of the same species, logically prior to (A). The chief point here upon which I should like supplementary information is as to whether the observed presence of any other dominants could mask the presence of **W**. If this is not possible, I think the conclusion of a selective aversion of **W** from most of the other dominants is well established, and it is interesting and important that this selection seems to act in alternate generations on the summer brood.

(C) A discussion, much of which I think you have seen, of *Paratettix cucullatus.* ...

I have a good deal more stuff, but am sending this so that we can get on with it bit by bit.

Fisher to R.K. Nabours: 7 September 1938

Very many thanks for your letter of July 11th. I am enclosing a short list of papers on grouse locusts which I do not possess and which I should be glad to add to my collection.

This year, at the British Association, I took the liberty of discussing the data you obtained with one species, *Paratettix texanus*, in your expedition of 1933, using your facts as a demonstration—which I think they validly are—of the existence of high selective intensities in wild conditions. I had been feeling, like you, that it was time the publication of discussion of these results was begun, and I thought, for my own part, that research would be furthered by the knowledge of how much you had succeeded in doing. If you think it fitting, I propose to publish, from time to time, papers on different aspects of the data which you sent me, with the obvious acknowledgements for this kindness, and with the quite unabashed hope that you will send me more when you come by it.[80]

Perhaps I told you that I tried to breed the two British species in this Laboratory, but was unsuccessful. Perhaps I shall try again later if I have the opportunity.

Fisher to A.J. Nicholson: 5 May 1955

Thank you for your letter. ... The difference in the matter of adaptation is indeed, I think, rather fundamental, for I feel sure that Darwin would never have made his discovery had he not been remarkably strongly impressed with the reality and intensity of adaptations. It was, I think, only the fading of this impression towards the end of the nineteenth century, which opened the door to theories of de Vries' 'mutation theory' type.

Fisher to J. Rasmusson: 8 August 1933

I was very glad to have your offprints and especially the Contribution to the Theory of the Inheritance of Quantitative Character.

With respect to yield, I am sure you are right that an interaction in the sense of a mutual inhibition of quantitative effects occurs in the neighbourhood in the maximum yield obtainable. I do not, however, like to apply this explanation to a character like plant height, which I am sure could be much increased in the case of cereals, at the expense of yield, if anyone cared to select solely for this character. But the delayed inbreeding effect, for which good published data seem almost lacking is certainly as recognizable in height as in yield and I wonder whether you have considered from this point of view the delay introduced in species, perhaps of recent tetraploid origin, in which many of the deleterious recessives occur as duplicate pairs or triplicate trios.

I am inclined to suggest, in fact, that good data on progressive inbreeding might in some characters afford a basis for estimating the proportion of recessives which belong to duplicate pairs, but this calculation would only be valid if interactions could be neglected entirely.

When you have time let me know what you think about this.

Fisher to J. Rasmusson: 1 January 1934

I have just received your very welcome letter of December 21st, but have scarcely considered all the good points in it. I am very glad that we do not really disagree as to the possible influence of duplicate factors, and its relation to interaction, which term I have been inclined to think of rather physiologically than genetically, if such a distinction may be permitted. I mean that the effect on the gene might be expressible to a good approximation in terms of some phenotypical quantity, such as the height of plant. At different heights then, the gene would have different effects, but at the same height much the same effect by whatever complex of other genes that height is determined. This would be what I think of a physiological kind of interaction, but it might be also that the effect of a gene is expressible to a good approximation in terms of the other genes present, or some few of them, and not simply related to their aggregate phenotypical expression, and this I would call a genetical interaction. Some day you and I must devise experimental procedures fit to disentangle these two possibilities.

I do not at all understand Haldane's remarks about 'Dominance Theory'.[81] I am in doubt, as I suppose all good men of science must be, in the sense that there is very little that I would wish to be dogmatic about, but I am more firmly convinced than I was when I wrote in 1928, and not less firmly so, as to (1) the modifiability of dominance, (2) that most mutations now recessive have become so progressively since their first appearance, (3) that the dominants in polymorphic species produce external effects which are beneficial and balanced in nature by a lower viability in the homozygote, (4) that most of the so-called dominants in poultry are really quite incompletely dominant. There is a great deal more that I should like to be sure of, especially in relation to the complex linkage systems in the polymorphic species.

I was interested in re-reading East and Jones's *Inbreeding and Outbreeding* to see what I had overlooked, that in 1919 they already felt the need of an evolutionary explanation for the great excess of recessives among mutations, and suggest that natural selection has eliminated those types which would be most inclined to dominant mutations. They do not, however, discuss numerically the selective intensity available to alter the mutation rates, and indeed such a selective action would really be trifling in magnitude for mutation rates not much higher than one in a million. It might, I think, be reasonably argued that the type of selection suggested by East and Jones provides the reason why mutation rates in general do not seem as high as one in a thousand, or one in ten. ...

Fisher to C. Tate Regan:[82] 7 February 1927

Many thanks for your letter. ...

Re Mendelism and Evolution, I will not inflict on you a full argument, but put more briefly a few points on which I should particularly like to have your opinion, and which can be enlarged upon if they interest you.

As you know, I regard the 'saltation' view as a pre-Mendelian preconceived idea which has led to a quite erroneous interpretation being put upon the bearing of Mendelian laws of inheritance upon evolution theory.

Where the Mendelian facts seem really to help is on the questions of variation, discussed in the first two chapters of the *Origin*; and here, I suggest, they require a somewhat fundamental rearrangement of ideas. About 1857 the idea crossed Darwin's mind (letter to Huxley, *More Letters,* Vol. [1] No. [57]) that inheritance might not be of a 'blending' but of a 'particulate' character. Possibly sexual dimorphism suggested the idea, but it was not followed up, and the reasoning of the Chapters referred to, and especially of the corresponding sections of the earlier essays, is based on blending. As I understand it the following argument is developed (I should immensely like to know if you think I have reproduced it rightly); by pure blending inheritance sexual reproduction will rapidly produce uniformity (in modern terms the variance will approximately be halved in every generation); consequently variation must be ascribed to the almost contemporary action of external conditions, the effect of this action being much influenced by the nature of the reacting organisms. Great variability is shown by domesticated animals and plants of very different kinds; consequently we may look for pecularities in the environment common to all domesticated species as probable causes of variability. The two peculiarities which seem to be common to all cases are 'changed conditions' and increased food, with crossing of varieties already formed, which is regarded as acting in a manner analogous to changed conditions, as a secondary cause.

One difficulty here did not escape Darwin; comparing those species which have been longest domesticated with those more recently domesticated, the former seem to be not less but more variable. But the great change of conditions took place long ago, and the food cannot have continued throughout the whole period to increase greatly. It is inferred that there must be some delayed or cumulative action upon the reproductive system which shall explain this fact.

In order to apply selection theory to wild species, it was necessary to show that they, like domesticated species, actually showed heritable individual differences; on this point Darwin had little direct evidence, especially when the first chapters were sketched out in the earlier essays. But, if the cause has been rightly assigned for the case of domesticated species, it can be argued that occasionally in nature the conditions change abruptly, and sometimes increased food will be available, and so to infer that analogous heritable individual differences will be produced. All this inference can be placed on a definite basis of observation by showing that the wild species do in fact show individual heritable differences.

What difference will it make to the above argument if we replace blending by particulate inheritance? First, whereas in blending inheritance heritable variability will only be maintained if almost every individual of every generation is a mutant (shows or possesses heritable novelties), in a particulate system there is no inherent tendency for the variability to die out. The genes will merely be recombined in each generation with a total variability almost unchanged. Two causes may be pointed out which do tend towards uniformity: (i) random survival, and (ii) selective survival. With random survival a gene will occasionally become exterminated by chance; the effect of this on the variance (which has been thought to be very great by the Hagedoorns) may be easily calculated, and I find that if n individuals reproduce in each generation, the variance will be halved in $2.8 \times n$ generations.[83] This will be an enormous time with most species, and the effect in any case is quite negligible compared to that of moderate rates of selection. Selection does really produce a tendency to uniformity, and this must be counterbalanced by occasional mutations. I have made some calculations to get an idea of the order of quantities involved. Take mean selection rates at 1%, representing that owners of a particular gene leave on an average 1% more or less offspring than owners of its allelomorph; take a population of only a million parents of each generation. Then if one in a million of the offspring is a tolerably good mutant, the number of factors maintained in the species will not fall below 100. By a tolerably good mutant I mean one which is not quite hopeless, but which in certain circumstances, or in certain genetic combinations, may be advantageous, but on the whole is neutral.

In interpreting this last calculation one may note [the following points]. (i) 100 factors form a somewhat ample reservoir of heritable variability. The number of pure breeding genotypes is 2^{100}, the number of heterozygous types bringing the total up to 3^{100} (48 figures in decimal notation). A population of a billion or so can only test a minute fraction of such combinations in each generation. By gradually varying the gene proportions, combinations which at first would be hopelessly improbable in a population of 10^{12}, would be made quite frequent, and vice versa so that continuous progressive evolution of the specific type would not have to wait upon the occurrence of fresh mutations. If mutation were altogether to cease, evolution would still go on carrying the species mean far beyond the original limits of individual variation, though of course in this case progress would ultimately cease when the supply of variance became exhausted.

(ii) Mutations themselves must be much more frequent that 1 in a million. The measured mutation rates for individual factors in *Drosophila* and Maize are of the order of 1 in 10^5, and there are evidently some thousands of different mutations possible. Probably about 20 million fruit flies have been examined from experimental cultures and at least 500 mutants (of the limited class which are useful to geneticists) have turned up. The lethals are distinctly more numerous; in view of these facts it does not seem improbable that mutations of the equally limited class designated by tolerably good should appear once in a million new individuals.

(iii) The population number of 10^6 parents in each generation represents a somewhat small species. I suppose most species lie between 10^6 and 10^{12}, though some, such as some of the millipedes, certainly exceed the latter figure. The larger the population the less frequent need mutations be to maintain a given stock of segregating factors, or in other words, with the same mutation rates the larger will the variance (when equilibrium is attained) be.

I suggest that if Darwin had ever recast his argument in terms of particulate inheritance he would have perceived at once the solution of the delayed or cumulative effect of domestication upon variability, namely that existing variability is due to mutations which may have occurred at any time since the first domestication. The greater variability of domesticated species would then be due not necessarily to any change in mutation rates, but to the greater chance of the survival of oddities under domestication. The increased variability found after crossing distinct varieties finds an obvious explanation, which throws much doubt on the analogy between crossing and changed conditions. The emphasis laid by Darwin upon the view that the most important effect of changed conditions was to produce a general variability through indirect action on the reproductive system, while he could only find slight evidence of direct action with a uniform heritable response, accords with the modern view that environment seldom or only with difficulty acts in determining specific mutations, while it is all-powerful in determining whether mutations in general shall or shall not survive and contribute to the general variability.

The main feature which distinguishes the particulate from the blending theory of inheritance is the great rarity of mutations in the former, and their extreme frequency on the latter theory. The exclusive applicability of the former theory even to cases incapable of Mendelian analysis, such as the quantitative normally distributed characters which seem to blend, like human stature, is shown by a variety of facts, of which the only one I need mention is their behaviour in pure lines. Johannsen has reported two heritable mutations among many thousands of his beans, but apart from these, heritable variability appears to be totally absent, selection over ten or more generations producing no visible effect. Now in blending inheritance almost all the heritable variability is less than 10 generations old; so practically the full heritable variability of the blending type, if any existed, would be available. I conclude that the inheritance appears to be exclusively particulate.

Now for your vertebrae![84] In herring samples only 3 or 4 vertebrae numbers appear, but these are distributed numerically like grouped normal date; i.e. they suggest an underlying continuous variate of vertebra potentiality which can only express itself in development to the nearest whole number. The *Zoarces* inheritance tables strongly confirm the same view, and Schmidt's diallel experiment with fowls seems to prove it conclusively with this group. In the latter the potential value deduced from averages of offspring may differ by more than half a unit from the actual, which is what would be expected if either developmental environment played a part as in human stature, or if Mendelian dominance produced a discrepancy between the parental genotype and its average expression in the offspring. In *Zoarces* the fact that the fraternal correlation is higher than the parental is direct evidence for Mendelian dominance.

In groups in which all or nearly all the individuals have the same vertebra number, two views are possible: (i) there is no genetic variability, (ii) neither genetic variability, nor the variability of the developmental environment, is sufficient to produce frequent departures from the central integer. The first view is improbable in view of the previous conclusions, because a mutant gene affecting vertebra number potential, unless it have other effects, will be exempt from selection, and consequently such mutations as have occurred in the past should accumulate, at least so long as the vertebra number is not actually changed.

If we take the second view, heritable individual variation exists in respect of the tendency to produce a given number of vertebrae, and the species is therefore potentially plastic in this respect. Supposing the mean of this distribution coincides with the modal integer (which of course is not the case in herring samples), one would have (i) if the S.D. of the distribution was 1/6 of a unit, only 3 exceptions in a thousand individuals taken at random, (ii) for 1/8 of a unit only 63 in a million, (iii) for 1/10 of a unit only 1 in two million, and so on. Very large counts would be needed to exclude these possibilities, which would, however, supply a *point d'appui* for selection.

Here I expect you to protest that in the case I have sketched there would be no reason for a large assemblage of related species to have the same number, but that more probably each would find it convenient to fix upon its own optimum number. The agreement of many different species is, in fact, an argument for genetic invariability. The case is singularly like that of the neck vertebrae in mammals. If I make a suggestion, it is one which I confidently expect you to be able to obliterate, but I hope you will consider whether it cannot be replaced by a better informed suggestion of similar effect.

My suggestion is that a certain extra-stability in respect of meristic changes might be expected in species, because it might reasonably be anticipated that the introduction of an extra vertebra should cause some degree of disorganization in the associated structures, attached muscles, nerves, blood vessels, etc., and even if there were a slight advantage to be gained by a complete reorganization on the basis of one more vertebra, it might well be that such slight advantage might be less than the disadvantage suffered owing to such disorganization in any individuals which happened to have the higher number. I imagine that in species such as the herring with variable vertebra numbers the morphological repetition of associated parts is complete, as far at least as can be traced morphologically, though even here one cannot be sure that all quantitative physiological adjustments, such as blood supply and nervous reflexes, have been completely coordinated. The occasional occurrence of fused vertebrae is an example of a partial morphological failure. In species with more constant vertebra number such disorganization is perhaps more confidently to be expected, if any individual happens to develop an abnormal number of vertebrae, because the developmental mechanisms, which must effect such readjustments, can have less opportunity of being perfected by selection.

Of course, I imagine that the selective differences both *pro* and *con* are exceedingly minute; modification follows so rapidly upon any pronounced selective advantage that the latter can scarcely ever come into play.

If there is any truth in this view it would follow that conservatism should often be the rule in meristic matters, in spite of the existence of heritable variability in the innate tendencies; but that if ... any pronounced change in habit, especially one affecting the use or attachments of the musculature, should be in progress, the merely conservative tendencies would cease to act.

Can you tell me if such modifications of associated structures are in fact found in the neck of sloths, or in the flat fishes, or other examples among the fishes of a break away from the conservative tradition of the parent stock?

I have not been so brief as I had hoped, but, believe me, I have put a great deal, through attempted brevity, much less convincingly than it ought to be put. You will, I am sure, not condemn any part of the argument on slight verbal grounds, but I should be pleased to explain any point which I have left in too hopeless obscurity.

Fisher to C. Tate Regan: 24 March 1928

Perhaps you will remember writing to me some time ago about fish vertebrae, when I suggested the possibility that variation was kept within bounds by the extreme variates being more frequently abnormal in development.

I had not then any numerical data, but put forward the possibility solely on the group of facts which you put before me. Since then, by the kindness of E. Ford at Plymouth, I have some data for herrings which bring out the point very beautifully (*Journ. Marine Biol. Ass.*, XIV, 413).

Ford has 95 fish with abnormal skeletons and nearly 7000 normals for comparison. If each element in a double or triple formation is counted as 1 vertebra, the means of the two groups agree closely, but the variations do not agree.

The abnormals are relatively infrequent in the central classes 55 and 56, which comprise about 90% of the fish, while they show an excess of frequency in classes 53, 54 and 57, 58. This seems to demonstrate, in the herring, the effect I postulated. It is well shown by the percentage abnormal in each class:—

Class	53	54	55	56	57	58
Percentage	46	4.1	1.2	1.1	2.6	10

You will see from this that there is a tendency for the rarer genotypes to produce abnormalities; and this, I suggest, explains the great constancy of vertebra numbers in groups in which no variations have been observed, without postulating the absence of genetic variability.

Fisher to C. Tate Regan: 3 April 1928

I am a little puzzled by your last, as you have not, I think, referred to the correspondence of last year. Very briefly the point is this. In the absence of evidence to the contrary, the Darwinian assumes that every character is affected by hereditary variations. The constancy of number in a meristic series in any one species is no argument against this view, for the heritable variation may have effects small compared to one unit; but, an assemblage of such species would be a difficulty, unless there were some tendency always or usually in action eliminating meristic variations as such. It seemed not improbable that such a tendency should exist, but if so, one might expect to find that malformations were more frequent in conjunction with rare vertebra numbers than in conjunction with common ones. The fact that this is so in the herring confirms what seemed at first sight to be a hazardous conjecture. This view of meristic variability has the advantage that it admits of the accumulation of heritable variance and of consequent changes in vertebra numbers at periods in which the reorganization of structures associated with the skeleton is in progress.

Fisher to C. Tate Regan: 12 April 1928

I am afraid you have got my views inside out, as I suggested that the constancy in vertebra numbers was due to the heritable variation being less than one unit in extent, and have been chiefly concerned to show how it is possible for it to have been kept so low. I have had the evolutionary part of my long letter of last year retyped so that you may have a copy by you, if you care to reply to this. I should be exceedingly glad to know if the attachments of the musculature, or other associated structures, do in fact show signs of modification in the groups which have broken away from the 24 vertebrae tradition.

Fisher to O.W. Richards: 21 February 1927

I was glad to get your letter, but am sorry my pamphlet[85] was so obscure. I have evidently failed altogether to make clear the conditions for the initial kick-off. I do not know if you have ever had to select animals or men for a specific purpose. People who have to do so usually have their own little fads and preferences; a man who wants a good milking Shorthorn will feel if the shoulder blades are thin, and Capt. Fitzroy disliked the shape of Darwin's nose (was it not as an index of lack of determination!).

Imagine a genealogical census of all the members of a species in 1927, and ten generations before, say 1915. To every mature male of the 1915 enumeration there will correspond 0, 1, 2, ... descendants in 1927, with some millions in each of the principal classes. I imagine that these classes will be differentiated to a minute extent in every measurement you could make, and in growth curves, colour, seasonal responses, etc. In general, every characteristic will be either positively or negatively correlated with survival (zero is but a point of zero measure). If any one of the positively correlated characteristics is conspicuous, and if the conditions at the mating are such that some only of the males mate, or mate with different frequencies and at more or less favourable times, according to their success in exciting a physiological response in the females, then those females who by reason of coyness or differential excitability in fact succeed in mating with the better adapted males will themselves be more heavily represented in future generations, and their selective taste or differential excitability will be more and more strongly represented.

There is no necessity for a simultaneous competition, though this must often help. The differential excitability might show itself in the female, as she matures, being ready to mate with the more attractive males earlier than she would be with the less attractive.

In your second paragraph, why do you suppose that the difference in display should be *outweighed* by variations in maturity and environment? This implies a negative correlation, else such variations will on the average be equally distributed between the two scale pans; such differences would dilute, but not neutralize the effect of display. The evidence that the secondary sex characters are suddenly developed agrees well with the view that they are due to a runaway process[86] in which each increase in the secondary male equipment produces increased *selection* in the female temperament, and vice versa, so that both changes must go on at increasing speed until the conditions (ratio of sexes at mating, natural selection, etc.) are altered. For the same reason one would expect very seldom to catch the runaway process actually at work, just because it works so quickly when everything is favourable. In the majority of cases some check must already have supervened, and if this check is detected it may be used, quite illegitimately, as an argument that the structures observed are not due to sexual selection. ...

Fisher to J.A. Fraser Roberts: 18 January 1935

... There is one point in which Hogben and his associates are riding for a fall, and that is in making a great song about the possible, but unproved, importance of non-linear interactions between hereditary and environmental factors. J.B.S. Haldane seems tempted to join in this. What they do not see is that we ordinarily count as genetic only such part of the genetic effect as may be included in a linear formula and that we make a present to the environmentalists of such variation due to the combined action of genetic and environmental causes as is not expressible in such a formula. Consequently, the more important non-linear interactions were, the more thoroughly would we underestimate the importance of the genetic factors. This is, of course, another point in favour of speaking of the residue as non-genetic, rather than as environmental, though I have no doubt that in this residue the direct environmental effects are probably larger than the portion due to interaction.

Fisher to J.A. Fraser Roberts: 20 May 1935

... Yes, I do agree with you quite strongly that selection would be at its most efficient under uniform conditions, and, among these, probably at a higher than at a lower level of environmental well-being. That is, that any serious environmental disabilities scattered in the population would tend to frustrate any favourable selection for genetic potentialities. In expressing this argument, one has, of course, to admit that the existing selection is certainly very unfavourable, so that the less efficient it is, the better. But to anyone who seriously aims at improving the environmental conditions of the population and appreciates what has already been done in the last few generations, it is a most important point that this desirable action is making genetic differences more and more important, the more completely bad environments can be eliminated. ...

Fisher to R.N. Salaman: 10 February 1933

Moore has sent on your letter to me. Perhaps I can explain what was in the minds of the Editorial Committee when they discussed the point.[87] A large proportion of children are from families of 1 and 2, and if easy sex control were possible, I personally am quite confident that a very large proportion of the single children would be males, and that about half of the families of 2 would be of two boys. The larger families might be more equally distributed, and of this it is difficult to judge, but the question before most parents is not whether to have 9 boys and a girl or 6 boys and 4 girls, but whether their sole or few offspring will be, as things stand, something of an asset or something of a liability. Naturally this is only a judgement of the probable preponderant action, not a justification for it. I should personally anticipate very high sex ratios in the age groups produced in the first 20 years after such a discovery.

I doubt myself if 'Society' would show any initiative in seizing control of any situation, before great and serious damage had resulted from action in private interests. In my view the present birth-rate is far below what any organized Society would aim at in the National interest; that, of course, is a matter of opinion, but the inertia of Society in the matter is an observable fact.

Fisher to E. Selous: 1 November 1932

I am venturing to write to you, through your publishers, to express my personal appreciation of your great book, *Realities of Bird Life,* ... I had heard a little of your work through Julian Huxley, though without appreciating its importance. I particularly regret that I knew nothing about it at the time of writing a chapter on sexual selection in my book, *The Genetical Theory of Natural Selection,* which came out in 1930.

From an arm chair, as you weather beaten adventurers still scornfully say, though, if you watched *our* activities, you would soon correct it to a laboratory desk, I had come to conclusions as to the value of Darwin's theory of sexual selection and of the criticisms of Wallace and others levelled against it, not so different from your own as you would expect from so suspicious a source, and had ventured to add an excrescence of my own on the psychic evolution, through the same selective process, of female taste. This aspect of the problem Darwin left alone, I cannot suppose he overlooked it, and I do not know how large a part in the reluctance of biologists to give due weight to this part of Darwin's theory has been due to an unwillingness to ascribe to the female bird, merely for the sake of its consequences, such extravagant and useless tastes as would seem to be necessary. However, the ecological situation which you have succeeded in observing and disentangling in the cases of the Ruff and the Blackcock fulfil so neatly the requirements of my runaway process, by which I believe particular preference patterns are evolved, as well as demonstrating the fact of preference itself, that I should particularly have liked to have had your facts (rather like a mannequin) to exhibit my theory on.

I do not know whether anything that I can say or do can avail to encourage you and your publisher to give us the second volume which you had, and I hope, still have, in mind. If so, let me say or do it.

Fisher to C.S. Sherrington: 22 January 1947

Talking to Mrs. Cameron[88] last night she gave me your kind message and made me recall that I had once attempted, though quite without success, to form ideas as to the bearing of the principle of indeterminacy on such questions as human character, moral responsibility, and so on.

I have been thinking a little further on the subject, and you may be amused, and I hope not bothered in any way, by the five disputable propositions that I have put down on the enclosed sheet. As, of course, everything depends on the development and workings of the nervous system, I hope you will peremptorily blue pencil anything which reads like absolute rot from this point of view.

Of course, my chief difficulty hitherto has been to allow the evolutionary process, which depends upon the permanent and therefore deterministic properties of genes, to take any part in the development of such a capricious quality as the possession of powers of individual choice. The enclosed is therefore essentially an attempt to set out a possible relationship between these two things.

Of the real existence of amplification on the scale required, there can be no doubt, since men, i.e. physicists, are in fact materially influenced by quantum events, amplified in succession by cloud chamber, camera, and the physicist's brain. It is, of course, quite another matter whether in the organization of the unity of the individual among higher organisms and the development of their capacity to be conditioned by experience, amplification on the same scale is an ordinary feature. I suppose for my own part that it must be.

[Enclosed sheet]

The development of a given genotype (even in given environmental conditions) is indeterminate in that undirected chance happenings intervene at all stages, each such event having perhaps permanent or increasing consequences, as development proceeds, on the integration of the nervous system and the formation of character.

Individual action, e.g. choice, is always in part predetermined by the genotype, in part by the subsequent effects of physically fortuitous developmental happenings in the past, and in part undetermined and ascribable to fortuitous contemporary happenings.

Both the course of development, and the instantaneous state of the nervous system, are such as to amplify the effects of initially minute (quantum) events, so as to have molar consequences.

This general principle of amplification has been of importance to survival, in some way at present obscure, perhaps connected with the organization of the whole bodily mass into individual unity, perhaps in orienting its reactions towards the future (as purpose or intention), and has evolved to its present high degree by reason of its survival value. It, though not the particular modifications which if favours, is determined by the genotype.

It is open to a man, religiously inclined, to assert that the primary elements of indeterminacy in development and choice are fortuitous only in the physical sense, being in reality divinely guided, much as the apparatus of games of chance were regarded as guided by the Goddess Fortuna.

C.S. Sherrington to Fisher: 3 February 1947

Thank you for writing, although your letter by its conundrums adds to the puzzlement of life. Your questions, beautifully clearly put, lie beyond the boundaries of any special competence I can claim. In a wholly 'man-in-the-street' fashion I have been tempted to suppose that life's 'progress'—if that is the word—was an upshot of gene-heritage on one side and 'conditioning' on the other. E.g. the domestication of man's friend the dog, an upshot of generations where 'conditioning' disfavoured 'wildness' and encouraged 'tameness' by breeding from stock which evidenced this latter but not from such as evidenced the former. Of course that presupposes an *anlage* (e.g. genotype) which (material, though it be) disposes the individual rather to 'wildness' than to 'domesticity' or vice-versa. Is that permissible? Your questions gaily involve the matter-mind dilemma throughout. I interpret that as that you discount it? When I was first in Berlin the 'conditioning' there was toward evil, because Bismarck though a strong man was not a 'good soul', and the young Kaiser, who easily overthrew him, was worse. The Berliners were I take it conditioned to be what they are.

I always feel at a disadvantage about the gene because I find it always put forward as a purely *material* thing. I expect other physiologists feel the same. If the gene carries the psyche, might it not be clearer to start with it so *ab initio*. Inherited qualities are at least as clear in the 'psyche' as in the 'body'. Some of course adopt the term mystic, but that confuses worse and leads nowhere.

What you say about 'amplification' is very interesting to me—indeed exciting. Is not an outstanding example the life history of the gene itself as unfolded in the development of the individual organism? There it is met both in plant and animal, but in the latter it applies to transcendent reactions, through the nervous system, e.g. the toad immobilized by a tiny retinal image of a fly, or ourselves by the faint footfall of a supposed ghost—Hamlet when he caught the rustle of something behind the arras and lunged! It is creditably reported that a *single photon* can induce through our retina a *percept* and a percept can move the individual. Clearly, in the 'higher' animal, e.g. human, the system *par excellence* exhibiting amplification is the nervous system—in physiology we call the principle 'integration' rather than amplification, stressing that it is a principle which tends to make the whole individual react as a unity—that is the foundation of the 'ego', the 'self'. The old-time philosopher tended to suppose what he called the 'will' was the cause of solidarity of the 'individuum'. The truth is really the direct reverse as traced ontogenetically and physiologically. As you say—and no one I think can have put it forward better—'The general principle of amplification has been of importance to survival, in some way at present obscure, perhaps connected with the organization of the whole bodily mass into individual unity', i.e. integration and the system which does that most is the nervous, and it is *in* that system that mind has its seat.

Your remark about the goddess Fortuna and the piety of classic times is delightful! I wish glorious old Anatole France could have lived to read it. ...

Fisher to G.D. Snell: 9 November 1943

I have just received your letter of September 25th, a few days after the mice arrived, on the whole with very little loss. I should like to thank you immensely for co-operating so kindly with the Rockefeller Committee in obtaining these lines for me.

I have run a little mouse colony now for more than fifteen years, but it was only when I accepted the Arthur Balfour Chair of Genetics in Cambridge, formerly held by R.C. Punnett, that I decided to put into practice what I had long felt needed doing, namely the creation of permanent inbred lines covering all (or as near as makes no matter) of the genes recognizable in mice. I believe that the advantages offered by segregating inbred lines have never been fully appreciated. They give one the true single factor manifestations without disturbance due to other factors, such as ruins the value of so many specimens used for demonstration or museum exhibition. They can be used to illustrate all points of interest, such as factor interactions or linkages; they supply permanent standard material for quantitative studies and the means of obtaining improved standard genotypes in mice used as test material in human and veterinary medicine.

I daresay I shall run into plenty of difficulties, but it seems to me that only by doing the thing on a comprehensive scale will these be adequately explored.

Fisher to C.S. Stock: 24 October 1932

Thanks for your letter. ...

I think you have stated the functions of sex exactly. I imagine forms like the dandelion which are believed to be wholly non-sexual may thrive immensely for a time, but would eventually be so slow in modifying themselves to suit changed conditions that they will not contribute to the ancestry of the flora of the remote future. For this purpose, however, a very low percentage of crossing would, I believe, be effective. The penchant for obligatory cross-breeding seems to me explainable only by the predominantly unfavourable nature of mutations. ...

Fisher to C.S. Stock: 13 February 1936

... I am very glad you like the article on Determinism and Natural Selection [*CP* 121], as N.S. has so often been represented as a mechanistic, fatalistic or deterministic doctrine, whereas, in reality, it differs from nearly all causal laws in requiring no rigid determinism whatever. The only other important exception I know is provided by thermodynamics and statistical mechanics. ...

Fisher to C.S. Stock: 18 September 1943

Many thanks for your kind letter on my appointment at Cambridge. You may be amused at one circumstance in connexion therewith. When in 1916, Dampier-Whetham, as he was then called, submitted a screed of mine, on the genetical intepretation of the biometrical work Galton had inspired, to the Royal Society, the referees appointed are rumoured to have been Karl Pearson and Reginald Punnett. The Society's action was impeccable; these were two leading lights in statistics and genetics respectively, with the additional advantage, when two referees are appointed, that they were not very likely to agree. In fact, I suspect that the rejection of my paper was the only point in two long lives on which they were ever heartily at one. Lest this sad story seem depressing, it has the point that the author of the paper was chosen to succeed each pundit in turn.

It is great news about your book. I suppose you must be right about it not selling, though really one can never tell, and the fact that a book is not understood doesn't prevent it being widely read. Anyway, I wish it the best of luck.

Fisher to C.S. Stock: 28 July 1945

... At the moment I suppose the principal safeguard[89] most obviously required is that the true father should be known and declared under personal attestation by the physician. This would, I suppose, regularize the business from a good many legal points of view, including that of the later possible incestuous marriage of the child produced, or, what is equally serious, suspicions or aspersions that such marriage was incestuous. I am not sure how far this would go to meeting the psychological requirements arising from the fact that our aesthetic and emotional nature must very largely have been hammered into its present shape, as in the case of other animals, through pressure of sexual selection.

Fisher to C.S. Stock: 31 July 1957

I am extremely glad you liked the Eddington Lecture [*CP* 241]. It was delivered in London and had a small and, I suppose, distinguished academic audience. I think they were interested at the time, but, on the whole, biological workers like those in physics are not much, or often, concerned with the larger issues, e.g. as to whether in the development of human character there are, in fact, developments of importance not to be ascribed either to nature or to nurture; as it were 'branch points', at which something happens, which, viewed from earlier in time, may be thought of in statistical terms as pure chance, which at least supplies a method of calculation appropriate to our state of uncertainty in such forecasts, but which, viewed in retrospect, may well seem providential to the individual most importantly concerned.

Fisher to P.V. Sukhatme: 6 May 1940

... Yes, I have followed with some interest Lotka's and Kuczynski's work in the measurement of population growth, and your impression is correct that I developed the formal theory as expressed in 1930, in independence of both writers, some years earlier.[90] Actually, if I remember right, I set out the whole formulation, probably including the notion of reproductive value as a function of age, in correspondence with the late Dr Brownlee about the year 1925. You may remember that Brownlee was one of the first writers in England to stress the inadequacy of our birth-rate for maintaining a stationary population, expressing his ideas in terms of standardized birth- and death-rates. As I agree with him strongly on the importance of emphasizing the facts, I had a good deal of correspondence with him with a view to relating them more directly to the actual happenings, than is possible through standardized rates. I found later that Lotka is exceedingly touchy, and anxious to claim priority for his ideas, but as he (and apparently Kuczynski also) seems to have failed to grasp the notion of reproductive value, I should prefer it to be known that my own development is quite independent of theirs. I did not, however, publish anything on the subject prior to 1930,[91] though I could, when University College is again accessible, hunt up my correspondence with Brownlee.

Fisher to H.G. Thornton: 29 November 1950

Thanks for your note. Some time when you feel like it, you must tell me what is this tendency for 'increasing complexity in the inorganic world', which someone ought to start explaining.[92] I do not feel a comparable difficulty about new products of the human intellect, because after all, people are new, and each one capable perhaps, of doing some particular job usefully well, and meanwhile the jobs waiting to be done are changing. I mean both the aims and the tools available are different in each generation, so that a certain amount of novelty ought to result.

I quite agree that Smuts meant by Holism something much wider than evolutionary theory could explain, and it is really not very clear to me exactly what operational principles Smuts did mean to specify. Some such phrase as 'tendency to completeness of integration' is about as near as I can get.

Thanks also in other ways for your letter.

Fisher to R.E. Threlfall: 30 September 1953

Thanks for sending me the cutting from *The Glass Industry.*[93] To me it was an entire surprise that my work in *The Genetical Theory of Natural Selection,* 1930, which I presume was the source to which Dr. Preston refers, had been of any technological use. It just shows, to my mind, how well supplied with library and bibliographical facilities American workers in applied fields are, and how thoroughly, in fact, they must be used, for though my book is now fairly well known, very few copies of it were sold and it is quite untrue to say that the technical details of its contents are at all well known. Yet someone must have read and noted the method and presumably from that point it has filtered through into some reference collections.

I find it all very astonishing. When are you going to be in Cambridge?

Fisher to J.F. Tocher: 20 June 1940

Thanks for your letter. I am not a little attracted by what you say, and by the suggestion you make,[94] and as there seems to be time for consideration, I will seriously try from time to time to get my ideas in order.

It is now full two generations since Galton began to point out that those rare men who make a success of administrative responsibilities in difficult times must owe their gifts principally to heredity, and must be growing rarer rather rapidly in countries with a distribution of birth-rate like that which has prevailed in our Island ever since. A crude prediction made at the time *Hereditary Genius* was published might well have been that in 1940 three posts out of four involving important decisions would be held by incompetents. Of course such predictions can never be verified, because, as in the later centuries of the Roman Empire, it always looks as though *circumstances* had changed so much. ...

Fisher to C. Todd: 23 April 1930

I am indebted to J.B.S. Haldane for calling my attention to the genetical importance of your most remarkable work[95] on the serology of oxen and poultry. If I am not mistaken, the methods you have developed may prove capable of elucidating some very obscure points in genetics and in evolutionary theory.

A genetic point of great interest to me, and I think of some general importance, is the biochemical relationship of alternative (allelomorphic) genes, and the meaning of 'dominance'. The rule you have discovered of the negative response of corpuscles of the offspring to serum exhausted for both its parents, suggests that the isolytic or agglutinative reaction is determined by the direct products of individual genes rather than of secondary reactions, which in many cases produce substances such as pigments which are absent from both parents. On this view your results can have two interpretations:—

(a) that the liability to respond by agglutination to any particular ingredient in the serum is always completely dominant, or
(b) the liability of recessives so to respond is always shared by the heterozygotes.

These two interpretations correspond to the two views (a) that dominance is a primary biochemical phenomenon, the recessive gene being defective, inactive or less active in some special respect than the corresponding dominant gene, and (b) that dominance is wholly a superficial or phenotypic phenomenon, which has been brought about by the evolutionary modification of the heterozygote in a desirable direction, the two allelomorphic genes each initiating characteristic but different reactions.

Now is it possible that serological methods can discriminate between these two contrasted views? I am quite ignorant of the practical limitations of serological methods, so perhaps you will tell me without compunction if you think the following is impracticable:

Make a serum using recessive donors.
Exhaust with corpuscles from numerous dominant homozygotes (until reaction is negative with all dominant homozygotes in the group to be tested).
Test with heterozygotes and recessives.

If (a) is true, the test should be negative in both cases; [if] (b) is true, it might be positive in both. The test fails if the exhaustion is inadequate, but this can be checked by a parallel test:

Exhaust with corpuscles from numerous heterozygotes.
Test with recessives; if the exhaustion is sufficient, the result should be negative on both theories.

The point is to obtain a serum sensitive to a particular gene. If this were possible, it would not only, as it seems to me, settle the dominance question, but throw a great deal of light on other points.

First, the magnitude of the reaction due to a single gene in comparison with those ordinarily observed would give an idea of the number of such genes in which the group of individuals tested ordinarily differ.

Next, if the technique can be pushed so far as to detect a single gene, the total mutation rate in genes having no visible effects would appear in a small proportion of perhaps feeble exceptions to your general rule as to parentage. Lethal mutations in *Drosophila* seem to be common enough to give an appropriate percentage of such exceptions.

I am sending a copy of this letter to Haldane. Please do not trouble to answer in any hurry. I know how troublesome it must be to have to deal with suggestions for laborious and perhaps useless side-lines, but I should much appreciate an exchange of ideas with a view ultimately to clearing up the genetic implications of your work.

Fisher to C. Todd: 6 October 1931

I was sorry to hear of the catastrophe at the farm and a little sorrier to hear that you have not yet been able to set up the complete experiment on the sex effect.[96] I am rather a fanatic on the subject of fully designed and complete experiments, but shall none the less be interested to hear if the other tests you mention give any guiding indications.

Your finding that two fowls immunized in parallel with the same corpuscles give qualitatively different antibodies is especially interesting to me as confirming the correspondence between immunological and genetical differences, for undoubtedly two sister fowls will generally differ qualitatively in their gene complexes and will therefore find different elements in the corpuscles, which are alien to them, and to which, on this view, they will react.

I believe you have made this point, though perhaps more tentatively, in your printed papers and I am glad to hear that you now regard it as fully confirmed.

I think I mentioned that in my experiment with wild *Gallus* I was developing lines differing in a single recognizable factor, such as Feathered feet, and at least not greatly different in the rest of their genetic outfit. If your accommodation is at the moment under-stocked, you might find it useful to take pairs of heterozygous birds which I could supply you with this winter and from each of which two homozygous strains and the heterozygote could be made available in two years' time, if, as I hope, after the sex effect, you will be attracted to the idea of developing sera reactive only to a specific gene.

Fisher to C. Todd: 5 February 1932

Seeing you yesterday afternoon, reminded me rather belatedly, that is, after getting home, that there was a point I wanted to put to you.

The point arises because I have been asked to serve on a newly formed committee of the Medical Research Council devoted to Human Genetics. As you know, I am inclined to think that your serological work is going to lead to a greater advance, both theoretical and practical, in the problems of human genetics than can be expected from any further work on biometrical or genealogical lines. This, at best, would be looking rather far ahead and I cannot hope to convince people until you have at least the sex effect pegged out; but I fancy expert committees are liable more usually to err, and therefore to waste public money, by taking too short rather than too long a view. What I want to know, is this: could you make any use of it if I were to persuade the committee that yours is the work best worth backing? You did not seem particularly keen on it when I suggested some time ago that an assistant might be useful, but I suppose a *good* assistant would always be useful in enabling you to explore by-paths, and in other cases might enable you to carry out tests on a scale which would be decisive, and which you could not undertake single-handed. …

Fisher to C. Todd: 9 February 1932

… The present opinion that there are two mutually exclusive classes of genes, one capable of serological detection and having no other effects, and the other familiar to geneticists, but having no serological effects, is firmly established, and will only be shaken by the direct demonstration that sera can be prepared sensitive to the genes that produce sexual differentiation and other effects.

This seems to me the primary point, beginning appropriately enough with the sex experiment, and this part of the work must be done with animals. It would seem all to the good in the meanwhile to have someone experimenting on the development of a parallel technique in man, i.e. one that will detect individual blood, and consequently sweep up a big aggregate of 'serological' factors. This would be useful for testing identity in twins and triplets, apart from what the animal work ought to lead to.

Fisher to C. Todd: 14 April 1932

I think that is very bad luck; also that it was very good of you to pursue the possibility so far.[97] You have shown that the reactions produced by the polyvalent cock were not conditioned by the sex of the corpuscles. He thus confirms the two other cocks, which, if I have the story right, failed to react at all to some hens' corpuscles. One might take these other two also as showing that the sex effect (if any) must be too slight to detect, within the range of the technique employed. (Your previous sex effect must on this view be due to sex-linked factors).

One possibility has occurred to me that might be of interest to you. I do not think there is any escape, unless your observational findings are revised, from the view that the whole of the reaction developed is a reaction to alien genes (or, of course, their immediate products). It is evidently possible to form antibodies to an enormous number of such alien genes, and perhaps to all, but your results do not prove that all possible reactions always take place; i.e. it may be that the reaction is conditioned by some other circumstance, as if the reacting mechanism needed to be stirred up somehow. Men, who do not react to alien human blood, might, on this view, do so if some bull or rabbit blood was injected at the same time, so that the serum would then react not only to the alien species, but to the alien human corpuscles. But, of course, the conditioning might have to be of an entirely different kind. The main point of my suggestion is that there may be conditions necessary to bring off the different kinds of reaction which are potentially available, and that your experience might well suggest some other sorts of conditions which might be effective.

Of course, on the sex question it may well be that the ♀ chromosome is entirely (genetically and serologically) inactive, and that the thing would work without difficulty in other factors.

Fisher to C. Todd: 22 November 1935

You might like to know that the serological research in human genetics that

I have long been planning is now a going concern here at the Galton Laboratory. Dr Taylor, who was formerly in Dean's School of Pathology at Cambridge, has been getting the laboratory into condition since the beginning of October, and we now have immune sera coming in from a number of rabbits.

I am planning to extend the animals utilized to sheep, pigs, and horses, and perhaps more widely.

In any case, I have long been looking forward to the possibility of your caring to keep in close touch with this work and giving us the benefit of your advice. Nothing, indeed, would give me greater pleasure than that you should, if convenient from time to time, make use of the bench room and facilities which we should always be glad to put at your disposal. I do not know, however, what your plans are, and whether you are likely to have time to maintain your interests in this line of research.

Perhaps you will be able, at all events, to give us a visit, to see the apparatus which Taylor has installed, and to discuss points of interest in connection with our programme.

Fisher to A. Vassal: [March 1930]

I am sending you a copy, which you may care to have, of a book of mine on Natural Selection. I wonder if you remember, in your lectures at Harrow, describing the numerical oddity of the neck vertebrae of the sloths, and if I remember right, of some odd manatee. The riddle interested me enormously at the time, and my interest was revived a few years ago when I heard that Tate Regan was using a rather similar group of facts in fishes as a basis for what seemed to be some rather fantastic Neo-Lamarckian conjectures. I had some correspondence with Tate Regan, making, I think, no impression upon *him*, but clarifying the matter so far to myself that when Ford and Bull published the herring data, which I quote in Chapter V, I was ready to spot its significance.

I hope at any rate that my shot at the riddle of the sloth will interest you, and that you will not turn down all the rest as unreadably mathematical.

Fisher to N. von Hofsten: 26 June 1950

... I suppose the difference between your 'actual curve' and your 'mixing curve' is that between two populations having the same gene ratio though different proportions of heterozygotes. This is a distinction which, if I were rewriting *The Genetical Theory,* I should certainly stress more heavily that I did there. For though the principal evolutionary agency is undoubtedly change of gene frequency, changes in the mating system with important secondary consequences can be brought about by changes in population frequencies without change of gene ratio.

I did not know about your paper, which is, I gather, of eugenic purport, though a trifle pessimistic. I do not see ground for pessimism in the genetic situation presented by Man, but I think it is quite inconceivable that any existing national state should have the courage to treat it as it requires.

Fisher to L.G. Wigan: 31 August 1942

... if the requirements of the environment fluctuate, and so are constantly inducing genotypic changes in the population of organisms, this will, at least slightly, hasten the extinction of genes, but I do not see that it does very much in this respect. I could well imagine the population of grasses in a region such as Syria adapting themselves progressively for 100 years at a time, or so, to moister or drier conditions without losing the capacity of reversing this change as quickly as ever. In fact, whereas in experimental populations extinctions of genes can occur with a gene frequency of only about 10^{-1}, it will need to be about 10^{-8} before it can conceivably occur in a really big population. ...

Fisher to E.B. Wilson: 2 August 1930

... As to the eugenic effect of class difference in fertility, I do not see that what you say about luck throws any doubt on it at all.

If desirable characters, intelligence, enterprise, understanding of our fellow men, capacity to arouse their admiration or confidence, exert any net average social advantage, then it follows that they will become correlated with social class. The more thoroughly we carry out the democratic programme of giving equal opportunities to talent wherever it is found, the more thoroughly we insure that genetic class differences of eugenic value shall be built up. Chance can only dilute this process, it does nothing to neutralize it. Of course, direct intelligence tests in this country show considerable differences between the children of parents of different occupations attending the same schools; but I do not stress this because a great many other qualities more important than intelligence must be sorted out by the same process. ...

Fisher to S. Wright: 6 June 1929

I was much interested in your note in the *American Naturalist* on the evolution of dominance, though of course sorry that you should consider the numerical values too small to be effective.[98]

I do not think there is any use in controversy except when the point at issue is perfectly clear to both parties, and I should therefore like to have your opinion of the enclosed,[99] which is the kind of thing I should now be inclined to write, before publishing anything on the matter.

Perhaps you would find it worth while to work out the case you cite making allowance for the effect of the more favourable factors on the frequency of the heterozygotes, and dropping the assumption that the modifier is dominant.

What I mainly want to know, however, is whether you agree with me that a very slight selective effect acting for a correspondingly long time will be equivalent to a much greater effect acting for a proportionately shorter time. Or, whether, on the other hand, you think I have underestimated the ratio of the selective intensities, or overestimated the ratio of the times. I cannot see how a conclusion can be reached without considering the latter.

Fisher to S. Wright: 10 July 1929

I was very glad to get your letter, and see what your point[100] really is. As others besides myself may have missed it, and fancied that you desired to establish insufficiency of selective intensity in relation to time available, I think it will be worth while to reply, little though either of us can know on the real point at issue.

I enclose what I am sending to the *American Naturalist* so that, if you think it desirable, you can have another go, in the same issue as mine. ...

Fisher to S. Wright: 13 August 1929

Many thanks for your interesting letter and the copy of your comment[101] on my reply. I am inclined to think your comment carries the discussion of your main point as far as it can be usefully carried in the present state of our knowledge, and I do not see that I can usefully add anything.

The point about using selective intensity[102] $i = \delta p/\{p(1-p)\}$ was of course aimed at comparisons with the selective value of 'multiple effects', in which also δp will contain the factor $p(1-p)$ depending on the gene ratio. From this point of view counter-mutation is infinitely powerful against the prevalent type of gene, as is illustrated by the power of mutation to keep a gene in existence against powerful selections.

You see, of course, that the principle of multiple effects, if carried far enough, greatly increases the number of factors available for modifying dominance, though possibly it does not increase the number whose fate will be settled by the effect in modifying dominance.

I am not sure that I agree with you as to the magnitude[103] of the population number n. To reduce it to the number in a district requires that there shall be *no* diffusions even over the number of generations considered. For the relevant purpose I believe n must usually be the total population on the planet, enumerated at sexual maturity, and at the minimum of the annual or other periodic fluctuation. For birds twice the number of nests would be good. I am glad, however, that you stress the importance of this number. ...

Fisher to S. Wright: 9 September 1929

Many thanks for your letter of August 28th, which is not only exceedingly interesting in itself, but helps me to understand the larger paper,[104] which I have been puzzling over occasionally for some time.

I have so far published nothing on the diffusion problem,[105] but have in the Press a book on The Genetic Theory of Natural Selection, which has part of a chapter on the cohesion of species in relation to the problem of their fission. I think it must be generally true that the ancestry of all individuals of a species is practically the same except for the last 100 or perhaps 10 000 generations, and that a gene frequency gradient is maintained by selection between different parts of a species' range. So that well marked local variations may or may not be incipient species, according as real fission, cessation of diffusion, ultimately supervenes. My discussion of this point is necessarily superficial and qualitative, but may have some points to interest you. ...

Fisher to S. Wright: 15 October 1929

I have reason to be immensely grateful to you for sending me your paper, which, I fear, I have kept all too long, as I have now fully convinced myself that your solution is the right one.[106] It may be of some interest that my original error lay in the differential equation.

$$\frac{\partial y}{\partial t} = \frac{1}{4n}\frac{\partial^2 y}{\partial \theta^2}$$

which ought to have been

$$\frac{\partial y}{\partial t} = \frac{1}{4n}\frac{\partial}{\partial \theta}(y \cot \theta) + \frac{1}{4n}\frac{\partial^2 y}{\partial \theta^2}$$

the new term coming in from the fact that the mean value of δp in any generation from a group of factors with gene fraction p, is exactly zero, and consequently the mean value of $\delta\theta$ is not exactly zero but involves a minute term $-(1/4n) \cot \theta$. (You might care to give this correction from me when you publish.)

With this correction I find myself in entire agreement with your value $2n$ for the time of relaxation, and with your corrected distribution for factors in the absence of selection. Re-examining the whole work has been a great gain to me in clarifying my ideas, and I appreciate what I had not realized before, that selection, except when directed to an optimum value, is not important in keeping down the variance.

I have done a good deal of work on the terminal conditions, which, when it is fit to be seen, will, I hope, be of interest to you. A very striking result is that a mutation can only be regarded as effectively neutral if the selective intensity multiplied by the population number is small, so that the zone of effective neutrality is exceedingly narrow, and must be passed over, one way or the other, quite quickly in the course of evolutionary change.

Fisher to S. Wright: 19 March 1930

I am sending herewith a complimentary copy of my new book *The Genetical Theory of Natural Selection.* It was written too soon to include the later developments of dominance theory which threaten to be extensive. This is really an advantage for it would be a pity if the interest of this special development were to draw attention away from the more general questions.

In some ways the first chapter is the most important, and in some the second. The sixth chapter and the group on Man will attract very different sorts of readers. However, I am sure you will think it an attempt worth making, and should you happen to review it anywhere, remember that I shall be most interested to see your opinion.

S. Wright to Fisher: 10 June 1930

I wish to thank you very much for sending me a copy of your recent book. I have found it extremely interesting and stimulating. I presented my paper on the subject before the American Association for the Advancement of Science last December. It should appear soon in *Genetics.*[107] In reading your book I have naturally attempted comparison at every point with the views which I had reached. Our basic assumptions are, of course, very similar.

Certain differences in detail are of a rather superficial nature and can doubtless easily be ironed out. There appear to be some rather important differences in emphasis, however. You would probably not approve at all of the conclusions which I gave in the abstract of my paper which was published (*Anatomical Record*, 44:287, 1929). This somewhat exaggerates the difference, since I was forced by limitation of space to express my views in a balder and more unqualified form than I would care to maintain fully. The main differences all seem to trace to the greater role which I have attributed to random differences among local strains of a species brought about by local inbreeding.

I have not yet been able to follow the mathematics in Chapter IV to my satisfaction but hope to be able to do so. There appears to be substantially complete agreement with the results of my method in the case of no mutation and slight mutation. Your determination of the exact character of the terminal frequencies seems to agree well with the conclusions which I had drawn from consideration of very small populations. There may be a trifling discrepancy at the bottom of page 86 [*GTNS*, p. 94]. I obtained $1/(2N)$ as the exact rate of decay in the case of a population of monoecious organisms with completely random combinations of gametes, and a formula for the case of separate sexes which does not seem to be exactly the same as yours, but which applies exactly to the case of brother-sister mating. In the case of low mutation rates, my formula for the number of genes maintained by a given mutation rate $2[0.577+\log(2N-1)]$ (in the case of one mutation per generation) differs only slightly from yours.

I was a good deal troubled by the difference between your formula for the selection effect (page 92) [*GTNS*, p. 99] and that which I had reached—$e^{2aNp}\{(C_1/p)+(C_2/q)\}$ in your symbols.

I had not considered the exact case which you give, flux equilibrium (because of the general difference in viewpoint) but on solving for it, I find a ratio of C_2 to C_1 in the above formula which gives results in close agreement up to a certain point ($a<1/(2N)$) but widely divergent beyond this. Your approximation is clearly a better one in this region, indeed, mine rapidly becomes wholly valueless in cases in which the terminal frequencies are large. Have you a general demonstration that the chance of fixation is $2a$? The example given on page 76 [*GTNS*, p. 83] for $a = 0.01$ seems to depend on repetition of a formula for the case in question. I have not, however, as yet gone carefully through the reasoning.

I liked very much your opening chapter with its comparison of the consequences of blending and particulate heredity, also the chapters on sexual selection, mimicry and human evolution.

I have been asked to review the book for the *Journal of Heredity.*

Fisher to S. Wright: 23 June 1930

Many thanks for your letter. I have not the summary from the *Anatomical Record,* so will await the appearance in *Genetics* before going into some of the small discrepancies you mention.

The method by which I should relate selective advantage when not necessarily small to chance of survival in a large population would be to say that the substitution of

$$f(x) = e^{c(1-x)} \text{ for } x$$

is without effect only if

$$x = e^{-c(1-x)};$$

writing the solution of this equation in the form $1-P$, P will be the limiting probability of survival, and

$$-\log(1-P) = P+\frac{1}{2}P^2+\frac{1}{3}P^3+\ \dots$$

$$= cP$$

whence $$P = 2(c-1) \qquad \text{approximately,}$$

or if a is the selective advantage

$$c = e^a$$

$$P = 2a-\frac{5}{3}a^2+\frac{7}{9}a^3-\frac{131}{540}a^4+\ \dots$$

as far as I have worked it. ...

I do not think the equation has any biological interest except when a is small.

Did I tell you that the cases of polymorphism mentioned by Haldane in connection with dominance theory really fit in exceedingly well? I am publishing a note on them primarily to encourage workers on these species to pay attention to the further predictions of the theory.

I shall be very much interested in your review, and hope you will give yourself space enough to deal with the many different aspects of the book on which I want to know your opinion. I am particularly glad you like Chapter I, as I suspect many biologists will be tempted to leave it out (i) because they will naturally expect a first chapter to be trite as well as elementary, (ii) because they are tired of introductory expositions of Mendelism, and (iii) because they have believed almost since boyhood that they know all about what Darwin thought!

S. Wright to Fisher: 15 October 1930

I should have thanked you long ago for your letter of June 23rd, which entirely cleared up for me the derivation of your value $2a$ for the chance of survival of a mutation in a large population. I think that I have cleared up the apparent discrepancy between the result which I gave for the distribution of genes under selection ($s = -a$) and irreversible mutation (at a rate u such that $4nu$ is negligibly small), vis. $y = Ce^{2nsq}/1-q)$ and your value $(2dp/pq)\ (1-e^{-4anq})/(1-e^{-4an})$ which seems clearly to be correct. The two formulae agree (with proper choice of coefficient) when ns is less than 1 but diverge rapidly above this. I had been aware of the limited range of applicability of my formula (which in fact I first reached in the form $y = C(1+2nsq)/(1-q)$), but had not seen how to deal with second order terms involving ns^2, n^2s^3, etc. in the derivation. I find now that these condense into a simple expression the inclusion of which gives identically your formula in this case. In the case of reversible mutation, however, the corrected formula appears to be $y = Ce^{4nsq}/q(1-q)$ for all values of ns (up to the point at which ns^2 approaches 1) in place of my previous formula $y = Ce^{2nsq}/\mathrm{q}(-q)$, and for mutation rates $(u,\ v)$ which are not negligible in comparison with $1/(4n)$, the formula seems to become $y = Ce^{4nsq}\ q^{4nv-1}$ $(1-q)^{4nu-1}$ to at least a much better approximation than the result which I gave in one of my papers in the *American Naturalist* last fall, viz., Ce^{2nsq} $q^{4nv-1}\ (1-q)^{4nu-1}$.

Fortunately (assuming my present formula to be sufficiently accurate) I have merely had to make all my statements on interpretation in my forthcoming paper in *Genetics* apply to intensities of selection just half as great as before and my graphs merely needed relabelling.

I have included these corrections to my formula in the review of your book for the *Journal of Heredity* (which should appear next month) to show that there is now no mathematical difference between our results in the cases which can be compared. I have discussed at some length the rather different interpretations of the role of selection which we have reached and will be much interested in getting your criticism of my view.

I was much interested in your discussion of dominance in *Paratettix*, etc. The situation certainly seems to conform well to the expectation from your theory, and the objections which I made in the case of ordinary recessive mutations do not seem to hold here.

Fisher to S. Wright: 25 October 1930

Thanks for your letter. I am glad to hear the little discrepancies are clearing themselves up. With respect to the polymorphism work, the important thing from the mathematical standpoint is to ascertain in what manner the chance of success depends on selective advantage in the case of restricted recombination discussed in the last section [*CP* 87]. As far as I can see, this might be a matter of great difficulty, but this may be merely because I have not spotted some simple way of looking at it. It would evidently include the problem, the quantitative treatment of which I shirked at the beginning of Chapter VI, and would certainly throw light on the equally elusive problem of the effect of a stream of gene substitutions in loosening the linkage to which I refer in Chapter V.

Mathematicians always tend to assume that the hardest mathematics will be the most important, and this is perhaps true enough in the well worn topics. It is certainly not true of my book, where the apparently non-mathematical parts, where I have left the mathematics undone, are often of the greatest ultimate interest.

I shall be much interested to see your review for the *Journal of Heredity*.

Fisher to S. Wright: 19 January 1931

I was delighted to see your review of my book in *The Journal of Heredity* for August last, which for some reason has only just appeared in this country. Your opening paragraphs especially will be most valuable in getting the less genetical sorts of biologists to see that the evolutionary bearings of genetical discussion are not at all what they were supposed to be; but indeed I ought not to praise one part rather than another for I liked it all heartily. It is in fact the most understanding review of my book which has yet appeared anywhere, and apart from personal vanity, which will of course absorb any amount of mere praise, that is really what an author craves for.

I was extremely interested in your more critical discussion, but what a shame that they should have printed your formulae so illegibly. You must really take some later opportunity to set out your views more fully, for I am willing to be convinced, not of the importance of subdivision into relatively isolated local colonies, which I should agree to at once, but that I have overlooked here a major factor in adaptive modification, which is what at present I am not convinced of. The point is very well worth going into in detail. I fear though that an adequate discussion will be above the heads of many biologists.

I hear that I have recently been attacked in the Zoological Society for daring to *intrude* in biological discussions; perhaps you have had occasionally a similar experience. I do not think it is this kind of thing which does any real harm; it makes a few old pundits feel more comfortable on their perches, but it carries mighty little weight with the younger men.

I had not intended to take up any special point in this letter, but I am tempted to mention this one, (p. 353) 'The formula itself seems to need revision in the case of another important class of genes, ones slightly deleterious in effect but maintained at a certain equilibrium in frequency by recurrent mutation' (I can leave migration aside here). The point here is that the average fitness *is* continually being increased by selection, at exactly the same rate as it is being decreased by mutation. This cause of deterioration of adaptedness, due to mutations of the organism, is, in my treatment, classed with the parallel deterioration due to changes in the environments. This supplies an amendment to the corresponding statement on p. 352, 'The only effective offset to undeviating increase in fitness, which he recognizes, is change of environment'. I think, if you happen to re-read p. 41 [*GTNS*, p. 44], you will see that I class deleterious mutations equally as an offset.

I wonder if you would agree that in attributing somewhat less weight than I to what selection always is doing, you are *ipso facto* attributing more to what it has already done. I mean that the situation sketched at the end of p. 353 would be undoubtedly right if selection had in the recent past been infinitely effective, or infinitely rapid, as a means of modification, and is only therefore ineffective now. This is what I was driving at in saying that the difficulties encountered by natural selection were chiefly of its own making, i.e. the high perfection of existing adaptation.

When the spirit moves you, I should be exceedingly interested to hear if you think this is rightly put.

Fisher to S. Wright: 17 February 1931

I very much hope I shall have a chance of seeing you again during the summer.

I do think that differential selective action in different stations or regions may be exceedingly important, even if there is a steady diffusion of germ plasm between them. ...

Fisher to S. Wright: 31 May 1931

I arrived in U.S. yesterday ... .

If I can catch you at Chicago I propose to come over on Saturday June 27 returning to Iowa the next day. ... I especially want to come on a day that will be convenient to you and when I can see something of the experimental work you are developing.

Let me know if the weekend I suggest will suit ... .

Your letter of Feb. 3rd contains a point about non-optimal points of genetic stability[108] which I should like to take up with you. In one dimension a curve gives a series of alternate maxima and minima, but in two dimensions two inequalities must be satisfied for a true maximum, and I suppose that only about ¼ of the stationary points will satisfy both. Roughly, I should guess that with n factors only 2^{-n} of the stationary points would be stable for all types of displacement, and any new mutation will have a half chance of destroying the stability. This suggests that true stability in the case of many interacting genes may be of rare occurrence, though its consequences when it does occur are especially interesting and important.

Fisher to S. Wright: [*late June 1931*]

This is just a note to thank you and Mrs. Wright for your kindness and hospitality to me in Chicago. I wish I could better understand your views on those points on which I differ from you, but on the points I have discussed with Lush,[109] I see little chance that I shall ever do so. However, there is a substantial body of theory on which I think we do agree and that after all is of infinitely more interest to the world at large than the very obscure points still in dispute.

Fisher to E. Wynter: 30 May 1945

... The subject of inbreeding especially with farm animals, interests me greatly, and I should be very glad to visit Dr. Corner's farm and discuss possibilities if ever this seems likely to prove useful. The preparation of inbred stocks is such a lengthy process that it should be started at once on [an] adequate scale and carried out by methods that will, as rapidly as possible, give closely inbred material. Of course, its importance will not be obvious to the farming community for another fifty years.

Notes

1. Dr J.R. Baker, Department of Zoology, Oxford University, had written asking Fisher whether he would agree that in the following statement, one part (the first and third sentences) was first pointed out in print by C.S. Elton though it was independently thought of by E.B. Ford, whereas the other part (the second sentence) was due to Fisher.

When, after a period of great scarcity, a species is rapidly increasing in numbers, non-advantageous mutations tend to spread through the population. In the course of their spreading, they are likely to become incorporated with certain gene-complexes with which they give rise to characters having selection value. Thus periodical increases and decreases in numbers may result in more rapid evolution than stationary populations.

See also correspondence between Fisher and Ford (p. 196).

2. Lady Barlow, daughter of Charles Darwin's son, Horace.
3. Barlow, Nora (Ed.) (1945). *Charles Darwin and the voyage of the Beagle.* Pilot Press Ltd, London.
4. Barlow, Nora (Ed.) (1958). *The autobiography of Charles Darwin 1809-1822.* Collins, London.
5. For Fisher's review, see Appendix C (p. 292).
6. From Part iii of *The Rime of the Ancient Mariner* by S.T. Coleridge.
7. E.W. Barnes, Sc.D., F.R.S., who was Bishop of Birmingham, 1924-53, had been one of Fisher's mathematical teachers at Cambridge. Fisher had sent him a copy of *GTNS.*
8. Darwin, C.G. (1930). Review of *The genetical theory of natural selection. Eugenics Rev.* **22**, 127-30.
9. Bishop Barnes, in commenting on a lay sermon given by Fisher, had asked if he could offer an explanation of the relation between the divine and evil 'which seems to be the repellent part of the same mode of being.'
10. Julia Bell, M.A., F.R.C.P., (1879-1979), was a member of the Medical Research Council's external staff attached to the Galton Laboratory. She had stayed in London during the 1939-45 War and in February 1941 was seeing to the removal of various Laboratory records and other possessions for sake keeping.
11. The American biometrician, C.I. Bliss, writing to Fisher from the USSR, had enquired about the translation of Fisher's statistical books into Russian and had then added, 'Incidentally, if there has been a delay in translating your *Genetical Theory,* it is possibly caused by the anti-Marxian character of the last part of it, at least so several biologists have suggested. In the Soviet Union this is more than a slight technicality.' See also Fisher's letter of 10 February 1942 to K. Mather (p. 236).
12. Dr W.C. Boyd, Boston University School of Medicine, had written seeking Fisher's views on the role of selection and dominance in the human blood groups which he noted were not referred to in *GTNS.*
13. See Fisher's letters to C. Todd (p. 267).
14. See *GTNS*, p. 87.
15. Boyd had referred to studies with rodents which were said to show few blood-group differences and had then asked Fisher if he was justified in supposing that many genetic differences would be distinguished serologically.
16. Fisher was seeking advice from Dr L.P. Brower at Yale University on whether he should include a note on the butterfly *Limenitis* in the Dover edition of his book (see *GTNS*, p. 145). See also his letter of 25 November 1955 to E.B. Ford (p. 202).
17. Hope Professor of Zoology (Entomology), Oxford University, 1933-48.
18. See Fisher's contribution to the discussion of Protective Adaptations of Animals—especially insects, *Proc. R. ent. Soc. Lond.* **7**, 87-9 (1933), where he says, 'Approaching the problem of selective intensity from the genetical stand-

point, I have come to the conclusion that the effective selective intensity in Nature can seldom exceed 1 per cent per generation, else evolutionary modification would be a much more rapid process than it is known to be. Probably we should think of intensities of 0.1 per cent as more typical.'

19. Dr R.B. Cattell had just been awarded a Leonard Darwin Studentship by the Eugenics Society and Fisher was writing to him about his programme of work. See Cattell, R.B. (1936). Is national intelligence declining? *Eugenics Rev.* **28**, 181-203.
20. See Crosby, J.L. (1940). High proportions of homostyle plants in populations of *Primula vulgaris. Nature* **145**, 672-3.
21. Dr J.F. Crow had written asking Fisher to comment on a discussion paper on the roles of inter- and intra-population selection.
22. In 1947, Darlington and Fisher together founded the journal, *Heredity.*
23. Dr J. Davidson who had been a colleague at Rothamsted had recently become Head of the Entomology Department in the Waite Agricultural Research Institute in the University of Adelaide. He was an authority on the taxonomy of the *Aphidae.*
24. C. Tate Regan gave the Presidential Address on Organic Evolution to Section D (Zoology) at the Southampton meeting of the British Association for the Advancement of Science in 1925.
25. See Fisher's letter of 7 February 1927 to Regan (p. 252).
26. On the question of 'pouched mice', Davidson sought the advice of Professor F. Wood-Jones at the University of Melbourne; Wood-Jones said they were 'excessively difficult to deal with in any way' and that it was not practicable to obtain and ship such animals to England.
27. Muller, H.J. (1932). Further studies on the nature and causes of gene mutations. *Proc. 6th Int. Cong. Genet* ., Vol, 1, pp. 213-55.
28. Plunkett, C.R. (1932). Temperature as a tool for research in phenogenetics: methods and results. *Proc. 6th Int. Cong. Genet.* Vol. 2, pp. 158-60.
29. Fisher was awarded the Darwin Medal of the Royal Society in 1948 for 'distinguished contributions to the theory of natural selection, the concept of the gene-complex and the evolution of dominance'.
30. See *CP* 87, p. 402.
31. This letter and the following ones shed light on the development of ideas concerning the evolutionary effects of fluctuations in population size. See Fisher's letter of 24 April 1931 to J.R. Baker (p. 178).
32. See *GTNS*, p. 103.
33. Ford, H.D. and Ford, E.B. (1930). Fluctuations in numbers and its influence on variation in *Melitaea aurinia. Trans. R. ent. Soc. Lond.* **78**, 345-51.
34. Ford had said Fisher's suggestion that Mendel had reached his conclusions as a generalization of wide rather than local application raised a difficulty in regard to Mendel's strategy for it would then seem extraordinary that Mendel should have verified and demonstrated his conclusions with only a single species when, perhaps with no more work, he could have used two widely different organisms to strengthen greatly his position.
35. See Fisher's letter of 31 May 1931 to Wright and also *CP* 185.
36. Ford had asked Fisher if he would contribute to a volume on evolution in honour of Julian Huxley. See Huxley, J.S., Hardy, A.C., and Ford, E.B. (Eds.) (1954). *Evolution as a process.* Allen and Unwin, London.
37. Fisher was seeking advice on whether he should insert a note on the butterfly *Limenitis* in the Dover reprint edition of his book (see *GTNS*, p. 145). See also his letter of 29 November 1955 to L.P. Brower.

38. Hagedoorn, A.L., and Hagedoorn, A.C. (1921). *The relative value of the processes causing evolution.* Martinus Nijhoff, The Hague. See *CP* 17 and Darwin's letter of June 1921 to Fisher (p. 74).
39. Dr A.B.D. Fortuyn was Professor of Anatomy, Peiping Union Medical College, China.
40. See Section 32 of Fisher, R.A. (1925-70). *Statistical methods for research workers.* Oliver & Boyd, Edinburgh.
41. After reading *GTNS*, Professor R.R. Gates, Botany Department, King's College, London, had written seeking Fisher's views on the relative importance of migration and crossing in producing the observed differences in racial frequencies of the ABO blood groups. Gates wrote of two genetic factors being involved in the ABO blood groups which, he said, were apparently without selective effect.
42. See *CP* 87, p. 402.
43. See Fisher's letter of 23 April 1930 to C. Todd (p. 267), a copy of which Fisher had sent Haldane.
44. Haldane, J.B.S. (1930). A mathematical theory of natural and artificial selection. Part VII. Selection intensity as a function of mortality rate. *Proc. camb. Phil. Soc.* **27**, 131-6.
45. Haldane had lost track of the manuscript of the review of *GTNS* he had written for *Eugenics Review* after the editor (Mr Elton Moore) said he did not want it.
46. Edin, K.A. (1929). The birth rate changes. Stockholm 'upper' classes more fertile than the 'lower'. *Eugenics Rev.* **20**, 258-66. See Fisher's letter of 24 November 1938 to Sir James Marchant (p. 233).
47. Haldane, J.B.S. (1931). Mathematical Darwinism. A discussion of *The genetical theory of natural selection. Eugenics Rev.* **23**, 115-17.
48. At University College, London.
49. At the John Innes Horticultural Institution, Merton, where Haldane held a part-time appointment.
50. Haldane, J.B.S. (1939). The spread of harmful autosomal recessive genes in human populations. *Ann. Eugen.* **9**, 232-7.
51. See Fisher's letter of 10 February 1942 to K. Mather (p. 236).
52. Haldane, J.B.S. (1940). The conflict between selection and mutation of harmful recessive genes. *Ann. Eugen.* **10**, 417-21.
53. University College, London.
54. Rothamsted Experimental Station.
55. Heckstall-Smith, H. (1957). Review of *Nuclear explosions and their effects.* (Government of India) *Friend* **115**, 33-6.
56. Lancelot Hogben, Professor of Social Biology at the London School of Economics, had written asking if Fisher was working on the problem of the contribution of a sex-linked locus to the correlations between relatives.
57. See also Fisher's letter of 18 January 1935 to J.A. Fraser Roberts (p. 260).
58. Huxley, A. (1923). *On the margin.* Chatto and Windus, London.
59. See Fisher's letter of 1 November 1932 to E. Selous (p. 261).
60. Fisher was recovering from an operation and Huxley was to take his place at a discussion on Population in the Zoology Section of the British Association for the Advancement of Science.
61. See Darwin's letter of 30 April 1931 to Fisher (p. 138). Fisher's paper was not published until 1954 (*CP* 258). See Fisher's letter of 23 October 1951 to E.B. Ford (p. 202).

62. Huxley had asked Fisher about what he could say on selection for closer linkage in an article he was writing on polymorphism. See Huxley, J.S. (1955). Morphism and evolution. *Heredity* **9**, 1-52.
63. A draft of an article on Fisher's fundamental theorem of natural selection.
64. The term *genetic variance*, as used by Fisher, refers to the component of the genotypic variance which is now commonly called the *additive genetic variance.*
65. In the following two letters, Fisher discusses several points arising from a draft of Kimura, M. (1958). On the change in population fitness by natural selection. *Heredity* **12**, 145-67.
66. Fisher had once pulled Lowdnes up in conversation for stating that natural selection is concerned with the benefit of the species and had emphasized that in reality it is only concerned with the benefit of the individual. Later, when Lowdnes was unable to find a reference to this in *GTNS*, he wrote to Fisher for further information. Fisher's reply is notable for its reference to the evolution of altruism by kin selection and for the distinction drawn between individual and species benefit in natural selection. In 1958, Fisher inserted a passage dealing with this distinction in *GTNS* (p. 49).
67. After a broadcast on the BBC's Third Programme in which Fisher and three other British scientists—C.D. Darlington, J.B.S. Haldane, and S.C. Harland —gave their views on the Lysenko controversy (*Listener* **40**, 873), Mr A.H. Machino, Programme Organizer of the Russian Section, wrote saying that the BBC would like to include a shortened version of these talks in their Russian broadcasts for Soviet audiences. He suggested that the quotations from Lysenko could be omitted from Fisher's contribution 'as we think we can assume that the average Soviet listener is well acquainted with the various steps which led to the recent developments in biological research in the U.S.S.R. and with the role played by Lysenko in this matter'. The letter printed here is Fisher's reply. For Fisher's talk, entitled, 'What Sort of Man is Lysenko?', see *CP* 229.
68. Sir James Marchant, Secretary of the National Birth-Rate Commission, in writing to Fisher said doctors had experienced a greatly increased demand for information on birth control methods.
69. See Note 46.
70. See Note 27.
71. See Fisher, R.A. (1942). The polygene concept. *Nature* **150**, 154 (*CP* 191).
72. Early in 1935 Fisher had received an offer of 1000 roubles from the President of the State Publishing House of Biological and Medical Literature, USSR, for a translation of the first seven chapters of *GTNS*. See also Fisher's letter of 15 February 1937 to C.I. Bliss (p. 183).
73. Lewis, D. (1942). The evolution of sex in flowering plants. *Biol. Rev.* **17**, 46-67.
74. Mather, K. (1943). Polygenic balance in the canalization of development. *Nature* **151**, 68-71.
75. Jolly, A.T.H. and Rose F.G.G. (1943). The place of the Australian aboriginal in the evolution of society. *Ann. Eugen.* **12**, 44-87.
76. Morgan, T.H. (1932). *The scientific basis of evolution.* Faber, New York. See also Fisher's letter of 15 November 1932 to Darwin (p. 159).
77. After reading Fisher's Herbert Spencer Lecture, *The social selection of human fertility* (*CP* 99), Dr. C.S. Myers had written asking if Fisher regarded it as *proven* that 'those who rise in the social scale ... are involuntarily (i.e. congenitally) less fertile' and whether voluntary infertility could be excluded.

78. Fisher's letters to Dr R.K. Nabours, Department of Zoology, Kansas State College, have special interest becasue of their early and novel suggestions on practical and theoretical questions which arise in the study of polymorphic species involving dominance and close linkage. See *CP* 87 and *CP* 167.
79. Nabours, R.K., Larson, I., and Hartwig, N. (1933). Inheritance of colour patterns in the grouse locust *Acrydium arenosum*. *Genetics* **18**, 159-71.
80. See Fisher, R.A. (1939). Selective forces in wild populations of *Paratettix texanus*. *Ann. Eugen.* **9**, 109-22 (*CP* 167).
81 Dr J. Rasmusson, writing from Svalöf, Sweden, had asked about a comment attributed to Haldane that Fisher was in doubt concerning dominance theory.
82. This letter to Dr C. Tate Regan, Direct of the British Museum (Natural History), contains the earliest known outline of the argument which Fisher later presented in Chapter I of *GTNS*. See Fisher's letter to J. Davidson (p. 190) and also Darwin's letter of 27 April 1928 to Fisher (p. 84).
83. The correct value is 1.4 *n* generations. See *GTNS*, p. 95.
84. See *GTNS*, p. 127. See also Fisher's letter to A. Vassall (p. 271).
85. Pamphlet on sexual selection, probably *CP* 6.
86. See *GTNS*, p. 152.
87. After editorial comment in *Eugenics Rev.* **24**, 174, (1932), Dr R.N. Salaman wrote questioning the assumption that the male ratio would be greatly increased if it were possible to control sex determination in Man. He suggested that 'Society' would seize control of the situation before that happened.
88. The wife of Dr J.F. Cameron, Master of Gonville and Caius College, Cambridge, 1928-48. Sir Charles Sherrington had resided in the Master's Lodge as a guest in 1943 when Fisher was also resident in Caius.
89. With Artificial Insemination Donor.
90. Dr P.V. Sukhatme had written asking if Fisher could confirm his impression that the theory of population growth included in Chapter II of *GTNS* had been developed by Fisher independently of the work of Lotka and Kuczynski and several years before publication of the book in 1930.
91. Fisher, in fact, published a short article on this subject in 1927 (see *CP* 60). Shortly afterwards, when a letter from Lotka appeared in *Eugenics Rev.* **19**, 257-8, claiming priority, it was accompanied by the following editorial note, 'Dr. Fisher writes: I am much interested to see how closely Dr. Lotka's work, which I had not previously seen, agrees in aim and method with the recommendations I have made. Evidently the only absolutely novel suggestion in my article lies in the estimation of a definite "reproductive value" for each age of life. Dr. Lotka's suggestions and mine are still unfortunately in the future as far as British official birth data are concerned.'
92. Dr H.G. (later Sir Gerald) Thornton, in commenting on Fisher's Eddington Memorial Lecture, *Creative aspects of natural law* (*CP* 241), had written that whilst Natural Selection must be the operative factor in the development of a higher structure in a living organism, it 'does not seem to explain the tendency for increasing complexity in the inorganic world or the appearance of new products of the human intellect such as works of art or original concepts.'
93. See Preston, F.W. (1953). Lecture version of Paper on annealing as genetics. *The Glass Industry* **34**, 485-6. Preston shows that Fisher's functional equation $f(x+1) = \exp(f(x)-1)$, considered in Chapter IV of *GTNS*, provides a good description of the process of annealing.
94. Dr J.F. Tocher, editor of *The book of Buchan*, had asked Fisher if he would contribute a chapter on 'National efficiency from the standpoint of heredity' in which he might 'give a lead in how to improve the physique, character, and

ability of the British Nation'. Fisher's contribution entitled, 'Heredity, environment, and national efficiency', was published as Chapter 4 of the Jubilee Volume of *The book of Buchan* (1943).

95. Todd, C. (1930). Cellular individuality in the higher animals, with special reference to the individuality of the red blood corpuscles. *Proc. R. Soc. B 106*, 20-44. See Haldane's letter of 29 April 1930 to Fisher (p. 209) for his comments on Fisher's letter to Todd. See also Fisher's letter of 25 November 1930 to Darwin (p. 134) and *FLS*, p. 338.
96. Fisher had suggested that Todd should test serologically for the female-determining chromosome. (See Fisher's letter of 10 June 1930 to Haldane, p. 212). On 2 October 1931, following Fisher's enquiry as to progress, Todd reported that he had not been able to tackle the complete experiment on the sex effect. In fact, there had been high mortality in his fowls which had been fed some alcohol-extracted protein residues in error. Todd went on to tell Fisher of his interesting finding that two fowls immunized in parallel with the same doses of the same red blood cells produced qualitatively different antibodies. This was an important discovery because it had been generally assumed until then that the nature of the immune antibodies produced depended solely on the character of the antigens used.
97. Todd had written that after spending much time trying to find a more delicate method of detecting small amounts of iso-agglutinin in the serum, he had not found any indication of a sex difference.
98. See Wright, S. (1929). Fisher's theory of dominance. *Am. Naturalist* **63**, 274-9. Wright suggested that the selective pressures on the modifying genes were too small to be effective.
99. An outline of Fisher, R.A. (1929). The evolution of dominance: a reply to Professor Sewall Wright. *Am. Naturalist* **63**, 553-6 (*CP* 81).
100. Wright had agreed that the main question at issue was whether a very slight selective pressure acting for a correspondingly long time would be equivalent to a much greater pressure acting for a proportionately short time. He said that his criticism of Fisher's theory rested on the assumption that modifying factors would nearly always be subject to other selective pressures more important than those involved in the modification of dominance.
101. Wright, S. (1929). The evolution of dominance. Comment on Dr. Fisher's reply. *Am. Naturalist* **63**, 556-61.
102. Wright maintained that it was proper to use δp, the change in frequency of a modifier gene, as the basis for comparison of the effects of selection and mutation. He had asked Fisher about the significance of his usage of the selective intensity i in *CP* 81.
103. Wright (see Note 101) had suggested that because of population subdivision and other factors, natural populations will often be of restricted size so that random drift will be important in affecting the frequency of genes subject to very small selective differences.
104. Wright's manuscript on gene frequency distribution which he had sent Fisher on 13 August 1929. See Chapter 1, p. 41.
105. Wright had asked Fisher if he had written anything on the effects of diffusion referred to in Fisher's previous letter.
106. See *GTNS*, p. 95 and *CP* 86.
107. See Appendix A (p. 287) for a review by Fisher of Wright's paper.
108. Wright's letter included an outline of his ideas on 'adaptive surfaces'.
109. J.L. Lush, Professor of Animal Breeding, Iowa State College, Ames.

APPENDIX A: A REVIEW OF 'EVOLUTION IN MENDELIAN POPULATIONS' (S. WRIGHT, 1931)

A review of Wright, S. (1931). Evolution in Mendelian populations. *Genetics* **16**, 97-159 by R.A. Fisher (1932). Reprinted from *Eugenics Rev.* **23**, 88-90.

More than half of this number, pp. 97-159, is occupied by Professor Sewall Wright's long paper on Evolution in Mendelian populations. The mathematical consequences of Mendelian inheritance are here developed in a number of separate investigations, which together form a valuable collection of old and new material, brought together under a common notation. Professor Wright was among the first in the United States to appreciate the importance for evolutionary theory of researches of this kind, which have developed independently in this country, and later in Germany. The results are in striking contrast to the opinions early formed, and tenaciously adhered to by several early writers on Mendelism, in its bearing on evolution. Professor Wright sums up this aspect in the words: 'The conclusion seems warranted that the enormous recent additions to knowledge of heredity have merely strengthened the general conception of the evolutionary process reached by Darwin in his exhaustive analysis of the data available seventy years ago.'

Aside from the scientific conclusions which the independent contributions of workers in several different countries have now set on a firm foundation, Professor Wright makes some philosophical observations on the nature of the evolutionary process, which are of great interest, although necessarily more personal and subjective:

> 'Evolution as a process of cumulative change depends on a proper balance of the conditions, which, at each level of organization—gene, chromosome, cell, individual, local race—make for genetic homogeneity or genetic heterogeneity of the species. While the basic factor of change—the infrequent, fortuitous, usually more or less injurious gene mutations, in themselves, appear to furnish an inadequate basis for evolution, the mechanism of cell division, with its occasional aberrations, and of nuclear fusion (at fertilization) followed at some time by reduction make it possible for a relatively small number of not too injurious mutations to provide an extensive field of actual variations.

One of the most important factors on which this balance depends, according to Professor Wright, is size of population. He points out that in very small populations the effect of selection is much reduced, so that the chances of individual survival must lead to the occasional establishment of deleterious mutations, with consequent degeneration and extinction. The reviewer is convinced of the reality of this effect, though the fact that the human breeder working with not very large populations can make substantial progress by the exercise of stringent selection, shows that it is possible to over-emphasize its importance. On the other hand Professor Wright considers that: 'In too large a freely interbreeding population ... there is great variability, but such a close approach to complete equilibrium of all gene frequencies that there is no evolution under static conditions.' He therefore argues that the subdivision of species into partially isolated local races of small size is an important condition not merely, as is obvious, for fission into distinct species, but for progressive evolution. This conclusion is much more debatable, for even under static conditions, unless it is postulated that the organism is as well adapted as it could possibly be (in which case, obviously, evolutionary improvement is impossible), the equilibrium will be broken by the occurrence of any favourable mutation, of which a steady stream will doubtless occur in one or other of the very numerous individuals produced in each generation. The advantage of the large populations in picking up mutations of excessively low mutation rate seems to be overlooked, possibly because the author has throughout his argument taken as the standard of mutation rate, such values as are found in the best known loci in *Drosophila*, mutations which are well known probably only because their mutation rate is high. Moreover, static conditions in the evolutionary sense certainly do not occur, for, apart from geological and climatological changes, the evolutionary progress of associated organisms ensures that the organic environment shall be continually changing.

APPENDIX B: A REVIEW OF *THE CAUSES OF EVOLUTION* (J.B.S. HALDANE, 1932)

A review, hitherto unpublished, of Haldane, J.B.S. (1932). *The causes of evolution.* Longmans Green, London by R.A. Fisher.

In his preface to this brilliant book Professor Haldane states that it

> 'is based on a series of lectures delivered in January 1931 at the Prifysgol Cymru, Aberystwyth, and entitled *A Re-examination of Darwinism.* These lectures were endowed by the munificence of the Davies family, with the provision that their substance should be published in book form. This admirable condition ensures that, unlike the average university lectures, which stale with great rapidity, they should only be delivered once, and also that they should be made available before any novelty which they may possess has worn off.'

To the advantages of making books out of lecture series, might be added the brightness and vivacity of Professor Haldane's lecturing style, carrying with it, however, the countervailing disadvantage of an unduly discursive treatment, even to the point of being sometimes merely allusive, of the wide field of topics mentioned; and, what is perhaps more serious, of an unusual prominence of the first person, associated with the bare statement of personal opinions, in many cases where we should have been glad of a presentation of the evidence. Thus in the introduction, p. 33, the sentence 'I can write of natural selection with authority because I am one of the three people who know most about its mathematical theory' has been allowed to stand. On p. 96 it appears that the two other 'authorities' are Professor Sewall Wright, of Chicago, and the reviewer. The last would urge, therefore, that the fact that these three writers have published their analytical efforts more copiously than others need not make them overlook three serious considerations.

(i) The probability that some 300 readers or more have probably assimilated everything of value that they have written, and may well know more about the mathematical theory than any of the three writers named.

(ii) That the points in which these writers are agreed have so far consisted chiefly in clearing the ground of the *debris* of anti-Darwinian criticism, which occupied so much attention in biological literature towards the end of the nineteenth, and the beginning of the twentieth century. As Professor Haldane says (p. 215), statements such as 'Natural selection cannot account for the origin of a highly complex character' will not bear analysis; or, as he emphasizes in his preface (p. vi), a Lamarckian transformation, even if physically operative, would, with particulate inheritance, be demonstrably ineffectual in producing evolutionary change. While it is, perhaps, of some value to have shown that on such issues the early followers of Darwin were right, and their critics mistaken, the practical test of the mathematical theory of natural selection as a means for the advancement of science, must lie in its power of giving a rational interpretation to biological phenomena, hitherto obscure, and of predicting others not yet observed. Short of this, there is not much to make a song about.

(iii) The third criticism, therefore, of the theory of 'three authorities' is that they show wide disagreement in questions of interpretation, such as the evolutionary modification of dominance, and the existence of selection in species showing a stable polymorphism. Professor Haldane evidently dissents largely, or entirely, from the reviewer's opinions on these points, and it follows unmistakably either that Professor Haldane, or that I, would be a less satisfactory guide than any judicious reader who had formed a just view of the state of the evidence.

How much the book would have gained by expansion considerably beyond the volume of the lectures—the length could easily have been doubled—and especially by supplementing bare, though impressive, opinions, with the reasons on which they are based, may be judged from the four passages in which the theory of the evolutionary modification of dominance is alluded to. (i) (page 134) 'Wright (1931) and I (Haldane 1930a) have criticized this theory, and I doubt if it can stand in its original form. Nevertheless it undoubtedly has some truth in it, and there can be little doubt that mutation pressure has been a cause of evolution, if perhaps a less important one than Fisher believes.' (ii) (page 142) [Fisher's theory of dominance is] '(in my opinion probably false)' (iii) (page 195) 'Fisher's (1930) analysis of the effect of selection on such a population involves his theory of the evolution of dominance, which I do not myself hold. His analysis is very greatly simplified if we restrict ourselves, as I shall do here, to the case where all the genes concerned are fully dominant.' (iv) (page 193) 'Fisher (1931) has based a theory of the evolution of dominance on this basis. He believes that abnormal genes are originally intermediate in dominance, rather than recessive. But modifiers are selected which render the heterozygote normal in its viability. I have criticized this theory (Haldane, 1930a) though I believe it to be true in some cases. Fortunately, however, it is susceptible of experimental proof or disproof (Fisher, 1930, p. 62), and since Fisher is undertaking the necessary experiments there is no need to state the arguments for and against this theory here, since at least one of these arguments will be shown to be fallacious in the near future.'

The reader who is curious to know on what evidence divergent opinions are held is kept guessing. He is not even told whether Haldane still adheres to his former theory that modification of dominance has taken place by the selection of multiple allelomorphs rather than by the selection of modifying factors as proposed by the reviewer. He is left wholly in the dark even as to what truth Haldane holds the theory 'undoubtedly' to contain, or in what class of cases he believes it to be true; and, without an answer to these questions he can scarcely judge of the relevance of much of Haldane's mathematical treatment, for it is of little use that the analysis should be very greatly simplified, if this is at the expense of making an unjustified assumption. But little expansion would have been needed to replace *ex cathedra* pronouncements (including one very curious prophecy) by a reasoned contribution to the subject.

The fact of the evolutionary modification of dominance has been demonstrated by Harland's work for a particular example in cotton, though Harland hesitates to accept the selective theory from which this fact was previously inferred. His experiments demonstrate, moreover, that the differentiation in this case is due to modifying factors, and not to Haldane's proposed mechanism of multiple allelomorphs. It is difficult to imagine why Haldane should not make it clear (i) whether he accepts Harland's observational findings, (ii) whether he questions Harland's genetical analysis of the situation, and (iii) whether, accepting these, he believes in some alternative evolutionary process by which the situation could have been brought about.

The reviewer must protest that Haldane's allusion to the experimental work he has undertaken, with two species of land-snails and with jungle fowl, is highly misleading. These experiments concern possible, though at present uncertain, extensions of the theory to two cases showing rather exceptional dominance phenomena. It should be obvious that the reviewer is not likely in his spare time to attempt to verify the great body of observational data, already well established by others, on which his views on the evolution of dominance have been founded.

The necessity of clearing up a personal point has necessitated giving more space to it than would be otherwise warranted. The examples quoted, however, are not unrepresentative of the style and manner of the rest of the book. One receives the impression more of able conversation on a series of interesting topics, than of a considered treatise on genetical theory; and Haldane's philosophical attitude towards the evolutionary process, developed in Chapter VI, will be found thought-provoking by many who are little concerned with the merely mechanical and scientific aspect of this process.

APPENDIX C: A REVIEW OF *THE AUTOBIOGRAPHY OF CHARLES DARWIN 1809-1882* (ED. NORA BARLOW, 1958)

A review of Barlow, N. (Ed.) (1958). *The autobiography of Charles Darwin 1809-1882.* Collins, London by R.A. Fisher (1958). Reprinted from *Nature* **182**, 71.

Lady Barlow keeps adding to our debt of gratitude for her untiring care in editing or de-editing the literary remains of her illustrious grandfather.

It is good to have Charles Darwin's original biographical sketch as it was written and left for the information of his children and grandchildren 'with original omissions restored'. His grand-daughter's notes are helpful and informative, and do not trouble or interrupt the narrative.

About half the book is, however, devoted to new material. There are two appendixes, one of eighteen pages 'On Charles Darwin and his grandfather Dr. Erasmus Darwin', and one of more than fifty entitled 'The Darwin-Butler Controversy'. The six notes which complete the volume are of personal and bibliographical interest, and take only twenty-six pages.

The relationship between Charles Darwin's evolutionary doctrine and that of Erasmus Darwin is treated here in terms of the theories, if that is not too strong a word, held by Charles on the subject of scientific inference. I believe this point of view does less than justice to his grandfather, who wrote in the tradition of didactic poetry, and was, to the taste of his century, one of the greatest of poets. I do not understand that this fact should be ignored merely because, eighty years later, the function of poetry in contemporary literature had changed; and people like Coleridge had written spitefully.

The charge that Charles plagiarized his grandfather's work, and took credit for his ideas, was indeed nothing but a malicious falsification due, I suppose, to Samuel Butler relying on the public's lack of direct familiarity with the work of either. I could wish that Lady Barlow had given half a dozen pages in this first appendix to quotations from *The Botanic Garden* and from the *Zoonomia.* The sonorous lines could be annotated from Buffon or Lucretius, lest the reader forget that Erasmus as an eighteenth century *philosophe* was expressing his appreciation of an old and richly poetic idea and not assembling the evidence for an inductive proposition. It would be apparent that Erasmus was not trying to do what his grandson later did, and this not from any lack of understanding of the proper procedure of the natural sciences.

I have, for myself, no doubt that Charles would never have undertaken the large task of marshalling the evidence for 'descent with modification', which had indeed become much more impressive since Erasmus's time, without having hit upon a truly naturalistic explanation. Speculation, indeed, has an important part to play in inductive reasoning, but speculation supported by a theory which both Cuvier and Lyell had been forced to reject was to Charles Darwin a major obstacle.

APPENDIX D: 'THE CENTENARY OF DARWINISM' BY R.A. FISHER (1959)

This paper, hitherto unpublished, was read at a meeting held in Adelaide in 1959.

The great advantage of celebrations of Centenaries lies in the opportunity they afford to consolidate what has been learnt in a century, and to fix in orderly relation to each other, and to the whole, the diverse movements, some fruitful, some abortive, which confuse the history of current events. A century affords an opportunity of taking a bird's eye view, and of eliminating unjust and erroneous opinions more speedily than would happen in the absence of such a periodic stocktaking.

What was accomplished by Darwin was not one task but two. Each [was] of considerable magnitude, requiring the marshalling of bodies of evidence, each detail of which was familiar to many of his predecessors, but [which] had not been assembled to constitute a coherent doctrine. Each side of his task encountered much prejudice and opposition, and required the strict logical examination of many related possibilities. Each also had been a subject of some controversy, with its tendency to the taking of sides, and the hardening of prejudice. Neither was capable of doing much without the other, for the two things that had to be done were, *first*, the establishment of the Historical Fact of descent with modification throughout the organic world, and *secondly*, production of a philosophically rational explanation of the fact, or a theory of the *means* of modification in the course of descent.

In each of these fields Darwin had many predecessors; what was unprecedented was their treatment by Darwin as but two aspects of a single problem.

The conjecture of transformism

As a philosophic conjecture, similar to some of the cosmological conjectures of our own day, the idea of transformism is extremely ancient. Greeks, and probably Indians, played with the notion. Lucretius, in many ways a precursor of modern science, certainly took it literally. Buffon, to whom the eighteenth century philosophy of the Age of Reason owed much, was also attracted. He had the wisdom not to discuss possible means, but to stick to the evidence for the fact. By about 1790, thinkers in many countries, Erasmus Darwin, Isadore Geoffrey de Saint-Hilaire, and Goethe all advocated the idea, with somewhat vague speculation as to causes. Lamarck was much more ambitious. His ideas were, however, equally speculative, and were exposed to trenchant criticism and rejection. It was not logically necessary, but quite in accordance with scientific controversy in fields where little is known, that the rejection included transformism itself, as well as its supposed mechanism, so that from the time of Cuvier to Charles Lyell's *Principles of geology* (1831), and indeed until the *Origin* itself, orthodox opinion ignored or dismissed the genealogical unity of the animal and plant kingdoms. The movement of thought started by Buffon had been frustrated by premature and unconvincing speculation, rather as the early geological evidence for continental movements, before the decisive evidence of Rock Magnetism, was largely neutralized by the speculative discussion of its possible but implausible causes. Still, the persuasive evidence for transformism remained, and was indeed quietly receiving massive accretions with the progress of the biological sciences, so that before the *Origin* was published, many new writers, though often timid and confused, had given support to the principle.

The first part of Darwin's task, then, was to present the historical fact of organic evolution for the reconsideration of the biologists of his day, in spite of a congealed and indurated doctrine to the contrary. His contribution was to transform the theory from an arid speculation to a *unifying principle* in which whole vast bodies of fact could be given coherence and intelligibility. His observations on the *Beagle* enabled him to mobilize an avalanche of facts relating to such fields as Geographical Distribution, Geological Succession, the principles of Classification, the affinities displayed in Embryology.

These facts were, of course, due mostly to the labour of others during the two generations since his grandfather's time. The suggestive character of each element had probably been appreciated by others. The labour of the collection and organization of the whole *corpus* was Darwin's, and it is a labour which he could scarcely have attempted and still less brought to completion had he not found in Natural Selection the key which his mind was seeking. His logic demanded not merely a *theory of causation* for the transformation of species, but a theory dependent on *known*, or independently verifiable causes. It was only with such a key that he could hope to persuade such weighty and critical minds as those of Hooker, Lyell, and Thomas Henry Huxley.

It is, I believe, only in the light of contemporary literature and private letters that it is possible to dispose of the rather trivial stress often laid by later writers on the numerous partial anticipations of many of Darwin's ideas. This exaggeration seems to flow out only from an imperfect acquaintance with what was known to others—often it had been known for generations—but to the illusion that original thought in the sciences is to be thought of as having no roots at all, but to be imported like Fire by Prometheus. However, originality in the sciences, as in practical life, is usually displayed by perceiving the application of a particular thought or process. The basic idea of Evolution was unimportant and sterile in the generation before Darwin's return in the *Beagle*; after 1859 it became the most fruitful idea in the biological sciences. Equally, it might be said that the idea of Selection, widely familiar as it was to stock breeders from ancient times, gave little to Biological Science until Darwin married it to the theory of the organic transformation in plants and animals.

Natural selection

Good writers, however, oversimplifying by taking the part for the whole, have often written as though the bare idea of selection was the whole of Darwin's contribution. The attitude is illustrated and, I think, intentionally satirized in Huxley's reaction to the *Origin*, 'How stupid of me not to have thought of that'. For the notion of selective modification is very simple, and was in certain circles very familiar. The bridge between the traditional lore of the stock breeder, and the Theory of the Organic World was not however easily crossed; very few could imagine that the effects of selection transcended specific boundaries. Consequently, and especially by reason of the immense fame of Darwin's work, the curiosity of the learned world has been rewarded by the discovery of a great many so-called 'anticipations', of particular fragments of Darwin's theory.

Samuel Butler, a witty and imaginative writer, without the discipline of mind to be gained from serious study in the Natural Sciences, recklessly accused Darwin of plagiarizing of, among other people, Lamarck, whose theory had formed the major obstacle to the learned world building on the foundation provided by Buffon and his followers.

With respect to the principle of Natural Selection, Darwin affixed to the later editions of the *Origin* an 'Historical Sketch' in which he refers among other works to Wells' *Two Essays upon Dew and Single Vision* (1818) in which, however, Wells applies the principle only to Man, and to Patrick Matthews' work on *Naval Timber and Arboriculture* (1831) in an Appendix to which there is a discussion showing that Matthews understood the principle perfectly. Since then the late Professor E.B. Poulton has called attention to J.C. Prichard's *Researches into the Physical History of Mankind* in the second edition of which (1826), though not in subsequent editions, Prichard goes far to anticipate Darwin and very thoroughly anticipates Weismann. More lately, L.C. Eiseley in the *Proceedings of the American Philosophical Society* (Vol. 103, pp. 94-158 (1959)) has given 60 large pages to exhibiting one Edward Blyth, as the true progenitor of Darwin's ideas.

The correspondence of words and thoughts adduced are really trivial. The men were nearly of the same age, both sedulous readers of the same periodicals, and therefore having the same oddities, such as the Ancon sheep, frequently brought to their notice. They were both inheritors of a tradition of animal and plant breeding in which the practical efficacy of artifical selection was universally recognized. Blyth was not even an evolutionist, but like Lyell at the same period, accepted the theory of *Special Creation*, with its closed species. He had no stimulus to explore the exciting possibility that the very tool on which breeders of animals and plants had learnt to rely was in verity the means by which these species had come into existence. His reasoning could supply little inspiration to young Darwin, save possibly as a foil, or a reminder of fallacious arguments which ought to be answered. If forerunners are wanted, many more interesting ones have been uncovered than Edward Blyth.

No case could illustrate more strongly the fact that any reconsideration of Darwin's contribution should consider its scope and magnitude as a work of co-ordinated reasoning, and that it is fatal to lay stress on singular details.

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NAME INDEX

An asterisk indicates a correspondent, the page references to the letters being shown in italics.

SUBJECT INDEX