# 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.<sup>1</sup> 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<sup>2</sup>: 26 July 1948

On the boat from Sweden I happened to pick up in the library your interesting book on Darwin<sup>3</sup>. 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<sup>4</sup>, 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.<sup>5</sup>...

#### 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.

[F.S.] Copy of draft feview 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.'<sup>6</sup>

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<sup>7</sup>. I ought to say, though, that I think Prof. C.G. Darwin<sup>8</sup> 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<sup>9</sup>, 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<sup>10</sup>....

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*, <sup>11</sup> 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<sup>13</sup> 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,<sup>14</sup> 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?<sup>15</sup> 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.<sup>16</sup>

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<sup>17</sup> to Fisher: 7 August [1934]

I.

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.<sup>18</sup>

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 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.<sup>19</sup>

#### Fisher to J.L. Crosby: 5 July 1940

... The case you have found<sup>20</sup> 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.<sup>21</sup> 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

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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. Bio*metrika* 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.<sup>22</sup>...

## Fisher to J. Davidson:<sup>23</sup> [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?<sup>24</sup> I had come in unprepared to speak and funked it quite shamelessly. However, I took up the matter with him in correspondence<sup>25</sup> 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<sup>26</sup>. ...

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

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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<sup>27</sup> or Plunkett's, <sup>28</sup> 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<sup>29</sup> 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.<sup>30</sup>

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<sup>31</sup>....

## 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;<sup>32</sup> 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.

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#### 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.<sup>33</sup> 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  $\chi^2$  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.<sup>34</sup> 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

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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,<sup>35</sup> 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  $\times$  3 lattice of 9 possible genotypes, and for n a 3<sup>n</sup> 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.

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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,<sup>36</sup> 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.

FISHER'S OTHER CORRESPONDENCE

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<sup>37</sup>. 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....