

16 May 1934.

My dear MacBride,

Thanks for your letter. I should be especially glad if you could come down sometime to Harpenden, see the experiments, as far as they have gone this year, and lunch with me on the same day. I am getting Morgan to do this sometime this week, but he has not yet fixed his date and when he does it may not suit you, so to make it certain would you care to sacrifice Saturday.

The experiment has now reached an extremely interesting stage. The story of the experiment is this: As you know, poultry geneticists have reported quite a number of the characters found in domestic races as dominant to those found in the wild species, for example feathered feet are supposed to be dominant to the featherless or clean feet. There are regularly feathered breeds, such as the Japanese Silky, whereas the jungle fowl and most other breeds have no feathers on the feet. In the same way polydactyly has been spoken of as dominant to the normal four toes, rose comb to the normal single comb, the white of the White Leghorn to the normal coloured plumage and the barred feathers of the barred breeds to the normal unbarred feathers.

I believe nearly 20 such factors could be listed, which the geneticists who have bred them at one time or another have called dominant. In addition to these, however, other characters of the fowl are quite ordinary recessives, such as silky plumage and the recessive white usually found in the Wyandottes.

Domestic poultry are exceptional in showing all these dominants, for in most species, both animal and plant, which have domesticated varieties these varieties are nearly all either quite recessive or if not that have an intermediate heterozygote, so that dominance is absent or incomplete, for example the budgerigars shown by Punnet at the last sioree exhibited two or three completely recessive mutations and one with an intermediate heterozygote. As more information has been accumulated about other species, like Gammarus or Drosophila, this rule has been found to be very general and the situation in poultry has looked more and more exceptional.

Some years ago (1928), arguing from the fact that different species of Drosophila, as also of rodents, had shown homologous mutations, which in the case of Drosophila could be shown by crossing to be really homologous. I argued that these mutations must have been occurring in the species for probably millions of generations and that this provided a possible explanation of the fact that they are so prevalently recessive. It is characteristic of mutations of the kind which geneticists

study, at least to be injurious to viability, and probably more so in wild conditions than in culture, and to be decidedly variable in manifestation, or as I should say, that the reaction of the organism to the mutation which was introduced into it is sometimes violent, leading to severe deformity and sometimes much milder, in which case it is fair, I suppose, to think that somehow the rest of the organism has managed to compensate for or repair the damage normally done by the mutation. Moreover, the degree of manifestation is certainly inheritable for mutant stocks, which to begin with were found to be scarcely viable had very frequently increased in viability after a number of generations and become useful genetic material, with at the same time less extreme manifestation of their peculiarities.

I argue, therefore, that if for a million generations or so a small proportion of heterozygotes for some defect, such as albinism, were maintained in the species, the heterozygotes which were least influenced by the mutation, and therefore most normal in appearance, would survive best and so gradually modify the species until in its heterozygous manifestation the mutation had become completely recessive, and that probably dominance was absent and the heterozygote intermediate in appearance when the mutation first occurred. This theory has been a good deal strengthened since I first put it forward, by facts that I was then unaware of, and which I have summarised in a paper called

"The Evolution of Dominance", published in Biological Reviews, of which, I think, you have a copy.

Now for the special case of poultry, it is on any view exceptional, but it would certainly be a score to my theory if it could show why this case was exceptional, and it occurred to me that human selection, especially in the earlier stages of domestication, presumably by jungle tribes in Burma and Assam, might account for this odd group of apparently dominant mutants. The point is that breeders always preserve novelties and oddities and that when parentage is under control, as with both species, any recessive which might turn up will breed true and constitute new domestic varieties, but that in jungles, full of the wild species, the domestic flocks would certainly be sired frequently by wild cocks. Indeed, even in England, cock-pheasants make a certain amount of trouble in domestic pens. The only novelties then which would reappear in subsequent generations, let us say among sacred fowls kept at some jungle shrine, would be those that were partially dominant, or at least not completely recessive, and if, like white elephants and Apis bulls, and indeed some breeds of poultry in the East, their sanctity depended on their being freaks it is certain that those heterozygotes which showed the strongest reaction would be consistently preserved.

Anyhow, whether I have got the details of the story right or not, it seemed possible to suggest one quite definite

experiment , which would throw light on the matter, for if I am right that the dominance in domestic breeds of fowl is due to human selection, then it should be absent, or nearly so, in the wild jungle stock, and if it is absent then poultry, at least in the wild phase, is no longer an exception to the general rule about dominance. What I set out to do was to introduce mutant factors, such as that for dominant white, into a stock of jungle fowl of wild origin. In each generation I selected poulets showing the mutant character and mated them to cocks of pure wild stock, obtaining mixed broods with about half showing white and half the normal plumage. This crossing back to the wild I have now done for most of the mutants chosen for five generations, and this year I am mating the heterozygotes to each other to see whether the homozygous mutants, which should constitute about a quarter of this year's broods are (1) indistinguishable from heterozygotes, in which case the mutant is properly described as dominant, or (2) show the mutant character so much enhanced that they can be distinguished from the heterozygote, in which case dominance is absent or incomplete.

In choosing what characters to work with I soon found that a large number of those commonly called dominant were not really so, even in the crosses between domestic varieties this is true of frizzled plumage, for example of spangled feathers and of sex-linked silver (v. gold). I, therefore, chose, as far as possible, characters that had a good reputation for being

dominant. The list I have been using is as follows:

- (1) Feathered feet
- (2) Polydactylly
- (3) Dominant white
- (4) Crest
- (5) Rose comb
- (6) Black skin
- (7) Barred (sex-linked)

Since last year I have been sure that feathered feet and polydactylly are not really dominant when tested in the wild germplasm. For last year I interbred birds with feathered feet of the fourth generation and they threw a few with enhanced feathering, which I suspect were homozygotes, though they both died and I have had to repeat the crossing this year, - but in addition they gave some with extra toes, although all the parent birds in the pen had normal feet, showing that polydactylly, at least, can be carried as a recessive by apparently normal birds. This has also been found in some breed crosses, and was at first ascribed to an inhibitor, which, I believe, was completely imaginary. I have only a few broods of chicks this year yet, but these certainly demonstrate my case for barred plumage, and are strongly suggestive for black skin. To complete the experiment beyond criticism, it will be necessary to carry it on for another year or two, to demonstrate, not only that enhanced types appear in the matings

where they are expected, but that these particular birds and not the others are the homozygotes.

My stock is now, as one would expect from their ancestry, almost pure, wild jungle fowl, apart from the particular mutants suggested. The great difficulty in breeding them is that the early flush of eggs in February and March is almost completely infertile. I get my best broods in late April, May and June, which is already dangerously late, since chicks hatched in August make very little growth before the autumn and usually die^{or} that season. I should, however, very much like to show you what I have now, as I cannot tell how long individual chicks will live or how the plumage contrasts will develop as they grow older.

Yours sincerely,