GENETIC STUDIES IN POULTRY.

II. INHERITANCE OF EGG-COLOUR AND BROODINESS.

BY R. C. PUNNETT AND THE LATE MAJOR P. G. BAILEY, R.F.A.

(With 13 Text-figures and Plate IX.)

Introductory.

IN 1910 we started some experiments with the intention of attempting to work out the genetics of egg-colour and of broodiness in poultry. At the time at which they were begun there was a fair prospect of means being found to carry them to a definite conclusion. This prospect was shattered by the advent of war, and the work was gradually curtailed until eventually it had to be abandoned. Nevertheless, the experiments, fragmentary as they are, present some points of interest which seem worthy of being placed on record.

Few observations concerning the genetics of either egg-colour or broodiness have hitherto been published. Hurst (1905) found on crossing the two non-sitting breeds, White Leghorn and Houdan, that none of the F_1 hens went broody; but that from the cross Black Hamburgh × Buff Cochin the F_1 pullets all went broody like the Cochin. With regard to egg-colour he states that from the former cross all the pullets laid only white eggs, while from the Hamburgh-Cochin cross the F_1 ♀♀ all laid "eggs of varied hue, none being so brown or so white as the parent breeds." Neither character appears to have been the subject of investigation beyond the F_1 generation.

A remarkable account of the mode of transmission of egg-colour was published by Holdefleiss in 1911. He contended, among other things, that the colour of the egg laid by the hen is affected by the cock that fertilises it: that the hens resulting from a cross between birds belonging to brown- and white-egglaying strains lay both brown and white eggs: and that such F_1 hens mated to a brother produce both brown and white eggs in the ratio 3 : 1. Though we regard Holdefleiss' paper as open to destructive criticism we do not consider it necessary here to do more than state that we have encountered no phenomena of the kind in the course of our work.

Inheritance of Egg-Colour.

The experiments, of which an account is now given, were designed for the investigation of egg-colour and of broodiness on the same material. For convenience the crosses made will be considered first in connection with egg-colour. In 1910 and 1911 F_1 birds were produced from the mating Brown Leghorn ♀ × Black Langshan ♂, and in 1912 from the reciprocal. The Brown Leghorn hens belonged to a strain which had been under observation for some years previously. The eggs were white, and broodiness was never observed. The Langshans were purchased in 1910, and during this season and the following one they were used for breeding pure Langshan as well as for crossing. Those bred all laid brown eggs of a depth similar to that of the egg figured on Pl. IX, fig. 5, though perhaps not quite so pink in tone. The variation in the depth of the colour in the various birds was slight. Subsequently a further set of experiments was made in which the non-broody white egg breed used was the Gold Pencilled Hamburgh, the brown egg broody race being, as before, the Langshan.

At this point a brief digression is necessary in order to explain the procedure adopted in recording the colour of the egg. After consideration of several methods we decided to make use of the standard colour charts published by the Société française des Chrysanthémistes. It was not always possible to match the tint of a given egg exactly, for some had slightly more pink, and others again slightly more yellow than the nearest colour on the chart. Nevertheless we felt that the record was sufficiently accurate for our purpose, since it was the depth of colour rather than the exact tint that we wished to register. Six sheets of the chart, each with four different shades, were made use of, viz.:

Jaune maïs/36[1].
Saumon jaunâtre, 65.
Chair tendre, 68.
Saumon rougeâtre, 73.
Chair rosé, 136.
Rose de Nymphe, 137.

The sheets were carefully collated by eye and the following 12 grades were established for use in the experiments:

Grade 1. White.
" 2. Very slightly tinted.
" 3. R. de N. 1.
" 4. R. de N. 2.

[1] The number after each colour denotes the number of the sheet in the publication referred to.

Grade	5.	R. de N. 2, Ch. t. 1.
,,	6.	R. de N. 4, Ch. t. 2, Ch. r. 1, J. m. 1.
,,	7.	Ch. t. 3, Ch. r. 2.
,,	8.	Ch. t. 4, Ch. r. 3.
,,	9.	Ch. r. 4, J. m. 2.
,,	10.	J. m. 2, S. roug. 1, S. jaun. 1.
,,	11.	J. m. 4, S. roug. 2, S. jaun. 2.
,,	12.	S. roug. 3, S. jaun. 3.

These grades are of course arbitrary, and in passing from the lowest to the highest there is no regular quantitative accession of colour. The difference between grades 2 and 3 for example is certainly much less than between grades 9 and 10. Where the amount of colour is slight a difference is more easily apprehended than where the shade is deeper.

In practice a difficulty arises from the fact that the tint of a given hen's eggs often varies to some extent during her laying period. Our experience has been that the eggs laid earlier in the series are generally rather darker than those laid later on in the season, and in the case of the more deeply tinted eggs there may even be a difference of several grades between those laid in March and those laid in July. Sometimes also the first few eggs laid by a pullet are variable in tint. Our practice therefore has been to neglect the first few eggs and to base our record on several eggs laid in the earlier part of the season. Our experience has been that, in the great majority of cases, such eggs show practically no variation in tint.

In the case of a few birds a further difficulty has arisen in attempting to grade the egg. In these cases a tinted egg is laid which has the appearance of being covered with a delicate chalky film. That the texture of the shell plays a part in the tint of the egg is obvious, but the extent to which the two are interdependent would necessitate research directed upon this special point. In the case of these "chalky" eggs we decided, after some hesitation, to record their grade as they appeared when moistened and rubbed. After such treatment the egg appears several grades darker than when fresh from the oviduct.

We may now turn to the experimental results, taking first the Leghorn-Langshan cross. Originally this was made between a Leghorn ♀ and a Langshan ♂. The Leghorn belonged to the strain procured by Mr Bateson from Mr Boys-Smith in 1900–01. Even at that time the birds were closely inbred[1]. The strain was kept pure from admixture with any other strain until it was used in 1910–11 for crossing with the Langshan. By that time hens alone remained. Though large numbers of chicks were hatched it was found impossible to raise a cockerel. The healthiest survived until about one-third grown and then succumbed to sudden and mysterious fits. The majority died soon after hatching. Pullets were more easy to rear, though even here the mortality was considerable. Those reared were slow growers, on the small side, and

[1] Cf. Bateson and Saunders, 1902, p. 92, where a pedigree is given.

with that delicacy of appearance so often characteristic of the highly inbred thing. On being crossed with the Langshan ♂ the chicks left nothing to be desired from the point of view of health and vigour. The black down of the Langshan proved to be dominant over that of the brown stripe of the Leghorn, and a simple 3:1 ratio was realised in F_2. In adult plumage the F_1 hens were full black with dark eyes and shanks; the F_1 cocks were, on the whole, black with a varying amount of orange in the neck, shoulder and saddle hackles: the eye was orange and the shanks were horn on light. The sexual differences in the last two characters are doubtless due to a sex-linked inhibitor introduced by the Brown Leghorn hen. The eggs laid by the F_1 birds were tinted, though rather lightly, approximating to grades 4 and 5[1]. In 1911–12 a number of F_2 ♀♀[2] were reared, and 65 were subsequently tested in respect of egg-colour. The results are shown schematically in Fig. 1. The range is from white up to grade 10, i.e. almost as deep as the Langshan's eggs. The great majority however laid white or light-tinted eggs.

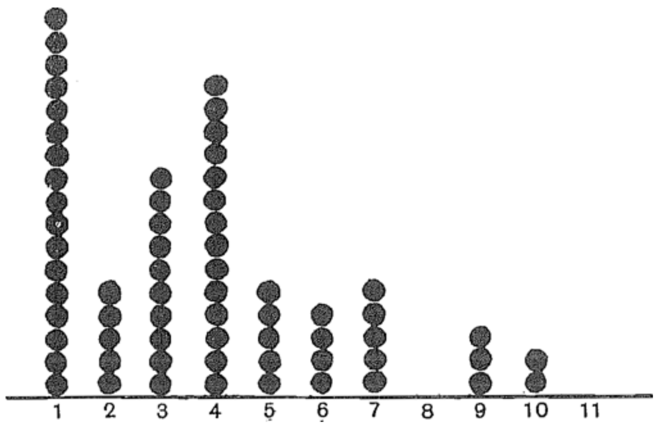


Fig. 1. Distribution of grades of egg-colour in F_2 generation ex Brown Leghorn ♀ × Langshan ♂.

Before passing on to the Hamburgh-Langshan cross, a further experiment with the Brown Leghorn and Langshan calls for attention. In 1912 we made the cross reciprocal to that described above, mating a Brown Leghorn ♂ with a Langshan ♀. The Leghorn ♂ was purchased,

[1] This statement is from recollection. The original records of the F_1 birds were in the keeping of my colleague. In the turmoil of war they appear to have gone astray, and I was unable to trace them among his papers after he had been killed. [R. C. P.]

[2] 3 F_1 ♂♂ and 12 F_1 ♀♀ in all were used for producing the F_2 generation.

and there is no reason for supposing that it was in any way related to our original stock. Of the F_1 birds the cockerels were very similar to those bred from Brown Leghorn ♀. The pullets however had orange eyes, though often with a few small patches of pigment, and their shanks were horn on light instead of horn on slaty. This is doubtless due to the Leghorn ♂ having been homozygous for the inhibitor for which we found the Leghorn ♀ heterozygous. Of interest here is the fact that the distribution of egg colours in the F_2 pullets[1] raised from this cross was quite different from that found in the reciprocal. As Fig. 2 shows

Fig. 2. Distribution of grades of egg-colour in F_2 generation ex Langshan ♀ × Brown Leghorn ♂.

the range is complete, from white to grade 11; but there is no excess of white and light tinted eggs as in the previous case. The mean grade is higher here than in Fig. 1, viz. 6·0 as compared with 3·7. It should be stated that the F_1 ♀♀ ex Langshan ♀ laid a more deeply tinted egg than the F_1 ♀♀ ex Brown Leghorn ♀.

The F_2 generation ex Langshan ♀ × Hamburgh ♂ forms an interesting commentary on the Leghorn-Langshan results. Eggs laid by F_1 pullets were tinted, belonging to about grades 6—7 (cf. Pl. IX. fig. 6). The distribution of egg-colour among the 51 F_2 pullets[2] is shown in Fig. 3. There is a complete range from the white of the

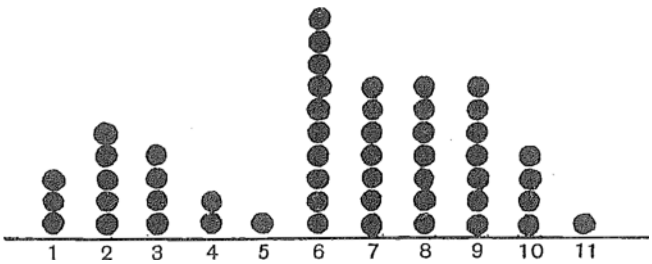


Fig. 3. Distribution of grades of egg-colour in F_2 generation ex Langshan ♀ × Hamburgh ♂.

Hamburgh up to the deep colour of the Langshan. The curve is evidently bimodal, and can readily be separated into two portions—a smaller one in which the colours range from 1—5, and a larger in which the range

[1] Raised from 2 F_1 ♀♀ and 1 F_1 ♂.
[2] Raised from 2 F_1 ♂♂ and 3 F_1 ♀♀.

is from 6—11. Those belonging to the more deeply tinted group are about thrice as numerous as the white and faintly tinted ones.

These are the chief facts with regard to egg-colour that have come from our researches, and before passing on to some special points we may consider their possible orientation. The data are clearly insufficient to justify any attempt at precise factorial analysis. Such analysis as we can pretend to must obviously be rough, and our only excuse for making it is that it may perhaps offer hints for future work to others.

We suggest then that the cases of the Langshan ♀ × Brown Leghorn ♂ (Fig. 2) and of the Langshan ♀ × Hamburgh ♂ (Fig. 3) are on the same plane, and may be taken together (Fig. 4)—that we are

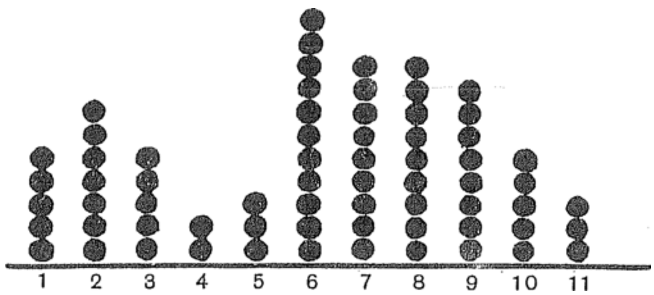


Fig. 4. In this figure the data given in Figs. 2 and 3 are combined.

concerned here with a principal factor leading to increased tint of egg—that this factor is present in a homozygous state in the Langshan, but absent from the Hamburgh and the Brown Leghorn—that in the heterozygous state the tint is intermediate. Further we suggest that the egg tint is also dependent upon one or more minor factors, which are present in the Langshan but not in the Hamburgh or the Leghorn. The effect of their presence is to lead to tinted shell, but only to a minor degree. The really dark egg must owe its colour to the principal factor, but the colour will be deeper if the minor factors are also present.

Our suggestion may perhaps be made clearer if we attempt to illustrate it by a concrete example. Let us suppose the dark egg breed to be homozygous for a major, and for one or more minor factors, while the white egg breed with which it was crossed contains none of these factors. If the various factors are inherited alike by either sex the distribution of egg-colour in the F_2 generation will be not unlike the scheme shown in Fig. 5. One-quarter of the F_2 birds will lack the major factor, and their eggs may be supposed to range between grades 1—4 according to their constitution with regard to the minor factors. The other three-quarters will contain the major factor and will vary between grades 5—11 according as this major factor is associated with one or more of the minor factors. Moreover the depth of tint may further depend upon whether the bird is homozygous for the major or for the minor factors. In this way we can form a rough interpretation of the nature of the F_2 generation such as that shown in Fig. 4.

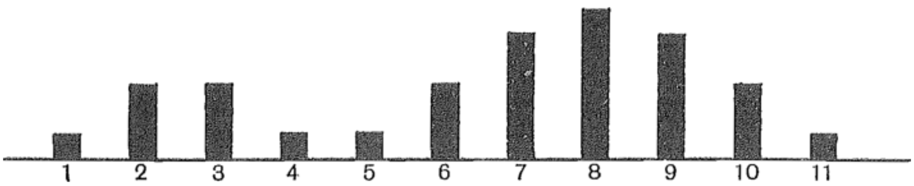


Fig. 5. Ideal scheme of distribution of grades of egg-colour in F_2. For explanation see text.

We have already seen however that the F_2 curve of egg-colour for the birds ex Brown Leghorn ♀ × Langshan ♂ is of quite a different type (Fig. 1), and is characterised by the enormous preponderance of white and of lightly tinted eggs. Now a curve of such a nature can be readily formed from our ideal curve (Fig. 5) if we suppose that the F_1 birds are of similar constitution with regard to the factors leading to pigment production, but at the same time are heterozygous for a factor leading to the inhibition of pigmentation in the eggs. Suppose that this inhibitor turns grades 1—6 into grade 1, grade 7 into grade 2, 8 into 3, 9 into 4, 10 into 5, and 11 into 6: and suppose further, for the sake of simplicity, that its action is similar whether the bird be homozygous or heterozygous: then our ideal curve shown in Fig. 5 is transformed into the curve shown in Fig. 6. Without harrying the point too closely it is clear that such a curve bears a fair resemblance to the actual curve met with in Fig. 1. If we accept this interpretation we must suppose that the Boys-Smith strain of Brown Leghorn was homozygous for this postulated inhibitor, which was lacking in the purchased Brown Leghorn ♂ and in the Hamburgh. There is the point of course that where the white egg breed was the mother one type of F_2 family appeared, and that where it was the father another type appeared: but in the absence of further data it seems hazardous to regard this as anything but a coincidence.

Though the interpretation which we have suggested is in fair accordance with the experimental data so far given, there is one further set of experiments which offer a difficulty to that interpretation. The two F_1 ♂♂ ex Langshan × Hamburgh were crossed with several Hamburgh ♀♀. Since such F_1 ♂♂ mated with similarly bred F_1 ♀♀

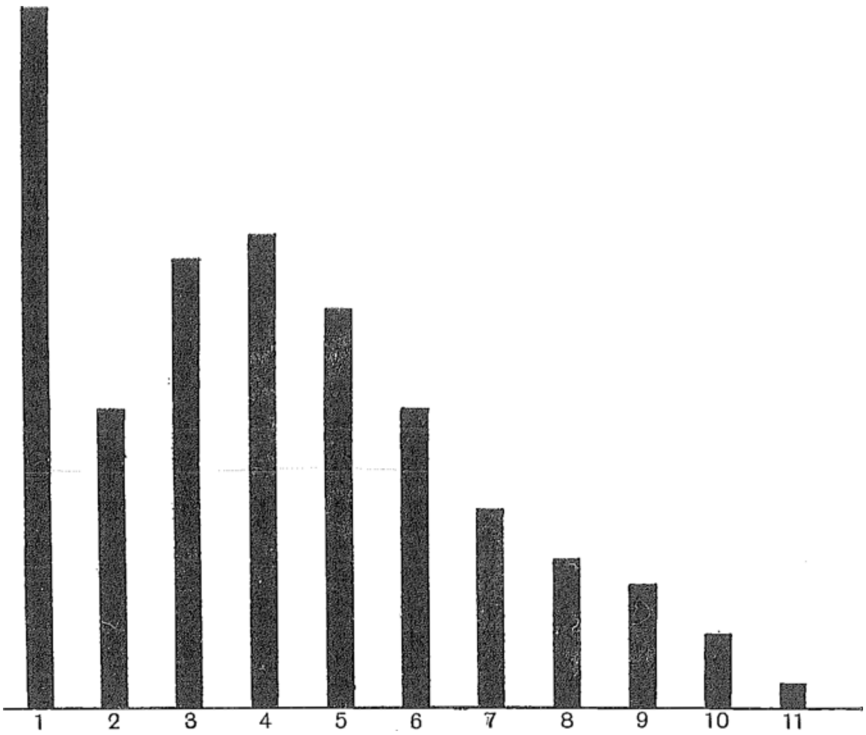


Fig. 6. Illustrating the alteration in the nature of the curve presented in Fig. 5 when the F_1 birds are supposed to be also heterozygous for a factor inhibiting the production of pigment in the egg-shell.

gave a bimodal curve (Fig. 3) we should look for a bimodal curve also when such males are mated with Hamburgh ♀♀; though we shall of course expect both modes to be shifted in the direction of lower grade. The curve actually obtained is shown in Fig. 7, and is certainly not

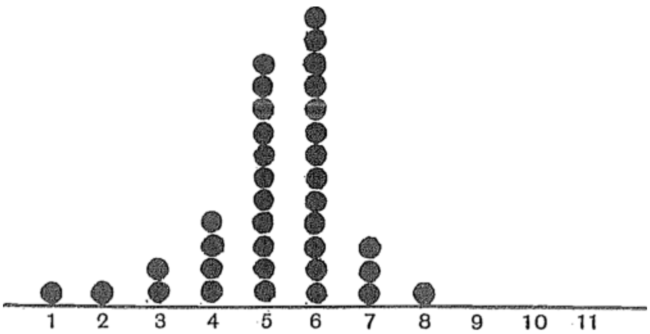


Fig. 7. Distribution of grades of egg-colour from F_1 Hamburgh-Langshan ♂♂ × Hamburgh ♀♀.

bimodal. A higher mode at about grade 6 was to be expected, but so also was another one at about grades 2—3. It is clearly not there and we cannot account for its absence.

Egg-colour and down-colour.

A. In the Brown Leghorn-Langshan cross.

We have already mentioned that in the Langshan and Leghorn cross the brown-striped down behaves as a simple recessive to the black. F_2 pullets black in the down develop for the most part into full blacks, though some may show a little gold in the hackle, and a little brown mossing in the wings. The brown-striped F_2 chicks feather up into various types of brown, a bird not far removed from the Dark Dorking type being perhaps the most common. The typical Brown Leghorn reappears but rarely. Of the 65 F_2 ♀♀ tested for egg colour ex Brown Leghorn ♀ × Langshan ♂ (Fig. 1) 19 were brown-striped in the down, and 46 were black. If the two down classes are considered apart a remarkable difference is noticeable in the distribution of the egg tints. For nearly all of the birds laying a white or almost white egg belong to the blacks (Fig. 8), eggs of such tint being but rarely found among the browns (Fig. 9). At first sight it seems tempting to

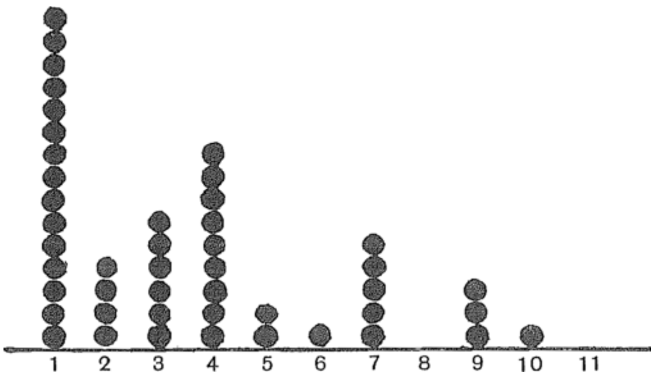


Fig. 8. Distribution of grades of egg-colour in the black F_2 birds ex Brown Leghorn ♀ × Langshan ♂.

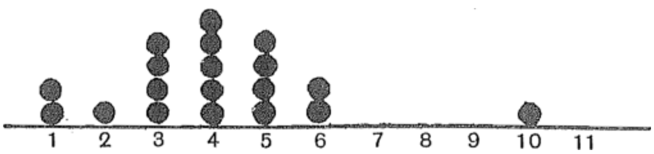


Fig. 9. Distribution of grades of egg-colour in the brown F_2 birds ex Brown Leghorn ♀ × Langshan ♂.

suggest that there is some form of linkage between the factor for black down and that for our postulated inhibitor of egg-colour. But when it is recollected that the inhibitor originally entered the cross from the side opposite to that from which the black entered, it is clear that we cannot be dealing with an ordinary case of linkage.

B. In the Hamburgh-Langshan cross.

The down-colour of the Gold Pencilled Hamburgh is pale golden with dark brown spotty markings on the back of the head, and generally also on the body. The down-colour of F_1 birds is that of blacks. In the F_2 generation four main types of down could be distinguished, viz. black, brown stripe, pale gold (similar to that of the Hamburgh), and chocolate. The last mentioned exhibited considerable variation. The predominant colour was always rich chocolate, but in some cases the chick could be described as a chocolate stripe, while in others the colour was uniformly distributed, and in others again their might be a slight admixture of black. Chick black in down developed into blacks: the pale golds developed into gold barred birds of various sorts: the brown stripes into a miscellaneous lot of browns and gold browns. The chocolates however gave two distinct classes of plumage, viz. gold barred of various kinds, and blacks, these last always with some brown mossing in the wings or else with some gold in the hackle[1]. No full black was actually reared from a chocolate chick though this may have been due to paucity of numbers. Of 31 chicks with chocolate downs reared 11 developed into blacks.

Out of the four kinds of down the actual numbers recorded for the several F_2 families were

Blk.	Choc.	Br. Str.	Gold
96	50	31	16

But if we reckon one-third of the chocolates as potential black-plumaged birds our ratio for the plumage characters, black as opposed to non-black, becomes

Black	Non-Black
96 + 17 = **113**	33 + 31 + 16 = **80**

This is very close to a 9 : 7 ratio where expectation would be 109 blacks : 84 non-blacks. The conclusion that the Hamburgh lacks two factors necessary for black is supported by the results of crossing F_1 birds with Hamburghs.

[1] These descriptions refer throughout to the pullets. For reasons of economy the cockerels were killed off at an early stage.

The four types of down appeared as follows:

Black	Choc.	Br. Str.	Gold
17	36	30	38

Reckoning one-third of the chocolates as blacks our ratio of blacks : non-blacks in respect of plumage becomes $17 + 12 = 29 : 92$. The blacks form almost exactly the quarter of the total that theory demands.

Where black plumage depends upon two factors, as in this cross, it is clear that an association between egg tint and plumage colour would be less easy to demonstrate statistically, even should it occur. In Figs. 10 and 11 the F_2 blacks and non-blacks have been set out with reference

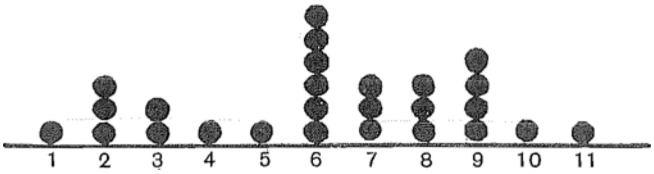


Fig. 10. Distribution of grades of egg-colour in black F_2 birds ex Langshan ♀ × Hamburgh ♂.

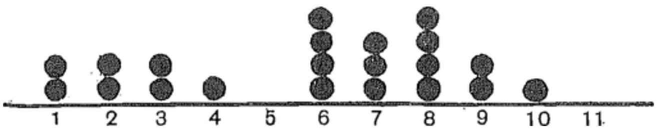


Fig. 11. Distribution of grades of egg-colour in brown and gold birds of F_2 generation ex Langshan ♀ × Hamburgh ♂.

to the egg-colour. So far as they go the two curves are obviously of a similar nature, and there is no reason for supposing that any factor influencing egg-colour is here associated with blackness of the plumage.

Broodiness.

Our data regarding broodiness are less satisfactory than those concerned with egg-colour. The character is a difficult one to classify. Between the obviously broody bird that will sit regularly each year and the equally obviously non-broody that never shows the least inclination to sit, there are many grades, as indeed is well known. In the earlier part of our experiments we kept the birds during their pullet year, and classified them as non-broody if they showed no tendency to sit during that period. After their first year we got rid of all the birds tested through lack of space. Only after several years did we realise that a bird might show no inclination to sit during her pullet year, and yet might become a reliable broody the following season. We have also encountered cases where a bird might go broody in her pullet year, and yet show no sign of broodiness the following season.

The material was the same as that used in the egg-colour work. Both the Brown Leghorn and the Hamburgh strains were under observation for some years and in neither of them did we ever observe any sign of broodiness. The broodiness of the Langshan we took on trust when we purchased our original birds. Such hens as we bred and had under observation went broody, though we never actually made use of them for sitting.

As in the case of egg-colour we found a marked difference in the Hamburgh × the Brown Leghorn crosses. F_1 birds ex Brown Leghorn ♀ × Langshan ♂ went broody, and this was also true of the reciprocal.

In the F_2 birds the distribution of broody and non-broody was as follows:

	Broody	Non-Broody
Ex Brown Leghorn ♀ × Langshan ♂	19	47
Ex Langshan ♀ × Brown Leghorn ♂	8	8

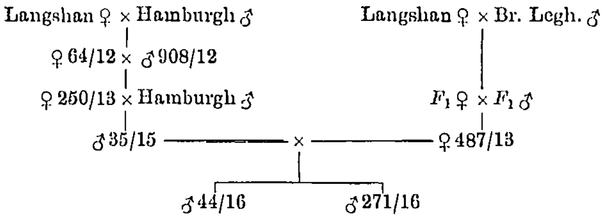
The birds were kept only during the pullet year and had we been able to keep them for another season it is possible that the proportion of broody birds would have been increased.

The data from the Hamburgh cross are of very different type. Three F_1 ♀♀ were used, of which one, ♀ 64/12, never went broody over three seasons, while the other two (♀ 453/13 and ♀ 454/13) only showed slight signs of broodiness. Two ♂♂ were used, viz. ♂ 908/12 and ♂ 452/13. Presumably both carried some factor for broodiness since ♂ 908/12 gave broody daughters with the non-broody ♀ 64/12 and ♂ 452/13 gave a broody daughter with pure Hamburgh ♀♀. As is shown by the figures set out below the proportion of broody birds arising from the Langshan × Hamburgh cross is very much lower than that from the Leghorn × Langshan cross.

		Broody	Non-Broody
F_2 generation	♀ 64/12 × ♂ 908/12	2	2
	♀ 453/13 × ♂ 908/12	1	19
	♀ 454/13 × ♂ 452/13	1	13
F_1 × Hamburgh	♀ 64/12 × Hamburgh ♂	—	8
	Hamburgh ♀ × ♂ 908/12	—	6
	Hamburgh ♀ × ♂ 452/13	1	21

The small proportion of broody birds produced from the Hamburgh cross is also shown by the following experiment. One of the two non-broody birds of the F_2 generation from ♀ 64/12 × ♂ 908/12 was ♀ 250/13, a hen which was full black in plumage, laid a deeply tinted egg (Pl. IX.

fig. 5), and was never observed to go broody during the four years she was kept. Mated with a Hamburgh ♂ this hen produced among other birds ♂ 35/15. He was mated with ♀ 487/13, a black broody F_2 ex Langshan ♀ × Brown Leghorn ♂, and a layer of deeply tinted eggs (Pl. IX. fig. 2)[1]. Two of the male offspring, as shown in the accompanying pedigree, were mated with hens belonging to a pure non-broody strain[2].



Of the daughters of ♂ 44, 13 were tested for broodiness, and all were found to be non-broody. Of the 16 daughters of ♂ 271 that were tested two became broody. This cock, with a father extracted from the Hamburgh cross and with a broody mother, recalls in its behaviour the F_1 Hamburgh-Langshan. For both of them appear to produce but a small proportion of gametes which give rise to broody daughters. We are inclined to think that ♂ 44 was of the same nature, and that he would have produced an occasional broody daughter had it been possible to rear more birds from him. It is tempting to suggest that the Hamburgh may have been carrying a factor, or factors, tending to inhibit the development of the broody habit; but to decide this point far more ample experiments are required.

Mention may be made here of some experiments undertaken with the Silky fowl in which this breed was crossed with the Brown Leghorn (Bateson and Punnett, 1911). The F_1 birds, as is usual in Silky crosses, were all markedly broody, nor did there appear to be any difference between those that had a Silky mother and those whose father was a Silky. Of about 24 F_2 pullets which were kept for a year or more all except one became broody. This low proportion suggests that the manifestation of broodiness, particularly where the character is well marked, may depend upon more than one factor. Should this turn out

[1] The experiment was part of a series designed to establish a non-broody strain laying a deeply tinted egg. Owing to conditions brought about by the war it had to be abandoned though we have little doubt from our general experience that the object could have been achieved.

[2] Extracted from a Hamburgh-Brown Leghorn cross, and belonging to a strain in which no sign of broodiness ever appeared.

to be the case the evidence from the Silky suggests that either factor, if two are concerned, is capable by itself of giving rise to broodiness.

We do not know of any instance in which broodiness has arisen through the crossing of two strains which experience had shown to be pure for the non-broody character. In the course of our experiments during the past ten years we have tested considerable numbers[1] of hens arising from complex crosses between the three non-broody breeds, Pencilled Hamburghs, Sebrights, and Brown Leghorns. Not a single bird has appeared which showed the slightest sign of broodiness. Such data as we have accumulated afford no grounds for the suggestion that the broody habit may depend upon the meeting of complementary factors[2].

Broodiness and dark eggs.

It is well known that most of the races of poultry that lay dark eggs belong to the broody section, whereas the non-broody strains lay white eggs. These facts suggest that there may be some form of linkage between egg-colour and broodiness, a point upon which we hoped that our experiments would throw some light. Figs. 12 and 13 show the

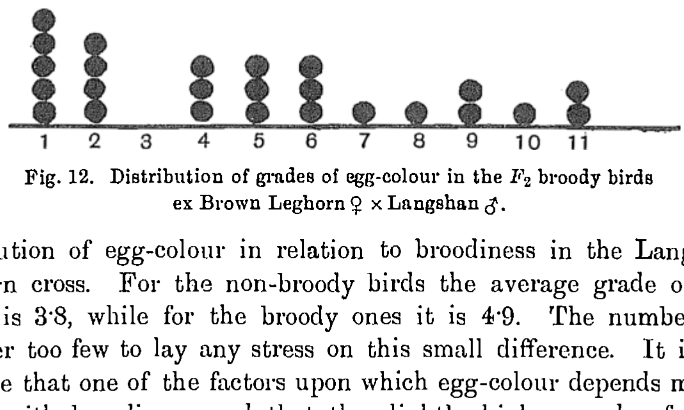


Fig. 12. Distribution of grades of egg-colour in the F_2 broody birds ex Brown Leghorn ♀ × Langshan ♂.

distribution of egg-colour in relation to broodiness in the Langshan-Leghorn cross. For the non-broody birds the average grade of egg-colour is 3·8, while for the broody ones it is 4·9. The numbers are however too few to lay any stress on this small difference. It is conceivable that one of the factors upon which egg-colour depends may be linked with broodiness, and that the slightly higher grade of colour among the broody birds is significant. Nor must it be forgotten that the non-broody birds were, with few exceptions, only tested during their pullet year. Some of them were doubtless potentially broody, and if

[1] Certainly more than 200.

[2] Broody birds, as is well known, may appear in breeds which are nominally non-broody, e.g. White Leghorns. We are inclined to think that in such cases the cock is responsible. After an occasional cross with a broody race it is not enough to rebuild the strain solely by selection of non-broody hens. The cock may also carry broodiness, and should be carefully tested before he is put into the breeding pen.

among these were the few layers of the darker eggs, the difference in grade between the two classes would become much more marked. It is to be regretted that the layers of darker eggs among the birds recorded as non-broody were not more thoroughly tested for broodiness, by

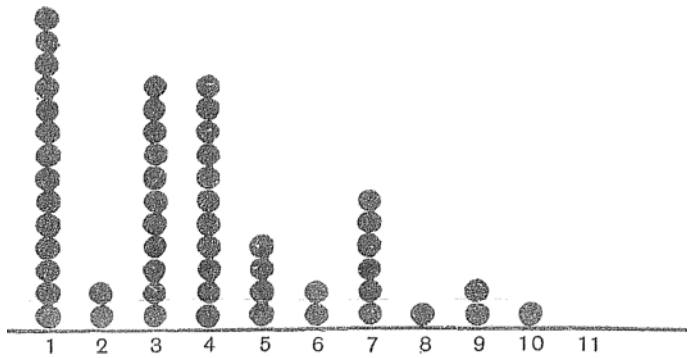


Fig. 13. Distribution of grades of egg-colour in the F_2 non-broody birds ex Brown Leghorn ♀ × Langshan ♂.

keeping them for several years, and we hope that this will be done by anyone who undertakes experiments on similar lines.

That the deeply coloured egg may be laid by a non-broody hen is clear from the case of ♀ 250/13, an F_2 bird ex Langshan × Hamburgh (cf. p. 288). But in this case there are some grounds for supposing that the Hamburgh may carry a factor inhibiting the broody instinct. It is possible that ♀ 250 was potentially broody, and that the manifestation of the instinct was prevented by an inhibitor factor. It is clear however that in practice it would be possible to establish a strain of non-broody birds laying dark coloured eggs.

SUMMARY.

1. F_1 birds from a cross between a white egg laying and a dark egg laying strain lay eggs of an intermediate tint.

2. Segregation occurs in the F_2 generation, the two parental grades, together with all intermediate ones being found.

3. There is evidence for the existence of an inhibitor of pigmentation in one of the white egg strains used, and there is some evidence for regarding this inhibitor as being associated with the factor for black plumage.

4. Broodiness is a highly complex character. F_1 hens are generally broody. The proportion of broody to non-broody birds in F_2 varies greatly in different crosses.

5. The factors for broodiness and for egg-colour are transmitted by the cock as well as by the hen.

6. Though there is slight evidence of some association between the brown egg and the broody habit, the two characters may be dissociated. It is clearly possible to establish a non-broody strain laying brown eggs.

EXPLANATION OF PLATE IX.

Fig. 1. Egg of Brown Leghorn.
Fig. 2. Egg of F_2 ♀ (487/13) ex Langshan ♀ × Br. Legh. ♂. Classed as grade 11.
Fig. 3. Egg of F_1 ♀ ex Br. Legh. ♀ × Langshan ♂. Classed as grade 5.
Fig. 4. Egg of Hamburgh ♀.
Fig. 5. Egg of F_2 ♀ (250/13) ex Langshan ♀ × Hamburgh ♂. Classed as grade 11.
Fig. 6. Egg of F_1 ♀ ex Langshan ♀ × Hamburgh ♂. Classed as grade 6.

LITERATURE.

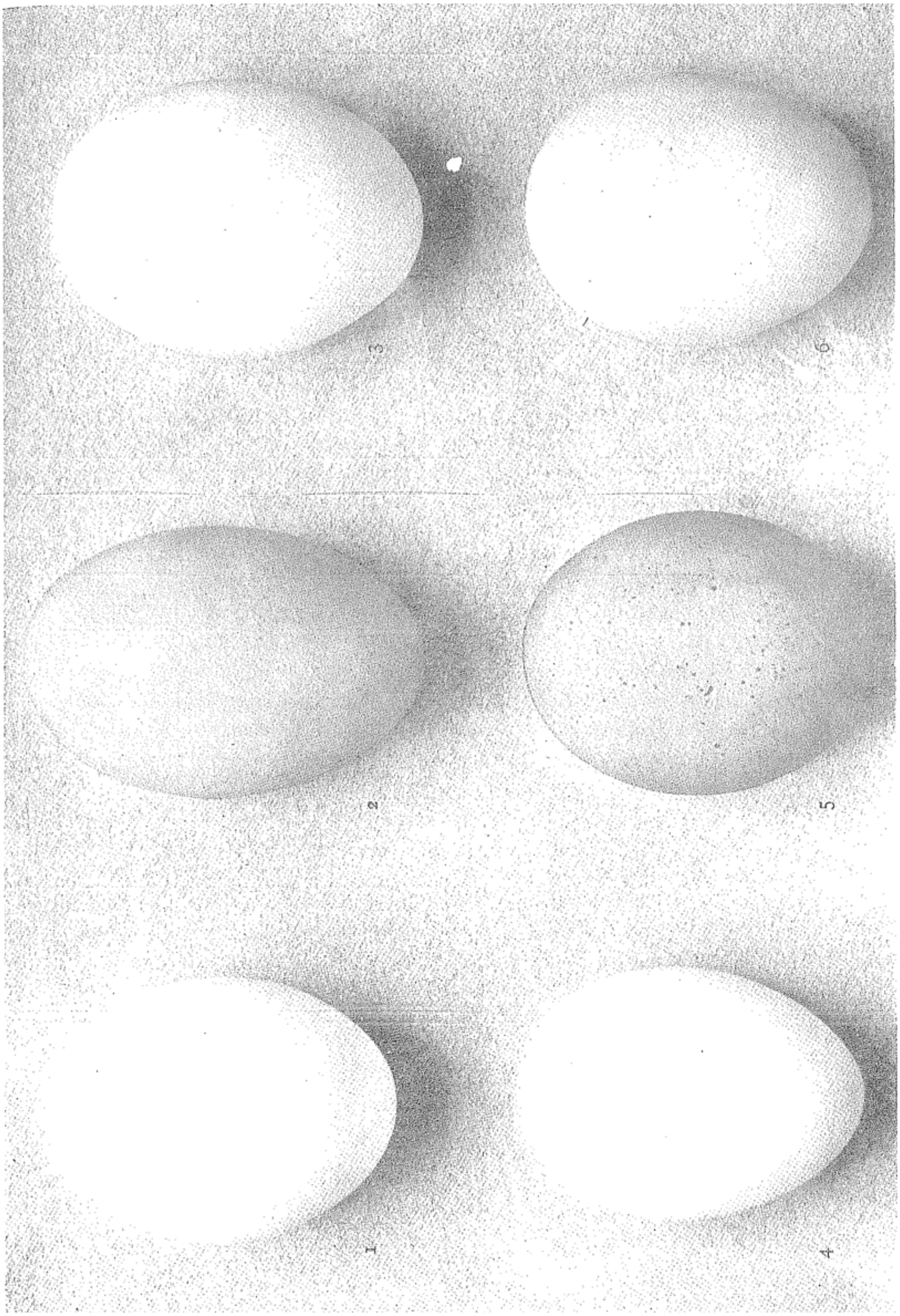
BATESON, W. and SAUNDERS, E. R. *Reports to the Evolution Committee of the Royal Society*. Report I. 1902.

BATESON, W. and PUNNETT, R. C. "The Inheritance of the Peculiar Pigmentation of the Silky Fowl." *Jour. Gen.* I. 1911.

DAUTHENAY, H. *Repertoire des Couleurs*, publié par la Société française des Chrysanthémistes et René Oberthür avec la collaboration de Henri Dauthenay. 1905.

HOLDEFLEISS, P. "Versuche über Xenienbildung und Vererbungsgesetze bei der Kreuzung von Hühnern." *Ber. phys. Lab. u. Versuchsanst. landwirt. Inst. Univ. Halle*, 1911.

HURST, C. C. *Reports to the Evolution Committee of the Royal Society*. Report II. 1905


3
6
2
5
1
4