

# Genetics of Buff and Related Color Patterns in the Fowl<sup>1</sup>

J. A. BRUMBAUGH<sup>2</sup> AND W. F. HOLLANDER

*The Department of Genetics, Iowa State University of Science and Technology, Ames*

(Received for publication September 4, 1965)

ONE of the landmarks in the history of poultry breeding was the importation of huge Chinese fowl into Europe about 1845. Tegetmeier's (1873) account indicates that the names "Cochin-China" and "Brahma" were less correct than "Shanghai." Fanciers crossed these into many other stocks, to give rise to American dual-purpose breeds and new color varieties of others, especially the buff, cinnamon, ginger-red, and light or Columbian.

Genetic analysis of these color types has been sporadic and incomplete. A good review of such studies was presented by Jull (1932), indicating considerable complexity. Nevertheless he applied the symbol  $e$ , for restriction (non-extension) of black, following Dunn (1923). This practice was continued by Hutt (1949), as well as by a number of subsequent writers, e.g., Kimball (1956).

In recent years evidence has been accumulating that a rather large number of multiple alleles of  $E$  exist (Brumbaugh and Hollander, 1965). These affect primarily the chick-down pattern. Most of the adult male plumage phenotypes are alike (wild-type). The relation of buff to these pattern types is the subject of the present paper.

Probably the chief reason for confusion and delay in analyzing the color patterns genetically has been failure to define the goal of analysis. The use of a standard reference type, preferably the wild type, has

been advocated by Jaap and Hollar (1954), so that other types can be analyzed in terms of mutant factors.

This procedure was almost followed by Davenport (1909). He crossed Buff Cocker bantam with a White Silkie, known by a previous breeding test to conceal the black-breasted-red game or wild-type pattern. The  $F_1$  were described as "washed-out black color . . . the Jungle pattern shows itself in the black tail and slightly redder buff on the wing-bar and hackles in the male." Only chick-down descriptions were given for  $F_2$ ; excluding the recessive whites, there were 34 buff or "buff and black," and 16 game (wild-type). Davenport's interpretation was that a dominant or incompletely dominant "xanthic" factor,  $X$ , was necessary for buff coloration, and also a recessive factor  $j$  for absence of jungle-fowl pattern.

Cock and Pease (1951) reported a cross of Light Sussex with autosex Black-Brussbar, essentially a barred black-red. "The  $F_1$  birds resemble Columbians, though in some the black pigment is much more extensive; but in backcrosses to Black-Brussbar the proportion of black-reds to their silver counterparts) varies widely among different families, and in most is too low to be explained by a single gene."

Kimball (1956) states that Columbian Wyandotte crossed with Brown Leghorn (essentially wild-type color pattern) gave a typical Columbian  $F_1$ . In successive backcrosses of the Columbian-pattern bird to Brown Leghorn, he obtained 1:1 segregation, recognizable both in chick down and adult plumage. However, he continued to use the symbol  $e$ .

<sup>1</sup> Journal Paper No. J-5210 of the Iowa State University Agricultural and Home Economics Experiment Station, Ames, Iowa. Project No. 1380.

<sup>2</sup> Present address: Department of Zoology and Physiology, University of Nebraska, Lincoln, Nebraska.

Because of these conflicting reports, we decided to make an extensive analysis of buff, using *Gallus gallus*, wild-type red jungle fowl, for the initial test.

#### MATERIALS AND METHODS

Our breeding stocks and methods have been described elsewhere (Brumbaugh, 1963; Brumbaugh and Hollander, 1965), and are too extensive to repeat here in detail. Most of the breeding, hatching, and rearing was carried out on the Poultry Farm of the Iowa State University Poultry Science Department, to which we are indebted for technical assistance.

Our stock of Red Jungle Fowls was developed from a blend of two lines: one from Dr. Walter Landauer of the University of Connecticut, and the other from the Lincoln Park Zoo in Chicago. Our only other source of wild-type color pattern was several Brown Leghorns of both Light and Dark varieties. The latter type was found to be heterozygous for another allele in the *E* series, which we have designated  $e^p$  (partridge), and which Smyth (1965) designated  $e^b$  (brown).

One of our principal testers was a stock of recessive wheaten type, symbolized  $e^x$ , derived in part from the Jungle Fowls of Lincoln Park and in part from mongrel bantam sources.

Another recessive allele in the *E* series we had extracted from an exceptional White Giant cock. This allele was called "blurred" and considered probably the same as that previously reported by Morejohn (1955) and termed "speckled head," with symbol  $e^s$ . This Giant cock, as well as most of our other pure stock birds except Rhode Island Reds, came from the Murray McMurray Hatchery of Webster City, Iowa. Our Rhode Island Reds were Parmenter strain, maintained by the Poultry Science Department.

Some chicks of the recessive wheaten

type are clear buff, though more often trace smudges of darkness are present in the dorsal region where the wild type has black stripes. In any case, unlike true buff chicks, wheatens develop dark feathering, and the males mature as essentially wild type.

At hatching, chicks were all carefully examined and recorded. Eggs failing to hatch were opened, and if the embryos were about full term they were also described. Coloration and pattern could be best examined after washing, drying, and fluffing the down. Representative chicks' skins were preserved flat for reference. The inner surface was dried with borax.

At the age of two months or later, the surviving birds were again recorded for plumage and foot colorations. Unless needed for further breeding they were then killed. Representative plumage samples were also preserved for record.

#### RESULTS

A Buff Minorca cock was crossed with two jungle fowl hens, and 63  $F_1$  chicks resulted. All were considerably lighter than standard wild type, the down color being described as tawny-buff with pale narrow striping (Fig. 1). However, none of the stripes was absent or interrupted. The beak was brown like that of buff breeds, or darker, in contrast to the flesh-colored beak of the jungle-fowl chicks. In mature plumage, the  $F_1$  cocks were rich coppery-buff with some black in the tail. The  $F_1$  hens (Fig. 2) were buffy-yellow with a mossy sprinkling of black over the tail and back, and in the flights. In both sexes the feet were blue, lighter than those of the wild type.

Matings of  $F_1$  *inter se* produced 464  $F_2$  chicks, most of which were buffy. Only 8 were classified as strictly wild type. The 381 birds surviving to plumage description were of numerous intergrading shades, including dark red, buff, wheaten, and the  $F_1$  phenotype. Five of the wild-type chicks



FIG. 1. Comparison of chick-down patterns. Left, standard wild type; center, female  $F_1$  from Rhode Island Red hen  $\times$  standard cock; right,  $F_1$  from Buff Minorca  $\times$  standard.

survived and remained standard. This complex segregation indicated that buff cannot be considered a single mutant.

Backcrosses to wild type were next made, to help in the analysis. Using the  $F_1$  hens, we obtained 238 chicks; the reciprocal matings gave 116 chicks. In both groups, chick-down phenotypes ranged between that of the  $F_1$  and wild type, with the latter greatly in the minority. Of the 277 survivors, 28 were described as standard wild type, while the remaining birds showed various grades of restriction of black. These were confusing at first, but

with close study we found it possible to recognize qualitative groupings. First was the group indistinguishable from the  $F_1$ . Second were "reds," much redder (darker) than the  $F_1$ . Third were "gingers." These as chicks were well striped but had tawny faces and ventral regions, and brown beak. As they matured, the plumage showed more buffy-red than in wild type, with dark fluff, the breast feathers of the cock having a coppery hour-glass pattern. Fourth were "mahogany-infused"; these as chicks were indistinguishable from wild type but in mature plumage were redder, the breast feathers of the cock being spangled (red base, black tips) to varying degrees. Fifth were "dilutes," which in chick down were pale-striped, but when mature, only the female was lighter than wild type.

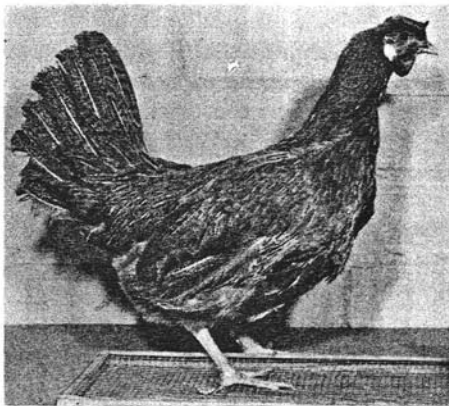


FIG. 2.  $F_1$  hen from Buff Minorca  $\times$  jungle fowl. Most of the plumage is buff, black being greatly restricted.

Second backcrosses of representatives of each of the above groups were made with jungle fowls. Twenty or more chicks were desired from each mating for reliability of ratios, and in most cases, this number was obtained. Matings of the first group (resembling  $F_1$ ) tended to repeat the complex segregation obtained in the first backcross. From two females however, single male progeny of a still different coloration showed up: though wild type as chicks, they showed diluted phaeomelanin in the mature plumage, somewhat similar to

TABLE 1.—Segregation data from presumptive monohybrid derivations of Buff  $\times$  jungle fowl (mature plumage)

Mating		Number of Matings	Progeny	$\chi^2$	P >
Cock	Hen				
Gr/+ +/+	+/+ Gr/+	4 0	62 Gr/+ : 57 +/+		
Total		4	62 Gr/+ : 57 +/+	.22	.5
Mh/+ +/+	+/+ Mh/+	5 2	113 Mh/+ : 88 +/+ 28 Mh/+ : 28 +/+		
Total		7	141 Mh/+ : 115 +/+	2.41	.1
Di/+ +/+	+/+ Di/+	1 3	8 Di/+* : 5 +/+* 12 Di/+* : 15 +/+*		
Total		4	20 Di/+* : 20 +/+*	0	
Cb/+ Gr/+ Mh/+	+/+ Gr/+ Mh/+	1 4 5	13 Cb/+ : 25 +/+ 42 GrGr : 58 Gr/+ : 41 +/+ 27 MhMh : 36 Mh/+ : 20 +/+	3.78 4.46 2.64	.05 .1 .25

\* Only female progeny classified.

"golden duckwing." We have called the coloration "champagne blond." One of these males was again backcrossed to standard. All the progeny were standard in chick-down color, but the survivors were easily classified in mature plumage (13 champagne blond : 25 standard). The champagne blonds all died, mostly of anemia, before two years old. No further analysis has been attempted.

Second backcrosses involving the "reds" all produced four or more types of progeny, including all the above types except that resembling the F<sub>1</sub>. We therefore infer that the "reds" are at least dihybrid.

In the case of second backcrosses from ginger, four matings were made, and monohybrid segregation was evident in each. The next step was to mate ginger heterozygotes *inter se* (four matings). Three classes of chicks were produced by each mating, with fair approximation to a 1:2:1 ratio (Table 1). The presumed homozygotes were more tawny than the heterozygotes, with less distinct striping (Fig. 3), and in mature plumage both sexes resembled the F<sub>1</sub> from buff  $\times$  standard. The plumage

fluff was dark gray. Most of these homozygotes were low in vigor and died before two years old.

Four second-backcross matings were made using dilutes. In each case, only the two classes of chicks were produced, indicating monohybrid constitution. Classification in later plumage was possible only with females. There were not many, but the totals make a 1:1 ratio. Attempts to mate dilutes *inter se* were quite discouraging because of poor egg-laying. Three classes of chicks were again obtained, however. The new phenotype here was pale and lacked the lateral black back stripes (Fig. 3). Unlike wheaten chicks, these showed fairly well developed head stripe and eye stripe. In mature plumage these birds became reddish, with very pale nearly white feet.

Mahogany birds in second backcrosses (seven matings) produced chicks all classed as standard. Of the 257 survivors, 141 were classed mahogany and 116 standard, a reasonable approximation to a 1:1 ratio. Five matings of heterozygotes *inter se* again produced chicks entirely standard

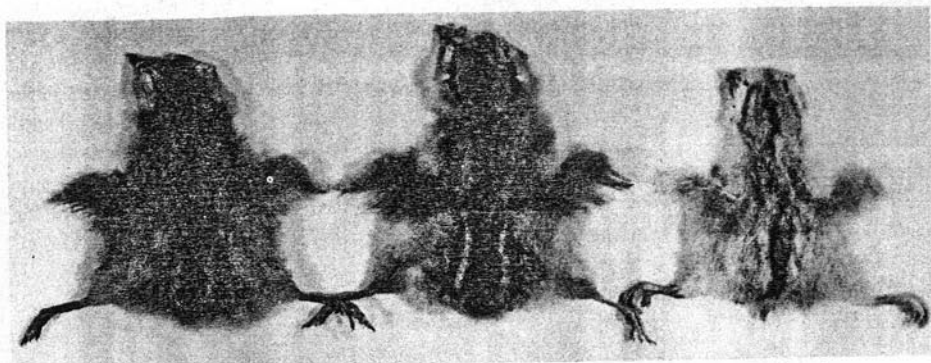


FIG. 3. Comparison of chick-down patterns of standard wild type (center), homozygous ginger (left), and homozygous dilute (right).

in phenotype. Survivors were classified into three groups with fair 1:2:1 ratio (Table 1). The presumably homozygous mahogany in both sexes is much redder than the heterozygote, and approaches the Rhode Island Red coloration.

The buff  $\times$  standard in  $F_2$  had produced some birds which appeared to be wheaten. To test this interpretation, we made individual crosses of 15 first-back-cross birds to wheaten and made chick classifications. Three kinds of results were obtained: (1) in five tests, all chicks were standard (i.e., not wheaten); (2) in three tests, half the chicks were standard and half wheaten; and (3) in seven tests, half the chicks were standard and half were quite light with some disruption of the striping, similar to that of the Buttercup breed. There was no relation between the outcome of these tests and the phenotype of the tested parent. We interpret the results of these tests to mean that, in addition to the semi-dominant factors indicated earlier, the Buff Minorca had  $e^y$  (wheaten) and  $e^{bc}$  (buttercup). These recessives at the  $E$  locus would preclude the possibility of any of the other factors being alleles of  $E$ .

Supplementary breeding tests, made to learn more about the relation of buff and

red breeds to the  $E$  locus, will be briefly summarized:

Buff Leghorn hen  $\times$  blurred ( $e^s e^s$ ) cock produced 30  $F_1$  chicks, all of which were buffy with faint striping on the back and blurred-speckled head markings. In mature plumage the  $F_1$  were similar to the Buff Minorca  $\times$  jungle fowl, but with green feet.  $F_1 \times F_1$  gave 149  $F_2$  chicks, of which none were wild-type—all were buff or blurred or something intermediate. These results agree with the interpretation that at the  $E$  locus the Buff Leghorn is homozygous for  $e^y$ .

Speckled Sussex hen  $\times$  blurred ( $e^s e^s$ ) cock produced 51  $F_1$  chicks, all with blurred head pattern and variable back-striping. Speckled Sussex hen  $\times$  jungle fowl cock produced 33  $F_1$  chicks, all of standard down-pattern phenotype. In mature plumage, these birds were mahogany.  $F_2$  chicks totaled 173, composed of 129 standard:44 wheaten. These results indicate that the Speckled Sussex is also homozygous for  $e^y$ .

Rhode Island Red hen  $\times$  jungle fowl cock produced 35  $F_1$  chicks, all with pale narrow striping (Fig. 1) and brown beak. As adults, these birds were mostly red. Two  $F_1$  females were tested with wheaten males; 102 chicks were obtained, of which

51 were wheaten and 51 had complete striping (standard or varyingly pale and narrow). We consider this result good evidence that the Rhode Island Red, like the Buff Leghorn and the Speckled Sussex, is homozygous  $e^s$ .

In 1961 Dr. Lewis T. Smith of the Iowa State University Poultry Science Department gave us a red cock, superficially almost identical in coloration with the Rhode Island Red, which had been black as a chick. It was  $F_2$  from crossing Rhode Island Red with White Leghorn. We crossed this cock with jungle-fowl hens and obtained a range of chick colorations including  $E$ -type black, rusty black of fairly uniform distribution, and wild-type. The striped:non-striped ratio was approximately 1:1, suggesting that  $E$  was segregating with a modifier, probably mahogany. Here is evidence that  $e^s$  is at least unnecessary in the red phenotype.

One further note on red is pertinent here. We crossed monohybrid ginger  $\times$  monohybrid mahogany birds, and obtained four phenotypes in the ten mature progeny: two standard, four ginger, two mahogany, and two red, which is about a 1:1:1:1 ratio. This result confirms the previous analysis of reds from the first backcross.

#### DISCUSSION

Although our study is incomplete, the results are sufficient to show that the symbol  $e$  as used by Jull (1932) and later workers is invalid. The "restricted black" condition is not a simple one. Kimball's (1956) claim that monohybrid segregation resulted from Columbian Wyandotte  $F_1$  backcrossed to Brown Leghorn is the outstanding case of disagreement with our conclusion. Even if the Columbian Wyandotte should be confirmed as an exception, which we consider most unlikely, there has been no evidence that the restriction factor concerned is allelic with  $E$ . The restriction effects of  $E$  alleles which we have iden-

tified (Brumbaugh and Hollander, 1965) do not occur in adult male plumage.

It may be asked, if  $e^s$  for example is ineffectual in adult males, why do buff and red breeds have this mutant? Of course, the wheaten phenotype of the adult female would seem a major step toward buff or red, and might have been selected for. However, another explanation is selection in the chick stage, where this mutant is a potent restrictor. Fanciers probably would prefer chicks of buff or red breeds to be buff rather than black, or striped, or other dark phenotype. Apparently it is possible with  $E$  to have a pure breed which would be black in chick down and red in the adult. By contrast, with homozygous wheaten and recessive black we have produced a pure type which is buff in the chick and black in the adult (Brumbaugh and Hollander, 1965).

Our data indicate that the buff adult phenotype depends on four autosomal mutant factors, which we have named ginger, mahogany, dilute, and champagne-blond. We propose for these the symbols  $Gr$ ,  $Mh$ ,  $Di$ , and  $Cb$ , respectively. None of these individually can be considered a "buff gene"; the buff phenotype is an interaction effect. For this reason we have not used the symbol  $X$  of Davenport (1909) or Knox' (1927) symbols  $Bu$  and  $Bu'$ .

Tegetmeier (1873) described a color variety of Game fowls called ginger-red. The term ginger is still current among cockfighters, and an old-timer applied it to our mature homozygous ginger birds.

While the Rhode Island Red and the Speckled Sussex have the sex-linked  $Id$  factor for light-colored feet, this gene is not involved in the Buff Minorca or Buff Leghorn. The light feet of such birds seem attributable to the dilute factor,  $Di$ . None of the other factors seems to affect the feet.

Champagne-blond,  $Cb$ , is the least-well-established factor of the four we propose in buff, yet it seems essential. It appeared in

monohybrid condition only in the second backcross to jungle fowl, and then only in two individuals. As an explanation, we suggest rather close linkage with *Gr*. It is quite possible that a high proportion of our apparently monohybrid ginger birds had *Cb* as well, since the latter is not evident in the chick. The observation that most of the *Cb* birds died of anemia is inexplicable at present. Also it is curious that *Di* birds and homozygous *Gr* were low in vigor. The Buff Minorca and Buff Leghorn and the F<sub>1</sub> did not show such troubles.

The differences between adult Buff Orpington, Rhode Island Red, and New Hampshire (light red) have been investigated by Somes and Smyth (1965) by all possible reciprocal crosses and F<sub>2</sub>, as well as some backcrosses. A multiple-factor interpretation was proposed, with no evidence for sex linkage. The authors were unable to identify the effects of any individual genes. According to our interpretation, all these breeds presumably have *Gr* and *Mh*, as well as *e*<sup>h</sup>, so that the differences among them would rest primarily with *Cb* and *Di*. Whether this is an oversimplification or not may best be answered by individual analysis of the breeds as we have done with the Buff Minorca.

#### SUMMARY

A reinvestigation of the genetical basis for "restriction of black" plumage patterns indicates that the previously postulated gene *e* is invalid. Distinction between chick-down and adult plumage effects is necessary. The Buff Minorca crossed with standard *Gallus gallus* produced F<sub>1</sub> striped as chicks but more resembling buff as adults. Backcrosses to jungle fowl, as well as F<sub>2</sub>, indicated segregation at five loci, the only recessive factor from the Buff being at the *E* locus. The other four factors from the Buff were named ginger (*Gr*), mahogany (*Mh*), dilute (*Di*), and champagne

blond (*Cb*). *Cb* is thought to be closely linked with *Gr*. Additional tests of *E*-locus constitution in Buff Leghorn, Rhode Island Red, and Speckled Sussex revealed only *e*<sup>h</sup>, which cannot account for the restriction phenotype of these adult males.

#### REFERENCES

- Brumbaugh, J. A., 1963. A study of the genetic control of black-red pigment patterns in the fowl. Thesis (Ph.D.), Iowa State University.
- Brumbaugh, J. A., and W. F. Hollander, 1965. A further study of the *E* pattern locus in the fowl. Iowa State J. Sci. 40: 51-64.
- Cock, A., and M. Pease, 1951. The genetics of the white pile pattern in the domestic fowl. World's Poultry Congress, 9th, Paris, 1951. Official Report 1: 49-53.
- Davenport, C. B., 1909. Inherited characteristics in the domestic fowl. Carnegie Institution of Washington Publication 121.
- Dunn, L. C., 1923. Color inheritance in fowls: The genetic relationship of the black, buff and Columbia colorations in the domestic fowl. J. Heredity, 14: 23-32.
- Hutt, F. B., 1949. Genetics of the Fowl. McGraw-Hill Book Company, New York, New York.
- Jaap, R. G., and W. F. Hollander, 1954. Wild type as standard in poultry genetics. Poultry Sci. 33: 94-100.
- Jull, M. A., 1932. Poultry Breeding. John Wiley and Sons, New York, New York.
- Kimball, E., 1956. Genetic relation of wild type and Columbian plumage patterns in the fowl. Poultry Sci. 35: 1274-1284.
- Knox, C. W., 1927. The genetics of plumage color in poultry. Iowa Agricultural Experiment Station Research Bull. 105: 106-131.
- Morejohn, G. V., 1955. Plumage color allelism in Red Jungle Fowl (*Gallus gallus*) and related domestic forms. Genetics, 40: 519-530.
- Smyth, J. R., Jr., 1965. Allelic relationship of genes determining extended black, wild type, and brown plumage patterns in the fowl. Poultry Sci. 44: 89-98.
- Somes, R. G., Jr., and J. R. Smyth, Jr., 1965. Feather phaeomelanin intensity in Buff Orpington, New Hampshire, and Rhode Island Red breeds of fowl. 2. Inheritance studies from whole feather extracts. Poultry Sci. 44: 47-52.
- Tetemeier, W. B., 1873. The Poultry Book (second edition). George Routledge and Sons, London.