PLUMAGE COLOR ALLELISM IN THE RED JUNGLE FOWL (GALLUS GALLUS) AND RELATED DOMESTIC FORMS

G. VICTOR MOREJOHN

Department of Zoology, University of California, Davis, California

Received December 9, 1954

THE lack of an ancestral "standard of reference", "normal" or "wild type" for use in genetic studies of the domestic fowl has been of little concern to many poultry geneticists (for a recent discussion of this topic see JAAP and HOLLANDER 1954). In the field of plumage color inheritance, however, a standard of reference seems necessary in describing the action of mutant genes. What the standard should be has yet to be determined, since the ancestry of the domestic fowl is still unknown. One or more of the four known species of jungle fowl may have contributed to the ancestry of the fowl, or some yet undiscovered fossil prototype may have been the major contributor. In view of this uncertainty, the use of the red jungle fowl (*Gallus gallus* L.) as a standard of reference for mutant genes in the fowl is entirely unwarranted without definite proof of allelism to genes manifest in the red jungle fowl. However, the lack of proof of allelism of genes to those of red jungle fowl need not disprove the "wild type" nature of a given allele since other jungle fowl species may have been involved.

Crosses between domestic breeds and red jungle fowl will be reported herein which demonstrate that a multiple allelic series of genes controls the differentiation of certain plumage colors and patterns. On this evidence, wild type designation of the character expressed in the red jungle fowl is justified.

Only a few attempts have been made to correlate the many color patterns in the down of chicks with adult plumage type. Often no correlation exists. In the multiple allelic series herein described, however, the same alleles are shown to regulate plumage color patterns in both the chick and the adult.

The three other groups of multiple alleles reported for the domestic fowl affect leg morphology (polydactylism, WARREN 1941; 1944), rate of feather growth (JONES and HUTT 1946), and blood groups (BRILES *et al.* 1950).

HISTORY

The phenotype represented in the brown Leghorn and red jungle fowl is commonly called black-red or black-breasted red and is based on the phenotype of the cock. KIMBALL (1951) was one of several workers who attempted to analyze the black-breasted red complex in the domestic fowl, and later (1952a, b) he published evidence of relationships of patterns in the down with respect to the wild type down pattern in the red jungle fowl and many domestic breeds. His analysis led him to assign the symbol e^+ to a gene governing wild type plumage and down. KIMBALL's reason for assigning the symbol e^+ to the black-breasted red pattern was that he found the latter to be allelic to a dominant gene E (extended black) which produces self black in both sexes of adults and chicks. The genetic basis for extended black was first recognized by LIPPINCOTT (1918). KIMBALL also assumed allelism to *e* (Columbian restriction) first described by DUNN (1923). This gene (*e*) restricts black pigment to the feathers of the neck, wings (primaries and secondaries) and tail. The relationship of *E* to *e*, however, is not always clear. COCK and PEASE (1951) state that in their work with the brussbar (barred black-red), F_1 heterozygotes (brussbar × Columbian) backcrossed to brussbar produced progeny in which "... the proportion of black-reds (or their silver counterparts) varies widely in different families, and in most is too low to be explained by a single gene." It is obvious from the above account that much more evidence is to be needed on the *extended black-Columbian restriction-black-red* relationship.

PEASE and COCK (1951) have extracted from the light Sussex breed of fowl a recessive gene called "retarded"* which, apparently, in homozygous state dilutes the down of chicks from a very pale striped wild type, with reduced mid-dorsal back stripe, to an all white chick. The adults (black-reds) are not similarly affected—cocks are more intensely colored; and hens are predominantly salmon-chestnut throughout with paler salmon breasts, black in tail and wing primaries, and the neck of deeper chestnut tint. PEASE and COCK also feel that the retarded gene may be found in Indian game (dark Cornish) fowl and in the salmon Faverolle breed. Regarding the latter breed, KIMBALL (1952b) states that the non-striped white down of the salmon Faverolle (and wheaten game) is governed by a dominant dilution gene, *Wh* (wheaten). Heterozygotes (*Whwh*), however, have white down with a mid-dorsal chestnut band and no black stripes. It seems evident that the retarded gene of PEASE and COCK, apparently completely recessive, may not be the same gene *Wh* which KIMBALL has described. Furthermore, KIMBALL (1953b) states that homozygous *WhWh* (wheaten game) cocks are indistinguishable from black-red (wild type) cocks, except for white undercolor of plumage; hens (*WhWh*) are of a red wheat coloration with no stippling, and black pigment is found in rectrices and remiges.

The author (1953) described a recessive mutation (yellowish-white down) discovered in a red jungle fowl cock of Siamese origin. The effects of this gene were to dilute the down of chicks of both sexes to a yellowish-white (fig. 1, D) and to depigment or dilute the plumage of juvenile and adult hens to creamy-buff or cinnamon. Adult cocks were not affected and were indistinguishable from normal wild type cocks. The gene was completely recessive, and in adult cocks homozygous for the gene, the undercolor of the plumage was not affected.

It can be seen from the above that three very similar phenotypes prevail: wheaten, retarded and yellowish-white. Minor differences in them can be accounted for in several ways. The two most logical are, (1) different genetic backgrounds (polygenes) affecting the expression of a mutant gene, or (2) three non-allelic genes producing similar phenotypic effects (a phenomenon not infrequently found in other animal forms). Genetic differences, if any, will only be found when the three phenotypes are brought together and analyzed genetically in proper matings.

* The term "retarded" has been used by WARREN (1933) for a condition affecting rate of growth of feathers. The symbol t^s has been given to this gene by JONES and HUTT (1946). The term is used here only with reference to the phenotype described by PEASE and COCK (1951).

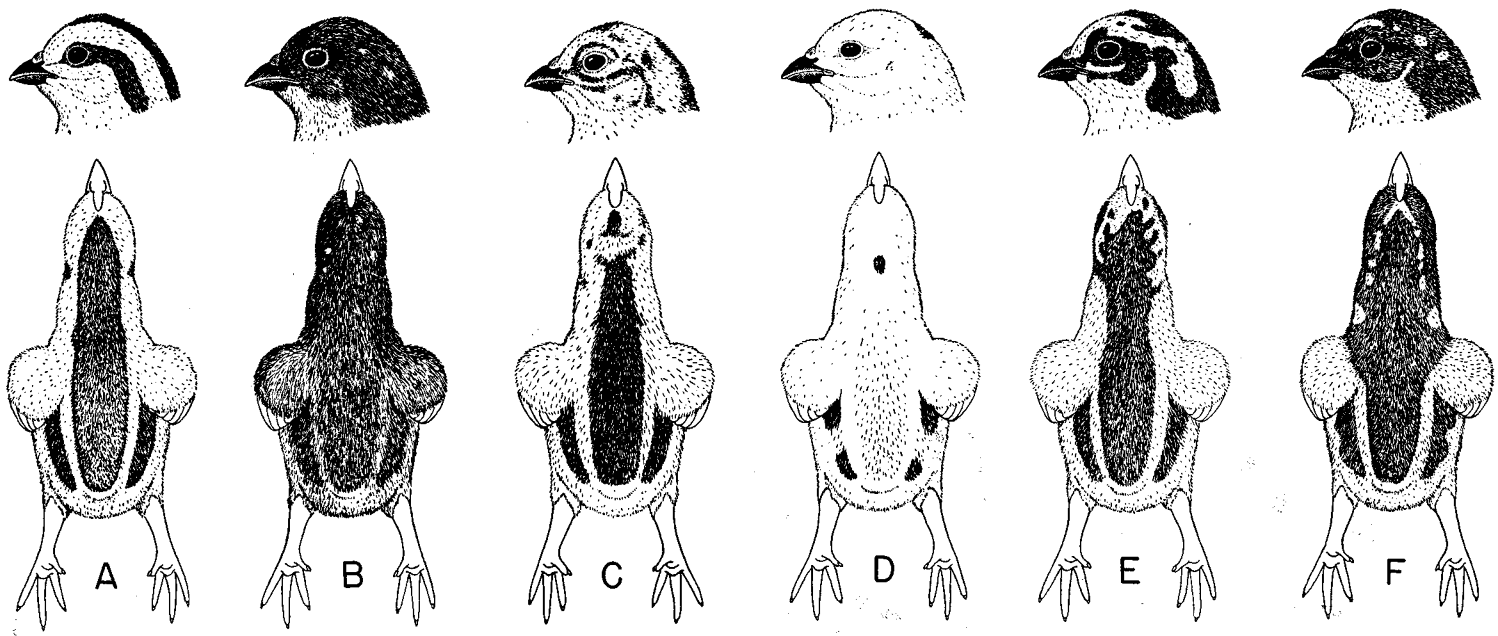

FIGURE 1.—Semi-diagrammatic drawings of lateral views of heads and dorsal views of chick down phenotypes: A, wild type striped (e^+e^+); B, brown (e^be^b); C, speckled head (e^se^s); D, yellowish-white (e^ye^y); E, heterozygous speckled head (e^be^y); and F, heterozygous brown head (e^be^s).

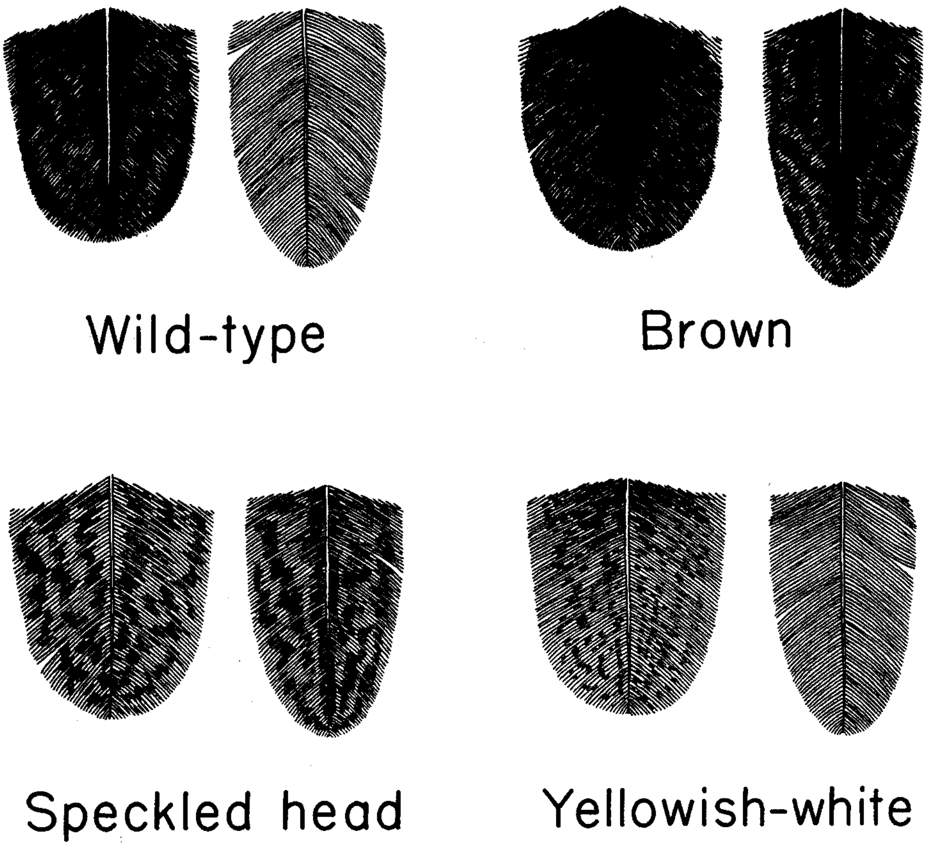

FIGURE 2.—Feather apices from the mid-back and upper breast of adult hens. Within each group the feathers from the back are at the left; feathers from the breast are at the right. Wild type (e^+), brown stippled feather of back and non-stippled salmon-colored feather from breast; brown (e^b), brown stippled feathers; speckled head (e^s), grayish-brown lightly stippled feathers; yellowish-white (e^y), cinnamon-buff lightly stippled feather of back and salmon-colored feather of breast.

DESCRIPTION

Since the primary concern of this investigation was with mutants affecting the wild type plumage and down pattern, the following description of the wild type, as seen in the red jungle fowl, is in order:

Cocks—Lanceolate orange-yellow feathers on the neck and rump; bay colored secondaries; blackish-brown primaries; and metallic-green tail feathers.

Hens—(fig. 2) Stippled (black spots on greyish-brown to brown ground color); light, salmon-colored breasts; and yellow-orange neck feathers.

Chicks—(fig. 1, A) The head has a median dorsal stripe, dark brown to light brown; it extends along the back of the head to a point along the neck. This stripe gradually disappears on the lower neck and continues wider along the dorsal surface of the back and rump. Lateral to this mid-dorsal back stripe there is a whitish-yellow stripe (approximately 5–8 mm in width) extending from a point lateral to the pygostyle and running anteriorly to a point along the scapula at the base of the wing. This stripe is margined along the ventral edge with black. A line of dark brown down runs through the eye to a point posteriorly on the side of the head, slightly above and posterior to the auditory orifice. The other areas of the down on the chick vary from yellowish-white to buffy-yellow.

The phenotype of these chicks is presumed to be an expression of the gene e^+ which theoretically controls in part adult wild type phenotype. Probably several genes contribute to the production of a perfected wild type plumage color. In conformity with current usage, alleles of this locus will be designated with superscript letters. Use of the symbol e^+ is based on data which shows that other mutant alleles of e^+ are allelic to E (extended black). The symbol e^+ is herein used only with reference to the normal or wild type birds used in this study and does not necessarily assume identity with other genes. Mutants used in this study were obtained in several ways. The red jungle fowl mutants (yellowish-white) were originally obtained from matings involving a heterozygous Siamese cock obtained from a game bird breeder (see MOREJOHN 1953). A strain of dark Cornish purchased from a breeder of commercial cross-bred poultry was also used and found to carry the same mutant allele (yellowish-white). The new mutant alleles to be described were discovered originally in a brood of day-old brown Leghorn chicks obtained from a commercial poultry hatchery. Extended black birds originally derived from the Australorp breed of domestic fowl, were obtained from DR. E. M. PLOCHER of Watsonville, California.

Following is a list of the mutants to be discussed. All adult cocks were phenotypically wild type.

Brown, (e^b)

The phenotype of the chick (fig. 1, B) may be described as being primarily all brown. The back was darker than the underside. Occasional small light brown spots seemed to delimit what may be taken to be the outer edge of the dorsal head stripe as found in wild type chicks. Dorso-lateral light brown striping was greatly suppressed and in most cases was absent. The adult hen differed from the wild type hen in being dark brown stippled throughout and not having a salmon-colored breast (fig. 2). Shanks and toes very frequently showed dark bluish-brown pigment in individual scales, and brown pigment was distributed along the distal edges of most scales.

Speckled head, (e^s)

The phenotype of the chick (fig. 1, C) was somewhat variable. In general, the body down color was very similar to the normal wild type striped phenotype. In the head region, however, the mid-dorsal head stripe was irregularly represented. Several spots and streaks also occurred in the area between the dorsal head stripe and the eye stripe and often were united giving the appearance of spectacles around the eyes. Adult hens (fig. 2) were similar to e^b homozygotes but were not as dark, i.e., feathers were not as darkly stippled.

Yellowish-white, (e^y)

The chick phenotype (fig. 1, D) appeared to be an extreme dilution of buff and brown pigment. The chick was uniformly yellowish-white with no head stripes and only a vague suggestion of the mid-dorsal brown stripe. The dark outer edges of the mid-dorsal stripe and the dorso-lateral black stripes were variable. Adult hens (fig. 2) were creamy-buff in color with dark stippled feathers of the back and rump. Hackles of the neck were yellow-orange, and the breast was light salmon-colored. Red jungle fowl homozygous for e^y were used in some of the experiments to follow, and a strain of dark Cornish was used which was demonstrated to carry the allele e^y.

EXPERIMENTAL MATINGS

Three parallel groups of breeding experiments were undertaken involving the groups of alleles: (I) e^+, e^b, e^s, and e^y; (II) e^+, e^b, e^s; and (III) E, e^b, e^s. Group I matings employed brown Leghorns and red jungle fowl; group II matings consisted only of matings between brown Leghorns; and group III matings were between brown Leghorns and extended black birds derived from the Australorp breed of fowl. A series of matings (IV) between brown Leghorn, dark Cornish and red jungle fowl were also undertaken to investigate the possibility of linkage of e^+ with pea comb (P). In the following experiments it should be kept in mind that in all cases except with extended black, all cocks were phenotypically e^+ as adults, i.e., only hens showed the mutant phenotype. Both sexes were equally affected as chicks.

I. *Genetic tests with* e^+, e^b, e^s, *and* e^y. Crosses were made between brown Leghorn mutants and red jungle fowl mutants. In table 1, the results of matings (1), (2), (3), (4), (5), (6) demonstrate that e^y is allelic to both e^+ and e^b. The progeny of mating (7) is important in that it represents the only evidence that e^s and e^y are not at different loci since the wild type striped phenotype was not realized.

II. *Genetic tests with* e^+, e^b, *and* e^s. Brown Leghorns alone were used in these matings. Matings (1) and (2) of table 2 demonstrate homozygosity of mutants e^b and e^s. The relation of these two alleles to e^+ is clear in mating (3) producing a 2:1:1 ratio together with the 1:2:1 segregation of e^b and e^s homozygotes from e^be^s individuals of mating (4). Considered with matings (5), (6), (7), (8), and (9), these data support the concept of a series of alleles of e^+.

III. *Genetic tests with* E, e^b, *and* e^s. Heterozygous cocks and hens of the genotype

TABLE 1

Segregating phenotypes of matings made between red jungle fowl and between brown Leghorns and red jungle fowl

Chick down phenotypes

Type of mating			Wild type (e^+)			Brown (e^be^b)			Speckled head (e^be^y)			Speckled head (e^se^y)			Yellowish-white (e^ye^y)			Expected ratio	Total
No.	Sire	Dam	♂♂	♀♀	Total	♂♂	♀♀	Total	♂♂	♀♀	Total	♂♂	♀♀	Total	♂♂	♀♀	Total		
(1)	e^+e^y	e^+e^y	17	18	66*	—	—	—	—	—	—	—	—	—	3	6	19*	3:1	85
(2a)	e^+e^y	e^ye^y	—	—	6	—	—	—	—	—	—	—	—	—	—	—	6	1:1	12
(2b)	e^ye^y	e^+e^y	15	9	29*	—	—	—	—	—	—	—	—	—	18	13	33*	1:1	62
(3)	e^ye^y	e^be^b	—	—	—	—	—	—	3	2	5	—	—	—	—	—	—	all	5
(4)	e^be^y	e^be^y	—	—	—	13	13	32*	13	27	50*	—	—	—	6	19	28*	1:2:1	110
(5)	e^ye^y	e^be^y	—	—	—	—	—	—	9	5	15*	—	—	—	16	5	21*	1:1	36
(6)	e^ye^y	e^ye^y	—	—	—	—	—	—	—	—	—	—	—	—	24	30	76*	all	76
(7)	e^ye^y	e^se^s	—	—	—	—	—	—	—	—	—	1	1	2	—	—	—	all	2

* The totals are greater than the sum of the male and female totals since the sexes of some or all of the chicks were not determined.

TABLE 2

Segregating phenotypes of matings made between brown Leghorns

Chick down phenotypes

Type of mating			Wild type (e^+)			Wild type speckled head (e^+e^b)			Brown (e^be^b)			Brown head (e^be^s)			Speckled head (e^se^s)			Expected ratio	Total
No.	Sire	Dam	♂♂	♀♀	Total	♂♂	♀♀	Total	♂♂	♀♀	Total	♂♂	♀♀	Total	♂♂	♀♀	Total		
(1)	e^be^b	e^be^b	—	—	—	—	—	—	23	33	74* (a)	—	—	—	—	—	—	all	74
(2)	e^se^s	e^se^s	—	—	—	—	—	—	—	—	—	—	—	—	5	6	25*	all	25
(3)	e^+e^s	e^+e^b	18	19	46*	6	8	14	—	—	—	10	3	17*	—	—	—	2:1:1	77
(4)	e^be^s	e^be^s	—	—	—	—	—	—	25	20	51*	38	31	78*	25	20	51*	1:2:1	171
(5)	e^+e^b	e^+e^b	0	3	12*	4	2	11*	1	1	8* (b)	—	—	—	—	—	—	1:2:1	31
(6)	e^be^b	e^+e^b	—	—	—	3	3	9* (c)	4	4	14* (d)	—	—	—	—	—	—	1:1	23
(7)	e^+e^s	e^be^b	—	—	—	8	6	23* (c)	—	—	—	8	12	28* (e)	—	—	—	1:1	51
(8)	e^be^b	e^be^s	—	—	—	—	—	—	2	5	14*	2	3	12*	—	—	—	1:1	26
(9)	e^be^s	e^se^s	—	—	—	—	—	—	—	—	—	5	4	10* (f)	4	3	10*	1:1	18

* The totals are greater than the sum of the male and female totals since the sexes of some or all of the chicks were not determined.

(a) Three chicks resembled a dark e^be^y phenotype.
(b) Two chicks resembled the e^be^s phenotype.
(c) Two chicks resembled the e^+e^+ phenotype.
(d) Three chicks resembled the e^be^s phenotype.
(e) Two chicks resembled the e^be^b phenotype.
(f) Three chicks resembled the e^be^b phenotype.

TABLE 3

Segregating phenotypes of matings made between brown Leghorns (e^be^s) *and birds derived from the Australorp breed of fowl of the genotype* E e^s. *Hens of this genotype were entirely black, and* E e^s *cocks were primarily black (black breast, tail, primaries, secondaries; dark red neck and rump hackles; and maroon colored back)*

Chick down phenotypes

Type of mating			Black (E)†			Brown head (e^be^s)			Speckled head (e^se^s)			Expected ratio	Total
No.	Sire	Dam	♂♂	♀♀	Total	♂♂	♀♀	Total	♂♂	♀♀	Total		
(1)	$E\ e^s$	e^be^s	29	46	81*	15	15	33*	19	15	37*	2:1:1	151
(2)	$E\ e^s$	$E\ e^s$	28	25	72*	—	—	—	2	6	15*	3:1	87

* The totals are greater than the sum of the male and female totals since the sexes of some of the chicks were not determined.

† Most chicks were black with whitish belly and chin or throat; some chicks were entirely black, and others (4) had whitish areas and/or spots on the sides of the head. All chicks were predominantly black except for the areas mentioned.

Ee^s were employed to test allelism of E to genes e^b and e^s. This test was accomplished in two ways: (1) An F_2 progeny was secured from the mating $Ee^s \times Ee^s$; (2) a cock Ee^s was mated to hens of the genotype e^be^s. Results of these matings are shown in table 3, matings (1) and (2). Results of these tests considered with results of the other tests strongly suggest a series of multiple alleles at the e^+ locus.

IV. *Linkage test with pea comb.* The dark Cornish breed of domestic fowl possessing pea comb (P) as a breed characteristic was locally available and was used in these tests. It has been demonstrated (see HUTT 1949 for complete data) that pea comb is linked with the gene for blue egg (O) and the gene for marbled down (ma). The gene for naked neck (Na) is also a member of this autosomal linkage group.

TABLE 4

Test for linkage between e$^+$ *(striped wild type) and* P *(pea comb). An* F_1 *female of the genotype* P/p, e^y/e$^+$, *derived from dark Cornish and brown Leghorn parents, was backcrossed to a red jungle fowl male* (p/p, e^y/e^y). *There is no significant deviation from a 1:1:1:1 ratio on the basis of independently assorting genes*

Segregating phenotypes

Striped wild type (e^+)						Yellowish-white or Cornish modification (e^ye^y)†					
Pea comb			Single comb			Pea comb			Single comb		
♂♂	♀♀	Total	♂♂	♀♀	Total	♂♂	♀♀	Total	♂♂	♀♀	Total
7	5	13*	8	4	16*	9	7	17*	9	6	16*

* The totals are greater than the sum of the male and female totals since the sexes of some of the chicks were not determined.

† See text for explanation.

Dark Cornish exhibit sexual dichromatism: Cocks are black with dark red backs and chestnut secondaries; wing coverts, neck and rump hackle feathers may have a shade of mahogany-red. Hens are penciled (chestnut feathers with black crescentic marks) on the back, breast, wings, and tail, and have black necks. Ground color of chicks in the strain used was greyish-white with irregular black or slate-grey dorso-lateral back stripes and grey mid-dorsal back stripes. The latter stripes were extremely variable in outline. The dorsal neck region was striped, but this stripe was broken in several spots on the head. Other strains of dark Cornish chicks have dark brown down (KIMBALL 1952b) or wild type striped down (PEASE personal communication).

Down color of the strain of dark Cornish used was found to be basically governed by the allele e^y; however, it was subject to some modification in phenotype by other plumage genes of dark Cornish. One F_1 double heterozygous hen was used to test for linkage. She had a Cornish dam (P/P, e^y/e^y) as one parent and the sire was a brown Leghorn, single comb, striped wild type (p/p, e^+/e^+). The F_1 hen thus was presumably of the genotype P/p, e^y/e^+ (pea comb, striped wild type). This hen was backcrossed to a double recessive male red jungle fowl (p/p, e^y/e^y). Data presented in table 4 indicate that e^+ is independent of P.

THE CORNISH DOWN PATTERN

The possibility of another allele at the e^+ locus was investigated. Attempts were made to extract birds with Cornish striping as chicks and non-penciled phenotypes as adults. Ideally, if Cornish striping represented another allele of e^+, then removal of the penciling character might reveal a new mutant phenotype in the adult hen and, theoretically, phenotypically wild type cocks.

In the test for linkage (table 4) the segregating phenotypes expected (disregarding P and p) were striped wild type and Cornish striped or yellowish-white in a ratio approximating 1:1. The mutant phenotype realized, however, ranged from typical yellowish-white (e^y) to an imperfect Cornish striped phenotype. This result, however, might have been expected since (as mentioned previously) the down pattern of the

Cornish strain used was somewhat variable. Polygenic modifiers seem to provide an explanation for this variation. Chicks having an imperfect Cornish down pattern (refer to table 4) were raised to maturity. Although only one cock and one hen survived to be definitely classified as adults, the cock was phenotypically wild type and the hen showed an e^ye^y phenotype. It is on this evidence that the down pattern of the dark Cornish strain studied is believed to be basically governed by the e^y allele.

HORMONAL CONTROL OF ADULT PHENOTYPE

In another study, the author (1953) demonstrated that adult red jungle fowl males of the genotype e^ye^y and e^+e^+ were indistinguishable from each other; whereas female red jungle fowl of the same genotypes were phenotypically distinct. Gonadectomy of e^+ and e^y males resulted in no change of phenotype in regenerating feathers. Males (e^+ and e^y) each given a 15 mg pellet of a synthetic estrogen (diethylstilbestrol) under the skin of the neck, however, showed differences in phenotype of regenerating feathers. Feathers of e^+ males approximated feathers of e^+ females; feathers of e^y males approximated feathers of e^y females. Diethystilbestrol elicited the same response in castrates as it did in intact males.

In the present study the same method of diethystilbestrol pellet implantation was used. Adult males of the genotypes e^be^b, e^be^s, and e^se^s, phenotypically indistinguishable (wild type) as adults, were each given a 15 mg pellet implant of diethystilbestrol. At this time feathers of the rump and breast were plucked so that new emerging feathers would grow under the influence of estrogen. Reaction responses of these cocks were as expected; new emerging feathers approximated the corresponding female adult phenotype in each instance. From these results it can be seen that estrogen (diethylstilbestrol) can be used in genotype determination of wild type males when doubt exists as to homozygosity of e^b, e^s, or e^y. The phenotypes of e^+, e^b, e^s, and e^y adult females are obviously only manifest under the influence of ovarian hormones.

DISCUSSION

Validity of the concept of multiple alleles of e^+

Tables 1, 2, and 3 present the types of matings which were made to establish allelism between E, e^+, e^b, e^s, and e^y. In most cases heterozygotes were phenotypically intermediate relative to their respective homozygotes. The allele e^y is presumed to be recessive to all other alleles, although it has not been tested with E. Homozygosity of each mutant phenotype (e^be^b, e^se^s, e^ye^y) is demonstrated. The mating brown Leghorn females (e^be^b) $\times$ red jungle fowl male (e^ye^y) was made (table 1, mating 3). F_1 individuals of this mating (fig. 1, E) resembled e^s homozygotes to some degree. However both phenotypes could be distinguished from each other, since the hybrids (e^be^y) had dark slate-brown undersides and other speckled headed chicks (e^se^s) did not. In general e^be^y individuals were darker throughout and speckling of the head was more extensive. Since the e^y homozygote tends to produce an extreme dilution of buff and brown pigment and the e^b homozygote, conversely, tends to darken down color, the allelic compound (e^be^y) in down color below the head approaches and very nearly duplicates the wild type dorsal back striping. It is not as light as the wild type nor as dark as the mutant e^be^b. Incomplete or no dominance, however, prevails in the head region of the compound. As mentioned previously, an irregularly shaped dorsal head stripe is found with dark brown spots and streaks along the lateral sides of the head. From this it can be seen that the action of e^b is to extend brown pigment over the head, for it is in this region that intermediacy is found. As adults e^be^y hens resemble the e^be^s phenotype.

Brown Leghorn heterozygotes (e^be^s) were intermediate in phenotype between e^b and e^s homozygotes, whereas e^+e^b heterozygotes (= speckled head wild type) usually differed from wild type only by the presence of small spots between the dorsal head stripe and the eye stripe. In one mating (table 2, mating 6) an occasional wild type individual was produced, which indicated that the threshold of phenotypic change from wild type to speckled head wild type is probably under polygenic control so that e^+ acts as a complete dominant. A similar situation exists in the e^be^s heterozygote. In most matings this phenotype (called brown head, fig. 1, F) was clearly recognizable, however, occasional individuals resembled e^b homozygotes (table 2, mating 7). Conversely, in matings of e^be^b *inter se* individuals may approach and almost duplicate the brown head phenotype. The allele e^s is apparently completely recessive to e^+.

As adults, e^be^s individuals were intermediate in phenotype: greyish-brown stippled breasts and backs. Adult individuals of the genotype e^+e^b and e^+e^s were wild type (breasts were non-stippled salmon-colored).

The allele e^b in an e^+e^b combination may act as a complete recessive, for an occasional e^+e^b chick is phenotypically wild type as in mating (6). It may therefore be said that the e^b allele occasionally lacks "penetrance". Polygenic modifiers apparently are present and in matings involving alleles e^+ and e^b segregation of e^be^b zygotes may not always be apparent. In mating (5) presumed homozygotes (e^be^b) resembled the e^be^s phenotype. The converse may also be true in matings where brown heads (e^be^s) are expected. In this case e^be^s zygotes may resemble e^be^b zygotes as in mating (7).

A mating between a homozygous speckled head (e^se^s) brown Leghorn female and a red jungle fowl mutant male (e^ye^y) produced F_1 chicks which had the speckled head phenotype (table 1, mating 7). This mating indicated that e^y was recessive to e^s.

The relationship between E, e^b, and e^s was adequately demonstrated in matings (1) and (2) of table 3. Mating (1) alone, however, cannot establish allelism of E, e^b, and e^s since the 2:1:1 ratio can also be produced with independently assorting non-allelic genes. Since the same cock used in mating (1) was mated with his sibling of identical ancestry and in F_2 produced a 3:1 segregation of black to speckled head, it indicates that at least e^s is allelic to E. Considering the known relationship of E to e^+ and the relationship of e^b, e^s, and e^y to e^+, it follows indirectly that E, e^+, e^b, e^s, and e^y can be considered to represent a series of multiple alleles. The relationship between e^y and E has not been determined. Arranged in order of decreasing dominance the alleles may be listed as follows: E-e^+-e^b-e^s-e^y.

The genotypes postulated for the sires and dams in tables 1, 2, and 3 were determined, when possible, from the parentage and phenotypes of the birds crossed and from segregation observed in their progeny. In most cases parentage and progeny segregation from diallel crosses were the main criteria used for genotypic determination. However, where known homozygous strains were used, homozygosity for the particular allele was assumed. Individual birds used in crosses involving ratios of 2:1:1 were always used in crosses involving different combinations of alleles, i.e., table 2, mating 3, sire e^+e^s was used in mating 7; dam e^+e^b was used in mating 6. Likewise, in table 3, sire Ee^s was used in both matings, and dam e^be^s was used in mating 4 of table 2. In most of the other matings the same method of "overlapping" sires and dams in different matings was employed. All data yielded results consistent with expectation.

Many other domestic breeds possibly carry other mutants of e^+. The only evidence of the occurrence of the mutant e^b in the wild state is a female red jungle fowl collected in February, 1908 by L. L. KRIBS near Illigin on the Island of Mindanao, Philippine Islands (University of California, Museum of Vertebrate Zoology Number 30947). It has the adult e^b phenotype (dark brown stippled breast) and presumably is of the genotype e^be^b.

Primary and secondary plumage pattern genes

KIMBALL (1953a) defined a primary pattern gene as one determining ". . . pterylar and multipterylar distribution of specific black feather pigments, *viz.*, e^+, e, and E." He defines a secondary pattern gene, such as stippling (Sg), ". . . as a factor determining distribution of black pigment within the individual feather." This classification of gene action on pigment distribution is useful in specific instances, but it necessarily becomes useless when attempts are made to apply it to a series of multiple alleles. Gene action in relation to color deposition can be classified in several ways (dilutions, extensions, inhibitors or suppressors, etc.), and the fact that the potentialities of alleles of one locus can be extremely variable (affecting the same character in different ways) has been shown by studies on other forms (CASTLE 1930, 1940; GRUNEBERG 1943). Well known examples are the alleles at the C^+ locus in domestic rabbits. Here the mutant chinchilla (c^{ch}) can be classed as a secondary pattern gene, whereas Himalayan (c^H) and albino (c^a) can be considered primary pattern genes. Considering the mutants of e^+, the allele e^y can be classified as a dilution gene. Alleles e^b and e^s, although producing nearly identical adult phenotypes, are clearly distinct in their action on down plumules. These can be classified as secondary pattern genes. From the evidence submitted it follows that the author disagrees with the classification of primary and secondary pattern genes, postulated by KIMBALL, as applicable to a series of multiple alleles.

SUMMARY

1. Evidence supporting the concept of multiple alleles in the fowl is presented.

2. Descriptions and relationships of three mutants, e^b (brown), e^s (speckled head) and e^y (yellowish-white) to E (extended black) and e^+ (wild type striped) are discussed.

3. Evidence presented demonstrates no linkage with P (pea comb).

4. All mutants with the exception of E affect both sexes as chicks, but as adults, cocks are not affected and hens demonstrate the mutant phenotype.

5. Down pattern in the strain of dark Cornish used is believed to be basically governed by allele e^y.

ACKNOWLEDGMENTS

The author wishes to express sincere thanks to DRS. M. A. MILLER, V. S. ASMUNDSON and M. M. GREEN for constructive criticism of the manuscript and for many helpful suggestions.

LITERATURE CITED

BRILES, W. E., M. R. IRWIN, and W. M. MCGIBBON, 1950 On multiple alleles effecting cellular antigens in the chicken. Genetics **35**: 633–652.

CASTLE, W. E., 1930 *The Genetics of Domestic Rabbits.* Cambridge (Mass.), Harvard Univ. Press.
1940 *Mammalian Genetics.* Cambridge (Mass.), Harvard Univ. Press.

COCK, A., and M. PEASE, 1951 The genetics of the white pile pattern in the domestic fowl. Report of the IX World's Poultry Congress, Paris **1**: 49–53.

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.

GRÜNEBERG, H., 1943 *The Genetics of the Mouse.* Cambridge (England), Cambridge Univ. Press.

HUTT, F. B., 1949 *Genetics of the Fowl.* New York, McGraw-Hill Book Co., Inc.

JAAP, R. G., and W. F. HOLLANDER, 1954 Wild type as standard in poultry genetics. Poultry Sci. **33**: 94–100.

JONES, D. G., and F. B. HUTT, 1946 Multiple alleles affecting feathering in the fowl. J. Heredity **37**: 197–205.

KIMBALL, E., 1951 Pyle-black plumage in the fowl. Am. Naturalist **85**: 265–266.
1952a Genetic relation of extended black to wild type plumage pattern in the fowl. Poultry Sci. **31**: 73–79.
1952b Wild type plumage pattern in the fowl. J. Heredity **43**: 129–132.
1953a Genetics of secondary plumage patterns in the fowl. Poultry Sci. **32**: 14–17.
1953b Genetics of buttercup plumage pattern in the fowl. Poultry Sci. **32**: 683–692.

LIPPINCOTT, W. A., 1918 The case of the blue Andalusian. Am. Naturalist **52**: 95–115.

MOREJOHN, G. V., 1953 A gene for yellowish-white down in the red junglefowl. J. Heredity **44**: 46–52.

PEASE, M., and A. COCK, 1951 Retarded pigmentation. A recessive gene affecting down colour and pattern. Report of the IX World's Poultry Congress, Paris **1**: 63–67.

WARREN, D. C., 1933 Retarded feathering in the fowl. J. Heredity **24**: 430–434.
1941 A new type of polydactyly in the fowl. J. Heredity **32**: 2–5.
1944 Inheritance of polydactylism in the fowl. Genetics **29**: 217–231.