INHERITANCE OF WHITE PLUMAGE IN *PHASIANUS*

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Plate 18

THE data herewith presented deal with the inheritance of white plumage in the Ring-necked Pheasant, *Phasianus colchicus torquatus.* In a previous publication (1939) the author has pointed out the scarcity of knowledge concerning the genetics of this species and reported on the inheritance of an incompletely dominant, autosomal gene for melanin. A general review of the literature on the genetics of the pheasant is given in that paper and accordingly will not be repeated here.

The pheasant fancier has long had blue-eyed white pheasants in his aviary, but the origin of this variety is apparently unknown. Occasionally reports are publicized of pure-white pheasants being shot in the wild. Whether such birds result from mutations occurring in the wild population or have escaped from aviaries cannot be proven, but the latter alternative seems unlikely.

White plumage among wild species which are normally colored is not uncommon and albinos have been reported in many birds as well as in mammals, reptiles, amphibians, etc. In very few birds, however, is the exact nature of the white determined and in many cases the specimen described is not a true albino at all but merely a bird with more or less depigmentation of the plumage. In the bird with complete albinism melanin is absent in all parts of the body. The eye appears pink in color because of the blood in the capillaries of the iris and retina. In most white birds the eye is black, brown, orange, or bluish, and all of these colors indicate the presence of melanin. True albinism is rare but birds in which a colored eye is associated with white plumage are common.

During the past nine years, approximately a million pheasant chicks have been hatched at the New York State game farms and among these but one true albino has been found. It is not uncommon to find white chicks, but usually these have some pigmented down on the wings. Almost without exception such chicks develop some pigmented feathers as they assume the juvenal and adult plumages and 'pied' birds, not white ones, are the final result.

Inheritance of color in the Domestic Fowl, a species in the same subfamily as *P. colchicus,* may give some indication of what might

be expected of color in the pheasant. In that species white plumage may be due to any one of three different genes. The White Leghorn fowl carries a unifactorial, incompletely dominant, autosomal gene which inhibits the formation of melanic pigment. Fundamentally the White Leghorn is a colored bird, but the presence of the inhibiting gene in homozygous form prevents the expression of black. In heterozygous individuals some color is evident. This type of white plumage is found occasionally in other breeds, but so far as is known is the result of crossing with White Leghorns.

The second kind of white plumage is that found in Plymouth Rocks, Wyandottes, Dorkings, Langshans, and other breeds of fowl. This white is autosomal and recessive and is apparently due to the absence of a gene necessary for the formation of melanin. Since the eyes are pigmented in both the dominant and the recessive whites, neither is a true albinism and both should be considered as a kind of white in which the manifestation of melanin is usually restricted to the eye. Bateson and Punnett (1908) described another 'complementary' white in Silkie fowls, but no other workers have been able to detect it in that breed.

True albinism is so rare in the fowl that in the thirty-nine years since the rediscovery of Mendel's laws only one case has thus far been reported. The condition was found by Warren (1933) to be a simple autosomal recessive character.

The white pheasant shows no signs of pigmentation in the plumage, but beak and shanks are a pearl white and the eyes are blue. It can be seen that the white plumage of the pheasant might possibly be any one of the genetically different types of white reported above, or possibly still another, since in these white pheasants the eye is blue, a condition not found in any of the white fowls mentioned above. Moreover, the shank color is affected in white pheasants but not in most white fowls. It is possible, of course, that in these white pheasants the shank- and eye-color dilution are due to other genes closely linked with that for white plumage.

In the absence of definite information of the genetic basis for white plumage in the pheasant an investigation was begun in 1938. While it was under way another report of 'hereditary albinism' was found. Taibell (1928) concluded that white is a monohybrid recessive character. He called his white specimens 'albinos', but the description furnished indicated that they were blue-eyed whites. Since his studies were somewhat limited, it seems advisable to report the present experiments.

GENETIC ANALYSIS

The first crosses were made in 1938. A male and two female white pheasants were purchased from a fancier with the assurance that they had bred true for many generations. These birds had white plumage, blue eyes, and pearl-white beak and legs. There were no colored feathers anywhere in the birds nor did they show any after the adult molt.

The male was mated with four Ring-neck females and the two white females were mated to a Ring-neck male with the following results:

Parents	*Progeny*	
	Number	*Color*
White ♂ × Ring-neck ♀ ♀	89	Ring-neck
Ring-neck ♂ × white ♀ ♀	14	Ring-neck

This is what would be expected in the F_1 generation if the white plumage were due to a recessive, unifactorial, autosomal gene.

If the character were sex-linked and recessive, that would be shown by differences in the progeny from reciprocal matings. The mating of normal, colored, Ring-neck males to white females would then produce F_1 progeny with normal plumage, but in the reciprocal mating of white males to Ring-neck females, the female progeny would be white, while the male progeny would be Ring-neck color. Since such 'criss-cross' inheritance was not found, these first matings demonstrated the autosomal nature of the gene.

At maturity most of the F_1 birds were identical in appearance with the Ring-neck stock, but an occasional bird exhibited a completely white primary or tail-feather. Others had a patch of white feathers on the throat but in the majority white was not in evidence. All progeny had dark-pigmented eyes, beak and shanks.

F_2 GENERATION

In 1939, the F_1 progeny of the white ♂ × Ring-neck ♀ ♀ were mated *inter se* to produce the F_2 generation (pen 1-39). This was also done for the progeny of the Ring-neck ♂ × white ♀ ♀ (pen 2-39). In these F_2 generations the expectation was 3 colored : 1 white, if the white were a simple, recessive character. Classifications at hatching, including embryos dying late in which color could be determined, were as follows:

	Hatched		*Late dead embryos*		*Combined*	
	Ring-neck	White	Ring-neck	White	Ring-neck	White
Pen 1–39	70	25	25	6	95	31
Pen 2–39	44	13	10	4	54	17
			Combined total		149	48
			Expected (3 : 1 ratio)		147.75	49.25

Taken either separately or together these matings yield an unusually close fit to the 3 : 1 ratio expected. About one hundred of these birds were reared to maturity and in none of them did any of the white segregates assume the Ring-neck plumage or show the pied condition.

It was noted that a number of these (adult) birds had an occasional dark feather, particularly on the head. Conversely, some of the F_2 Ring-necks had an occasional white feather in the wing or a small white patch of feathers on the throat. Doubtless these were individuals heterozygous for white. Birds of that genotype must have comprised two-thirds of the F_2 population, but since only a few of the Ring-necks showed any white feathers, it is clear that the white plumage is usually completely recessive in the heterozygote.

The symbol *c,* which is used to denote the gene for recessive white in the fowl, is assigned to this gene responsible for the absence of color in the pheasant. The normal wild Ring-necked Pheasant would thus be *CC,* while the pure-white birds would be *cc.*

BACKCROSSES

The expectation here, as in any backcross to the recessive form, was a ratio of 1 colored : 1 white. Backcross matings of F_1 progeny were made to the white male and females. One of the original white hens died during the breeding season and, accordingly, two additional white hens were obtained from the original source of the stock used in the experiment. The results were as follows:

	Hatched		*Late dead embryos*		*Combined*	
	Ring-neck	White	Ring-neck	White	Ring-neck	White
Pen 3-39	33	21	21	15	54	36
Pen 4-39	61	66	30	15	91	81
			Combined total		145	117
			Expected (1 : 1 ratio)		131	131

There is a deficiency of white chicks in both these backcrosses. Application of the χ^2 test for goodness of fit of observed and expected ratios (in combined totals) yields a value for χ^2 of 2.992 and, with $n = 1$, the value for p is .083. This means that the deviation from expectation is not significant, and, therefore, the hypothesis that a single gene causes the recessive white is not invalidated. Dunn (1923) reported a lethal gene linked with recessive white in White Wyandotte fowl. The deficiency of whites in these pheasant backcrosses does suggest that embryonic mortality is higher in *cc* embryos than in *Cc* ones. However, there was no deficiency of the homozygous recessives in the F_2 generation and the discrepancies in the backcrosses should therefore be ascribed to chance. Since the deficiency of whites was evident in the embryos dying late, any lethal effect of the white in the homozygous condition must have been exerted in embryos dying at some stage before the plumage color could be determined. It is noticeable that the major deviation from the expected 1 : 1 ratio was in pen 3-39, which yielded a ratio of 54 Ring-neck to 36 white chicks, whereas pen 4-39 gave a ratio of 91 Ring-neck to 81 white chicks. The latter is a reasonably good fit to the normal ratio.

Some of the white birds from the backcrosses showed an occasional dark feather and a few of the Ring-necks showed a white feather or two as was the case in the F_2 matings.

F_3

In order to check further the conclusion as to the genetic basis for white plumage, the white segregates from the backcross matings, pens 3-39 and 4-39, were mated *inter se* in 1940. Two such matings were made with the result that 75 chicks were hatched. These chicks were all pure white when hatched, and at maturity showed no signs of colored plumage.

DISCUSSION

The source of the white pheasants as bred in captivity is not definitely known, but, as has been mentioned, white individuals in wild birds of other species are not uncommon. Some of these wild specimens are true albinos, but they are relatively rare. Game breeders differ in their opinions as to the origin of this variety. Some believe it to be a true mutation or 'sport' while others think that it is the result of selection from 'pied' or 'spotted' stock. This latter aberrant form is relatively common. Correspondence with observant game breeders has indicated that white mutations from Ring-neck and melanistic pheasants have been known to occur.

It is evident from the data presented in this paper that white plumage in the pheasant, *Phasianus colchicus,* is due to the presence in the homozygous condition of a unifactorial, autosomal gene. Dominance of the allele, *C,* for color, is sometimes incomplete since heterozygous individuals often show occasional white feathers. Conversely, homozygous recessive individuals may show a slight ticking or a colored feather. Recessive white segregates from backcross matings breed true when mated *inter se.*

It would seem that white plumage in *P. colchicus* is similar in character to the recessive white found in White Wyandotte, White Plymouth Rocks and other varieties of fowls. However, in the pheasant the pigment in the eye, beak and shank is so reduced that these structures appear bluish, whereas these areas are not affected in white fowls. This suggests that the genes responsible for white plumage in the two species are not comparable or else, possibly, that the pheasant carries a gene, or genes, for the dilution of eye, shank and beak color closely linked with the gene *c* responsible for absence of color in the plumage. However, since in all the white birds raised in this study no exceptions were observed to the rule that white pheasants have blue eyes, beak and shanks, it seems most probable that the single gene, *c,* is responsible for the dilution of melanin pigment in these areas as well as for its elimination from the feathers.

SUMMARY

White plumage in the genus *Phasianus* is due to a single, autosomal, recessive gene, *c,* present in the homozygous condition. This is shown by ratios observed in 103 F_1, 262 backcross, and 197 F_2 pheasants following crosses involving white and Ring-neck Pheasants.

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EXPLANATION OF PLATE 18

UPPER FIGURE: Normal Ring-necked Pheasant, *Phasianus colchicus,* used in study of the inheritance of white plumage. F_1 hybrids between this bird and pure-white pheasants cannot be distinguished from the common Ring-neck except in rare instances where one or two main tail- or wing-feathers may be white.

LOWER FIGURE: Pure-white pheasant used in this study. The white segregates in the F_2 and backcross matings are identical in appearance and breeding behavior with the original white stock.

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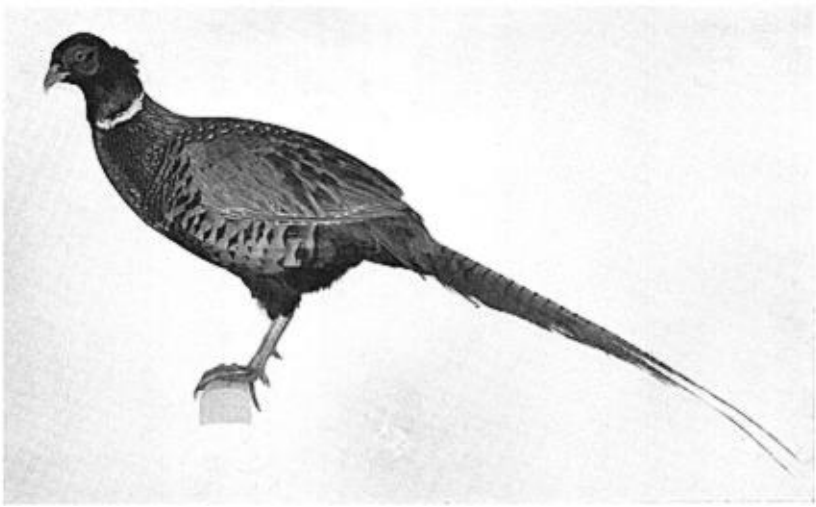
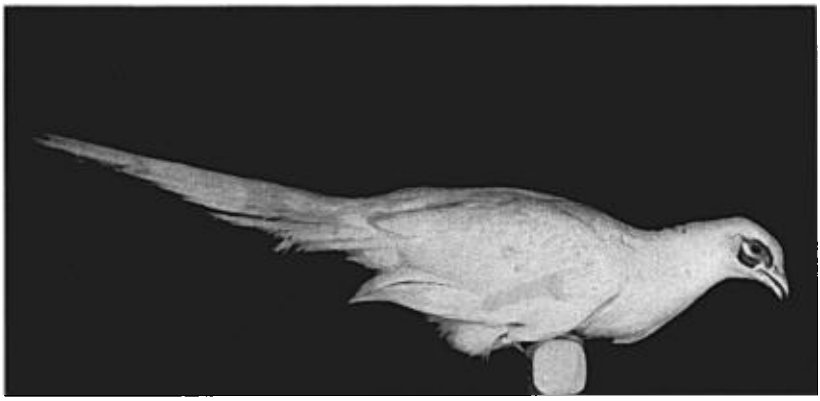


NORMALLY PLUMAGED RING-NECKED PHEASANT



PURE-WHITE RING-NECKED PHEASANT USED IN THIS STUDY