

# A FURTHER REPORT ON SPECIES CROSSES IN BIRDS

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## TABLE OF CONTENTS

INTRODUCTION.....	366
Mallard Duck × Florida Duck.....	367
Mallard Duck × Black Duck.....	370
Mallard Duck × Pintail Duck.....	371
Gold Pheasant × Lady Amherst Pheasant.....	371
Back-crosses.....	372
Segregation.....	472
Segregation in back-crosses of Amherst and Gold Pheasant.....	373
Linkage of character-complexes in extreme variates.....	376
Fertility.....	376
Sex of hybrids.....	376
Black Kalij Pheasant × Silver Pheasant.....	376
Silver Pheasant × Swinhoe Pheasant.....	378
“Freak” Mallard crossed with various wild species.....	378
“Freak” Mallard × Black Duck.....	378
“Freak” Mallard × Australian Duck.....	379
DISCUSSION AND CONCLUSIONS.....	380
LITERATURE CITED.....	383

## INTRODUCTION

In 1915, several controlled crosses with ducks and pheasants were described. The data for the present paper are in part from a continuation of these experiments, and in part from new crosses carried on during 1916 and 1917. In a sense it is a final report, since the exigencies of the war caused the abandonment of the investigations in 1917.

Analysis of the material, taken as a whole, presents a picture which may be of some interest. At least it brings a certain amount of order out of an apparent chaos, presumably caused by sporadic reports of numerous hybrids between different species of birds in which the number of individuals under observation has been insufficient for arriving at any proper conception of the mechanism of heredity. The impression appears to have been created that there is seldom anything approaching a Mendelian phenomenon in species-mating among birds. But definite types of segregation do occur, and these types are dependent upon the degree of relationship of the genetic constitution, as I shall hope to show here.

## MALLARD DUCK × FLORIDA DUCK

In 1915 the following cross was produced. The male parent was *Anas fulvigula maculosa*, a resident of the Gulf Coast of Louisiana and Texas, and a very poorly marked subspecies of the Florida Duck (*Anas fulvigula*) from which it differs by only one or two doubtful characters. The female parent was the Mallard. This cross was undertaken chiefly with the idea of testing the systematic position of the Florida Duck as compared with the common Black Duck (*Anas rubripes*), as seen in their hybrids with the Mallard.

*Anas fulvigula* (the subspecific name is dropped for convenience) resembles a light-colored Black Duck. The sexes are the same, except for the color of the bills, both resembling the female Mallard very closely. The only marked difference is that the white speculum band of the latter is not present. From the genetic standpoint the Florida Duck may be regarded as a Mallard with the male plumage (secondary sex characters) dropped out.

The first-generation hybrids were very different from the Mallard × Black-Duck combination, being much lighter-colored and more Mallard-like, and showing a slightly greater range of variation than is usual in a first-generation cross (figure 1). 17 males and 14 females were reared.

The next year (1916) an F<sub>2</sub> generation of 23 males was produced (see figure 2); and in 1917, 15 more were reared,—the number of females being approximately the same. The result is shown better in the photograph than by description, but it is so striking as compared with most other series of second-generation species hybrids, that it deserves special mention. These 38 males, when arranged in a linear series, present birds approaching the Mallard parent at one end, birds with solid-green heads, white neck-rings, chestnut breasts, and light-colored, vermiculated abdomens; while at the other end are birds with almost no male secondary sex characters, plain brown types, looking almost exactly like F<sub>1</sub> females, and to be distinguished from females only by the color of their bills, by their voices, and by the presence of testes. Between these extremes is a continuous series showing every gradation, including a few mixed types, such as birds with very Mallard-like body-coloring and small white neck-ring, but with female-like, brown heads.

Taking the body regions separately, there is the following result in the F<sub>2</sub> generation.

*Heads.* Solid green to solid brown. There were 2 with solid green heads, 5 or 6 with mottled heads and the remainder with little or no green.

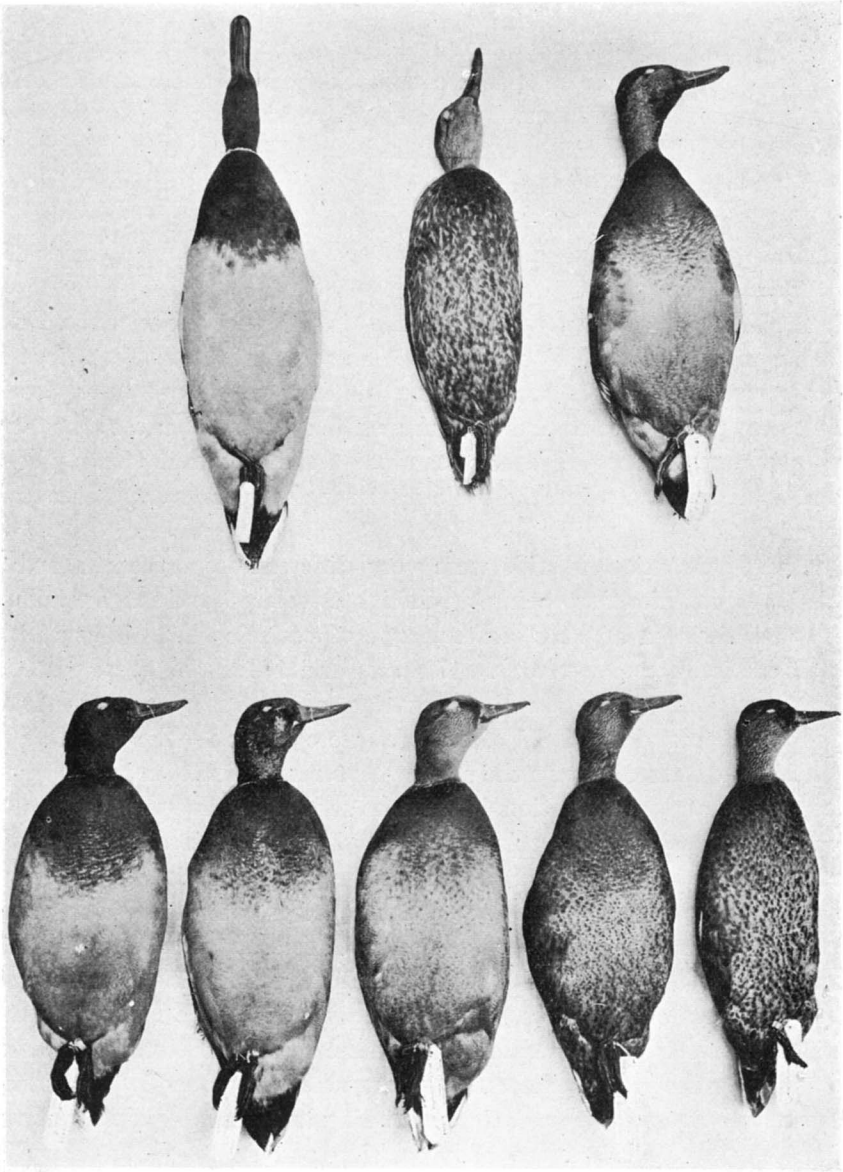


FIGURE 1.—Mallard Duck  $\times$  Florida Duck. All males. Upper row, left to right: Mallard, Florida,  $F_1$  hybrid. Lower row, selected  $F_2$  types, left to right: No. 1, extreme Mallard type; No. 2, Mallard type with spotted head; No. 3,  $F_1$  breast and abdomen, but with brown head; No. 4, approaching Florida type; No. 5, extreme Florida type showing scarcely any male secondary sex characters.

The birds with the greatest amount of green on the head, as a rule, were the most Mallard-like.

*Bills.* No great difference in series.

*Neck ring.* A trace in 4 specimens, absent in all others.

*Breast.* From almost solid chestnut with a few black spots, through mottled chestnut, to pure female type of breast color (mottled brown).

*Abdomen.* Unspotted and almost pure Mallard type in 4 specimens, through many intermediate types, to pure female type.

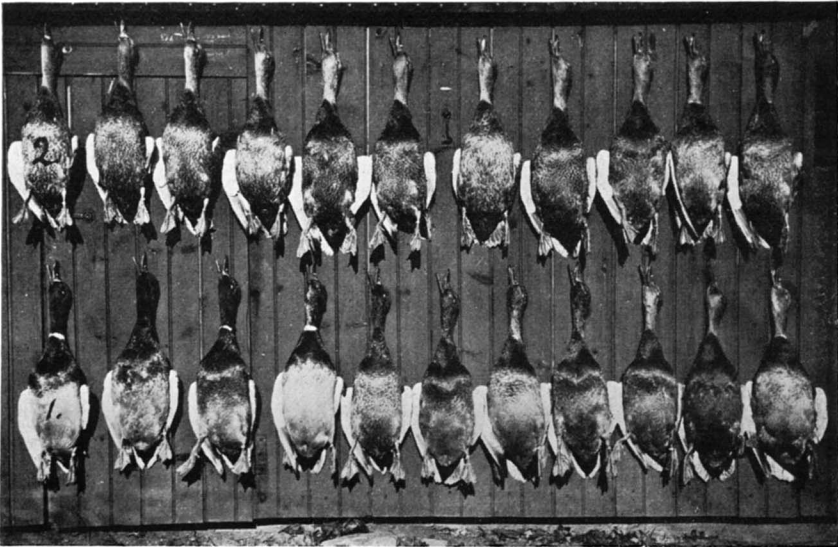


FIGURE 2.—Mallard Duck  $\times$  Florida Duck. Male  $F_2$ 's. 1, extreme Mallard variate; 2, extreme Florida variate. Arranged in series, upper row left to right, lower row right to left.

*Under-tail coverts.* All more or less of Mallard type, that is to say, black. The amount of black varies directly with Mallard-like appearance. Traces of the dark under-tail coverts persist in males that have lost practically every other trace of secondary sex characters.

*White anterior wing-bars.* More marked in Mallard type and always absent in the female or the neutral types.

*Rump.* In series the more Mallard-like birds have darker rumps. This is not universal. There is one intermediate individual with a very black rump.

*Color of legs.* The markedly Mallard types have brighter, more orange-colored legs than those at the other end of the series.

*Back and scapulars.* Rather dark and uniform throughout the series, but as one approaches the intermediate and the female type of male, the ends of the feathers become edged with lighter colors.

*Tails.* The lighter, brownish tails (upper surface) appear as a rule at the Mallard end of the series, but not in every case. The upturned sex feathers (central tail feathers) are more pronounced in Mallard-like individuals.

The females show about the same variation that one finds among the specimens of pure-Mallard females.

It is apparent then that in this species cross we have a nearer approach to orthodox Mendelism than in any other thus far reported among birds. Out of 38 males two are nearly pure Mallard types, and three almost pure female types, these latter closely resembling the Florida-Duck parent.

A back-cross made in 1917 between a female Mallard and an  $F_1$  Mallard  $\times$  Florida resulted in a series of 13 males which were very uniform and extremely close to Mallard. They do not show the variation characteristic of the  $F_2$  series, in fact they present very little more variation than one sees in a normal  $F_1$ . All except three are birds with solid-green heads, white neck-rings, and light-colored abdomens. Two approach the  $F_1$  type and one other has a partly green head. The white neck-ring is never complete as in pure Mallard, but broken on the dorsum. There are no "female" types like those in the  $F_2$  series. The females of this back-cross, 23 in number, show some specimens impossible to distinguish from pure Mallard.

#### MALLARD DUCK $\times$ BLACK DUCK

A cross between the Mallard and the Black Duck was described in a former paper (PHILLIPS 1915, p. 76). The cross was again made in 1916 and 1917, yielding 7 more  $F_2$  males and 4 females. Thus there are 23 male and 27 female  $F_2$  individuals from this combination. The extreme Mallard variates of this series, males 174 and 2262, do not approach the Mallard variates of the Mallard  $\times$  Florida-Duck  $F_2$  series; neither do the variates towards the Black Duck approach that species as closely as in the other cross. In other words, the Mallard-Black-Duck crosses do not show anything like as close an approximation to Mendelian behavior as do the Mallard-Florida crosses. The same thing is true of the Mallard-Australian crosses. Here even less segregation is seen than in the Mallard  $\times$  Black-Duck crosses. There was no approach to the Mallard types in the Australian crosses, a result shown in my former paper (PHILLIPS 1915). The scheme therefore is as follows:

*Results*

- Mallard  $\times$  Florida Duck 38  $F_2$  males obtained. 2 nearly pure Mallard types, 3 nearly pure Florida types. Back-crosses to Mallard females bring out many nearly pure Mallards.
- Mallard  $\times$  Black Duck 23  $F_2$  males obtained. 2 most extreme Mallard variants lack solid-green head, white neck-ring, and light-colored, vermiculated abdomen. Back crosses to Mallard females show no pure Mallard types.
- Mallard  $\times$  Australian Duck 15  $F_2$  males obtained. Very slight segregation. Most extreme Mallard type scarcely differs from  $F_1$  individuals. Back-cross to Australian female was the only one made, so not directly comparable with the other back-crosses.

MALLARD DUCK  $\times$  PINTAIL DUCK

For comparison with the crosses just described may be mentioned the Mallard-Pintail crosses reported in 1915. It was then shown that in this mating between the two genera, *Daifila* and *Anas*, the smallest possible amount of segregation was found, both in the straight  $F_2$  generation and in back-crosses with the Pintail male. The character complexes in the parent species are here wholly unrelated, the color patterns and the colors themselves being very different, and the hybrids show a resulting tendency to stability. This experiment has not been continued since 1915.

GOLD PHEASANT  $\times$  LADY AMHERST PHEASANT

In the paper mentioned above (PHILLIPS 1915), I described part of a series of crosses between the two pheasant species known as Gold and Lady Amherst, and at that time called attention to a supposed difference in the  $F_2$  hybrids of the reciprocal crosses. In order to test this matter further I repeated the reciprocal crosses in 1914; but this time used only stocks which had been tested for several generations in my own pens. These hybrids were carried to the  $F_2$  generation in 1915, the males reaching maturity in 1916. There were thus 12 additional males available for study, and these show without question that there is no difference in the reciprocal hybrids. The question then comes up, what produced the opposite result the first time the cross was made? The explanation of this seems to me to be as follows. It was found that in the  $F_2$  individuals of 1911-1914, the Gold  $\times$  Amherst mating produced second-generation hybrids with considerably more Gold Pheasant characters than did the Amherst  $\times$  Gold mating. I suggested then (PHILLIPS 1915, p. 99), that the

male Amherst used might have been a bird of hybrid origin, and that latent Gold characters influenced the offspring and produced the different  $F_2$ 's of the reciprocal hybrids. I still think this is the correct explanation; and this last repetition of the experiment fully bears out the conclusion that there is no evidence of sex-linkage.

#### *Back-crosses*

Besides the crosses enumerated above the following 8 matings were carried out between Gold-and-Amherst hybrids:

If we designate Gold female  $\times$  Amherst male as cross "C," and Amherst female  $\times$  Gold male as cross "H," the scheme will be as follows:

Gold female $\times$ C male	Gold female $\times$ H male
C female $\times$ Gold male	H female $\times$ Gold male
Amherst female $\times$ C male	Amherst female $\times$ H male
C female $\times$ Amherst male	H female $\times$ Amherst male

Males from all these matings were finally secured and 41 were brought to adult plumage (14-16 months of age). Twenty-one specimens were preserved and careful notes made on all those discarded. All extreme variates were preserved.

Sixty-eight females were produced in the course of these eight matings, and sixteen were preserved.

It is sufficient to say here that all of these hybrids show exactly what would be expected from back-crosses of the types made. All four of the back-crosses with pure Gold stock are alike, and show a plumage intermediate between  $F_1$  hybrids and the pure Gold parent. We need not therefore consider these eight matings again. There is no evidence of sex-linkage.

#### *Segregation*

We come now to the question of segregation. These two species of the genus *Chrysolophus* present a number of sharply defined and vividly contrasted characters which could not be better for a genetic study. Those characters which present the widest contrasts may be described as follows, the male sex alone being considered, as the females in the two species are almost identical (figures 3 and 4):

<i>Character</i>	<i>Male Gold</i>	<i>Male Amherst</i>
Top of head	Golden yellow	Bronze green
Crest	Golden yellow	Blood red
Mantle	Orange, banded with black	White, banded with black
Under parts	Uniform scarlet	Chest dark green, abdomen pure white
Middle tail feathers	Black with rounded spots of brown	White with black bars and lines

It is apparent that from the genetic point of view—assuming that we are dealing with closely related sets of characters—there is here an excellent chance for the reappearance of new types in  $F_2$ ; but with the number at hand such is not the case.

The  $F_1$  hybrid males show some green on the breast, and nearly always have a yellow band, or at least a yellow area, at the point of junction of the Amherst green breast and white abdomen. This character, however, is somewhat variable. In one specimen the yellow "break" consists of a few yellow feathers on the sides of the breast, in another the band is 3.7 cm broad all across the lower surface. These represent the two extreme  $F_1$  variates. All other characters are intermediate and extremely constant.

The  $F_2$  generation (excluding that from the presumably hybrid Amherst male) is merely a repetition of the  $F_1$ , but with the extreme variates slightly extended. The nearest approach to the Gold parent has uniform scarlet underparts, mantle dirty yellow and black, head and crest pinkish straw-color, and tail vermiculated, not barred. At the other end of the scale, the most Amherst-like bird is characterized by a yellow band across the chest 5 cm wide at the sides, the scarlet of the underparts not so deep in tone, the mantle pure white and black, and the central tail feathers yellowish-white, irregularly barred and mottled with black. Segregation is manifested far less than in the Mallard  $\times$  Florida-Duck cross.

#### *Segregation in back-crosses of Amherst and Gold Pheasant*

Let us next consider results obtained from mating pure Amherst with  $F_1$  (the four matings designated above). This series of 18 males shows some rather marked variates. No. 1765 has the lower parts nearly all red, and separated from the green breast by a whitish area. The tail is very clearly barred, the occiput and the crest deep scarlet (see figures 3 and 4). No. 1502 is nearly pure Amherst underneath, with only a little red on the lower part of the abdomen. The top of the head is nearly all green and the crest is blood red. The middle tail feathers are well barred, but not so white as in the last specimen (see figures 3 and 4).

Similarly we may describe the results obtained from mating pure Gold with  $F_1$  (the four matings designated above). This series of 23 males shows a marked variation in the crest, from light straw-color in No. 999 to light scarlet in No. 1160. In No. 640 the ground color of the mantle is orange, and in two others it is nearly white. The scapular feathers show considerable variation. The lower parts are all a uniform red except



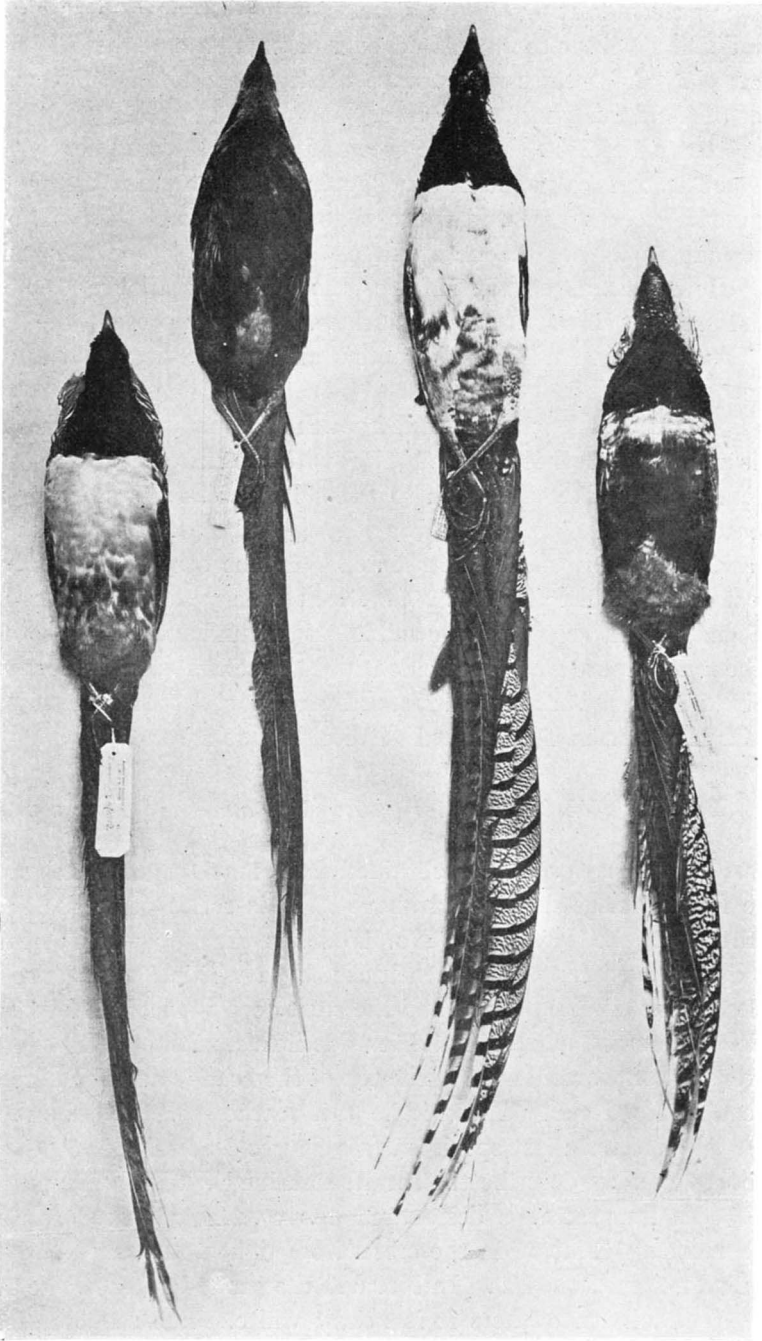


FIGURE 3.—Gold Pheasant  $\times$  Lady Amherst Pheasant. All males. Upper row, left Gold; right Lady Amherst; lower row, left No. 1502,  $F_1$   $\times$  Lady Amherst showing no Gold characters on lower parts; right No. 1765 of same cross showing posterior parts to white band pure red, like Gold parent.

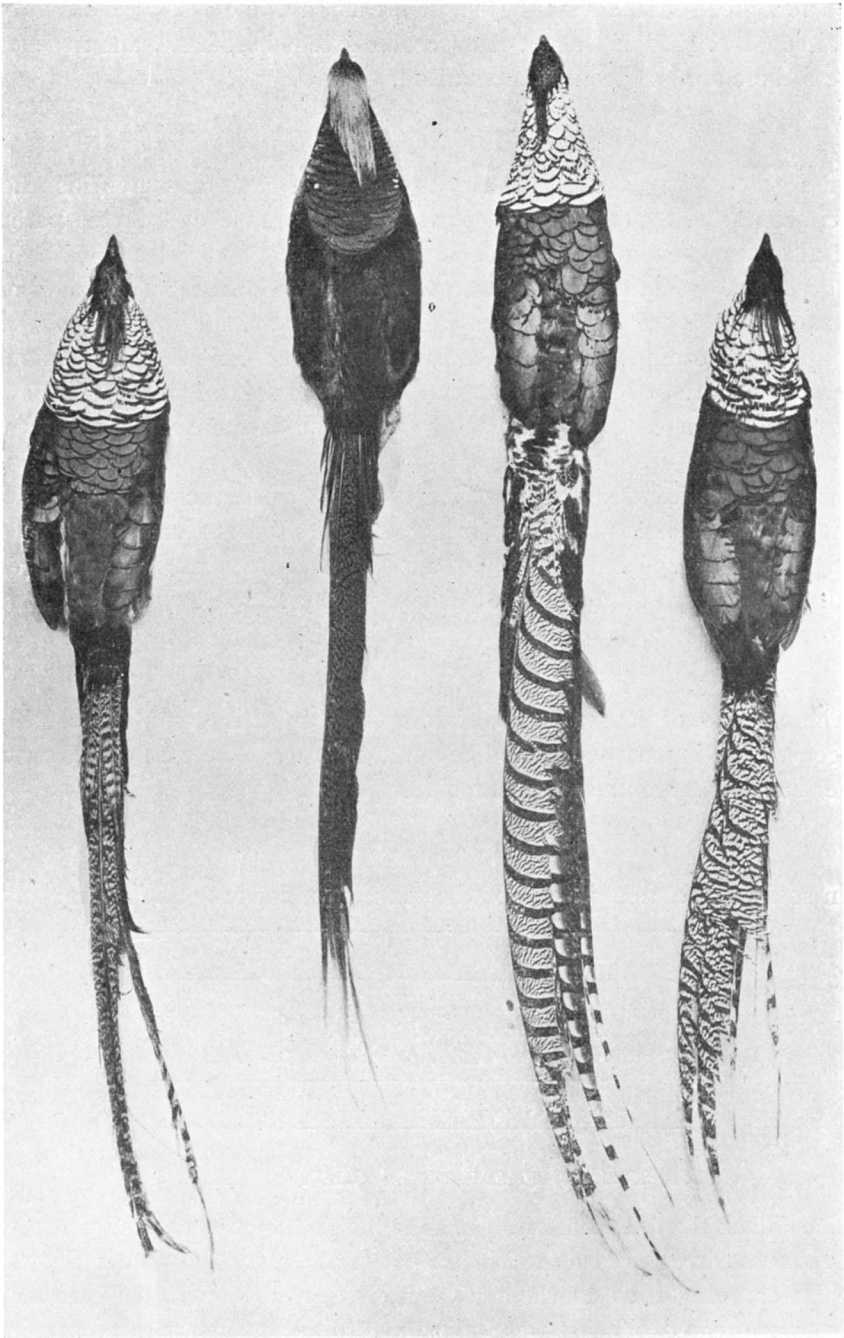


FIGURE 4.—Dorsal view of birds of figure 3.

for a few green feathers on the upper breast in a few cases. Only in one specimen, No. 1160, is there a considerable green chest-band, and in several others there are no green feathers at all.

*Linkage of character-complexes in extreme variates*

In a general way, through this entire series of back-cross hybrids, those specimens showing one character varying towards the Amherst parent, will also show several others. The same is true of variates towards the Golden parent. In other words, the character-complexes for different tracts of the plumage are more or less linked. This linkage is not, however, absolute. For example, the three-fourths-Amherst hybrid No. 1765, though having a very red (Golden character) breast, has central tail feathers even more clearly barred and Amherst-like than the extreme Amherst variate No. 1502 (see figure 3).

In the three-fourths Golden series, No. 999, with the palest head and crest, does not possess the most deeply colored (Golden) mantle, the latter being found on specimen No. 806, a bird having a pink head and crest. Thus the Golden characters are not completely linked any more than are the Amherst.

*Fertility*

There is no direct evidence of infertility in this cross. The inbred F<sub>2</sub> generation is very feeble and difficult to rear. The first cross, on the other hand, is more vigorous than either parent.

*Sex of hybrids*

In so far as records were kept the sex proportions are as follows:

GENERATION	MALES	FEMALES
F <sub>1</sub> .....	31	40
F <sub>2</sub> .....	28	27
Back-crosses.....	41	64
Total.....	100	131

BLACK KALIJ PHEASANT × SILVER PHEASANT

The Black Kalij Pheasant, *Genaeus melanotus* was crossed with the well known Silver Pheasant, *Genaeus nychthemerus*, in 1915 (cross F, 1915), the latter being used as the male parent. In 1916 and 1917, eight F<sub>2</sub> males were reared. These were kept until full plumage appeared at about eighteen months of age, and then killed for specimens.

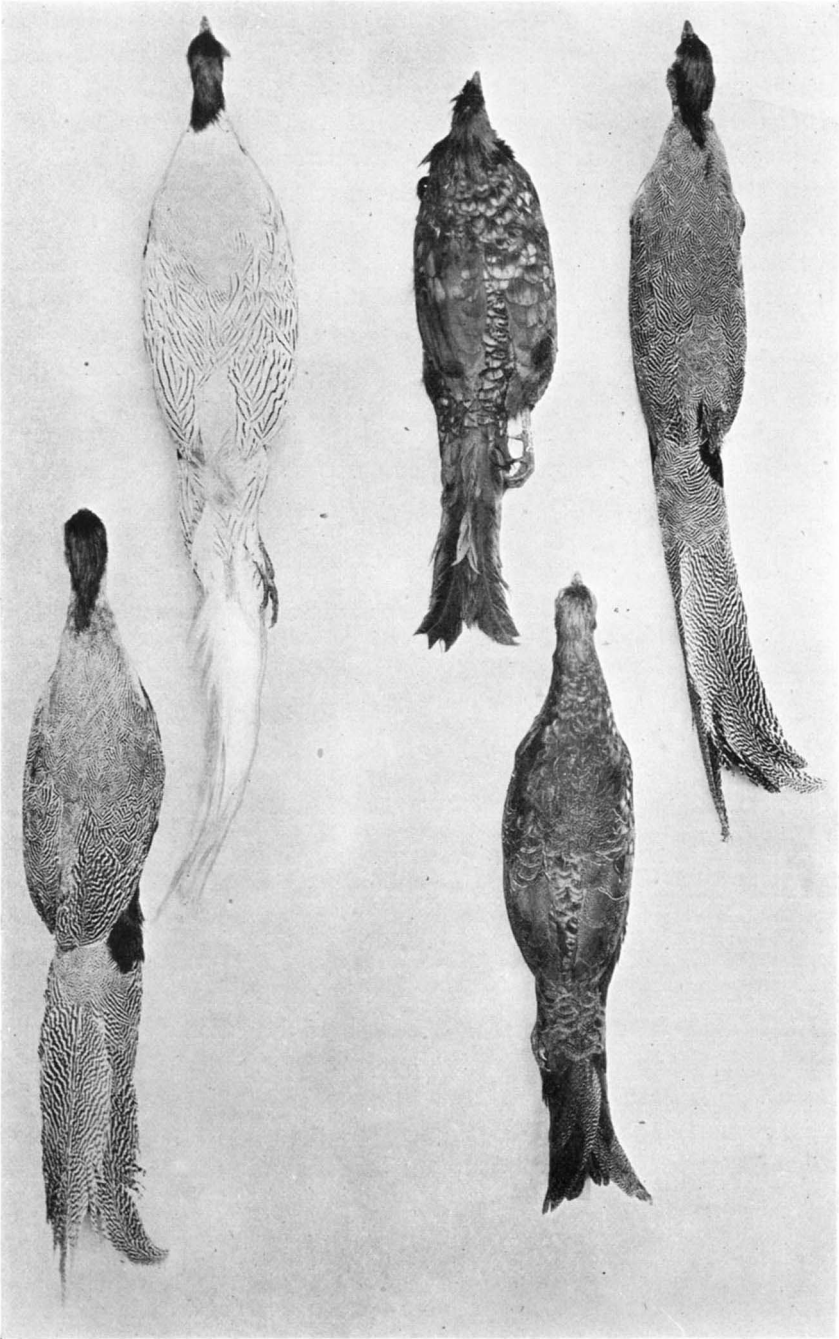


FIGURE 5.—Silver Pheasant  $\times$  Black Kalij Pheasant. All males. Upper row, left to right: No. 1, Silver, No. 2, Black Kalij, No. 3,  $F_1$  hybrid. Lower row, left to right: No. 1 extreme Silver variate of  $F_2$ , No. 2, extreme Black Kalij variate of  $F_2$ .

The parents of this cross differ remarkably in color, although there is no apparent infertility in the  $F_1$  individuals. With the exception of head and crest, the male Silver has the whole upper surface white, with narrow black concentric lines on each feather. The top of head, crest and underparts are black. The male Black Kalij Pheasant is entirely black with a purplish gloss. The females of the two species are not markedly different.

The first cross is intermediate. The birds resemble the Silver Pheasant, though darker and more heavily barred on the upper surface, and with enough white to give them a distinct silver-gray appearance (figure 5). The eight  $F_2$  males are very interesting, as they vary from the  $F_1$  type to a bird (No. 1219) almost black all over, particularly so marked on mantle, wings and tail. A vermiculated appearance is seen on back rump and secondaries, but this individual might easily be taken for three-fourths pure *melanotus* (see figure 5).

#### SILVER PHEASANT $\times$ SWINHOLE PHEASANT

Swinhoe's Pheasant was crossed with Silver Pheasant in 1914. These hybrids were partially sterile, and only 2  $F_2$  males were reared to maturity. These two individuals are extremely different in appearance, and neither of them is like an  $F_1$  bird. Partial sterility has already been reported in this cross by others (GHIGI 1908).

#### "FREAK" MALLARD CROSSED WITH VARIOUS WILD SPECIES

In my 1915 paper I described a variety of domestic Mallard showing in the male an absence of chestnut breast and white neck-ring, and a black instead of a green wing speculum. The female was plain-colored about the head, and the young were jet black in down plumage. This variety behaved as a simple, clear-cut, Mendelian recessive, in crosses with Mallard stock, and showed no tendency to variation.

In 1915 it was thought of interest to cross these "freak" Mallards with other pure wild species, to see how this new Mallard variety would be affected by meeting another set of germ characters. Accordingly female "freaks" were mated both with pure wild Black Ducks and pure Australian Ducks with the following result:

#### "Freak" Mallard $\times$ Black Duck

The first cross (cross S, 1915) produced 5 males and one female, all normal and just like the birds of the Mallard  $\times$  Black cross described in the former paper.

The next year the second, generation ( $F_2$ , cross L, 1916), produced five normal and six freak young, the latter black in down. When these grew up there remained:

	FEMALES	MALES
Normal.....	3	1
Freak.....	0	2

In addition one doubtful male (No. 2422) was obtained, looking like an  $F_1$ , but with a very dull-colored speculum. It was marked "normal" when in down plumage.

This series agrees with Mendelian expectation as far as it goes. The male "freaks" tend to segregate into two types, extreme Mallard with solid-green head and vermiculated breast, and a more female-like type, plain-colored all over. The doubtful male cannot be classified with certainty, but was probably a normal, slightly influenced by "freak" characters.

*"Freak" Mallard × Australian Duck*

In 1914 a female "Freak" Mallard × male Australian (cross B, 1914) produced 4 males and 7 females, all normal  $F_1$  types.

In 1915 and 1916 sister × brother matings produced 28 ducklings, 19 normals and 9 "freaks." On maturity, 3 "freak" males and 4 normal males were saved as specimens. Again no "freak" females reached maturity. There were as adults:

	FEMALES	MALES
Normal.....	6	11
Freak.....	0	4

The "freaks" are all clearly separable, both in downy plumage and as adults. The only thing which here runs counter to expectation is the great variation in "freak" males. They tend to segregate into a very Mallard-like "freak" type with solid-green head and vermiculated breast and abdomen, and another type looking like a female "freak" Mallard. The normal  $F_2$  males show more segregation than that seen in the Mallard × Australian cross (PHILLIPS 1915), but none shows the solid-green Mallard-like heads of the "freak."

As far as these two crosses go they show that the "freak character," or set of inhibitors, whatever one chooses to call it, acts normally when

brought into contact with the germ-plasm of two other true species. It even appears to have the effect of increasing the segregation in  $F_2$  hybrids. There may be a lethal factor which inhibits the development of  $F_2$  "freak" females, or else kills them in the shell. One very interesting young bird ("Freak" Mallard  $\times$  Australian  $F_2$ , No. 1991) which was lost before reaching adult plumage, showed a curious bilateral difference in first plumage. A note on August 1st, 1915, describes this bird as having the whole right side lighter colored than the left side, the difference showing especially on the wing and the occipital and orbital head-streaks. Possibly this bird may have been a mixed "freak" and normal type, or a gynandromorph.

The lack of virility of the "freak" stock was mentioned in 1915 and it was always very difficult to maintain the strain with pure "freak" (recessive) matings.

#### DISCUSSION AND CONCLUSIONS

Looking over the various matings between species described here, and those described in former papers, let us see whether some order can be brought out of the apparent chaos. It was suggested in 1915 (p. 110) that in closely related forms there is, under experimental conditions, a nearer approach to orthodox Mendelism than in crosses between more widely separated species; and the present work has, I think, gone far enough to fully bear out this point.

I will arrange the various species matings made at Wenham in a column, beginning with the most distantly related generic crosses and ending with species most closely related.

Reeves  $\times$  Prince of Wales Pheasant (PHILLIPS 1916)

Reeves  $\times$  Ring-neck Pheasant (PHILLIPS 1913)

Intergeneric crosses between genera only distantly related.

Hybrids sterile. Reciprocal hybrids unlike.

Malformation or absence of sex organs in females.

The cross difficult to obtain on account of sterility of most of the eggs of parents.

Muscovy Duck  $\times$  Mallard

Intergeneric cross said to produce unlike sterile reciprocal hybrids, but females sometimes lay eggs. (These reciprocal crosses were not produced by me. POLL 1910).

Silver Pheasant  $\times$  Swinhoe (SMITH and HAIG-THOMAS 1913, and present paper)

A species cross accompanied by partial sterility of hybrids (found sterile by GHIGI 1908), and producing probably abnormal types of hybrids, but not a large enough series to draw definite conclusions.

Mallard Duck  $\times$  Pintail (PHILLIPS 1915)

Intergeneric mating showing no sterility. The genera *Dafila* and *Anas* are closely related, and give results very different from the above-mentioned crosses. The parental colors and patterns differ, plumage character

complexes are unrelated, and  $F_2$  hybrids show the smallest amount of segregation. Back-crosses show even less tendency to segregate than does the second generation. This is the best example of hybrids "breeding true."

Golden Pheasant  $\times$  Lady Amherst (present paper)

A species cross between parents having several well marked alternative characters. Pattern in general the same, but colors very different. Hybrids show a moderate amount of segregation. On the theory of two closely related species, this mating ought to show a closer approach to simple Mendelian behavior than it does. This is possibly accounted for by the very complicated nature of the colors and color patterns in the parents. Back-crosses appear to show more segregation than  $F_2$ .

Black Kalij  $\times$  Silver Pheasant (present paper)

A species cross where the parents have well marked alternative characters. Hybrids show no apparent sterility and  $F_2$  exhibited a clear-cut type of segregation (see figure 5).

Mallard  $\times$  Australian Duck (PHILLIPS 1915, and present paper)

A cross between two closely related species showing a moderate amount of segregation. Less segregation in back-crosses.

Mallard  $\times$  Black Duck (PHILLIPS 1915, and present paper)

Comparable with last cross, but parent species more closely related and segregation somewhat pronounced.

Ring-neck  $\times$  Prince of Wales Pheasant (PHILLIPS 1915)

A cross between two nearly related species, one of which, the Ring-neck, is probably not pure, but made up of *Phasianus colchicus* and *P. torquatus*. Alternate characters showing well marked segregation.

Mallard  $\times$  Florida Duck (present paper)

Showing most extreme example of segregation thus far discovered in species crosses between either ducks or pheasants. Parental types are almost recovered from among 38  $F_2$  males. Back-crosses to Mallard parent produce a more uniform generation of nearly pure Mallard types. The Florida Duck must be supposed to represent, from the genetic point of view, substantially a Mallard, with the male secondary sex characters not expressed. It must thus be regarded, according to the breeding test, as more closely related to the Mallard than is the Black Duck, or the Australian Duck. (Figures 1 and 2.)

These differing results do not, of course, necessitate the consideration of a different mechanism of heredity, as the types used become more and more closely related in a genetic sense. The results of hybridization are in *appearance* different because of partial sterility in the most extreme matings, because of great numbers of factorial differences affecting the characters—but without sterility—in the next cases, and because of few factorial differences in the last case.

Two types of domestic variations in ducks have also been investigated. In one of these, the "East India" melanistic Mallards were shown to be dominant over pure Mallard stock (PHILLIPS 1915), but extracted normal Mallards entirely free from melanism have not been obtained from the cross. The ratio between extracted normals and "East Indias" remained,



however, a simple Mendelian one. The other variation investigated was the "freak" Mallard, a type acting in crosses as a pure Mendelian recessive unit character. The "freak" character, though behaving as a unit, has produced many profound changes in plumage, in down-coloring of young, and in viability and fertility. When crossed with other distinct species, the "freak" Mallards do not lose their identity, but actually appear to segregate more readily than normal Mallards in the same crosses.

We have, therefore, a gradation of results in species crosses starting with sterile monstrosities, whose sex organs may even be absent, and ending with species combinations showing, in spite of small numbers, such a near approach to parental types in the segregates, that their plumage characters may be supposed to differ from each other by only three or four principal factors.

How then shall we explain the behavior of stable hybrids like those between the Pintail and Mallard Ducks? My own preference would be the assumption of two character-complexes, very distantly related, and presenting such an enormous series of possibilities in  $F_2$ , that with the small numbers at hand only the very centre of the curve of frequency has thus far been brought to light in experiments. There is absolutely no evidence of infertility in this cross and therefore I see no reason to assume the presence of selective elimination due to balanced lethal factors.

In these species-crosses we have found no true sex-linked inheritance. In species crosses the more important plumage characters are not recombined independently, but nearly always reappear together, so that the most extreme individual in a series will contain several plumage characters of an extreme parental type. This does not always hold, however; and quite important characters at times become disassociated in hybrids, and crop up at random. This is seen in the matings between *Phasianus torquatus* and *P. principalis* and also in back-cross Gold-Amherst matings. As a rule, however, we may say that plumage characters of species, even for widely separated feather tracts, are closely linked.

The fact that complicated male color patterns *can* be at times broken up in inheritance, even in a very limited series of individuals, tends to show that some of the elements of the secondary sex color-patterns may be carried in separate chromosomes.

The series of crosses here reported give results in accordance with the views of those who believe that genetic factors are carried by the chromosomes. In the more distantly related species, the plumage patterns and colors are affected by so many factors that the majority of segregates are more or less intermediate; but in the more closely related species, decidedly

different patterns and colors may result because of the interaction of relatively few inherited factors. In the latter case the visual result of segregation will be more marked.

The independence of color factors, and factors underlying fertility and sterility, is striking, especially in ducks. Ducks afford interesting material because of the presence of fertility in wide crosses.

The sterile and unlike reciprocal hybrids between Reeve's and Ring-neck Pheasants should be carefully investigated by a competent cytologist. The writer some years ago possessed a large amount of this material which was, unfortunately lost in the laboratory to which it was sent before it could be studied.

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