

ALLELES¹ OF THE MALLARD PLUMAGE PATTERN IN DUCKS²

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Very little information has been published on the genetic composition of the various breeds and varieties of ducks. The present investigation was started to study the inheritance of these varietal differences. The Standard (American Poultry Association 1930) varieties, Rouen and Gray Call, have a plumage pattern similar to that commonly found in their wild ancestor, the Mallard. The most outstanding difference between these two Standard varieties is in size rather than color, the Rouen being selected for large, and the Gray Call, small size. The term "mallard" is used to designate this pattern type wherever it occurs; "Mallard" (capitalized) refers to the wild duck or stock reared from it in captivity. This mallard plumage pattern was used as a starting point since it represents the wild-type. It was early noted that variations occur in this pattern which are rather constant in expression. A series of three patterns produced by three allelic genes, all of which give an adult color pattern approaching the generally accepted wild-type, are herein discussed.

Early in the work the stock consisted of partially domesticated Mallards. Some of these were obtained through the courtesy of the State Conservation Commission, others consisted of stock bred by the Poultry and Genetics Departments of the UNIVERSITY OF WISCONSIN, and a few were secured from local breeders. Later White Pekins were used, which proved to be genetically mallard in plumage pattern; that is, having this pattern as a cryptomere under the recessive white. For sake of clearness, as in a previous report (JAAP 1933) the pure white segregates have not been included in the material presented.

DESCRIPTION OF TYPES

The three down color types and their corresponding adult patterns have been designated as mallard, dusky mallard, and restricted mallard. The following is a description of these types.

The "mallard" pattern

The dorsal surface of mallard ducklings (figure 2A) is of a dark color closely approaching olivaceous black. Four dull yellow spots (see figure 1),

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irregular in outline, are invariably found on the back. These may vary somewhat in brightness but their location is constant. The sides of the head are dull yellow, with one or two dark ocular stripes extending from the base of the bill to the dorsal dark area. The variability in these dark ocular stripes is considerable. Mallards always have at least one of these stripes and this is the main character used in classification. When there is only one stripe it extends across the eye and may or may not unite with the dorsal dark area. The second of these stripes may appear as a mere spot near the back of the head and another at the base of the bill where the two mandibles meet. All gradations are found between this latter type and those having two complete ocular stripes. On some ducklings the two stripes may fuse below and just posterior to the eye. On others,



FIGURE 1.—Dorsal view of “mallard” duckling showing the location of the four light colored spots on the back.

neither of the oculars may unite with the dark area of the dorsal surface. The ventral surface, from the base of the bill to a point where the white neck ring appears on the adult male, is yellow in color. The down here is very short, which makes it impossible to distinguish any difference between the surface and undercolor. The same is true for the ventral surface of the wings. The remainder of the ventral surface is also dull yellow but the down here is characterized by a dull black to slate undercolor. On some ducklings the dark undercolor may extend out to the surface, giving the region a mottled appearance. The upper surface of the bill, the legs and the feet, are dark horn-color, while the under surface of the bill shows only the yellow carotinoid pigment.

In adults (see figure 4) “mallard” conforms very closely to the description as outlined by the American Standard of Perfection (American Poultry Association 1930). Both males and females of the stock used, however, are usually of a somewhat lighter shade owing to a reduced size of the dark brown markings as compared with the ideal feather. The precise regularity of feather pattern described in the Standard seldom, if ever, occurs. The color of the upper mandible of the drake, and of that part of

the duck's bill not covered with dark pigment, varies considerably. It ranges from greenish yellow through dark green to leaden. Narrow white tipping on the claret breasts of the males is common and, in extreme cases, may make the median area appear white. The sides of the head on females and the first feathering of both sexes in the head region tend to vary with the down color. The dark portion of the feather pattern is usually lacking

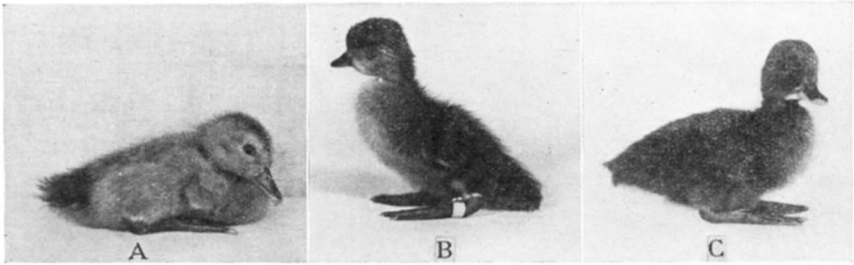


FIGURE 2.—(A) “Restricted,” (B) “mallard,” and (C) “dusky” ducklings.

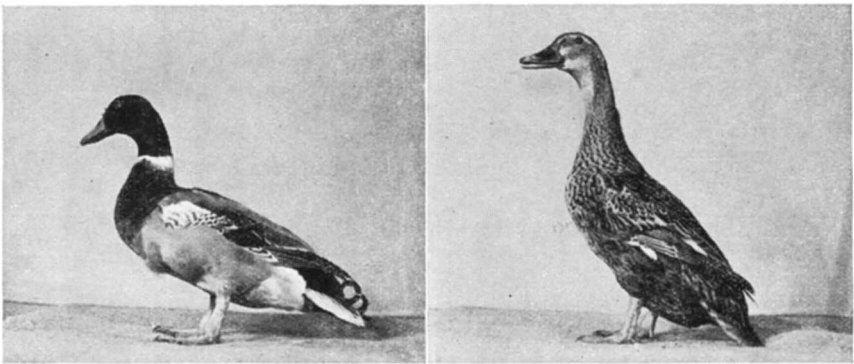


FIGURE 3.—Adult “restricted” male and female. Note the white on the dorsal wing surface of the male. The white on the female’s wing is limited to the wing front, which is nearly covered by body feathers. The feathers on the remainder of the dorsal wing surface have a wide lacing of buff.

for some distance from the base of the bill on the ventral side of the neck of females. Several “mallard” females, however, have been recorded in which this area has the dark feather pattern.

Dusky “mallard”

The “dusky mallard” or “dusky” pattern has been obtained from the Mallard, White Pekin, Buff, and black breeds. Dusky ducklings (figure 2C) exhibit a uniform olivaceous black over the entire dorsal surface, gradually becoming lighter to a dark-olive-gray on the ventral side. There

are no dull yellow spots on the back of dusky, this being a constant difference from mallard. The ventral surface of the wing is deeply pigmented. The bill, legs and feet have a dark color which always shows a distinct brownish cast. As in mallard the under surface of the bill usually lacks the dark color, but a small spot may appear at the tip. Dusky ducklings, as evidenced by their plumage pattern when adult, have been described

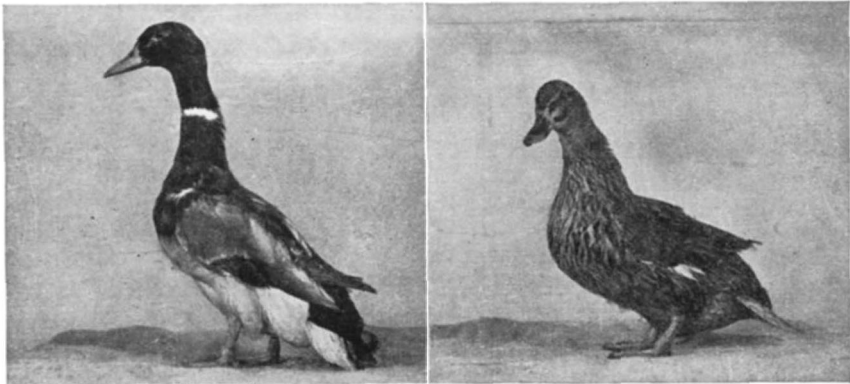


FIGURE 4.—Adult “mallard” male and female.

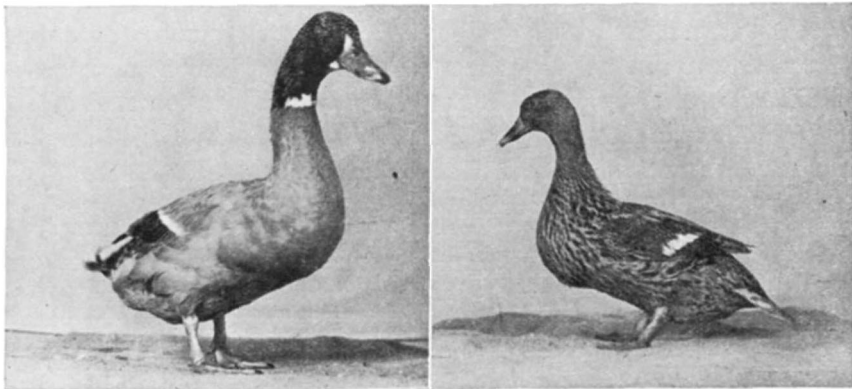


FIGURE 5.—Adult “dusky” male and female. Note the absence of claret-brown on the breast of the male and the irregular white spot on the throat. This white spot occurs equally often on females as males. The uniform coloration of the head is characteristic of the female.

in the literature as “*vrais petit negrillons*” by ROGERON (1903), “sooty black” by FINN (1913), and “coal black” or “freak” by PHILLIPS (1915, 1921). A “sooty aberrant” type described by PUNNETT (1932) was probably dusky.

Adult dusky drakes usually deviate from mallard by a complete ab-

sence of the white neck ring. If white is present in the neck (figure 5) it is not a secondary sexual character and always appears in the first feathering of both sexes. The claret breast of most dusky males is reduced to a very small amount in a region close to where the white neck ring is located on mallard. Quite a few individuals, however, show even more claret than is minimum for mallard. The iridescent bar on the secondary wing feathers is invariably obscured and the secondary coverts have more white (figure 5). Dusky females show no sign of the light ocular stripes usually present on mallard ducks. Though the females are usually somewhat darker in shade, some duskies have been raised which are even lighter in color tone than the darkest of the mallards. The only part of the plumage in which dusky invariably differs from mallard is the ventral wing surface. In dusky this region is always pigmented. Furthermore, the feather pattern is similar to that of the body, while in mallard it is white.

GOODALE (1911) is the only author who has noted the pigmented ventral wing surface of dusky, but he failed to associate it with the dusky down pattern. The only uniformly colored ducklings raised by GOODALE were reported to have been black when adult. The association of the uniform head color of the females, and the obscured wing speculum of both sexes, with a pigmented ventral wing surface in the adult is shown by him in tabular form along with some other variations. The males described by PHILLIPS (1915, 1921) had very little, if any, claret-brown on the breast, while FINN (1913) observed a gradation from a mere trace to an amount of claret similar to mallard. GOODALE (1911) has recorded one male without and one with claret-brown in the anterior breast region. ROGERON (1903), FINN (1913), and PHILLIPS (1915, 1921) report an absence of the white collar, or neck ring, while both the males given in the table presented by GOODALE (1911) had a white neck ring.

Restricted "mallard"

The term "restricted" has been given to the other variant since, in the down, the dark area of the dorsal surface is restricted to a patch on the head and tail (figure 2A). The remainder of the dorsal surface is dull yellow with a dark undercolor. The ventral surface, bill, legs and feet are the same as described for mallard. About the only variation occurring within this type is in the general color shade of the duckling. This is due to the extent to which the dark color at the base of the down feather extends out towards the tip. In some cases the dark tail area may extend a short way up the back, gradually blending into the dorsal surface color.

Restricted mallards as adults (figure 3) are almost indistinguishable from mallard. The only constant difference is in that area designated by the Standard (American Poultry Association 1930) as the wing front and

bow. In "restricted" this area always shows considerable white in the males, the white appearance being due to partially white rather than to completely white feathers. Restricted females have white spotted feathers on the wing front, and the wing bow is much lighter in color than mallard or dusky owing to a very wide lacing of buff. This restricted type of mallard plumage coloration has not, to the writer's knowledge, hitherto been described in the literature.

GOODALE (1911) obtained from Rouen-Pekin crosses a new type of down pattern in about one-half of the progeny, the remainder having the typical Rouen coloration. These were described as "dull yellow, very different from the Pekin color, and with an under color of dull black which usually came to the surface on the wings and tail." The adult males had much claret on the dorsal side of the lower neck and the more anterior parts of the dorsal wing surface had an admixture of white and rufous. One F_1 male with color pattern similar to that of the Rouen was raised. Since the down colors of each individual were not reported it is not known whether the above mentioned types of down and adult colors correspond. FINN (1913) records that three yellow ducklings with a dash of black on the crown were observed in the progeny of a Mallard. These ducklings as adults were described as being pale brown with dark markings. No inheritance studies were undertaken on either of these two types.

EXPERIMENTAL

The following material, except where specified, is gathered from matings in which both parents are known. The exceptions consist of pen matings of one male with two or three females. Since the adult and duckling classifications correspond, the records presented in the following tables are the down color descriptions. By this procedure many of the ducklings could be disposed of at hatching and thus make it possible to increase the number classified. The letter M designates the wild-type (mallard) and m^d the recessive, dusky. Since restricted is dominant and allelic to the others it is designated by the symbol M^R .

The relation of dusky to mallard

The results of the matings involving only mallard and dusky are given in table 1. In mating 2 a dusky female mated to an unrelated mallard male produced 34 mallard ducklings. Fifteen ducklings were described from the reciprocal cross (mating 6), all of which were mallard. In the F_2 generation (Y18-1, U354, 29, 36, and 59) there were 97 mallard to 43 dusky, a deviation of 8 from the expected 3:1 ratio, with a probable error of 3.45. Matings 9, 41, and P41 are backcrosses of F_1 progeny to dusky. These produced 90 mallard and 104 dusky ducklings, a deviation of 7 ± 4.69 from

the expected 1:1 ratio. Dusky segregates mated together, in matings 3, 19, 21, 24, 52, 62, and 67, produced 253 ducklings, all of which were duskies. These matings demonstrate a single gene difference between mallard and dusky. PHILLIPS (1915, 1921) also reported dusky a simple recessive to mallard.

TABLE 1

	MATING NO.	TYPE OF MATING		OFFSPRING	
		MALE × FEMALE		MALLARD	DUSKY
(a)	2	<i>MM</i>	<i>m^dm^d</i>	34	0
	6	<i>m^dm^d</i>	<i>MM</i>	15	0
	Total			49	0
	Expected			49	0
(b)	Y18-1	<i>Mm^d</i>	<i>Mm^d</i>	47	17
	U354	"	"	4	3
	29	"	"	16	10
	36	"	"	13	7
	59	"	"	17	6
	Total			97	43
	Expected			105	35
		Deviation		8 ± 3.45	
(c)	9	<i>m^dm^d</i>	<i>Mm^d</i>	51	41
	41	<i>m^dm^d</i>	<i>Mm^d</i>	29	47
	P41	<i>Mm^d</i>	<i>m^dm^d</i>	10	16
	Total			90	104
	Expected			97	97
		Deviation		7 ± 4.69	
(d)	3	<i>m^dm^d</i>	<i>m^dm^d</i>	0	44
	19	"	"	0	43
	21	"	"	0	40
	24	"	"	0	36
	52	"	"	0	57
	62	"	"	0	23
	67	"	"	0	10
	Total			0	253
		Expected		0	253

With the exception of matings 59 and P41, the birds used in table 1 were entirely of Mallard origin. Therefore, as ROGERON (1903), FINN (1913), and PHILLIPS (1915) have found, the dusky gene is present in some races of the wild Mallard. Mating 59 is a mating of two buff ducks obtained from a local fancier. Both mallard and dusky pattern appeared in the young. Since none of these were raised to feathering the adult patterns were not checked. Both parents in this mating must accordingly have been heterozygous for dusky. The male used in mating P41 is the same buff drake as in 59 and the female was an F₁ of a Pekin-dusky cross (mat-

ing P8, table 3). These two matings demonstrate that Buff ducks may have either the gene M or m^d , or both. Since dusky ducklings were produced in mating P8, and in other Pekin-Mallard matings, it is evident that White Pekins also may carry both mallard and dusky. Data not presented here show, in the same manner, that black ducks (a breed known as East India) may also carry both these genes.

TABLE 2

	MATING NO.	TYPE OF MATING		OFFSPRING	
		MALE	FEMALE	RESTRICTED	MALLARD
(a)	P1	$M^R M^R$	MM	130	0
	P5	$M^R M^R$	Mm^d	91	0
	P16	$M^R M^R$	MM	10	0
	P31	Mm^d	$M^R M^R$	31	0
	P37	$M^R M^R$	MM	12	0
	Total			274	0
	Expected			274	0
(b)	P9	$M^R M$	$M^R M$	34	15
	P11	$M^R M$	$M^R M$	15	7
	P12	$M^R M$	$M^R M$	23	8
	P13	$M^R (m^d)$	$M^R M$	13	4
	P15	$M^R m^d$	$M^R M$	4	1
	P17	$M^R m^d$	$M^R M$	18	10
	P36	$M^R m^d$	$M^R M$	22	7
	Total			129	52
	Expected			135.75	45.25
	Deviation	6.75 ± 3.93			
(c)	40	$m^d m^d$	$M^R M$	27	28
	P6	$M^R m^d$	MM	19	22
	P10	Mm^d	$M^R M$	16	26
	P14	$M^R m^d$	MM	3	3
	P30	$m^d m^d$	$M^R M$	12	12
	P32	Mm^d	MM	31	21
	P44	$M^R M$	$M.M$	21	15
	Total			129	127
	Expected			128	128
	Deviation	1.5 ± 5.38			

The relation of "restricted" to mallard and dusky

The data on the heritable relation of restricted to mallard and dusky are presented in tables 2 and 3. In table 2 (a) mating P1 consisted of a White Pekin male (1.6) mated with 3 Mallard females known to be MM . This mating produced 130 ducklings, all restricted in pattern. The same male (mating P5) mated to 3 females known to be Mm^d gave 91 restricted ducklings. An F_1 mallard female from another Pekin-Mallard cross was mated to male 1.6 in each of matings P16 and P37. These produced 10

and 12 colored ducklings respectively, all restricted. Mating P31 consisted of the Buff male, previously cited in matings 59 and P41, mated to a White Pekin female. The 31 ducklings described from this cross were restricted. From these matings it is evident that restricted is completely dominant to mallard and dusky and was obtained from the Pekin.

In table 2 (b) are included matings in which a ratio of 3 restricted to 1 mallard was expected. The total of 129 restricted to 52 dusky approaches the calculated reasonably well with a deviation of 6.75 ± 3.93 . The females used in all of these matings and the males of P9, P11, and P12 were progeny of mating P1, and thus a further check on their genotype was provided. The male of mating P13 is a White Pekin and has not been tested further. The males of P15, P17, and P36 have all been tested further,

TABLE 3

	MATING NO.	TYPE OF MATING MALE \times FEMALE		RESTRICTED	OFFSPRING MALLARD	DUSKY
(a)	P23	$M^R m^d$	$m^d m^d$	7		3
	P24	$M^R m^d$	$m^d m^d$	21		22
	Total			28		25
	Expected			26.5		26.5
	Deviation	1.5 ± 2.45				
(b)	44	$M^R m^d$	$M m^d$	17	14	8
	P8	$M^R m^d$	$M m^d$	19	7	7
	Total			36	21	15
	Expected			36	18	18
	Probability = .5 to .7					

proving that they were genetically $M^R m^d$. In the matings included in part (c) of this table a fair agreement with the expected equality of restricted and mallard is noted, 129 being restricted and 126 mallard. Each of the parents has been tested further in other matings which confirmed their genotype.

The relation of restricted to dusky is further analyzed in the matings given in table 3. In part (a) of this table an equality of the two types is expected. The actual numbers described were 28 restricted and 25 dusky, a deviation of 1.5 ± 2.45 from the calculated. The male of P23 was also mated in P17, table 2. Both matings demonstrated that he was heterozygous for dusky. Similar confirmation is made of the genotype of the male in mating P24, since he was used the previous season in mating P8. A ratio of 2 restricted, 1 mallard and 1 dusky is expected in both matings 44 and P8. The females of these matings were mallards known to be $M m^d$ and the male of mating 44 was from a cross of restricted by dusky and

should accordingly be $M^R m^d$. The total results of 36 restricted, 21 mallard and 15 dusky are a reasonably close approximation to the calculated 2:1:1. The probability of these deviations being due to chance alone, as measured by the X^2 method of goodness of fit, is between 0.5 and 0.7.

EVIDENCE FOR ALLELISM OF M^R , M AND m^d

The data presented in tables 1, 2, and 3 show: (1) that mallard is a simple dominant to dusky; and (2) that restricted is due either to a dominant allele or to an independent factor pair, the dominant member of which would be epistatic to mallard and dusky. A crucial mating was planned to test these two possibilities. The results are presented in the two charts on the following page.

These charts represent the expected and observed results on the basis of the two alternative postulates. On each hypothesis the original male is assigned a genotype which fits the results obtained by mating him to three known types of females. In chart 1 the female selected for the final mating received the restricted gene from her sire and mallard from her dam whereas in chart 2 the sire contributes both restricted and dusky. By mating this female to a dusky male the progeny would be half restricted and half mallard in the first case while on the second hypothesis a ratio of 2 restricted: 1 mallard: 1 dusky would be expected. Of the 55 ducklings classified from this mating, 27 were restricted and 28 mallard. Since no dusky ducklings were obtained it is apparent that the allelic and not the two factor hypothesis is consistent with the actual results.

RELATION OF M^R , M AND m^d TO WHITE SPOTTING

In a previous article (JAAP 1933) the inheritance of three types of white spotting was analyzed. Two of these types, bib (b) and recessive white primaries (w), were found to be simple recessive genes. The other type (R) exhibited incomplete dominance. In the homozygous condition, RR , white markings similar to those of the Fawn and White Indian Runner variety result. The heterozygous condition, Rr , is detected by the presence of white primary wing feathers when the bird is not ww . The alleles of the mallard pattern are distinguished in adult ducks by the presence or absence of white in certain regions of the plumage. Mallard has a secondary sexual white neck ring occurring only in the male. The ventral wing surface in both sexes is white. Dusky mallards are always colored underneath the wing and the male dusky never has a secondary sexual white neck ring. White in the neck when it does occur is present on approximately the same number of females as males. Again the only constant difference between restricted and mallard is the white spotting on the dorsal wing surface. White never occurs in this region on either mallard or dusky. In the

CHART 1

Observed and expected results of certain matings tested on the hypothesis of three allelic genes;
 M^R (restricted), M (mallard), and m^d (dusky). Restricted is dominant to mallard and dusky.

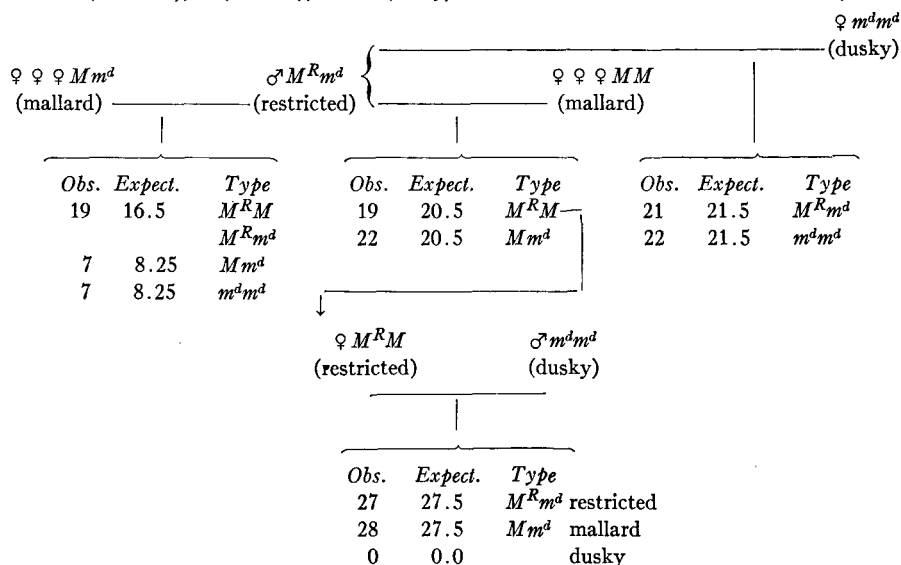
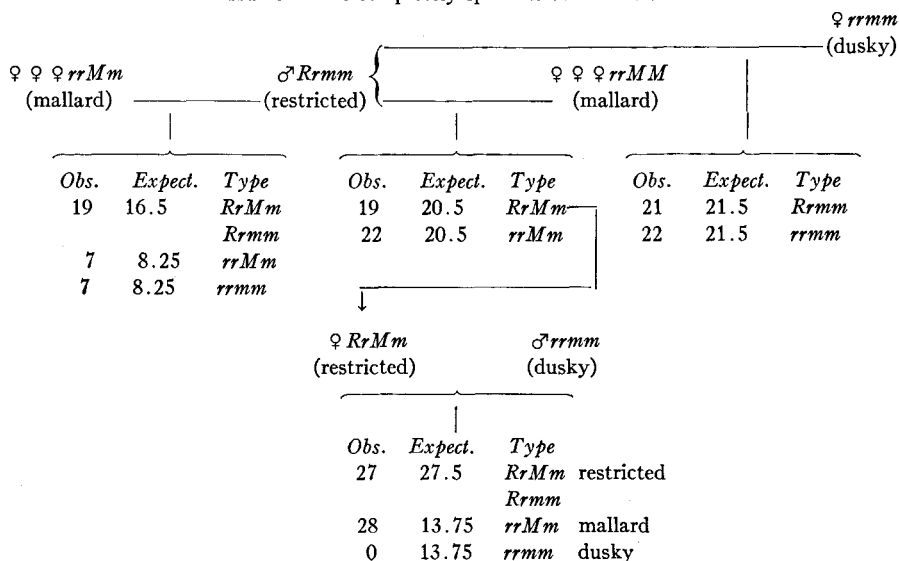


CHART 2

The same matings as in chart 1 showing that the hypothesis of two factor pairs will not fit the results obtained.

R =restricted r =not restricted M =mallard m =dusky

R is assumed to be completely epistatic over M and m .



adult restricted male there is considerable white on the wing front and wing bow. In the female also the wing front has much white, but the remainder of the wing differs from that of mallard and dusky by a restricted dark brown area and an extremely wide pencilling of light brown or buff on each feather. It is, therefore, evident that these alleles form three additional genes influencing white spotting.

A summary of the genes at present known in ducks which affect white spotting in the various parts of the body is as follows:

Section of the plumage	Genes producing	
	White	Color
anterior breast	<i>b</i>	<i>B</i>
posterior breast	<i>RR</i>	<i>Rr, rr</i>
ventral wing surface	<i>M^R, M</i>	<i>m^d</i>
dorsal wing surface	<i>M^R</i>	<i>M, m^d</i>
neck ring of male	<i>M^R, M</i>	<i>m^d</i>
neck ⁴	<i>RR</i>	<i>Rr, rr</i>
primaries	<i>RR, Rr, w</i>	<i>rr, W</i>
secondaries	<i>RR</i>	<i>Rr, rr</i>

SUMMARY

1. Three distinct variations of the mallard plumage pattern, namely, restricted mallard, mallard, and dusky mallard are described.

2. The down pattern of each type corresponds to a definite type of adult plumage color.

3. The inheritance of these patterns is explained on the hypothesis of three allelic genes. Restricted (*M^R*) is completely dominant to mallard (*M*) and dusky (*m^d*). Mallard is dominant to dusky. All the possible homozygous and heterozygous combinations have been obtained.

4. The gene *m^d* has been obtained from the Mallard, White Pekin, Buff, and East India Ducks.

5. Restricted was obtained from the White Pekin breed, where it was not expressed owing to the absence of the gene for the production of color in the plumage.

6. All the known genes affecting white spotting are discussed in relation to the different parts of the plumage. Restricted and mallard produce a white ventral wing surface while the dusky gene causes this region to be colored. The dorsal wing surface of dusky and mallard is colored, whereas restricted produces white spotting on the feathers. Dusky eliminates the secondary sexual white neck ring of the male.

⁴ The term "neck" refers to the entire neck of the bird from the head to the body, as contrasted with the narrow white collar present on mallard and restricted males, which is designated by the term "neck ring."

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