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FURTHER EXPERIMENTS IN INHERITANCE OF  
COLOR IN DOMESTIC PIGEONS

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The following paper contains an account of breeding work with domestic pigeons since 1921. The experiments have been subsidized by the University of Michigan since 1924.

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The general results of breeding work on pigeon colors were summarized, in a paper read before the Michigan Academy of Science, Arts and Letters in 1926, in a table of colors. This table is published also in a pamphlet, "Color Breeding in Pigeon Plumage."<sup>1</sup> In this table the three colors: "recessive

<sup>1</sup> Color Breeding in Pigeon Plumage. Jan Metzelaar. Amer. Pigeon Keeper, Geneva, Illinois, 1926; 45 pp.

red," "brown," and "black" are arranged in a serial order, according to their mutual dominancy. It has been found, since that table was published, that this serial order should be changed. The brown pigment in domestic pigeons is one subject of this paper.

Orren Lloyd Jones has devoted an elaborate paper<sup>2</sup> to the results of a microscopical study of pigeon colors. In typical black the black pigment granules are evenly spread through the cells of the barbules. In blue this same pigment is clumped together, leaving wide interspaces free of pigment (segmented arrangement). Between typical blue and black, intermediate shades called "smoky" occur in certain parts of the feathering and on the wings of some individual birds. These are based on various intermediate degrees of "segmentation."

Although brown has a wide distribution among domestic pigeons, it has never been recognized as such prior to 1926. Neither in breeders' publications nor in scientific literature was there any definite reference to brown as a distinct and independent color.<sup>3</sup> The fanciers have commonly confused it with dun, as, for instance, in Nuns, Maltese, Carriers, Dragons, Turbits. Dun, however, is nothing but the dilution of ordinary black. (Dilution is the accepted term for the occurrence of about one third of the number of pigment granules per square unit as compared with the intense phase, this relation being ruled by a sex-linked factor. See Cole, 1914.)<sup>4</sup> Brown ranks with black, blue, red, etc., in the group of intense colors, and reminds one distinctly of the color of milk chocolate.

Before discussing the breeding experiments with brown I wish to stress the fact that brown is in every respect an exact counterpart of black. In other words, all the physical features,

<sup>2</sup> *Journal Experimental Zoology*, 1915, Vol. XVIII, pp. 453-509.

<sup>3</sup> A short note on "chocolate," which is identical with my "brown" has been very recently published by Christie and Wriedt; *Zeitschrift. Ind. Abst. Vererbungsl.*, XLIII, 1927, pp. 391-392.

<sup>4</sup> *Studies in Inheritance in Pigeons*, by Leon J. Cole. *Agric. Exper. Sta., Rhode Island State Coll.*, 1914, Bull. 158.

the particular combinations of black pigment granules found in nature, are possible also with brown. For instance, I have materialized the diluted series by mating yellow (which is diluted red) with some phase of brown and raising an  $F_2$  generation from their progeny. An even spreading out of the brown pigment granules results optically in a deep brown color, but, just as blue is the clumped phase of black, so brown-silver is the result of the clumping of the brown pigment. In fact brown appears to be the only pigment with which are possible *exact* counterparts to the colors and patterns formed with black pigment. Here follows a full list of these in both the intense and dilute series.

BLACK*	blue	blue-check	black-check	black	} Intense
BROWN*	brown-silver	brown-silver check	brown-check	brown	
BLACK*	blue-silver	blue-silver check	dun-check	dun	} Dilute
BROWN*	drab-silver	drab-silver check	drab-check	drab	

*Drab* has been previously called "lavender" by me, but the name is inadequate. The color is identical with that of ring neck doves and corresponds to Ridgway's "drab" on plate XLVI. *Drabsilver* corresponds to Ridgway's "drab gray" on the same plate.

All of these so-called colors are simply physical phases of two pigments: black and brown. In order to simplify the discussion we shall henceforth designate any member of the group based on black pigment as black\* and any belonging to the group based on brown pigment as brown\* regardless of the clumped or non-clumped condition of the pigment.

Dr. Leon J. Cole (*loc. cit.*, 1914) clearly outlined the characteristics of so-called recessive red in its relations to black. The basic red is symbolized by R and a factor B is assumed whose presence is responsible for turning this red into black. Apparently this theory is now to be modified with reference to the finding of brown.

Experiments were started by mating red with brown\*. The red was exactly the kind used by Cole (1914). As will be seen in the tabulation below, in about half the number of cases

this kind of mating produces brown\* in  $F_1$ . Eight young were raised of this color. Three pairs were saved and have so far produced an  $F_2$  of 4 browns\* and one red, pointing to a single factor difference between brown\* and red, which may be symbolized by E. This result might have been expected. Just as the extracted reds of Cole, which he obtained out of his black to red crosses, frequently showed bluish rumps and tails, so my extracted reds from these and similar matings frequently show tails and rumps with a decidedly brownish cast. In other words, there are pure recessive reds and also reds with some additional (terminal) brown, which subjects our tentative unit character E to criticism.

To those not intimately familiar with pigeons it may now be surprising to learn that the other half of my recessive reds, if mated to brown\*, produced black\*. To be exact: 6 matings together produced 9 blacks\* and 2 reds, the brown parent of the latter apparently being heterozygous. Two more matings of red with brown\* gave together 6 blacks\* and 3 browns\*, which means that in those cases the red parent must have been heterozygous. Because of this striking feature, close account was kept of the pairs which produced black\* in this way, and all the viable young were saved. Unfortunately there was, in this year of experimentation, unusually high mortality in the lofts, due to various diseases, and practically all the surviving young were males (the male birds having a higher vitality than the females). Only 2 black females of  $F_1$  could be saved. Later on, running water was installed and the food was regularly treated with cod liver oil, which enormously reduced the mortality of the female sex. From two pairs of the black\*  $F_1$  set an  $F_2$  generation has been raised, composed (to date, fall of 1927) of 17 blacks\*, 10 browns\*, and 4 reds.

Recessive red, then, may behave in two very different ways when mated to brown\*: either it produces black\* or the parental brown\* is reproduced. To explain this it will be assumed that the first kind of red carries a factor B, which modifies brown\* into black\*. In accordance with Cole's

nomenclature a recessive red of this kind would be RB, a red of the second type would be Rb (producing just brown\* with brown\*). Brown\* itself would be in all cases just RE. The synthetic black\*, from a mating of red RB with brown\* RE, would then be REB. These blacks\*, mated together, would produce an F<sub>2</sub> generation of blacks\*, browns\*, and reds in the following proportion :

	black* REB	brown* RE	red Rb	red RB
Expected .....	9	3	3	1
Found, to date .....	17	10	4	

One male black F<sub>1</sub> has been crossed back to red Rb, and in F<sub>2</sub>.

	black*	brown*	red
Expected .....	1	1	2
Found .....	3	2	14

This shows an abnormally high number of reds, quite in line with the findings of Cole (*loc. cit.*, 1914, p. 348); for interpretation see below, pages 11-13. (A later test showed this bird to carry factors for dominant red.) In addition it may be noted that recessive reds quite frequently and unexpectedly crop out in different breeds of pigeons. One such bird was obtained from a pair of spangled Gazzi (a variety of Modena), another one from a cross of a Suabian with a solid black, which was born from a union of a Suabian and a black tumbler; in Suabians recessive red is unknown. Bronze tipplers ("branders") will also occasionally throw solid red young. Strange as these results may seem, they are in accord with our knowledge of recessive red, which may be summarized thus: Solid red always appears phaenotypically in the presence of R and absence of E, irrespective of the presence or absence of any other factors. Cole, in 1914, drew attention to the very remarkable fact that this recessive red, at least in the adult bird, never shows any clumping of the pigment. A pigeon may genetically have the characters of a barred or a checkered pattern, which involves the clumped condition of

the pigment of large parts of the plumage, and yet this bird, in the absence of E, will be solid red, showing no trace of clumping whatever. In other words, this red pigment cannot be clumped: recessive red has no patterns like black or brown. This remarkable fact involves a phaenotypic identity of a good many different genotypes. In 1923, I found that this recessive red may carry the factors for practically all the different types of dominant red (see below) without any phaenotypic difference resulting from these factors. To this list the present paper now adds the factor B. In view of these facts it becomes very probable that the fundamental factor E is essential for the expression of all other color factors (with the exception, of course, of R), and that all  $R_e$  pigeons look identical to the eye; viz., *red*. This red, when pure, is solid and even over the entire bird; the bases of the feathers are always white, never dusky.

Mention has been made of a short paper by the late W. Christie and Chr. Wriedt, which asserts that the factor B (as I call it, in accordance with Cole) is sex-linked.

So close is the mutual relationship of black\* and brown\*, in all their phases, that the possibility of stereochemical isomerism is strongly suggested. The question naturally presents itself as to the behavior of brown toward the various agents responsible for turning black\* into the different reds (and whites) which are usually called dominant reds (and whites). For a better understanding of these relations it will be necessary briefly to review the main facts about the different kinds of dominant red.

It has been found in the course of our recent breeding work that not less than three different sets of factors are responsible for reducing the ordinary black pigment, as found in the wild *Columba livia*, to some kind of "red," each of them in its own peculiar way. A short characteristic of each of them will be given first, after which the three groups will be discussed in more detail.

I. A sex-linked factor A, attacking clumped and spread pigment, reducing the former to brick red, the latter to the

corresponding color "mealy," according to Cole and Kelley<sup>5</sup>, who assume that A is a single factor.

II. A set of factors responsible for what I have termed "centrifugal reduction" of the pigment, resulting in "centrifugal mahogany" acting exclusively on pigment in its spread-out phase. I have symbolized this with the letter M, M, M, each single factor being assigned to a definite area of the feathering. In this type of coloration the mahoganized area of the individual feather is always separated from the clumped or unaffected zone by an unaffected zone or line. If the basic pigment is black then these lines are black, which results in a very characteristic design, called *spangling* if the fundamental pattern of the bird under consideration is a check. *Lacing* results if the background simply is a self color like black, dun, brown, etc. (Plate I). The technical names spangling and lacing have reference to the unaffected remnants of the fundamental pattern and color, occupying a marginal position. The base of the feathers of the body are never mahoganized (quills excepted).<sup>6</sup>

<sup>5</sup> Genetics, IV, March, 1919.

<sup>6</sup> In a mixed population there is an enormous variety in the degree of affection of the different elements of the plumage. Suppose a rather full check forms the basic field of operation. We may encounter the following phases: For the wings, the interior part of the wing bars, especially the second one, is the center of operation. Starting from this point the successive blocks of these bars may become affected and show anything from the merest trace of bronze to a maximal reduction.

Forward, the successive blocks of the wing coverts may or may not become affected to the same varying degree. Considering the wing shield (entire wing minus primaries) as a whole there is an endless variety of reduction patterns, though the centrifugal system is strictly maintained. The black fields of the wing tips may or may not be individually affected. The black terminal blocks of the twelve tail feathers may or may not be affected, and to differing degrees. The elements of these three main fields of operation (shield, flight tips, and tail bar) may again be combined in different ways. Again, the reduction may stop at mahogany or go down to white; the white may completely overtake the red, or it may be less complete, in which case rosy residues are left. This particular relation may vary in the various subfields.

III. A set of multiple factors Q, Q, Q, attacking exclusively spread-out pigment, that is, operating in close conjunction with accessory agents which seem first to spread out the pigment granules of certain areas *which normally have clumped pigment* (so that blue becomes dull black). This color is very common in the primaries of commons and the breasts of Archangels, but best developed in bronze tipplers, for which reason I call this type of color technically "*tippler-bronze*." The *optical* effect of the resulting shade of red is absolutely *identical with the mahogany* of the former group, but no spangling or lacing is ever produced. The bases of the small feathers are never mahoganized; the tips of quills are usually unaffected, but in extreme cases the whole bird is solid mahogany on its exposed parts. Tippler-bronze frequently, but by no means always, accompanies centrifugal-mahogany in spangled pigeons (Modenas).

These, then, are the three groups of dominant reds as they stand today. It should be emphasized that the factors involved affect the plumage of the pigeon in a strictly symmetrical way in all three cases. Furthermore, for each of the three types a corresponding white form is known, which in the adult bird (not in the young) shows the pigment further reduced from red to white.

A rather striking but unexplained fact presents itself when red in pigeons is being considered: neither recessive red nor mahogany has ever been found in the clumped phase in adult birds. The different reds will now be reviewed in more detail.

#### I. *Dominant (brick-) red*

The only kind of red definitely known to occur in the clumped phase is dominant red, or "brick" red, as I have termed it on previous occasions. Cole and Kelley in their classical paper of 1919<sup>7</sup> fully discuss the properties and features of this type of color. A single sex-linked factor, A, is

<sup>7</sup> Leon J. Cole and Frank J. Kelley, Studies on Inheritance in Pigeons, III. Description and linkage relations of two sex-linked characters. *Genetics*, IV, March, 1919.



supposed to be responsible for all the rather complicated color-phases of this group (*loc. cit.*, pp. 187-188).

It may here be recalled that in a general way the A-birds follow the different phases of clumping and spreading of pigment which we meet in the blue, checkered, and black pigeons, but with one striking exception. Certain parts of the feathering, most generally the tips of the flights, the rump, belly, and tail show a coloration which is very appropriately called "washed out." Instead of finding the basic black and blue parts simply turning into the corresponding red and mealy, the pigmentation of these parts is just weakened and faded out. The black parts become bluish and thus assume a similarity to the originally blue parts, and both, having become indistinguishable, tend to fade out to a kind of pale gray, approaching *white*. (Frequently unaffected black edges and "ticks" remain in the field.) In extreme cases, called "dominant gray" (described by Cole and Kelley in the text and in the appendix to their paper), the entire plumage of the bird is affected by this "washing out," even the red wing bars being attacked and reduced to mere vestiges. On the other hand, very mild cases are known in which an A-bird is practically blue with some red in the wing-bar region and only the tips of the flights and tail quills slightly washed out.

Cole and Kelley have assumed that this washing out is an essential and quite normal feature of all A-birds, inherent in and inseparable from dominant red. As will be seen from the following paragraphs I do not agree with this, but consider the factors responsible for producing "A-red" on one hand and for "washing out" on the other hand as separate entities. I do so on the following grounds:

In mixed populations we sometimes meet otherwise typical red A-birds, but obviously lacking the typical washed out features. We may roughly group such pigeons in three classes.

a. The bird has the general features of a mealy: head, neck, and breast a rather uniform red, a diffuse red on the shoulders (that is, the part of the wing in front of the bars) which does

not definitely show checkering; back and upper surface of tail of a reddish blue which might well be called "pseudo-brown silver," the tail bar being more strongly brownish-red; belly strongly washed out, almost white.

*b.* The wings are practically solid, self red, sometimes with a shadowy checkering; back, tail, and belly as in class *a*.

*c.* The entire bird is practically solid red, the color being only a trifle paler on belly, or belly and tail.

In other words, A-pigeons of this group show a supernormal amount of solid red; this red is to my eye indistinguishable from recessive red, as now recognized and described by all authors in the field. There is an obvious and striking parallelism between the three classes as described here and some representatives of the well known blue-black series; if we consider the occurrence of the spread-out red color we should compare class *a* with a sooty or rather a "dirty" blue<sup>8</sup>; class *b* with blue-tailed black, which is sometimes called "black-check"; and finally class *c*, red or "near red," with black.

On these types of red I have made the following observations:

1. One red male of class *b* mated to a brownsilver female produced two young colored like the father and another one with more bluish color on back and less washing out on belly.

2. One female of class *b* mated to a bluecheck male produced two characteristic red check A-young with strongly washed out tail and flights, and another young of more smoky color with red wing bars and strongly washed out tail and flights, all these young probably males.

3. A female of class *c* mated to a bluecheck produced two bluechecks and two strongly washed out red young.

4. A solid red "flight" male mated to brownsilver produced a dominant red young of type *a*.

5. This young F<sub>1</sub> male again mated to another brownsilver flight produced 3 brownsilver young, 6 dominant red young,

<sup>8</sup> C. J. A. C. Bol. Genetische Analyse van Kleuren Veerpatronen Tinten en Afteekeningen by Postduiven, 's Gravenhage, M. Nyhoff, 1926, summary.

generally belonging to the same type as the father, but some with considerably more and one with less spread-out red in shoulders and tail, one young almost solid red (class *c*), and 2 typical mealy ones with genuine washed-out tails.

6. A red Carneau *c* male mated to brown produced one solid red young like the father and one strongly washed-out red.

7. One of the 6 red  $F_2$  young cited above mated to blue produced one  $F_3$  young with genuine washed-out tail.

8. An  $F_1$  *c* female mated to a male of type *a* produced one bluecheck young and one of class *b*.

9. A pair of A homers with vestigial washing out produced one young like themselves and one with strong washing-out.

I interpret these observations as follows:

I. Washing out has primarily a clumping effect on pigment, whether this is black or red.

II. Normal washing out can be partly or entirely inhibited.

III. Dominant A-red can only exist in the clumped condition with cooperation of the washing out factor. If the action of the latter is inhibited by another factor the pigment tends to spread out to solid red. As the washing out recedes the true solid red grows.

I conclude from this that, inasmuch as washing out and red are affected separately by interfering agents, they are controlled by separate factors, and I suggest the following new definitions.

**A.** A sex-linked factor turning black and brown pigments, whether clumped or spread, into red.

**G.** A sex-linked factor having a clumping and washing out effect on all phases of black, brown, and A-red pigments; never observed in the absence of A.

**S''.** An inhibitor of the factor G, having thus the effect of spreading on A-red. Its effect on the clumped phases of other pigments is not known.

The letter G has been adopted in accordance with the nomenclature of Christie and Wriedt in 1923<sup>9</sup>, but the definitions

<sup>9</sup> W. Christie and Chr. Wriedt. Die Vererbung von Zeichnungen, Farben, und anderen Characteren bei Tauben. Zeitschr. Indukt. Abstamm. und Vererbungslehre. 1923. Bd. XXXII.

are different. I am satisfied that the broad term "Nicht-durchfaerbung" of these authors comprises certain seemingly similar but essentially unrelated phenomena. The letter  $S''$  has been chosen with reference to the established symbolizing of complete spreading by  $S^{10}$ . It is quite possible that further investigation may force us to split up the factor  $S''$  into a multiple complex of which each component affects a certain region.

Turning back to the list of observations given above, we find that the appearance of normal washing out in Nos. 2, 6, 7, and 9 can be readily explained by heterozygosity for  $S''$  of the A-parent(s). The activity of the inhibitor  $S''$  is apparent in No. 4, where its effect seems to be weakened in the young through heterozygosity. In No. 5 the presence of  $S''$  in the 7 red young and its absence in the 2 mealy ones is obvious and very striking.

Thus we have rather complicated conditions in the A group. One powerful reducing factor tends to paint the entire bird solid red. This is checked by a second one, G, which tends to reduce the color to a uniform whitish gray, the action of which in its turn is checked by a third factor,  $S''$ . This complicated balance of power might explain, in part at least, the immense variety of colors and shades in the A group.

The fact that a dominant red pigeon, through complete inhibition of the washing out factor, becomes or tends to become a solid red pigeon throws a new light on some hitherto unexplained facts. In his 1914 paper Cole mentions the fact that after crossing recessive red with black, and from their offspring raising an  $F_2$  generation, the number of reds was unexpectedly high. This may very well be due to the presence of dominant self-red among his parental stock, these factors being carried by the "recessive reds." Cole's  $F_1$  is classed as "black"; it showed, however, considerable red, and the term "black" is debatable.

In the same way the unexpectedly high number of reds in my own back crosses of black with red may very well be due to the same cause. (See page 5.)

In his 1914 paper, just referred to, Cole mentions the well known blue cast on the rump and tail of his extracted reds. Every trained

<sup>10</sup> Sarah van Hoosen Jones. Studies on Inheritance in Pigeons, IV. Checks and bars and other modifications of black. Genetics, VII, Sept. 1922.

fancier has had the same experience. Now, it is extremely interesting that these "bad reds" very closely resemble some dominant near-reds as described by me, belonging to class b. The off color affects exactly the same parts; the same prevailing of red in the tail-bar region over the proximal parts of the tail. The same tendency to shadowy checks or bars. The only appreciable difference is the more washed out shade of the off colored parts in the A-birds. And this resemblance is just what might be expected. Recessive red and dominant red are closely related after all. The factor, B, which is absent or latent in the first is supposed to be suppressed or inhibited in the second. (Bol, *loc. cit.*, p. 66.)

Now if there is such a thing as solid, self dominant red, phaenotypically indistinguishable from recessive red, only cross-breeding can distinguish between the two. I have tried such a test cross with blue in two instances, and in both cases I had both types of red in the red parent. In other words, the two kinds of red have probably for a long time been mixed and intercrossed by the fanciers, so that inquiry into their nature, except in carefully selected and inbred strains, is very discouraging.

The evidence obtained by me is by no means considered complete, and experiments in this field are being continued on a larger scale.

## II. *Centrifugal Reductors*

The first experiments on "spangle" were carried out with Modenas of the variety called Gazzi. The neck and breast of this variety are white; head, wings, and tail, colored. The tail shows hardly any reduction; in the mahogany spangled birds the tail is blue and the primaries show a large amount of tipler bronze, which will not be considered here. Every black fleck on the wing shields has the characteristic mahogany center.

On crossing the black variety with the spangled one it soon became apparent that the blacks contained factors for mahogany spangling as recessives and that it is therefore not feasible to obtain ratios in the customary way. All  $F_1$  blacks

were crossed back to mahogany spangled. The  $F_1$  and  $F_2$  generations, obtained in this way, together comprised 26 blacks and 25 mahogany spangled. Of these 25 spangled birds, 22 are fairly completely "mahoganzed," sometimes with a sprinkling of black barbs in the mahogany fields, apparently due to heterozygosity. The other three represent a lower stage, as the reduction is confined to the wing-bar region and a few checks immediately in front of this. In addition to the 51 young ones listed here, I obtained three near-blacks with shadowy checker-marks and more or less reduction in the wing-bar region.

The ratios obtained clearly establish black as a unit character dominant over mahogany, or rather as a single-factor inhibitor of centrifugal reduction.

Since Modenas were found unsuitable for the present purpose, I mated a dozen Hyacinths and Suabians with black tumblers and homers, which could hardly be suspected of carrying mahogany reducers as recessives. A Hyacinth is a blue check with a centrifugal reduction in the wing shield, leading down either to mahogany, to white, or to an intermediate stage. Suabians are very similar, but are based on very dark black checks or on true blacks. They have the tips of the primaries also affected and show considerable "dominant-white" in addition to the other markings, which will not be considered here. For the sake of simplicity we shall consider all centrifugal reduction, irrespective of the particular shade produced, under the same headings. In this way I obtained the following ratios in  $F_1$ :

- 20 solid black (including a few with vestigial kite flecks on wings),
- 1 black with incomplete mahogany checkering (from Suabian parents),
- 1 black check (in the sense used by Bol),
- 6 show complete centrifugal reduction (spangling),
- 3 are checks with this reduction largely confined to the wing bars,

15 are blue checks with diffuse traces of reduction in the wing bars or both wing bars and checker marks.

Total blacks: 21.

Total non-blacks: 25.

Those black  $F_1$  birds raised from Suabians were mated back to Suabians and an  $F_2$  generation was obtained consisting of 4 blacks, 4 spangled, and 1 black with "kite" checker marks on the wings.

The features of the checkered (non-black)  $F_1$  birds illustrate in an extremely interesting way the chemical "struggle" between the black pigment and its reductors:

a. Clumped pigment is absolutely irreducible by centrifugal reductors.

b. The marginal black around the central reduced areas is unaffected in all cases in which there is any blue between that area and the edge of the feather. If, however, the black of the basic pattern reaches the edge of the feather, the centrifugal reduction may overtake it and may also reach the edge; in this way the marginal black disappears, and if the basic pattern is a black check the wing covert becomes solid mahogany.

c. In accordance with the results obtained from the Modena crossings, it appears that *black* is a condition *sui generis* in which ordinary spangling factors, like those occurring in Hyacinths, have no effect. As all the parental blacks apparently were heterozygous it is clear from the ratios obtained that black is controlled by a single factor, which is in line with findings of earlier workers in the field.

d. All non-blacks appearing in  $F_1$  are due to heterozygosity of the parental blacks. They are all checkered and the reduction of their checkermarks shows a bewildering variety from which only a few facts seem to stand out rather clearly: I. Centrifugal reductors in the heterozygous condition *may* succeed in completely reducing the entire wing shield. II. Usually, however, the effect is very much less, as the mahogany areas are sprinkled with black or are confined to mere vestiges. These extreme conditions may be shown by two young in the same nest.

e. The maximal development of centrifugal reduction is obviously limited by the extent of the spread pigment on the wing shields. Now the various patterns formed by normal black marks on a blue back ground constitutes a well-known phaenotypical series in pigeons which has been puzzling scientists ever since the time of Darwin, viz:

- barless blue;
- blue with traces of bars;
- blue with two bars;
- blue with two bars and traces of a third one;
- checkering in all stages from very light to very dense;
- black check (no blue left in exposed parts of wing covert).

Out of the series Bol recognizes barless blue, barred blue, blue check and black check as separately controlled by single factors which *inter se* behave as multiple allelomorphs.

Returning now to the series of spangled  $F_1$  birds, one outstanding fact at once comes to the fore: except for imperfect development on account of heterozygosity, any spangled pattern formed by centrifugal reduction of a certain wing pattern always corresponds to a lower link in the series of patterns just listed above. For instance, it may correspond to the stage with two wing bars on the background of a bluecheck or, usually, to a more restricted checkering. The former features were found by me only in three out of 46  $F_1$  young raised in the black x spangle crossings. These birds have mahogany wing bars superimposed on a true blue checkering and should be distinguished from imperfect spangling due to heterozygosity. I am raising an  $F_2$  generation from these birds which I expect to breed true to type (that is, with mahogany wing bars and no mahogany checker marks) in accordance with what we know about the breeding of blue and all other colors with two wing bars, including solid colors with mahogany or white bars (which really belong in the *laced* group). Other reasons have made further delay of the present publication undesirable; further experiments, now under way, will be published later. In the meantime I have made sure that the diffused, more or less sprinkled condition of some spangled



wings is indeed due to heterozygosity. Two such birds (Modenas) produced at least one  $F_2$  young with a completely developed spangling. Furthermore, on crossing a Polish Lynx female with a normal blue common, I obtained  $F_1$  birds with imperfectly reduced wing bars and out of 6  $F_2$  young one showed complete centrifugal reduction of these bars and the rest incomplete or vestigial reduction.

It has been stated by me before, that centrifugal reduction of non-black patterns extends its action over three main fields: wing shields, tips of primaries and tips of tail quills. The first is by far the most common; the second occurred in my birds only in swallows, Suabians and blondinettes, and the third in blondinettes only. These pigeons are more rare and slow breeding and consequently the data obtained concerning reduction of the quill tips are much less complete than those concerning the wing coverts. In a general way it can be stated that when there is reduction of the flight tips the wing coverts are usually—but not always—also affected. The reductions of wing shields, primary tips and tail quill tips are separately controlled by reduction factors. Furthermore in case of heterozygosity the reduction of the pigment in the tips of the quills may be vestigial or, in more developed cases, the reduction is graded from the median quills down to the outer ones in the wings and from the outer quills down to the median ones in the tail, and bilateral symmetry is maintained throughout.

In the present chapter we have been watching the chemical "struggle" between melanins—which are oxidized derivatives of tyrosin compounds—and certain centrifugally operating reductors tending to rob the melanin of some of its oxygen, and we have marked the scores in the different phases of this battle. We have seen that the (dull) black checkermarks on pigeon wings offer the weakest resistance against these reductors and that solid black is practically invulnerable by those reductors which successfully turn a checkered into a spangled bird. But right here it must be admitted, that like Achilles, solid black is by no means absolutely invulnerable.

In some breeds solid black actually gives way under the attacks of certain powerful reductors, not only dull self black, but even real glossy black. In certain rare breeds such as Schietti and Blondinettes we meet a condition in which a solid black wing actually shows a definite pattern (bars or checkermarks) carved out in mahogany or in white from the black background. Even the tips of all the quills may be affected and there is a very rare, extreme condition in which every center of every feather of the plumage of a self colored bird is reduced, leaving only the margins tainted with the original color. This condition never develops before the bird is fully mature and only under favorable circumstances of nutrition and general health.

To be exact I will define the features just described here as *lacing*, as patterns comprising mahogany or white wing bars, checks and more complete stages of centrifugal reduction with a solid self color as a basis. In other words, the background of a *laced* pigeon never shows clumped pigment. Regardless of the use of the terms among the fanciers I define *spangling* as: any pattern resulting from centrifugal reduction of the pigment, operating on a checkered or barred bird. In other words, the background of a spangled bird always shows some clumped pigment.

Naturally the question arises: what decided the battle here in the laced Blondinettes and made the melanin yield its oxygen? Cross experiments with different types of black have made it very probable, that the successful attack of reductors on glossy black where a cross with an ordinary spangled pigeon would have failed is *not* due to a lowered resistance of the black, but to a more vigorous attack of the reductors. So I feel rather safe in stating that Oriental Blondinettes contain the most powerful reductors of melanin known in pigeons. Related breeds are rated accordingly. Here is a rather striking illustration: Quaker Starlings are black and show either white bars or white checks; the white bars breed true. A male of this variety, mated to a common bluecheck homer, produced one young with beautiful, complete spangling of the

entire shoulder: the Starling must have carried the less powerful reductor as a recessive.

A further complication is a fact upon which, for the sake of simplicity, I have been silent hitherto: centrifugal reduction may go either to mahogany or to white. Almost half the  $F_1$  spangles (from black\* white spangled) were mahogany, and these never again produced white in  $F_2$ . In those cases the whitening factor was lost by the outcross. I find that between two simple spangled birds, one mahogany and one white, there is a single factor difference: the two series run exactly parallel. For factorial reasons, the whitening may be less complete than the mahoganizing and then we get reddish residues and edges.

Coming now to the crucial task of interpreting the contrasting, almost paradoxical facts related here on a factorial basis I encounter the old difficulty of interpreting physiological phenomena, involving individual, age and health variations in terms of genetics. When we observe that in test matings one reductor readily reduces the melanin pigment of dull black wing bars to mahogany and fails to affect glossy black we may perhaps conclude that the latter black represents a more highly oxidized melanin. If *this* melanin in its turn can be reduced to mahogany in a second crossing and to white in a third one we may perhaps conclude that the stronger reducers at work here represent two chemical compounds different from that in the first case and that the corresponding genetic factors are different in each case. But, with the available evidence at hand, speculation ought to stop here; our information on the subject, though rich, is by no means exhaustive. So I tentatively propose the following new color factors controlling centrifugal reduction.

a. *Reduction of checkered and barred patterns*

- |  |                                    |
|--|------------------------------------|
| $M_b$ for reducing wingbars to mahogany  | $W_b$ ditto from mahogany to white |
| $M_c$ for reducing bluecheck to mahogany including the wing bars ("spangling") | $W_c$ ditto from mahogany to white |

M <sub>p</sub> for reducing tips of primaries to mahogany	W <sub>p</sub> ditto from mahog- any to white
M <sub>t</sub> for reducing tips of tail quills to mahogany	W <sub>t</sub> ditto from mahog- any to white

This system is in accordance with the latest analysis of the blue- to blackcheck series by Bol.

b. *Reduction of solid self colors*

M' <sub>b</sub> for producing mahogany wing bars	W' <sub>b</sub> white wing bars
M' <sub>c</sub> for producing mahogany checks	W' <sub>c</sub> white checks
M' <sub>p</sub> for producing mahogany pri- maries	W' <sub>p</sub> white primaries
M' <sub>t</sub> for producing mahogany tail quills	W' <sub>t</sub> white tail quills

I am fully aware of the probable necessity of further differentiating the present scheme in the future, as further detailed information becomes available. Also, there probably is a certain amount of overlapping in the action of the "regional" factors on account of their correlation in the same chromosome.

### III. *Tippler bronze*

Tippler bronze represents the third type of red discussed in this paper. It occurs in a wide range of breeds of pigeons and is best developed in the ordinary bronze tippler which is solid bronze with black tips to all quills and which is sometimes called "chimney sweeper" in Germany, Denmark and Holland, sometimes "coffee brown" and again "brander." Among my own birds this type of color furthermore occurs in Archangels, Larks, Suabians (breast) and in the inner vanes of the primaries of most spangled pigeons such as Modenas. In the latter breed this feature is so interwoven with the spangled pattern that it seems to almost form a part

of it. In Suabians and Archangels it has a very dark purplish hue due to accessory factors. Typical tippler bronze is optically identical with mahogany resulting from centrifugal reduction and is physiologically produced in a very similar way. Circumstantial evidence makes me suspect, that the factors for both are located in the same chromosome which is *not* the sex chromosome.

Tippler bronze offers some paradoxical characteristics: although the reductors responsible for its production seem primarily to attack clumped pigment, yet no one has ever seen this color in the clumped phase. We therefore at once suspect the presence of certain agents breaking up the clumps of melanin and spreading out the pigment, thus opening up the field for the action of the bronze producing factors. In crosses of tippler bronze with blue, for example, we quite frequently find that clumped fields, spread out by these accessory "spreaders," are imperfectly bronzed, thus leaving dull black edges or "pseudo-spangling." I observed this in many Modenas and also in Archangel  $\times$  Nuernberg Lark crosses. On this rather meager evidence I conclude that a multiple complex  $S', S', S'$ , operates in conjunction with the bronzing factors  $Q, Q, Q$ . To date in crosses with blue I have failed to obtain this type of black in larger areas, but in strains of good bronze tipplers I have frequently obtained a considerable partial reversion to dull black, especially in the tail region, which shows that the color certainly is based on a fundamental *dull* black.

Archangels are among the most beautiful and interesting pigeons in existence. The most common variety is solid bronze with the wings glossy black and the tail quills blue. I also have some with the wings blue and bluecheck. From the blue winged Archangel again is derived what in Germany is called "Kupfergimpel," having red wing bars and washed out tail quills. The Kupfergimpel carries the dominant factors  $A$  and  $G$  discussed above, but they have not the least effect on the solid bronze colored ventral side of the bird. The corresponding yellow variety we call here Goldgimpel, the name being

adopted from the German and being introduced in America by me although in Germany this name has a wider application.

The most striking feature of all is the fact that the bronze in Archangels may completely turn to golden yellow while the black or blue upper parts remain entirely unaffected. This obviously means, that tippler bronze can be diluted quite independently from the non-bronze parts of the bird.<sup>11</sup>

Attention should be duly drawn to the occurrence of the intensifier I in the same breeds in which the diluter D occurs, which is liable to cause confusion. But whereas I affects the entire plumage of the bird D affects only the bronze parts. For instance Nuernberg Larks, having a yellow head and neck and dun check shoulders are ii birds. Heterozygous Dd birds are usually paler than dd birds.

This feature is very obvious in bronze Archangels. Unlike Larks, this breed invariably has intensely pigmented wings; ii birds are unknown here. All male birds are II, all females Ii. Now, if we cross a dark bronze (dd) with a light bronze (DD), the heterozygous male cross is orange, the female is normal light bronze. This remarkable feature is easily explained by the interaction of the Intensifier I and the Diluter D, DdII being orange and DdIi light bronze. Optically light bronze approaches a very rich, lustrous golden yellow. All the nestlings have a dense coat of down.

In its mode of inheritance tippler bronze differs but slightly from centrifugal mahogany; the factors controlling the latter have been zoned by me in accordance with the originally black parts of the fundamental pattern in pigeons. In the former

<sup>11</sup> This phenomenon is entirely independent from the intensity caused by the presence of the sex-linked factor I of Cole, admirably described by him in his classical 1914 paper. I mated male bronze Archangels to golden females and *vice versa* and raised a total of 14 young; the dilution from bronze to golden appears to be effected by a dominant factor with no evidence of sex linkage, and to be strictly confined to the mahoganyed parts of every single feather. I tentatively propose to symbolize this type of dominant dilution with the letter D.

I have not succeeded in doing this because the materialisation of the tippler bronze involves the fading out of all such patterns by spreading of all the pigment that theretofore was clumped. Imperfectly bronzed tipplers never show a distinct zoning of their bronze areas, and birds of this character always show a mixed sprinkling of black and bronze with a more perfect development of the bronze in certain ill defined areas such as the head or the shoulders, the breast, the inner vanes of the primaries, etc. I attribute this to heterozygosity of some of the factors of the "bronzing set." I have bred this color for five years and have been unable to definitely isolate regional factors on the basis of zoning. Yet I think this will eventually be possible. The *black* tips of both tail and wing quills turn bronze in extreme cases only; usually they are unaffected by bronze and inherited very tenaciously. This points to zoning. The same applies to the inheritance of bronze in Archangels and Larks. I have had several pairs of incompletely bronzed tipplers and from those I have raised two young with the perfect colors of the standard bronze tippler, showing a cumulative effect of the factors involved.

For these reasons I assume the presence of a multiple set of bronzing factors Q, Q, Q, each of them covering a certain area of the pigeon in a strictly symmetrical way with the possibility of extending its field of action to neighboring areas. I think that the entire modus operandi of these factors is identical with those responsible for *lacing* and that the phaenotypical differences between the results of both are of a secondary nature.

Bronzing factors are absolutely powerless against glossy black as might be expected. One good female "Danish brander," imported from Europe, was mated to a good jet black tumbler and produced a solid black  $F_1$  offspring. From these an  $F_2$  generation was raised consisting of 22 birds, of which 14 were black at the time of their death (some died young and perhaps would have developed some bronze if they had lived); one was black with small bronze patches and 7 showed intermediate stages between black and bronze, ranging

from black-blue-tail with bronze in the inner vanes of the primaries to the other extreme which exactly reproduced the brander grandmother. No two young of this group are exactly alike. The ratios show in a very fair way that black contains a single factor inhibitor of bronzing factors, which probably is the same as the one inhibiting the action of centrifugal mahogany. In fact, the Modena experiments have shown that they are inhibited simultaneously.

Just as there is a centrifugal white corresponding to centrifugal mahogany, there exists a kind of white corresponding to tippler bronze. In my 1926 paper I termed this "tippler white"; but inasmuch as white tipplers appear to carry other whitening factors outside the ones referred to at present I will drop that name. The present kind of white is at once recognized by the fact that just as in tippler bronze the bases of the small feathers always remain unaffected. We find it in the neck of Suabians and starlings and in the inner vanes of the primaries of various white spangled breeds. No extensive data have been gathered regarding this color except such as were incidentally obtained from Suabian matings; the mode of inheritance appears to be identical with that of tippler bronze of which it certainly represents a further stage of reduction.

Just as there is a single factor difference between corresponding patterns in centrifugal mahogany and centrifugal white, so there is a single factor difference between tippler bronze and its corresponding white (dominant white). The set of whitening factors, which I will call V, V, V, runs exactly parallel to the set of bronzing factors Q, Q, Q. Again, in its mode of inheritance we note the same difference between Q and V as there is between M and W. Suabians have a white neck and inner primary vanes; in outcrosses we may lose the white color here and get bronze in its stead: if we raise an  $F_2$  from such hybrids we do not get back the white. This means that the white Suabian neck, etc., is controlled by two factors, the first Q reducing to bronze, the second V reducing the bronze to white.

Mutual relations of the three types of red. If we cross a centrifugal mahogany bird with a brick red one, the typical



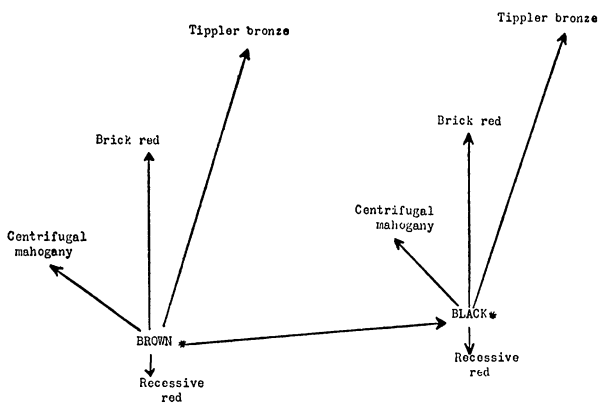
pattern of the former is, of course, destroyed. Again, a barred or checkered bird of the red AG type has its pigment all clumped and its pattern destroyed by introducing tippler bronze; at the same time the typical black roots of the feathers in a tippler bronze are whitened by the AG complex. We therefore have to call the latter dominant to the former in each case, but these relations are purely technical and non-essential, as I have shown that tippler bronze is much more closely related to mahogany than to brick red.

#### *Conclusion*

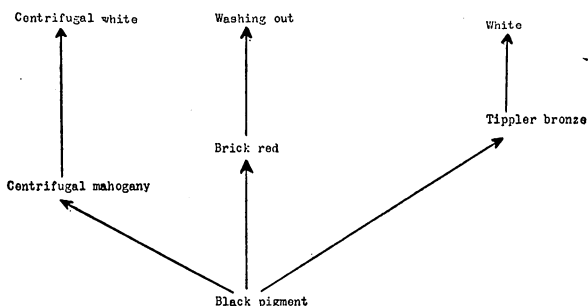
Returning to the original subject of this paper, the behavior of brown toward the other color factors and the way in which the "dominant reducers" affect it, we find, as we might expect, that brown is reduced to red (and to white) just as black is reduced. These conditions are so obvious that no extensive experiments have been started to verify the facts. I mated, in one case, a mahogany tippler (type Q) with brown\* and obtained two young with regular mahogany flights, as expected. Again, in hatches of centrifugal-mahogany oriental frills based on brown\*, this color could not be distinguished from mahogany based on black\*. Again, nine members of a brick-red family (A), obtained by introducing the factors for brick-red into a strain of brown "Flights," all show a brick-red which, to my eye, is absolutely identical with brick-red based on black.

In view of the striking similarity of brown\* and black\* in all their physical features, their behavior toward recessive red and toward factors which reduce both pigments to other chemical compounds affecting the eye as some shade of red, we may consider black and brown pigment to be closely related, this relation being of a different order from that of other pigments known in pigeons.

The writer suggests the following schemes of colors in pigeons, in which a higher level symbolizes dominance, and a lower level symbolizes recessiveness.



General scheme of colors, not including whites.



Partial scheme of colors, showing derived whites  
In both schemes a higher level symbolizes dominance,  
a lower level recessiveness.

#### SUMMARY OF FACTORS DISCUSSED IN THIS PAPER

- R Fundamental factor for red in pigeons.  
 E Responsible for brown (chocolate) pigment if added to R.  
 B Turns brown pigment into black pigment (*sexlinked*)  
 M, M, M A differentiated set of factors turning spread-out black or brown into centrifugal mahogany.  
 W, W, W A differentiated set of factors turning centrifugal mahogany into centrifugal white.

- Q, Q, Q A multiple set of mahoganizing factors working on black and brown pigment.
- S', S', S' An incompletely known set of spreading factors, affecting clumped black and brown pigment in association with Q, Q, Q being together responsible for tippler bronze.
- V, V, V A multiple set of whitening factors working on bronze.
- D A dominant diluter of tippler bronze, non sex linked.
- A A sex linked factor turning black and brown pigment into red.
- G A sex linked factor having a clumping and washing out effect on all phases of black, brown and A-red and eventually turning it into white; closely associated with A.
- S'' An inhibitor of G, thus having a spreading effect on clumped A-red. Its effect on other pigments not known; perhaps sex linked.

SCHEMATIZED COLOR ANALYSIS OF PRINCIPAL BREEDS OF  
PIGEONS USED IN THIS WORK

The symbol (B) means that B may be present or absent.

Recessive red R(B)ee, or any combination with ee, in Tumblers.

Brown\* or chocolate RE in Dragoons, Kings, Flights.

Black\* REB in Tumblers.

Brick red, washed out RE(B)AG in Homers.

Brick red, solid RE(B)AGS'' in Carneaux.

Centrifugal mahogany, spangled RE(B)M in Modenas.

Centrifugal white, spangled RE(B)MW in Hyacinths, some Suabians.

Centrifugal mahogany, laced RE(B)M' in Schietti.

Centrifugal white, laced RE(B)M'W' in Blondinettes, some Suabians.

Tippler bronze, dark RE(B)QS' in Tipplers, Archangels, some Larks.

Tippler bronze, light RE(B)QS'D in Archangels.

Dominant white RE(B)QS'V in Suabians, Starlings.

Probably Q = M

" R = W

## PLATE I

- FIG. I. Typical spangled wing of a Hyacinth. The basic pattern or background is bluecheck.
- FIG. II. Typical laced wing of a swallow (whitecheck). The background is solid black.

