

INHERITANCE OF CERTAIN "BLUE-BLACK" PATTERNS
AND "BLEACHED" COLORATIONS IN THE
DOMESTIC PIGEON¹

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INTRODUCTION

TWO objectives are concerned in the following study: to clear up as far as possible the questions concerning the inheritance of certain "blue-black" patterns previously discussed by JONES (1922) and by BOL (1926), and to analyze several previously unrecognized color types.

The coloration of the ordinarily accepted wild type of *Columbia livia* is here used as a standard of reference. The plumage is basically a light bluish gray; the remiges become black distally, and the ends of the rectrices also show black distally but in the form of a broad band with a faint bluish terminal edge. The tertiary wing feathers exhibit a black area in the vanes, as do the secondary coverts and often the median coverts; these rows of black areas form two black bars across the closed wing. The neck and crop feathers are dark, with much iridescence. The rump and underwing feathers are albescent or whitish terminally; the outer vanes of the outer rectrices are also albescent. The iris of the eye is red at the margin and more yellow centrally, giving an orange appearance. The beak and claws are very dark brown or black.

A list of factors incidentally involved in the present study and descriptions in terms of deviations from wild type follow. Wild type factors are symbolized "+."

d—"dilution"; sex-linked. Nestling down short, fine; beak, claws, and skin pale; retinal pigmentation less intense; plumage tawny with dun pattern. The symbol *i* has also been used for this factor. CHRISTIE and WRIEDT (1923).

B^A—"ash"; sex-linked. Plumage ashy gray with reddish brown neck, crop, and wing pattern. Also has been termed "dominant red" and "A-factor." HAWKINS (1931).

b—"chocolate"; sex-linked, allele of *B^A*. Beak, claws, and skin pale; iris less yellow; plumage tawny with brown pattern. STEELE (1931) and HAWKINS (1931).

e—"recessive red"; beak, claws, and skin pale; plumage more or less uniformly chestnut red, least effect on albescent areas and in proximal part of tail. STEELE (1931).

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S—"spreading"; plumage dull black, usually with wing bars still faintly visible. JONES (1922).

G—"grizzle"; finely stippled decolorization (whitening) in plumage, least in distal parts of remiges and rectrices. BOL (1926).

Studies of feather development in general show that the source of pigment is mainly large chromatophore cells, whose branching pseudopodia deposit pigment in the cornifying structures. These chromatophores appear to arise in the growth ring at the root of the feather germ. Microscopic examination of the pigment left in the mature feather of the wild *C. livia* has shown that only one kind of pigment, black, is present. The

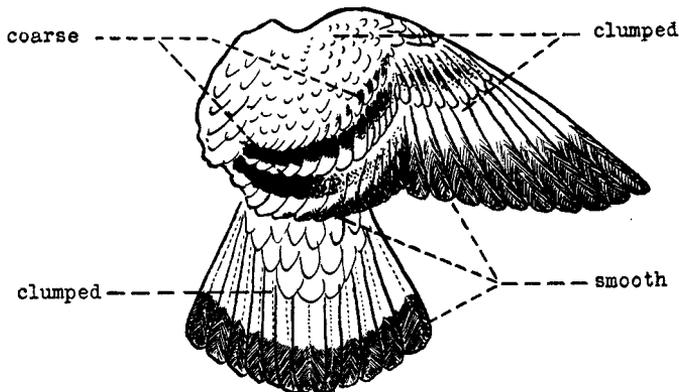


FIGURE 1.—Diagram of wild type color pattern, showing the positions of the clumped and spread phases of the pigment.

appearance of "blue" portions of the plumage under the microscope resembles a half-tone print, each barbule showing striations or clumping of black granules. The black portions of the plumage reveal only traces of the clumping or striation, if any, the clumps being so wide as to coalesce. These two phases of the blackish pigment have been called "clumping" and "spreading" respectively (LLOYD-JONES 1915).

Two slightly different sorts of "spreading" should be recognized. One of them involves the distal portions of the remiges and the tail band, while the other affects the wing bars (fig. 1.) Examination of these areas of a wild type specimen reveals in the first case a smooth transition from black to blue, while in the second case there are usually slight irregularities and "freckling" in the transition. For convenience the two types of spreading will be referred to as the "smooth" and the "coarse" types, respectively. There is apparently no microscopic difference, but as will be seen further on, the two react differently in many color combinations. The effect of S seems to be chiefly to cause deposition of pigment of the "smooth" spread type throughout the plumage.

The tendency for spreading of pigment to occur in specific areas of the plumage and individual feathers results in patterns. A wide variety of such patterns is found in the Columbidae, and has furnished ground for voluminous speculations on evolutionary relationships (WHITMAN 1919). Within the limits of domestic breeds also a remarkable range of pattern may be observed.

"BLUE-BLACK" PATTERNS

Fanciers and most students of pigeon inheritance have adopted a simple system of "blue-black" pattern nomenclature based on the modal types, namely barless, bar (wild type), and checker. Appropriate adjectives designate deviation from these modal conditions. The checker pattern has been subdivided according to the amount of spreading into several sub-types; extremely dark checker has been termed the "T" type. Another condition which JONES (1922) named "sooty" has often been lumped with checker. Specimens showing the various patterns are well illustrated in the works of WHITMAN, JONES, and BOL.

The patterns differ from each other only in the amount and position of coarse spreading. The barless pattern lacks it almost entirely; the other patterns show in serial array increasing invasion in the wings, the crop, and finally nearly all the body feathers anterior to the tail.

JONES considered the patterns "barless," "bar" (wild type), "sooty," "checker," and "T" as independently inherited but forming an epistatic series. BOL considered them to be alleles. Neither gave due treatment of intermediate conditions, and the evidence for their respective hypotheses is insufficient.

From the above studies we can accept two conclusions: that despite a perfectly graduated series of patterns, sharp segregations occur frequently; and that in general dominance is parallel to the amount of "spreading" involved in the pattern.

A restudy of the problem has been made. It seemed obvious at the start that the "sooty" type is not homologous with the other patterns, since "spreading" occurs along the shaft and end of affected feathers. In other patterns spreading encroaches from the side toward the shaft. Since no satisfactory source of sooty was available at the time, this type has not been studied further.

Breeding data obtained in the study of the patterns are summarized in table 1. Barred birds, of several color classes, and chiefly of Homing pigeon ancestry, have been used as the wild type pattern. In all cases they have been typical, but not entirely alike. A family of barless Strassers and a checker Strasser cock whose dam was barless constituted the source of the barless character.

Two matings of barless male by bar female gave 16 offspring, all barred. Some tendency to narrowness and shortness of the bars was observable. Three matings of the F₁ produced 47 F₂; of these only seven were barless. In the others the character of the barring was decidedly variable, the bars being mere rudiments in two cases. That a single factor differentiates bar-

TABLE I
Results of matings involving T-pattern, checker, bar, and barless.

MATING	PHENOTYPE OF OFFSPRING			
	<i>C</i> ^T	<i>C</i>	+	<i>c</i>
Barless × ++ (bar)			16	
F ₁ × F ₁			40	7
T pattern (origin 2380F) × ++	33		31	
T-pattern (origin 2707.1) × ++	4		6	
Medium checker (origin 7-29-1) × ++		117	131	
Checker, heavy grade (origin 2267N) × ++		25	19	
Checker, light grade (origin 2835.1) × ++		7	5	
T-pattern (origin 2380F) × barless	3		6	
F ₁ T-pattern × barless	18			17
T-pattern × checker (medium, heterozygous for bar)	8			
<hr/>				
F ₁ (T-pattern) × ++	27	25		
	8		10	
	35	35		
Checker (origin 8-33-14) × barless		6		4
Checker (origin 8-33-14) × ++		3	6	
F ₁ bar × F ₁ bar			9	1
T-pattern (origin 2380F) × checker (medium, heterozygous for bar)	23	10	6	
T-pattern (origin 2707.1) × checker (medium, heterozygous for bar)	3	1	1	
F ₁ T-pattern × ++	24		26	
Medium checker × ++		32		
F ₁ × ++		19	19	

less from barred is not excluded by these facts, but the presence of modifying factors must be considered.

The backcross method is more suitable for analytical purposes and has been used in most of the remaining work. Two birds of unrelated stock form the sources of all T-pattern birds used: one, 2707.1, was heterozygous for bar; mated with bar he gave ten squabs, four T-pattern and six bar. The other, 2251F, was not heterozygous for bar, since in a mating (2380) with a bar female none of the eight offspring were barred. A daughter, 2380F, was mated with a bar male. Of sixteen offspring nine were T and seven bar. Some of the former were crossed with bar, and the process

repeated for two more generations. Of a total of 64 offspring so produced, 33 were T-pattern or very heavy checker, and 31 bar. No definite distinction between T-pattern and very heavy checker seemed feasible, and since on a two-factor basis a ratio of 48:16 would be expected, it seems clear that T-pattern and very heavy checker are, in this case at least, slightly different expressions of one dominant factor.

In a similar study three checkered birds were sources of separate families. All three birds were heterozygous for bar. One was a heavy grade male, 2267N; another was a medium heavy grade female, 7-29-1; the last was a very light grade male, 2835.1. In each family approximate equality of checker and bar descendants was obtained. The factor for checker in each case then behaved as a simple dominant. But instead of a regression to a common modal condition for all families, it was found that the condition in each family was similar to that of its source bird. The family derived from 7-29-1 was the largest and most varied; the modal condition here was medium grade, but some individuals were fairly light, and a few even heavier than the source bird.

The conclusion is that a different chief factor or allele for checker was introduced by each source bird, but that modifying factors are capable of shifting the grade of the checker to some extent, as in the case of the T-pattern. At the extremes of this variation the phenotype of one factor may overlap that of the next higher or lower grade factor and the highest may even be confused with T-pattern. It is advisable then to use breeding tests to classify intermediate individuals of unknown origin.

To determine whether the more distinct types (barless, medium checker, and T-pattern) might be allelic, tests were made as follows. A female, 2670J, T-pattern (heterozygous for bar) and descendant of 2380F, was crossed with a barless male Strasser. Nine offspring resulted—three very heavy check and six barred. The former were back-crossed to barless Strasser, producing 18 very heavy check and 17 barless. Barless and the T factor from 2380F are therefore alleles. The male 2251F (homozygous T) was crossed with a medium grade checker heterozygous for bar. Seven offspring (all T-type) were mated to bar. Five produced 52 offspring, of which 25 were medium grade checker and 27 T-pattern or very heavy checker. The other two produced a total of eighteen young, of which ten were barred and eight T-pattern or very heavy check. Therefore the T factors from 2251F are allelic with the medium-grade checker factor.

Only one mating was made to test the allelism of checker with barless. The checkered Strasser 8-33-14, whose dam was barless, was mated with barless. Of the ten offspring, six were checker and four barless.

To sum up: T-type, heterozygous, by other types gave 143 T:139 others. Checker, heterozygous, by bar or barless gave 178 C:187 others.

Bar, heterozygous for barless, inbred, gave 49 bar:8 barless (expectation 43:14).

In all tests allelism of these three patterns is found. There is little reason to suspect a different mode of inheritance in the other cases although they have not been tested.

The above findings explain the results of a number of other available matings. Two matings of T-type, heterozygous for bar, by medium grade checker, also heterozygous for bar, gave 26 T:11 checker:7 bar (expectation 22:11:11). Two T-type offspring crossed to bar, gave a total of 50:

TABLE 2A
Results of matings involving opal.

MATING	PHENOTYPE OF OFFSPRING			
	INFERTILE, DEAD EMBRYO	DEAD YOUNG, ETC.	+	OPAL
Opal×opal	136	87		261
Opal male×++female	11	16	113	
++male×opal female	25	19	20	
Opal male×F ₁ female (or equivalent)	63	100	300	258
F ₁ male (or equivalent)×opal female	115	57	133	134
F ₁ ×F ₁ (or equivalent)	8	10	49	21
Totals:				
in outcross			133	
in back-cross			433	392

24 T and 26 bar. Male 8-33-14, checker heterozygous for barless, when mated with a bar gave nine young—three checker and six bar. The latter barred birds carry the barless factor. Two of them were inbred, and did produce a barless squab, but as in the previous case of barred carrying barless, the ratio is poor (9 barred:1 barless), and variability of the barring was marked. Homozygous checker 8-33-6 mated with bar produced 32 offspring, all checker. No marked difference between the homozygote and most of his heterozygous offspring has been found. These in turn mated with bar gave a total of 19 checker and 19 bar.

The symbolization of the factors in this allelic series as suggested by JONES and by BOL seems at present undesirable. DE HAAN'S (1933) method will be followed in general. Barless will be *c*, checker *C*, and T-pattern *C^T*. The dominance relations in the series may be represented as follows: *C^T* > *C* > + > *c*.

"BLEACHED" COLORS

The "bleached" appearance of the "ash" (*B^A*) plumage is imitated to some extent by four new factors. These have been given the names "opal,"

“dominant opal,” “faded,” and “milky.” Experience and the use of suitable breeding methods are necessary in differentiating these types from each other as well as from B^A .

Opal

“Opal” seems widely distributed in Homing pigeons, since it has been obtained or observed by the writer in many separate flocks. Probably WHITMAN (1919) was dealing with it in his chapter on “Color and Weakness in Homers” (vol. II, chap. IX). Figures representing the condition are given in his vol. I, plate V, A and B. WHITMAN considered the cause of any such color to be low vigor in one or both parents.

In appearance most opal birds are faded black to grayish ashy in the regions of “smooth” spreading; the remiges generally show less “bleaching” than the tail band. The “coarse” spread areas generally exhibit a distal edge which is blackish, while proximally a narrow ashy line and then reddening are found. Clumped areas of the wing plumage are practically normal (blue) except in the more extreme cases; in these the clumped areas are bleached out also, resembling the condition found in B^A . The blue of the rectrices and tail coverts, however, becomes bleached to some extent in all cases.

Breeding data involving opal are given in table 2a. Since in outcrosses no opals were produced the character is recessive; in F_2 it occurred in a frequency of 30 percent, with standard deviation of 5.47 percent. In the backcross the opals are slightly in the minority but chance can easily account for the discrepancy. And finally, opals breed true. The inheritance is therefore definitely monofactorial; the symbol o will be used.

Variability in the degree of “bleaching” in opal birds is most striking. Almost every case shows slight banding of the feathers, representing variation in effect at different times while the pigment is being deposited. Definite “banding” is frequent, and easily induced by starving. The starvation period is marked by a very light bar across the feathers. RIDDLE (1908, p. 357) states that “pale-colored” pigeons are most suitable for studies of “fundamental bars.” Opal birds were observed by the writer in RIDDLE’S “family 133.” At the time, RIDDLE commented that such a color type was referred to by the term “pale-colored.”

Opals sometimes also exhibit marked change of color at different molts. Since such variation seemed due to physiological states, a test was made to see whether thyroid feeding would have similar effect. A male with little “bleaching” was chosen, 2652F. Secondary covert feathers were removed from both wings. Five days later, just before the new quills came through the skin, feeding of capsules of thyroid powder (Armour’s, 0.2 percent iodine) was started. Two doses a day of .15 gram each were

given over a period of five days. By this time the feathers were well out of the skin and pigmentation nearly complete. These feathers were much more bleached than the previous set; the new ones were removed two weeks after cessation of thyroid feeding. The next regeneration (no thyroid feeding) grew in dark again.

In another case the same total amount of thyroid (1.5 grams) was given to a dark opal male, 2730D, in one dose. Apparently its effect wore off before pigmentation of new feathers began, since they were dark.

If the first case above is to be considered significant, it may be surmised that the activity of the birds' own thyroid is correlated with the variability

TABLE 2B
Reproductive behavior of females in opal matings. Standard deviations given.

TYPE OF FEMALE	TOTAL EGGS	INFERTILE?,	BROKEN EGGS,	SURVIVORS
		DEAD EMBRYO %	DEAD YOUNG %	
Normal	964	8.6 ± .9	13.0 ± 1.08	78.4 ± 1.32
Opal	956	22.1 ± 1.11	15.3 ± 1.16	62.6 ± 1.57
Extreme opal	122	53.3 ± 4.5	13.1 ± 3.0	33.6 ± 4.3

of opal. Just how much of the variation can be accounted for on this basis is questionable since the "extreme" opals (closely resembling B^A) do *not* show any fluctuation at different molts or in the individual feathers. The possibility that the extreme condition is due to another opal allele has no genetic support at present.

Opal females have been decidedly poor breeders, as is shown in table 2b. The chief point of trouble seems to be the egg; no matter what kind of male is involved, apparent infertility and embryonic death is considerably greater than in eggs from females of other colors. It seems unlikely therefore that the genotype of the embryo is responsible. Further evidence in this direction is afforded by the fact that once hatched, opals and other squabs seem equally hardy, and that the segregation ratios are approximately correct for a simple recessive.

Opal has been found closely linked with the locus of the pattern series treated earlier in the paper; the details of this study are to be published separately.

Dominant opal

A coloration known to fanciers as "white bar" or "white checker" (according to the pattern) in the Strasser breed greatly resembles the ordinary opal, though less reddish appears in the wing pattern: also, the bleaching is often more obvious in the primaries than in the case of recessive opal.

Illustrations of Strassers of this color may be seen in WITTIG part VI, pp. 33-37.

One male Strasser of this type, 8-33-14, has been the source of the type in this study. The breeding data are summarized in table 3. No inbreeding was practiced, and therefore no homozygotes produced. About half the offspring of affected parents were of the type; a female (2694D) produced daughters of the color. The trait is then dominant and autosomal, and will be termed "dominant opal," with the symbol *Od*.

This same female, 2694D, being the daughter of a recessive opal dam, is heterozygous for *o*. Backcrossed to an opal male, she gave 22 offspring; among them was one wild type, and six were apparently the combination of both opal types. Dominant opal is therefore not an allele of recessive opal. The expression is not nearly so variable as in the case of recessive opal. Occasionally a few small reversionary (blue or black) flecks have been observed in the plumage.

Faded

A third "bleached" coloration type was kindly given the writer by Dr. H. W. FELDMAN from the pigeon colony at the University of Michigan. The ancestry was Tippler \times Parlor Tumbler; probably the latter was the actual source of the trait, but the coloration has not been given a name by fanciers. The phenotype resembles a low-grade opal in many respects, but the clumped areas are more definitely bleached. The plumage of both sexes shows frequent reversionary (blue or black) flecks.

One male, 2707.1, was used. The procedure followed was the same as in the case of dominant opal, repeated outcrosses, and testing for allelism with recessive opal. Here again dominance was demonstrated. As yet no females have been bred, so that whether the trait is sex-linked or not is unknown. At any rate the factor is not an allele of recessive opal; it will be given the name "faded," and the symbol *Of*. A summary of the breeding data is given in table 3.

Milky

The last type of "bleached" coloration to be discussed here has been given the name "milky." The origin was a single male street pigeon, 8-33-15; no other sources of the trait are yet known. It has proved very uniform in phenotype, the "bleaching" always being quite pronounced, with little reddening in the "coarse" spread pattern.

The original male was crossed with a blue and with an opal, respectively; all progeny were blue. He was mated with a daughter, and produced eight young, only one of which was milky. Matings of the F_1 however, gave a fair 3:1 segregation (table 3). No other information is available on this

trait, but it seems safe to assume that a simple recessive autosomal factor is responsible, not an allele of opal; the symbol *my* will be used.

Smoky

“Smoky” plumage color is well known in several breeds of pigeons and occurs sporadically in many others. In this study the trait has been introduced by several Homing pigeons and by the Archangel breed. Smoky

TABLE 3
Results of matings involving dominant opal, faded, milky, and smoky.

MATING	PHENOTYPE OF OFFSPRING			
	DOM. OPAL		+	
		27	30	
Dominant opal × ++	<i>Od</i>	(<i>Od</i>)	+	<i>o</i>
		<i>o</i>		
Dom. opal × recessive opal	3		4	
F ₁ dom. opal × rec. opal	6	6	1	9
	Faded		+	
		16	10	
Faded × ++		2	3	
Faded × recessive opal				
	<i>Of</i>	(<i>Of</i>)	+	<i>o</i>
		<i>o</i>		
F ₁ faded × recessive opal	5	5	6	4
	+		<i>my</i>	
Milky × ++	9			
Milky × recessive opal	7			
F ₁ × F ₁	23		9	
F ₁ × milky	7		1	
	+		<i>sy</i>	
smoky × ++	78			
F ₁ (or equivalent) × F ₁	148		46	
F ₁ (or equivalent) × smoky	44		45	
Smoky × smoky			78	

birds have light skin and base of beak, especially noticeable in squabs; the wing pattern is blurred through a darkening of the blue portion and less richness of the “coarse” spreading. The bluish tip edges of the rectrices are accentuated, and the albescence under the wings, on the rump, and in the outer rectrices is replaced by slaty blue.

This group of features was found to breed true in all cases. Other breeding data (table 3) show that a single factor is responsible for this syndrome. In the heterozygous condition the beak is slightly light, and there may be slight loss of albescence, or accentuated blue-tipping of the rec-

trices, but the trait may best be treated as a recessive. It is symbolized *sy*.

Modern Carriers, Barbs, and Magpies seem all to be smoky, according to show standards and numerous examples which the writer has observed. In addition, the ordinary varieties of Archangel seem always smoky.

STAPLES-BROWNE (1908) used the Barb in some of his crosses. Two "blue" segregates are pictured in his paper (plate V); the one on the left, except for beak color, which may have been darkened by sunlight, seems a typical smoky in the T-pattern.

COMBINATIONS

Despite the fact that all the eight factors described have to do with only one general process, namely pigmentation, most of the combinations which have been obtained have not usually been difficult to detect phenotypically. Generally the phenotype may be predicted from knowledge of the effects of the single factors.

In combinations of *C* or its alleles with *S* and with *e*, the latter are epistatic.

Combinations of recessive opal with B^A , *b*, *d*, and *e* have generally been difficult to classify as opal without breeding tests, but many individuals show unmistakable bleaching.

The combination of recessive with dominant opal resembles the dominant opal mainly, but also possesses certain features of the recessive opal which are recognizable with experience.

In the combination of recessive opal with faded, a more or less additive effect is seen; the general appearance is recessive opal with marked bleaching of the clumped areas as well.

Smoky in combination with *S* gives a rich, even black; the base of the beak is light. It is very easy to confuse the homozygous and heterozygous conditions, and it is safest to classify such specimens by breeding test.

Smoky is even more difficult to recognize in combination with *e*; the lack of typical albescence is characteristic, especially in the rectrices, but the phenotype is mainly that of *e*.

SUMMARY²

A series of at least three alleles has been shown to be concerned in the inheritance of the patterns involving the extent of one phase of pigmentation. These are *c* (barless), *C*, (checker, medium grade), and C^T (T-pattern and very heavy checker). The variability in expression of *C* and C^T seems to be due to modifying factors. Other alleles are indicated but not proved to exist; variability hinders their recognition.

² Detailed data have been filed in the editorial office of GENETICS and may be consulted by anyone interested; they are also to be found in the writer's thesis (University of Wisconsin, 1937).

Four factors responsible for "bleached" phenotypes somewhat similar to that produced by the sex-linked B^A factor have been identified. Opal and milky are recessives, while Dominant opal and Faded are dominants. The first three are autosomal; Faded has not been tested for sex-linkage. Opal is not an allele of the other three; it is closely linked with C and its alleles. Furthermore, poor hatchability has been observed with eggs produced by females of the opal type. Opal is the most variable of the four factors studied; a large share of the variability seems the result of metabolic variability during feather growth.

The color modification smoky has been found to be a simple autosomal recessive; it is apparently a characteristic color feature of several breeds.

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