The Journal of Heredity 66:177-202. 1975.

Sectorial Mosaics in the Domestic Pigeon: 25 More Years

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SINCE MY 1949 review on problems of mosaicism in the pigeon[9], the vista has expanded with the accumulation of many new spontaneous cases. Also, considerable new data and discussion have been reported concerning other species, notably a 1955 review by Cock[4] on the fowl.

Sectorial (sometimes half-and-half) mosaicism usually can be clearly distinguished from the more common variegated or flecking effects that have been attributed to instability of certain mutants[8,10]. Not infrequently in sectorials two or more mutants are involved simultanenously. Among various hypotheses for such cases, some sort of binucleate origin seems most probable, and development of tissue from supernumerary sperms was indicated in some well-documented examples. I proposed the term "bipaternity" for such origin; the term "androgenesis" has been preferred in studies of honeybees[6] in which the phenomenon has been thoroughly demonstrated. Strangely, Hannah-Alava did not include either in her 1960 review[7].

The present paper summarizes data coming to my attention since 1949 on 182 spontaneous cases in the pigeon. Most of them have not previously been reported (other than in the informal *Pigeon Genetics News Letter*). Only the most unusual can be given detailed comment. For many others, data have been fragmentary or equivocal, but overall some new insight is gained.

Sectorial Contrasts

Discovery of a mosaic by a pigeon fancier usually is dependent on obvious and superficial contrast of an unexpected sort. Numerous plumage-pigmentation mutants are available and readily recognizable in contrasting areas. The mutants are described and illustrated in Levi's treatises[11,12], together with gene symbols. Those encountered in the present study are as follows:

Sex-linked			Autosomal		
Ash-red	B^A	allelic	Grizzle	G	
Brown	b		Checker	C	allelic
Dilute	d		T-pattern	C^T	
Reduced	r		Spread	S	
Almond	St	allelic	Recessive red	e	
Faded	St^F		Opal	o	
			Dominant opal	Od	
			Indigo	In	
			Milky	my	

The wild-type alleles of all the mutants will be designated only by the symbol +.

In pigeons the great majority of sectorial mosaics have been "patchworks." For tabulation I have used a colon to separate the contrasting components; the larger area is arbitrarily on the left of the colon, except in cases where there was half-and-half arrangement—there, the mutant area arbitrarily is given to the left. Table I gives a breakdown of "simple" mosaics—those showing only two allelic phenotypes in contrast. Some possible contrasts did not occur, as might be expected by chance. Table II presents data on most of the more complex cases.

Sex Ratios

It seems evident from examination of the tables that no significant difference from expected 1 : 1 sex ratios exists. The slight tendency to an excess of males agrees with the usual condition in adult populations of pigeons. Adding in mosaics not classifiable for the tables, we obtain totals of 72 males, 60 females, and 50 not sexed or questionable. This last group consists mainly of young examples or specimens not used for breeding and not examined internally; there is little reason to suspect that these would have had sexual abnormality. Only one case was reported to be a gynandromorph, that of Regenstein[15]. It was a Racing Homer, about half-and-half, the left side of wild-type coloration and with an ovary, while the right side showed the ash-red (B^A) coloration, with a testis.

The scarcity of gynandromorphs may reflect the irregular arrangement of contrasting tissues. Also, it is possible

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The author is professor of genetics, Iowa State University, Ames, Iowa, 50010. Journal paper no. J-8179 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project no. 1380. Most of this research was privately supported, and the generous aid of nearly a hundred breeders and fanciers in the United States and other countries is hereby acknowledged. Special gratitude is due to: E.M. Blaine of Des Moines, Iowa; Robert B. Clark of Livermore, Calif.; Ove Fossa of Sandnes, Norway; Harold Gordon of New Haven, Conn.; C.M. Gottfried of Stamford, Conn.; Gerhard Hasz of Indianapolis, Ind.; Kerry Hendricks of South Lyon, Mich.; Ramon Kinkade of Union Lake, Mich.; Robert J. Mangile of Pittsburg, Kans.; George Neuerburg of North Hollywood, Calif.; Joseph W. Quinn of Atwater, Ohio; David A. Rinehart of Tallmadge, Ohio; Arvil G. Stone of Murray, Utah; John S. Tidwell of Tucson, Ariz.; and for assistance in defraying publication costs, Carl F. Graefe of Cuyahoga Falls, Ohio; and Wendell M. Levi of Sumter, S.C.

FIGURE 1—Examples of complex pigeon mosaics. *A*—Female Giant Homer from Harold Goodman. The right side is mostly spread black (*S*), the left mostly wild-type, but smaller areas of indigo (*In*) are scattered in both sides. (Photo by Paul J. Hollander.) *B*—Male French Mondain from H.J. Anthony. The whitened area involves the effect of the grizzle factor (*G*). This effect is not present in the area that shows the sex-linked brown (*b*). (Photo by Louis Facto.) *C*—Female King from C.M. Gottfried. Most of the plumage is brown (*b*), but the left wing shows the two sex-linked dominants faded (St^F) and ash-red (B^A). (Photo by Louis Facto.) *D*—Female Tumbler from Harold Gordon. The white primaries are a type of piebaldness, usually not so asymmetrical. The remaining areas are recessive red (*e*) and spread (*S*) with the sex-linked reduced (*r*). (Photo by Louis Facto.) *E*—Male Racing Homer of R.J. Mangile. Most of the plumage shows grizzle (*G*) with ash-red (B^A) but they are not present in the left wing shield (+). (Photo by Kerry Hendricks.) *F*—Male mongrel of the author. Most of the plumage is variegated almond (*St*) and brown (*b*), while the right wing shield is faded brown ($St^F b$). (Photo by Paul J. Hollander.) *G*—Female Tumbler bred by Jim Wilson. The contrasting areas differ only in the sex-linked ash-red factor. This female produced a similar son and he produced a similar daughter (3 generations). (Photo by Don Livengood.) *H*—Female Racing Homer from William Trapp. This is the most common type of "simple mosaic," with contrasting areas different only in the sex-linked ash-red factor. (Photo by Paul J. Hollander.)

that mixed gonads may have existed in some of the specimens that functioned as essentially normal males or females. Several of the complex mosaics ultimately died with gonadal tumors. Mintz[14] also has reported rarity of gynandromorphism in artificially composite ("allophenic") mosaic mice. In any event, a distinction is needed between gynandromorphic vs. intersexual conditions in birds. The "hermaphrodites" reported by Riddle *et al.*[16] were evidently hormonal rather than mosaic in origin.

Incidence Notes

My 25-year total of 182 cases far exceeds the number of all previously reported, and I am certain that my sampling has been haphazard at best. Have mosaics been increasing in recent times? It seems incredible that such acute observers as Charles Darwin and C.O. Whitman[21] did not note a single example among the thousands of pigeons they studied. Could they have seen some and ignored them? But hardly any other reports appeared before the 1930 period[13].

Several factors however must be considered in relation to this problem. First, there has been a large increase in the total pigeon population kept by fanciers since 1850. Second, education in regard to genetics, especially in coloration, has gradually been seeping into the fanciers' minds, and there has been more tolerance of crossing. Also, my hammering on the subject probably has saved many a "mismarked" bird from an ignominious end. Instead of something ridiculous or despicable, the creature becomes newsworthy.

A geographic analysis of incidence shows cases from 28 states and 6 foreign countries. California and Kansas had the most, 23 each. Other highs were Iowa and Ohio (15 each), Connecticut (11), Texas (10), and Arizona (7). In my judgment, the distribution merely indicates general density of fancy pigeon populations and the extent of fancier interest in esoteric topics such as biology. That New Zealand leads all the foreign countries in cases is largely the result of zealous reporting by one fancier (Mrs. Madelon Gilligan of Christchurch).

It might be suggested that very widespread occurrence and apparent increase in recent decades really indicates the effect of some new and pervasive environmental factor. DDT perhaps, or other chemical pollutants, or radioactive fallout all might be suspect. While granting the possibility, I do not consider the probability more than remote.

The question of whether a possible hereditary tendency to produce mosaics may exist also is difficult to answer. Analysis of incidence by breeds shows no obvious tendency; many breeds are represented, roughly in proportion to their popularity and their color crossing. On the other hand, I have had reports of families in which several cases occurred, and at least half a dozen instances of mosaics produced by mosaics.

"Simple" Mosaics

Many of the specimens included in Table I had pedigree and progeny-test data, but nothing significant can be concluded, usually because the parents were in flock pens and the mosaics could equally well be heterozygotes or germinal composites. Of particular interest, however, are the females showing two sex-linked alleles. Their sons from progeny-test matings are informative. Six of the 16 females showing ash-red (B^A) and wild-type areas were tested, and in each case, the sons received only the allele shown in the mosaic's larger area. Similarly a female showing wild type:dilute (*d*) produced only non-dilute sons. Regrettably, no other progeny tests of such females succeeded.

Two males are of special interest in the sex-linked group. One of these, #50 H 14868, from Earl A. Klotz of Cleveland, Ohio, was $+:d$; the mother was +, the father $B^A\ d / / + +$, so that the dilute areas in the mosaic could have been derived from a *d* crossover sperm. At least 16 daughters from the mosaic were classified, and none was dilute. The second mosaic male was a Racing Homer bred in 1959 by James Foster of San Antonio, Texas. The bird's parents were both ash-red (B^A) but the mosaic looked mostly wild type. Foster tested him with a wild-type female and got 7 progeny, all ash-red. It seems probable, therefore, that this mosaic was not germinally heterozygous. These two males are exceptions to the more usual finding that mosaic males are heterozygous, germinally.

Complex Mosaics

Eleven of the better-documented cases listed in Table II will now be considered in more detail.

Case no. 1. ♂ French Gros Mondain NPA 51 I 749

Table I. Distribution of "simple" mosaics according to mutant factors. Contrasting phenotypic areas are separated by a colon, with the larger area on the left. In case of equal apparent area, the mutant is arbitrarily considered larger. + represents wild type. The upper half of the table concerns sex-linked mutants

Allelic contrast	Males	Females	Sex?	Total
$+:b$	1	2		3
$b:+$		2	1	3
$+:B^A$	3	3	4*	10
$B^A:+$	24	14	7	45
$B^A:b$	1	1		2
$St:+$	4	4		8
$d:+$	1	3		4
$+:d$	3	2	4	9
$r:+$		1		1
$+:e$	6	5	5	16
$e:+$	1	3	7	11
$+:S$			1	1
$S:+$	1		1	2
$C:+$			2	2
$C^T:+$		1		1
$Od:+$			1	1
$+:Od$		1		1
$+:O$	2			2
$In:+$	1			1
$my:+$	1			1
Totals	49	42	33	124

* Includes one gynandromorph

(see Figure 1*B*), from H.J. Anthony of Grimes, Calif. Left wing and right half of tail brown (b): rest of plumage mostly whitened (G) and not brown. Sire black-and-white splashed (G); dam white (G?). Progeny tests showed that the mosaic transmitted both mutants (b and G). He lived to 14 years. Postmortem examination revealed that the left testis was tumorous.

Case no. 2. ♀ of the King breed, NPA 52 F 1651, from C.M. Gottfried of Stamford, Conn. Most of plumage brown (b) except left wing, head, and part of body ash-red with faded ($B^A\ St^F$) (see Figure 1*C*). Sire's genotype $St^F B^A / / + b$; dam's genotype $St^F b/--$. Progeny test with a brown male yielded a total of six young: two brown females and four $B^A\ St^F$ males. The mosaic died at 5 years with a huge tumor in the position of the right gonad.

Case no. 3. ♀ Racing Homer AU 49 SAN 152, from Oscar Desrochers of Sanford, Maine (see Figure 800 in Levi[12]). Left side mostly ash-red T-pattern ($B^A\ C^T$), right wing-shield wild-type coloration in checker pattern (C). No pedigree data. Progeny test showed transmission according to her left side and heterozygosity for pattern ($C^T / / +$). She lived to age 10 years.

Case no. 4. ♀ Tumbler #8135, from Harold Gordon of New Haven, Conn., in 1953 (see Figure 1*D*). Most of left side recessive red (e) with white primaries (a piebald condition); right side has large areas of reduced (r) with spread (S) pattern. Sire was reduced (r), dam white (piebald etc.?), but the mating was in a flock pen, and one of the other males was recessive red. Progeny tests of the mosaic showed that she transmitted recessive red (e) and reduced separately. Also, one of her daughters was a mosaic. The old mosaic died at 11 years from an ovarian tumor.

Case no. 5. ♂ of the African Owl breed, NPA 55 R 305, from John S. Tidwell of Wichita, Kans. Plumage mostly black with patches of brown (b) on sides of body and yellow patches ($d\ e$) on the back and throat. Sire brown (b), dam yellow ($d\ e$). This mosaic sired two mosaic progeny (one described below, case no. 6). Also he was progeny-tested and found to transmit all of his phenotypically evident mutants. He died in 1960, aged 5 years.

Table II. Individual "complex" mosaics, the contrasting areas being indicated as in Table I. In group 1 only sex-linked loci are involved; in group 2 only autosomal loci; and in group 3 both sex-linked and autosomal loci. An asterisk (*) indicates that the individual is discussed further in the text

Contrasting areas	Sex	Breed	Year	Breeder
Group 1				
*$b:St^F B^A$	♀	King	1952	Gottfried
$St^F B^A:b$	♀	King	1955	Gottfried
$d\ b:+$	♂	Giant Homer	1953	Hasz
$+:d\ B^A$	♀	?	1956	Telford
*$b:B^A:+$	♀	Racing Homer	1963	Stone
*$B^A/b:+$	♂	King cross	1963	Johnson
$+:d\ B^A$	?	F_2 Homer × Tumbler	1964	Ellis
$B^A:d$	♂	F_1 Homer × Roller	1968	S. Dakota
$d\ B^A:+$	?	Fantail	1970	Isle
$d\ B^A:+$	♂	Tumbler	1971	Blaine
Group 2				
$C:S$	?	Racing Homer	1963	Hasz
*$S:+:In$	♀	Giant Homer	1968	Goodman
*$+:In\ In:S$	♀	Giant Homer	1969	Hasz
Group 3				
*$B^A\ C^T:C$	♀	Racing Homer	1949	Desrochers
*$G:b$	♂	French Mondain	1951	Anthony
*$e:r$	♀	Tumbler	1953	Gordon
$d\ e\ :+$	♀	Carneau	1956	Neuerburg
$d\ e\ :+$	?	Giant Homer	1956	McKenzie
$d\ e\ :+$	?	Modena	1957	Lindsay
$d\ e\ :+$	♀	Roller	1964	Smith
$d\ e\ :+$	?	Strasser	?	Saetveit
$d\ e\ :+$	♀	Fantail	1970	Isle
$St^F:d\ e$	♀	Giant Homer	1963	Clark
$St:d\ e$	?	Giant Homer	1964	Hasz
$+:d\ e$	?	Roller	1964	Pauli
$G:d\ e$	♂	Dragoon	1961	Neuerburg
$S\ G:d\ e$	♂	Trumpeter	1964	Wetzel
$S:C:d\ e$	♀	Giant Homer	1967	Clark
*$G\ e:b:+$	♀	French Mondain	1960	Dill
$G\ b:S$	?	Giant Homer	1964	Hasz
$e:d\ b$	♀	Tumbler cross	1967	Moore
$d:e$	♀	Tumbler	1962	Tidwell
$B^A:S:d\ B^A$	♂	Roller	1969	Gilbert
*$e:S$	♀	Roller	1969	Quinn
*$S:b:d\ e$	♂	Owl	1955	Tidwell
*$+:e:d\ e$	♀	Owl	1958	Tidwell
$B^A\ G:+$	?	Racing Homer	1961	Stovin
$B^A\ G:+$	♂	Racing Homer	1974	Mangile

FIGURE 2—Male mosaic of the Swing Pouter breed obtained in 1970 from John McCarroll. Plumage of almost the entire right half of the bird is defective; general coloration black, with patches of recessive red (*e*) on the back. The limb bones of the right side were found to be considerably shorter than those of the left. (Photo by Lyman Greiner.)

Case no. 6. ♀ African Owl, bred in 1957 by John S. Tidwell of Wichita, Kansas. Most of plumage wild type, with a recessive red (*e*) patch on the back of the head and a yellow patch on the back (*d e*). This mosaic was a daughter of the preceding case, no. 5. No other data available.

Case no. 7. ♀ Racing Homer, bred 1963 by Dal M. Stone, Santa Ana, Calif. Plumage mostly brown (*b*), with patches of ash-red (B^A) and also a couple of black feathers (+). Pedigree not detailed, but this mosaic had two mosaic close relatives.

Case no. 8. ♂ King-cross NPA 63 SC 2233 from Chester E. Johnson of Tucson, Arizona. Pied (wing primaries all white), with most of left side ash-red (B^A), T-pattern (C^T); right wing-shield wild-type color (+), checker pattern (C); tail mixed, left half ash-red with brown flecks (variegation) as expected in heterozygote ($B^A/ /b$). Pedigree uncertain. Progeny test only for color, showing transmission of all three sex-linked alleles (B^A, *b*, and +).

Case no. 9. ♀ Giant Homer NPA 68 GH 3776, bred by Harold Goodman of Chadron, Nebr., and obtained for me by Don Roscoe (Minn.) and E.M. Blaine. Right side mostly spread black (*S*), left mostly wild-type pattern; scattered patches of indigo (*In*) on both sides (see Figure 1*A*). Sire was spread indigo (*S In*), dam spread black (*S*). This mosaic was not progeny-tested but was fertile for a time.

Case no. 10. ♀ Giant Homer #84 bred 1969 by Gerhard Hasz of Indianapolis, Ind., and obtained for me by David Rinehart (Ohio). Plumage shows roughly equal areas of light, probably homozygous indigo (*In/ /In*) and wild-type (+) coloration. Also on the right side there are scattered areas of spread black (*S*) with characteristic longitudinal striping of some feathers (see cover). Sire was spread indigo (*S In*), dam dilute indigo (*d In*). This mosaic has not been progeny-tested, having laid few eggs. (Note added in proof: this bird has finally produced one progeny by a wild-type male; its plumage shows indigo and checker.)

Case no. 11. ♂ Racing Homer USA 74 PHP 0667, raised by Robert J. Mangile of Pittsburg, Kansas. Plumage mostly ash-red and grizzle (B^A *G*), with left wing-shield and other patches wild-type coloration (see figure 1*E*). Sire was ash-red grizzle (B^A *G*) and the dam dilute (*d*). Progeny test is in progress.

Discussion and Conclusions

Because of the haphazard source of the mosaic data, inconclusiveness is not surprising. Most of the cases were produced in flock pens that would encourage bipaternity. Probably the best support for the bipaternity hypothesis is the rather high frequency of complex cases, especially those involving sex-linked and autosomal mutants simultaneously. Double fertilization of a binucleate egg, however, could explain most cases equally well.

Chromosome loss could be invoked in some cases, but not with much cogency. Several mosaics showed structural as well as color contrasts (these and a number of other mosaics not readily classifiable are not included in the tables). One of these is illustrated in Figure 2; almost the entire right side has defective feather structure and shorter bones, similar to the mosaic of Figures 13 and 14 in the 1940 report of Hollander and Cole[10]. The present mosaic also had patches of recessive red coloration (*e*). Another example, a female Roller bred in 1960 by Joseph W. Quinn of Atwater, Ohio, was a patchwork of black and red, and the left side "from beak to tail" failed to molt for at least 2 years.

Spontaneous mosaics are just as informative as artificial graft examples such as those of Cock[5], Mintz[14], Brumbaugh[2], and Volpe[20] for some physiological questions. All the mutants involved have shown autonomy of expression; there has been no indication of hormonal effects. With the exception of the *S* and *C* loci, the genes seem to act in the melanocytes rather than in the integumental tissues. The erratic placement of patches probably depends on the migratory history of the melanoblasts[17,18], in contrast to the usual right-left arrangement seen in *S* mosaics. Histocompatibility seems to have been complete—no depigmentation effects have been noted, and the specimens often have lived in health for many years.

It is regrettable that, to date, no karyotype studies have been attempted with such mosaics. Especially with the "half-siders" it would be interesting to know if haploidy is or is not involved.

Questions of frequency (see incidence notes, above) are tantalizing also. Only a few mosaics have been reported during the same period in other species[1,4]. In chickens, the prevalence of white plumage may be an obscuring condition, in addition to reduced interest in noncommercial problems[3]. Experimental production of mosaic conditions has been limited to X-ray effects[19], and here the complication of natural mosaicism may be confusing.

The possibility of testing the bipaternity hypothesis by means of artificial insemination with mixed semen remains to be explored. With pigeons this is a very difficult procedure, but simple with domestic fowls.

Summary

The hypothesis of bipaternity—incorporation of tissue derived from supernumerary sperms into an embryo—to explain the origin of sectorial mosaicism in pigeons was advanced in 1949. Since then, 182 additional examples have come to my attention. Only one was reported to be a gynandromorph; sex ratios generally have been near 1 : 1. No environmental variable has shown significant relation to the origin of the mosaics, and only a slight familial tendency has been indicated. At least 15 color and pattern mutants have been involved, usually contrasting only two alleles. The frequency of each mutant corresponds roughly to its gene frequency and its use in crosses. Complex mosaics, involving two or more loci in the contrasts numbered at least 38 cases, of which 11 are examined in more detail, and 6 shown in photographs. Several instances of germinal as well as somatic mosaicism were demonstrated by progeny tests. The bipaternity hypothesis has not been ruled out by evidence in any case.

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