DARK-BLOND-WHITE: Sex-linked alternatives in Ringneck Doves

by
Wilmer J. Miller

Genetics of Ringneck Doves V.

The sex-linked nature of the dark, blond (fawn), and white colors in ringneck doves, Streptopelia risoria, was worked out by L. J. Cole. In 1930 (Aviculture 2:27-30 and Anat. Rec. 47:389) Cole demonstrated that blond was a sex-linked recessive to dark and that white is recessive to both. C. O. Whitman's data: Orthogenetic Evolution in Pigeons, Carnegie Inst. of Wash. Vol. 1, was published posthumously in 1919. But it was essentially completed before Mendelism was well analyzed and it also evinced the sex-related association. See, for example, p. 150, Table 138, of a cross of a white male risoria x S. humilis yielding 18 white daughters and 11 classified dark sons (+ 7 dark unsexed).

Sex-linkage is the major exception to genetic characters having equal reciprocal crosses. Such equality in reciprocal crosses was noted by pre-Mendelian researchers such as Kölreuter and Von Gärtner. That is, ordinarily a male of stock A crossed with a female of stock B gives the same results as a male of stock B crossed with a female of stock A. But with sex-linkage, reciprocal crosses are not equal.

Cole's analysis included the dark allele from species crosses such as Pearlneck or the Senegal Palm dove. The Dark color we have now is from an importation by J. W. Steinbeck near Walnut Grove, California in the early 1950's. Steinbeck imported 6 "red-eyed" doves from Holland. He sent them to the University of Wisconsin at Madison for sexing. I was the one who sexed them. They were all females, so I had no chance to hear the different voice they are reported to have, assuming that they are S. decaocto that were spreading through Europe at that time. I got "hybrids" of them with ringnecks before returning them. So presumably all our dark ringnecks are from that source. I still have not heard the "different voice". S. decaocto had no blood type or other differences noted in comparison with S. risoria other than the color. I probably missed noting the undertail coverts and dark outer web of the outer rectrices (tail) feathers that are described by P. William Smith in his recent paper "the Eurasian collared-dove arrives in the Americas", 1987 American Birds 41:1370-1379. I regard decaocto as conspecific with risoria or roseogrisia, the likely progenitor of risoria. Their hybrids are perfectly fertile with ringnecks (risoria).

I have extensive records verifying the sex linkage of dark, blond, and white and their allelic inheritance (alternatives at the same spot on the chromosome). No matter what other colors also may be involved, this relationship holds true,although it may be hidden by albino. For purposes of this report I have excluded the more recent data involving mixtures of other mutant colors to reduce confusion of actual phenotypes (their appearance) as dark,blond or white.

The remaining data is reduced in numbers, but still more than adequate to confirm earlier conclusions.

First let us diagram the reciprocal crosses.

purebred <u>stocks</u> $\qquad$ F_1 $\qquad$ symbol d is used for the dilution locus

blond ♂ d^B d^B → 1/2 blond ♂ d^B d^W (carries white)

white ♀ d^W ⇢ 1/2 blond ♀ d^B

reciprocal crosses are not equal

white ♂ d^W d^W → 1/2 blond ♂ sons d^B d^W (carries white)

blond ♀ d^B ⇢ 1/2 white ♀ daughters d^W

These colors are controlled by genes (alleles) on the sex chromosome (Z chromosome). The male has 2 Z's and the female has only one plus a "W" (W = no chromosome <u>or</u> else an inert pairing partner for the Z). This is the reverse of mammals and insects in which the sex chromosomes are called X and Y, and XX→♀; XY→♂.

The genes for these colors (dark-blond-white) are located on the Z chromosome. So males have any 2 of these three genes. The d^B d^B male is "pure" (= homozygous) for it. The males in the hybrid generation (F_1) having d^Bd^W are carriers (of white) and are heterozygous. But females have only one of these genes (nothing on the W), and are hemizygous. So females <u>show</u> whatever sex-linked color gene they get from their father. For completeness, one could tag the Z chromosome with the gene symbol as superscripts. This is done in the next figure for dark and blond instead of blond and white. However, these symbols get a bit too involved for most people.

purebred stocks		F_1	
Dark ♂ Z^{D^+} Z^{D^+}	→	1/2 Dark ♂ Z^{D^+} Z^{d^B}	(carries blond)
Blond ♀ Z^{d^B} W	⇢	1/2 Dark ♀ Z^{D} W	

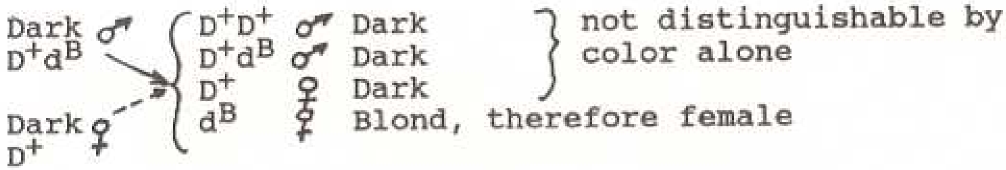
Blond ♂ Z^{d^B} Z^{d^B}	→	1/2 Dark ♂ Z^{D^+} Z^{d^B}	(carries blond)
Dark ♀ Z^{D^+} W	⇢	1/2 Blond ♀ Z^{d^B} W	

The reader or student now should try diagramming the reciprocal crosses of dark x white colors.

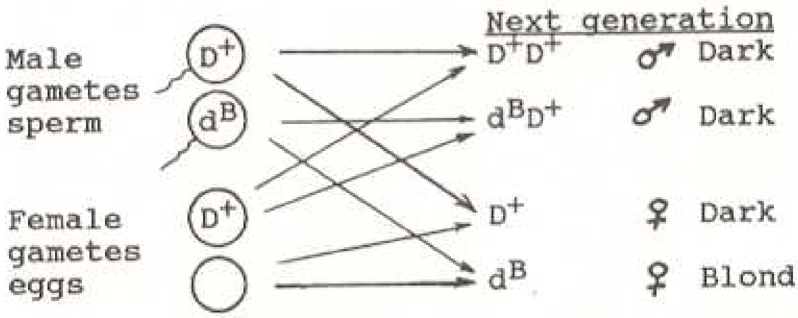
Table 5 includes reciprocal crosses for all possible genotypic combinations (15) at this locus. 164 matings totaled 853 progeny sexed. It was not practical to keep all birds for sexing, since the data was incidental to other research.

The first 4 matings are "sex-linked" in the sense that the color of the offspring implies their sex immediately at hatching, as well as by the later plumage color. White squabs have no bill ring, a very light skin and down color (near white) and unpigmented eyes which will progressively pigment, unlike albinos. Blond squabs have a dilute bill ring and a light pigmented skin color with a tannish down. Dark squabs have an "intense" (= normal amount of pigment) bill ring and skin color with a tan down. The adult plumage of whites is very, very slightly pigmented (extreme dilution). The pigment shows mainly in the ventral aspect (bottom side of the feathers of the basal (proximal) tail bar to about half way out on the major tail feathers. Whites have no bill ring as new hatchlings. Blond doves are "diluted" darks.

Some genotypic mating combinations can be called partially sex-linked, since half the female offspring are detectable at hatching. As an example let us diagram the first of the next 4 combinations.



How sex cells combine in this particular sex-linked mating.



The remaining 7 matings do not allow us to infer the sex by the color, since white colors occur in both sexes among the progeny.

The X^2 statistical test fits 13 of the 15 combinations. The low numbers yielding the X^2's of 14.73 and 8.22 are interpreted as chance deviation from inadequate sampling.

The bias in the "partially" sex-linked matings or remaining ones results from our being able to sex males earlier than females and discarding extra birds before all were sexed.

Any questions??? "Practice (tends) to make perfect".

Table 5. Results involving only the sex-linked Dark, blond and white colors in ringneck doves, S. risoria. Offspring sexed by behavior or by method of Miller and Wagner (1955, The Auk 72:279-285) at 6+ months of age.

Genotype of mating ♂ x ♀		Number of matings	Expected ratio	Color and sex of offspring Dark ♂	Dark ♀	Blond ♂	Blond ♀	White ♂	White ♀	Subtotal ♂	Subtotal ♀	Not sexed	Total sexed	df	X^2	P
d^Bd^W x D^+	S.L.	9	2:1:1	25	·	·	14	·	15	25	29	31	54	2	.33	.88
d^Wd^W x D^+	S.L.	2	1:1	8	·	·	·	·	1	8	1	14	9	1	–	
d^Bd^B x D^+	S.L.	8	1:1	20	·	·	·	·	28	20	28	23	48	1	1.33	.25
d^Wd^W x d^B	S.L.	11	1:1			25	·	·	14	25	14	22	39	1	3.10	.08
			S.T.	53		25	14		58	78	72	90	150			
D^+d^B x D^+	S.L.P.	14	2:1:1	34	18	·	11	·	·	34	29	53	63	2	1.95	.39
D^+d^W x D^+	S.L.P.	3	2:1:1	3	·	·	·	·	3	3	3	9	6	2	–	
D^+d^W x d^B	S.L.P.	6	1:1:1:1	4	7	12	·	·	3	16	10	14	26	3	7.74	.05
d^Bd^W x d^B	S.L.P.	12	2:1:1	·	·	40	28	·	19	40	47	51	87	2	2.42	.34
			S.T.	41	25	52	39		25	93	89	127	182			
D^+D^+ x D^+		7	1:1	15	15	·	·	·	·	15	15	31	30	1	0	" 1. "
D^+d^B x d^B		25	1:1:1:1	47	34	38	33	·	·	85	67	94	152	3	3.21	.36
D^+d^B x d^W		13	1:1:1:1	12	17	10	12	·	·	22	29	31	51	3	2.09**	.5
D^+d^W x d^W		8	1:1:1:1	16	4	·	·	6	3	22	7	46	29	3	14.73	.0025
d^Bd^B x d^B		22	1:1	·	·	73	63	·	·	73	63	91	136	1	.74**	.4
d^Bd^W x d^W		7	1:1:1:1	·	·	16	9	6	5	22	14	49	36	3	8.22	0.04
d^Wd^W x d^W		17	1:1	·	·	·	·	48	39	48	39	60	87	1	.94	.38
15 combinations		164		184	95	214	170	60	130	458	395	619	853			

S.L. actually the sex of the progeny is known from the color of these sex-linked matings.

S.L.P. sex-linked in part. A bias for males results from colony management.