SEXUAL DICHROMATISM IN TWO SPECIES OF THE COLUMBIDAE

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It is obvious that many birds exhibit sexual dimorphism of color. But the causal mechanisms resulting in sexual dichromatism have been well demonstrated for only a few species such as chickens and finches. Sex hormones control the plumage color and form in the brown leghorn (Greenwood and Blyth, 1938). Witschi (1935, 1937) and students have shown that within the weaver finches, three kinds of control are involved: sex hormones, gonadotrophic hormones, and genetic constitution.

The auto-sexing varieties of chickens and geese (Hutt, 1949; Quinn, 1939) and of domestic pigeons reveal sex dichromatism by the time of hatching and in the first plumage. Auto-sexing refers to a genetic method of detecting sex in birds and requires a sex-linked gene with dosage effects easily detected early in the birds' development. A wild species exhibiting auto-sexing is the Snow Bunting, *Plectrophenax nivalis* (Pitelka, personal communication). Auto-sexing is difficult to explain by known hormonal mechanisms, and relatively direct gene control of such sexual dichromatism is indicated (Hollander, 1942).

Among the approximately 14 species of doves in the genus *Streptopelia* only one, the Dwarf Turtle Dove (*Streptopelia tranquebarica*), exhibits marked sexual dichromatism. This dove is native to the Philippines, southeastern Asia, and India. Immature and female *tranquebarica* are "gray." The mature male has a bluish head, with the color extending to the neck ring, and a reddish brown "back."

Several auto-sexing pigeons and *tranquebarica* were available from a pigeon colony housed in a barn by the Department of Genetics at the University of Wisconsin, Madison, Wisconsin, and since they seemed to represent opposite extremes of early and late dichromatism within the Columbidae the following experiments with hormones were conducted.

The data on the domestic pigeon or Rock Dove (*Columba livia*) were collected in connection with another study (Miller and Wagner, 1955) in which the hormones were donated by Dr. W. H. McShan and the implants and some of the injections were made by Frederic H. Wagner.

MATERIALS AND METHODS

The sex of the mature Dwarf Turtle Doves was ascertained by their color. This diagnosis agreed with the method of sexing described by Miller and Wagner (1955) and Hanson (1953). Female doves were injected with testosterone propionate, the males with estradiol benzoate, and the controls were injected with sesame oil (the diluent for the hormones) according to the following plan:

Dove	Sex	Daily injection intramuscularly
D801.136	Male	0.1 ml. sesame oil
D801.134	Female	0.1 ml. sesame oil
D801.112	Male	0.1 ml. estradiol benzoate (0.166 mg.)
D801.140	Female	0.02 ml. testosterone propionate (0.1 mg.)
D801.171	Female	0.08 ml. testosterone propionate (0.4 mg.)

On the third day after injections were begun, some feathers were plucked from the right half of the bird's head and from the right wing. The wing feathers plucked were lesser secondary and marginal coverts. Eleven days after plucking, the last injections

were given to the controls and to D801.171 since the regenerating feathers were already showing their color. D801.112 and D801.140 received their last injections 20 days and 28 days after plucking, respectively, since their feather regeneration was slower. D801.171 died 18 days after plucking, but most of the regenerating feathers were about two-thirds regrown and were saved. The head feathers of D801.112 were extremely delayed in regeneration and very probably had no effect of the injected hormone since the injections had been stopped at least 30 days previously.

The feathers grown before and after treatment were compared and colors checked with Ridgway's "Color Standards and Color Nomenclature."

Auto-sexing strains of the domestic pigeon have been made utilizing the mutant "faded," St^F, which has been described by Hollander (1942). The faded gene is sex-linked and causes sparse down and absence of pigment on the bills of homozygous males just hatched but permits nearly normal down and pigment on the bills of hemizygous females. The first feathers of the homozygous faded male squabs are white with rare flecks of color, usually black but often reddish in color. The first plumage of a homozygous faded male does not differ in color from later plumages except that the flecks may become more numerous and larger. The hemizygous faded female has nearly normal-colored plumage but has a "washed out" appearance.

Five-week-old, opposite-sexed siblings from a pure line of faded pigeons received intramuscular injections daily of the opposite sex hormone—0.25 ml. of testosterone propionate was given the female (equivalent to 12.5 mg. per injection and equal on a weight basis to 0.04 ml. or 0.2 mg. if given to a Dwarf Turtle Dove), and 0.5 ml. of estradiol benzoate (0.83 mg.) was given the male.

Some tail feathers, secondaries from the right wing, and feathers from the back were plucked from each bird at the first injection of hormone, and these of course were saved for comparison with the regenerated feathers. Injections continued for 18 days until the regenerating feathers were nearly fully regrown.

Two additional males six weeks of age were implanted with diethylstilbesterol pellets; they were similarly plucked and the feathers compared.

RESULTS

Several birds other than those listed were given different doses of the hormones at the beginning of the experiment. These birds died in a Newcastle epidemic before results could be obtained (see Hanson and Sinha, 1952, and Miller and Wagner, 1955).

The faded female of *Columba livia* injected with testosterone propionate developed typical male cloacal papillae during the first week of injections, that is, at six weeks of age (Miller and Wagner, 1955). Papillae are not ordinarily distinguishable until males are four to six months old. No color change was observed in any of the regenerated feathers of the injected or pellet-implanted pigeons when these were compared to the original plucked feathers. There was a slight increase of black flecks in the males' feathers but this is normal for such males.

All Dwarf Turtle Doves receiving the "reverse" sex hormone showed intermediate color and pattern of feathers tending to be much more like the opposite sex. As Salomonsen (1940) has indicated, the influence of hormones on feather color and pattern is not "all or none" but often may be intermediate. New feathers of the control birds D801.134 and D801.136 were one grade darker than the previous old feathers, except for the male wing color which showed little difference. This kind of change had been noticed for new feathers of this and other species of doves, probably resulting from sun fading or weathering of the older feathers.

Comparisons of the feather color of the Dwarf Turtle Doves are given in table 1.

Table 1

Results of Reversing Sex Hormone on *Streptopelia tranquebarica*

Specimen number and sex	Standardization of untreated feathers	Standardization of regrown feathers
D801.134 ♀ control	Wing: army brown edges deepening gradually to deep mouse gray in the proximal half of the feather	natal brown (next grade to army brown) deepening to deep mouse gray
	Head: deep mouse gray	dark mouse gray lightening to deep mouse gray
D801.136 ♂ control	Wing: Hay's brown changing abruptly to deep mouse gray in the proximal half of feather	Hay's brown changing abruptly to deep mouse gray (no change)
	Head: dark gull gray	slate gray (next darker grade to dark gull gray)
D801.112 ♂ 0.1 cc. estradiol	Wing: colors same as in D801.136	Hay's brown *edges* only, grading* to deep mouse gray
	Head: colors same as in D801.136	(delayed regeneration of feathers) no change, dark gull gray
D801.140 ♀ 0.02 cc. testosterone	Wing: army brown edges but larger than in D801.134	very large area of the edges Hay's brown with an *abrupt change* to deep mouse gray in the proximal part of the feather
	Head: color same as in D801.134	*dark gull gray*
D801.171 ♀ 0.08 cc. testosterone	Wing: colors same as in D801.134	feathers "two-thirds" regrown; *Hay's brown* slightly "peppered" with and deepening to deep mouse gray
	Head: colors same as in D801.134	no feathers; bird died

* Italics indicate hormonal influence.

Standardization was made twice under fluorescent and "ordinary" bulb lighting using Ridgway's "Color Standards and Color Nomenclature."

DISCUSSION

In spite of the loss of some birds before results could be obtained, it has been demonstrated that sexual dichromatism in *Streptopelia tranquebarica* is under the immediate control of the sex hormones. In the auto-sexing *Columba livia,* "direct" gene action without sex hormonal influence is indicated as the cause of sexual dichromatism.

It has been shown that sex hormones control the plumage form and color in brown leghorns (see Juhn, Faulkner and Gustavson, 1931; Domm, Gustavson and Juhn, 1932; and Greenwood and Blyth, 1938). Sex hormones alone do not explain sexual dichromatism in all birds even for those which show marked hormone influence (Danforth, 1937). Half-and-half or sectorial mosaics, male on one side and female on the other, with regard to color are known (Hollander, 1944), and species showing seasonal plumage changes complicate the problem. Witschi (1935) and students have explained some of the complications in their work on weaver finches, in which a complex interaction of sex hormone, gonadotrophic hormone, and genetic constitution is shown. Also see Miller (1935) for some effects of thyroxin.

Much work remains to be done to clarify the mechanisms of sexual dichromatism. For example, what is the genetic basis for the differences of *S. tranquebarica* from other species of *Streptopelia* that enable it to exhibit sex hormonal control of its sexual dichromatism? Certainly the genetic interactions with the environment both internal (especially hormones) and external can be complex.

SUMMARY

Sexual dichromatism in two species of the Columbidae exemplify the two extreme types of control: "direct" genetic control, and sex hormonal control.

Reversal of the predominant sex hormone by injection of testosterone propionate or estradiol benzoate in mature individuals of the Dwarf Turtle Dove (*Streptopelia tranquebarica*) resulted in a corresponding change in the feather color in the head and wing which in this species shows sexual dichromatism. Control *tranquebarica,* male and female, injected with sesame oil, showed no change.

Reversal of the predominant sex hormone in the auto-sexing domestic pigeon (*Columba livia*) had no effect on the plumage color.

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