

in August, was a bird captured in the Bay of Panamá off Balboa, some 8 degrees north of the equator in 1937 (Murphy, 1938).

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The genetic basis of color differences observed in the Mute Swan (*Cygnus olor*)¹.—The downy young of the Mute Swan appear in either of two color phases, a white or gray. The white phase was first reported in 1868 among the swans on Lake Geneva, Switzerland (Hilprecht, *Hocherschwan, Singschwan, Zwergschwan*, Wittenburg Lutherstadt, Die Neue Brehm-Bucherie, 1956); it is usually less common than the gray phase, but becomes more frequent as one moves eastward across Europe, and it is sometimes referred to as the Polish variety. Cygnets with gray down have slate-gray bills and feet; the white phase birds have tan colored bills and feet. The foot color of each phase persists in the otherwise identical white-plumaged adults, and may be used to determine its down color phase. This study was undertaken to determine the genetic basis of the color phase.

Methods and materials.—In 1963 the State Division of Conservation initiated a banding program to determine the status of the Mute Swan in Rhode Island. Nesting sites were watched and location and down color were recorded by the senior author.

In the 1967 hatching season 53 nesting sites were kept under observation. Cygnet data were obtained from only 36 nests; 11 were lost by flooding during adverse weather and 6 were destroyed by predation.

Color phase was observed as soon as possible after hatching to reduce any effect of possible differential mortality. Unhatched eggs were broken and color phase determined on embryos far enough advanced to exhibit down color.

Adult color phase was determined for all nesting pairs, and additional adult data were obtained from previous banding records.

Results and discussion.—The 1967 nesting color phase data summarized in Table 1 indicates that color difference is determined by a single gene and that the gray allele is dominant to white.

Examination of sex data indicated a preponderance of white females. As birds follow an XO method of sex determination, the male being homogametic XX or hav-

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TABLE 1
1967 MATING DATA

Type of mating	No. of adults		No. of cygnets		Total individuals
	Gray	White	Gray	White	
Gray × gray	58	0	145	2	205
Gray × white	5	5	18	12	40
White × white	0	4	0	12	16

ing two sex chromosomes, and the female heterogametic XO or having one sex chromosome, a sex-linked recessive would result in a greater number of visible recessives in females.

Banding data from previous years included 488 swans whose sex and color phase had been recorded. Of the 288 males, 29 or 10 per cent were white phase; of the 200 females, 51 or 26 per cent were white phase.

If in a random mating population we let the frequency of the dominant allele (A) of an autosomal gene be p and the frequency of the recessive allele (a) be q , then the frequency of the three genotypes are:

$$p^2 AA, 2 pq Aa \text{ and } q^2 aa$$

If a gene is sex-linked, the frequency of the genotypes within sexes will differ. In the case of the male, which is homogametic (XX) the ratio of the recessive genotypes to the total number of individuals represents q^2 , just as if the gene were autosomal. In the case of the female, which is heterogametic (XO), there can be no heterozygotes (Aa) and the possible genotypic frequencies are $p AO$ and $q aO$ and the ratio of recessives to the total number of individuals represents q .

If the gene is sex-linked, the estimated value of q based on females is $q_f = \frac{51}{200} = .255$. An estimate based on males and the assumption of random mating is $q_m = \sqrt{\frac{29}{288}} = .316$. The estimates q_f and q_m do not differ by a statistically significant amount and matings can be assumed to be at random. The estimated value of q for the population then can be a weighted estimate of $q_{f+m} = .293$.

Further evidence of sex-linkage was obtained by examining families that would yield a sex-linked result, i.e. recessive (white) male × dominant (gray) female or the male contributing the sex chromosome carrying the recessive allele to his daughters. Only two such families appeared in the 1967 matings; these yielded 9 males and 7 females. All male cygnets were gray and all females (XO) were white, obtaining their sex chromosome from their recessive (white) sire. This clearly indicates the color phases to be sex linked.

Summary.—Examination of banding data and parents and progeny at nesting sites of the feral population of Mute Swans in Rhode Island indicated that the gray and white color phase segregating in the population was due to a single sex-linked gene. The gray was dominant to white and the gene frequency of the recessive allele (white) was estimated to be .293.

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