Recognizable Forms

Ecological Significance of the White and Grey Colour Morphs of the Mute Swan

by
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Introduction
The Mute Swan (Cygnus olor) is one of seven species of swans in the order Anseriformes. In Eurasia, it occurs from the British Isles, southern Scandinavia and Russia, southeast through central Europe to Asia Minor and east to Siberia and Ussuriland (A.O.U. 1983). It was introduced to North America as an ornamental species in the early 1900’s (Palmer 1976; Belrose 1976; Campbell et al. 1990) and has established feral populations throughout parts of Canada and the United States.

Yarrell (1838) suggested that the Mute Swan was actually two species of morphologically distinct birds. He separated these two species by the leg colour of individuals and by the down and juvenal plumage colour of cygnets. Those swans which had black legs, were covered in grey-brown down, and had a grey-brown juvenal plumage, he named C. olor. Pink-legged individuals which were covered in pure white down as cygnets and had a white juvenal plumage he named C. immutabilis (in reference to their unchanging plumage colour). We now know that the species described by Yarrell are simply two readily identifiable colour morphs of the Mute Swan (C. olor).

This note describes morphological differences between the grey and white colour morphs of the Mute Swan, explains how the expression of the colour morph trait is genetically controlled and examines the potential ecological impact Mute Swans may have on native populations of waterfowl and on native North American habitat.

Plumage, Moult and Morphology
The two colour morphs of the Mute Swan are easily distinguished from each other at any age by leg colour and are named to reflect the down and juvenal plumage colour of the cygnets. Illustrations of adults and juveniles of both white and grey morphs are contained in Cramp (1977: 374).

Grey-morph cygnets are covered in grey-brown down with white underparts. Legs are slate-grey or black and bill colour can range from grey to purplish. Sometime after the seventh week posthatching, the down is completely replaced by the first juvenal plumage. At this time, juveniles are mostly grey in colour; the grey-brown streaking is concentrated on the head, neck and dorsum, but nowhere on the plumage are there any large areas of white (Palmer 1976).
Mute Swans undergo one complete annual moult somewhere between July and August. Cygnets, however, begin to moult from their juvenile plumage into their first basic plumage approximately 4.5 months after hatching (Palmer 1976). This first moult proceeds gradually, over the winter (Birkhead and Perrins 1986). It is not complete and some juvenile flight feathers are retained. Although individuals may acquire large patches of white on the freshly moulted primaries, from their first winter until early the next summer the first basic plumage remains largely streaked with greys and browns (Palmer 1976; Birkhead and Perrins 1986). By the end of their second summer, grey morphs will have moulted into their second basic plumage. Upon completion of the second annual moult, grey morphs assume the white plumage of an adult.

It may be possible to distinguish these second year grey morphs from reproductively mature adults by bill colour and by the size of the knob at the base of the bill. The bills of second year birds are light orange in colour and have not yet attained the bright reddish-orange of breeding adults (Cramp 1977; Belrose 1976; Birkhead and Perrins 1986). However, Palmer (1976) noted that bill colour varies a great deal between Mutes of the same age, hence bill colour cannot be reliably used to indicate age. Reproductively mature males generally have larger knobs at the base of their bills than adult females or immatures. Although the knob begins to enlarge in second year birds, it may not approach the knob size of a breeding adult until the third year (Belrose 1976). Therefore, adult knob size also varies with time of year (Palmer 1976). Because knob size and bill colour can only be used to indicate the age or sex of birds beyond their second basic plumage, and because the appearance of soft parts of second year birds may not stabilize until their third or fourth year when individuals begin to form pair bonds and reproduce, the third basic plumage is considered to be the definitive basic (adult) plumage (Palmer 1976).

White-morph cygnets are easily distinguished from grey individuals by their pure white down and pink, flesh-coloured legs (Munro et al. 1968; Palmer 1976; Cramp 1977; Birkhead and Perrins 1986; Dierschke 1988). From the time juveniles moult into their first basic plumage, they are entirely white and will retain this plumage colour throughout the normal succession of moults (Palmer 1976; Birkhead and Perrins 1986). From the time white Mutes are fully grown as juveniles, they cannot be distinguished from a reproductively mature white-morph adult, save for possible differences in bill colour and knob size.

**Morph Genetics**

The sex, appearance and function of all living organisms are controlled in part by the genetic material present in the body’s cells. This genetic material is organized into chromosomes; each chromosome is subdivided into units called genes. Either a single gene or a group of genes is responsible for the expression of one trait. Alleles are alternative forms of a gene and are chemically different from one another. For example, if there is one
gene on a chromosome that determines eye colour, one allele may result in blue eyes while another chemically different allele may result in brown eyes.

In higher animals, chromosomes occur in pairs. An organism receives one of each pair from the mother's egg and the other from the father's sperm. Each chromosome consists of many thousands of genes; those genes responsible for the expression of various traits are sequentially located at the same relative positions on each chromosome of a pair. If alleles are chemically identical, then the individual is homozygous for that trait. If alleles are chemically different, that individual is heterozygous. In heterozygous individuals, if one allele is dominant to the other, that allele will be expressed and will mask the effects of the recessive allele located on the opposite chromosome. Homozygous individuals will express either the recessive form or the dominant form of the gene, depending on which alleles are present on their pair of chromosomes.

The sex chromosomes are generally the exception to the rule described above. Organisms still receive a pair of sex chromosomes (one from the mother and one from the father), but there are two different types and each controls the expression of different traits from the other. The expression of any genetic information present on these sex chromosomes will be influenced by the sex of the individual and are therefore said to be sex-linked.

In birds, the different sex chromosomes are designated as X and O. The X-chromosome controls sex-related and other traits, while the O-chromosome is mainly responsible for female sex determination. In order to be female, therefore, a bird must receive an O-chromosome from its mother's egg. Females receive their second sex chromosome (X) from their father's sperm and are thus symbolically represented as XO. Males, on the other hand, are represented as XX because they receive one copy of the X-chromosome from their mother and another copy from their father.

If the genetic material for a particular trait is located on the X-chromosome, males will have two copies of the gene(s) responsible for the trait's expression. Heterozygous males will express the dominant form of the gene present on one of their X-chromosomes, and will "carry" the recessive allele present on the opposite X-chromosome. Either X-chromosome can be passed on to an offspring with equal probability.

Females, because they have only one copy of the X-chromosome, will only have one copy of the gene(s) responsible for the expression of a particular trait. This is the allele which will be expressed, regardless of whether it is the dominant or recessive allele. Because females must receive their O-chromosome from their mother, the expression of a sex-linked trait depends on which allele (on the X-chromosome) a female receives from her father. (For a more detailed explanation of the genetics involved here see Hartl 1988: 37-38).

In conjunction with a banding program initiated to determine the status of the Mute Swan in Rhode Island, Munro et al. (1968) undertook a study to determine the genetic mechanism which controls the
Figure 1: A punnet square illustrating the way the grey (X) and white (x) alleles can be passed on to offspring in the Mute Swan (Cygnus olor). The grey male "carries" the white allele and can pass either the grey or white allele on to his male (XX) or female (XO) cygnets. The white female must pass her O-chromosome on to her female cygnets. The white allele on her X-chromosome is passed on to her male cygnets. In a mating between a grey, carrier male and a white female, half of both the male and female cygnets will be grey and half will be white.

expression of colour morph in Mute Swans. Results from the study showed that colour morph is determined by a single gene, where the grey allele is dominant to the white allele. Furthermore, the gene for colour morph was found to be sex-linked and located on the X-chromosome. Figure 1 illustrates the method by which males (XX) and females (XO) pass the white allele on to their offspring.

That the white allele is sex-linked recessive, means that, overall, there should be more white females than males and a much greater proportion of grey birds than white birds in a given population. In a randomly mating population with equal numbers of white, carrier and grey adults, 1/4 of all male offspring would be grey, 1/2 would carry, but not express the white allele and 1/4 of all males would be white. Half of all female offspring would be grey and half would be white. However, the frequency with which white-morph cygnets are produced will depend on the frequency of the white allele (and therefore on the proportion of grey, carrier and white adults) in natural populations.

Morph Range, Distribution and Status
Within their native European range (see Cramp 1977), white- and grey-morph Mute Swans occur together and interbreed. However, the frequency of white morph Mute Swans in the population is distributed along a geographical cline. White morphs occur with a greater frequency as one proceeds eastward from Britain across the European continent. In Britain white individuals are relatively rare and occur at a rate of about 1% in the general population, whereas in the Netherlands, Poland and Russia, white Mute Swans can comprise up to 18 to 20% of a population (Bacon 1980; Dierschke 1988). Indeed, the name "Polish" swan was used by London poulterers to refer to the white morph, because the groups of birds imported from the Baltic frequently contained white individuals (Bacon 1980; Birkhead and Perrins 1986).

Aside from occasional description and mention in European literature, (e.g. Bacon 1980; Birkhead and Perrins 1986; Dierschke 1988), there has been little study of the white
morph itself. Perhaps this is due to its low frequency of occurrence in British populations where most long-term research projects have been conducted (e.g. Reynolds 1972; Coleman and Minton 1979, 1980; Bacon 1980; Perrins and Ogilvie 1981; Birkhead and Perrins 1986; Sears 1988, 1989).

Introductions of the Mute Swan to North America are known from 1889 in Victoria, British Columbia (Warren 1970 in Campbell et al. 1990) and from a museum specimen from Boston Market, 1875 (Griscom and Snyder 1955 in Palmer 1976); however, historical data are poor. Phillips (1928 in Palmer 1976) documented two major importations of 216 and 328 Mute Swans in 1910 and 1912, respectively. Belrose (1976) states that one pair, imported in 1919, gave rise to the Michigan population which numbered approximately 1500 individuals in 1987 (Lumsden 1987).

Since its introduction to North America very early in this century, unpinioned cygnets and breeding adults have escaped captivity to establish feral breeding populations (Palmer 1976; Belrose 1976; Birkhead and Perrins 1986; Campbell et al. 1990). The first feral breeding in North America was reported in 1910 from the Hudson River (Allin 1987 in Lumsden 1987). Localized populations are now distributed throughout North America from southern British Columbia and Saskatchewan to northern Wisconsin, central Michigan, southern Ontario, New York and Connecticut, south to central Missouri, Illinois and Indiana, and Virginia in the Atlantic region (A.O.U. 1983). The densest populations are known from Michigan and along the eastern seaboard from Delaware to Massachusetts (Root 1988).

Populations on Vancouver Island and in Regina, Saskatchewan are known from at least 1967 and 1963, respectively (Root 1988). Although breeding Mutes had likely been present for some time in Ontario, Peck (1966) first documented feral breeding Mute Swans in 1958 at Georgetown, Halton County.

Munro's et al. (1968) found that 13% of the Rhode Island population is white. Birkhead and Perrins (1986) state that some 15% of all North American Mute Swans are white and suggest that North American Mute Swans were imported from eastern European rather than from British populations. In the Long Point population, however, the frequency of white morphs ranges from 76 to 87% (Knapton and Enright 1993). Because there are no other data, the range, distribution and status of the white morph in North America are virtually unknown!

Population Status in North America

Numbers of feral breeding and wintering Mutes in North America are increasing. Belrose (1976) estimated the Michigan population's annual rate of increase to be 18% and Davies (1981) recorded an annual increase of 12% in the Vancouver Island population. Wood and Gelston (in Belrose 1976) measured the annual mortality of the Michigan population to be 15%; it is unclear whether Belrose's increase estimate of 18% takes the annual mortality rate into account. Mortality rate in the Vancouver population of Mutes has not been reported (see Campbell et al. 1990).
The Ontario Mute Swan population appears to be increasing as well. Feral populations have established themselves on the shores of Lake Ontario between Bowmanville and Hamilton (25 nesting pairs in 1985; Lumsden 1987) and on the shores of the Inner Bay, Lake Erie at Long Point, Ontario (McCracken et al. 1981; Knapton 1993). While Lumsden (1987) states that there were 120 feral birds in the province around 1985, he also mentions that over 600 Mute Swans were kept in captivity under permit from the Canadian Wildlife Service. On the 1992 Christmas Bird Count, there were 227 Mute Swans found in Ontario alone (American Birds 1993). The Long Point population, established in the early 1970’s has increased from one breeding pair along the Causeway at Long Point (McCracken et al. 1981) to an estimated population of 148 individuals in 1991 (9 nesting pairs), 172 in 1992 (22 nesting pairs) and 105 in 1993 (14 nesting pairs) (Knapton 1993; Knapton and Enright 1993).

Bacon (1980) suggested that the Polish morph is naturally selected for in expanding, low density populations. The reasoning behind his hypothesis is as follows. Mute Swans are monogamous and pair for life, generally with birds of the same age. Few breed in their second year, although some may begin to form pair bonds, defend a territory and build a nest (Palmer 1976; Cramp 1977; Birkhead and Perrins 1986). Third and fourth year birds breed more frequently. Although clutch size is not correlated with age, it is positively correlated with season (Perrins and Reynolds 1967). Clutches laid earlier on in the breeding season contain significantly more eggs and because females breeding for the first time tend to lay their clutch later on in the breeding season, they tend to lay smaller clutches.

Now white females will appear to be reproductively mature adults by the autumn of their first year. If first or second year white females are able to pair bond with older, reproductively experienced males who can defend a territory from intruders, then they can begin breeding in their second or third year, earlier than grey females. In effect, white-morph females get a one year head start over grey females. They therefore are expected to have a higher reproductive success over their lifetime.

Despite the poorly documented status and distribution of the white morph in North America, the continuing increase in Mute Swan numbers both across the continent and in Ontario, together with the relatively high estimate of white swans made by Munro et al. (1968), Knapton and Enright (1993), and Birkhead and Perrins (1986), lend support to this hypothesis.

Ecological Significance
In light of the increasing Mute Swan population in North America, many birders, ornithologists and conservationists are concerned that this introduced species could have adverse effects on native species of waterfowl and on native habitat. No studies have yet focused on the issue, and only anecdotal data are available (see Tiner 1993).
Mute Swans defending their territory will show aggression toward humans and other waterfowl (Palmer 1976); male swans have attacked ducks and their broods coming too close to the nest site, possibly to reduce the occurrence of disease in the area (Birkhead and Perrins 1986). Stone and Marsters (1970) actually documented, in some detail, fatal attacks on Canada Geese (Branta canadensis), Bean Geese (Anser fabalis), Snow Geese (Chen caerulescens), Mallards (Anas platyrhynchos) and Black Ducks (Anas rubripes). These attacks took place in a zoo pond of approximately one half hectare, which also held about 110 captive ducks and 20 geese. Feral Mute Swans may nest on small ponds and lakes or in confined areas of a marsh and may thus have similar effects on native species in the wild.

In southern Ontario, Mute Swans probably compete directly with other marsh or shore nesting species such as Pied-billed Grebe (Podilymbus podiceps), Mallard and Canada Goose, not only for breeding territories, but for food as well. Competition is expected to be especially pronounced in those areas with little or diminishing habitat. Moulting adults uproot aquatic macrophytes and consume only the tubers; they require up to 4 kg of wet vegetation per day (Cramp 1977). Unknown quantities of food are needed to supply growing cygnets. Aside from using food resources which would otherwise be used by native species and their broods, Mute Swans disturb much of the vegetation in a marsh or along a shore. Often a sharp line, devoid of vegetation, is left along many shoreline and marsh edges of cattails and reeds (pers. obs.).

Dierschke (1988) states that Mute Swans breeding in the Baltic Sea show no interspecific aggression to other waterfowl or gulls and have little effect on the native vegetation or general habitat. References therein do document Mute Swan aggression toward native European waterfowl; however, additional references cited within the text state that these reports of aggression were exaggerated and over-simplified.

Conclusions
Any study and documentation will further our knowledge of the effects of the Mute Swan on native species and of the distribution and occurrence of the white morph in North American populations.

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