THE MOULTING GROUND'S RELATION TO BREEDING AND WINTERING AREAS AS REVEALED BY NECK-BANDED *CYGNUS OLOR*

S MATHIASSON

Introduction

There are three important biological and geographical elements in the annual life cycle of *Cygnus olor:* the reproduction and the breeding area; the moult and the moulting ground; and the winter quarters. They are connected by migration and resting grounds.

Before the 1930s *C. olor* was unknown as a breeding bird along the Swedish west coast. The swans had traditional haunts in eastern Sweden, where they have been known since the 17th century (Fig 1). These ancestral Swedish swans passed western Sweden on their migration to winter quarters along the coasts of southern Sweden and Denmark, as their descendants still do (Mathiasson 1973a). Gradually

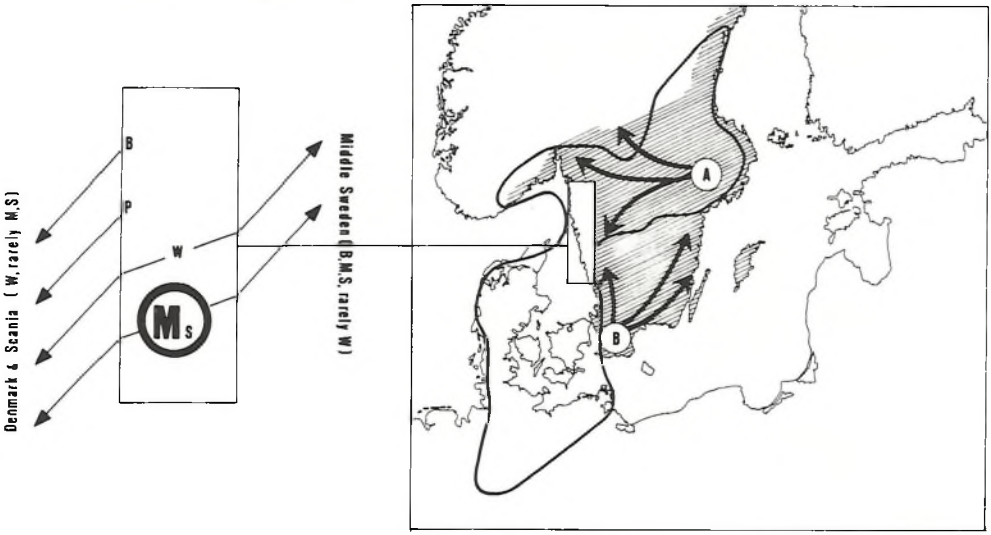

Fig 1. The present breeding distribution of *C. olor* in Sweden and Norway (hatched area), the preceding geographical extension of the former bicentric breeding populations (A and B) and the living space (all the year round) of swans occurring on the Swedish west coast (broad solid line).

The schematic illustration shows the migratory behaviour of different categories of west coast swans. Breeding birds (B) and their cygnets (P) occur only in the west coast area (rectangle) or migrate towards the southwest to winter. West coast winter swans (W) may use the whole living space, as do the moulting non-breeders of the summer (M_S).

they extended their breeding range to westernmost Sweden. The coast nowadays harbours no less than 83% of the population of about 300 pairs breeding in the Swedish west coast counties (total area 10 000 km^2). The coastal breeders have become more or less resident. The inland swans are still migratory and contribute non-breeders to the western Swedish moulting grounds and summer haunts.

More than 2500 moulting *C. olor* have been ringed in the 1960s and 1970s.

The moulting ground and the moulting flock

The moulting ground of Kungsbackafjorden (Mathiasson 1973a, 1973b) provides food and shelter. The total water area is about 53 km^2, of which 13 km^2 is of a depth less than 2 m. The vegetation of the latter area is accessible to the swans, in its deeper parts only during low water (Fig 1). It has been calculated that during their stay the moulting flock of about 1000 swans eat about 425 tonnes of seaweed, mainly *Zostera marina* but to a smaller extent also *Ulva lactuca.* This means that not more than 8% of the total production of *Z. marina* is consumed by that number of swans (Mathiasson 1973b and Borjesson 1974). The length of stay of the swans depends mainly on intrinsic factors connected with the moult. Fig 2 shows the regularity in annual fluctuation of numbers of swans at Kungsbackafjorden.

Counts throughout the year, biometrical data and movements of marked birds present general information on the migratory behaviour of *C. olor* in the Swedish west coast area as well as special information on the 'demographic' structure of the moulting flock and the behaviour of its members.

Fig 3 illustrates the structure of the moulting flock and the dynamic involved in the annual change of numbers. As can be seen from the graph to the left there has been a decline in the number of moulting swans during the decade of studies. The same graph shows the proportion of one-year old swans (hatched in the previous year). It is clear that the number of young produced in the preceding year (average 20%) strongly affects the total number of moulting swans present. There is also a clear decline of the proportion of one-year old birds, from 30% in 1972 to 6% in 1979. The very low figure of 1971 reflects lowered reproduction in 1970 due to the effect of the severe winter of 1969/70. The decreasing number of swans is also brought about by increased death rates (Fig 3: categories 6 and 4).

Shift of moulting ground has also had a strong influence. In the early 1960s up to 1800 moulting swans were present at Kungsbackafjorden and no other grounds were found along the Swedish west coast. Today there are six additional moulting grounds, established in the 1960s, which in 1978 held about 2500 moulting swans, compared with 625 at Kungsbackafjorden. Today such shifts seem to play a minor role. The numbers coming or going balance one another.

We find three clearly definable categories in the moulting flock. The 'floating'

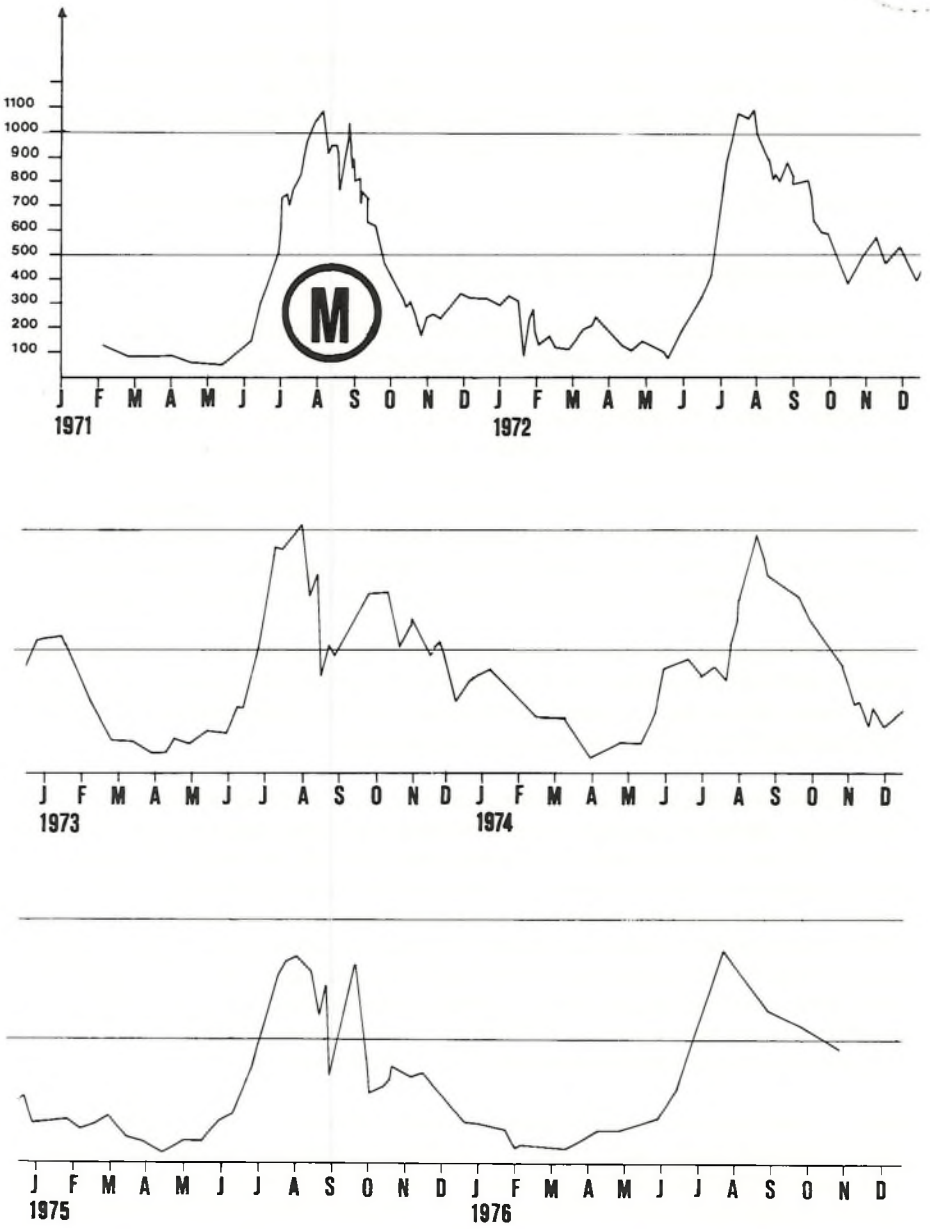

Fig 2. Annual fluctuations of *C. olor* at the Kungsbackafjorden moulting ground.

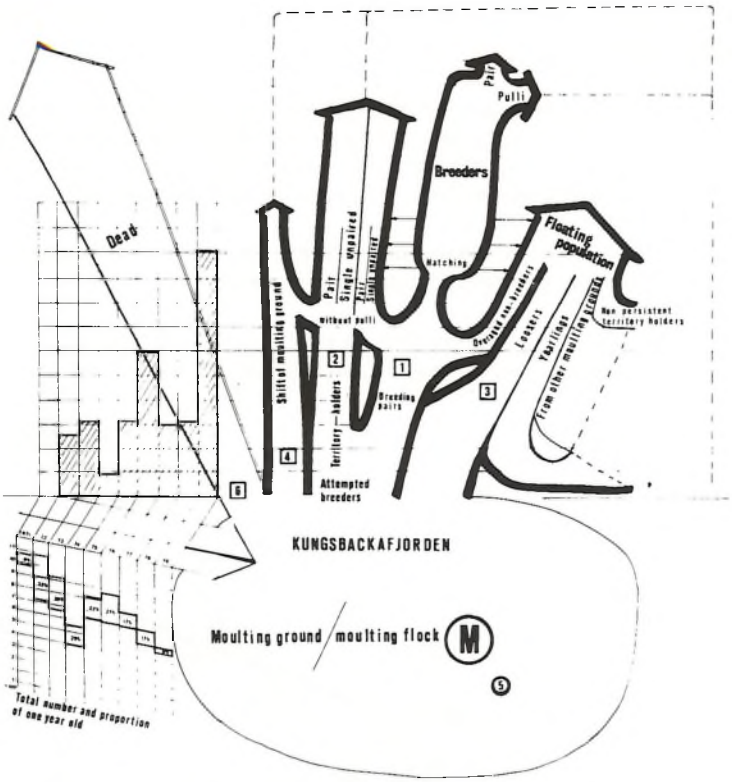

Fig 3. Illustration of the structure of the moulting flock at numerical peak (category 2) and the dynamic involved in the annual dispersal over the living space (category 1) and the rebuilding of the moulting flock.

The percentage of one-year-old swans in different years is presented to the left. The percentage of swans reported dead is also shown.

population which circulates between moulting ground, resting grounds and winter quarters (Fig 3: 3) and is built up mainly of yearlings, subadult non-breeders (but presumptive breeders), non-persistent territory-holders, over-aged breeders, swans which shift from other moulting grounds, and a large number of 'loosers', which never or very rarely attempt to breed, in spite of having reached the age of sexual maturity. The attempted breeders may take up a territory and stay there even during the moult and thus break the annual circulation characteristic of the first category (Fig 3: 2). The breeders, having reached sexual maturity, become successful territory-holders and stay at the breeding ground to moult (Fig 3:1). If the eggs are destroyed or the cygnets lost, they may, however, return for that particular season to their former moulting ground.

Migratory behaviour of individuals representing different categories of moulting swans

Mathiasson (1976) discussed the role of learned behaviour and tradition in the migratory habits of *C. olor.* Here are some examples of migratory behaviour connected to the function of the moulting flock model in Fig 3 and its relations to breeding grounds and place of birth, respectively, and winter quarters.

The way of the cygnet to its winter quarters, its future moulting ground and its subsequent breeding place (Fig 3: categories 1 and 2)

a) A pair of coastal breeders (female H4252, male H4154) of the Gothenburg archipelago produced four cygnets (001H—004H) in 1972 (Fig 4). The parents

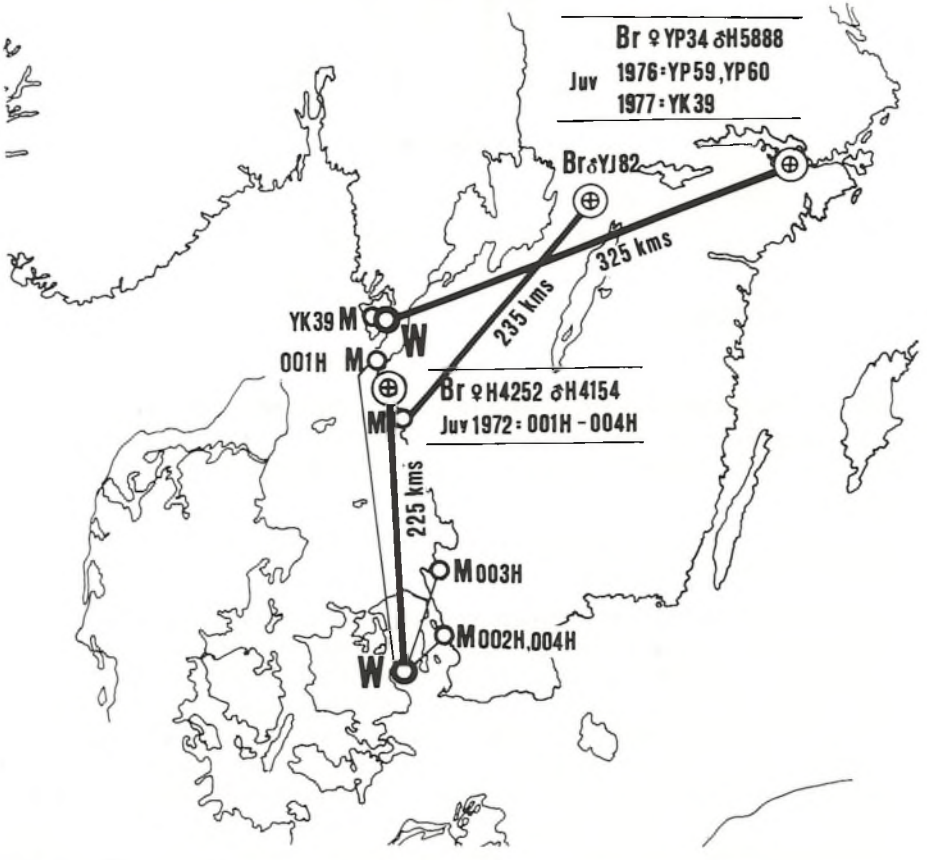

Fig 4. Three different migratory patterns between breeding places (birth places), winter quarters and moulting grounds.

reared their young and moulted as usual in the breeding ground. The cygnets wintered in Denmark, at Køge Bugt, southern Sjaelland. From there they dispersed the following spring. As yearlings, three of them were at different moulting grounds in Scania (southernmost Sweden) and Sjaelland (southern Denmark). From those moulting grounds they returned to their former and common winter quarters. They did so up to the age of 2 to 4 years. At that age they also returned for spring visits to the vicinity of their birth place but still recurred at their southern moulting grounds (about 225 km south). One female (004H) recurred during breeding time in 1976 with her mate at her birth place at the age of four. Being non-persistent territory-holders the pair disappeared. She was seen later on at her southern moulting ground (Landskrona, Scania), still later at her winter quarters. The following spring she returned to her place of birth and laid her first clutch of eggs but failed to incubate them. She returned to her winter quarters at the age of six (in 1979) and she succeeded in raising two cygnets in a nest 12 m from her own birth place. The pair that year moulted with their cygnets at the breeding place.

b) One pair of inland *C. olor* (female YP 34, male H5888) has its breeding place at Lake Hjalmaren, eastern central Sweden (Fig 4B). For five years they regularly changed between their breeding place at Lake Hjalmaren and their winter quarters 325 km away at Svanesund on the Swedish west coast. They arrive at their winter quarters in December and depart in late March or early April. In 1976 they brought two cygnets with them, in 1977 one (1976: YP 59, YP 60; 1977: YK 39). These cygnets stayed, as far as we know (records in summer), at west coast haunts when their parents left for their breeding ground in spring. The cygnets mingled with west coast non-breeders. One of them joined the moulting flock at Kalvofjorden. During subsequent winters the offspring rejoined their parents at Svanesund.

Shift of unsuccessful breeders between breeding ground and moulting ground (Fig 3: category 1)

A male (YJ 82/H4534) was ringed at Kungsbackafjorden moulting ground on 25 August 1973. Between 19 and 21 September 1974 it was caught when moulting there. On 23 November 1974 it was reported from Laxa, Narke, central Sweden, where it was courting one of two females (Fig 4C). They formed a pair and stayed for the winter. The following spring (1975) they bred and six cygnets were hatched but perished in June. On 17 June the parents were seen without cygnets at Laxa and in July they disappeared. On 20 August the pair was moulting at Kungsbackafjorden moulting ground, where they were still seen on 28 September. On 16 November they recurred at the breeding place at Laxa. Thus, when failing to breed, they left the breeding place for a flight of 235 km to the west coast moulting ground whence they returned, having completed the moult.

The examples given illustrate the traditional shifts between breeding place, moulting ground and winter quarters. The cygnets learn their way between birth place and their first winter quarters with their parents, because of family bonds.

Repelled by their parents in the winter quarters they join by chance flocks of older, more experienced swans from which they learn the way to their first moulting ground. Programmed in this way, they then continue their shifts year after year in the same manner. When reproductively mature, they reorientate themselves to their place of birth, where they settle to breed. Failing to breed, they go back to their programmed movements.

'Floating' population (Fig 3: category 3)

Obviously the moulting flock includes a number of less clearly definable groups. One such seems to be overaged non-breeders (eg former breeders). There also seems to be a fairly high number of swans never making any attempt to breed. We may name them 'loosers' as they seem to be of a low rank in both social and physical hierarchies. We have many records of neck-banded as well as tarsus-ringed swans of advanced age which have never bred. No less than 38% of the swans moulting at Kungsbackafjorden in 1979 (about 600) were considered to be at least six years old (a rough calculation based on capture/recapture). However, we need to be careful in judging whether a certain bird belongs to the 'loosers'. The start of breeding may take place very late in life. Continuous observations of single swans showing a permanent state of non-breeding are so far limited.

There are technical difficulties in permanent monitoring due to the long time span from the date of ringing (our oldest swan up to 1979 is 16 years old). Two examples of permanent non-breeders were:

- In July 1979 a healthy 9-year-old moulting female (3756) was controlled on Kungsbackafjorden, where she had been ringed as a moulting yearling in 1972. The shape of the cloaca showed that she had never laid eggs. As she was only tarsus-ringed, the records from the elapsed period were few. But she wintered at Hammer Bakke, Sjaelland, Denmark, prior to moving 200 km to the moulting ground;
- YA 94 (H4297), a female neck-banded as an adult (3 years old or more) in 1973 at the Lake Takern moulting ground. In 1974, 1975, 1976, 1977, 1978 and 1979 she was recorded in the moulting flock at Kungsbackafjorden. All the year round she was observed at the Swedish west coast and proved not to breed.

Shift of moulting ground (Fig 3: category 4)

Swans from the Kungsbackafjorden moulting ground have been found moulting not only at adjacent moulting grounds along the Swedish west coast, but also elsewhere within the living space of that population, as shown in Fig 1.

The rate of recurrence at a moulting ground of two-year old swans marked there as yearlings is between 55% and 70%. The recurrence in 1979 of swans marked as

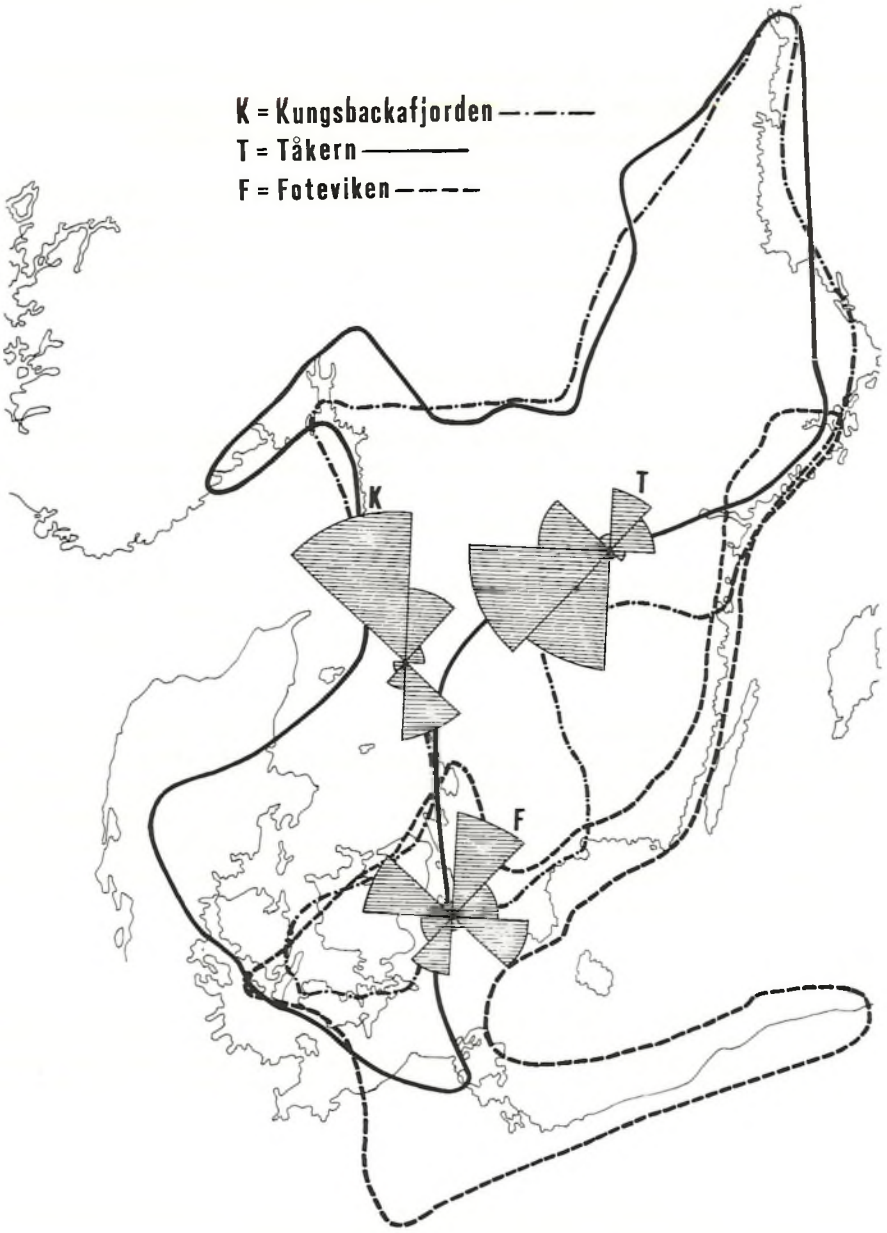

Fig 5. Geographical distribution during breeding season of *C. olor* ringed in preceding years at three important Swedish moulting grounds.

T = Lake Takern, K = Kungsbackafjorden, F = Foteviken-Hollviken. The circle diagrams show the proportional distribution in various directions from the moulting ground during breeding season.

two-year olds and older at Kungsbackafjorden moulting ground in 1978 was 37%, as compared to 65% for those marked as yearlings. Those figures are not compensated for mortality, so they should probably be at least 10% higher.

The lower recurrence rate of adult swans is connected with their incorporation into the breeding population and territory holders, which moult in their territories. There is, however, also a slight indication that adults shift more than yearlings; 15% of 85 swans shifted moulting ground in their second year of life, against an average of 20% yearlings.

The relations between different moulting grounds

The Swedish swans can be divided into two geographical populations. Their main living space is separate, but the winter quarters overlap to some extent (cf Mathiasson 1973a, Mathiasson 1976). The separate living spaces can be studied in relation to the main Swedish moulting grounds.

Numerical investigations show that the moulting swans of the different grounds have an identical time schedule in their in- and outflux, as well as synchronous numerical peaks. The different moulting flocks also seem to function as in Kungsbackafjorden (Fig 3).

Fig 5 shows the geographical affinities of the two moulting grounds of Kungsbackafjorden and Lake Takern, and the segregation between those two and the moulting ground of Foteviken, southern part of the Sound. The close connection between Kungsbackafjorden and Lake Takern is indicated by 22 swans alternating between the two grounds, but only 2 between Foteviken and Kungsbackafjorden and Takern. Fig 5 also indicates the clear connection between a certain breeding area (population) and special moulting grounds.

Summary

Cygnus olor has since the 1930s extended its breeding range to the west coast of Sweden. Kungsbackafjorden is the main moulting ground, and 2500 have been ringed since 1960. Marking with neck-collars allows different categories (floating population, attempted breeders and breeders) to be defined in the moulting flock and to illustrate subsequent movements and behaviour.

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S MATHIASSON
Naturhistoriska Museet
Box 11049
400 30 Goteborg
Sweden

PRELIMINARY RESULTS OF NECK-COLLARED *CYGNUS CYGNUS CYGNUS*

N O PREUSS

Introduction

During unusually cold weather, 129 *Cygnus cygnus cygnus* were ringed in Denmark during the first three months of 1979. Of these, 116 were additionally marked with a plastic neck-collar and a plastic tarsus-ring, both engraved with letters and ciphers. The neck-collar is 85 mm high with an inside diameter of 57 mm, the inscription is white on blue, 3 mm wide and 27 mm high. The tarsus-ring (94 mm high and 27 mm inside diameter), having the same inscription as the neck-collar, is engraved with 2 mm wide and 17 mm high ciphers and letters. With a telescope these neck-collars can be read from up to a distance of 500 m in good viewing conditions. This form of marking facilitates control in nature of live birds and does not depend entirely on recoveries of dead birds.

Up to 1 February 1980, we have received information concerning 40 such sight records from Denmark in the period up to April 1979, when the swans left for their breeding grounds. From Sweden we have sight records up to the end of April and from Finland from May. The autumn migration was demonstrated by records from south Finland and Sweden in October and November. From December and January 1980 we have received some records from the Danish winter-quarters.

Even at this early stage of the programme it is evident that the 116 neck-collared swans produced much more information that the 266 *C. c. cygnus* ringed without neck-collars in the period 1953 to 1978. Of the 116 neck-collared swans 26 (22.4%) were seen abroad (some individuals were recorded several times), compared with 24 (9.0%) recoveries of the 266 previous ringed.