POPULATION DYNAMICS OF *CYGNUS OLOR* IN DENMARK

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Introduction

The Zoological Museum started swan investigations in 1966 on a breeding population of solitary *Cygnus olor* pairs nesting in Copenhagen and North Sjaelland. Since 1971 they have been enlarged bv investigations on colonially breeding swans in Roskilde Fjord, a brackish water area 30 km west of Copenhagen.

In addition, about 17 000 swans were ringed in winter and during moult in summer. All data concerning ringed swans are transferred to Electronic Data Processing (EDP), but computer processing has not yet started. It has therefore been possible to make only a few preliminary calculations.

Climatic conditions

The data on which the main part of this paper is based can be divided into two parts: 1964 to 1969 and 1971 to 1978. The first period was quite normal as far as the severity of the winters is concerned, whereas there has been a series of very mild winters in the 1970s. In 1963, 1970 and 1979 the winters were very severe. This must be kept in mind as the mortality, shown below, is especially high during the winter months.

Production of young

Solitary breeding swans: As there is little variation from year to year in the onset of the breeding, 1 October has been taken as the time for fledging, even though poorly developed young actually fledge later.

In the period from 1966 to 1975 the number of young in North Sjaelland varied between 1.9 and 3.8 per pair, with 2.6 as the average. A breeding pair is one which built a nest and laid at least one egg.

Colonially breeding swans: Colonially breeding swans in Roskilde Fjord generally had a lower production than solitary swans. By the end of September (1971 to 1979) it varied between 0.6 and 1.5 young per pair, average 0.9. The production is very low even in areas in Guldborgsund (Clausen and Lind *in litt* and the author's own observations) and Ringkøbing Fjord (Eskildsen 1979), and it is possible that the numbers on more exposed areas are lower still. It has been possible to find only a few broods from the big colony of about 100 pairs at Ragø north of Lolland (Preuss pers comm).

In North Sjaelland the proportion of solitary pairs which do not start the breeding cycle at all varies. Normally it lies between 10% and 20%, but after the very severe winter in 1970, 42% of all surviving potential breeders did not nest. The total production of young in North Sjaelland appears to have varied from about 75 to 200. The lowest number was produced in 1970 but those birds which actually bred had the highest average brood size ever found. A part of the colonially breeding swans also did not start to breed.

Age at first breeding

Estimates made in 1975 on data from cygnets ringed from 1967 to 1969 show that the average age of first breeding for females was 4.7 years (n = 24), and for males 5.0 years (n = 19). However, it was clear that some birds from the years in question had not yet bred, so that the values most probably should be higher. Less than 10% of the birds in their fourth calendar year breed, and swans breeding in their third calendar year have not been found in Denmark at all. Indeed, we have the impression that a few birds never join the breeding population, even at the age of more than ten years.

Below we have used five years as the mean age of the first breeding.

These figures refer to solitary swans in North Sjaelland. Corresponding values for colonially breeding birds are not yet known but may be still higher.

Mortality before fledging

Calculation of mortality up to 1 October is based on direct observation.

The average number of eggs per breeding pair in North Sjaelland is 5.6. For colonially breeding swans the corresponding value is 5.2. As the figures for fledged young are 2.6 and 0.9 respectively, the loss is 54% for solitary breeding and 83% for colonially breeding swans. Solitary breeding swans lose young especially during their first month of life. Colonially breeding swans also lose many young during the first month, but in addition 40% to 50% of the eggs are lost, so that the number of young hatched in colonies is about 2.6 per pair, equal to what is left with a solitary pair four months later.

There is more disturbance in colonies, where nests are situated close together. There is much walking about during the egg-laying period, and the consequent conflicts among the pairs result in many eggs being broken. The higher the density of nests, the more eggs will be lost.

The mortality among young is higher among colonially breeding than in solitary breeding swans because the former are in more open and wind-exposed areas. The young weigh less in years with much wind and the average brood size is also lower in such years, which means that the mortality of young during the first four months is higher (Andersen-Harild 1981a).

Mortality after fledging

Material: The material can be subdivided as follows:

- Recoveries of *C. olor* ringed in Denmark and Sweden before 1957.
- Mortality calculations based on recoveries of birds ringed in the ice-winter 1962/63.
- Mortality calculations based on breeding birds in North Sjaelland in the period 1963 to 1974.
- Mortality calculations based on swans ringed as young at breeding places in North Sjaelland from 1961 to 1974.
- Estimate of the mortality among birds ringed as moulting non-breeding birds in 1970 and 1971.
- Estimate of the mortality of birds ringed as young in Roskilde Fjord and Guldborgsund 1972 to 1977.

Sources of error: This heterogeneous material contains a number of specific sources of error. Among the more general sources of error are loss of rings and differential chances of recovery of birds according to geographical area or age. Baltic swans stay in shallow areas near coasts until they start to breed, when the majority migrate to lakes and peatbogs. We do not know whether there is any difference in chances of recovery in these two habitats. Dead swans are so big that they take a long time to disappear on land, and they drift around on the surface before sinking. Thus the chances of recovery are high and it is assumed that all age groups have the same recovery chance.

Possible differences in recovery prospects between geographical areas are assumed to be without consequence as the population remains throughout the year in rather densely populated areas where ringing is well known and where there is good communication between ringing centres.

Loss of rings may therefore be the most serious source of error. The Zoological Museum in Copenhagen has used four different ring types for swans (see Table 1).

The highest loss occurs when rings of type 3 (with no clip) are used. In investigations in North Sjaelland and Copenhagen, swans were ringed with an aluminium ring of type 3 on one leg and an individually coded plastic ring on the other. It soon became obvious that there was extensive loss of the aluminium rings, estimated at 7% to 8% per annum, which is of almost the same order as the annual mortality (Andersen-Harild 1971). The loss of rings does not appear to be connected with wear or correlated with how long the ring has been on the swan. In several cases the ring, although correctly applied, was lost a few months after it

Table 1. Ring types used by the Zoological Museum in Copenhagen for ringing of swans.

No.	Material	Inner diameter (in mm)	Thickness (in mm)	Closing method	In use
1	Aluminium	32	1.5	Clip	1954–61
2	Aluminium	28	1.0	Clip	1962–68 (70)
3	Aluminium	20 x 30	1.0	No clip; butted	1964–66
4	Aluminium	28	1.5	Clip	1968–

had been put on. The data originating from this type of ring are without value and are not included in the mortality calculations.

As far as the other ring types are concerned, the loss (according to calculations on birds with coloured plastic rings) is much lower. The loss of type 2 and 4 is less than 0.5% annually and, therefore, we do not consider it necessary to correct calculations. The cause of loss is not quite clear but it seems that rings with clips can be so distorted by a blow that another blow can open them completely.

Wear of rings: As far as ring type 1 is concerned, the wear is rather limited, even after ten years. In addition, some of the rings were applied above the heel joint, which further reduced wear.

Ring type 2 wears much more quickly and some were nearly worn down after five years. In most cases the wear was not so extensive as to cause loss of the ring but in some the address was difficult or impossible to read. In many cases worn rings were replaced by new ones. In this way ring type 4 replaced more than half of the older ring types on swans which were still alive in the winter of 1969/70. Wear of rings does not seem to have had essential influence on the recovery frequency.

Mortality during the first winter (1 October to 31 May)

Solitary breeding swans: In the Copenhagen area the swans are ringed with an aluminium ring and mostly with additional colour rings. Since 1971, a 40 mm wide plastic ring with a number consisting of three cyphers was used. It can be read from a distance of up to 100 m. During the preceding years about half of the birds were ringed with an individual combination of colour rings. As the birds are rather tame and congregate in spring, it has been possible to check a rather large portion of them in the study area.

It is difficult to calculate the mortality during the first winter of cygnets of solitary breeding swans. The birds leave the breeding places during the first autumn or winter and most of them leave the study area during their first flight-feather moult. Thereafter they usually spend some years away from the study area but return for shorter or longer periods in spring until they settle down as breeding birds.

As only rather few young were ringed (usually 100 to 175 annually) recoveries of dead birds are insufficient for mortality estimates. It is possible only to calculate a 'disappearance percentage' based on birds which have not been recorded after 31 May in their second calendar year. However, a bird may be found dead and reported to the ringing centre, it may be observed in the study area or it may be controlled alive on a winter feeding place or on a moulting place. Some of the birds surviving the first winter are never recorded, so the disappearance percentage is a maximum figure. This will apply to birds which die after the first winter and before their potential return to the breeding area up to five years later. However, since the mortality in this period is very low (see page 170) the margin of error will, at most, be 10% to 12%.

Table 2 shows the 'disappearance percentage' for 1967 to 1974 (1970 being excluded). The latter was the year after the severe ice-winter, and only a few birds produced young for ringing. The Table shows 56% as the mean, which, as mentioned above, should be reduced to about 45%. The highest losses occurred in 1969 when the young had to face the severe ice-winter. Some 10% to 30% of the cygnets fledged in the study area spent the winter there and, being fed by man, were subject to less starvation than cygnets which emigrated. On the other hand, they were more endangered by collisions with wires. A disappearance percentage of 74% in the study area was thus relatively low and probably 90% of the young died in Denmark during this very severe winter.

Table 2. The percentage of young in solitary breeding swans in North Sjaelland and Copenhagen which have not been observed later than 31 May in their second calendar year.

Year of ringing	'Disappearance percentage'
1967	63
1968	50
1969	74
1971	58
1972	45
1973	48
1974	54
Average	56

Colonially bred swans: Mortality during the first winter of colonially bred swans can be followed better as they have been marked with neck-collars and 'mortality' is close to the true die-off (Table 3).

Table 3. Mortality during the first winter (1 October to 31 May) of cygnets of colonially breeding swans from eastern Denmark.

Year of ringing	Mortality percentage	
	Roskilde Fjord	Guldborgsund
1972	24	
1973	54	6
1974	21	
1975	13	75
1976	71	95
1977	78	81
Average	44	(64)

Mortality in this group varies much more than in those from solitary breeders because of the greater variation in weight from year to year (Andersen-Harild 1981). The mild winters in the 1970s resulted in a very good survival rate, certainly higher than in the 1960s.

Proportion of second calendar year birds in the moulting places

The proportion of second calendar year birds present on the moulting places is highly variable and was lowest in 1970 after the severe ice-winter (Fig 1).

The moulting flocks in Roskilde Fjord consist mainly of local swans (Andersen-Harild 1981b) and the proportion of young birds closely reflects the mortality data of cygnets fledged in this area (Table 3).

Swans from Sjaelland and southern Sweden moult at Saltholm and the proportion of second calendar year *C. olor* recorded accords well with that in midwinter in southern Sweden (Nilsson 1979). Nilsson did not find any correlation between the winter temperatures and the percentage of young (ie second calendar year birds) the following winter, indicating that breeding success in *C. olor* does not depend on weather conditions in the previous winter.

The percentage of second calendar year birds moulting does, however, correlate with the temperature and ice conditions in the preceding winter, but it must be remembered that the age composition of the total population varies from year to year. Therefore differences in the second year percentage do not reflect only differences in production and/or mortality.

The moulting swans at Rødsand come mainly from the German Democratic Republic and the conditions influencing this population differ from those affecting birds moulting at Saltholm.

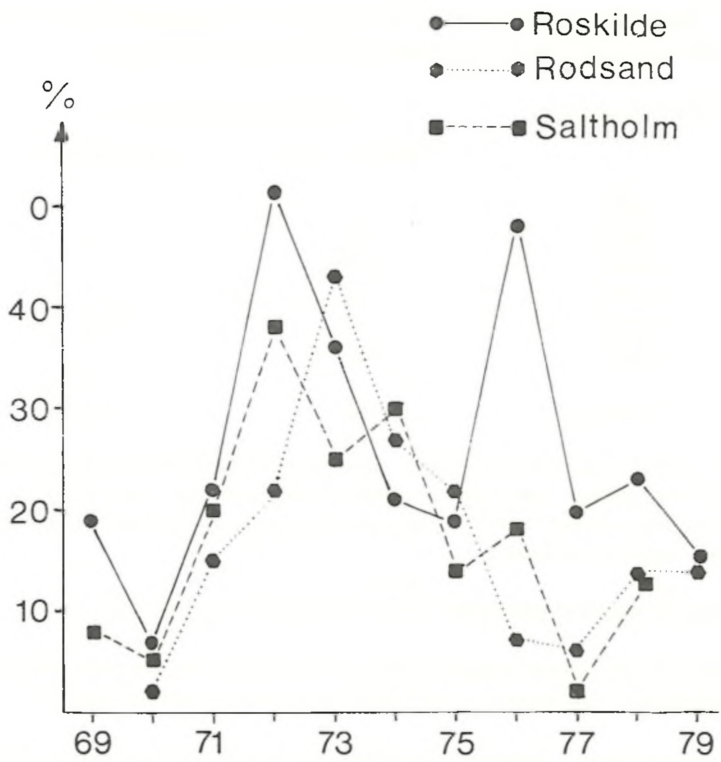

Fig 1. Variation in the percentage of second calendar year birds at three moulting places, 1969 to 1979.

Mortality of older swans

Here different material has been used:

1) *Birds ringed before 1957:* All recoveries are of birds ringed in winter in North Sjaelland (1953, 1954, 1956) or of birds ringed on the Swedish coast of Øresund (1941, 1947). All birds reported dead before 1 January 1977 are included. Table 4 shows the age of the birds when recovered. The average annual mortality is calculated using the formulae in Lack (1951) and Haldane (1955): $m = N/\sum xd_x$, where N represents the total number of recoveries, x the age group and d_x the total number of recoveries in a given age group. This gives m = 36/271 = 0.133. The uncertainty $\delta = m\sqrt{(\frac{1-m}{N})}$ is 0.021. Thus the annual mortality will be 13.3% ± 2.1%. This calculation is based on the assumption that the original ringed population is extinct. We can still expect one or two recoveries of birds ringed between 1954 and 1956, so the mortality rate will decrease to below 13%.

Table 4. Number of recoveries of swans found dead in different age groups.

The age groups follow the calendar year. Recoveries in the same calendar year as ringing have been omitted.

Age group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
No. recovered	5	2	3	2	3	3	3	2	1	3	0	2	1	2	0	1	1	1	0	1

2) *Birds ringed in winter 1962/63:* The winter of 1962/63 was more severe and longer than usual. *C. olor* gathered in big flocks in places where currents maintained open water, and in many there was extensive artificial feeding activity. Some 1800 *C. olor* were ringed, most of them in the beginning of March 1963. It can be assumed that about 1500 of these survived the winter. The number reported dead up to 31 December 1976 is shown in Table 5.

Table 5. Recoveries of *Cygnus olor* ringed in winter quarters in east Denmark during the ice-winter of 1962/63.

The recovery year runs from 1 June to 31 May.

Year of recovery	Number of recoveries: Actual	Number of recoveries: Calculated (assuming constant mortality)	Mortality (%) calculated (assuming constant reporting rate)
1963/64	22	33	8
1964/65	34	29	15
1965/66	26	25	13
1966/67	14	22	8
1967/68	18	19	12
1968/69	23	17	17
1969/70	81	15	70
1970/71	7	13	7
1971/72	10	11	11
1972/73	10	10	13
1973/74	6	9	9
1974/75	4	7	7
1975/76	10	6	20

Calculations of the annual mortality based on these recoveries require that the frequency of reporting is constant during the whole period and that mortality does not fluctuate too much. The formula of Haldane (1955) can be used but if the recoveries involve only birds ringed in a single year it is easier to use a regression

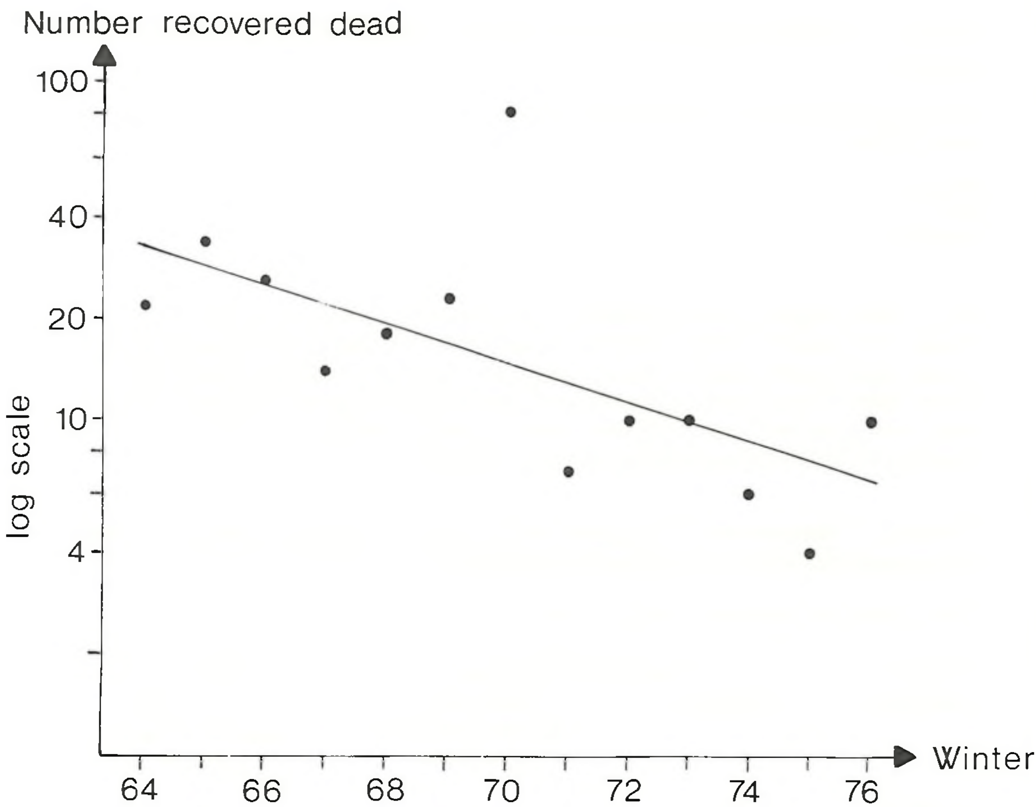

Fig 2. Number of recoveries of birds ringed in winter 1962/63 as a function of time.

The line is the regression line, the decline of which shows the average mortality.

analysis. Fig 2 shows the number of recoveries in relation to time, the line being the regression line. The regression coefficient shows the mortality, which is 12.8%.

We can calculate how many recoveries we should have received. If the result of the calculation differs from the number actually received, this can mean that the mortality has not been constant and/or that the reporting rate varies.

If it is assumed that the reporting rate is constant, the difference between expected and actual numbers of recoveries must be due to differences in mortality. The actual mortality can be found by multiplying the average mortality by a factor ^{Y} actual/^{Y} calculated. This has been done in Table 5.

The calculated mortality has been compared with the severity of the winter (Fig 3). This clearly indicates that those winters with the highest mortality have been the

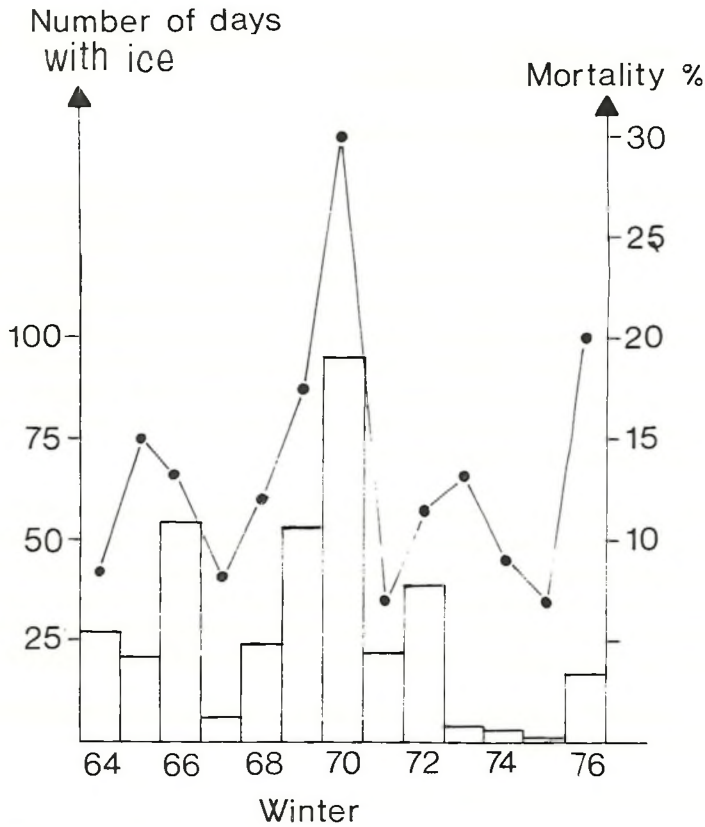

Fig 3. The calculated mortality (curve) during the winters 1963/64 to 1975/76 for *Cygnus olor* ringed in the ice-winter of 1962/63, in relation to the number of days with ice in the inner Danish waters (columns).

most severe (1968/69 and 1969/70) and mortality has been lowest in especially mild winters (1966/67, 1970/71 and 1973/74). There are indeed annual fluctuations in mortality.

On the other hand, the prospects for reporting in severe winters must be higher than normal because the birds gather in large numbers at a few localities visited by many people. The calculated mortality of 70% in 1969/70 is too high. Counts of the swan population in northern Europe (especially Denmark) suggested a much smaller reduction. Calculations of other parts of the population suggest 30% to 35% as more reasonable. Mathiasson (1974) has shown in Sweden that only 61% of the rings from dead swans were reported to the ringing centre, but the proportion would be higher in 1969/70 because of the intensive ringing activities which resulted in many additional ringed swans being collected directly and through contacts with local people at feeding places.

Mortality of birds ringed during moult

Since 1970 many birds have been ringed at moulting places, mainly younger ones (up to four to five years old) which have not yet bred and a few failed breeders. Only after severe winters did the latter increase. This means that there will be a higher proportion of potential breeders among those caught in the summer of 1970 than among those caught in 1971. In both years there would be relatively few birds in their second and third calendar year (Fig 1), these age groups having suffered severe losses during winter 1969/70. The breeding success in 1970 was very low, so that only a few young joined the moulting population in 1971. Thus the two years chosen are untypical but calculations for later years have not yet been made. It will always be hard to find a 'normal' year.

It is difficult to adjust the recovery material from moulting swans to formulae for calculation of mortality. We need to know what proportion of dead ringed swans is reported to the ringing centre. Even though we still receive recoveries for the 1963 group, the number is now so low that we can estimate the final recovery proportion with confidence as around 20%. Thus only 20% of dead birds are reported, and the mortality for birds ringed in 1970 and 1971 can be calculated (Table 6).

Table 6. Mortality calculations of swans ringed as non-breeders during moult in July and August.

The recovery year runs from 1 June to 31 May.

Year of recovery	Number recovered dead	Estimated total number of deaths	Number alive in the beginning of the period	Mortality (%)
a) Birds ringed in 1970:				
1970/71	11	55	931	6
1971/72	15	75	876	9
1972/73	23	115	801	14
1973/74	20	100	686	15
1974/75	15	75	586	13
1975/76	23	115	511	23
b) Birds ringed in 1971:				
1971/72	15	75	948	8
1972/73	17	85	873	10
1973/74	10	50	788	6
1974/75	17	85	738	12
1975/76	20	100	653	15

Mortality is somewhat lower during the first year than during later years because moulting birds stay in a marine environment during the first three to four years of their lives. A large part of Danish swans die by collision with wires when flying to potential breeding places and this hazard is lower for non-breeding swans.

Mortality in the birds' second winter

Mortality seems to be considerably reduced in the second winter. This is shown by ringing of moulting birds in 1970 and 1971. Of swans ringed in their second calendar year, 1.7% were recovered during the year after ringing, compared with 1.6% of those older swans. The 1970/71 winter was mild but the 1971/72 winter normal (Fig 3).

Mortality of breeding birds

In North Sjaelland most of the breeding birds were ringed with an aluminium ring and additional colour rings which enabled individual recognition at some distance. The mortality may be calculated from the number of ringed birds that disappears between two breeding seasons (Table 7). Usually *C. olor* is faithful to the breeding territory and even when partners are changed a new territory is rarely established more than a few kilometres away. Only a small part of those swans which disappear are reported to the ringing centre as dead. In the severe winter of 1969/70, when there was an exceptional opportunity to control birds on the wintering places, only one of those which had disappeared from a breeding site was seen alive and this bird actually returned to breed one year later.

Table 7. Mortality in solitary breeding swans in North Sjaelland.

Breeding seasons	Number alive in the preceding breeding season	Number disappeared before the next breeding season	Mortality (%)
1963/64	7	1	(14)
1964/65	20	2	(10)
1965/66	27	5	19
1966/67	70	8	11
1967/68	100	21	21
1968/69	90	22	24
1969/70	104	37	36
1970/71	49	6	12
1971/72	90	9	10
1972/73	120	20	17

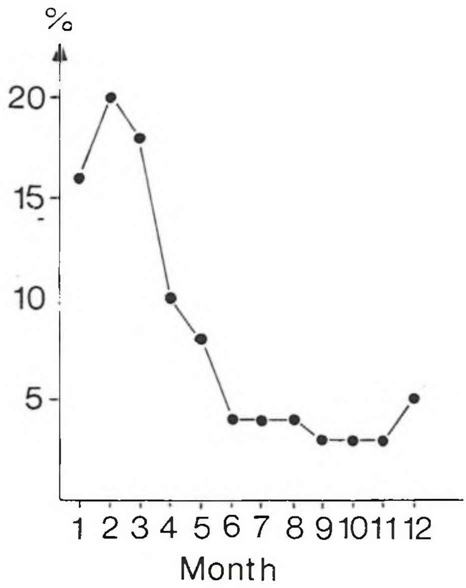

Fig 4. Distribution by month of ringed swans found dead.

The mortality rate in colonially breeding swans seems to be similar to that of solitary breeding ones.

Causes of death during the year

By far the majority of swans ringed in Denmark die in the winter. Fig 4 shows the distribution by month of all swans recovered as dead. About 54% are recovered from January to March. In severe winters thousands of swans die, usually from starvation.

Oil pollution is a special problem in the early spring (Fig 5) and occurs at the same time as oil catastrophes for diving ducks. Most oil pollution occurs in the Kattegat area where swans are sparse (Joensen 1972 and 1977). Extensive oil pollution in southern Danish waters might have very serious consequences for the population, even though *C. olor* seems to have a better chance of surviving oiling than other waterfowl.

Of recoveries received with an indication of the cause of death, 14% died from oil pollution and 36% by collision with overhead wires. However, many reports give no cause of death, many being from winter and probably involving starvation. Collisions with wires occur mostly in spring, when the birds fly to the breeding places, and in autumn, when they leave them again.

It has to be added that even though swans are totally protected in Denmark some illegal shooting takes place. X-ray investigations of dead birds have shown that about one-fifth had pellets in their tissues.

In later years several cases of lead poisoning caused by ingestion of spent lead pellets have been observed in areas where there are shooting-ranges orientated towards shallow coastal waters. Up to 150 to 200 dead swans were found in such areas (Clausen and Wolstrup 1979). The usual concentration of lead pellets in shallow areas in West Jutland is so high that death by lead poisoning seems to be fairly common (Petersen and Meltofte 1979).

Balance in the population

It is difficult to make calculations on the balance of the populations because of the variation in winter mortality and in age composition. In order to maintain the population level, production of about 1.5 young per pair is necessary, but calculations show that enough young from solitary breeding swans survive to give an annual population increase of about 15%. Contrary to this, the population of colonially breeding birds should decline.

The increase in colonially breeding swans would seem to be due to immigration of surplus young from the solitary breeding population. In North Sjaelland we have controlled about 15 swans breeding in colonies which had been hatched in lakes. Young hatched in colonies have never been found breeding as solitary pairs.

Variations in the age of first breeding do not change the calculations much and cold winters seem to occur at such long intervals that their overall effect must be comparatively small.

Even though the Danish swan population has increased considerably, the breeding population rising from 750 pairs in 1954 to 2800 in 1966 (Block 1971), mortality of swans after their second calendar year does not seem to have changed since 1950.

On the other hand, a change in mortality during the first four months of life could be documented. In 1954, when no colonially breeding swans existed, 3.1 fledged young were produced per pair (Paludan and Fog 1956). In 1966 Bloch (1971) gives an average in July of 3.5 young per pair in freshwater lakes and 1.9 for colonially breeding birds. The present material shows 2.6 young per pair for solitary breeding and 0.9 for colonially breeding swans in the period 1966 to 1975. This means that the change to colonially breeding has caused an increase in mortality of young. It is more difficult to ascertain whether mortality in young of solitary pairs has increased, but it seems likely that the spread to less appropriate lakes, caused by the increase in the population, has also resulted in a higher cygnet mortality rate in this group.

We cannot say for certain whether mortality during the first winter has also increased. Still, it has to be pointed out that the utilization of marginal habitats during the last 20 years has resulted in lower weights of young, probably causing increased winter mortality.

More detailed analysis of the relation of weight, sex, age and habitat on mortality are desirable.

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The author would like to thank the numerous volunteers who have helped in ringing operations and reported thousands of sightings of ringed swans. Large-scale ringing was initiated by P Tholstrup and A Schat-Kielberg, and later increased by Peter Hermansen, Hans Lind and Leif Clausen. The study in North Sjaelland involved the close co-operation of Peter Hermansen during 15 years of field work. Erik Hansen has prepared computer programmes and carried out a lot of field work at Roskilde Fjord. N O Preuss has encouraged the study with never-failing interest and help. Jon Fjeldsa read the manuscript and suggested improvements. Ursula Friis made the English translation. Statens Naturvidenskabelig Forskningsrad enabled me to present the paper to the Second International Swan Symposium in Sapporo, Japan.

Summary

The paper presents preliminary data on studies carried out since 1966 on a solitary breeding population and since 1971 on a colonially breeding population of *Cygnus olor* in Denmark. Production of young was higher in solitary than colonial nesters and after severe winters many potential breeders did not nest. In solitary breeders, five was the mean age of first breeding. Mortality before fledging is higher in colonial breeders because of disturbance in the colonies, but mortality in young of solitary breeders is also high because of exposure to wind. Mortality during the first winter is calculated for solitary breeders by the 'disappearance percentage', normally 45%, but 90% in severe winters; in colonial breeders mortality in the first winter varies considerably from year to year because of variations in weight. Mortality in older birds averages under 13%, but there are considerable annual fluctuations, linked with the severity of the winter. Mortality of swans ringed during moult is difficult to calculate but is lower in the first year. Most swans die in winter, usually in severe winters from starvation; 14% of recoveries received come from oil pollution and 36% from collision with overhead wires. The population of solitary breeders shows a small increase, which compensates for a decrease in colonies. The change to colonial breeding apparently leads to increased mortality in young swans.

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AN ISOLATED POPULATION OF *CYGNUS OLOR* IN SCOTLAND

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Introduction

This paper presents a preliminary report on certain aspects of a study of *Cygnus olor,* begun in 1978, in the Outer Hebrides, Scotland. The main objective of the research project is to understand the processes underlying the regulation of numbers in a natural wild population.

Jenkins *et al* (1976) suggested that the numbers of adult *C. olor* were fairly constant between seasons, that an August peak might be due to a temporary immigration to the islands of 200 birds to moult, and that the constancy both of numbers of breeding pairs (around 86) and of adult non-breeders between seasons was due to regulation of numbers through social behaviour in relation to food supply. The population, unlike others studied in Britain recently, appeared to be stable, not declining in numbers, despite a low breeding output each year. Further-