Whooper Swan *Cygnus c. cygnus* population dynamics in Finland



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Population parameters are described, based mainly on earlier studies or their primary data. Thirty per cent of the spring population are breeding birds. No big flocks of non-breeders are found in Finland. Population density has been low. The density was highest in the 1970s in the northern boreal zone and declined to north and south. In northern Finland the habitat may become a limiting factor in near future.

Population growth has been 14.2% +/-0.7 per year in southern Finland and 7.5% in northern Finland. The constant rate of increase (11.0% +/-0.2 per year) throughout the whole country has continued since 1950. The recent population is about 5,000 birds.

The summer distribution now covers the whole country. The dispersal has been 25 km per year. Local populations have dispersed 2 km per year. Gross annual mortality rate is 15%. Probable mean annual mortality rates of first year, second year and older birds 30, 25 and 12% respectively.

The aim of this study is to analyse the population parameters of the Whooper Swan Cygnus c. cygnus population in Finland on the basis of some earlier studies such as Haapanen *et al.* (1973a and b, 1976), Haapanen & Nilsson (1979) and Haapanen (1987). The primary data in the study by Haapanen & Nilsson (1979) is analyzed here in a more detailed way than was possible earlier.

In the 1960s there was a fairly extensive Whooper Swan study project which produced information on the breeding biology, production and population size (Haapanen *et al.* 1973a), changes of distribution (Haapanen *et al.* 1976) and habitat use (Haapanen *et al.* 1977). In the 1970s the population was censused twice (Haapanen & Nilsson 1979, Hyytiä *et al.* 1983). In the 1980s the population of southern Finland was censused again (Haapanen 1987).

Material and methods

The methods of the previous studies on the Finnish Whooper Swan population have been described in them and will not be repeated here.

Haapanen & Nilsson (1979) took into account only paired birds. Here the material comprises all the Whooper Swans seen. Some aerial counts were also made south & 64° N. These results were not included in the 1979 paper but are used here. The total area covered in aerial counts was 199,000 sq. km, 59% of the whole of Finland.

The size of the breeding population in southern Finland is known in each year 1949-70 (Haapanen *et al.* 1973a). Later it was censused in the early 1970s (Haapanen & Nilsson 1979), in late 1970s (Hyytiä *et al.* 1983) and 1984 (Haapanen 1987). The breeding population of the whole country has been censused five times between 1949 and 1979 (see Haapanen 1987).

A Whooper Swan pair with a nest, a single bird close to a nest or an incubating female were regarded as a breeding pair. All other birds were regarded as non-breeders, either single, paired or birds in flocks.

As the female spends 85% of its time incubating, feeding takes place often close to the nest (Haapanen *et al.* 1977), the pair criteria used here are fairly reliable. The aerial counts were made in the middle of the incubation period (see Haapanen & Nilsson 1979).

Results

Population structure and flock size in early summer

In this paper the population structure can be

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studied only as far as the relation between the non-breeders and breeders are concerned. Haapanen *et al.* (1973a) have shown that the non-breeders formed 71% of the total in the acrial surveys made in 1968-70. In aerial surveys made in 1973-76 73% of censused swans were non-breeders in the same area.



Fig. 1. Whooper Swan population densities in Finland and in adjacent areas of the Soviet Union in the middle of 1970s in the subarctic zone (A) and different parts of the boreal zone (B-D). The figures for the Soviet Union are according to Bianki (1981). Figures are birds per 1000 sqkm.

The population structure varies in different vegetation zones. In the subarctic vegetation zone the breeders formed only 5% of the population. In this area about half of the summers are too short for the Whooper Swan to produce fledged cygnets (Haapanen *et al.* 1973a). The non-breeders can, however, find good feeding habitat in this zone.

The non-breeders occur during the summer time in small groups very scattered over wide areas. 85% of the birds recorded in aerial surveys in 1973-76 occurred as singles or in pairs. No flocks comprising more than ten swans have been counted.

Density

In the early 1970s the density of the Finnish population was highest in the northern boreal zone and decreased to both north and south (Fig. 1). There is strong positive correlation between the amount of good habitat and the number of Whooper Swans in the northern boreal zone (Fig. 2) (r-square=0.48), although the regression may not be linear in high densities because of territorial behaviour.

Population surveys compared with estimates of available breeding territories show that Lapland is nearly saturated (430 breeding or non-breeding pairs and 450 territories) (Haapanen 1987). There are in southern Finland plenty of potential territories and the low densities are not related to shortage of the habitat (Haapanen 1987).

Population growth

There has been a constant rate of increase of 14.2% +/-0.7 per year (r-square = 0.98) in the southern part of Finland since 1950. The constant rate of increase for the whole country was 11.0% +/-0.2 per year (r-square=0.99) at least from 1950-77. The rate of increase in the province of Lapland has been 7.8% per year (Haapanen 1987).

Haapanen *et al.* (1973a) showed that as a result of the climate and lower habitat quality the production and population growth of swans has been smaller in the northern part of the country. The constant rate of increase suggests that density dependent factors have not limited growth.

The size of the spring population was in mid 1980s about 3,000 birds (Haapanen 1987), in the late 1980s probably 5,000 birds.

Dispersal

Haapanen *et al.* (1976) have given the distribution maps 1950-75. The most recent distribution map is published by Hyytiä *et al.* (1983).

During the last 30 years changes in distribution have been of two types. The most common change has been the slow increase of the population range around the initial breeding sites. The most dense subpopulations are found around those sites where breeding Whooper Swans were found in 1950.

Some single pairs, however, suddenly appeared



Number of potential territories

Fig. 2. Correlation between the numbers of potential territories (Haapanen et al. 1973a) and the numbers of Whooper Swans (Hyytiä et al. 1983) in the province of Lapland. Figures are numbers per 1000 sqkm.

far from the former range. Later on gradual population increase occurred around these new grounds. The first "jump" took place in the early 1950s when there had not been any population pressure within the normal borders of their distribution. Six such sudden new sites have been identified. The distances between the new sites and the nearest site of former distribution averaged 185 +/-75 km (range 100-325 km).

The Finnish Whooper Swan population has dispersed from the eastern border of Finland to the southern coast in 23 years. The total distance is 580 km. The mean dispersal rate is 25 km per year. The population consists of local subpopulations with large non populated areas in between. These subpopulations have dispersed only 2.1 km per year.

Production and mortality rate

Cygnet production has been very stable at 3.2 +/-0.3 cygnets per pair measured in late August from 1964-70. The mean number of fledged cygnets in early September was 3.2 +/-1.4 (N=59) in southern Finland and 2.5 +/-1.3 (N=17) in Lapland and Kuusamo. There was a statistically significant higher cygnet mortality rate in north Finland than in south Finland

(P=0.002) (Haapanen et al. 1973a).

There are no banding studies in Finland which would give direct information on the mortality rate. It is, however, possible to get a picture of the mortality rate based on the productivity and the population structure.

Based on data on the productivity, the percentage of breeders and that of losers the structure of the theoretical autumn population is as follows:

| successful breeders | 19.8% |
|-----------------------|-------|
| unsuccessful breeders | 2.3% |
| non-breeders | 51.8% |
| fledged cygnets | 25.9% |

As the constant rate of increase is 11%, the gross mortality rate is:

(25.9 - 11)% = 14.9%

Adult mortality rate shall be less than gross mortality rate. The first and second year mortality rates and the age of first breeding are unknown. According Dement'ev & Gladkov (1967) breeding starts at the age of five years in Soviet Union and according to Gardarsson & Skarphedinsson (1984) breeding starts at the age of seven years in Iceland.

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Testing with different adult mortality rate figures (less than 15%) it is possible to gain different figures of first and second year mortality rates and the age of first breeding. These figures result in the observed number of nonbreeders and with a given figure of adult mortality rate the known number of first breeders. In fact the number of immatures must be less than the observed number of non-breeders as 10% of breeders have failed and some widows and widowers may not breed.

The results suggest that the most probable mortality rates are 30% for first year birds, 25% for second year birds and 12% for the older birds. The mortality rates are valid only if the average age of first breeding is six years. In this case 92% of the non-breeders are immatures. If the adult

Table 1. A life table for the Whooper Swan in Finland. The survival rates of early development stages are according to Haapanen *et al.* (1973a).

| Each pair of swans lays 4.4 eggs | |
|---|--|
| hatches 2.9 young (90% of pairs successful and 74% of eggs hatch) | |
| raises 2.6 young to late September raises 1.8 young to 1 year (survival 70%) raises 1.4 young to 2 year (survival 75%) raises 1.2 young to 3 year (survival 88%) raises 1.1 young to 4 year (survival 88%) raises 0.9 young to 5 year (survival 88%) | |
| raises 0.8 young to 6 year (age of first breeding) | |

As the adult survival rate is 88%, (1-0.88)x2 = 0.23 birds per pair die each year.

mortality rate is bigger than 12%, the number of immatures is unrealistically high. If the adult mortality rate is smaller than 11%, the immature mortality rates become unrealistically high.

Table 1 presents a life table for the Finnish Whooper Swan population calculated by the method used by Perrins & Reynolds (1967) and Perrins & Ogilvie (1981). From an average brood with 4.4 eggs, 0.8 Whooper Swans reach the age of first breeding.

Discussion

The percentage of breeders in relation to all birds over one year old have been found to be similar in several Whooper and Trumpeter swan populations: for Whooper Swans; 30% in spring in Iceland (Gardarsson & Skarphedinsson 1984) and in Finland: for Trumpeter Swans; 26-27% in summer in the population studied by Banko (1960), in Alaska (Hansen *et al.* 1971) and in the easternmost Soviet Union (Gusakov 1987).

In Finland the non-breeders are found scattered among the breeders as in Alaska (Hansen *et al.* 1971), but in Iceland there are large flocks of non-breeders (Gardarsson & Skarphedinsson 1984).

The densities in Finland in the 1970s were much lower than in nearby areas in USSR (Fig. 1). In Iceland the densities (14 birds per 100 sq km, based on Rüger *et al.* 1986) are much higher than in Finland (0.9 birds per 100 sq km, based on Haapanen 1987).

There are few bird populations which have shown such a constant rate of increase for so long time as the Finnish Whooper Swan population. The Trumpeter Swan population studied by Banko (1960) grew over twenty years at a constant rate of 10% per year.

The same type of sudden appearance of breeding Whooper Swans far outside their normal breeding range has also been found in Latvia in 1973 (Baumanis 1975) and in Poland (Kawenczynski *et al.* 1976).

Gross mortality rate of the Icelandic-British population is the same as found in Finland. This can be concluded on the fact that the population is stable and the average percentage of cygnets is 15% in that population (Thom 1986). The adult mortality rate of the Trumpeter Swan population in Red Rock Lakes National Wildlife Refuge is found to be also 12% (Anderson *et al.* 1986).

It is quite obvious that the Finnish Whooper Swan population still has good possibilities to continue its growth, especially in the south. In the north the population pressure may in the near future cause more of the non-breeders to find summer habitat outside the breeding range.

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