Eurasian Whooper Swan *Cygnus cygnus* migration, with particular reference to birds wintering in southern Sweden

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The Whooper Swan, a breeder of the Palearctic taiga lakes, spends the winter in both Atlantic and Pacific areas, as well as in lakes and streams of central Asia. The population is split into fractions by migration dividers, also smaller subpopulations display specific migration characters. Factors influencing the migratory behaviour are discussed, partly based on sightings of neck-collared birds, partly based on field observations.

We may presume that Whooper Swans *Cygnus cygnus* strive to maximize their life-time reproductive success, and to minimize their chances of mortality. Migratory behaviour between wintering and breeding areas is an important integral component of such a strategy.

Whooper Swans need about 3.5 months to complete reproduction, but are restricted in the time available in summer on their northern breeding grounds. There is no advantage for swans to leave suitable winter quarters too early in spring in order to move into frozen areas as losses during migration could be high and costs for reversed migration may exceed any potential benefits. Conversely, to stay as long as possible in winter quarters may promote individual winter survival, but completely eliminate chances for reproduction.

The nature, rate and timing of migration is a critical factor in resolving this conflict. Indeed it becomes more pronounced the further to the north and east Western Palearctic winter birds have their breeding areas. In central and eastern parts of the Palearctic region Whooper Swans face similar problems.

Arising from this background, we can identify a number of elements of a migration strategy of a positive beneficial nature and related potential risks or costs to a migratory swan.

Beneficial behaviour will include:
- restricting the migratory route to cover the shortest distance between breeding grounds and favourable winter quarters - swans may benefit from external stimuli (releasers), for the appropriate timing of spring and autumn migration - gross mortality may be reduced and reproductive capacity increased by different timing of the migration of adult breeders and immature non-breeders (by reducing competition for food at resting grounds and breeding sites, as well as in winter quarters).

Potential costs arising from these behaviour patterns include:
- increased mortality to early migrating breeders which may face adverse weather and food scarcity
- reduced breeding success in certain years due to unseasonal weather conditions (late spring and early autumn frost)
- increased mortality for inexperienced birds migrating on their own.

These costs may be reduced by experience (knowledge by learning), which could be promoted by social organisation:
- by experienced birds repeatedly using routes and resting grounds which have been proved successful in the past
- by cygnets accompanying their parents on first migration cycle (imprinting "the right and best")
- by flock movements (based on an appropriate number of experienced birds forming geographical cohorts).

This behaviour itself may, however, under certain circumstances involve negative elements and costs, for example:
- dependence on fixed routes and localities may be catastrophic in unstable habitats - too big flocks may cause intraspecific competition when available open water and food is limited.

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This paper examines some of these aspects of migration strategy as revealed by studies of Whooper Swans in Sweden and in general through the western Palearctic.

The Whooper Swan in Sweden

The Whooper Swan is considered an arctic fauna element. The present distribution of the subspecies *C. c. cygnus* is holarctic; the nominate form breeding in the taiga lakes of Eurasia, the subspecies *buccinator* (the Trumpeter Swan) replacing it in North America.

Whooper Swans have occurred all over Sweden since the last glaciation. The first documented breeding refers to an eggshell, found near Falsterbo, Scania, southernmost Sweden, dated back to about 14,000 years BP (cf. Löppenthin 1952).

In recent times, however, the breeding distribution has been restricted to the northern parts of the country. In recent decades this formerly exclusive and rare breeder of the northernmost parts of Sweden, however, has also established a breeding population in southern Sweden (cf. Hansson 1968, Holmgren & Karlsson 1982, Arvidsson 1987). The total Swedish breeding population is estimated at 400-500 pairs, about half of them breeding in middle and southern Sweden.

Western Sweden forms the north easternmost part of the regular winter distribution of Whooper Swans breeding in Western Palearctic. The recent winter population is of the order of 2,500 individuals (Nilsson 1987), the most important winter quarters being found along the Swedish west coast. During autumn and spring migration, on the other hand, thousands of Whooper Swans pass and rest in southern Sweden, indicating that most migrants are of non-Swedish origin.

Materials and definitions

Up to now, ringers attached to the Swedish Bird Ringing Centre (and previously, before centralization in 1960, to other ringing bodies, such as the Natural History Museum of Gothenburg), have ringed 38 Whooper Swans in hard winters, mainly in The Sound, a semi-marine coastal strait in south westernmost Sweden, resulting in seven recoveries of dead birds.

My own, recent studies of wintering birds are restricted to two different flocks in two habitats in the west coast area of Sweden - one in a freshwater lake, Stensjön, Mölndal, another in a coastal,

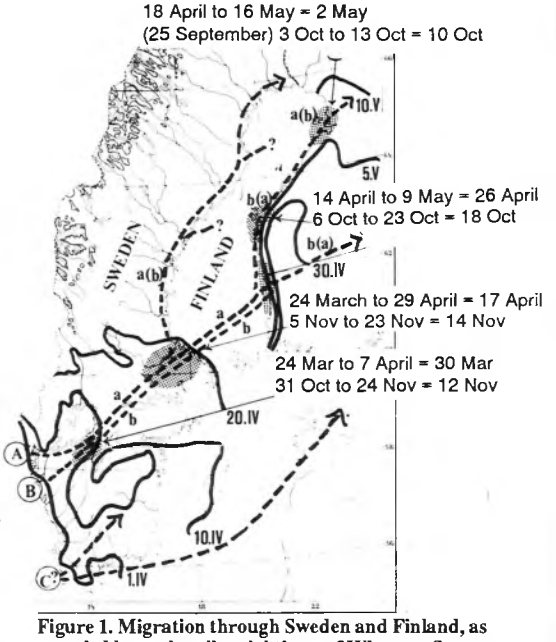

Figure 1. Migration through Sweden and Finland, as revealed by neck-collar sightings, of Whooper Swans wintering as A = Malö Stömmar, B = Stensjön, C = The Sound (öresund) shown by broken lines (small letters refer to winter quarters). Solid curves = isotherms for +3°C (Sweden) and +5°C (Finland) in spring (period: 1.IV to 10.V) Shaded areas = major resting areas, visited by A and B swans. To the right is shown the interval in which neck-collar swans have been observed during spring and autumn migration, and average migration, and average date for all observations.

marine habitat, Malö Strömmar, Dragsmark, Bohuslän (Fig. 1). Since 1977, we have ringed 118 Whooper Swans - 85 with neck-collars (international codes: one figure, one letter, two figures, white on blue background, e.g. 1P15). They have produced several hundred resightings of living birds, and eight reports of dead birds.

This study is based on recoveries of ringed birds from these three localities, and numerical counts throughout the year, as well as field studies and some replacement experiments.

In this paper I use the term "winter haunt" for the localities used by the swans during their winter stay in a certain "winter quarter" (composed of proximate and ultimate haunts respectively). The swans of a certain winter quarter are dispersed over a wider area (proximate haunts) during milder winter conditions. The proximate haunts are normally better ones from a nutritional and habitat point of view. Open water, equally important as natural food, however, becomes inaccessible because of ice or snow cover. Ulti-

mate winter haunts offer none or very limited natural food, just open water; the swans depend on food supplied by humans. Several quarters (or "sub areas") form "wintering areas", which together constitute the "winter distribution" of the species. The site is just a place for swans, whether permanent or not.

Wintering Whooper Swans at Lake Stensjön, Malö Strömmer and Öresund (The Sound)

1) Numbers

The freshwater Lake Stensjön

Numbers fluctuated from 35 to 77 birds between the years 1978-87. The overall average is 57; the average proportion of yearlings being 19%. The average brood size is 2.5 cygnets per successful pair.

The maximum numbers were 40 in 1986-87 and 61 in 1986-87. The proportion of yearlings was 25 and 34% of the total number; the proportion of successful breeding birds was 33% and 40%. The average brood size was 2.0 and 2.6 cygnets.

Twenty-three adult swans, one immature and 23 cygnets have been neck-collared.

The marine habitat Malö Strömmar

During some years numbers were very low, or the swans were absent, due to weather conditions.

The maximum numbers were 200 in 1986 and 337 in 1987. The proportion of yearlings was 9 and 8% of the total number; the proportion of successful breeding birds was 9 and 7%. The average brood size was 1.9 and 2.5 cygnets per successful pair.

Forty-five adult swans, 8 immature and 19 cygnets have been neck-collared.

The brackish öresund (The Sound)

Numbers fluctuated very much depending on winter conditions (between 500 and 2000 birds). No figures on cygnets were available.

About 30 have been leg-ringed. One neck-collared swan, initially ringed in Denmark, has stayed in the area.

Summing up, we can see that:
the proportion of juveniles as well as the proportion of successful breeders differ between the winter flocks of the three winter quarters, though the average brood size of the haunts, however, was the same.

2) Exchange of individuals between the three winter quarters

In spite of the very close distance (72 km) between Stensjön and Malö Strömmar no exchange of swans has been noted between the two flocks, nor between Stensjön and The Sound (Barsebäck, 220 km apart).

An adult pair from the flock of Malö Strömmar was found wintering in The Sound (Barsebäck, 290 km S). The swans might have been passing migrants when ringed at Malö Strömmar on 5 March 1985, as they were observed at Rekekroken, Skälderviken (230 km S) on the 23rd in the same month. They were checked again in the subsequent winter (on 2, 8 and 12 March 1986) in öresund (Barsebäck), having passed Nibe at Jutland, Denmark on their migration. They were never resighted at Malö Strömmar.

3) Recurrence, flock structure and social behaviour

Resighting of marked birds in the winter quarter is normally high (*Mathiasson* in press). However, some individuals have been found during subsequent winters, either to stay in the northern sector of their migration zone, or to prolong their migration southwestward. The swans of Malö Strömmar prolong their migration to Jutland and further on to the Netherlands, but those of Lake Stensjön follow a more eastern route to Sjaeland and Fyn in Denmark and further on to Rostock in Germany.

Swans in their second winter tend to return to the same winter quarter, where they spent their first winter with their family. The cygnets from previous years were still accepted by their parents at ages of two, three and four years (even when they were paired). Their parents, however, at the same time vigorously rejected other swans in their immediate surroundings.

Some replacement experiments:
We have brought foreign swans to the flocks on four occasions, and found that they were mobbed by the flock members wherever they occurred in the flock. One swan was forced to land, where it was later found dead (killed by fox). The other three were expelled from the flock and escaped flying.

Five neck-collared swans were separately relocated to sites 100 km from the flock of their

ultimate winter haunt. They returned immediately and were accepted with calls and neck-stretching.

We may stress the following facts, based on resightings of neck-collared swans (details in press):
- the families migrated as a unit to the winter quarter and stayed together during winter. Spring migration was still performed as a family group
- the family groups moved between proximate haunts and their ultimate winter haunt
- adult swans as well as independent juveniles/subadults recurred in succeeding seasons in the same places during migration and in winter
- when later migrating on their own, the offspring proved able to adjust for great deviations in relation to their first winter quarter, to which they returned - some of the offspring changed winter quarter when paired.

Migration of Swedish west coast swans

1) Geographical course

Recoveries and resightings of marked swans indicate different geographical routes for swans wintering in south western Scania to those wintering in the northern west coast area (Stensjön-Malö Strömmar). Furthermore, there are differences between the sub-populations wintering in Lake Stensjön and those at Malö Strömmar (Fig. 1).

Whooper Swans wintering in The Sound (öresund) leave in an eastern direction, initially separated from the route of the two northern sub-populations as far as the Baltic states and the Leningrad-Ladoga area. On their way they pass the White Sea, from where they turn eastward. The only records so far from northern Russia are from the arctic coast.

The swans of Stensjön and Malö Strömmar also initially fly in an eastern/north-eastern direction passing and resting in the lakes of Västergötland and later on in (Närke) Västmanland-Dalarna. From here they veer towards the northeast, some of them following the Swedish coast northward, then passing northern Finland and so to the east.

One portion leaves the eastern middle Swedish resting grounds for a flight across the lower part of the Bothnian Sea reaching the Finnish coast between Björneborg and Wasa, from where they either turn northwards or fly to the east. Those following the more southern alternative are mainly the wintering birds of Stensjön; those following either the Swedish northern east coast or the Finnish west coast to the north are swans from Malö Strömmar. The ratio is 71:29 (Stensjön birds) and 38:62 (Malö Strömmar birds) for Vasa (Pori)-Björneborg/Oulu (Uleåborg).

The individual recurrence in certain resting haunts from year to year, from season to season, is high. Some birds have recurred five seasons at one and the same resting site.

Consequently, we may state that:
- geographically different sub-populations of wintering birds follow different migratory patterns
- the migration of such birds takes place in restricted zones (narrow front)
- the recurrence within a certain zone, and even the fidelity to certain haunts along the migration zone is high
- the routes of different sub-populations may converge in certain areas.

2) Timing

Whooper Swans from the three different haunts normally leave their winter quarters at the end of March and beginning of April. The time for departure depends very much on the weather and the severity of the winter.

Figure 1 suggests a relationship between the isotherm for +3°C/+5°C and spring migration, i.e. the migration is related to the time when the frozen, ice-covered lakes and streams are thawing. Whooper Swans in many areas during migration stay on fields inundated by meltwater. They may graze on land, but need open water for shelter.

It takes 3-4 weeks for the Whooper Swans to reach south western Finland, and another month to reach the northern Soviet Union. The eastern-most records of Whooper Swans ringed in Swedish winter quarters are from the area of Sorka and Naryan-Mar (about 52° 30′ E, 66° 45′ N; 2350 km northeast of the winter quarter, west of the Ural Mountains). These records were from 21 June and 7 June. The time of year suggests that those two birds were close to their breeding areas.

The swans quite often remain for up to a fortnight, especially at their middle Swedish resting grounds (e.g. northern Västergötland in the west of Sweden, and southeast Dalarna and Västmanland in the east) and in their western Finnish resting grounds (e.g. Wasa area in the southwest and Uleåborg in the northeast). However, usually an individual swan is only seen

two to four days at the same spot. Ice and snow conditions determine the actual migratory time-table. The flight between these important resting grounds, however, is mostly direct and fast. The swans rarely rest in between them.

As previously stated adult breeders, families and cygnets, migrate as units and have the same time-table during autumn and spring migration. After the young become independent in their first summer, they migrate on their own.

General migration of Palearctic Whooper Swans

We may subdivide the Palearctic Whooper Swans into four major groups:

I) The Icelandic populations (wintering in the British Isles).

II) Southwestern migrants (wintering in western continental Europe, breeding west of Ural Mountains). Tens of thousands (Atkinson-Willes 1981).

III) Southern migrants (wintering around the northern parts of the Black Sea and Caspian Sea, breeding east of the Ural Mountains between Ob/Irtysh and Yenisai rivers). Winter numbers tens of thousands (Lisenko 1987, Rusanov 1987, Ravkin 1991).

IV) Southeastern migrants (mainly wintering in Japan, but also in Kamtchatka, Korea). Winter numbers thousands (Horiuchi 1981).

This suggested subdivision is supported by data from field observations on numbers, time-tables and direction of flight, though not for all areas and populations by recoveries and resightings of ringed birds.

Migratory characteristics of different Palearctic Whooper Swan populations

Population I

The use of neck-collars on swans from Iceland has proved their wintering grounds in the British Isles, and revealed numerous other details (Gardarsson 1991).

Population II

Neck-collaring of swans breeding in southern and central Sweden winter in southwest Sweden, in Denmark and the Netherlands (Mathiasson unpubl.). Two northern Finnish breeding neck-collared swans were observed at Gävle in central

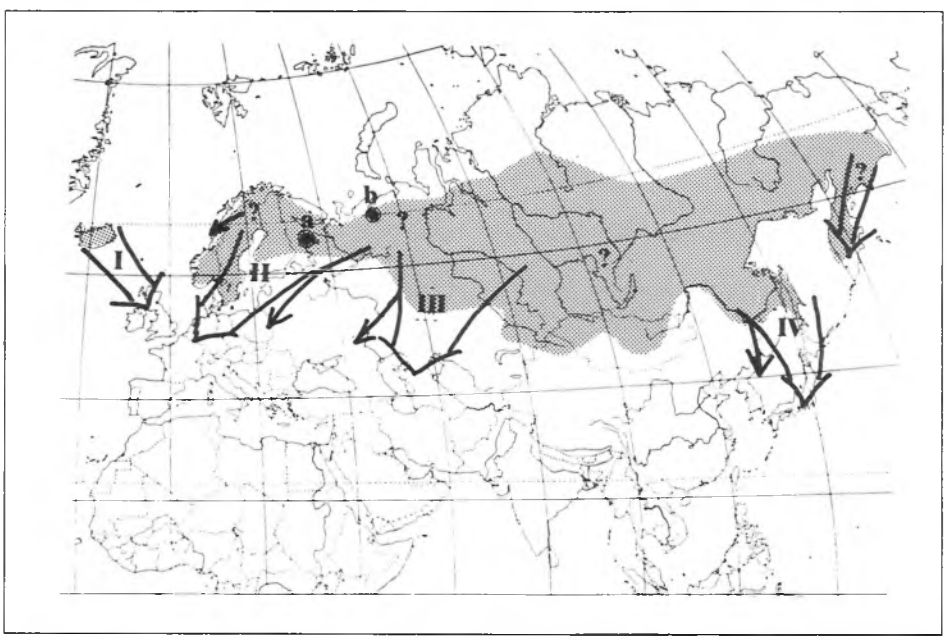

Figure 2. Migration of Palearctic Whooper Swans. Shaded section = breeding area. Arrow = direction to winter areas. Only movements of I, II and IV are revealed by marked birds. "Northern Nordic Swans" in the west and "Anadyr Swans" in the east are by many authors supposed to migrate as indicated. The migration divide between populations I and II needs further documentation, so do migration dividers in the far east. The migratory behaviour of central Asian populations is still not known.

Sweden, and a complete family close to Malö Strömmar (pers. obs. and Ohtonen pers. comm.) Danish wintering neck-collared Whooper Swans fly northeastward to unknown breeding grounds (Preuss 1981), as do south western Swedish swans (cf. above).

Baltic-Fennoscandia: These swans leave the winter grounds in late March to early April. The first northern Fennoscandian (Lapland) breeders appear at breeding grounds around 31 March to 1 April. The breeding sites, however, are not visited until 4-5 weeks later, when nest construction and egg-laying immediately takes place (Blomgren 1974, Haapanen 1991). Hatching occurs (11 June) 20-25 June (Swedish Lapland, Blomgren op. cit.). The swans leave their breeding sites around 20 September to 10 October (20 October) (southern Norway, Myrberget 1981).

Soviet Union: It seems that here the schedule is somewhat later for more eastern breeders. Hatching about 1-15 July (USSR Lapland, Bragin 1987). Consequently, the bulk of swans migrating through Sweden, and neck-collared swans (cf. above) arriving in western Finland between 14 April to 16 May (average 26 April to 2 May) are probably heading eastward. Furthermore, neck-collar sightings are reported from the White Sea, but none from the intensely studied Finnish breeding grounds (V.V. Bianki, A. Ohtonen pers. comm.).

Population III

The first spring migrants pass Kazakhstan between 13 March to 15 April (average 5-8 April), mass migration 7-12 April (Andrusenko 1987, Auezov & Gravhev 1987, Drobovtsev & Zaborskaya 1987, Gordienko 1987, Auezov *et al.* 1987).

The first arrive at the southern breeding grounds (Baraba) on 3 April, but mass migration continues to 20 April (Fyodorov & Khodkov 1987). In the northern breeding grounds the first swans return to lower Ob and southern Yamal between 9-24 April (average 14 April) and 6-29 May (average 16 May); the mass migration taking place between 1-12 May at lower Ob (Braude 1987, Kalyakin & Vinogradov 1987). Hatching at Baraba occurs about 6-15 June and, at Yamal, could be estimated to take place during early July. The swans leave southern Yamal about 1 September to 1 October, arriving and passing Kazakhstan about 15 September to 31 October (op. cit. above, and Varshavski 1987). The Caspian Sea and Lake Azov is reached between 23 October to 5 December (Karavayev 1987, Lisenko 1987).

Population IV

The Japanese wintering swans leave in April (Tamada 1981). In the Amur area of USSR mass migration occurs from 20 April to the first half of May with some still in June (Roslyakov 1987). The Whooper Swans breeding at Anadyr are supposed to winter in Kamnchatka (Kondratiev 1991). The Japanese wintering birds seem to belong to the breeders of central eastern USSR.

In central Yakutia, between the rivers Lena and Kolyma, the first migrants appear from 23 April to 7 May in the middle and central courses of Kolyma between 30 April to 12 May, and in the northern, lower Lena as late as 25 May. Hatching occurs in lower Amur in the first half of June (Roslyakov 1987), and northern Yakutia around 15 July to 8 August. Autumn migration started in Yakutia about 10 to 18 September (15 October) (Labutin *et al.* 1987), in lower Amur migration took place from 15 September to 15 November.

Discussion and Conclusions

The time-table of migration of the different Palearctic populations is similar. The swans of the central and northernmost Palearctic areas, however, normally have to wait longer for improved climatical conditions; their arrival at breeding grounds being later than for breeders to the west and east. The annual reproductive cycle involves early return for the breeders, which stay 4-5 weeks in "waiting grounds", near to the breeding sites. Swedish wintering swans needed approximately two months to reach their Russian breeding grounds.

Many observers (e.g. Finland, Haapanen & Hautala 1991, lower Ob, Braude 1987) have noted that Whooper Swan migration occurs locally in two or several waves. Haapanen & Hautala (op. cit.), suggest a different time schedule for breeders and non-breeders. My own results prove that different geographical populations have a different time schedule, passing one and the same area in different waves. The waves may under special climatological conditions be contracted to one (Braude 1987).

Migrating neck-collared birds follow the isotherms +3-5°C in spring through Sweden/Finland. A similar relationship was found in northern Kazakhstan (Drobovtsev & Zaborskaya 1987). The arrival of the first swans may be delayed by 15-20 days in cold springs (Braude 1987). However, swans have been observed to

arrive when temperatures were still around -20°C (Western Siberia, Fyodorov & Khodov 1987).

When the breeding sites are ice-free nest building takes just a few days and egg-laying begins. Egg-laying may take a week, incubation 33 days. The young are fledged after another eight weeks. Hatching in the western, southern and eastern-most parts of the breeding area takes place in June, while hatching in the central and northern parts may occur in July, and even sometimes in early August.

In the north eastern European USSR (Petchora) the loss of young increased, especially in late and immature broods, with adverse climatic conditions (frost, ice cover etc.) in September (Mineyev 1987). The average brood size just after hatching is of the same order for different populations (Swedish Lapland 3.8 (n = 26), North Norway 3.7 (n = 37), Yamal 4.0 (n = 9), Baraka 4.5 (n = 18)).

Pairs which have bred once, do not do so continuously or annually. The numbers of non-breeders in all northern populations are very high (northern Finland 70-80% (Haapanen 1976, 1989), Kola, Northern Karelia, Kanin Peninsula 35% (Bianki & Shutova 1987), Kamchatka 70-80% (Gusakov 1987)).

Temperature also influences the start and timing of autumn migration (external stimulae). Mass migration at the end of September has been related to freezing (Yakutia, Labutin *et al.* 1987).

Swedish winter quarters had a very restricted exchange, if any, of individual swans, though the recurrence of individual swans in succeeding winters in one and the same winter quarter was high. Displaced swans, not members of the actual winter flock (winter haunt), were rejected by the flock members. Swans caught in the flock and released at some distance returned to the haunt and were accepted by the flock.

Direction, time and distance are factors of migration. As in most life activities, the migration of the Whooper Swan is based on casual and functional elements. Furthermore, inherited functions interplay with learned or adapted behaviour. The basic time-table of migration in the Whooper Swan is inherited and has evolved in relation to general prevailing climatical conditions. The actual weather (external releaser), however, sets the exact date of departure, a flexible time from year to year.

Whooper Swans are long-lived, and successful broods may be large. Within the context of life-time reproductive success, the swans can adopt a migratory strategy including colonization of areas where reproduction may not be successful every year.

Reproductive success, among other things, depends on an accurate timing of the arrival at and the departure from the northern breeding grounds. Late arrivals will reduce the possibilities for the birds to improve their physical condition before breeding, and delay the start of breeding. Hatching later than July will be hazardous as autumn migration in most areas has to start in the middle of September. Fluctuations in numbers of successful breeders are influenced by the inconsistency of weather conditions.

Adaptations favouring optimum timing will be advantageous for different age and social classes of swans involved in migration. We recognize separate time-tables for immature non-breeders and adult breeding birds, and their cygnets. Potential breeders may by an early start either suffer death through adverse weather and food conditions, or increase the chances for successful reproduction. Non-breeders avoid the climatological hazards of an early migration by leaving the winter quarters later and moving slower. For cygnets, on the other hand, a delayed and separate departure could be disadvantageous because they would lose by not learning from the behaviour of their parents.

Eurasian Whooper Swans, as a consequence of the long time needed for reproduction, gain from wintering close to their breeding sites; thereby reducing costs for long-distance migration in time and energy. Birds flying to presumptive breeding grounds beyond a certain point will not have time to reproduce, and this behaviour consequently will not survive. This, and historical, factors may explain the position of the main migration dividers.

My Swedish studies indicate different geographical origin and migration routes of different wintering flocks, even those having winter quarters very nearby. Family migration and individual recognition (social organization) preserve population characteristics in migration. Consequently, the geographical course of the migration of different sub-populations depends highly on imprinting and tradition related to topographical and habitat factors.

References

Arvidsson, B. 1987. Sångsvanens *Cygnus cygnus* utbredning och populationsstorlek i Sverige. *Vår Fågelvärld* 46:248-255.

Atkinson-Willes, G.L. 1981. The numerical distribution and conservation requirements of swans in northwest Europe. In: G.V.T. Matthews & M. Smart (Eds.) *Proc. 2nd Int. Swan Symp.* Sapporo, 1980. IWRB, Slimbridge.

Blomgren, A. 1974. Sångsvan. Bonniers.

Gardarrson, A. 1991. Movements of Icelandic Whooper Swans *Cygnus cygnus* neckbanded in Iceland. In: J. Sears & P.J. Bacon (Eds.) *Proc. 3rd Int. Swan Symp.* Oxford, 1989. *Wildfowl.* Special Supplement No. 1.

Hansson, L. 1968. Sångsvanen som skånsk hackfågel. *Medd. SKOF* 7:45-50.

Haapanen, A. 1976. Breeding distribution and migration of swans in Finland. *Bird Migration*, Tallin 1976:189-190.

Haapanen, A. 1991. Whooper Swan *Cygnus cygnus*, population dynamics in Finland. In: J. Sears & P.J. Bacon (Eds.) *Proc. 3rd Int. Swan Symp.*, Oxford, 1989. *Wildfowl.* Special Supplement No. 1.

Haapanen, A. & Hautala, H. 1991. Bimodality of spring migration of the Whooper Swan *Cygnus cygnus*, in Finland. In: J. Sears & P.J. Bacon (Eds.) *Proc. 3rd Int. Swan Symp.*, Oxford, 1989. *Wildfowl.* Special Supplement No. 1.

Holmgren, V. & Karlsson, J. 1982. Sångsvanen fortsätter att öka i Skåne. Resultat från en inventering 1978-79. *Anser*:163-168.

Horiuchi, M. 1981. Ten years of swan counts in Japan. In: G.V.T. Matthews & M. Smart (Eds.) *Proc. 2nd Int. Swan Symp.*, Sapporo, 1980. IWRB, Slimbridge.

Kondratiev, A. Ya. 1991. The distribution and status of Bewick's Swan *Cygnus bewickii*, Tundra Swan *C. columbianus* and Whooper Swan *C. cygnus*, in the 'Extreme Northeast' of the USSR. In: J. Sears & P.J. Bacon (Eds.) *Proc. 3rd Int. Swan Symp*, Oxford, 1989. *Wildfowl.* Special Supplement No. 1.

Löppenthin, B. 1952. *Danske ynglefugle i fortid og nutid.* Odense Universitetsforlag.

Myrberget, S. 1981. Breeding of *Cygnus cygnus cygnus* in a coastal area of southern Norway. In: G.V.T. Matthews & M. Smart (Eds.) *Proc. 2nd Int. Swan Symp.*, Sapporo, 1980. IWRB, Slimbridge.

Nilsson, L. 1987. Internationella sjöfågelinventeringarna i Scerige 1986-87. *Vår Fågelvärd* 46:279-286.

Ohtonen, A. & Huhtala, K. 1991. Whooper Swan, *Cygnus cygnus*, egg production in different nesting habitats in Finland. In: J. Sears & P.J. Bacon (Eds.) *Proc. 3rd Int. Swan Symp.*, Oxford, 1989. *Wildfowl.* Special Supplement No. 1.

Preuss, N.O. 1981. Preliminary results of neck-collared *Cygnus cygnus cygnus*. In: G.V.T. Matthews & M. Smart (Eds.) *Proc. 2nd Int. Swan Symp.*, Sapporo, 1980. IWRB, Slimbridge.

Ravkin, Y.S. 1991. Number and distribution of Mute Swans *Cygnus olor*, Bewick's Swans *C. bewickii* and Whooper Swans *C. cygnus*, species in the West Siberian plain. In: J. Sears & P.J. Bacon (Eds.) *Proc. 3rd Int. Swan Symp.*, Oxford, 1989. *Wildfowl.* Special Supplement No. 1.

Tamada, M. 1981. The wild swans at lake Tofutsu-Ko, Hokkaido, Japan. In: G.V.T. Matthews & M. Smart (Eds.) *Proc. 2nd Int. Swan Symp.*, Sapporo, 1980. IWRB, Slimbridge.

Voous, K.H. 1960. *Atlas of European Birds.* Nelson.

The following authors are cited from "Ecology and Migration of Swans in the U.S.S.R.", Academy of Sciences of USSR, Institute of Evolutionary Morphology and Ecology of Animals, Moscow 1987.

Andrusenko, N.N. p.107; Auezov, E.M. & Gravhev, V.A. p.140; Bianki, V.V. & Shutova, Y.V. p.20; Bragin, A.B. p.142; Braude, M.I. p.97; Drobovtsev, V.I. & Zaborskaya, V.N. p.104; Fyodorov, Y.G. & Khpdlov, G.I. p.100; Gordienko, N.S. p.110; Gusakov, Y.S. p.126; Kalyakin, V.N. & Vinogradov, V.G. p.95; Karavayev, A.A. p.124; Auzov, E.M. *et al.* p.116; Labutin *et al.* p.132; Lisenko, V.I. p.66; Mineyev, Y.N. p.17; Roslyakov, G.Y. p.136; Rusanov, G.M. p.69; Varshavski, S.N. p.119; Shadilov, Y.M. & Orlov, V.A. p.77.

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