

Spring migration of Barnacle Goose *Branta leucopsis* and Dark-bellied Brent Goose *B. bernicla bernicla* over Sweden

MARTIN GREEN

Abstract

Numbers of migrants, flock sizes, influence of winds, geographical pattern, and timing of spring migration of Barnacle Goose *Branta leucopsis* and Dark-bellied Brent Goose *Branta bernicla bernicla* over Sweden during 1981–1995 are reported. Both species showed a general increase in passing numbers during the period, in good agreement with overall population trends. Flock sizes of Brent Geese in Sweden were larger than those at departure from the Wadden Sea while flock sizes of Barnacle Geese were similar in Sweden and at the Wadden Sea. Flocks migrating overland were larger than flocks following the coast for both species. There was a preference for migrating in

tailwinds. Normally 70–90 % of all observed birds (both species) were recorded in the most southern provinces. Median dates of passage was 19 April for Barnacle Goose and 25 May for Brent Goose. The time pattern of Barnacle Goose changed during the period with a higher proportion passing in May during the later years of the study. Timing of Brent Goose passage did not change, although it was delayed in headwind years.

*Martin Green, Dept. of Animal Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden
E-mail: Martin.Green@zoekol.lu.se*

Received 24 April 1998, Accepted 21 October 1998, Editor: Å. Lindström

Introduction

Each spring large numbers of Barnacle Geese *Branta leucopsis* and Dark-bellied Brent Geese *Branta bernicla bernicla* pass Sweden on their way from winter and early spring staging areas in western Europe towards their breeding areas, situated mainly in arctic Russia. The general timing and the geographical pattern of this passage are well known (see below) but no detailed national compilation of migration data have previously been made, only some good regional or local analyses (Hjort 1976, 1977, Hasselquist 1981, Wirdheim 1981, 1988). I have collected data from the regional bird reporting system of the Swedish Ornithological Society, certain bird observatories, observers at migration sites and from a special study in south Sweden. I give a detailed description, analysis and comparison between the species of numbers of migrants, flock sizes, influence of winds, geographical pattern and timing of the spring passage in Sweden during the fifteen year period 1981 – 1995.

The Barnacle Geese that pass Sweden winter mainly in the Netherlands (Ebbinge et al. 1991). About half the population leave this area in late

winter for a short flight to north-west Germany, which is a major early spring staging area (Busche 1991, Ebbinge et al. 1991). From the Netherlands and Germany they then fly to the next major spring staging areas in the Baltic (Gotland and Estonia) and during this flight they pass south Sweden. Usually the whole population is found in the Baltic area from late April to mid May (Leito 1991). About 90–95 % of the birds then continue to Russian breeding areas, mainly Novaya Zemlya and Vaygach (Ebbinge et al. 1991). An increasing number remain and breed in the Baltic area, mainly at the Swedish islands of Gotland and Öland (Larsson et al. 1988, Waldenström 1995, SOF 1997).

Dark-bellied Brent Geese winter mainly in France and England (Bergmann et al. 1994). They leave the wintering areas in March for their first main spring staging sites in the Wadden Sea. Here they increase heavily in mass and in late May they pass south Sweden when conducting a (probably) direct flight of about 2 500 km to the White Sea and surrounding areas in Russia (Ebbinge & Spaans 1995). In mid June they continue to their breeding areas, mainly at the Taimyr peninsula (Bergmann et al. 1994).

Material

The data in this study come from the following sources: 1) replies to inquiries sent to the majority of the regional report committees of the Swedish Ornithological Society, 2) communication with bird observatories and field observers, 3) literature search in local and regional ornithological bulletins, and 4) migration studies made in Lund, Skåne (55° 42' N 13° 12' E). The time period covered by the overall analysis of timing and geographical patterns was restricted to 1981–1995, since data before 1981 were too heterogeneous to be included.

Most of the regional report committees (24 of 27) that got the inquiry replied. Inquiries were not sent to the regions in the mountainous north-west part of the country where migration of these species never have been observed (selection made based on SOF 1990). The report committees compile records of voluntarily reported bird observations from ornithologists. Most regions collect data on migrating Barnacle Geese and Brent Geese, but not all. In south-east Sweden, i.e. the regions of Blekinge, Öland and Gotland, where migration is intense, no data are collected routinely. This is because these species are considered to be too numerous, making it difficult to handle all the data each year. However, data from peak migration days are in many cases collected in these regions and are included in this analysis. My belief is that this lack of total coverage should not affect the conclusions of this study since yearly data have been included from Ottenby (56° 12' N 16° 24' E), a major migration site on Öland with daily observations throughout the migration seasons. From 1985 and onwards more or less yearly data from Utlängan (56° 01' N, 15° 48' E), a major migration site in Blekinge, have also been included. Furthermore, the report committees in Skåne and Halland, the two remaining provinces with high migration intensities, do collect all migration data on these species. From the provinces where the report committees did not respond to my inquiry and from the ones that did not get the inquiry, data have been collected from their regional bulletins.

All observations were summarized day by day. By comparing numbers of migrants, flight directions, passage times and localities a minimum daily number of passing geese was calculated. This was done under the assumptions that both species migrate over south Sweden in one uninterrupted flight and that the migratory direction is between north-east and south-east. Thus, if large number of geese were recorded at the south coast of Skåne and at Öland

(see Figure 1 for locations) during the same day the figures were not added to each other. Instead the highest number of geese at one of these places was used as the days minimum total of that particular day. If large numbers were seen in Skåne during the evening and high numbers had been recorded at Öland in the morning the same day, these numbers were summed since birds passing Skåne will pass Öland afterwards and not the other way around. Also, if large numbers were recorded in Skåne during the evening one day and at Öland the day after the figures have been treated as separate ones as flight time from Skåne to Öland makes it most likely that the birds seen in Skåne in the evening will pass Öland already during the night. The minimum daily sums were then used to calculate total numbers of birds observed per season, numbers passing different geographical zones, median dates and concentration of passage.

Data on flock sizes and flight directions were collected in Lund, Skåne, in the years 1995–1997, covering the complete migratory season each year. In addition, data on flock sizes were collected at Kåseberga, south-east Skåne (55° 21' N 14° 4' E) during 1995 and at Ottenby, Öland in 1996. At Ottenby, data on flock sizes were collected for Brent Goose only. At both localities the entire migration period was covered. Flight directions at Lund were measured by tracking migrating flocks with an optical range finder (WILD, 80 cm, 11.25X) with azimuth and elevation scales, or with a short-range tracking radar (X-band, 200 kW peak power, pulse duration 0.25 μ s, pulse repeat frequency 500 Hz, 1.5° pencil beam width) from the roof terrace of the Ecology Building, Lund University. For flocks passing relatively close to the observation site, that were observed by telescope or binoculars only, flight directions were estimated to the closest 22.5° (i.e. NE, ENE, E etc).

Data on annual population sizes and breeding success were obtained from the Goose Specialist Group Data Base, Wetlands International (J.Madsen & P. Clausen pers. comm.)

Wind data were obtained from the European Meteorological Bulletin (EMB, Deutsches Wetterdienst) for the relevant periods each year. Wind speed and direction are indicated by flags in the EMB, each full flag representing a wind speed of 10 knots (=5.1 m s⁻¹). This way wind speeds are given in classes approximately corresponding to 0; 1; 2.5; 5; 7.5 m s⁻¹ etc. Assuming that most geese passing Sweden start the flight from the northern part of the Wadden Sea, wind data from north-west Germany was used to

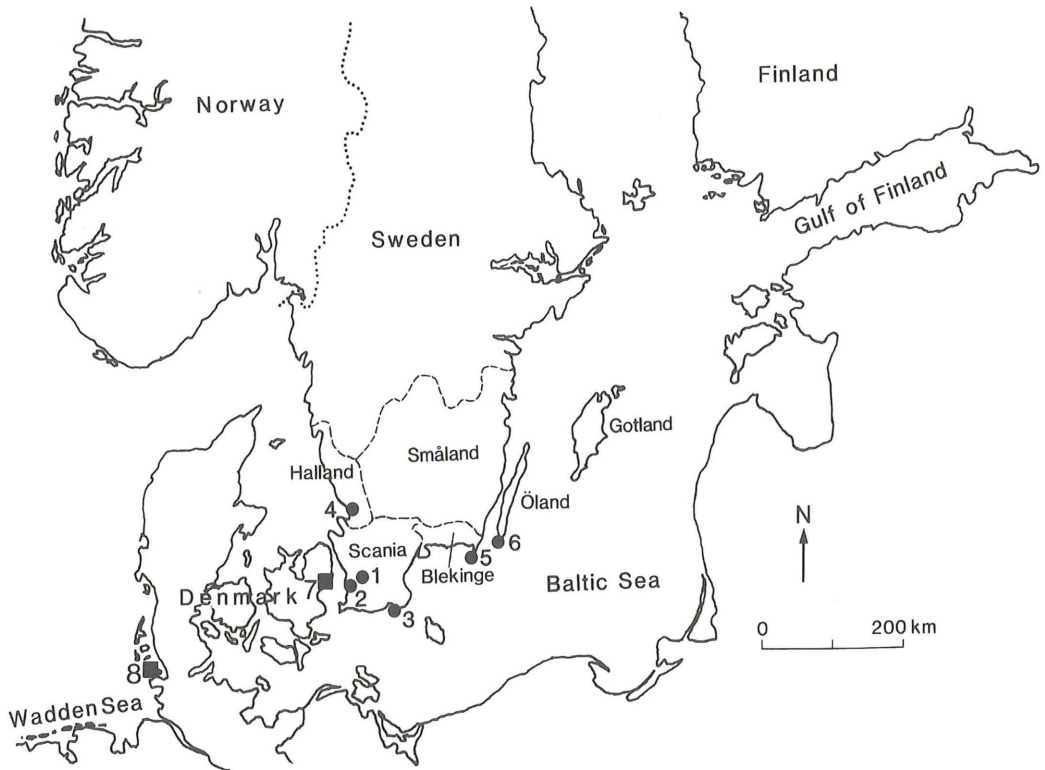


Figure 1. Map of south Sweden and the Baltic region. Main provinces mentioned in the text, main migration localities and wind measurement sites are shown. 1. Lund, 2. Lommabukten, 3. Kåseberga, 4. Laholmsbukten, 5. Utlängan, 6. Ottenby, 7. Copenhagen and 8. Wadden Sea.

Karta över södra Sverige och Östersjöregionen. Landskap och betydande sträcklokaler som omnämns i texten samt även vindmätningsslokaler visas. 1. Lund, 2. Lommabukten, 3. Kåseberga, 4. Laholmsbukten, 5. Utlängan, 6. Ottenby, 7. Köpenhamn och 8. Vadehavet.

analyze starting conditions. To analyze the passage over south Sweden, wind data from Copenhagen, Denmark were used since that was the closest weather station to south Sweden in the bulletin. Wind data in the EMB are given from 00 GMT and 11/12 GMT (= 02 and 13/14 local Swedish summer time). Depending on when during the day migration was observed over Sweden an assumed mean departure time was calculated based on flight speed measurements made in Lund (Green & Alerstam in prep.). Wind data closest in time to assumed departure or observed passage was used. For migration data with no exact time given, departure winds (Wadden Sea) from 00 GMT and passage winds (Copenhagen) from 11/12 GMT was used. All wind data in this report refer to ground level situations.

Migration data on Brent Geese from Finland and Denmark were taken from literature and personal correspondence with ornithologists. Finnish data

were only available from two years, 1987 (B. Ollberg and G. Nordenswan pers. comm. through N. Holmström) and 1993 (Leivo et al. 1995). Danish data were available for four years between 1988 and 1995 (Lindballe et al. 1993, 1994 and Preben Berg, pers. comm.).

Results

Number of migrants and flock sizes

For both species the number of reported migrants increased significantly during the period (Spearman rank correlation, Barnacle Goose: $r_s = 0.91$, $p = 0.0007$; Brent Goose: $r_s = 0.56$, $p = 0.03$, Figure 2). There were significant correlations between numbers observed in Sweden and overall population sizes in both cases (Kendall rank correlation, $\tau = 0.74$, $p = 0.0001$ for Barnacle Geese and $\tau = 0.39$, $p = 0.04$ for Brent Geese). The yearly numbers obser-

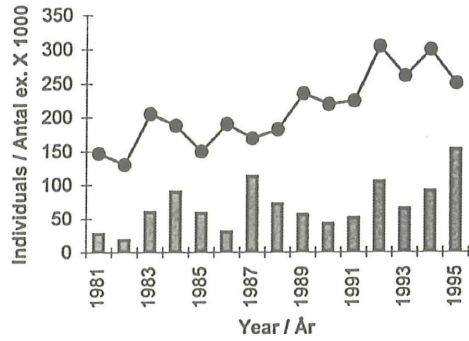
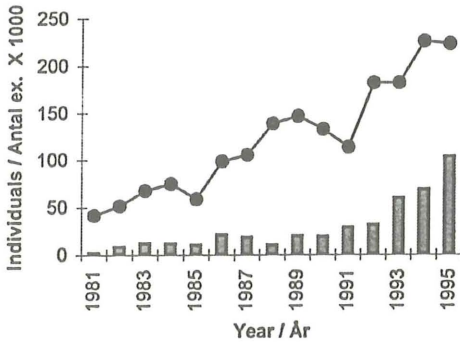


Figure 2. Seasonal totals of reported spring migrating Barnacle Geese (a) and Brent Geese (b) in Sweden 1981–1995 (bars) and overall population sizes (dots and line).

Säsongssummor av vårflyttande Vitkindade gäss (a) och Prutgäss (b) i Sverige 1981–1995 (staplar) och de totala populationernas storlek (punkter och linje).

ved in Sweden corresponded to between 6 and 47 % of the total population for Barnacle Goose, with a median of 18 %. For Brent Goose, between 14 and 67 % of the total population was seen every year, with a median of 29 %. Over the study period, significantly higher proportions of the Brent Goose population was reported (Mann-Whitney U-test, $n_1 = 15$, $n_2 = 15$, $z = -2.43$, $p = 0.02$) than for the Barnacle Goose. The proportion of the total population of Barnacle Goose seen in Sweden was relatively stable at about 15–20 % during the first twelve years of the period and then increased to 30–47 % in the last three years. The proportion of Brent Goose showed a much larger variation, with marked peaks in some years but no overall trend.

The distribution of flock sizes and individuals in different flock sizes at three main migration sites are shown in Table 1, whereas average flock sizes at the inland locality Lund and the coastal sites Kåseberga and Ottenby are presented in Table 2. Barnacle Goose flocks were significantly larger at Lund than at Kåseberga (Mann-Whitney U-test, $n_1 = 258$, $n_2 = 90$, $z = -4.28$, $p = 0.0001$). Also Brent Goose flocks passing Lund were significantly larger compared to those at the coastal sites Kåseberga and Ottenby (Mann-Whitney U-test, $n_1 = 310$, $n_2 = 111$, $z = -2.81$, $p = 0.005$ and $n_1 = 310$, $n_2 = 130$, $z = -2.81$, $p = 0.04$ respectively). Brent Goose flock sizes did not differ significantly between Kåseberga and Ottenby (Mann-Whitney U-test, $n_1 = 111$, $n_2 = 130$, $z = -0.84$, $p = 0.40$). Brent Goose flocks were significantly larger than Barnacle Goose flocks in Lund (Mann-Whitney U-test, $n_1 = 310$, $n_2 = 258$, $z = -2.15$, $p = 0.03$). At Kåseberga the tendency was in the same direction

(Mann-Whitney U-test, $n_1 = 111$, $n_2 = 90$, $z = -1.80$, $p = 0.07$) as can be seen from the mean and median values in Table 2.

Wind and migration intensity

Wind conditions (direction and strength) at Copenhagen during days with high migration intensity over Sweden are shown in Figure 3 a and b. A more detailed analysis of wind and weather patterns associated with the passage of arctic geese over Sweden will be presented elsewhere (Green in prep.).

A closer examination and categorization of the figures revealed some interesting patterns. I categorized winds from between SSW-WNW as true tailwinds, winds from between NNE-ESE as true headwinds, winds from ESE to SSW as sidewinds from the southern sector, winds from WNW-NNE as sidewinds from the northern sector and winds of not more than 1 m s^{-1} as neutral. Wind categories were chosen based on a generalized migratory direction towards ENE during the flight from the Wadden Sea over south Sweden. In Table 3 the number of days with high migration intensity in the different wind classes are shown together with the occurrences of winds during spring migration periods. The distributions of high migration intensity days were significantly different from the occurrences of winds for both species (Barnacle Goose: $\chi^2_{(4)} = 12.53$, $p = 0.01$; Brent Goose: $\chi^2_{(3)} = 8.30$, $p = 0.04$; in the statistical analyses for Brents both sidewind categories were pooled as the number of days with high migration intensity was too low during side winds from the north). During peak migration days, tailwinds were

Table 1. Distribution of number of flocks and individuals of spring migrating Barnacle Geese and Brent Geese at three localities in south Sweden in different flock size classes.

Fördelning av antalet flockar och individer av vårsträckande vitkindade gäss och prutgäss vid tre lokaler i södra Sverige fördelade på olika storleksklasser av flockar.

	Flock size <i>Flockstorlek</i>						N
	1-49	50-99	100-199	200-399	400-799	800-	
Barnacle Goose							
<i>Vitkindad gås</i>							
Flocks (%)							
<i>Flockar (%)</i>							
Lund	21.4	21.8	27.6	18.3	10.5	0.4	258
Kåseberga	40.0	27.8	13.3	16.7	1.1	1.1	90
Individuals (%)							
<i>Individer (%)</i>							
Lund	3.7	8.8	22.6	31.1	31.9	1.9	42 318
Kåseberga	11.0	18.3	16.8	40.6	4.5	8.9	8 986
Brent Goose							
<i>Prutgås</i>							
Flocks (%)							
<i>Flockar (%)</i>							
Lund	21.0	18.7	16.4	20.3	16.4	7.1	310
Kåseberga	32.4	18.9	19.8	14.4	12.6	1.8	111
Ottenby	32.3	15.4	16.2	20.0	11.5	4.6	130
Individuals (%)							
<i>Individer (%)</i>							
Lund	1.9	4.6	8.1	20.6	32.3	32.5	81 412
Kåseberga	2.7	7.6	14.8	22.7	39.2	12.9	20 365
Ottenby	3.6	5.0	9.7	26.3	26.7	28.6	27 265

used in a higher proportion than the occurrence of tailwinds. Winds from other directions (headwinds and sidewinds) were used in a smaller proportion than the occurrence of such winds. No difference between the species was found in this respect. High migration intensity days in headwinds were either in relatively low wind strength ($\leq 2.5 \text{ m s}^{-1}$); five of six occasions for Barnacle Geese, seven of nine occasions for Brent Geese; and/or late in the migratory season (after 20 April for Barnacle Goose, after 25 May for Brent Goose); three of six occasions for Barnacle Geese, six of nine occasions for Brent Geese; (Figure 3). Wind directions and strengths during peak days at the start of the flight from the Wadden Sea were very similar to the ones in Figure 3 and are therefore not presented.

Geographical pattern and flight directions

The passage of Barnacle Goose and Brent Goose over Sweden was mainly confined to the southern parts of the country. In Table 4 and Figure 4 I have divided Sweden in different geographical zones according to the amount of passing geese and arrows indicate the major migration corridors of both species.

The geographical pattern of Barnacle Goose passage was very stable between years with 70–97 % of all birds reported from the southernmost provinces (Skåne, Blekinge and Öland, zone 1) each year. Most birds were seen at Öland or in Skåne. Large numbers passed along the south coast of Skåne and then turned up towards the eastern part of Blekinge.

Table 2. Average flock sizes of Barnacle Goose and Brent Goose during spring migration at three sites of high migration intensity in south Sweden. Lund is an inland locality, Kåseberga and Ottenby are coastal sites.

Flockstorlekar hos vitkindad gås och prutgås under vårsträcket vid tre lokaler med hög sträckintensitet i södra Sverige. Lund är en inlandslokal, Kåseberga och Ottenby är kustlokaler.

Species <i>Art</i>	Locality <i>Lokal</i>	Mean <i>Medel</i>	Median <i>Median</i>	Range <i>Variation</i>	Year <i>År</i>	N <i>N</i>
Barnacle Goose <i>Vitkindad gås</i>	Lund	164	110	3-800	1995-97	258
	Kåseberga	100	60	4-800	1995	90
Brent Goose <i>Prutgås</i>	Lund	263	145	2-3000	1995-1997	310
	Kåseberga	183	97	2-1800	1995	111
	Ottenby	210	100	2-1700	1996	130

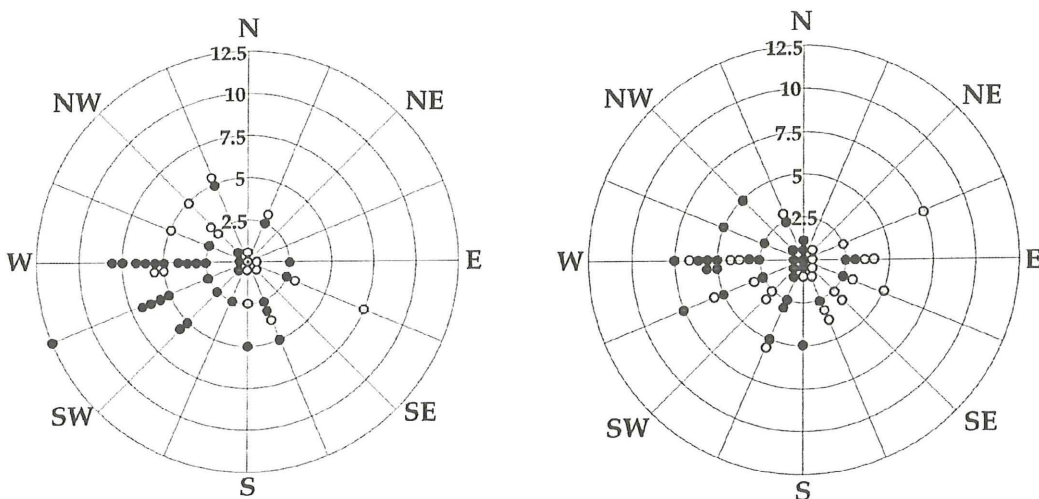


Figure 3. Wind conditions, direction (in 22.5° intervals, shown as a compass) and strength ($m s^{-1}$, increasing wind strength in outward going circles shown by numbers at the “North-axis”), at Copenhagen, Denmark during peak migration days of (left) Barnacle Geese (> 2 000 inds. observed) and (right) Brent Geese (> 5 000 inds. observed) in Sweden 1981–1995. The material has been divided in early (dots) and late (open circles) migration days. For Barnacle Geese, days up to 20 April was classified as early and days from 21 April onwards as late. For Brent Geese, days up to 25 May were regarded as early and days from 26 May onwards as late.

Vindförhållanden, riktning (i 22.5° intervall) och styrka ($m s^{-1}$, ökande vindstyrka enligt skala på “Nord-axeln”), uppmätta i Köpenhamn, Danmark under toppdagar av (vänster) Vitkindad gås (> 2 000 ex) och (höger) Prutgås (> 5 000 ex) i Sverige 1981–1995. Materialet är uppdelat i tidiga (punkter) och sena (öppna cirklar) sträckdagar: För vitkindad gås klassades dagar t.o.m. 20 april som tidiga och dagar fr.o.m. 21 april som sena. För prutgås klassades dagar t.o.m. 25 maj som tidiga och dagar fr.o.m. 26 maj som sena.

Table 3. Number of days with high migration intensity of Barnacle Geese (> 2 000 ind. observed) and Brent Geese (> 5 000 ind. observed), and the occurrence of winds (number of wind recordings, there are two measurements every 24 hours) during main migration periods (1 April - 5 May for Barnacle Geese, 11 May - 3 June for Brent Geese) in 1981–1995 in different wind classes (see also in text).

Antal dagar med hög sträckintensitet av vitkindad gås (> 2 000 ex observerade) och prutgås (> 5 000 ex observerade) och förekomsten (antal måttillfällen, två mätningar görs varje dygn) av vindar under vårflyttningssäsongerna (1 april – 5 maj för vitkindad gås, 11 maj – 3 juni för prutgås) 1981–1995 fördelat på olika vindkategorier (se texten).

Species Art	Tailwind Medvind	Headwind Motvind	Sidewind (left+right) Sidvind (vänster+höger)	Neutral winds Svag vind	N N
Barnacle Goose <i>Vitkindad gås</i>	24 (49.0%)	6 (12.2%)	5+6 (10.2+12.2%)	8 (16.3%)	49
Wind occurrence <i>Vindfördelning</i>	264 (26.3%)	190 (19.0%)	192+161 (19.2+16.1%)	195 (19.5%)	1002
Brent Goose <i>Prutgås</i>	24 (43.6%)	9 (16.4%)	3+6 (5.4+10.9%)	13 (23.6%)	55
Wind occurrence <i>Vindfördelning</i>	186 (26.3%)	144 (20.3%)	87+103 (12.3+14.5%)	188 (26.6%)	708

From there they passed Öland mainly on the eastern side of the island, heading for staging areas on Gotland or in Estonia. In some cases relatively large numbers crossed the southern parts of Öland but migration in Kalmarsund, between mainland Sweden and Öland, was usually less intensive. The numbers of Barnacle Geese crossing Skåne overland was similar to those following the south coast. Many of these birds flew in over land at Lommabukten, continued over Skåne and along the coast of Blekinge towards Öland where they took the same route as described above. Smaller numbers crossed mainland Sweden north of Skåne. A regular passage was observed in Halland, where the geese flew inland at Laholmsbukten, and over Småland (zone 2). Every year 2–30 % of the total numbers observed in Sweden were reported from these regions. Very small numbers were seen yearly north of Halland-Småland (zone 3 and 4), in many cases in association with the passage of *Anser sp.* geese.

Also the pattern of Brent Goose passage was fairly stable between years, although the variation was larger than for Barnacle Geese. Usually 72–94 % of all recorded birds were reported from the provinces of Skåne, Blekinge, Öland and Gotland (zone 1). Also here the main provinces were Skåne and Öland, but in some years equally large numbers were observed in Blekinge. The routes followed by Brent Geese

were similar to those described for Barnacle Geese. However, a higher proportion crossed Skåne overland. When reaching eastern Blekinge large numbers turned north and followed Kalmarsund. Normally 8–26 % of the birds each year were seen crossing mainland Sweden over the provinces of Halland and Småland (zone 2), mainly flying in overland at Laholmsbukten. Smaller numbers were seen annually in zone 3 (Figure 4 b). North of this, mostly single individuals were seen in flocks of other goose species, but in some years one or two flocks were seen as far north as the Gulf of Bothnia.

During two years, 1989 and 1992, the geographical pattern of Brent Goose migration was quite different from the pattern described above. In these years only 29 and 22 % of all birds were observed in the southernmost provinces (zone 1). Most birds were instead seen in Halland-Småland (zone 2) (51 and 67 %) and relatively large numbers were also seen in zone 3 (20 and 11 %). To analyse the variation in geographical pattern I plotted winds during the actual days when large numbers of Brent Geese (> 1 000 birds) were seen in zone 2–3 during 1989 and 1992. Almost all days with strong migration in zone 2–3 coincided with easterly winds, both at the start from the Wadden Sea and during passage of south Sweden (Figure 5).

Data on flight directions were collected for 192

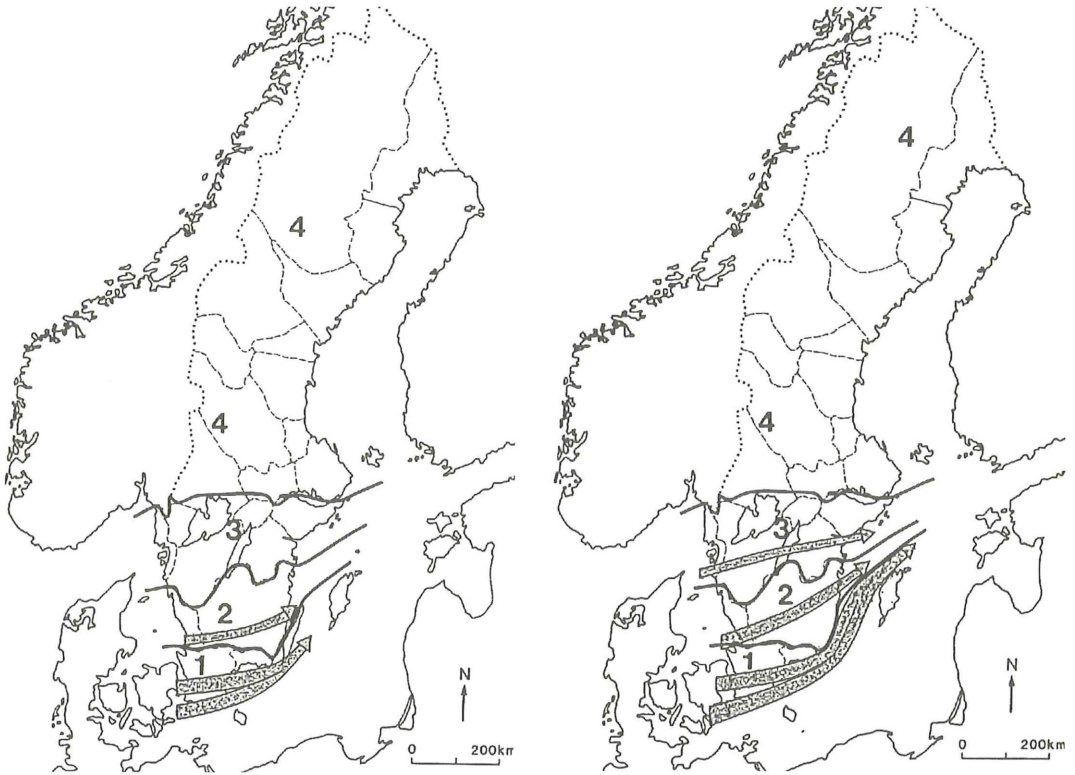


Figure 4. Main migration corridors and division in geographical zones according to observed migration intensity (see table 4 and text) of spring migrating Barnacle Geese (a) and Brent Geese (b) in Sweden 1981–1995.

Huvudsträckkorridorer och geografisk zonindelning efter observerad sträckintensitet (se tabell 4 och text) för vårflyttande Vitkindade gäss (a) och Prutgäss (b).

Table 4. Average percentages (\pm s.d.) of the total number of Barnacle Geese and Brent Geese passing different geographical zones of Sweden (see fig. 4 a and b) each spring during 1981–1995. A + sign means that the average percentage is below 0.5, but still the species is observed more or less annually. A – sign means that the species is not an annual migrant in the zone.

Procentuell fördelning (\pm s.d.) av antalet vitkindade gäss och prutgäss på olika geografiska zoner av Sverige (se figur 4 a och b) i medeltal per vårsäsong under 1981–1995. Ett +-tecken betyder att medelvärdet understiger 0.5 men att arten observerats i zonen mer eller mindre årligen. Ett - tecken betyder att arten inte är en årlig flyttare genom zonen.

Species	% in zone 1	% in zone 2	% in zone 3	% in zone 4
Art	% i zon 1	% i zon 2	% i zon 3	% i zon 4
Barnacle Goose Vitkindad gås	87.2 (\pm 7.5)	12.5 (\pm 7.2)	+	-
Brent Goose Prutgås	70.5 (\pm 22.4)	26.9 (\pm 18.6)	2.6 (\pm 5.5)	+

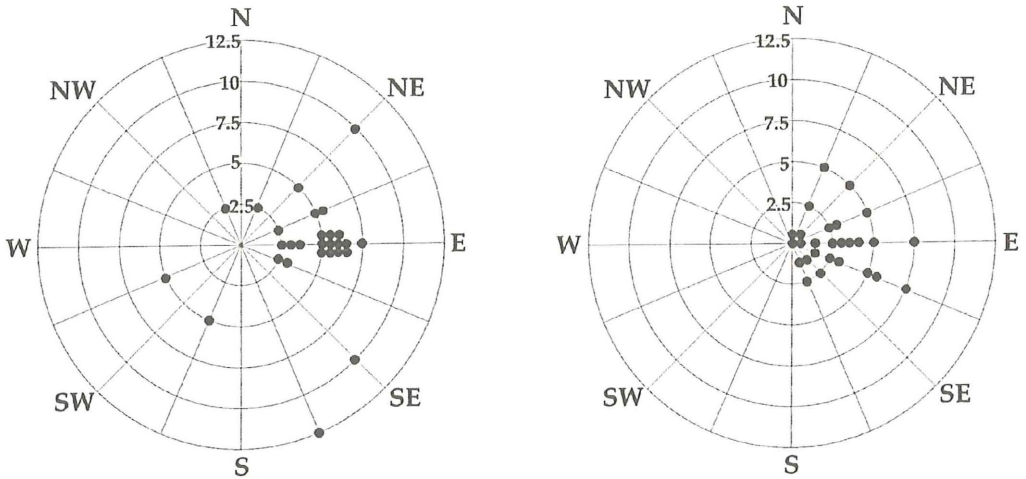


Figure 5. Wind conditions, direction and strength shown as in Figure 3, at the Wadden Sea (left) and Copenhagen, Denmark (right) during migration days of Brent Geese (> 1 000 inds. observed) in Sweden in 1989 and 1992.

Vindförhållanden, styrka och riktning, uppmätta vid Vadehavet (vänster) och Köpenhamn, Danmark (höger) under flyttmigrationsdagar för Prutgås (> 1 000 ex) i Sverige 1989 och 1992.

flocks of Barnacle Geese and 217 flocks of Brent Geese passing Lund. Of these flocks, 72 flocks of Barnacle Geese and 68 flocks of Brent Geese were tracked with optical range finder or tracking radar (exact migration directions measured). For the rest, flight directions were estimated visually. No significant differences were found between trackings and visual estimates or between years within the species so all data were pooled. Mean track direction of Barnacle Geese was 64° (\pm angular deviation 19°), more or less towards ENE (Figure 6a). For Brent Geese the mean track direction was 85° (\pm a.d. 21°), towards east (Figure 6b). The difference in mean flight directions between the species was highly significant (Watson-Williams test, $F_{1,407} = 99.8$, $p < 0.001$).

Flight directions from other localities or regions were reported to a varying extent but the data do not permit a detailed analysis. Within the main migration corridor over Skåne and Blekinge migratory directions were reported to be between NE and E for both species. In the region around Öland, Brent Geese shifted to more northerly directions while Barnacle Geese continued towards NE-E. At the northernmost point of Öland flight directions of Brent Geese were reported to be more or less towards

NE (about 50° according to the observer) during a peak migration day (27 May 1995). Around Gotland directions of Brent Geese were between N and NE. Deviations from this pattern occurred outside the main migration corridor. Along the west coast of Sweden, north of Skåne, about half of all observations of Barnacle and Brent Geese were of birds flying towards SSE along the coast. Ten to twenty percent of all reports referred to birds following the coast towards north. The remaining birds were heading inland with directions between NE and SE. In the south part of Halland more birds flew inland with flight directions between NE and SE than further north along the coast, but still around 40 % of all reports from this area referred to birds flying south along the coast. In inland areas of Småland and areas further north, almost all reported flight directions were between N and E.

Seasonal pattern

Migration of Barnacle Geese usually began in March when small numbers were observed. April was the main migration month, with an overall peak in the middle of the month. Numbers then decreased during May but passage occurred during most of the month.

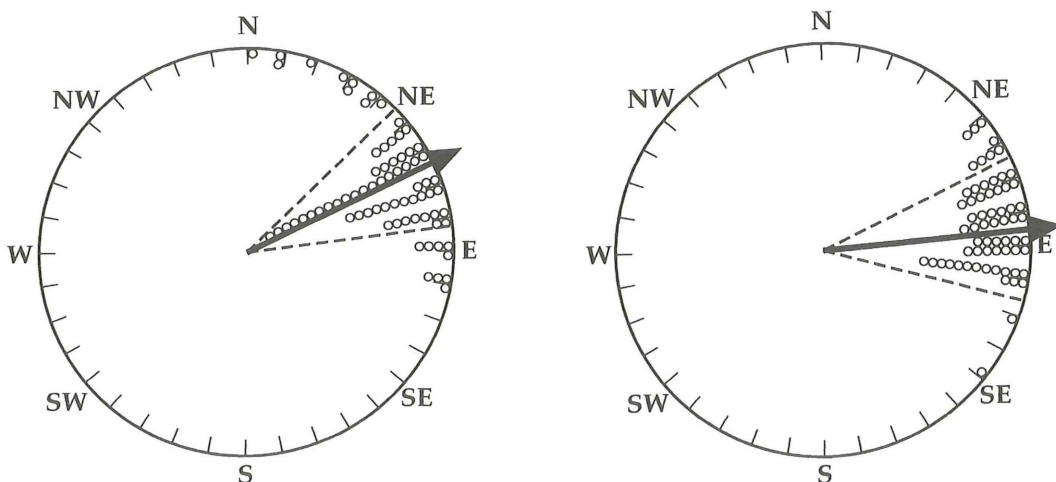


Figure 6. Measured flight directions (circles) of spring migrating Barnacle Geese (left) and Brent Geese (right) in Lund, Scania in spring 1995–1997. Arrow show mean flight directions of measured and observed flocks in Lund (see text). Stipled lines show angular deviations of mean directions. Barnacle Goose: mean 64° (\pm a.d. 19°), Brent Goose: mean 85° (\pm a.d. 21°).

Uppmätta flygriktningar (cirklar) hos vårflyttande Vitkindade gäms (vänster) och Prutgäss (höger) i Lund, Skåne 1995–1997. Pil visar medelflygriktning hos uppmätta och observerade flockar i Lund (se text). Streckade linjer visar vinkelavvikelsen hos medelriktningen. Vitkindad gås: medelriktning 64° (\pm 19°), Prutgås: medelriktning 85° (\pm 21°).

The last migrating Barnacle Geese every season were seen in the last days of May or the first days of June (Figure 7a).

Brent Goose passage was more or less exclusively a late May affair. Only small numbers were seen during March to early May. More numerous migration was observed from mid-May with an overall distinct peak in the last week. In some years high numbers were noted in early June but numbers decreased sharply during the progress of the month. The last migrating Brent Geese every season were seen in mid- or late June (Figure 7b).

Yearly median dates for Barnacle Geese varied between 4 April and 23 April. There was a tendency, although not significant, for median dates to be successively later during the period (Spearman rank correlation, $r_s = 0.50$, $p = 0.06$). Another sign of a successively later passage was that the proportion of birds seen in May increased (Spearman rank correlation, $r_s = 0.64$, $p = 0.02$). In 1981–1985, 0.1–3.2 % (yearly mean: 1.1 %) of the recorded birds were seen in May. During the later years, 1991–1995, the proportion of birds observed in May was 1.1–19.0 % (yearly mean: 10.0 %). The variation in median dates was compared to the proportion of time that headwinds or tailwinds occurred during the main migration periods for each year, but no significant relationships were found, neither for start winds at

the Wadden Sea nor for passage winds at Copenhagen (Kendall rank correlation, $t = -0.17$, $p = 0.37$ and $t = -0.09$, $p = 0.64$ for proportion of headwinds; $t = 0.06$, $p = 0.76$ and $t = 0.04$, $p = 0.83$ for proportion of tailwinds at the Wadden Sea and Copenhagen respectively).

For Brent Geese, yearly median dates were stable during the period. In ten years median dates were between 22 and 25 May. In four years passage was delayed and median dates were between 27 and 31 May. One year of early passage occurred with a median date of 19 May. No trend in median dates could be discovered (Spearman rank correlation, $r_s = -0.13$, $p = 0.63$). The variation was significantly associated with the proportion of time that headwinds occurred during the main migration period, passage being later in headwind years (Kendall rank correlation, $t = 0.61$, $p = 0.002$ and $t = 0.43$, $p = 0.03$ for winds at the Wadden Sea and Copenhagen). For start winds at the Wadden Sea, median dates were also significantly associated with the proportion of time that tailwinds occurred, being earlier in tailwind years (Kendall rank correlation, $t = -0.53$, $p = 0.006$), but only tending to be so for passage winds at Copenhagen (Kendall rank correlation, $t = -0.35$, $p = 0.07$).

The passage of both species was usually concentrated to a few days of mass migration every year

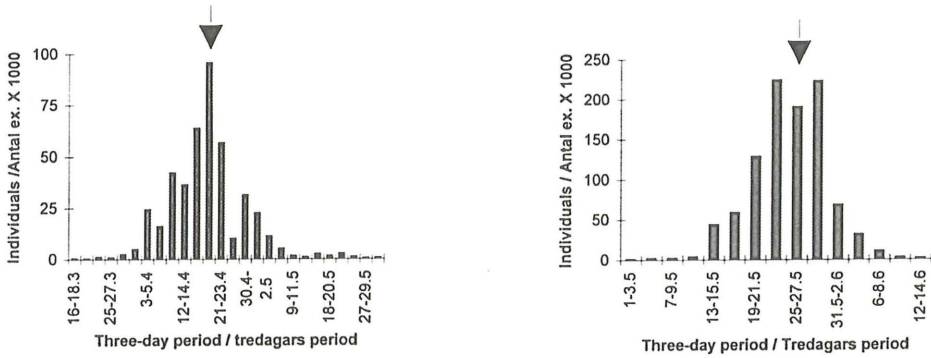


Figure 7. Overall seasonal pattern, in three-day periods, of spring migrating Barnacle Geese (left) and Brent Geese (right) in Sweden 1981–1995. Arrow show median dates.

Säsongsfördelning, i tredagarsperioder, av vårflyttande Vitkindade gäss (vänster) och Prutgäss (höger) i Sverige 1981–1995. Pilar visar mediandatum.

(Table 5). There was no difference between the species regarding the proportion of birds seen during the three best days every season (Mann-Whitney U-test, $n_1 = 15$, $n_2 = 15$, $z = -0.14$, $p = 0.88$) and no trends in this proportion could be detected during the period for any of the species (Spearman rank correlation, $r_s = -0.02$, $p = 0.95$ for Barnacle Geese; $r_s = 0.24$, $p = 0.37$ for Brent Geese).

There was a significant difference between the species in the time span during which 95 % of all birds were observed in any season (Table 5). Passage of Brent Geese was more concentrated in time than the passage of Barnacle geese (Mann-Whitney U-test, $n_1 = 15$, $n_2 = 15$, $z = -2.81$, $p = 0.005$). Furthermore the time period during which 95 % of all Barnacle Geese were recorded in each spring increased in length through the period (Spearman rank correlation, $r_s = 0.71$, $p = 0.008$) from 15–24 days in the early 1980s to 27–44 days in the early 1990s. No significant pattern could be detected for Brent Geese (Spearman rank correlation, $r_s = -0.35$, $p = 0.19$). Variation in the time period covering 95 % of the passage was not correlated to the proportion of time that tailwinds or headwinds occurred during main migration periods for any of the species (Kendall rank correlation, all $p = 0.20$ – 0.92).

International outlook

To analyze if Brent Geese fly over Denmark and the Baltic Sea in one go, numbers of migrating birds observed in Sweden were compared to observed numbers reported from Denmark and the Gulf of Finland. In Figure 8 a–f I have compiled data from

the years when numbers have been available from at least two of the three countries. Unfortunately no year was available with data from all three countries. Generally there was a good fit between Brent Goose numbers observed in Denmark and Sweden, and between numbers observed in Sweden and Finland. A peak in Denmark coincided with a peak in Sweden the same day and a peak in Sweden was followed by a peak in Finland the same day or the day after. In some cases a certain time delay in passage was observed between Denmark and Sweden and between Sweden and Finland, indicating that the birds do not fly the entire distance but sometimes stop to rest for shorter periods.

Discussion

Number of migrants and flock sizes

The significant increase in numbers of Barnacle and Brent Geese seen in Sweden during the study period coincide with the large increases in their overall population sizes in the last decades. The Russian-Baltic breeding Barnacle Goose population increased from around 40 000 birds in 1980 to 220 000 birds in 1994–1995 (Wetlands International, Goose Specialist Group database). During the same time period the population of Dark-bellied Brent Geese increased from 140 000 to 250 000–300 000 birds (Wetlands International, Goose Specialist Group database). The proportions of the total populations seen on migration in Sweden each year varied roughly between 20 and 50 %. The variation probably depends to a certain degree on the extent to which the migra-

Table 5. Median dates, proportion of the season total observed during the three best days and time-span during which 95 % of the season total was observed for Barnacle Goose and Brent Goose during spring migration 1981–1995.

Mediandatum, andel av totala säsongsumman observerade under de tre bästa dagarna samt tidsperiod under vilken 95 % av säsongsumman inräknats för vitkindad gås och prutgås under vårflyttningen 1981–1995.

Species Art	Median date (Range) <i>Mediandatum</i>	% during three best days <i>% under de tre bästa dagarna</i>	95 % within (days) <i>95 % inom (dagar)</i>
Barnacle Goose <i>Vitkindad gås</i>	19.4 (4-23.4)	62 (± s.d. 14.6)	26 (± s.d. 9.3)
Brent Goose <i>Prutgås</i>	25.5 (19-31.5)	62 (± s.d. 11.9)	17 (± s.d. 4.1)

tory seasons were covered by ornithologists at strategic migration sites and to what degree observed migration was reported to the regional report committees. The increase in relative numbers of Barnacle Geese is for example most likely caused by increased ornithological activity at strategic sites, as in Lund, during the migration period in the later years of the study period. Another possible explanation of the variation might be differences between years in wind patterns since it is likely that winds affect the altitude of migration, geographical patterns and maybe also the distribution of birds that migrate during day and/or night. As this data set does not contain any information on the differences in observation coverage between years, this question cannot be analyzed in detail. A higher proportion of the total Brent Goose than of the total Barnacle Goose population was generally observed in Sweden. This can of course be a result of a better coverage of the Brent Goose passage, but it may also indicate differences in, for example, diel migration patterns and departure areas. Generally, Barnacle and Brent Geese initiate their migratory flights either in the early morning or in the evening (Leito 1991, P. Clausen pers. comm.) but we have poor knowledge of the exact preferences of departure times and if there are any differences between the species in this respect. There is though a clear difference in observed passage times in south Sweden with the majority of Barnacle Geese recorded between early morning and midday while Brent Geese are more spread out during the day with marked peaks in early morning and in the evening (Green, unpubl. data). This pattern might be caused by a difference in departure areas between the species. Barnacle Geese leave from a more concentrated area of the Wadden Sea in

Germany and the north part of the Netherlands (Ebbinge et al. 1991) while Brent Geese are spread out over the whole Wadden Sea (Bergmann et al. 1994). In addition a couple of relatively large staging areas of Brent Geese are also present around the Danish islands (Madsen et al. 1990). Thus, Barnacle Geese probably pass south Sweden in more concentrated waves while passage of Brents will be more spread out during the day making it likely that a higher proportion of all birds will be observed.

Flock sizes of Barnacle Geese in Sweden (Table 1) were relatively similar to flock sizes reported from departure at the Wadden Sea, where 66 % of the flocks observed during spring departure contained 1-100 birds and 24 % of the flocks were in the size class 100–250 birds (Busche 1991). General flock sizes of Brent Geese in Sweden were larger than flock sizes observed at departure from the Wadden Sea. There, only 3 % of 73 observed flocks were larger than 300 birds (Prokosch 1991), while in Sweden 14.4–20.3 % of all flocks were larger than 400 birds (Table 1). The difference between Wadden Sea and Sweden indicates that smaller Brent Goose flocks merge into bigger ones somewhere along the route. If flocks frequently stop and rest along the route, there is a possibility of accumulation of birds and the formation of larger flocks at these occasions. Whether this is what the Brent Geese do is unknown, but a recent satellite telemetry study on Light-bellied Brent Geese flying from Denmark towards Svalbard and Greenland indicate that these birds pause now and then to rest (Clausen & Bustnes in press). Furthermore observations along the west coast of Sweden show that Brent goose flocks frequently go down and rest before flying inland (A. Wirdheim pers. comm., own obs, and see below).

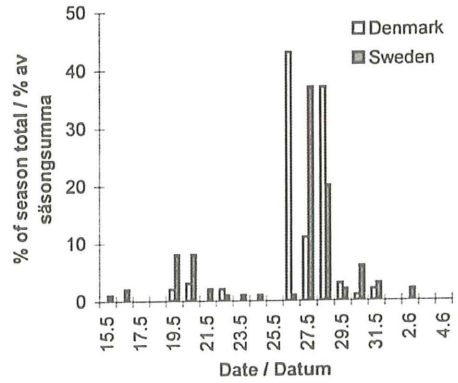
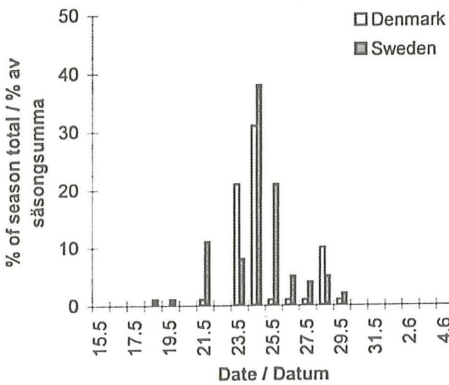
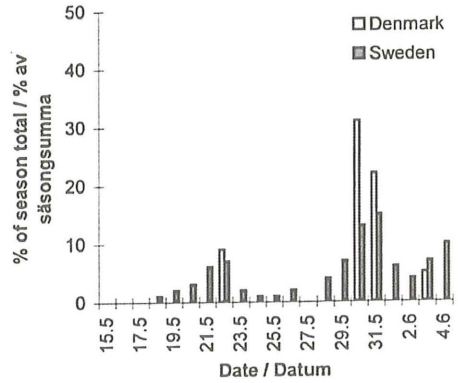
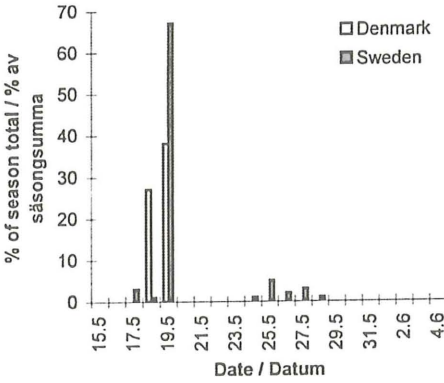
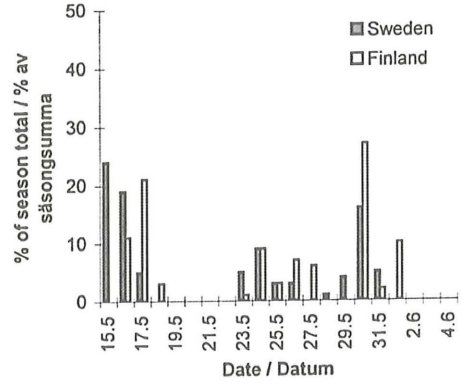
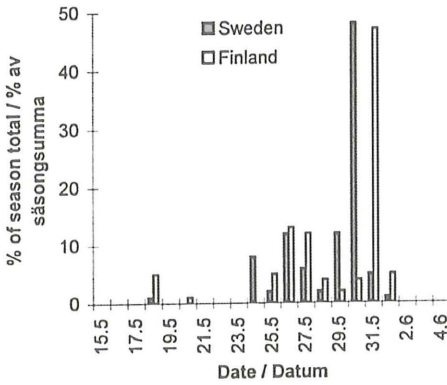


Figure 8. Comparison of observed migration intensities of Brent Geese between Sweden and Finland (a-b), and Denmark and Sweden (c-f). a) 1987, b) 1993, c) 1991, d) 1992, e) 1994 and f) 1995. See text.

Jämförelser av sträckintensiteter av prutgäss mellan Sverige och Finland (a-b) och mellan Danmark och Sverige (c-f). a) 1987, b) 1993, c) 1991, d) 1992, e) 1994 och f) 1995. Se text.

Flocks of Brent Geese were larger than those of Barnacle Geese at Lund and tended to be so also at Kåseberga. Both species depart from large staging concentrations in the Wadden Sea (Rösner 1993, Rösner & Stock 1995) so this difference is not likely to arise from differences in the size of staging concentrations (cf. Alerstam et al. 1990). A plausible explanation is that since migration of Brent Geese is more concentrated in time than Barnacle Goose migration, more Brent Geese are bound to migrate at the same time, thus making Brent Goose flocks larger.

Flock sizes of both species were higher during migration over land than along the coast. This has also been found for spring migrating Eiders *Somateria mollissima* in south Sweden (Alerstam et al. 1974). For the Eiders, Alerstam et al. suggested that the larger flock sizes of birds crossing land were due to the fact that when about to fly inland, Eiders generally circled above the shoreline for a quite a while. The circling behaviour led to the merging of several smaller flocks into larger ones that finally departed inland. The same argument may apply to Brent Geese which are frequently seen circling in the bays of west Sweden before flying inland (Wirdheim 1981, 1988, own obs.). Also, as mentioned above, Brent Geese relatively often land on the water for a while when reaching the west coast of Sweden before they depart inland. This behaviour may also lead to accumulation of birds into larger flocks than the ones that arrive at the coast. For Barnacle Geese circling behaviour at the coastline and the habit of going down and rest before continuing inland is not observed as frequently as for Eiders and Brent Geese (own obs.). The difference in flock sizes between overland flying birds and those following the coastline is thus more difficult to explain, but the same reasons as mentioned above might be responsible for the difference in Barnacle Geese as well. Another factor affecting the observed flock sizes may be associated with the fact that migration over land often takes place at higher altitude than migration along coasts. Small flocks might not be detected as easily over land by observers as along the coast, making the data set biased towards larger flock sizes at an inland locality.

Wind and migration intensity

High migration intensity was generally associated with favourable winds (49 % of peak days for Barnacle Geese, 44 % of peak days for Brent Geese). In addition several peak days occurred in winds from

the southern sector (S-SSE, Figure 3) which also could be categorized as relatively favourable from the birds point of view as these wind directions also hold a considerable tailwind component, at least during certain parts of the flight (see Figure 4). By including these days in the summary, 29 peak days (59%) of Barnacle Goose migration were in tailwinds and sidewinds from the southern sector. The corresponding figure for Brent Geese was 37 peak days (67 %). By choosing to fly in tailwinds the birds reach their destinations faster and with less energy expenditure than otherwise. Hence, there should be a high selection pressure towards choosing the right days with respect to wind (Alerstam 1979, 1990a). For both species several peak days were also recorded in weak winds. These days do obviously not give any wind assistance and energetic advantages compared to tailwinds but compared to a flight in headwinds a flight in no winds is clearly preferable both from an energy saving and time saving perspective. The importance of favourable winds, or at least to avoid unfavourable winds, during spring migration has been shown for Brent Geese. Ebbinge (1989) stated that "wind conditions during spring migration may have a marked impact on the eventual breeding condition of the birds" and showed that breeding success was low in years when headwinds prevailed during the spring migration period. Probably the birds these years arrived at their breeding areas in rather bad condition, having spent a lot of energy on flight in the headwinds. A majority of all studies on bird migration intensity and wind have shown a preference for migration in tailwinds or at least winds of low strength if they were opposing (Richardson 1978, 1990 and references therein). Studies of waterfowl migration in particular also show a positive correlation between following winds and migration intensity in most cases, both during spring and autumn, for short and for long flights (Alerstam et al. 1974, Blokpoel & Gauthier 1975, Blokpoel 1978, Wege & Raveling 1983, Owen & Gullestad 1984, Dau 1992).

Although both species predominantly migrated in tailwinds, some days with high migration intensity occurred in headwinds. These days were in several cases late in the season and/or with relatively low wind speeds ($\leq 2.5 \text{ m s}^{-1}$, see Figure 3). Probably, time gets increasingly important as the season progresses, especially for Brent Geese as these birds migrate over south Sweden only a couple of weeks before the onset of breeding. To be able to reach their staging areas to refuel for their next flight to the breeding grounds and still have the chance to breed

successfully in the short arctic summer, the geese can not afford to wait for favourable winds late in the season. At these occasions migration is commenced as soon as wind conditions get better (lower strength of headwind) but still not optimal.

Geographical pattern

The geographic pattern of migration shown in this analysis follow, in broad respects, general descriptions in the literature (Kumari 1971, Cramp 1977, Prokosch 1984, Madsen 1987, SOF 1990, Bergmann et al. 1994). Differing from the above mentioned descriptions are the number of geese flying over inland areas of south Sweden, especially for Barnacle geese. These numbers have previously been underestimated. I conclude that a substantial part of all Barnacle and Brent Geese in fact cross the southernmost part of Sweden overland.

Geographic pattern of Brent Goose passage showed a larger between-year variation than the one for Barnacle Goose. In some years the migration corridor was markedly shifted towards north, as in 1989 and 1992. In these years the geese migrated in winds mainly from the eastern sector as shown in Figure 5. The more northern migration corridor in 1989 was also observed in Denmark (Munk et al. 1991). Large scale wind drift might be responsible for this shift on some of the occasions. Birds migrating towards north-east from the Wadden Sea could have been drifted northwestwards by the wind. This seems likely in winds from east to south-east. Looking at Figure 5 one can see that not all migration days were in winds from these directions, so wind drift cannot be responsible for all occasions with migration further to the north than usual. In north-easterly winds the birds might instead have hesitated to fly in their preferred direction from the Wadden Sea, since this would have been straight into the headwinds. Maybe they set off in a more northerly direction, with less unfavourable winds, following the Wadden Sea coast and getting some shelter from the wind. When reaching the north part of the Wadden Sea the coast bends off towards north-west and west, more or less the opposite direction of the preferred migratory direction and the geese had to face the headwind if not to stray away from the normal route. Thereby the corridor would be shifted northwards. Why then was the migration corridor for Barnacle Geese more stable than the one for Brent Geese? This may be a consequence of the difference in destination areas and in time to onset of breeding between the two species. The majority of the Barnacle Geese are on

their way to spring staging at the Baltic islands with about two months to the start of breeding. Brent Geese head for the White Sea via the Gulf of Finland, just a few weeks before the start of breeding. For Brent Geese a general drift northwards is not totally unfavourable regarding the length of the flight and by letting themselves be wind-drifted instead of flying straight into the headwinds they also save energy which might be of crucial importance for the coming probability of a successful breeding since time for replenishing nutrient stores at the White Sea is limited (cf. Ebbinge 1989, Ebbinge & Spaans 1995). For Barnacle Geese on the other hand, the extra detour will make the flight substantially longer in distance, making the same behaviour unlikely to develop. They might also not be as pressured by time and thus by an energy conserving strategy, since they have about two months to go before the start of breeding and sufficient time to rebuild their stores at Baltic staging sites.

The difference in flight directions in Lund between the species is intriguing. Barnacle Geese flew more straight towards their destination (ENE) while Brent Geese were flying with directions towards the closest coast area on the east side of Skåne (E). Perhaps Brent Geese are more selected to maximize contact with marine habitats, where they can find suitable resting sites, than Barnacle Geese. The reluctance of Brent Geese to land on lakes in inland areas is illustrated by the fact that very few grounded flocks (only occasional single individuals) are reported from lakes in inland Sweden. In contrast, resting flocks of Barnacle Geese are sometimes reported (this study). Furthermore the relatively high numbers of Brent Geese seen following the Swedish west coast towards SSE, instead of flying straight on towards NE or E, indicates that they hesitate to fly inland when the coastline does not deviate completely from the preferred migratory direction. Another indication that Brent Geese try to maximize contact with the sea is the finding from Finland that almost all Brent Geese seem to take the shortest overland passage from the innermost Gulf of Finland to the White Sea. Barnacle Geese are more often seen inland, apparently taking the shortest way to the White Sea but not the shortest overland crossing (Saurola 1976).

General flight directions were in the sector between NE and E in Sweden with some deviations around coastlines, most pronounced for Brent geese. This is in good agreement with departure directions from the Wadden Sea (Busche 1991, Prokosch 1991). A constant compass route (rhumbline) from the

German part of the Wadden Sea towards staging areas for Barnacle geese at Gotland and in Estonia is about 65°, e.g. towards ENE. A rhumbline between the Wadden Sea and the White Sea is about 55°, e.g. towards NE-ENE. Flying along a great circle route, the shortest route between two places on the earth's surface, from the Wadden Sea to the White Sea would require a more northern initial flight direction, about 40°, continuously changing towards a more easterly direction of about 55° when approaching the White Sea (Figure 9). A great circle route between the Wadden Sea and the Baltic would not differ much from a rhumbline route, due to the short distance. If Brent Geese followed a great circle route large numbers should pass over zone 2 and 3 (Figure 4, Figure 9) and not as this study shows over zone 1. Instead it seems (Figure 4, Figure 9) that they follow a route similar to a rhumbline, but with substantial influences of topographical features, such as coastlines. The same behaviour have been observed for Knots *Calidris canutus* passing Sweden in late spring heading for breeding areas on Taimyr peninsula (Gudmundsson 1994) and might be a general behaviour of birds breeding in high arctic Russia during spring migration from western Europe. Even if a great circle route would be shorter than following a constant compass course there are certain advantages with the latter. By flying on a constant compass course during the flight from western Europe to the Russian tundra the birds increase the contact with

coastal areas compared to a great circle route (cf. Figure 9). Staying in contact with coastlines may increase security since it gives the birds both the possibility to use landmarks for orientation and a better choice of sites for emergency landings, for example if encountering bad weather, than flying over land or over open sea (Alerstam 1990 b).

Seasonal pattern

Seasonal timing of the passage of both species were in accordance with previously reported time patterns (Kumari 1971, Saurola 1976, Hasselquist 1981, Leito & Renno 1983, Wirdheim 1988, Ebginge 1989, SOF 1990, Busche 1991, Ebginge et al. 1991, Leito 1991, Prokosch 1991). Interestingly the time pattern of Barnacle Geese showed a certain change during the period, with a migratory period increasing in length (more birds seen in May) and a tendency for a successively later median date. The time pattern of Brent Goose passage on the other hand was very stable, just showing a delay in years when headwinds prevailed. No such association with wind was found for Barnacle geese. Migration of Barnacle geese during the 1970s took place mostly in early April (Hjort 1976). May migration was reported to be rare at that time. Peak migration in the 1980s was mainly in mid April and during the 1990s the peak has changed further towards late April. The change in time pattern might be connected with the increasing population size. Overall population size during the mid 1990s was four-five times larger than during the early 1970s. Furthermore the Barnacle Goose has established itself as a breeding bird of the Baltic with a present population of at least 10 000 birds (Larsson et al. 1988, Waldenström 1995). This heavy population increase has probably led to increased competition on Baltic staging and breeding grounds, which are of relatively limited size. It might thereby be more beneficial for some birds to stay longer in the Wadden Sea and build up reserves, with less competition than in the Baltic, for either a direct flight to the Arctic or to use the Baltic staging areas for a much shorter period. This scenario would also explain the longer migratory period of Barnacle Geese compared to Brent Geese. In the former case we probably have a mix of early migrating Baltic breeders (Forslund 1992), Russian breeders on their way to major spring staging in the Baltic, and Russian breeders flying directly towards the Arctic or just staging for a short time in the Baltic. In the Brent Goose case all birds are on their way to spring staging in the White Sea and the passage is very

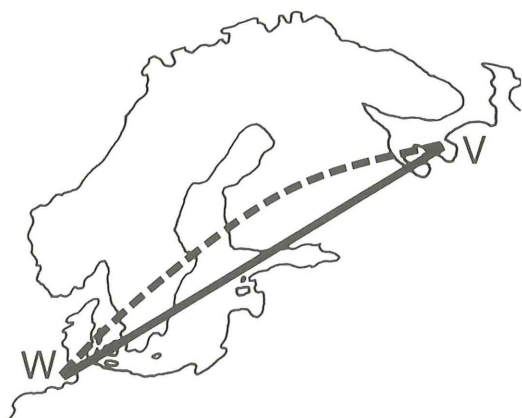


Figure 9. The great circle route (stipled) and constant compass route (straight line) between the Wadden Sea and the White Sea. Brent geese approximately fly along a constant compass route.

Storcirkelrutt (streckad kurva) och konstant kompassrutt (hel-dragen rak linje) mellan Vadehavet och Vita havet. Prutgäss följer ungefär en konstant kompassrutt.

concentrated. It is interesting to note that Barnacle Goose migration from the Baltic in mid to late May is very synchronized following very much the same pattern as Brent Goose migration from the Wadden Sea (Kumari 1971, Leito & Renno 1983, Leito 1991, Leivo et al. 1994, 1995).

International outlook

Brent Geese are assumed to fly from west European staging grounds to the White Sea, north-west Russia in one uninterrupted flight (Ebbing & Spaans 1995). Based on flight speed measurements on Brent Geese in Lund (mean groundspeed = $71 \text{ km h}^{-1} \pm \text{s.d. } 14 \text{ km h}^{-1}$, Green & Alerstam in prep.) the flight between the Wadden Sea and the Gulf of Finland should normally take about 20 hours. From Denmark to Sweden the geese have to fly for between half an hour and four hours depending on where they were observed in respective country. The flight from south Sweden to the Gulf of Finland should be covered in 10–14 hours if the geese fly non-stop. Geese passing Denmark should thus be seen in Sweden later the same day. Geese observed in Sweden one day should be observed in Finland later the same day or the day after, depending on when during the day they pass Sweden. As seen in Figure 8 there was generally a good fit between numbers seen in the different countries. On some occasions there was a small time delay though. What probably happens is that, for one reason or the other, Brent Geese make short stops along the route. This has, as previously mentioned, been observed for Light-bellied Brent Geese (Clausen & Bustnes in press) and also for Dark-bellied Brent Geese along the Swedish west coast (own obs.). What the geese do at these occasions and why they do this is unknown. The short stops and the locations where they go down indicate that it is not to eat and replenish nutrient stores. A possible explanation is that they need to drink since they might run the risk of dehydration during long flights with high body masses (cf. Carmi et al. 1992).

Bearing in mind that many geese pass Sweden by night, the high proportions of the involved populations observed in Sweden and the findings that Barnacle and Brent Geese are only observed in small numbers along the south and southeast coast of the Baltic (Rutschke & Litzbarski 1976, Raudonikis & Shvazhas 1991) the conclusion must be that for both species the majority of all birds pass Sweden or the waters surrounding the country during spring. Migration is however not as concentrated over Sweden as in the Gulf of Finland.

Acknowledgements

Observation records were provided by the courtesy of Mats Alderus, Martin Amcoff (Ottenby Bird Observatory), Preben Berg (Kongelunden Bird Observatory), Anders Blomdahl, Erik Borgström, Stefan Clason, Göran Darefelt, Ola Elleström, Thomas Ewelid, Jonas Grahn, Olof Hjelm, Niclas Holmström, Kurt Holmquist, Joakim Johansson, Ingela Kristoffersson, Hans Larsson, Sören Linden, Alf Lindström, Reno Lottman, Jan Pettersson (Ottenby Bird Observatory), Thomas Pettersson, Stig Rosen, Daniel Steen, Staffan Swedberg, Martin Tjernberg, Gunnar Wikman. Jesper Madsen and Preben Clausen provided the figures on population sizes and breeding success. Anders Hedenström, Thomas Alerstam, Åke Lindström and two anonymous referees gave valuable comments on the manuscript. Steffi Douwes helped in creating the maps. The studies on arctic goose migration in Lund have been financially supported by Gustaf Danielssons Foundation (Swedish Ornithological Society).

References

- Alerstam, T. 1979. Wind as a selective agent in bird migration. *Ornis Scand.* 10:76–93.
- Alerstam, T. 1990 a. *Bird migration*. Cambridge University Press, Cambridge.
- Alerstam, T. 1990 b. Ecological causes and consequences of bird orientation. *Experientia* 46: 405–415.
- Alerstam, T., Bauer, C.-A. & Roos, G. 1974. Spring migration of Eiders *Somateria mollissima* in southern Scandinavia. *Ibis* 116:194–210.
- Alerstam, T., Gudmundsson, G. A., Jönsson, P.-E., Karlsson, J. & Lindström, Å. 1990. Orientation, migration routes and flight behaviour of Knots, Turnstones and Brant geese departing from Iceland in spring. *Arctic* 43: 201–214
- Bergmann, H.-H., Stock, M. & ten Thoren, B. 1994. *Ringelgänse*. AULA-Verlag, Wiesbaden.
- Blokpoel, H. 1978. Weather and spring migration of Snow geese across southern Manitoba. *Oikos* 30: 393–397.
- Blokpoel, H. & Gauthier, M. C. 1975. Migration of Lesser Snow and Blue geese in spring across southern manitoba. Part 2: Influence of weather and predictions of major flights. *Can. Wildl. Serv. Rep.* Series 32.
- Busche, G. 1991. Nonnengans, Weisswangengans - Branta leucopsis. Pp. 89–100 in *Vogelwelt Schleswig-Holsteins. Bd 3: Entenvögel 1* (Berndt, R. K & Busche, G., eds). Wachholtz, Neumünster.
- Carmi, N., Pinshow, B., Porter, W. & Jaeger, J. 1992. Water and energy limitations on flight duration in small migrating birds. *Auk* 109: 268–276.
- Clausen, P. & Bustnes, J. O. 1998. Flyways of North Atlantic light-bellied brent geese *Branta bernicla hrota* reassessed by satellite telemetry. *Norsk Polarinst. Skr.* In press.
- Cramp, S. (ed) 1977. *Birds of the Western Palearctic*. Vol 1. Oxford University Press. Oxford.

- Dau, C. P. 1992. The fall migration of Pacific Flyway Brent Branta bernicla in relation to climatic conditions. *Wildfowl* 43: 80–95.
- Ebbinge, B. S. 1989. A multifactoral explanation for variation in breeding performance of Brent geese Branta bernicla. *Ibis* 131: 196–204.
- Ebbinge, B. S., van Biezen, J. B. & van der Voet, H. 1991. Estimation of adult survival rates of Barnacle geese Branta leucopsis using multiple resightings of marked individuals. *Ardea* 1979: 73–112.
- Ebbinge, B. S. & Spaans, B. 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent geese Branta b. bernicla in the high Arctic. *J. Avian Biol.* 26: 105–113.
- Forslund, P. 1992. *Effects of reproductive tactics and population density on breeding success in the Barnacle goose Branta leucopsis*. Ph. D. Thesis, Dept. of Ecology, Univ. of Uppsala, Sweden.
- Gudmundsson, G. A. 1994. Spring migration of the knot *Calidris c. canutus* over southern Sweden as recorded by radar. *J. Avian Biol.* 25: 15–26.
- Hasselquist, D. 1981. Prutgåsens Branta bernicla förekomst på Öland. *Calidris* 10: 139–150.
- Hjort, C. 1976. The migration of Barnacle geese (Branta leucopsis) at Ottenby. Pp. 165–174 in *Bird migration* (Kumari, E., ed.). Tallin.
- Hjort, C. 1977. Den vitkindade gåsens Branta leucopsis förekomst på Öland. *Calidris* 6: 59–71.
- Kumari, E. 1971. Passage of Barnacle goose through the Baltic area. *Wildfowl* 22: 35–43.
- Larsson, K., Forslund, P., Gustafsson, L. & Ebbinge, B. S. 1988. From the high Arctic to the Baltic: the successful establishment of a Barnacle goose Branta leucopsis population on Gotland, Sweden. *Ornis. Scand.* 19: 182–189.
- Leito, A. 1991. A note on migration ecology, population status and interactions with agriculture of Barnacle geese in Estonia. *Ardea* 79: 347–348.
- Leito, A. & Renno, O. 1983. Über die Zugökologi der an der Barentssee heimischen Population der Weisswangengans (Branta leucopsis) in Estland. *Die Vogelwarte* 32: 89–102.
- Leivo, M., Kontiokorpi, J. & Rusanen, P. 1994. Migration of Arctic waterfowl on the northern Baltic Sea in spring 1993. *Linnut* 29 (2): 12–19. (In Finnish with English summary).
- Leivo, M., Kontiokorpi, J. & Rusanen, P. 1995. Migration of Arctic waterfowl on the northern Baltic Sea in spring 1994. *Linnut* 30 (3): 28–31. (In Finnish with English summary).
- Lindballe, P., Christensen, R., Munk, M., Skov, H., Smidt, J. & Söby, T. 1993. Fugle i Danmark 1991. Årsrapport over observationer. *Dansk Orn. Foren. Tidsskr.* 87: 191–230.
- Lindballe, P., Christensen, R., Friis-Munk, M., Skov, H., Smidt, J. & Söby, E. 1994. Fugle i Danmark 1992. Årsrapport over observationer. *Dansk Orn. Foren. Tidsskr.* 88: 111–150.
- Madsen, J. 1987. Dark-bellied Brent goose Branta bernicla. In: Status and management of goose populations in Europe. *Dan. Rev. Game* 12: 38–52.
- Madsen, J., Frikke, J. & Laursen, K. 1990. Forekomst og habitatvalg hos Mørkbuget Knortegås Branta bernicla bernicla i Danmark, og specielt Vadehavet. *Danske viltundersøgelser* 45.
- Munk, M., Christensen, R., Skov, H. & Smidt, J. 1991. Fugle i Danmark 1989. Årsrapport over observationer. *Dansk Orn. Foren. Tidsskr.* 85: 109–144.
- Owen, M. & Gullestad, N. 1984. Migration routes of Svalbard Barnacle geese. *Norsk Polarinst. Skri.* 181: 67–77.
- Prokosch, P. 1984. Population, Jahresrhythmus und traditionelle Nahrungsplatzbindungen der Dunkelbäuchigen Ringelgans (Branta b. bernicla) im Nordfriesischen Wattenmeer. *Ökol. Vögel.* 6: 1–99.
- Prokosch, P. 1991. Ringelgans – Branta bernicla. Pp. 101–108 in *Vogelwelt Schleswig-Holsteins. Bd 3: Entenvögel I.* (Berndt, R. K. & Busche, G., eds). Wachholtz, Neumünster.
- Raudonikis, L. & Shvazhas, S. 1991. A short note on geese migration in Lithuania. *Ardea* 79: 123–124.
- Richardson, W. J. 1978. Timing and amount of bird migration in relation to weather: a review. *Oikos* 30: 224–272.
- Richardson, W. J. 1990. Timing and amount of bird migration in relation to weather: updated review. Pp. 78–101 in *Bird Migration. Physiology and Ecophysiology.* (Gwinner, E., ed.). Springer-Verlag, Berlin.
- Rutschke, E. & Litzbarski, H. 1976. Passage and wintering of geese in the GDR. In *Bird migration* (Kumari, E., ed.). Tallin.
- Rösner, H-U. 1993. Monitoring von Nonnen- und Ringelgänsen (Branta leucopsis, Branta bernicla) im Schleswig-Holsteinischen Wattenmeer: Das Gänsejahr 1991/1992. *Corax* 15: 245–260.
- Rösner, H-U. & Stock, M. 1995. Anzahl, Phänologie und räumliche Verteilung der Dunkelbäuchigen Ringelgans (Branta b. bernicla) in Schleswig-Holstein. *Seevögel* 16 (3): 73–80.
- Saurola, P. 1976. The role of the Finnish archipelago in the passage of northern sea- and shorebirds. In *Bird migration* (Kumari, E., ed.) Tallin.
- SOF, 1990. *Sveriges fåglar. 2:a upplagan.* Stockholm.
- SOF, 1997. *Fågelåret 1996.* Stockholm.
- Waldenström, J. 1995. Fortsatt framåt för de vitkindade gässen på Öland. *Calidris* 24: 64.
- Wege, M. L. & Raveling, D. G. 1983. Factors influencing the timing, distance and path of migrations of Canada Geese. *Wilson Bulletin* 95: 209–221.
- Wirdheim, A. 1981. Prutgås och Vitkindad gås i södra Halland. *Halmstad Ornitologiska Klubbs årsskrift* 1980. pp 25–30.
- Wirdheim, A. 1988. Vårsträcket av sjöfåglar i Laholmsbukten. *Fåglar i södra Halland* 1987: 11–30

Sammanfattning

Vårsträcket av vitkindad gås Branta leucopsis och prutgås Branta bernicla bernicla över Sverige

Varje vår passerar stora antal vitkindade gäss och prutgäss Sverige under sin flyttning från Västeuropeiska övervintringsplatser och tidiga vårrastningslokaler på väg mot häckningsområden, huvudsakligen i arktiska Ryssland. I den här artikeln redovisar jag antalet observerade fåglar, flockstorlekar, geografiskt och tidsmässigt mönster i Sverige, samt vindens generella inverkan på sträckaktivitet

under tidsperioden 1981–1995. Jämförelser med sträckdata från Danmark och Finland görs även. Materialet till denna sammanställning kommer från följande källor: 1) svar på förfrågningar till SOF:s regionala rapportkommitteer om samtliga observerade vårsträckande fåglar av båda arterna, 2) förfrågningar till vissa fågelstationer och enskilda observatörer verksamma på strategiska platser, 3) litteratursökning i (främst) lokala och regionala ornitologiska tidskrifter, och 4) en specialstudie gjord i Lund, Skåne (55° 42' N 13° 12' E).

Observerade antal och flockstorlekar

Antalet observerade fåglar av båda arterna ökade signifikant under perioden (Figur 2) parallellt med kraftiga ökningsgrad av de totala populationsstorlekarna. En signifikant högre andel av totalpopulationen av prutgås (median: 29%, variation: 14–67%) sågs per vår i Sverige jämfört med vitkindade gås (median: 18%, variation: 6–47% av totalpopulationen). Det relativa antalet fåglar av båda arterna som observeras i Sverige beror troligen till viss del på bevakningsgrad på strategiska platser och huruvida observerade flockar rapporterats in till de regionala rapportkommitteerna. Andra tänkbara faktorer som påverkar andelen observerade fåglar är t.ex. vindmönster som kan påverka val av flyghöjd, benägenhet att följa kuster samt sträckets dygnsrytm. Då detta material inte ger någon möjlighet att skilja på bevakningsinsatser mellan olika år har jag inte analyserat frågan vidare. Den högre andelen prutgäss jämfört med vitkindade gäss kan bero på skillnader i t.ex. dygnsrytm och/ eller i startområdets läge. Båda arterna startar normalt en flyttningsetapp antingen under tidig morgon eller sen kväll. Fåglar som startar från Vadehavet under kvällen passerar sannolikt Sverige nattetid och är därmed normalt ej möjliga att observera, medan de som startar på morgonen kan ses passera Sverige några timmar senare. Det finns tyvärr inte mycket detaljerade uppgifter på exakt när på dygnet de olika arterna påbörjar sina flyttningsetapper eller om det finns någon skillnad mellan arterna i detta avseende. Åtminstone i Skåne är det dock en tydlig dygnsrytmskillnad där huvuddelen av de vitkindade gässen passerar under morgon och middag, medan prutgässen är mer utspridda under dagen med tydliga toppar morgon och kväll (Green opubl.). En möjlig förklaring till detta är troligtvis det faktum att medan de vitkindade gässen startar från ett relativt begränsat område i Tyskland och norra Nederländerna (Ebbing et al. 1991) så startar prutgässen från hela Vadehavet samt även en

del danska rastplatser på ännu närmare håll (Bergmann et al. 1994, Madsen et al. 1990). Därmed blir sträckvägen av vitkindade gäss mer koncentrerad i tid på dygnet och sträckvägen av prutgäss mer utspridd under dygnet vilket i sin tur ökar sannolikheten för att fler prutgäss blir observerade.

Fördelningen av flockar och individer på några olika lokaler i södra Sverige visas i Tabell 1. Prutgäss observerades i större flockar än vitkindade gäss och för båda arterna var flockar observerade över inlandet (Lund) större än kustföljande flockar (Kåseberga och Ottenby) (Tabell 2). Prutgåssträcket är mer koncentrerat i tid under säsongen så fler prutgäss är flyttningsbenägna vid samma tillfälle än de vitkindade (se vidare under Säsongsmönster). När det gäller skillnaden mellan kust och inland så ligger förmodligen beteendemässiga faktorer bakom. Ofta sker en uppsamlingseffekt när sträckande vattenfåglar når en kustlinje på så vis att flera mindre flockar slås ihop till större i samband med insträcket över land (Alerstam et al. 1974). Dessutom går åtminstone prutgäss ofta ner och rastar en kort tid i bukterna längs västkusten innan de sträcker vidare in över land (A. Wirdheim muntl., egna obs.) vilket ger ytterligare tillfällen för flocksammanslagningar. Observerade flockstorlekar för vitkindade gäss i Sverige var i samma storleksordning som de som ses sträcka iväg från Vadehavet (Busche 1991). Flockstorlekarna för prutgås i Sverige var dock större än de som lämnade Vadehavet (Prokosch 1991), vilket pekar på att en sammanslagning av mindre flockar till större sker någonstans längs vägen. Troligen går prutgässen ner för korttidsrastning då och då längs flyggrutten och bland annat vid dessa tillfällen kan flocksammanslagningar ske.

Vindförhållanden och sträckintensitet

Dagar med hög sträckintensitet inföll för båda arterna främst vid medvind (Figur 3, Tabell 3). Sträck i medvind ger energimässiga fördelar och ovanstående resultat ligger helt i linje med tidigare studier av både fågelflyttning i allmänhet och sjöfågelsesträck i synnerhet. För båda arterna förekom några dagar med hög sträckintensitet i motvind. Dessa dagar inföll i regel sent på säsongerna och/ eller vid låga vindstyrkor. Förmodligen blir tiden en allt viktigare faktor ju längre säsongen lider, särskilt för arktiska häckfåglar. För att överhuvudtaget ha en möjlighet att nå nästa rastområde, fylla på förråden och flyga den sista etappen till häckningsområdet i tid för ett häckningsförsök under den korta arktiska sommaren, kan gässen inte vänta på fördelaktiga

vindar hur länge som helst. Under år med ihållande motvindar nås troligen till slut en tidsmässig gräns då flyttningen påbörjas så snart vindförhållandena blir bättre (lägre motvindstyrka) om än inte optimala.

Geografiskt mönster och flygriktningar

Hos båda arterna passerade normalt den största andelen av fåglarna över de sydligaste delarna av Sverige (Figur 4, Tabell 4) med 70–97% av säsongsummorna observerade i Skåne, Blekinge, Öland och Gotland. Skåne och Öland var normalt de landskap där de högsta siffrorna inräknades. Det geografiska mönstret hos de vitkindade gässen var mycket stabilt under perioden. För prutgässen fanns dock två år, 1989 och 1992, som skiljde sig markant från övriga år. Dessa år var flyttningskorridoren förskjutet norrut och 70–80% av säsongsummorna inräknades norr om de sydligaste landskapen. En analys av vindförhållanden under sträckdagarna dessa år visade att fåglarna huvudsakligen flyttade i vindar från E-sektorn (Figur 5), både vid starten från Vadehavet och under passagen av Sverige. Storskalig vinddrift kan ligga bakom det uppkomna mönstret framförallt vid vindar från E-SE. Då inte alla sträckdagar inföll vid vindar från denna sektor måste dock även andra faktorer ha spelat in. En möjlig förklaring kan vara att när fåglarna ger sig iväg från Vadehavet i NE-vindar undviker de att följa den normala ruten mot NE. Istället kanske de följer Vadehavskusten mot N så att de får ett visst skydd från vinden. När kusten sedan viker av mot NW och W i Vadehavets norra del måste de sträcka mot NE-E för att inte avvika alltför kraftigt från den önskade sträckkorridoren. På så vis skulle hela korridoren kunna förskjutas norrut. Skillnaden mellan arterna i flyttningskorridorens stabilitet kan bero på att de vitkindade har ett betydligt sydligare beläget mål för sin etapp (Gotland och Estland) jämfört med prutgässen (Vita havet via Finska viken). En förskjutning av flyttningskorridoren norrut för prutgässen innebär inte en helt ofördelaktig förändring. För de vitkindade däremot skulle en dylik förskjutning förlänga flygetappen ganska avsevärt och därmed är de kanske inte lika benägna att låta sig vinddrivas.

Flygriktningar uppmätta i Lund redovisas i Figur 6. Resultaten visar att medan de vitkindade flyger med direkt riktning mot rastlokaler på Gotland och i Estland (ENE) så flyger prutgässen snarare mot närmaste kustområde (E). Skillnaden antyder att prutgässen försöker maximera kontakten med kuster i större utsträckning än de vitkindade vilket även

stöds av iakttagelser på andra platser (Saurola 1976, se även nedan). Generella flygriktningar i övrigt låg mellan NE och E, i god överensstämmelse med uppgifter från Vadehavet. Vid ostkusten följde stora antal av prutgäss Kalmarsund mot norr medan de vitkindade i allmänhet fortsatte mot NE. Norr om Öland satte prutgässen mer eller mindre rak kurs mot Finska viken (NE). Avvikande flygriktningar från det generella mönstret observerades framförallt längs västkusten norr om Skåne där en relativt hög andel av fåglarna sågs sträcka mot SSE längs kusten innan de sträckte in över land i de södra delarna av Halland. Även här föreföll prutgässen mer påverkade av kustlinjer än de vitkindade. Det observerade storskaliga geografiska mönstret hos vårsträcket av prutgäss stämmer mer med en rak kompasskurs mellan Vadehavet och Vita havet än med en storcirkelrutt (den närmaste vägen mellan två platser på jordens yta), dock med stora influenser av kustlinjer. En storcirkelrutt skulle innebära att huvuddelen av prutgässen borde passera över zon 2 och 3 och inte över zon 1 (Figur 4, Figur 9) som observerats. För de vitkindade går det inte att skilja på en rak kompasskurs och en storcirkelrutt p.g.a. flygetappens ringa längd. Den observerade flygruten stämmer in på båda varianterna.

Säsongsmönster

Övergripande säsongsmönster för observerat vårsträck av båda arterna visas i Figur 7 och Tabell 5. Det säsongsmässiga mönstret för prutgässen var mycket stabilt med mediandatum i regel mellan 22–25 maj. Under år med ihållande motvindar låg passagen senare med mediandatum under majs sista dagar. Mediandatum för passagen av vitkindade gäss tenderade att senareläggas och andelen fåglar sedda i maj ökade under perioden. Inget samband med rådande vindförhållanden kunde hittas i detta fall. Anledningen till senareläggningen av passagen kan finnas i den kraftiga populationsökningen under perioden och möjliga förändringar i flyttningsstrategier relaterade till denna. I mitten av 1990-talet fanns fyra-fem gånger fler vitkindade gäss jämfört med i början 1980-talet. Vidare så har den vitkindade gässen etablerat sig som häckfågel på vårrastningsplatserna i Östersjöområdet, främst på Gotland, med en population på minst 10 000 fåglar (Waldenström 1995). Troligen har detta ökat konkurrensen på de relativt begränsade rastlokalerna och därmed kan det ha blivit fördelaktigare att stanna kvar i Vadehavet för att under mindre konkurrens bygga upp näringsförråden, antingen för en direktflygning

från Vadehavet till arktiska områden eller för att förkorta rastperioden i Östersjön. Detta scenario skulle även kunna förklara den längre sträckperioden som observerats för vitkindade gäss jämfört med prutgäss (Tabell 5). De vitkindade gäss som ses utgörs av en blandning av fåglar med olika häckningsområden och flyttningsstrategier. Tidigt flyttande Östersjöhäckare (Forslund 1992), ryska häckfåglar på väg till långtidsrastning i Östersjöområdet, och ryska häckfåglar som flyger direkt till arktiska områden eller enbart korttidsrastar i Östersjön. För prutgässens del är alla fåglar på väg till vårrastning kring Vita havet och passagen är mycket koncentrerad i tid. Intressant i sammanhanget är att när huvuddelen av de vitkindade lämnar Östersjön i mitten av maj är ivägsträcket synnerligen koncentrerat på samma sätt som när prutgässen lämnar Vadehavet (Kumari 1971, Leito & Renno 1983, Leito 1991, Leivo et al 1994, 1995).

Internationell utblick

I Figur 8 a-f har jag jämfört sträckförloppet hos prutgäss i Sverige med observerat sträckförlopp i Finland eller Danmark för att utreda om de flyger hela vägen genom Östersjöområdet i en obruten flygning. Tyvärr fanns inte uppgifter från samtliga länder tillgängliga från samma år. Baserat på flyghastighetsmätningar i Lund (Green & Alerstam, in prep.) bör flygningen från Sverige till Finska viken ta 10–14 timmar. Mellan Danmark och Sverige bör det ta gässen mellan en halvtimme och fyra timmar

att flyga beroende på vilka lokaler man utgår ifrån. Om flygningen sker i en obruten etapp bör gäss som passerar Danmark kunna observeras i Sverige senare samma dag. Gäss som ses i Sverige bör passera Finland senare samma dag eller dagen efter beroende på när på dygnet de observerades i Sverige. Figur 8 ger gott stöd för att prutgässen i många fall verkligen flyger igenom Östersjöområdet utan att stanna. I vissa fall finns dock en liten tidsförskjutning i passagerna mellan länderna som antyder att de ej har genomfört en direktflygning. Förmodligen går de stundtals ner och rastar kortvarigt längs ruttan. Detta beteende har även konstaterats för ljusbukiga prutgäss på väg mellan Danmark och Grönland/Spetsbergen (Clausen & Bustnes in press) samt längs den svenska västkusten. Varför de gör detta är än så länge relativt okänt men de korta stoppen och platserna de går ner på antyder att det inte är för att bygga på näringsförråden. Möjligen kan det vara så att de behöver dricka då stora fåglar med tunga fettförråd löper risk att uttorkas vid långa flygningar.

Med tanke på att många prutgäss och vitkindade gäss passerar Sverige nattetid och det faktum att ytterst få fåglar av båda arterna ses längs den södra och sydöstra Östersjökusten (Rutschke & Litzbarski 1976, Raudonikis & Shvazhas 1991) visar de relativt höga antalen observerade i Sverige att huvuddelen av de inblandade populationerna passerar över Sverige och närliggande havsområden under vårsträcket. Sträcket är dock inte lika koncentrerat som i t.ex. Finska viken.