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Spring migration of birds across the Greenland Inlandice

Thomas Alerstam, Christian Hjort, Göran Högstedt, Paul Eric Jönsson, Johnny Karlsson and Bertil Larsson

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Radar observations from a long-range surveillance station in SE Greenland (65°31'N, 37°08'W) during the end of May and beginning of June 1980 and 1982, demonstrated regular bird migration across the Inlandice in both E/SE and W/NW directions. According to supplementary field observations from SE and W Greenland 1980, -82 and -84, and to available information from the literature, the most probable species to carry out a transglacial E/SE-migration in spring are *Gavia immer, Clangula hyemalis, Mergus serrator, Anas platyrhynchos* and, possibly, *Alle alle* and *Larus hyperboreus*. These birds probably depart from the ice-free coasts in W Greenland towards breeding sites along the E Greenland coast and, at least in *Clangula hyemalis*, Iceland and possibly even further to the east. *Plectrophenax nivalis* and *Calcarius lapponicus* probably also travel eastwards over the southern Inlandice to SE Greenland breeding sites.

Species involved in the transglacial W/NW-migration comprise geese, *Anser albifrons* and *Branta bernicla,* and high arctic waders, *Charadrius hiaticula, Arenaria interpres, Calidris canutus* and *Calidris alba.* In addition, it is highly probable that also *Oenanthe oenanthe, Sterna paradisaea* and *Phalaropus lobatus* belong to this category. The geese and high arctic waders depart from staging areas in Iceland to undertake a long-distance flight to breeding grounds in W Greenland (*Anser albifrons)* or NW Greenland and N Canada. The flight route passes the Sermilik fjord region in SE Greenland, where the migrants shift from a W/WNW course over the Denmark Strait to a WNW/NW course across the Inlandice.

The route from Iceland via Sermilik to NW Greenland and N Canada is about 10% longer than the great circle route across the central and northern Inlandice. However, wind conditions for a high altitude transglacial flight are much less favourable along the great circle route. The observed migration patterns involve the crossing of 450–700 km of inlandice, reaching 2500–2800 m asl, with temperatures about −10°C. The total flight distance from Iceland to NW Greenland and N Canada is 2300–3000 km.

Staging areas for ducks and divers along the Greenland west coast, and for geese and waders in Iceland, are probably of crucial importance for the evolution of the observed transglacial migration patterns. The distance from Iceland to the northernmost part of the Nearctic is smaller than from corresponding spring staging sites in North America. Hence, Iceland serves as a spring-board to Nearctic breeding grounds for Old World winter populations of waders and geese. Staging sites probably have a dual effect as spring-boards and bottle-necks, respectively, for the evolution of migration patterns in arctic birds. Gaps in the circumpolar breeding distribution of arctic species, and a relatively low diversity of species breeding in the sector around Greenland, may be due to competition for limited staging resources in combination with the isolating effects in this sector of sea expanses and the Greenland Inlandice.

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Introduction

The Greenland Inlandice covers 1.7 million km^2, spans over more than 20 degrees of latitude, from about 61° to 82°N, and has an average height of about 2100 m asl, with maximum heights between 2500 and 3300 m asl at different latitudes. There exist no resting and sheltering places for birds in this vast ice desert. It is easy to understand why it was formerly assumed that the Inlandice must be a formidable obstacle to migratory birds, constituting a natural divide between species or populations breeding to the west of the Inlandice and taking part in American migration systems, and populations in East Greenland and Iceland taking part in European migration systems.

However, already field observations made between 1896 and 1923 by Johan Petersen in the Angmagssalik region, SE Greenland (in Helms 1926), demonstrated that migrating Brent Geese *Branta bernicla* pass west (spring) /east (autumn) rather than north/south. Obviously, these birds travel across the Inlandice between European winter quarters and breeding sites in NW Greenland and N Canada. This was confirmed by E. Knuth in 1936, on his crossing of the ice-cap between the Angmagssalik and Disko regions (in Salomonsen 1950). On 30 May large flocks of geese, altogether 500–600 birds, were recorded flying NW across the Inlandice.

Salomonsen (1950) concluded that, besides Brent Geese, also White-fronted Geese *Anser albifrons* breeding in W Greenland, migrate from wintering places in the British Isles via Iceland across the Inlandice. On the basis of extensive ringing studies of bird migration in Greenland, Salomonsen (1967a) could add at least three further species participating in a transglacial migration system between Old World winter quarters and New World breeding areas: the Turnstone *Arenaria interpres,* Knot *Calidris canutus* and Wheatear *Oenanthe oenanthe.* With the further accumulation of ringing and observation data, a regular transglacial migration pattern has been confirmed in the above-mentioned species, as well as in the Ringed Plover *Charadrius hiaticula,* and to a smaller extent also in the Purple Sandpiper *Calidris maritima* and, possibly, the Sanderling *Calidris alba.* During spring migration, the birds to a large extent travel via Iceland, which is used as a stopover and refuelling station before the final transglacial flight journey to the breeding sites (Morrison 1975, 1977, 1984, Wilson 1981, Meltofte 1985).

For the high arctic breeding birds, i.e. Brent Geese, Turnstones, Knots, Ringed Plovers and Sanderlings destined for the Thule region, Ellesmere and Axel Heiberg Islands and surrounding areas, the journey from Iceland extends over 2000–3000 km. Little is known about the detailed circumstances of this journey, although there are indications that it is completed in a rapid and direct flight, without refuelling and possibly without landing and resting at all, except when the migrants encounter unfavourable weather en route. Furthermore, a significant number of migrants seem to cross the Inlandice along the 600 km-route between the Angmagssalik and Disko regions (Meltofte 1985).

There are also bird species with populations breeding to the east of the Greenland Inlandice and wintering to the west of it, like various ducks, gulls and auks spending the winter along the ice-free coast of SW Greenland (Salomonsen 1967a). In these species the existence of transglacial migration has never been suspected, but it has been taken for granted that the migration proceeds along the coastlines or over the open sea, passing south of Kap Farvel. Furthermore, there are recent recoveries in North America of Snow Buntings *Plectrophenax nivalis* and Lapland Longspurs *Calcarius lapponicus* ringed during the breeding season in SE Greenland (Meltofte 1983, Zoological Museum, Copenhagen, unpubl.). Salomonsen's (1979a) review of various bird species encountered dead or alive on the ice-cap, indicates that transglacial migration flights may occur in more species than hitherto suspected.

In this paper, we present radar observations from a surveillance station on Kulusuk island, SE Greenland, of spring migration in two different years across the Greenland Inlandice. Regular migration was found to take place both in a westerly and easterly direction. Supplementary systematic field observations are described from both SE and W Greenland. All data refer to the period 20 May – 10 June, i.e. the spring migration peak in a majority of Greenland birds.

The results are analysed and discussed mainly from two different points of view. First, the circumstances of long-distance transglacial flights are unique in bird migration. The arctic birds' strategies to meet the difficulties and hazards associated with these flights, which often bring them far beyond the point of no-return, may throw light on the limits of migratory performance and capacity in birds. These strategies include the timing of migration, flight routes, mode of orientation and responses to weather and wind.

Second, the importance of the Inlandice as a barrier for migratory birds is of interest not only for reconstructing possible bird migration and distribution patterns during earlier glacial epochs, but also for interpreting the present-day distribution in arctic breeding areas of different wintering populations. More specifically, do Old and New World wintering populations compete for the Arctic breeding grounds on either side of the Greenland Inlandice, and to what extent are the migratory divides between American and European migration systems affected by the existence of this Inlandice?

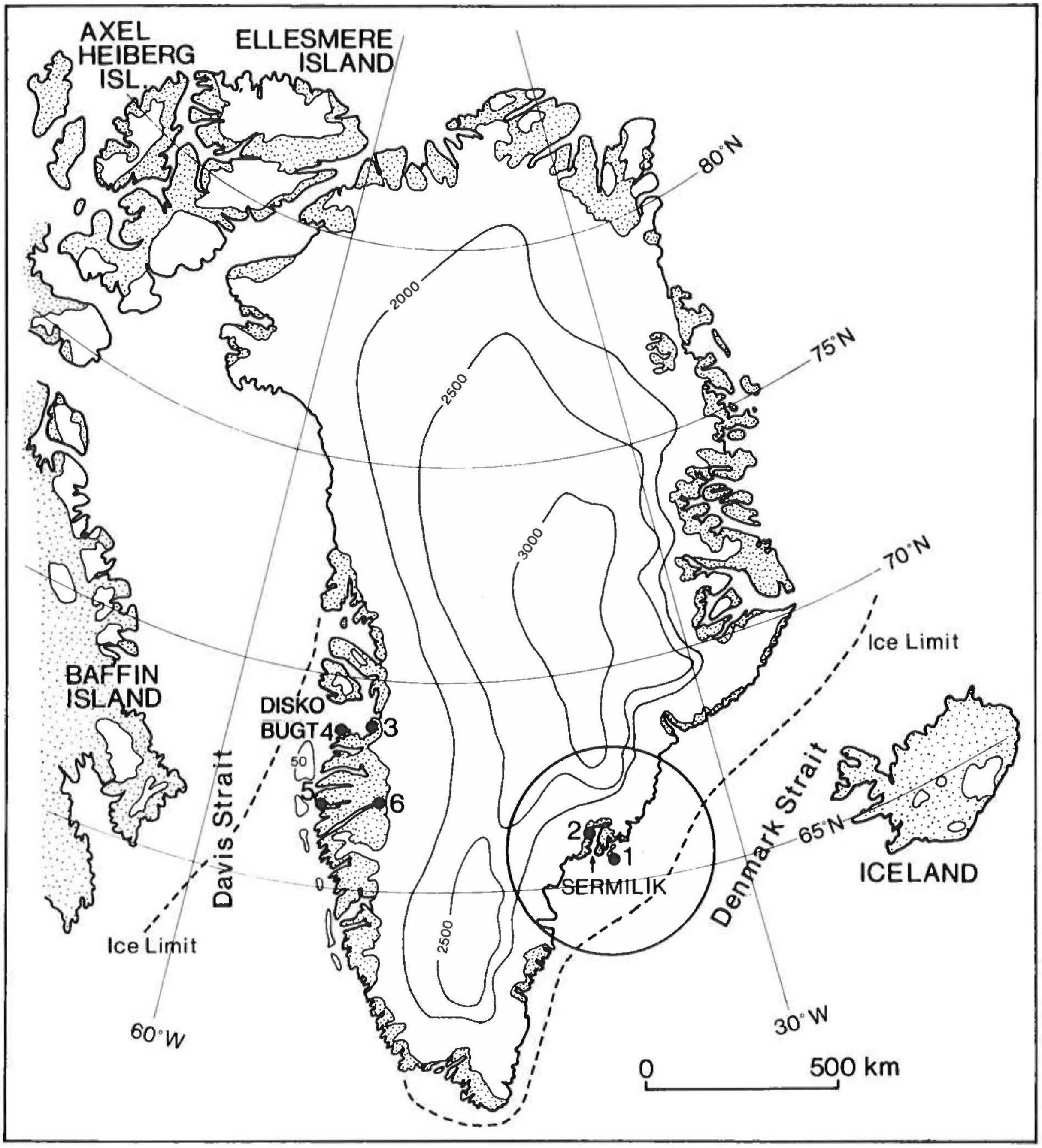


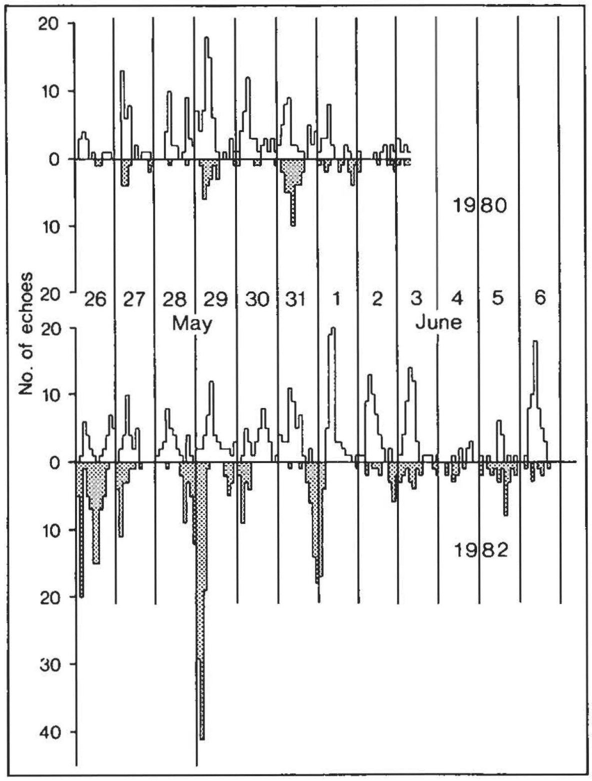
Fig. 1. Radar observations were carried out at a radar station on Kulusuk island, SE Greenland (site 1). The circle shows the approximate maximum range for registration of radar echoes from migrating birds. Supplementary field observations of bird migration were carried out at sites 1–6. The height of the Inlandice (m asl) is indicated, as well as the position of fishing banks (depths <50 m) off the Greenland west coast. Broken lines show the normal pack ice limit in May/June.

Radar observations

Observations were carried out 21 May – 3 June 1980 and 26 May – 7 June 1982 at DYE-4 radar station, situated approx. 300 m asl on Kulusuk island, SE Greenland (65°31'N, 37°08'W). This is a high-power surveillance station operating with a long pulse duration, and equipped with MTI (moving target indicator). The maximum range for detection of radar echoes from flocks of birds is about 250 km (Fig. 1). The methods of registration differed between the two years.

In 1980, an automatic camera mounted at the radar screen (PPI) was used to obtain continuous registration 24 hrs a day, from 26 May onwards. The exposure time for each photographic frame was 8 minutes, corresponding to 12 antenna revolutions. Films were developed at the radar site, and records of echoes from migrating birds were plotted on maps using a photographic magnification apparatus. The total number of echoes will be somewhat underestimated by this method, since weak and brief echoes, and echoes overlapping on a single 8 min. photographic frame, are missed. Persistent echoes were identified and plotted over several successive frames, and speed measurements given in this paper are restricted to echoes recorded over at least 5 successive frames, i.e. ≥40 minutes. Direct observation and plotting at the radar PPI were carried out each day 21–25 May (during altogether 23 hours), and such supplementary observations were also carried out during the succeeding period of photographic registration.

In 1982, 16 mm time-lapse filming (one frame per antenna revolution) of the radar screen provided continuous round the clock registration throughout the study period. We analysed our radar films at Colorado Springs, USA, in November 1983. The film records allow also weak and intermittent echoes from migrating birds to be detected and counted. Detailed plots of routes and determination of direction and speed were accomplished for a sample of bird echoes in each migratory wave. Unless otherwise stated, times given in this paper are local Greenland Summer Time (=GMT−2hrs).

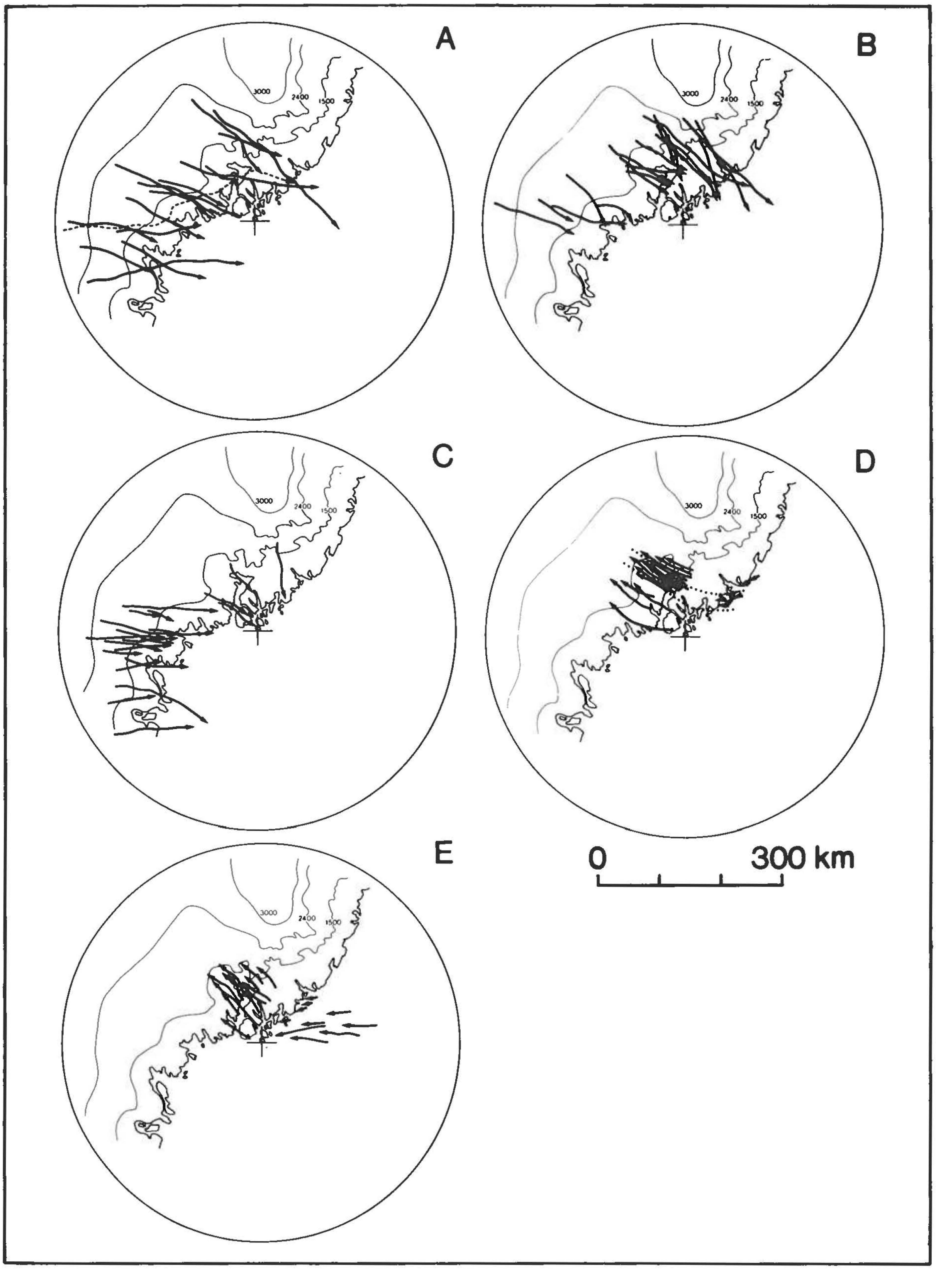


Fig, 2. Number of radar echoes in 2-hour intervals from bird flocks migrating E/SE (above the time axis) and W/NW (below the time axis) over the Inlandice. The data are based on continuous photographic registration of the radar PPI. Additional observations of the radar PPI were carried out 21–25 May 1980, revealing intensive and moderate E/SE migration on 24 and 25 May, respectively.

Number of echoes

Three different types of migratory pattern were distinguished: 1) offshore migration towards NE in the Denmark Strait; 2) W/NW migration across the Inlandice and 3) E/SE migration across the Inlandice. The first type was often impossible to analyse properly because

Fig. 3. Geographical patterns of transglacial E/SE (Figs A-C) and W/ NW (figs D, E) migration, according to radar registration. A sample of radar echo tracks are illustrated for each occasion.
A) 31 May 1982. E/SE-migration on a broad front. Echoes were strong and persistent. The echo indicated by the broken line was recorded between 08.05 and 12.22 hrs, with a mean ground speed at 25 ms^{-1}. The two echo tracks reaching far offshore towards SE and E over the Denmark Strait were recorded 06.45 – 09.08 hrs and 11.23–14.38 hrs, respectively. The average ground speed on this occasion was 26 ms^{-1}.
B) 29 May 1982. E/SE-migration taking place mainly north of the radar station. One echo detected at 07.08 hrs was split into two at 07.44 hrs, disappearing 40 km apart at the coastline at 08.01 and 08.23 hrs, respectively. The northernmost echoes traverse high mountainous terrain, like the Mount Forel area (3360 m asl). Average ground speed was 30 ms^{-1}.
C) 29 May 1980. E/SE-migration taking place mainly south of the radar station. Except for a few echoes arriving from the north, the main track direction was almost due east. Average ground speed was 22 ms^{-1}.
D) 29 May 1982. W/NW-migration, mostly within a well-defined corridor as indicated by the dotted lines. Radar echoes appeared at the coastline, later to reappear over the Sermilik fjord and the ice slope. In the intervening section of the route, the migrants presumably travelled mostly in radar shadow across an area with mountain peaks and glaciers 1500–2000 m asl. Average ground speed for the most persistent echoes was about 21 ms^{-1}. Part of this movement took place simultaneously with that shown in B.
E) 31 May 1980. W/NW-migration, with registration of birds arriving on a westerly course over the sea. A distinct shift in direction towards NW occurred over land. Average ground speed for the most persistent echoes was 18 ms^{-1}.


A
B
C
D
E
3000
2400
1500
0
300 km

of interference with sea clutter on the radar indicator, and will not be considered in this report.

The number of echoes from birds migrating W or E over the Inlandice is shown for 2-hour intervals in Fig. 2. According to the direct observations at the radar screen, there was no transglacial migration 21-23 May 1980, but E-migration took place on both 24 May (24 echoes plotted in four hours) and 25 May (7 echoes in four hours). From 26 May onwards, altogether 259 echoes of E-bound and 94 echoes of W-bound transglacial migrants were recorded in 1980, and the corresponding figures for 1982 were 441 and 396, respectively.

The echoes of W-migrants were generally weaker, and visible on the radar screen for a shorter time, than those of E-migrants. The number of radar echoes do not provide accurate estimates of the total number of migrating bird flocks, particularly not for the W-migrants, the majority of which pass a mountainous area north of the radar station where the birds fly in radar shadow at many places. Furthermore, the speed of W-migrants is slower than that of the E-migrants (cf. below), a fact which makes the former category more susceptible than the latter to suppression from radar registration by the MTI device (suppressing stationary and slowly moving targets).

Geographical pattern

The geographical pattern is exemplified in Fig. 3. E-migrants generally arrived on a broad front across the Inlandice. They were detected at high altitudes, often where the Inlandice reaches well above 2000 m asl. Flocks were regularly passing over the high mountain ranges, with peaks 2000–3000 m asl, north of the radar station. A few echoes were even seen crossing the Mount Forel area (3360 m asl). Most echoes disappeared at the East Greenland coast, almost certainly because the birds descended below radar coverage. However, some echoes could be followed far offshore over the pack ice in the Denmark Strait. On some days, most echoes arrived north of the radar station with a preponderance for southeasterly tracks (Fig. 3B), while tracks were on average more towards east on occasions when the main arrival occurred south of the radar station (Fig. 3C).

A few echoes arrived from the north on southsoutheasterly, or even southerly tracks. The most reasonable explanation is that they represent bird flocks that have veered from a more easterly track, in order to descend towards the Angmagssalik region.

Hence, the transglacial E-migrants seem to include both birds that are destined for the East Greenland coast, where the Angmagssalik region offers the most hospitable living conditions between Kap Farvel and Scoresbysund, and birds that continue their migration across the Denmark Strait.

W-migration occurred almost exclusively to the north of the radar station, with a majority of echoes crossing the northern part of the Sermilik. On some days the echoes were concentrated within a distinct migration corridor: radar echoes were briefly visible at the coastline, mostly around 66°N latitude, where the migrants obviously started to climb inland. The echoes were lost from the radar screen in the adjacent area with glaciers and mountain peaks reaching 1500–2000 m asl, reappearing over the Sermilik area. The echoes could then be followed up the ice slope, disappearing where the ice reaches about 1500 m asl, sometimes 1800 m asl (Fig. 3D).

A few echoes departed inland along a route slightly to the north of this corridor, across the mountains north of Sermilik, where there are many peaks above 2000 m asl. Furthermore, there were regular but scattered movements up the ice slope from the southern parts of Sermilik. Only very few W-echoes were recorded to depart over the Inlandice from further south along the coast.

A distinct feature of the W/NW-migration pattern was the change in migratory direction taking place in the study area. The direction of the migration corridor shifted from west towards northwest (Fig. 3D). Normally, echoes from W-migrants were not detected over the sea, probably because the birds travelled at low altitudes,below radar coverage (sometimes the detection of bird echoes was also prevented by sea clutter). However, on a few occasions such echoes were recorded (Fig. 3E), showing a distinct shift in direction from approx. west over the sea to approx. northwest over the ice slope.

As seen from Fig. 2 it regularly happened that E/SE- and W/NW-migration took place simultaneously. Sometimes flocks on opposite tracks passed so close to each other, that the echoes overlapped on the radar screen during the short period of passage. However, the vertical separation between the migrants was unknown.

Direction and speed

The distributions of track directions over the ice slope are presented in Fig. 4. The transglacial E-migration showed a rather wide scatter of directions, with 82% of the echo tracks between 80° and 140°. For W/NW-migration, 90% of all track directions fell in the range 290°–330°, with 69% between 290° and 310°. Only 4% of the echoes showed directions south of west (<270°) over the ice slope.

Speeds differed noticeably between the transglacial E- and W- migrants (Fig. 5). This difference is manifest for ground speeds as well as air speeds, calculated on the basis of wind measurements from the 850 mb-level (approx. 1500 m asl) at Angmagssalik. Of course, without a detailed knowledge of the birds' flight altitudes, the calculated air speeds are provisional estimates only.

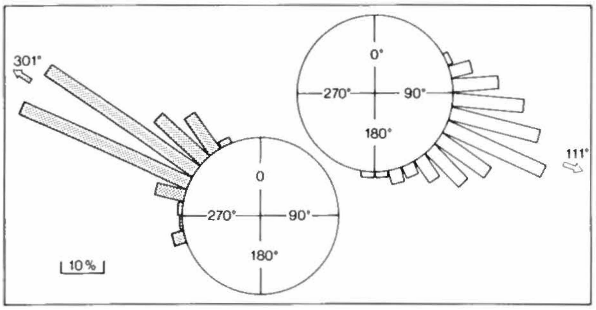


Fig. 4. Distribution of track directions of radar echoes from transglacial E/SE- and W/NW (shaded)-migration. The diagrams show the weighted percent distributions for the two study years combined. Median directions are indicated by arrows.

Most E-migrants travelled very fast, between 20 and 35 ms^{-1}, with a median air speed at 27 ms^{-1}. W-migrants were slower, with speeds normally in the range 15-25 ms^{-1} and with a median air speed at 21 ms^{-1}. Part of the difference between E- and W-migrants may be explained by the fact that many of the former probably descended while the latter were in a climbing phase over the ice slope. Because speeds were measured over very long time intervals and distances, this explanation probably is not sufficient to account for all of the difference in speed between the two categories. It seems highly probable that different types of birds, with different typical flight speeds, participated in the E- and W-migration, respectively.

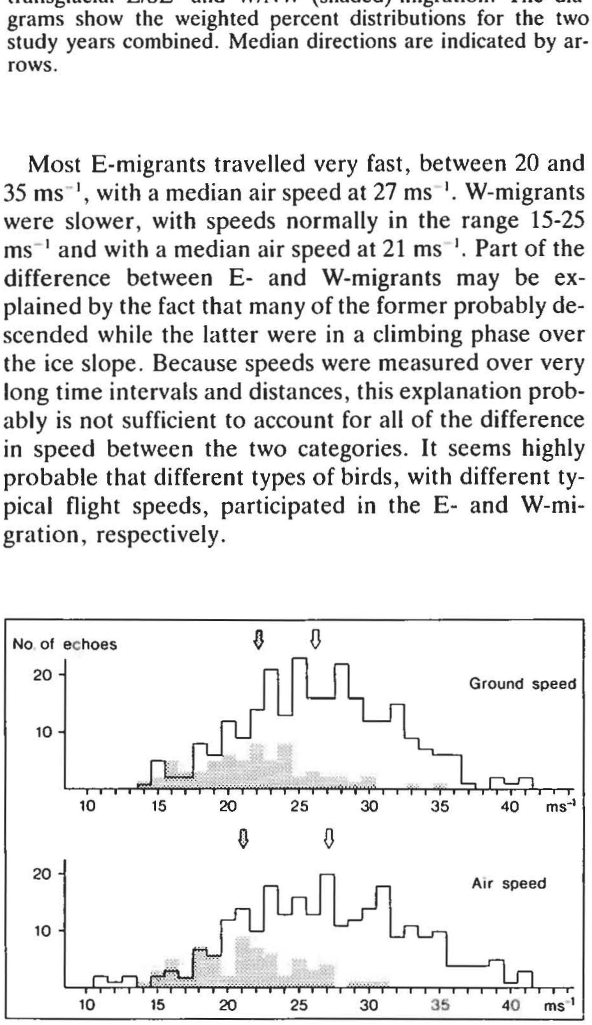


Fig. 5. Ground speed of transglacial E/SE-(open bars) and W/NW (shaded bars)-migrants, as determined from radar photographs and films for echoes registered during a time period of at least 40 min. In addition, speeds of a few echoes plotted directly ≥20min. from the radar PPI have been included. Air speeds (lower diagram) have been calculated on the basis of daily aerological wind data (850 mb-level) from Angmagssalik 09.00 and 21.00 hrs. Each set of wind data was used for air speed calculations for echoes recorded within ± 6 hours from the time of wind measurement. Median speeds are indicated by arrows.

Many echoes of W-migrants were weak and only briefly visible on the radar screen (perhaps intermittently suppressed by the MTI). The most persistent echoes, used for speed determination, may therefore represent a biassed sample of this category. If so, the overall difference in speed between E- and W-migrants is even larger than indicated in Fig. 5.

Variation in migratory intensity, timing and direction

As seen from Fig. 2, the daily occurrence of transglacial E-migration was highly regular. Exceptions were 21–23 May (direct observations of the radar screen), 26 May, 2–3 June 1980, and 4–5 and 7 June 1982, when there was little or no such migration. On six out of these nine exceptional occasions, a cyclone had passed along the W Greenland coast during the preceding evening and night (Tab. 1). Hence, this type of migration probably is primarily affected by the weather situation in W Greenland – cyclones with precipitation, poor visibility and strong winds preventing eastward departures across the Inlandice. On many days with transglacial E-migration, weather conditions for continued eastward flights across the Denmark Strait were highly unfavourable with strong headwinds (and on a few occasions cyclones at W Iceland). On such occasions one may assume that transglacial migrants destined for a continued eastward journey, descend to rest and wait for more favourable weather at the East Greenland coast.

Transglacial W-migration occurred much less regularly than E-migration. The main passage was concentrated to a few peak days each year (Fig. 2). These days were associated with favourable NE–E tailwinds over the Denmark Strait except 31 May 1980 when westerly winds prevailed (Tab. 1, Fig. 6). On this latter occasion the migration peak occurred unusually late during the day (cf. below). On several days with W-migration in 1982, easterly winds over the Denmark Strait were very strong, like 29 May – the major migration day of that year (Figs 6 and 7).

Weather conditions over the Inlandice and at the W Greenland coast were favourable, or at least not inhibitory, on the days when W-migration was registered in 1980 and 1982. However, it may be difficult or impossible for the migrants to forecast cyclone passages along the W Greenland coast, and in some years it may happen that transglacial W-migration coincides with cyclonic weather in W Greenland.

The distance from the W Greenland coast to the radar site is roughly the same as that from W Iceland to the radar (about 700 km). Hence, if the transglacial E-migrants start from W Greenland and the W-migrants from Iceland, they should arrive simultaneously in the radar study area provided that they depart at the same time and fly equally fast.

However, W Greenland and W Iceland are approxi-

Table 1. Cyclonic disturbances (fronts, precipitation) and winds (direction and speed in ms^{-1}; weak winds <5 ms^{-1} omitted) between W Greenland and Iceland within the latitudinal zone 63°N – 69°N. All data are from 00 hrs GMT = Greenland Summer Time 22 hrs the preceding date. Winds at W Greenland and Iceland are from radiosonde measurements at Aasiaat (Egedesminde) (850 mb level, approx. 1500 m asl) and Keflavik (low altitude wind), respectively. Over the Inlandice, winds were estimated from the 700 mb aerological chart (approx. 3000 m asl) and over Denmark Strait from the surface chart (low altitude wind). Based on the European Meteorological Bulletin, Deutscher Wetterdienst.

Date		W Greenland coast		Ice-cap	Denmark Strait		W Iceland	
1980								
May	21	Cycl.	S 12	S 17		S 12		
	22	Cycl.	SE 10	S 20	Cycl.	SE 20		
	23	Cycl.		S 15		S 10	Cycl.	S 5
	24		SSE 16	SSW 14		W 5		WSW 5
	25		SSW 7	SW 11	Cycl.	WNW 10		WNW 5
	26			W 5				NW 5
	27		SW 5			NE 5		NNE 12
	28	(Cycl.)[1]		S 5		ENE 5		NNE 11
	29			SSE 8		ENE 5		
	30					E 6		
	31		SSW 9			W 12		
June	1		S 9			S 7	Cycl.	
	2	Cycl.	S 12	SSW 20		NNE 8		
	3		S 14	WSW 5				NW 5
1982								
May	26			SE 5		ENE 14		
	27					ENE 12		
	28					E 8		
	29	(Cycl.)[3]		SE 5		ENE 20		E 8
	30					ENE 25	(Cycl.)[2]	E 6
	31		SSW 16			NNE 8		N 5
June	1			E 5		NE 22	Cycl.	NNE 9
	2					ENE 10		
	3					NE 15	Cycl.	ESE 9
	4	Cycl.	S 5	SSW 17		N 5		
	5	Cycl.	SSE 15	S 20				SSE 7
	6		S 7	S 10	Cycl.			ESE 8
	7			SE 10	Cycl.	E 8		

1) Occlusion front, little precip.
2) Occluding depression, rain showers
3) Weak depression

mately 30° of longitude apart, corresponding to a time difference of 2 hours. Hence, if the migration starts at the same time of the solar day from these two areas, the birds are expected to take off two hours earlier from Iceland. On the other hand, W-migrants have a lower airspeed (median 21ms^{-1}, Fig. 5) than E-migrants (27 ms^{-1}), and travel time over a 700 km distance in calm weather will therefore be expected to differ by 2 hours (9.3 versus 7.2 hours) between these two categories (neglecting the possible influence of climb and descent on the air speed estimates, cf. above). Hence, the effects of a longitudinal time difference and of different air speeds between E- and W-migrants cancel each other. Because of this, differences in time schedule at the radar site between the two migratory categories are probably the result of different wind conditions encountered during the preceding flights across the Inlandice and the Denmark Strait, respectively.

As seen from Figs 2 and 8, the morning peak of transglacial E-migration in the radar study area occurred between 04 and 11 hours. On days with a relatively late arrival, 08 – 11 hrs, head- and crosswinds often prevailed over the Inlandice. The median time with neutral winds was between 06 – 07 hrs (Fig. 8), indicating a departure time from W Greenland about 23 hrs the preceding night. Secondary afternoon peaks of E-migration were recorded on a few days.

W-migration over the ice slope at Sermilik most often culminated between 02-10 hrs in the late night or morning (Fig. 8). In addition, important migration peaks occurred early in the afternoon on 26 May 1982, and before midnight on 31 May 1982. On the latter day a cyclone reached W Iceland in the late afternoon and passed during the evening and night. The migrants probably departed in favourable ENE winds immediately before the arrival of the cyclone.

The early morning peaks, 02–04 hrs, of W-migration were all associated with very strong tailwinds providing an effective wind assistance of at least 10 ms^{-1} over the Denmark Strait. With an estimated ground speed 30–35 ms^{-1}, these birds would have crossed the Denmark Strait in only 6 hours' flight, taking off 20–22 hrs

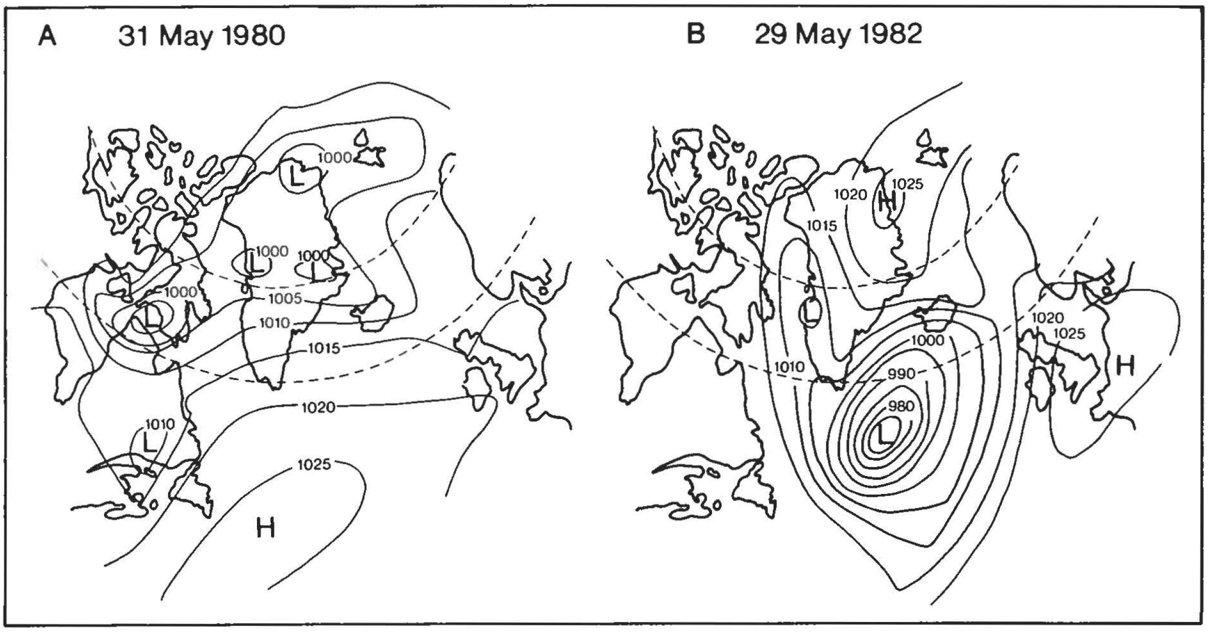


Fig. 6. Atmospheric pressure patterns on 31 May 1980 (A) and 29 May 1982 (B). Based on data from 00 hrs GMT(European Meteorological Bulletin, Deutscher Wetterdienst). Extensive transglacial migration, towards E as well as W , occurred on both occasions. The timing of W-passage at the radar site was considerably earlier on occasion B than A, while the reverse held for transglacial E-migration (cf. Fig. 2). This is consistent with an overall W-wind flow on occasion A, but an E-wind flow on occasion B. In A) the typical high pressure in N Greenland has temporarily disappeared, leaving room for a weak occlusion front extending across Greenland to N Iceland. A similar temporary reversal of the typical pressure pattern occurred on 24 and 25 May 1980. B) illustrates the most common weather pattern during the study period,characterized by high pressure in N Greenland and depressions moving south of Greenland towards Iceland. Sometimes, depressions also moved north in the Davis Strait along the W Greenland coast (Table 1). The deep depression moving towards Iceland 28–30 May 1982 was associated with strong ENE winds in the Denmark Strait.

(=22–24 hrs GMT) during the preceding night. In contrast, on 31 May 1980 when the culmination of the W-migration was delayed until 09–10 hrs, winds over the Denmark Strait were opposed at the surface (Table 1) and neutral at higher altitudes (850 mb level – note the tendency of higher flights over the sea on this day, Fig. 3E). Assuming that the birds came from W Iceland with an effective headwind of 5 ms^{-1}, the flight across the Denmark Strait would have lasted about 12 hours after the birds' main take off from Iceland 21-22 hrs (=23–24 hrs GMT).

This suggests that transglacial E- and W-migrants may depart at about the same local time, with a peak 2-3 hours before solar midnight, from W Greenland and W Iceland, respectively. The timing of their passage of the radar study area the following night or morning is dependent on wind conditions prevailing during the flights across the Inlandice and the Denmark Strait, respectively. There are a few migration peaks, e.g. during the afternoon (Figs 2 and 8), which do not fit into this schedule, indicating that departures may also occur at other times or from other starting areas.

The geographical pattern of transglacial E-migration was on average shifted slightly to the north in 1982 as compared to 1980. 39% of the radar echoes arrived north of 66°N latitude in 1982, with a daily variation 19–51%, while the corresponding proportion in 1980 was 14%, with a daily variation 8–20% (Fig. 9). Because track directions differed somewhat between arrivals north of 66°N latitude (median track direction 136° in 1980, and 122° in 1982) in comparison with arrivals to the south of this latitude (corresponding medians 102° and 111°, respectively), the overall track distribution was shifted slightly more towards the south in 1982 (median 114°) than in 1980 (median 105°). Furthermore, the total proportion of radar echoes of transglacial E-migrants with track directions north of east (<90°) was distinctly higher in 1980 (21%) than in 1982 (11%). Probably, these differences cannot be explained by effects of wind during the eastward flights across the Inlandice (cf. Table 1, Fig. 9). Rather, it seems likly that the departures from W Greenland of transglacial E-migrants occurred from, on average, more northerly latitudes in 1982 than in 1980.

Mean track direction for the transglacial W-migration, as estimated over the ice slope in the Sermilik area, varied between 290° and 319° during eleven different migration peaks (mean of the means 305°, S.D. 8°, n=11). The corresponding heading direction, calculated on the basis of the 850 mb wind at Angmagssalik, varied

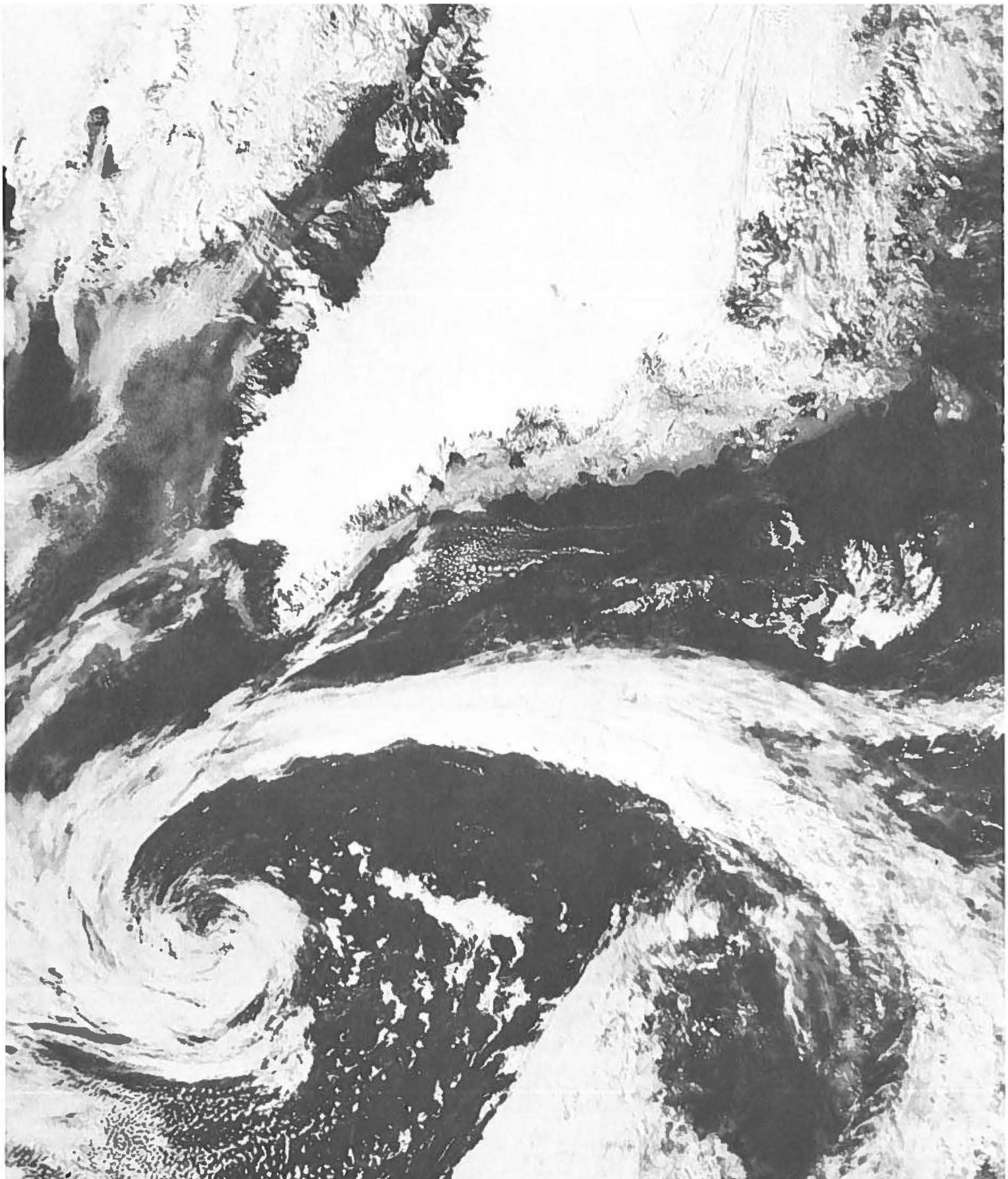


Fig. 7. Satellite photograph from 15.30 hrs GMT, 28 May 1982. A deep cyclone passes south of Greenland towards Iceland (cf. the corresponding pressure pattern nine hours later, Fig. 6B). Strong easterly winds and clear weather prevail over Denmark Strait, and maximum transglacial W-migration 1982 took place on this occasion (Fig. 2). The photograph also shows the extension of pack-ice along the E and S Greenland coasts as well as in Davis Strait. Note that most of Disko Bugt and the waters off the island of Disko are ice-free. Photograph by courtesy of the Meteorological Office at Søndrestrømfjord Airport.

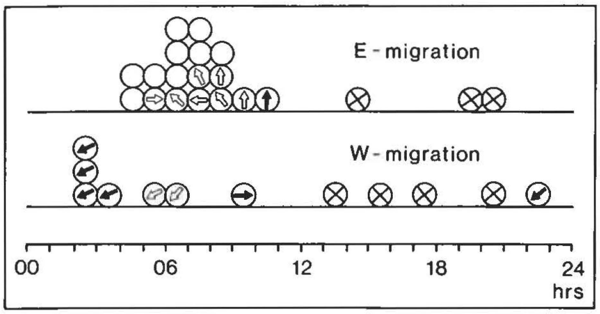


Fig. 8. Hour of culmination for different transglacial migration peaks, according to counts of radar echoes. Only migration peaks with ≥ 4 radar echoes during the hour of culmination, are included. Arrows indicate wind directions over the Inlandice (estimated from 700 mb aerological charts) and Denmark Strait (from surface charts, cf. Table 1), for the transglacial E/SE- and W/NW-migration peaks, respectively. Open arrows show instances with wind speed 5–10 ms^{-1} and filled arrows with wind speed >10 ms^{-1}, while no arrows are given with wind speed <5 ms^{-1}. Wind data are omitted for afternoon peaks.

between 297° and 326° (overall mean 314°, S.D. 9°, n=11). Analysing these data in relation to the angular difference between track and heading directions (Alerstam 1976), revealed no significant correlation either for track direction (r=0.14) or heading direction (r=−0.45,0.1<p<0.2). Hence, no firm conclusions about the occurrence of wind drift or compensation for such drift can be drawn from these data.

Field observations

In order to identify the species involved in the transglacial migration recorded by the radar we carried out field observations (basic equipment 10x binoculars and

		Arrivals N (%)
1980		
May	27	13
	28	18
	29	8
	30	12
	31	20
June	1	15
Total 1980		14
1982		
May	26	33
	27	19
	28	26
	29	59
	30	23
	31	36
June	1	51
	2	47
	3	47
	6	34
Total 1982		39

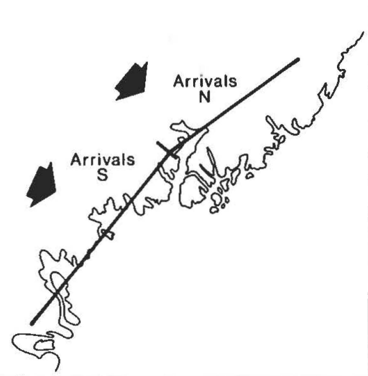


Fig. 9. Proportion of radar echoes of transglacial E/SE-migrants arriving north and south of approx 66°N lat. during different days (with ≥20 echoes). Echoes were counted when passing the transect lines shown on the map. Median directions for northerly and southerly arrivals vere slightly different, as indicated by the arrows (cf. text).

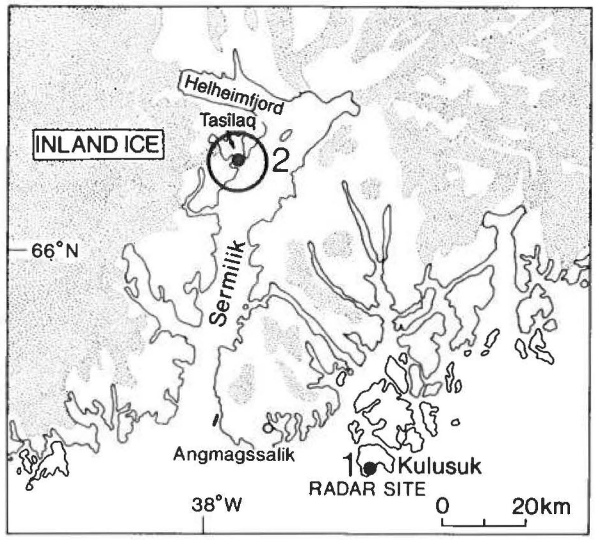


Fig. 10. Field observation sites 1 and 2, situated in the Angmagssalik region in SE Greenland (cf. Fig. 1). The radar station is situated at Kulusuk (site 1). Inlandice and glaciers are indicated by shading.

25x telescopes) in both SE and W Greenland (Sites 1–6 in Figs 1, 10 and 11).

Site 1. *Kulusuk*. Excursions on this island were made during the study period at the radar station 21/5 – 3/6 1980 and during transit stays 19–20/5 and 5–6/6 1982 on our way to and from site 2. No systematic counts of migrating birds were carried out.

Site 2. *Sermilik*. A small peninsula in Tasîlaq bay (66°11'N, 37°50'W) on the west side of Sermilik. After

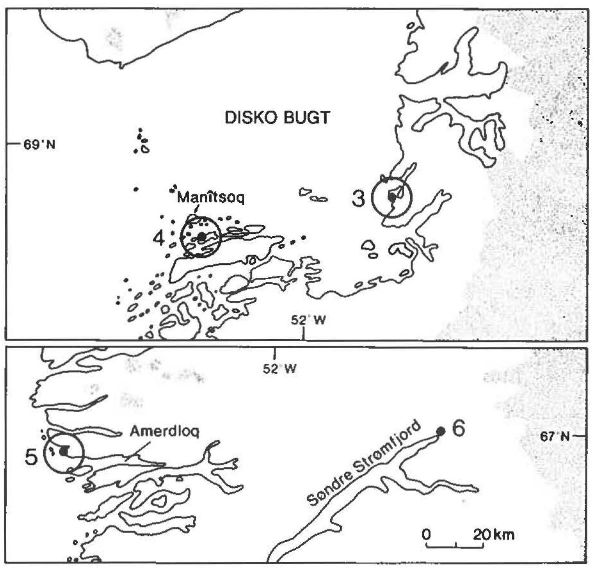


Fig. 11. Field observation sites 3–6 in two different regions of W Greenland (cf. Fig. 1), the southern Disko Bugt (top map) and the Sisimiut (Holsteinsborg) – Søndre Strømfjord region (below). Inlandice and glaciers are indicated by shading.

reconnaissance excursions 21-22/5, systematic counts of the visible bird migration was carried out by a team of four field observers 24 hours a day 23/5 – 4/6 1982. The observation post was situated close to our camp, 65 m above the fjord (entirely frozen throughout our stay) with free visibility in all directions. Between the camp and the Inlandice there were very poor resting and foraging areas for birds. About 90% of the surface of the peninsula (diameter 1.5 km, height 150 m) was glacially abraded bare rock, snow and water. The most suitable resting place for birds was a small marsh and pond area (approx. 1000 x 200 m) at the base of the peninsula. This area was gradually emerging from under the snow during our stay. It was used by geese and some waders and passerines, as recorded during our daily visits.

The weather was anticyclonic and fair, with occasional fog banks low over the fjord ice. Winds were normally weak, with only a few days with stronger, 8–10 m/s, southerly fjord winds (upper winds were easterly on these occasions as seen from the cloud drift). Temperature fluctuated between +8°C (afternoon maximum) and −4°C (night minimum).

Site 3. *Qasigiannguit (Christianshåb).* Systematic counts of bird movements were carried out each evening 24–28/5 1984 (two days with adverse weather). Two or three hours of further observations took place in the morning or afternoon 25–28/5. Total systematic observation time 24-28/5 was 28 hours. In addition, alertness for passing birds (but without systematic binocular/telescope surveys) was upheld during extensive outdoors activity in the vicinity of the village (also applies to sites 4 and 5).

The observation post was a small hill 110 m asl just outside the village. It was overlooking the inner Disko Bugt which was completely frozen, except for a few small open leads close to the shore and islands. Snow cover was close to 90%. During the last week of May 1984, Disko Bugt was still ice-covered westwards to about 52°45'W, with extensive areas of drift-ice further west, between site 4 and the island of Disko.

Site 4. *Aasiaat (Egedesminde).* Systematic counts of visible bird migration were carried out each evening 20.00–00.30 hrs 30/5–3/6 1984, with 2–4 hours of additional observations in the mornings or afternoons 31/5–3/6. Total systematic observation time 30/5–3/6 1984 was 32 hours.

The observation site, a small hill 20 m asl at the west end of the village, offered a good view of the archipelago to the north including Maniitsoq island, and to some degree even beyond that island. However, areas to the south of the observation island were completely blocked from view. The waters NE, N and W of the observation island were covered by drift-ice, whereas those to the E and S were still frozen. Snow cover in the area was close to 90%. Weather was fair with weak winds and high visibility.

Site 5. *Sisimiut (Holsteinsborg).* Systematic counts of visible bird migration by a team of three field observers were carried out each evening 19.00-24.00 hrs 30/5-4/6 1984, with 6-12 hours of additional daily observations 1/6-4/6. On 2/6 and 3/6 these additional observations were evenly distributed throughout the day (01–03, 04–06, 07–09, 10–12, 13–15 and 16–18 hrs). Total systematic observation time 30/5–4/6 1984 was 63 hours.

The observation site was a small hill, 50 m asl, in the southwest end of the village, from where the sea to the west (with offshore islands), southwest (open sea) and south-southeast (inlet to Amerdloq) could be surveyed. The view towards N, NE and E over land was restricted because of the hilly terrain. The sea was completely free of ice, and there was no fjord ice nearer than about 40 km inland. Weather was fair with weak winds and good visibility. Offshore fog banks were frequently seen far to the west. Snow coverage was about 10%.

Site 6. *Søndrestrømfjord Airport / Kangerdlugssuaq.* We entered and left Greenland via this place in all three years. 19–20/5 and 3–4/6 1980, 17–18/5 and 8–9/6 1982, 23–24/5 and 4-6/6 1984. A further transit visit took place 28–29/5 1984. On all occasions excursions were made in the vicinity of the airport, but no systematic counts of migrating birds were carried out. The floor of the valley was practically snow-free, and the weather was usually comparatively warm and sunny.

Observations from these sites are summarized below for the different species or species-groups, with comments about their possible participation in the transglacial migration systems. The results of the systematic counts of visible bird migration at sites 3, 4 and 5 are shown in Table 2. The counts of migrating waders and passerines at site 2 are presented in Tables 3 and 4, and in Fig. 12.

Red-throated Diver *Gavia stellata*

Site 1: 1 ind. 30/5-80.

Site 4: W-passage took place at 200–300 m asl along the southern shore of the ice-covered Disko Bugt at 23.24 and 23.35 hrs (2+2 inds.) 35/5, and at 21.16 and 21.20 hrs (2+1 inds.) 3/6.

Site 5: Three individuals (2+1) passed eastwards into the fjord low over the water surface, probably as a part of the sparse coastal migration.

Great Northern Diver *Gavia immer*

Site 4: 1 ind. passed E 50 m above the drift ice at 23.55 hrs 3/6, and it was probably the same individual which returned half an hour later.

Site 5: Regular northward coastal migration at altitudes up to 300 m asl was recorded, sometimes very close to the coastline. At 22.20 hrs 30/5 4 inds. arriving from the south circled and climbed for about ten minutes, and later continued towards E-ESE at approx. 500—700 m asl. A little later, at 22.57 hrs, a single individual passed in the same direction, into the fjord at 200 m asl. Low-altitude movements into the fjord were noted at 11.12 and 21.45 hrs (2+2 inds.) 4/6.

Comments: Transglacial E-migration may be suspected on account of the climbing behaviour of the divers departing eastwards across land.

Table 2. Counts of visible migration at site 3 (24–28 May), 4 (30 May – 3 June) and 5 (30 May – 4 June) in West Greenland during spring 1984. Observations took place each day from 20.00 hrs until midnight (estimated departure time for transglacial E/SE-migrants according to radar results), with additional daily observation periods as given in the text. Migratory directions are broadly classified into W- and E-migration at site 3 and 4. At site 5, coastal migration towards N or S is distinguished from E-migration across land or into the fjord.

	Site 3 Qasigiannguit (Christianshåb) W/E	Site 4 Aasiaat (Egedesminde) W/E	Site 5 Sisimiut (Holsteinsborg) E	Site 5 Sisimiut (Holsteinsborg) N/S
Red-throated Diver *Gavia stellata*		7/–	3	5/1
Great northern Diver *Gavia immer*		1/1	9	17/1
Gavia spp.			1	6/1
Cormorant *Phalacrocorax carbo*				3/–
White-fronted Goose *Anser albifrons*	9/–(2S)	(1S)		6/–
Canada Goose *Branta canadensis*		(9N)		4/–
Teal *Anas crecca*				–/2
Mallard *Anas platyrhynchos*				5/–
Eider *Somateria mollissima*		3/–	81	787/2
King Eider *Somateria spectabilis*				5/–
Long-tailed Duck *Clangula hyemalis*		10/15	25	124/8
Red-breasted Merganser *Mergus serrator*		–/13	10	32/–
Ringed Plover *Charadrius hiaticula*	1/–	18/–		3/1
Knot *Calidris canutus*		1/–		
Red-necked Phalarope *Phalaropus lobatus*		–/5		
Arctic Skua *Stercorarius parasiticus*		43/5	1	9/–
Long-tailed Skua *Stercorarius longicaudus*				1/–
Arctic Tern *Sterna paradisaea*		>1000/cf.text		
Glaucous Gull *Larus hyperboreus*	–/51			
Uria/*Alca* sp.				6/–

White-fronted Goose *Anser albifrons*

Site 3: Flock of 9 inds. arrived from the east at 17.30 hrs 26/5. The birds descended from inland, circled a small open lead along the shore before continuing towards SW across the Disko Bugt ice. 2 inds. flew south along the coast 27/5, and 5 inds. rested in company with 5 Canada Geese.

Site 4: 1 immature arrived from northeast over Disko Bugt 3/6, continuing towards S at 300 m asl.

Site 5: Flock of 4 inds. arrived from northeast 1/6, circled and turned northwards along the coast, climbing to 300 m asl. 2 inds. passed towards north later the same day.

Site 6: Local movements of 2–10 inds., mostly pairwise, recorded in all three years.

Comments: The White-fronted Goose has since long been known as a transglacial migrant, travelling from resting places in Iceland across the ice-cap to the West Greenland breeding area in the beginning/middle of May (Salomonsen 1976a). The staff at Søndrestrømfjord (site 6) have told us about the main arrival from the east of White-fronted Geese, ten to fourteen days before the beginning of our study periods. Numerous flocks, usually comprising 10-15 inds. in V-formation, then pass the valley, sometimes landing on or near the runway when there is much snow in the surroundings. The migration probably continues on a smaller scale until late May, as indicated by the arriving flock recorded at site 3.

Canada Goose *Branta canadensis*

Site 2: 1 ind. rested 25/5–4/6, often in company with Pink-footed Geese (Alerstam et al. 1984).

Site 3: Flock of 5 inds. rested 26–27/5, in company with White-fronted Geese.

Site 4: Flock of 9 inds. in V-formation passed over the observation island at 11.50 hrs 31/5, continuing in level flight across Disko Bugt at about 250 m asl, on a straight course towards approx. 16°.

Site 5: Flock of 4 inds. passed at 19.40 hrs 31/5, circled over the observation site and continued towards NE at 150 m asl.

Comments: The staff at Søndrestrømfjord (site 6) told us about the arrival in May 1984, before our study period, of a flock of Canada Geese, resting for some days at a short ice-free stretch of the stream at the airbase bridge. The Canada Goose population obviously is rapidly expanding in West Greenland (cf. Salomonsen 1967a). The birds probably arrive in spring by a NNE-migration from Labrador across Davis Strait. The bird at site 2 probably was a vagrant which had crossed the ice-cap to East Greenland.

Other geese.

Site 1: One pair of Pink-footed Goose *Anser brachyrhynchos* 5–6/6–82.

Site 2: Pink-footed Geese breed and rest locally in this area. A total of 18 inds. migrated past the observation site during the study period, mostly northwards along Sermilik, or arriving from the east (Alerstam et al. 1984). Notable is the behaviour of a flock of 3 inds. arriving and passing the observation site on a NW course at 12.00 hrs 22 May. The flock continued purposefully at approx. 500–600 m asl across Tasîlaq bay heading straight towards the Inlandice. Not until snow-covered land began to rapidly rise below the geese, merely three or four km from the ice slope, did they suddenly break off their migration, turning back east and descending. One pair of Barnacle Geese *Branta leucopsis* passed northwards along the western Sermilik shore at 06.52 hrs 28/5 (Alerstam et al 1984).

Comments: Both above-mentioned species of geese breed in

Northeast Greenland, and the Pink-footed Goose also, although sparsely, along the East Greenland coast southwards to the Angmagssalik district. Prolonged spring migration flights across the ice-cap are extremely rare. According to Salomonsen (1967a) there are only two records from West Greenland of Barnacle Geese and none of Pink-feet.

The complete lack of observations of Brent Geese *Branta bernicla* during our study period is notable in view of the regular occurrence that has been reported during spring migration in Southeast Greenland (cf. Helms 1926, Salomonsen 1967a) as well as in West Greenland (mainly the Disko region).

Mallard *Anas platyrhynchos*

Site 1: One female at the shore 25/5–80, two pairs at freshwater ponds 30/5–80, one male at freshwater pond 1/6–80.

Site 5: Sparse coastal migration towards the north, and one or two local pairs were recorded.

Site 6: At least 4 inds. resting in shallow freshwater at the airport on 23–24/5–85.At 22.00 hrs 23/5–84 one pair took off, circled and climbed for several minutes before departing over a ridge towards NE. No mallards were seen at this site 4–5/6–84.

Comments: Transglacial E-migration may be suspected.

Eider *Somateria mollissima*

Site 1: Flocks of 9 and 35 inds. rested close to the shore 24/5-80 and 20/5-82, respectively. Furthermore, flocks of 74 and 50 inds. were seen 5/6-82 from helicopter in open pack ice at the edge of the Angmagssalik Fjord ice.

Site 4: Flock of 31 inds. rested 3/6 in drift ice at offshore islands, and a few flew W low over the ice.

Site 5: Regular northward coastal migration was recorded close to the coastline as well as far offshore. Two large flocks, about 100 inds. in each, were observed, but most flocks were considerably smaller. By way of example; between 05.00 and 09.00 hrs 2/6, a steady N-migration, totalling fifteen flocks (4–15 inds./flock) with altogether 160 eiders was recorded.

Three flocks flew eastwards into the fjord low over the water surface: 23 and 50 inds. at 19.45 and 20.15 hrs 3/6 (all except 1 were immatures/females, a flock of 21 inds. returned from the fjord two hours later), 7 inds. at 22.20 hrs 4/6 plus a single female later the same night.

A few male King Eiders *Somateria spectabilis* were identified in the N-migrating eider flocks.

Comments: There is nothing in our observations to indicate transglacial migration in either direction. Flocks seem to be present in the coastal pack ice in Southeast Greenland already at the beginning of our study periods (cf. Salomonsen 1967a). The low-altitude E-migration at site 5 was probably of local character.

Long-tailed Duck *Clangula hyemalis*

Site 1: Flocks of 6, 2 and 10 inds., plus a single individual, were resting close to the shore 25/5, 29/5, 30/5 and 1/6-80, respectively.

Site 4: Flock of 7 inds. landed in drift ice at 21.46 hrs 30/5. Low-altitude movements over the drift ice were recorded at several instances: 1 + 2 + at least 3 inds. towards E at 21.08 hrs 1/6, 21.11 hrs 3/6 and 21.35 hrs 3/6, respectively, and 4 + 6 inds. towards W at 14.46 hrs 3/6 and 20.37 hrs 3/6. Flock of 9 inds. in dense and typically undulating formation climbed above 200–300 m asl, passing towards E at 21.37 hrs 2/6.

Site 5: Regular northward coastal migration, scattered throughout the day, with flock sizes between 2 and 25 inds. (mean 10 inds./flock). On each of the nights 31/5–3/6 between 19.30 and 23.16 hrs, one flock was recorded flying eastwards into the fjord (8+2+4+8 inds., respectively), mostly low over the water. In addition, 3 inds. flew E in the morning of 4/6.

Site 6: Flock of 5 inds., three males calling and chasing two females, passed about 150 m above the ground towards E at 22.00 hrs 5/6-82.

Comments: Transglacial E-migration may be suspected primarily on account of the flock at site 4 climbing to a high altitude flight eastwards above the southern shore of Disko Bugt. Most movements close to land, with recurrent eastward flights, occurred in the late evening, 21-23 hrs.

Red-breasted Merganser *Mergus serrator*

Site 1: One pair and a flock of 3 inds. were recorded 25/5–80 and 1/6–80, respectively.

Site 4: Recurrent E-movements were observed. Flock of 3 inds. passed at high altitude (at least 400 m asl) towards E at 20.30 hrs 1/6. 2 inds. passed towards E-SE across the observation island at 23.04 hrs 2/6, but broke off their migration, descended and veered back towards the west. Another 2 inds. climbed at 23.30 hrs 3/6 from about 75 m to at least 300 m asl by flying in circles over the observation site, before flying ESE across the observation island. Later the same night 4+2 inds. passed purposefully towards E at low altitude and about 150 m asl, respectively (at 00.05 and 00.16 hrs 4/6).

Site 5: Regular northward coastal migration took place, mostly by small flocks or pairs. Flock of 6 inds. flew inland towards E-ESE, after some violent aerial manoeuvres over the coastline at approx. 400 m asl, at 20.47 hrs 31/5. In addition, single individuals were recorded passing eastwards into the fjord on four occasions, between 19.00 and 21.30 hrs, usually at low altitude. Mean flock size for N- and E-migrants at site 4 and 5 was 2.2 (25 flocks with sizes ranging from 1 to 6 inds.).

Comments: Transglacial E-migration may be suspected on account of the recurrent eastward flights, including high altitude departures across land.

Arctic Tern *Sterna paradisaea*

Site 4: The spring arrival of Arctic Terns in Disko Bugt was a highly spectacular event. None were seen until after midnight, at 00.20 hrs 31/5, when four flocks (100+10+29+40) passed W in rapid succession along the small islands off the south coast of Disko Bugt, approx. 100 m above the drift ice. The terns travelled in well-defined, fairly dense flocks, in rapid wader-like flight. A similar rapid W-passage of a flock of 37 inds. took place the following night, at 21.23 hrs 31/5.

1 June was the date of the main tern arrival. None were observed during two hours of observation 13.30-15.30 hrs, but well over a thousand terns were counted during the evening observations 19.45-00.20 hrs. During the first hour 318 terns were counted passing W, and merely 2 passing E. The counts are, in effect, gross underestimates due to long observation distances. The terns travelled low over the pack-ice, sometimes rapidly in well-defined flocks, but more often slowly and easy-going, with intermittent diving

and fishing. The counts mainly refer to terns that passed inside the islands and skerries north of the observation site, but large numbers were vaguely visible beyond these islands over the open Disko Bugt.

As the evening passed, the number of foraging terns increased and they were not only passing towards W, but to an increasing degree also towards E. During the second hour 585 W-bound inds. and 197 E-bound inds. were counted. After 22.00 hrs the relative magnitude of W- and E-movements was rather similar, and it became increasingly difficult to distinguish directed movements among the terns foraging far offshore among the ice-floes. "Swarming" terns were seen as a barely visible "haze" low over the Disko pack-ice (25x telescope), comprising at least 2000 inds. The true number may well have been several times larger due to the restricted observation coverage.

Sample counts of the terns passing inside the islands north of the observation site were carried out during the following two days, giving a total of 482 W-bound/499 E-bound inds. 2/6, and 1014 W-bound/916 E-bound inds. 3/6. These movements probably comprised local flights within the concentration area of newly-arrived terns in southern Disko Bugt. A great deal of ice drifted away from the areas close to the observation site on 3/6 and hundreds of terns assembled there to forage. On repeated occasions during the late evening small parties of terns were seen to arrive in this area from E or ESE, descending steeply from high altitude, 150-500 m asl, towards the foraging terns at low altitude.

Comments: The large numbers of terns recorded at site 4 are all the more noteworthy because of the complete absence of records from the other sites. One observation from site 2 may possibly be relevant: a cascade of brief, slightly vibrating "jet-jet-jet" calls was heard from a bird flock high up towards the ice-slope at 23.55 hrs 29/5–82. Nothing was seen, and the birds were at that time left unidentified. In retrospect, however, terns might have given these calls.

Transglacial W-migration may be suspected on two grounds: 1) The large numbers of terns observed at site 4, where the influx seemed to occur from the east. 2) The complete absence of terns from site 5, where they would be expected to pass if their spring arrival was via Davis Strait.

Arctic Skua *Stercorarius parasiticus*

Site 4: A regular W/SW passage of skuas from southern Disko Bugt towards the open sea west of the observation site was recorded. The birds passed within the archipelago between Manîtsoq island (Fig. 11) and the observation site, mostly 30–100 m above the drift-ice. A few inds. were recorded flying the same route in an easterly direction. Totally 1,18,16,7 and 6 inds. were counted 30/5–3/6, respectively. The skuas were flying 1 to 3 together (mean = 1.6), mostly between 20–23 hrs, but they were also recorded in the afternoon as well as after midnight. Chasing of gulls or terns was never recorded.

Site 5: A sparse northward coastal migration took place. Piracy hunts by one or two Skuas among the large numbers of Kittiwakes, Glaucous and Iceland Gulls were repeatedly recorded.

Comments: The W-movements at site 4 indicate that transglacial W-migration may occur (cf. the Arctic Terns), but the observations at site 5 also show that there is probably a northward passage in Davis Strait.

Gulls and Fulmar

Generally, migration could not be distinguished from local movements among the gulls, and no counts of movements were carried out . One exception was the Glaucous Gull *Larus hyperboreus* at site 3. In addition to about 100 inds. resting on the Disko Bugt ice within observation range, a regular SSE/SE-movement was recorded in the afternoon and evening 24/5, 26/5 and 27/5 (not recorded during poor weather 25/5 and 28/5). The adult gulls arrived from the north along the coast, passed close to the observation site about 100m asl, circled to gain height ≥300 m asl to cross the peninsula south of the observation site. It is difficult to judge whether these movements were local flights to breeding colonies or departures on transglacial E-migration.

Observations at site 2 rendered no support for transglacial gull migration. Single Glaucous Gulls were noted to travel across the ice-bound Sermilik, twice towards NW, and once towards SE. Furthermore, calls from distant flocks of gulls were heard from northernmost Sermilik at 22.00 hrs 21/5, 01.45 hrs 25/5 and 09.25 hrs 3/6. *Larus hyperboreus, L. glaucoides* and *L. marinus* were recorded at sites 1 and 3, and, in addition, *Rissa tridactyla* and *Fulmarus glacialis* at sites 4 and 5. The number of gulls and Fulmars seen at site 5 often exceeded 1000 inds. At site 6, besides *Larus glaucoides* and *L. hyperboreus, L. ridibundus* was recorded (one adult 5/6–84).

Waders

Site 1. Ringed Plovers were recorded 26/5 and 1/6 1980, as well as 20/5 (2 inds.) and 6/6 (7 inds.) 1982. Display flights were noted in both years. One Knot rested close to a small marsh area 26/5-80. A flock of 5 Golden Plovers was flushed and departed from the island towards W 1/6–80, and this species was also recorded 18–20/5 (1 ind.) and 5–6/6–82 (3 inds.). One pair of Dunlin *Calidris alpina* was recorded at a small marshy bay 1/6–80, and one pair of Sanderling *Calidris alba* 6/6–82 (Alerstam et al. 1984).

Site 2. The records of migrating waders are shown in Table 3. Although there was a regular migration towards the W/NW, the number of birds counted was very low. This was probably due to the fact that the main stream of migrants passed at high altitudes beyond observation range. In fact, most of the passing waders were discovered by their calls and several were never seen, which means that calls registered as one passing bird may have represented several individuals. The intense glare from the ice and snow, and the sun shining in the clear blue sky, made visual observations difficult. Almost all waders actually seen were solitary birds, passing at low altitude, 25–200 m asl, sometimes even landing for a short time before taking off again.

The most numerous wader was the Ringed Plover. At least one third of them were seen or heard passing towards WSW-NW on straight courses towards the Inlandice. Others rested for a short time near the camp before taking off again in a westerly direction. Still others became more sedentary, and a few displayed in the marsh area at the base of the peninsula, or close to the camp. These birds obviously belonged to the local population, and were excluded from the counts.

Table 3. Migration of waders as registered by round the clock field observations at site 2, Sermilik, 23 May – 4 June 1982. Main migratory directions were in the sector SW-NW (Red-necked Phalarope) or W-NW (other species).

	May									June				
	23	24	25	26	27	28	29	30	31	1	2	3	4	Total
Ringed Plover *Charadrius hiaticula*	4	5	5	1	2	4	4	3	2	2	1			33
Red-necked Phalarope *Phalaropus lobatus*						2	1		5	2	1	3	7	21
Turnstone *Arenaria interpres*				3	5	1			1					10
Knot *Calidris canutus*	1						1							2
Sanderling *Calidris alba*			1											1
Golden plover *Pluvialis apricaria*											1		1	2
Redshank *Tringa totanus*									1					1

About half of the Red-necked Phalaropes passed straight towards the sector SW-NW, or they just circled the camp area before setting course in that direction. A few alighted on small meltwater ponds for a few minutes up to an hour before disappearing in a westerly direction. Finally, some rested for longer periods, mostly in pairs, and flew around in different directions. Some of these latter birds probably belonged to the local population (cf. Tinbergen 1935), and a few records have been excluded from the counts on this suspicion. Estimated migratory directions (SW-WSW: 6, W: 4, WNW-NW:4) indicate that many Red-necked Phalaropes travel on courses south of west in contrast to Ringed Plovers (directions south of west apply only to a minority, approx. 25% of available records) and, even more pronounced, to the high arctic species, Turnstone, Knot and Sanderling (all records of flight direction towards W-NW).

Of the latter three species all individuals passed on direct purposeful flight, except two Turnstones that alighted for a short time. There seemed to be a "wave" of Turnstone passage 26–27/5, best illustrated by a summary from the observation logbook.

26 May. 14.05 hrs. A Turnstone suddenly appeared and alighted at the camp. Disappeared within short.

19.30 hrs. One Turnstone passed WNW, about 20 m above the fjord ice, continuing into the Tasîlaq bay.

21.34 hrs. Another Turnstone is heard and seen arriving low over the fjord ice, again continuing WNW into the Tasîlaq bay.

27 May 02.47 hrs. One Turnstone heard and spotted high up, perhaps 400 m asl, climbing in rapid zigzag flight towards NW.

03.08 hrs. One Turnstone heard high up.

09.45 hrs. Another heard, again at high altitude.

13.50 hrs. One Turnstone heard high up , disappearing towards W.

14.45 hrs. Another heard passing towards NW at high altitude.

These examples of Turnstone migration also give a good view of the general character of all observation records of wader migration from site 2 (Table 3). For further details about the records of Golden Plover and Redshank, see Alerstam et al. 1984. One should keep in mind that although a record of SW-NW passage at site 2 provides a strong indication of transglacial migration, it cannot be regarded as conclusive evidence. Some birds may break off their migratory flight upon encountering the ice-slope, as earlier described for a flock of Pink-footed Geese.

The daily time distribution of the wader migration recorded at this site is shown in Fig. 12. Most records are from the morning and around noon.

In addition to the above-mentioned species, one pair of Purple Sandpiper *Calidris maritima* was stationary, some times displaying, throughout our stay at this site (already present on our arrival 21/5).

Site 3. One Ringed Plover passed W at 20.35 hrs 26/5.

Site 4. Recurrent W-migration of Ringed Plovers, mostly low over the drift-ice. 12 inds. passed in rapid succession between 23.14 hrs and 23.39 hrs 1/6 (1+1+2+8 inds.). 1+3 inds. passed the following night between 22 hrs and midnight, one further individual in the same time period 3/6. At 22.30 hrs 3/6 a flock of 5 Red-necked Phalaropes climbed above 200 m asl towards SE across the observation island. One Knot passed towards W low over the drift-ice at 09.45 31/5.

Site 5. Ringed Plovers were seen or heard on all observation days, but no consistent migratory pattern could be discerned. Local pairs as well as resting flocks of 5 and 7 inds. were noted 2/6 and 3/6, respectively. One pair and 3 inds. of Red-necked Phalaropes rested in the village 2/6 and 3/6, respectively.

Site 6. One pair of Ringed Plovers at the airport 4–5/6-84.

Comments: We conclude that there is a regular transglacial W-migration of Ringed Plovers, Turnstones and Knots, and probably also of Red-necked Phalaropes and possibly Sanderlings. We did not en-

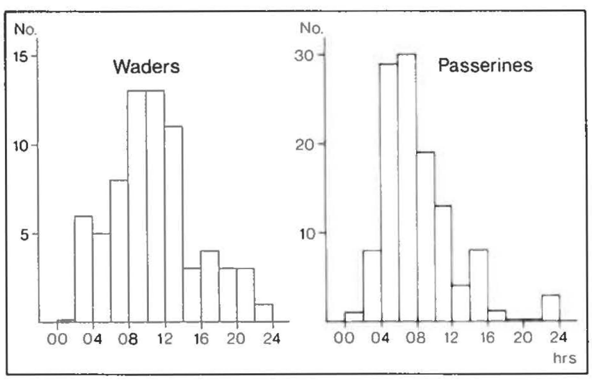


Fig. 12. Daily time distribution of visible migration of waders and passerines 23 May – 4 June 1982 at site 2, Sermilik (cf. Tables 3 and 4).

Table 4. Migration of passerines as registered by round-the-clock field observations at site 2, Sermilik, 23 May – 4 June 1982.

	May									June				
	23	24	25	26	27	28	29	30	31	1	2	3	4	Total
Snow Bunting *Plectrophenax nivalis* N-NE	5	4	16	2	4	1	1	1	5	1	4	2	2	48
Lapland Bunting *Calcarius lapponicus* N-NE	4	7	7	3		8		8	6	1	7	5	6	62
Lapland Bunting E-SE	3					1	1					1		6

counter any resting parties in the Kulusuk/Sermilik region, and obviously the waders normally migrate past this region without interruption, mostly at high altitudes. Waders that passed towards W at site 4 may have been destined for Baffin Island.

Small passerines

Redpolls *Carduelis flammea* were recorded at all observation sites, but migratory behaviour was never indicated. Hence, this species has been excluded from the following account.

Site 1. Counts of passerines within ± 50 m along approx. 5 km walking distance 20/5–82, totalled 12 Snow Buntings *Plectrophenax nivalis* (mostly territorial, sometimes in pairs), 45 Lapland Buntings *Calcarius lapponicus* (mostly small flocks, 93% males) and 26 Wheatears *Oenanthe oenanthe* (50% males). Fifteen Wheatears were concentrated at a sunbaked meadow by a small stream. Snow cover was approx. 90%. Some weeks later, 6/6–82, when there was considerably less snow, similar counts along a partly different but equally long route totalled 15 Snow Buntings, 4 Lapland Buntings and 4 Wheatears. Only a single Wheatear remained at the meadow. These figures demonstrate resting concentrations, which disappeared during our study period, of Lapland Buntings and Wheatears on Kulusuk island.

1–3 inds. of Meadow Pipits *Anthus pratensis* were recorded 29/5-1/6–80.

Site 2. A regular trickle of northbound migration of Snow and Lapland Buntings was recorded, with males clearly dominating (Table 4). The birds travelled singly or two and three together, normally below 100 m asl, along the western shore of Sermilik. Some maintained their northerly course after passing our observation site, heading across Tasîlaq bay towards a deep valley cutting through to Helheimfjord. Others veered northeast, to continue along the western Sermilik shore (cf. Fig. 10). A few Lapland Buntings flew towards E-SE across the Sermilik. There was a distinct peak of passage in the morning, 04–10 hrs (Fig. 12).

Somtimes the buntings temporarily halted their migration, flew around or even alighted. On several occasions Snow Buntings were chased off and forced to continue their migration by stationary territory owners. At our 2.8 km² observation peninsula we censused 31 stationary and territorial males of Snow Buntings. Twelve of these were or became paired during our study period, probably to females attracted from the stream of northbound migrants. There were also 1 male of Lapland Bunting (unpaired) and 15 males of Wheatear (4 paired). Except for a few male Lapland Buntings (1–4 at a time) sometimes attracted to a small seed deposit which we placed at our camp, there were no migrant buntings resting at this observation site.

However, there was a number of non-stationary Wheatears and at 23.35 hrs 28/5 one was actually seen leaving on migration. It flew in circles as it climbed, calling a few times (singing in flight high up), and finally disappeared northwards at more than 200 m asl.

Site 3. Altogether 8 Snow Buntings and 6 Lapland Buntings were seen to depart northwards between 22.05 and 23.15 hrs 24/5. Another 5 Snow Buntings and 5 Lapland Buntings passed on N-migration during the next hour. Another N-departure from the village by 8 Lapland Buntings occurred 22.45–23.25 hrs 27/5.

There were large numbers of resting passerines in the village of Qasigiannguit (Christianshåb), where the birds foraged on snow-free areas close to houses, dog-teams and roads (about 50% snow cover in the village). The total number of resting birds in the village (55 hectares) was estimated on two different occasions:

26/5: 840 inds., out of which 420 Lapland Buntings (97% males), 410 Snow Buntings (88% males) and 10 Wheatears. 28/5: 1160 inds., out of which 627 Lapland Buntings (91% males), 520 Snow Buntings (79% males) and 13 Wheatears (80% males of all Wheatears identified to sex).

Censuses in the surroundings (80–90% snow cover) gave densities of passerines 0.5–1.3/ha, i.e. only a faction of the density within the village (15–23/ha).

During a brief transit visit in the afternoon 29/5 to the village of Ilulissat (Jacobshavn), about 40 km north of site 2, concentrations of resting Lapland and Snow Buntings even larger than at Qasigiannguit (Christianshåb) were seen.

Site 4. No passerine migration was recorded, and the number of resting birds was negligible – no Wheatears were seen and only very few Lapland Buntings. Except for a flock of 20-30 individuals (mostly males) at a bird-feeder, Snow Buntings were territorial and dispersed throughout the village of Aasiaat (Egedesminde).

Site 5. Sparse N-migration across land was recorded. Altogether 10 Lapland Buntings and 4 Snow Buntings were counted on two nights, between 23 and 04 hours.

In the village of Sisimiut (Holsteinsborg) (86 ha), 85 territorial males of Snow Buntings (mostly paired) and 12 Lapland Buntings (mostly unpaired) were rather uniformly distributed according to our censuses. The number of resting migrants (nonterritorials) was very small – only 30–40 Snow and Lapland Buntings and no Wheatears.

Site 6. Three Lapland Buntings migrated E at high altitude at 22.25 hrs 23/5–84.

Snow and Lapland Buntings as well as Wheatears were recorded during all visits to this site. Lapland Buntings were particularly abundant 23–24/5–84, and even more 28–29/5, when several hundred (about 90% males) rested in flocks at the airfield. Later the same year, 4–5/6, they were distinctly reduced in numbers (no censuses were undertaken).

Comments: Greenland Wheatears are known to winter in the Old World (Salomonsen 1976a). Some of them probably reach their W Greenland/Canadian breeding places by transglacial migration via SE Greenland.

Whether there is a regular transglacial migration of Snow- and Lapland Buntings or not, is difficult to judge from the field observations. There are recent ringing recoveries of SE Greenland birds of these species from North America (Meltofte 1983, Zool. Museum Copenhagen), suggesting the possibility of a spring arrival from the west across the southern Inlandice (cf. next section).

Species involved, and areas of departure and destination

The species that are most likely to take part in the transglacial migration across Greenland during the end of May and beginning of June, are listed in Table 5. Below we discuss the results from our radar and field observations in relation to available knowledge about the bird migration pattern in and around Greenland.

Divers and ducks

The ice-free coast of SW Greenland, including highly productive offshore fishing banks (cf. Fig. 1), offers suitable wintering conditions for many ducks, auks and gulls. Additional coastal areas become accessible in spring, with the northward retreat of theWest Ice in Davis Strait. In May, there are usually ice-free conditions along the Greenland west coast up to 70°–72°N, including the Disko region (cf. Fig. 7).

This is in marked contrast to conditions along the coasts of S, SE and E Greenland, where the pack ice cover associated with the East Greenland Polar Current is at its maximum in April. In May, the sea ice in the Angmagssalik region may extend 100-200 km offshore into the Denmark Strait. Hence, there are few or no suitable wintering or spring staging areas for ducks, divers and gulls. For this reason, it can be assumed that breeding populations in E Greenland use the ice-free waters in SW/W Greenland during winter and/or spring, departing directly across the Inlandice towards their breeding sites. This may be particularly favourable for breeding populations from SE Greenland (from the Angmagssalik region and southwards), because the distance to this area from W Greenland is closer than from W Iceland (cf. Fig. 16b), the closest alternative wintering or spring staging area.

Of course, breeding populations from Iceland or even further east, may also form part of the transglacial E/SE-migration system. For the Great Northern Diver, there is some evidence for movements between America/Greenland and NW Europe. One individual, wounded by an Eskimo's arrow, has been caught at the Faroe Islands (Salomonsen 1939), and a study of gizzard grit from wintering birds at Iceland indicated that many birds were winter visitors from abroad (Gudmundsson 1972). Hence, these two reports suggest that birds from Canada/Greenland to some extent winter in NW Europe. This is contradictory to a transglacial E-passage in spring, as indicated by our field observations.

However, Bay (1894) reported from the inner parts of Scoresby Sund, E Greenland (at Danmark Ø, 70°30'N, 26°W), that in September Great Northern Divers were

Table 5. The birds most likely involved in E/SE- and W/NW-transglacial migration across Greenland at the end of May and beginning of June

Species	Transglacial direction	Destination
Great Northern Diver	E	SE Greenland, Iceland?
Long-tailed Duck	E	SE Greenland, Iceland
Red-breasted Merganser	E	SE Greenland
Mallard	E	SE Greenland
Glaucous Gull?	E	SE Greenland?
Lapland Bunting	E	SE Greenland
Snow Bunting	E	SE Greenland
White-fronted Goose	W	W/SW Greenland
Red-necked Phalarope	W	W/SW Greenland
Arctic Tern	W	Disko, NW Greenland?, Ellesmere and surrounding islands?
Wheatear	W	W Greenland, Baffin, Ellesmere
Ringed Plover	W	W Greenland, Baffin, Ellesmere
Turnstone	W	NW Greenland, Ellesmere and surrounding islands
Knot	W	NW Greenland, Ellesmere and surrounding islands
Sanderling	W	NW Greenland, Ellesmere and surrounding islands
Brent Goose	W	NW Greenland, Ellesmere, Axel Heiberg and Bathurst Islands

repeatedly seen flying west at a considerable altitude. He suggested that the divers departed on a transglacial flight, approx. 1000 km from Scoresby Sund to the Disko Bugt, later to continue southwards through Davis Strait towards winter quarters along the North American east coast. Hence, the existence in this species of a regular transglacial spring migration from W Greenland (where the Great Northern Divers arrive in the beginning/middle of May) to breeding sites in SE and E Greenland, is supported by Bay's observations.

Great Northern Divers are known regularly to undertake long-distance flights across land in North America, both during autumn and spring migration. With the aid of a tracking radar, Kerlinger (1982) measured flight altitudes of birds migrating singly or in small flocks (up to 4 inds) over eastern New York at 1500–2700 m asl (1000–2200 m above ground level), and their mean air speed was estimated at 34 ms^{-1}. This speed corresponds well with the remarkably fast air speeds, >30 ms^{-1}, that were estimated for a significant fraction of the radar echoes of transglacial E/SE migrants (Fig. 5).

Whether Great Northern Divers breeding in Iceland are also involved in the transglacial spring migration remains to be clarified. Migratory patterns may differ between immature and adult birds, and knowledge about the origin and age composition of the Great Northern Divers wintering in Iceland and other parts of NW Europe, is necessary for a better understanding of the migration systems of this species in the North Atlantic region.

The Long-tailed Duck is an abundant wintering bird in SW Greenland. During spring, there is a gradual northward movement along the Greenland W coast (Salomonsen 1967a). There are 9 recoveries from SW and W Greenland between November and May, of birds ringed at breeding places in Iceland (Salomonsen 1971). Three of these are from May, reported to be shot on 6 May at about 62°N, on 12 May at 61°N and on 27 May at 69°N, respectively. The latter recovery from the inner Disko Bugt is of particular interest in view of the timing and direction of the transglacial E/ES-migration as recorded by radar. These ringing recoveries indicate that Long-tailed Ducks destined for Iceland take part in the transglacial E-migration. Of course, it is highly probable that birds from breeding populations in SE and E Greenland use a transglacial migration route as well. Whether this applies also to Long-tailed Ducks breeding in NE Greenland remains an open question.

In the North Atlantic region, Long-tailed Ducks regularly winter, besides at SW Greenland, Newfoundland and surrounding coasts of E Canada and NE United States, at Iceland, N. Britain, along the coast of Norway and in the southern Baltic Sea. Hence, it is difficult to judge whether a majority or only a smaller fraction of Icelandic Long-tailed Ducks winter in SW Greenland. There is a surprisingly large exchange of individuals between the different wintering areas, as indicated by the recoveries of young ringed in West Greenland from Newfoundland (Nov.), Iceland (Nov.) and the Baltic Sea (Jan.). Hence, one cannot exclude the possibility that some birds from more distant easterly breeding areas than Iceland are participating in the spring migration across the Inlandice.

The Long-tailed Duck is well-known to undertake high-altitude flights overland, e.g. between the Gulf of Finland and the White Sea, where migration proceeds at 200–4200 m asl (average about 1000 m asl) and with air speeds 19–29 ms^{-1} (average about 26 ms^{-1}) according to radar studies by Bergman & Donner (1964), and Bergman (1978). Similar overland flights probably take place on a large scale through interior Alaska in spring (Richardson & Johnson 1981).

Besides Great Northern Divers and Long-tailed Ducks, it is highly probable that SE Greenland breeding populations of Red-breasted Merganser and Mallard undertake a transglacial spring flight from winter and spring quarters in SW/W Greenland. Greenland Mallards, including both W and SE coast populations, belong to a distinct subspecies *Anas platyrhynchos conboschas* Brehm. There is a report from May-June 1970, of a small flock of Mallards flying over the Inlandice at the DYE-2 station (66°N, 47°W), one duck alighting on the ice (Salomonsen 1979a).

The existence of regular transglacial Eider migration seems improbable in view of the total lack of supporting observations in this abundant species. Chapman (1932) recorded wintering Eiders in the Angmagssalik district, being fairly frequent in open water leads in January. Eiders ringed in NE Greenland have been recovered during the non-breeding season in Iceland (Meltofte 1978).

One cannot exclude the possibility that significant numbers of gulls, notably Glaucous Gulls, travel across the Inlandice to breeding sites at the Greenland E/SE coast and perhaps further east and northeast. Glaucous Gulls ringed as nestlings in Svalbard and Jan Mayen have been recovered, mainly as immatures, during the autumn in SW/W Greenland (Salomonsen 1971, Zool. Museum Copenhagen). Chapman (1932) observed a single gull (species uncertain) flying northwest on 4 October over the Inlandice about 200 km northwest of Sermilik (2600 m asl). It seems doubtful that gulls fly fast enough to account for any larger fraction of the radar echoes of transglacial E/SE-migrants (Fig. 5).

Large numbers of seabirds from N European breeding places, e.g. *Alle alle, Uria lomvia* and *Rissa tridactyla,* spend a large part of their non-breeding season in SW/W Greenland waters. The spring migration of these species is more or less completed before the period investigated in this study. Hence, it remains to be clarified whether these migrants engage in transglacial flights or not. Hans Meltofte (pers. comm.) informs us of the observations by a Greenlander from the Scoresby Sund district, E Greenland, that little auks have been repeatedly seen to arrive in spring in this region from the west. This strongly suggests regular spring migration towards the east across the Inlandice in this species.

There are four recoveries at North Sea coasts of Red-throated Divers ringed in Greenland, two of them ringed in W Greenland and two in NE Greenland (Salomonsen 1967a, Spencer & Hudson 1980). These recoveries demonstrate that NW Europe is a winter area for both adults (three recoveries) and immatures (one recovery) from Greenland. Possibly, birds from W Greenland migrate to and from Europe across the Inlandice. Large numbers of Red-throated Divers winter along the east coast of North America. Whether some of them come from Greenland and if so, how different breeding populations in Greenland and N Canada divide between winter quarters in NW Europe and North America is unknown.

Small passerines

Even if the migration of the Wheatear, Snow and Lapland Buntings was not registered by radar in our study (because of too low flight speeds in these small birds), our field observations throw some light on their spring migration.

Wheatears arrive via Britain or Iceland at the coast of SE Greenland, from where birds destined for W Greenland and N Canada continue across the Inlandice (Snow 1953, Salomonson 1967a, Luttik & Wattel 1979, Spencer & Hudson 1982). The relative importance of Iceland and SE Greenland as a stop-over area before the transglacial spring flight is unknown, although it would not be surprising if a majority of W Greenland and Canadian Wheatears depart from Iceland on a non-stop flight across the Denmark Strait and the Inlandice (cf. Salomonsen 1967a).

Snow Buntings migrate to Greenland along at least two, and perhaps three, main routes. The Snow Buntings of NE Greenland winter in the southern Soviet Union, passing the White Sea region and N Norway on migration (cf. ringing recoveries presented by Meltofte 1983). In N Norway there are large spring concentrations of birds storing heavy loads of fat before their final non-stop flight across the Norwegian and Greenland Sea (Bentz 1985).

There are numerous ringing recoveries demonstrating that W Greenland Snow Buntings winter in North America, migrating in spring via the St. Lawrence and Labrador regions before embarking on the flight across Davis Strait (Salomonsen 1979b, Orr et al. 1980). There are also three recoveries in North America of Snow Buntings ringed at Angmagssalik, SE Greenland (Zool. Museum Copenhagen and Meltofte 1983), indicating that Snow Buntings reach this part of Greenland by an eastward flight over the southern Inlandice and/or by crossing from Labrador to Kap Farvel, continuing northwards along the coast of SE Greenland.

Interestingly, there are also indications that some Snow Buntings arrive in SE Greenland across the Denmark Strait from Europe. Tinbergen (1939) pointed out that the arrival in the Angmagssalik region of the first Snow Bunting flocks in spring normally is associated with easterly winds. Furthermore, the dates of first arrival in this region are consistently earlier than in SW/W Greenland (Tinbergen 1939, Meltofte 1983). There are also observations from ocean weather-ship stations of a regular spring passage across the Denmark Strait (Williamson 1966, Luttik & Wattel 1979). These facts suggest that a fraction of the Snow Buntings in SE Greenland, particularly those arriving early in spring, come from NW Europe. Meltofte (1983) argued that these birds belong to the Icelandic population, overshooting their goal during spring migration from the British Isles. The Snow Bunting ringed one spring on Fair Isle and recovered next spring on Newfoundland (Williamson 1966) may have been a SE Greenland breeding bird. If so, the recovery indicates that Snow Buntings from this area may shift between Old and New World winter quarters in different years.

It is surprising that there seem to be so few Snow Buntings migrating to Greenland via Iceland, which would seem to be an ideal staging site at a relatively close distance from major parts of Greenland. Possibly, competition with the numerous and mainly resident Icelandic Snow Bunting population (Williamson 1966), prevents the use of this island as a major spring staging area for migratory populations (cf. below).

The Lapland Buntings of both W and SE Greenland populations winter in North America, according to ringing data as well as to field observations of migration across the Davis Strait (Salomonsen 1967a, Orr et al. 1980). There are two recoveries of SE Greenland birds from North America (Zool. Museum, Copenhagen). Like Snow Buntings, Lapland Buntings probably reach SE Greenland by a transglacial flight across the southern Inlandice. After this flight they may join a stream of northbound coastal migrants, travelling between Kap Farvel, Sermilik and further northwards (cf. our field observations of a regular northward passage of Snow and Lapland Buntings at Sermilik).

The migration pattern in southern Greenland of the Snow and Lapland Bunting, and the relative importance of coastal migration via Kap Farvel and transglacial migration to SE Greenland breeding sites, remain to be clarified.

There are several records of Wheatears and Snow Buntings from the Inlandice (Chapman 1932, Salomonsen 1979a), suggesting a regular occurrence of transglacial flights in these species. Furthermore, during our study period in 1980, a Lapland Bunting was encountered and given food at the DYE-3 station (identified by us from a detailed description given over the telephone by the station personnel). Several of the personnel had previous experience of small passerines encountered at this Inlandice station.

White-fronted Goose, Arctic Tern and Red-necked Phalarope

White-fronted goose. The Greenland White-fronted Goose *Anser albifrons flavirostris* is well-known as a transglacial migrant (Salomonsen 1967a). The population, presently numbering about 15 000 birds (Fox et al. 1983), winters in Ireland and Scotland. A large proportion of the geese uses Iceland as a stop-over site during spring migration, continuing from there by a non-stop flight across the Denmark Strait and the Inlandice to W Greenland. A major arrival and breeding region is around Søndre and Nordre Strømfjord (67°–68°N). The main arrival takes place already in the beginning and middle of May, and only a minor number of straggling flocks may be included among the radar registrations reported in this study.

Arctic Tern. Disko Bugt is a major breeding area for Arctic Terns, with many thousands of pairs. The species is widely distributed along the coasts of Greenland, although between 60°–68°N along the SW/W Greenland coast, and in many other areas as well, the occurrence is sparse (Salomonsen 1981). Besides Disko Bugt, the largest breeding colonies of Arctic Terns in the North Atlantic region are known from Iceland and Scotland (Glutz von Blotzheim & Bauer 1982).

Recoveries of birds ringed in W Greenland show that in autumn the Arctic Terns travel from Davis Strait across the North Atlantic to West Europe, continuing along the East Atlantic coast towards their winter quarters in the Antarctic pack-ice zone (Salomonsen 1967b, cf. Alerstam, in press). There are very few ringing recoveries during spring migration, giving no indications whether the majority of terns returns by the same general route as used in autumn or not. One tern ringed as young in W Greenland (Uummannaq) was recovered as breeding in E Greenland (Scoresby Sund district; Zool. Museum, Copenhagen.)

However, the observations by Wynne-Edwards (1935) of birds on the North Atlantic around 50°N demonstrate that there is a spring passage of terns from Europe to North America, with a mean flight direction towards WNW, almost exactly the reverse of the mean direction of autumn migrants. The spring passage is very concentrated in time. Wynne-Edwards (1935) suggested that in spring four-fifths of the trans-Atlantic flights take place within a week, about 28 May – 3 June. He described the terns' arrival in the Gulf of St. Lawrence: "When sailing down the Gulf of St. Lawrence on June 3 the ship passed through mile after mile of terns newly arrived from the ocean, all eagerly fishing in a thin white line stretching as far as the eye could see, where two streams of water met, one the olive-green outflow of the St. Lawrence tide and the other a blue cold stream setting in from the northeast. The serpentine partition was marked by a great accumulation of drifted seaweed and wreckage. I counted 360 birds as we passed, and more and more were arriving all the time from the east" (Wynne-Edwards 1935).

The St. Lawrence region is an important stop-over (and breeding) area for the terns, although not for Greenland populations, since the main arrival time in W Greenland is approximately simultaneous with that in St. Lawrence. Many of the St. Lawrence terns probably continue towards NW by an overland flight to James and Hudson Bay, as indicated by scattered field observations in late May and in the first two weeks of June (Godfrey 1973). Simultaneously, Arctic Terns having migrated from the Southern Hemisphere over Pacific waters, have been recorded to migrate east along the north coast of Alaska and the Yukon Territory. Hence, the migratory divide between Arctic Tern populations travelling via the Atlantic and Pacific Ocean, respectively, runs in the central Canadian Arctic (Richardson & Johnson 1981).

Do the Greenland terns make a trans-Atlantic WNW flight in spring, similar to that of the St. Lawrence birds but over more northerly latitudes, and involving a W/NW crossing of the Inlandice directly to W Greenland? Our observations of the main tern arrival in the Disko Bugt on 1 June 1984, in conjunction with the absence of migrating terns along the Greenland west coast south of Disko, strongly suggest this possibility. The observations by Rankin & Duffey (1948) in the Irish Sea are interesting in this context. Sailing down the North Channel (between Ireland and Scotland) on 22 May 1943, westward migration of Arctic Terns was recorded; "all the way down the Irish Sea till dusk, parties of terns crossed the ship's bows regularly, all flying from the English to the Irish side. This was evidence of the spring movement well under way. The urge to migrate must have been new and strong, as never again from a ship were terns seen whose flight was so steady and constant. On May 25th, 1945, single birds and flocks were seen frequently from the air flying west , between the Isle of Man and the Irish coast. Again on May 28th in the area north of the Isle of Man and in the North Channel many large flocks were seen,sometimes numbering over 50, all flying westwards" (Rankin & Duffey 1948).

The Irish Sea seems to be an important stop-over area for Arctic Terns arriving there already in late April. This is indicated by large numbers of terns encountered inland in England and Wales during southwesterly or westerly gales in spring (cf. Gibb 1948).

It seems reasonable to interpret the westward migration in the northern Irish Sea (55°N) as departures for Greenland and, perhaps, N Canada. The late time of the season suggests that the terns fly more or less non-stop to their breeding sites, making it all the more likely that they follow the shortest possible route, across the Inlandice to the Disko region.

However, some W Greenland terns may also rest around Iceland, where the main arrival of Arctic Terns occurs in the first half of May, before continuing westwards across the Denmark Strait and the Inlandice.

The terns arriving in the Disko region possibly comprise not only local breeders, but also birds destined for more northerly breeding areas, like NW Greenland and northernmost Canada. One cannot exclude the possibility that some Arctic Skuas follow the same transglacial migration route as suggested for the terns.

Arctic terns are known to make long overland flights, e.g. across the Scandinavian peninsula (Saurola 1978), climbing to 1000–3000 m asl, or even higher, according to tracking radar records (Alerstam, in press).

Red-necked Phalarope. There is little information about the migration of N Atlantic populations of the Red-necked Phalarope. Our field observations from SE Greenland, suggest that birds reach their breeding sites in SW/W Greenland, (and perhaps even further west, on Baffin Island) by a transglacial W-passage. Huge postbreeding concentrations of millions of Red-necked Phalaropes, possibly including birds from Greenland, occur in the Bay of Fundy, Nova Scotia. The winter destination for these birds is a matter of speculation (Richardson 1979). One possibility is the SE Atlantic off equatorial W Africa (Harrison 1983).

There seem to be virtually no spring records from W Europe, and one can only guess that the Atlantic Red-necked Phalaropes in spring travel via NW African waters, continuing more or less non-stop and unseen towards Iceland (Iceland and Greenland breeding populations) or Newfoundland (E Canadian populations). If this is correct, there are some obvious parallels between the migration pattern in the Arctic Tern and the Red-necked Phalarope (see also Richardson & Johnson 1981 about eastward spring migration of phalaropes into W Canada).

Alternatively, Red-necked Phalaropes from Iceland and Greenland may migrate towards SE to the same winter quarters as Scandinavian birds, i.e. the Arabian Sea (cf. Glutz von Blotzheim et al. 1977). However, this seems unlikely, in view of the scarcity of autumn as well as spring records of this species from NW Europe. Still, there are some observations of postbreeding concentrations at the Norwegian coast (Glutz von Blotzheim et al. 1977).

High arctic waders and Brent Goose

Waders. There is little doubt that the transglacial W/NW movements registered by radar in this study, mainly reflect the migration of high arctic waders including the Ringed Plover, Turnstone, Knot and Sanderling. Noer (1979) reported air speeds in the range 13–20 ms^{-1}, with a mean about 15 ms^{-1}, for Knots, Turnstones and Sanderlings flying south at low altitude along the Jutland west coast in July and August. Air speeds are expected to be higher than this for the transglacial migrants, flying with heavy fat loads at high altitudes, because optimal flight speed increases with body mass and decreasing air density (Pennycuick 1975). Consequently, the observed air speeds for transglacial W/NW migration (Fig. 5) are not unrealistic for these waders.

The field observations at Sermilik (site 2, Table 3) lend support to the conclusion that the above-mentioned wader species were most important in producing the W/NW-moving radar echoes. However, according to the radar, the daily peak of migration usually occurred in the late night or early morning (Figs 2 and 8), while the peak of visible (or audible) wader migration at Sermilik was in the late morning (Fig. 12). The explanation is probably that the birds registered by field observations to a large extent represented drop-outs and stragglers from the main migration stream climbing high above the Sermilik region beyond the range of field observations.

Ringed Plovers breeding in W and NW Greenland, Ellesmere Island and N Baffin Island winter in the Old World, presumably W Africa, passing W Europe on migration (Salomonsen 1967a). One bird ringed on spring migration in Great Britain was recovered on Ellesmere Island in July (Spencer & Hudson 1982). One bird from Disko has been recovered in SW France during autumn migration, and there are three recoveries in SW and W Greenland of birds ringed on spring migration in Belgium (3 May), England (30 April) and Iceland (1 June; ringing data from Salomonsen 1967a, 1971 and Zool. Museum, Copenhagen). The Ringed Plover is a fairly common breeding species in the Angmagssalik region (Helms 1926).

There are extensive ringing data to support the conclusion that Knots and Turnstones make a transglacial spring flight via the Sermilik region towards W Greenland, continuing to breeding grounds in NW Greenland and N Canada (Fig. 13). They depart on this flight from W Iceland, where since early May they have stored large amounts of fat for the final spring flight to the breeding range (Salomonsen 1967a, Morrison 1977, Wilson 1981).

Probably the flight from Iceland to NW Greenland and Ellesmere, normally proceeds non-stop (Meltofte 1985). Only in years when the migrants meet unfavourable weather en route, do they presumably become grounded. Other possible explanations of the large numbers of recoveries in W Greenland in certain years (mainly reported between the last days of May and 10 June, cf. Fig. 13), are that some migrants in years with a delayed spring temporarily interrupt migration in W Greenland, or retreat here from their breeding range.

Intensive visible migration of Knots and Turnstones was registered at Kap Atholl in NW Greenland by Ferdinand (1966 and unpubl.). During three days, 31 May – 2 June 1964 (21 observation hours), almost 400 waders (205 identified as Knots and 148 as Turnstones) were counted at this site. The migrants arrived, mostly in flocks between 5 and 25 inds. (sometimes mixed flocks) low over the sea (which was free of ice at this place) from south or southwest, and continued towards north or east across the rocky shore. Some of the birds

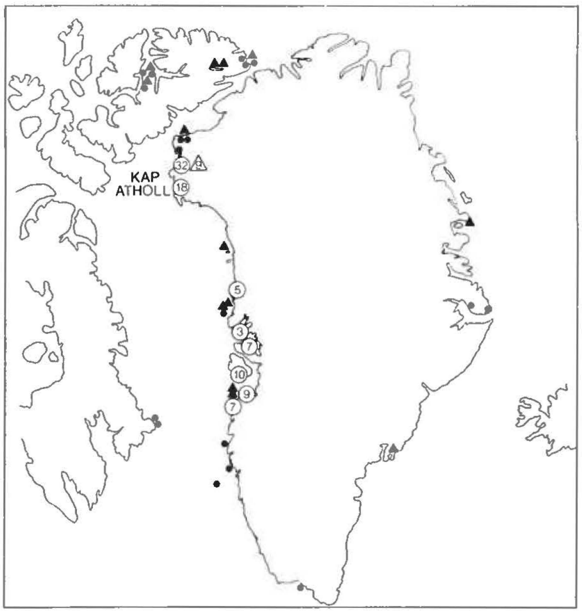


Fig. 13. Recoveries in Greenland and N Canada during May and June of Knots (circles) and Turnstones (triangles) ringed in Europe (Britain, Iceland, Norway, Holland, France). Eleven recoveries of Knots and five of Turnstones reported from Herbert Ø, Thule, by letter dated 2 July 1974 are included. Of the 93 recoveries of Knots in Greenland 1970–79, 30 and 52 were reported from 1972 and 1974, respectively. Ten of the twelve Turnstone recoveries in Greenland during the same period are from 1974.

seemed to be exhausted and landed on the ice edge at the shoreline, while others passed without pause, sometimes circling for a few minutes or briefly breaking out in songflight the moment they reached land. The reason why the birds arrived from S-SW over the sea may be that they had drifted west with winds over the Baffin Bay (Ferdinand 1966 and unpubl.).

In the following period, until the middle of June, hundreds of Knots were recorded resting at a heathland area, 200–350 m asl, where the snow rapidly melted away. Since long, this area, not far from Thule Air Base, is known as one of the first to become snow-free in the region. Similar pre-breeding concentrations of newly arrived waders at more or less traditional places, of a longer or shorter duration depending on snow conditions in different years, have deen described from other arctic regions (Meltofte 1985).

Nettleship (1974) observed a main influx of Knots to Lake Hazen, N Ellesmere Island (82°N, 71°W), on 5 June 1966, with seven flocks (flock sizes 6–60, average 27) passing along the lake towards southwest. This flight direction may indicate (with a reservation for local topographic influences) that the birds have migrated via the northern parts of Greenland (cf. Morrison 1975). As discussed in the next section, there may be a migratory divide in NW-N Greenland and N Ellesmere Island between wader populations reaching their breeding range by a flight via Sermilik or via NE and N Greenland .

There are also observations of Knots and Turnstones departing in August from Lake Hazen in northeasterly and easterly directions, again indicating a flight via N Greenland (Saville & Oliver 1964). The observation by Wulff (1917, published 1934) of a flock of four Knots migrating towards the east up the slope of the northern Inlandice (80°N, 56°W, about 1000 m asl) on 14 August is interesting in this context. As expected, the main migratory direction of Knots, Turnstones and Sanderlings observed in July in Peary Land and southeast thereof, is towards E or SE (C. Hjort, observations in 1979).

Autumn migration routes may differ to some extent from those used in spring. Wind conditions are probably more favourable for broad-front return migration across the Inlandice of northern and central Greenland than for spring migration over this area (cf. next section). Numbers of Knots and Turnstones resting in Iceland are apparently much lower in autumn than in spring, reflecting seasonal differences in the migration pattern (Morrison 1977, Wilson 1981). Resting Turnstones and Knots in August at Kangerdlugssuaq and Miki Fjord (68°N, 32°W), along the Greenland east coast between Angmagssalik and Scoresbysund (Degerbøl & Møhl-Hansen 1935, Hørring 1939), may be associated with transglacial autumn migration across central Greenland. However, there are also observations from W Greenland suggesting that many Turnstones on return migration travel southwards along the Greenland west coast to Kap Farvel, from where they depart on a trans-Atlantic flight to Britain (Salomonsen 1967a).

One Turnstone ringed in England was recovered on 28 July at the DYE 2 station on the Inlandice, 66°29′N, 46°17′W (Salomonsen 1971). There is also one observation from this site of an adult Knot on 21 July. Furthermore, observations (two from autumn and one from spring) of Turnstones on the central Inlandice have been reported from "Station Centrale" (70°54′N, 40°42′W) at 3000 m asl (Bourlière 1952).

The Sanderling is a sparse breeding bird in NW Greenland (Thule district) and on Ellesmere Island, but it is distinctly more common in N and NE Greenland (Salomonsen 1967a). One may assume that the relatively small number of birds destined for the former regions pass Sermilik on the same transglacial spring migration route from Iceland as used by the Knots and Turnstones with this destination. Besides our spring observations of Sanderlings in SE Greenland, Chapman (1932) spotted two individuals (and a Turnstone) at the mouth of Sermilik on 8 June 1931.

Numbers of Sanderlings resting in Iceland in May are modest in comparison with other high-arctic waders. Possibly, the Sanderlings using Iceland as a spring staging area mainly belong to the NW Greenland/Ellesmere population. Many Sanderlings (as well as Ringed Plovers, Dunlins and Turnstones) destined for NE

Greenland may depart directly from Britain, overflying Iceland. This is supported by observations of appreciable numbers of high-arctic waders, including several thousand Sanderlings, remaining in Britain as late as until the end of May and the first days of June (Wilson 1981).

Waders are renowned for storing large fat deposits and carrying out long non-stop flights at high altitudes in many parts of the world. One example is the autumn migration across the West Atlantic from North to South America. According to radar studies by Richardson (1979), the waders depart over the ocean at Nova Scotia and New Brunswick with median altitudes 1000–4000 m asl on different days (overall mean altitude 2000 m, top altitudes 5000–6650 m asl).

Brent Goose. That the Brent Goose uses a regular transglacial migration route between the Sermilik and Disko regions has since long been inferred from field observations. According to reports from the Angmagssalik district by Johan Petersen (Helms 1926), Brent Geese appeared commonly during the early decades of this century on spring and autumn migration, in the middle of May and in September. During both seasons, parties of Brent Geese were "found on the water, walking on land, often about the very houses, and flying over – sometimes in large numbers" (Helms 1926). The flight direction was towards west or north-west in spring, and the reverse in autumn, clearly suggesting transglacial migration (Helms op. cit.).

Obviously the geese were resting for some time in SE Greenland, since they do not appear in the Disko region until the last days of May or the first week of June (Salomonsen 1967a, Bertelsen 1932). They continue without much delay to their breeding grounds in NW Greenland and N Canada, where they arrive in the beginning of June.

Chapman (1932) noted the arrival of Brent Goose parties in the Angmagssalik district on 14 May 1931. On 31 May he reported a skein of 1000–1500 geese silently flying northwest up a small fjord at the mouth of Sermilik. It seems highly probable that they were Brent Geese, and not Pinkfooted Geese as suspected by Chapman. A similar observation by E. Knuth (in Salomonsen 1950) on 30 May 1936 of 500–600 geese, most probably Brents, flying northwest over the Inlandice between Sermilik and Disko, has been mentioned in the Introduction.

Probably, these large flocks have departed directly from West Iceland, where, during their spring staging period, Brent Geese regularly remain until about 1 June (Gardarsson in litt.). It may well be that the majority of Brent Geese fly directly from Iceland across the Inlandice about 1 June, and that only a minority use the Sermilik region for a stop-over. The total lack of Brent Goose observations during our study periods in this region, may indicate that resting here is less common nowadays than formerly.

The number of New World Brent Geese wintering in Europe, mainly in Ireland and possibly also in France, total between 10 000 and 20 000 birds (Ogilvie 1978, 1985). The vast majority migrate via resting areas in Iceland and probably follow the above-mentioned transglacial flight route via Sermilik. Only very few travel to NE and N Greenland, where the number of breeding pairs is small. During recent decades the species has become virtually extinct from this part of the breeding range (Meltofte 1975, 1976, Meltofte et al. 1981, Håkansson et al. 1981).

Recoveries of Brent Geese ringed in N Canada demonstrate that the migratory divide between populations wintering at the North American Pacific coast and in Europe, respectively, is about longitudes 100°–110°W, in the region of Melville Island and Bathurst Island. Brent Geese from these islands have been recovered in both wintering areas.

Of Melville Island (approx. 110°W) birds there are at least twenty recoveries on the Pacific coast, together with one sight record from Iceland and 19 from Ireland of birds with neck-collars. Of Brent Geese from Bathurst Island (100°W), there is one recovery in the State of Washington and one in Ireland. A third recovery is of a bird on spring passage at Disko on 4 June. In addition, 15 birds with neck-collars have been sighted in Ireland (Maltby-Prevett et al. 1975, Spencer & Hudson 1978, Zool. Museum Copenhagen).

Brent Geese ringed in northernmost Canada east of Bathurst, have been recovered exclusively in Greenland or Europe. There are six recoveries of Ellesmere Island birds, two from W and SW Greenland (autumn), three from Ireland and one from France. Of birds from Axel Heiberg Island (approx. 90°W), there is one autumn recovery from Angmagssalik and sight records from Iceland of 22 birds and from Ireland of 10 birds with neck-collars (Maltby-Prevett et al. 1975, Spencer & Hudson 1978, Zool. Museum, Copenhagen).

The Nearctic breeding range of the Brent Goose is divided into three main sectors, occupied by winter populations, besides from W Europe and the Pacific coast, also from the Atlantic coast of the United States. The breeding range of the latter population includes the Baffin and N. Hudson Bay regions. While the two Atlantic winter populations belong to the light-bellied race (*Branta bernicla hrota*), the Pacific population comprises Black Brant (*Branta bernicla nigricans*). Intergrading between the races is found around the migratory divides (Ogilvie 1978, Owen 1980).

Flight routes across the Inlandice

The radar observations demonstrate that migrating birds fly both in an easterly and westerly direction across the southern Inlandice (64–69°N), in spite of the high altitudes of the ice ridge, 2500–2800 m asl, and the low temperatures, often about −10°C in May/June. The distance from the coast of SW and W Greenland to the Sermilik region is about 700 km, with the major part, 450–600 km, extending over inlandice proper. The alternative route around Greenland along the coasts via Kap Farvel is more than twice as long. In view of this, it seems probable that transglacial migration in this area is of regular occurrence at other times of the year besides late May/early June, involving many of the bird species migrating to and from coastal W and SW Greenland and adherent waters in the Davis Strait.

The regular passage of high-arctic waders and Brent Geese via Sermilik, is interesting since this region is not positioned along the shortest routes between departure areas in Iceland and destinations in NW Greenland and N Canada. We do not know to what extent migration takes place further north over the Inlandice. However, the radar pattern of migratory passage at Sermilik, as well as available field observations and ringing results (cf. preceding section), indicate that the flight route via Sermilik is of major importance. One might think that the passage at Sermilik is due to drift from a great circle course, by E-NE winds over the Denmark Strait. However, this seems improbable in view of the peak passage at Sermilik on 31 May 1980, when westerly winds prevailed over the Denmark Strait (cf. Tab. 1 and Fig. 6).

After arriving at Sermilik from Iceland along a course around 287°, the migrants shift their flight direction towards NW (with 90% of all echo tracks between 290° and 330°, cf. Fig. 4). The shift takes place in a narrowly defined area, sometimes in a distinct migration corridor. Hence, the Sermilik area seems to represent a normal break-point for the high arctic migrants, between a first leg of the flight from Iceland, over the Denmark Strait, and a second leg, across the Inlandice.

Distances

The great circle routes between Iceland and different sites within the destination range for high arctic waders and Brent Geese are shown in Fig. 14. These routes should be compared with the rhumbline routes (along a constant compass course), with a first leg from Iceland to Sermilik and a second leg from Sermilik to the destination. Note that a major part of the destination area in NW Greenland and N Canada, falls within the extrapolated main range of transglacial flight directions from Sermilik, as recorded by radar (Fig. 4). The median direction according to the radar, 301°, falls between the constant compass direction towards Disko (295°) and towards Kap Atholl/Eureka (315°). In contrast, the compass courses from Sermilik to Alert (340°) and surrounding areas of NE Ellesmere and N Greenland fall outside the range of observed flight directions at Sermilik.

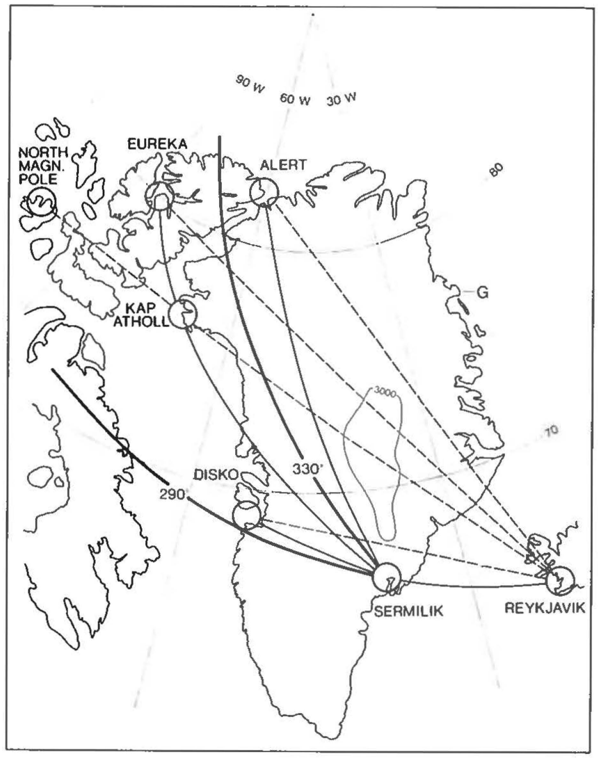


Fig. 14. Great circle routes (broken lines) from Iceland (Reykjavik) to different destinations in W/NW Greenland and Ellesmere Island (and to the North Magnetic Pole at Bathurst Island), and the corresponding rhumbline routes via Sermilik. Track directions of 90% of the radar echoes moving W/NW at Sermilik were between 290° and 330° (Fig. 4), extrapolated as thick lines in the above figure. G = Germania Land.

We suggest that high arctic waders and Brent Geese destined for NW Greenland and N Canada fly from Iceland via Sermilik, from where they proceed mainly within the 290–330° range of track directions shown in Fig. 14, thereby avoiding the central part of the Inlandice. Populations destined for N Greenland and NE Ellesmere may avoid the central Inlandice by flying from Iceland via NE Greenland or from N Norway (cf. below). Possibly the migratory divide runs across Nares Strait and NE Ellesmere Island, approximately as indicated by the 330° line in Fig. 14. This would be in accordance with the observations at Lake Hazen, NE Ellesmere (cf. preceding section), indicating migration of Knots and Turnstones via the northern parts of Greenland.

Comparisons of flight distances from Iceland along great circle routes and routes via Sermilik and NE Greenland, respectively, are presented in Table 6. Distances via Sermilik to the Thule region (Kap Atholl), parts of Ellesmere Island (e.g. Eureka) and further west in high arctic Canada, are shorter than via NE Greenland (Germania Land used as break-point for calculations), while the reverse holds for NE Ellesmere Island

Table 6. Distances in km from Reykjavik in Iceland to different destinations in W Greenland and Ellesmere Island along three different routes (cf. Fig. 14): 1) Great circle route, 2) Two-leg rhumbline route via Sermilik and 3) Two-leg rhumbline route via Germania Land. Distances were calculated from standard formulas for great circle and rhumbline navigation, using the following coordinates: Reykjavik 64°15'N 22°00'W, Disko 69°00'N 53°00'W, Kap Atholl 76°20'N 69°30'W, Eureka 80°00'N 86°00'W, Alert 82°30'N 62°20'W, Sermilik 66°20'N 38°00'W, Germania Land 77°00'N 19°00'W.

	Disko	Kap Atholl	Eureka	Alert
Great circle	1446	2130	2563	2286
Rhumblines via Sermilik	1477	2337	2883	2691
(diff. from great circle)	(+31)	(+207)	(+320)	(+405)
Rhumblines via Germania Land	–	2715	2934	2457
(diff. from great circle)		(+585)	(+371)	(+171)

(Alert) and N Greenland. Distances to northernmost Greenland are even a bit smaller from N Norway than from Iceland (cf. Fig. 16 below), a fact which may be relevant in view of recent indications that Knots resting during spring in N Norway are, at least partly, of Nearctic breeding origin (Davidson et al., in press).

Still, the flight distances around the central part of the Inlandice is 200–300 km longer than straight across it along the great circle routes. Why would the migrants travel via Sermilik rather than the shortest route across central Greenland?

Weather en route

A flight along the great circle from Iceland to NW Greenland or Ellesmere Island would involve a 1500 km passage across the Inlandice, including its highest parts 3000–3300 m asl. This is more than twice the transglacial distance of a crossing from Sermilik to the Disko and Uummannaq regions, 600–750 km, where the ice-cap reaches 2500–2600 m asl.

However, a long transglacial distance *per se* is probably not preventive for bird migration, because many high arctic birds obviously complete their flight from Iceland to the breeding grounds non-stop (cf. Meltofte 1985). It also seems unlikely that the altitude of the central Inlandice represents a problem for the migrants, even if the mean temperature in May and June at the weather station Eismitte/Station Centrale (71°N 41°W; 3000 m asl) is as low as −20°C and −14°C, respectively (Putnins 1970). This is about 5–10 degrees colder than on the ice cap between Sermilik and Disko (cf. data from Watkin's ice cap station 67°N 42°W, 2500 m asl, in operation for seven months only, and unfortunately not in May and June; Mirrlees 1932), but similar to temperatures on the northern Inlandice (Station Northice 78°N 38°W; 2300 m asl; Putnins 1970).

Table 7 shows wind conditions during the end of May/early June, at low altitude over the Denmark Strait and over northern Greenland, and at high altitude (at the 500 mb level, corresponding to approx. 5500 m asl) over the Inlandice between Sermilik and Disko (66–70°N) and over the central Inlandice (70–78°N)

The air flow over the Denmark Strait is often easterly, which is favourable for a flight towards SE Greenland, but less favourable for departures towards NE Greenland. This air flow is associated with a high pressure cell residing over the Arctic Basin or N Greenland and cyclones moving south of Greenland towards Iceland. Sometimes cyclones and adherent weather fronts move up the Denmark Strait, bringing weather that is highly unfavourable for departures from Iceland. Still, on average weather and winds permit a flight from Iceland to SE or NE Greenland on about 75% of the days during the period 21 May – 9 June (based on five years of weather data, cf. Table 8). For a flight to Sermilik, conditions are favourable, with considerable tailwinds (cf. Figs 6 and 7), on 27% of the days, while winds are

Table 7. Wind directions in different parts of Greenland as estimated from daily aerological charts (00 hrs GMT) for the period 21 May – 9 June 1980 – 1984 (a total of 100 days). Based on the daily European Meteorological Bulletin, using the surface pressure chart for the Denmark Strait and N Greenland, and the 500 mb chart for the Inlandice.

	Wind				
	Variable <5 ms^{-1}	NNE-ENE	E-S	SSW-WSW	W-N
Denmark Strait (66°N), surface	24	35	27	7	7
Inlandice (66–70°N), 500 mb	17	1	41	23	18
Inlandice (70–78°N), 500 mb	12	3	14	33	38
N Greenland, surface	67	4	4	4	21

Table 8. Number of days with weather and wind conditions permitting migration between Iceland and Ellesmere Island along three different routes (cf. Fig. 14). Weather and wind conditions refer to the period 21 May – 9 June 1980-1984 (a total of 100 days), as estimated from the daily European Meteorological Bulletin (00 hrs GMT). The occurrence of cyclones, weather fronts with precipitation and/or strong (>10 ms^{-1}) cross/headwinds is considered as preventive for migration. Number of days with favourable weather (F), i.e. with tailwinds ≥5 ms^{-1} within ±45° from the migratory direction, are given in brackets. Winds above the Inlandice have been estimated from 500 mb pressure charts.

	Iceland- E Greenland coast (surface)	E Greenland coast- Ellesmere (500 mb)	
Route 1 Great circle	73 (4F) out of 100	34 (9F) out of 73	
	Iceland- Sermilik (surface)	Sermilik- Disko (500 mb)	Disko- Ellesmere (surface)
Route 2 via Sermilik	71 (27F) out of 100	52 (26F) out of 71	44 (21F) out of 52
	Iceland- NE Greenland (surface)	NE Greenland- Ellesmere (surface)	
Route 3 via NE Greenland	76 (1F) out of 100	74 (–) out of 76	

not equally favourable for birds travelling towards more northerly areas in East Greenland, because of their northwesterly or northerly flight directions over the Denmark Strait.

High altitude winds differ significantly between the central Inlandice and the Sermilik-Disko section. Over the former region, upper winds are frequently westerly and strong, often 15–25 ms^{-1} (Table 7). This means that transglacial high altitude flights are at all feasible on less than half of the days during the spring migration period, and on these days the probability of having any wind assistance for the flight is small (Table 8).

Because of an upper high pressure cell or ridge frequently appearing over SE Greenland, high-altitude winds between Sermilik and Disko are generally not so strong, and they often blow from southeast or southwest. Hence, weather readily permits a transglacial flight on about three quarters of the days during the spring migration period, and on half of these days the migrants can expect considerable wind assistance.

There is a small risk, about one in six, that migrants, after a transglacial flight from Sermilik, will encounter unfavourable weather in the form of a cyclone moving north along the West Greenland coast. Probably it is difficult or impossible for the migrants to adjust the timing of their flights in relation to this risk. However, the danger may be mitigated by the possibilities to alight on the W Greenland coast and wait for the bad weather to cease. Normally, a northward flight along W and NW Greenland is unproblematical, with weak winds or with tailwinds along the coast and along the edge and slope of the Inlandice.

Weather in N and NE Greenland is rather stable, and seldom preventive for migration via the northern parts of Greenland. Generally winds are weak, but since the dominant wind direction is more or less opposed to the migratory direction in spring, flight conditions are not very favourable.

Hence, comparing the overall flight conditions between the three alternative routes from Iceland to Ellesmere Island given in Table 8, one finds that the shortest route across the central Inlandice is the least favourable. This route is quite dangerous, and possible to fly on merely about one third of the days during the migration period. The flight via NE and N Greenland is probably the safest, but rather unfavourable because of opposed winds. The route via Sermilik is intermediate in reliability. However, by departing from Iceland towards Sermilik on days with favourable winds over the Denmark Strait, migrants have reasonably good prospects of completing the journey with favourable flight conditions.

The above reasoning presupposes that migrants fly high, hundreds of meters or more above the Inlandice surface. For these altitudes, 500 mb winds apply as reasonable estimates. One may note that in May/June the mean temperature at the 650mb level (approx. 3500 m asl, i.e. 300–1000 m above the top of the Inlandice) is about −15°C (Putnins 1970).

Quite different wind conditions prevail low over the Inlandice surface. Here the wind is usually katabatic, blowing downslope with a large component, inflicted by the Coriolis force, parallel to the contours of the ice surface topography. The vertical extent of this wind is small, only a few hundred metres. As a consequence, the predominant wind direction close to the surface of the Inlandice differs radically between the east slope, with much northwesterly winds, and the west slope, with southeasterly winds most frequent. Generally the overall pattern of low altitude air flow over the Inlandice and its edges is anticyclonic.

The katabatic wind over the Inlandice is very persistent, but wind speeds are not strong, below 9 ms^{-1} for more than 90% of the time. The average air speed at Eismitte in May/June is about 4 ms^{-1} (Putnins 1970).

Consequently, migrating birds should be able to avoid the unfavourable upper winds over the central Inlandice by flying at a very low altitude over the ice surface, in the regime of katabatic winds. However, such a flight strategy would expose the birds to other difficulties: At Eismitte, about one third of the days in spring are cloudy, with low stratus or stratocumulus occurring on half of the cloudy days. Fog was reported at 15% of all weather observations at Eismitte, although it is less common in spring than other times of the year. "White-out" is an atmospheric condition at the Inlandice surface, in which there is a lack of contrast between the sky and the snow surface. It is normally produced by a solid overcast of stratus, sometimes in conjunction with fog or blowing snow (cf. Putnins 1970 for a detailed description of the ice-cap climate). Presumably, these conditions make a flight low over the Inlandice surface very hazardous (although the total risks during a long crossing of the central Inlandice cannot be assessed). Furthermore, such a low-altitude flight may render orientation difficult.

Hence, the hazards and difficulties involved in a low altitude flight over the Inlandice surface, and the unfavourable winds prevailing higher up over the central Inlandice, may explain why many high arctic waders and Brent Geese travel over the Inlandice via Sermilik, or via the northern parts of Greenland, rather than the shortest route across the central Inlandice. For the return journey in summer and autumn, a high altitude flight on a rather broad front across the central Inlandice, may be a more favourable option.

The geomagnetic field

With a total geomagnetic field intensity between 52000–55000 nT, and an angle of inclination 80–85°, the horizontal component of the geomagnetic field at the Greenland Inlandice is weak, 5000–9000 nT. Whether birds are able or not to use a magnetic field with such a small horizontal component for their orientation, has not been investigated (cf. Wiltschko & Wiltschko 1976). The North Magnetic Pole of the earth is presently situated at Bathurst Island, approx. 76°15'N 100°30'W (cf. Fig. 14). Hence, from the point of view of geomagnetic orientation, the simplest way to fly between Iceland and NW Greenland/N Canada across the Inlandice would be to follow a magnetic course more or less due north. This would lead the birds along a route closely similar to the great circle route between Iceland and the North Magnetic Pole (passing Kap Atholl) as shown in Fig. 14.

Consequently, a detour flight via Sermilik, as demonstrated in this study, probably cannot be primarily explained with reference to geomagnetic orientation. However, this does not preclude that the migrants use magnetic orientation during their flight via Sermilik. If the geomagnetic field is of importance for the orientation of birds in the Arctic, difficulties may be expected in N Canada. Whether such difficulties have affected the evolution of migration patterns around the North Magnetic Pole, is a matter of speculation.

Evolution of bird migration patterns in the Arctic

The capability of migratory birds to perform long non-stop flights, at high altitudes and low temperatures, has made possible the development of regular transglacial migration across the Greenland Inlandice by many different species. What are the most important selection forces for the evolution of these and other migration patterns in the Arctic?

For the evolution of a migration link between the Nearctic and Europe, Nørrevang (1963), Prater (1981) and Hale (1984) have discussed the historical conditions, in terms of the distribution of glacial refuges during the Ice Ages, and of the postglacial climatic development. It seems likely that arctic migratory birds colonized Greenland and N Canada refuges and early ice-free areas from Europe rather than from North America, because of the slow postglacial disintegration of the North American (Laurentide) ice sheet. It still had a wide extension 8000 years BP, when the inlandice had completely disappeared from Northern Europe (Denton & Hughes 1981). Prater (1981) and Hale (1984) also point out that the migratory journey for the Nearctic birds to European winter areas was much shorter than to American coasts with a similarly favourable winter climate.

However, in order to understand why the Nearctic-European migration link persists today, we must probably seek the answer in present-day ecological conditions, favouring through natural selection the maintenance of this migration pattern rather than alternative flight routes and winter areas. It seems improbable that tradition *per se* in migrating birds is of so great importance as to seriously hamper adaptive migratory changes in response to changing environmental conditions.

Long-distance flights from spring staging areas

Longitudinal breeding segregation between populations from different winter quarters, as well as wintering segregation between different breeding populations, may arise because of differential migration costs and asymmetric competition (individuals arriving late being competitively disfavoured) for wintering as well as breeding resources (Lundberg & Alerstam, in press). Hence, there are two complementary sides to the problem of segregation between migratory populations of birds: 1) the competition for different winter areas between different breeding populations and the associated costs of migration, and 2) the competition for different parts of the breeding range between different winter populations, and the associated differences in migratory costs.

Spring conditions presumably are of particular importance for the population segregation of arctic birds, because food resources for long-distance flights may be limited. The migrants are probably hard pressed not to become delayed, but to arrive in time at the breeding destination, preferably with some surplus energy reserves remaining after the migratory journey.

A characteristic feature of the spring migration of many arctic species is the existence of a major staging area. Here the birds store large energy reserves before their remaining long-distance flights more or less directly to their breeding grounds. Hence, the positions of these staging areas, and the amount of food resources available there for fat accumulation, may be of crucial importance for the migration pattern and breeding distribution of different competing populations.

As a first approximation, one may compare the positions of different staging areas, and the possibilities birds using them have to reach different parts of the breeding range with a minimal flight distance. Of course, a reduction in flight distance will generally be associated with reduced costs of migration, because of a smaller energy expenditure for the journey, smaller risks, and an earlier arrival at the destination. In Figs. 15 and 16 major spring staging sites are exemplified for different types of species. The sector adherent to each staging site, demarcates the region of closest distance (calculated on the basis of great circle distances) from this site in comparison with any of the other staging sites. Other things, like wind conditions during migration, being equal, one should expect a population associated with a certain staging site to have the best possibilities of occupying breeding areas within the adherent sector of minimal flight distance.

As mentioned earlier, populations migrating between Europe and the Nearctic, use Iceland as a spring staging area of crucial importance (cf. Wilson 1981). For the Brent Goose and Knot, there is sufficient information about other resting places in spring to allow a provisional circumpolar plotting of the main staging areas, as in Figs 15A and 16A, respectively. As seen from these maps, Iceland is clearly the best staging position, from the point of view of minimal flight distance, for migration to major parts of Greenland and to parts of high-arctic Canada. The sectors of closest flight distance seem to correspond well with circumpolar population segregation in these species (cf. Ogilvie 1978, Roselaar 1983).

Possibly the Knots of Nearctic breeding origin recently discovered to rest during spring in N Norway (Davidson et al. in press), are destined for northernmost Greenland and, perhaps, adjoining areas of N Ellesmere Island. The flight distances to these regions are slightly smaller from N Norway than from Iceland (Fig. 16A), and wind conditions en route may add to the favourability of a flight from N Norway rather than from Iceland. One may speculate that also the small N Greenland population of Brent Goose migrates in spring via N Norway in company with the population destined for Svalbard.

The Old World winter populations of high arctic waders arrive earlier in Ellesmere Island and adjacent breeding areas, than the New World winter populations arrive in their parts of the breeding range. This may be explained by the former populations' advanced spring position in Iceland, in combination with relatively less snow cover, and consequently earlier breeding opportunities (cf. Meltofte 1985), in northernmost Canada as compared to central arctic Canada (Morrison 1984, Fig. 17).

Fig. 15B shows, for the Greenland region, the sectors of closest flight distance from three spring staging areas used by Snow Buntings. The population migrating from Soviet winter quarters via N Norway, has the shortest final spring flight to NE and N Greenland, while birds from North America migrating via Labrador are in a good position for access to SE Greenland and the major part of W Greenland. This is in reasonable agreement with the observed migration pattern (Meltofte 1983). Snow Buntings departing from N Great Britain in spring, have only a small area in E Greenland which they can reach by a shorter spring flight than birds from the other two populations. Whether there is any significant migration of Snow Buntings between Great Britain and E Greenland is unknown. Birds wintering in NW Europe may be of Icelandic rather than Greenlandic origin.

As seen from the broken lines in Fig. 15B, Iceland comprises a most favourable staging position for Snow Buntings destined for most parts of Greenland. The reason why, in spite of this fact, there is no major passage of migrating Snow Buntings through Iceland, may be lack of food resources in spring, in combination with a competition pressure from the local Icelandic breeding population. There are of course other aspects, besides the position of staging areas, that affect the evolution of migration patterns, like the total distance between breeding and winter quarters, and the carrying capacities of different breeding and winter areas,etc. With the main winter resources for Snow Buntings in North America and far to the east in Europe, staging in Iceland may not fit well with the most reasonable migration routes and time schedules.

The sectors of closest distance for divers or ducks departing from staging waters in W Greenland, Scotland and Norway, respectively, are shown in Fig. 16B. The W Greenland coast is a favourable position to reach the whole of Greenland, provided that the migrants destined for E Greenland fly across the Inlandice. It is

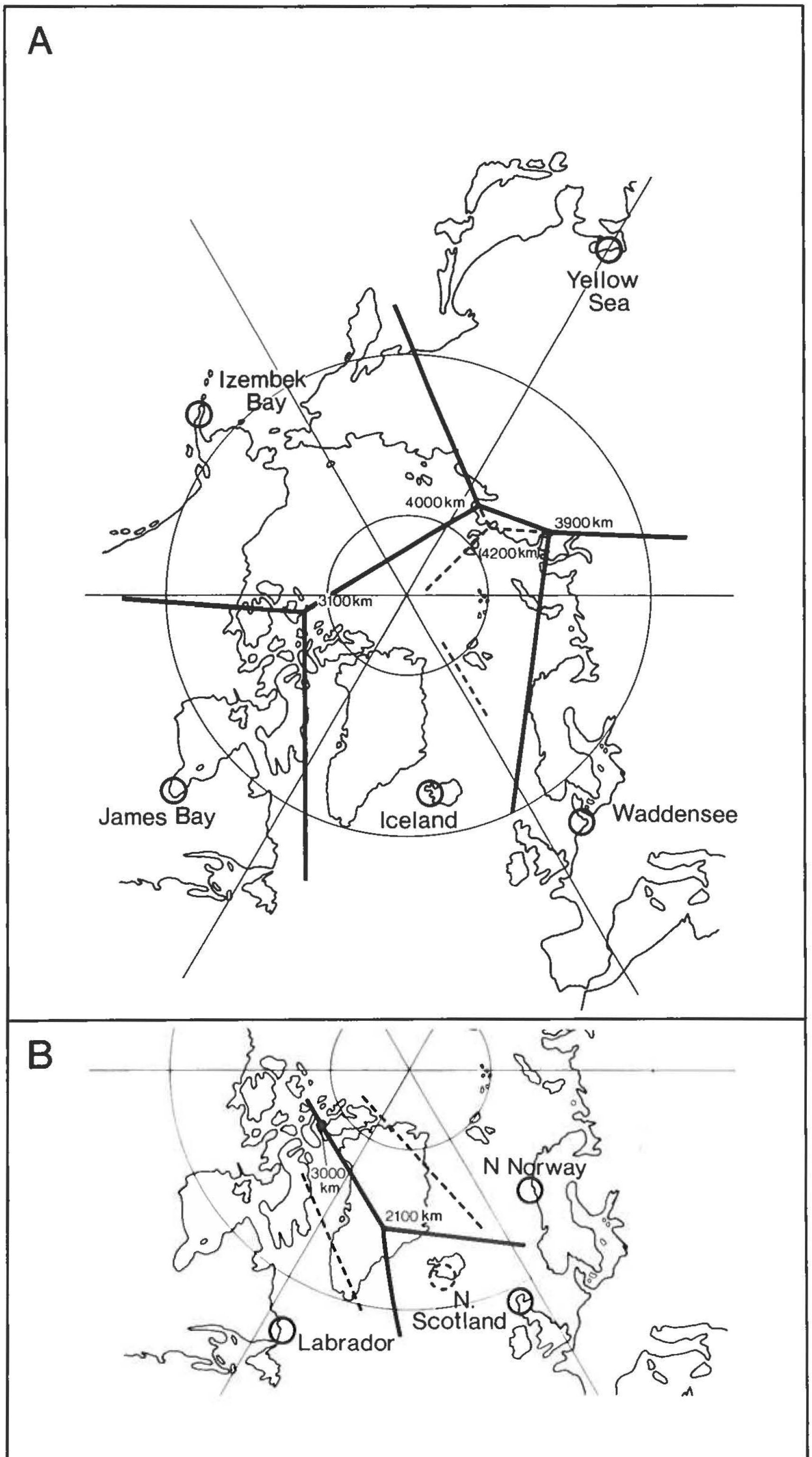
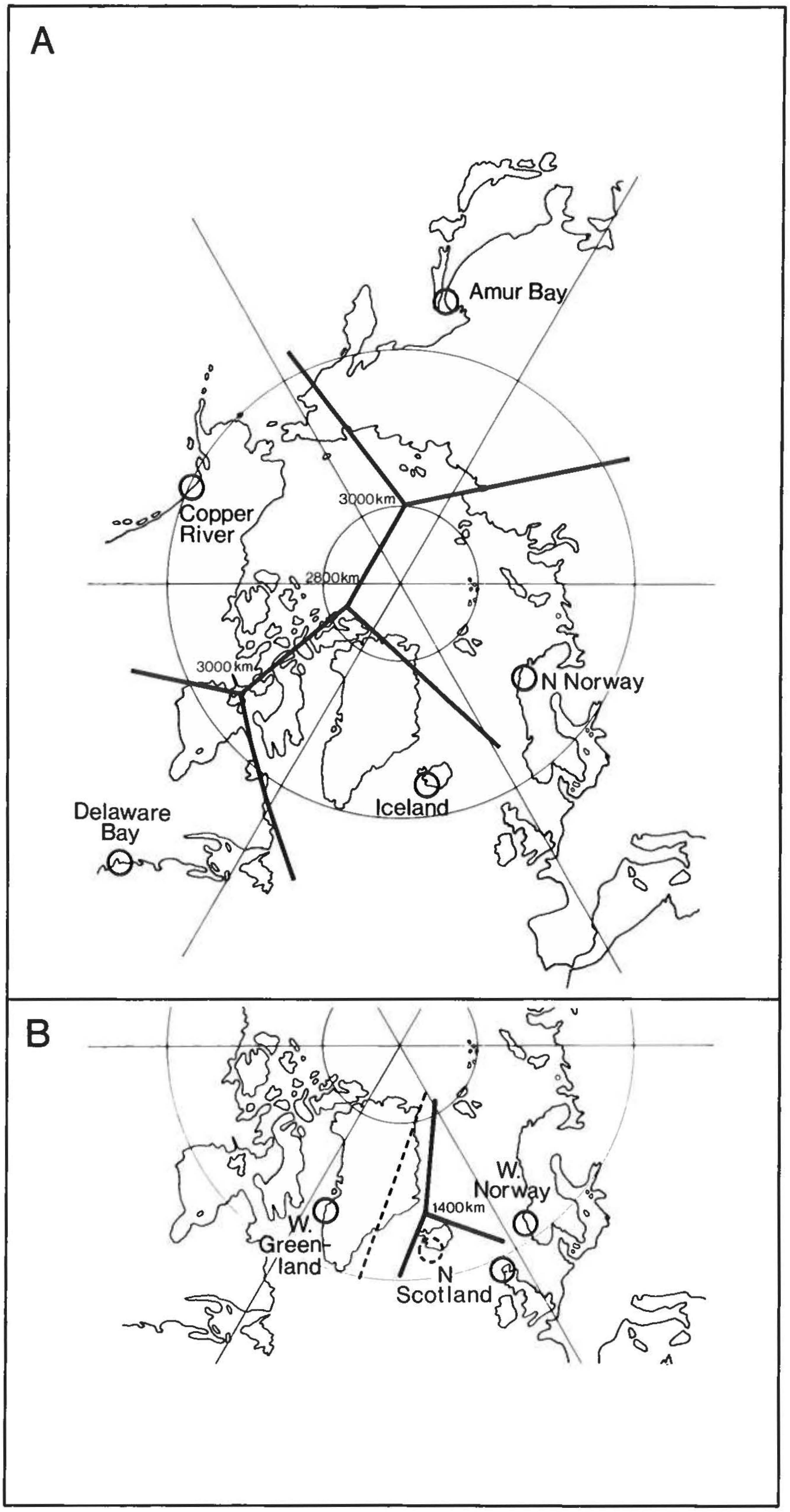


Fig. 15. Main spring staging areas with adherent sectors of closest distance (great circle distance) for Brent Goose (A) and Snow Bunting in the North Atlantic region (B). Great circle distances are indicated at points of insection between adjoining distance sectors.
A. Information about staging areas is mainly based on Ogilvie 1978 and Owen 1980. Brent Geese do not migrate to Palaearctic breeding areas via Iceland, in spite of the relatively close distances from Iceland to Svalbard, Franz Josef Land and parts of the Taimyr region. One possible explanation is the prevalence of unfavourable polar easterlies blowing over the Arctic Ocean between Iceland and these areas. The effect of excluding Iceland as a staging area for Palaearctic breeding populations is shown by broken lines. A spring staging area for the small Svalbard population is in N Jutland, Denmark, not shown in the figure (and perhaps also in N Norway, cf. Fig. 16A). The great circle distance between N Jutland and Svalbard is approx. 2430 km, i.e. about 450 km longer than between Iceland and Svalbard.
B. Based on data from Salomonsen 1967a, 1979a, Meltofte 1983, Haftorn 1971 and Bentz 1985. Including Iceland as a potential staging area for Snow Buntings, gives an adherent sector of closest distance covering most of Greenland, as shown by the broken lines.

Fig. 16. Main spring staging areas with adherent sectors of closest distance (great circle distance) for Knot (A), and divers and ducks in the North Atlantic region (B). Great circle distances are indicated at points of intersection between adjoining distance sectors.
A. Based on data from Dick et al. (1976), Morrison (1977, 1984), Isleib (1979), Wilson (1981), Håland & Kålås (1980), Dunne et al. (1982), Roselaar (1983), Senner & Howe (1984), and Strann (1984). Part or all of the West Palaearctic breeding population does not use the newly discovered spring staging sites in N Norway, but depart from final spring staging areas at Waddensee (cf. Fig. 15A). According to recent findings, at least part of the Knots resting in N Norway are of Nearctic breeding origin (Davidson et al. in press). B. W Greenland, N Scotland and W Norway are potential spring staging areas for ducks and divers like *Clangula hyemalis, Mergus serrator, Anas platyrhynchos* and *Gavia immer*. The broken line shows the equal-distance division between W Greenland and Iceland, respectively.



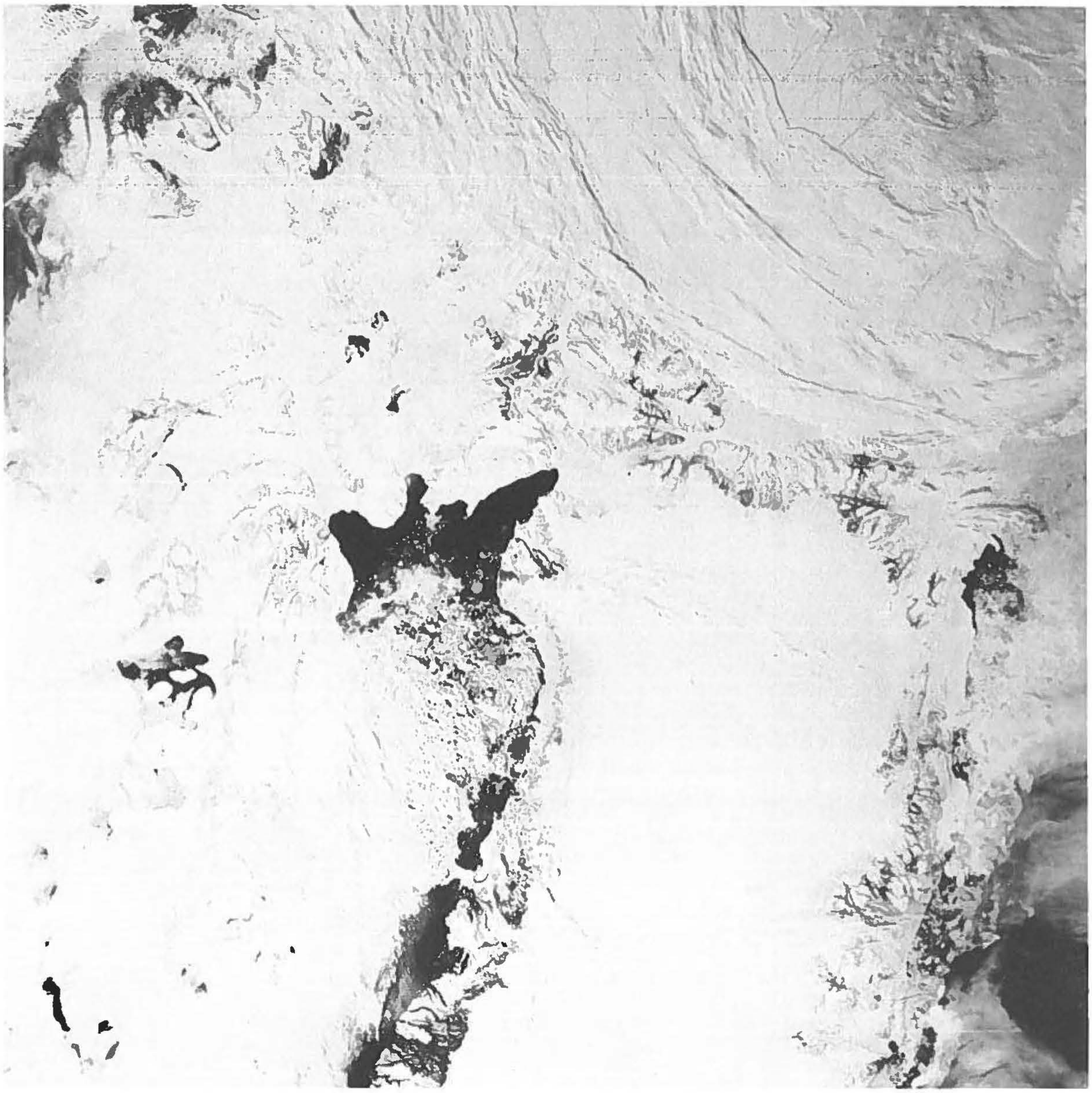


Fig. 17. Satellite photograph (4 June 1984), illustrating conditions at the normal time of arrival of high arctic waders and geese to northernmost Greenland and Canada. Large areas free of snow are to be found in NW Greenland, on Ellesmere- and Axel Heiberg Islands, as well as on Melville-, Banks- and Victoria Islands (top left corner of photograph). This makes it possible for migrants to arrive earlier in these areas than in the central parts of arctic Canada, where there are greater amounts of snow. Photograph by courtesy of the Meteorological Office at Søndrestrømfjord Airport.

closer to Iceland from N Scotland than from either W Greenland or Norway, although the differences in distance are small. Hence, there must be other factors, besides a short migration distance, to account for the wintering in SW Greenland of at least part of the Icelandic population of Long-tailed Ducks.

Divers and marine ducks to some extent winter also in the waters around Iceland (like Eiders from NE Greenland , cf. Meltofte 1978). Here, as indicated by the broken lines in Fig. 16B, they are in a favourable position for migration to E and NE Greenland, while birds starting from the W Greenland coast still have the shortest migration route, by way of transglacial flight, to the Sermilik region and more southerly areas in SE Greenland.

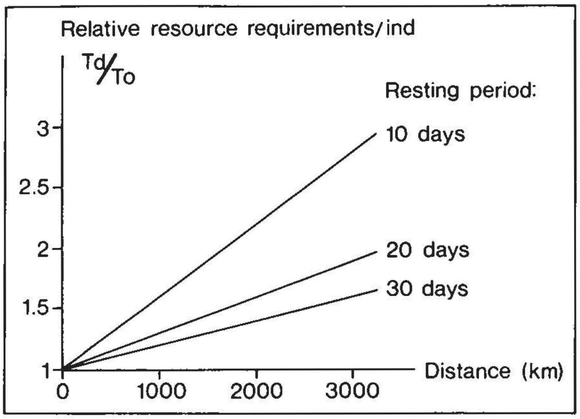


Fig. 18. Energy requirements of a bird accumulating fat during a certain resting period for different distances of migration, in relation to the existence metabolism (no net accumulation of fat) during the corresponding period. The threshold of energy required during a resting period *t* for migration of a distance *d* in relation to the existence metabolism during the same period is given by $T_d/T_0=1+(TC/EM)\ (d/t)$. Transportation costs (TC, energy/distance) and existence metabolism (EM, energy/time) have been estimated according to Kendeigh et al. (1977). For small and medium-sized birds, this relationship approximates to $T_d/T_0=1+\ 0.006\ (d/t)$, where *d* is the migratory distance in kilometres and *t* the resting period in days.

Resource limitation and competition at staging areas

According to the above discussion, Iceland is of crucial importance as a staging area, particularly in spring, for the evolution of the European-Nearctic migration system. The favourable resting and wintering opportunities for ducks and divers along the SW/W Greenland coast , is probably of primary importance for the evolution in these species of eastward transglacial migration in spring.

However, staging areas may not always serve as spring-boards to distant parts of the breeding range. With limited staging resources and competition between different local and migratory populations, the outcome may be quite the opposite: Migrants, during the available resting period, will be unable to accumulate enough fat for reaching distant parts of the breeding range. Unless there is an alternative migration route, these parts of the breeding range will then remain unoccupied even if providing ideal breeding conditions.

The total energy requirements of a bird storing fat for different distances of migration in relation to an energy consumption restricted to the existence metabolism, are calculated in Fig. 18. Hence, a bird storing fat for a 3000 km-flight during a resting period of 20 days requires approximately twice as much food resources as a stationary individual with no net accumulation of fat during this period.

With limited and non-renewable food resources, the amount of food per individual will decrease with increasing population density at the staging site (Fig. 19). With large enough carrying capacities for populations breeding close to the staging site, birds of these populations will suppress the amount of staging resources available per individual below the threshold for long-distance migrants to accumulate enough fat for a spring migration flight to distant breeding areas. As a result, birds migrating farthest from the staging site will become outcompeted. The competitiveness of long-distance migrants may be increased by selection for increased or reduced body size, depending on whether the competition at the staging site operates mainly through interference or exploitation, respectively.

Gaps in the circumpolar breeding distribution of many species may be explained by the dual effects of spring staging sites as spring-boards and bottle-necks, respectively. By way of example, the large breeding populations in Iceland of Golden Plovers and Dunlins,

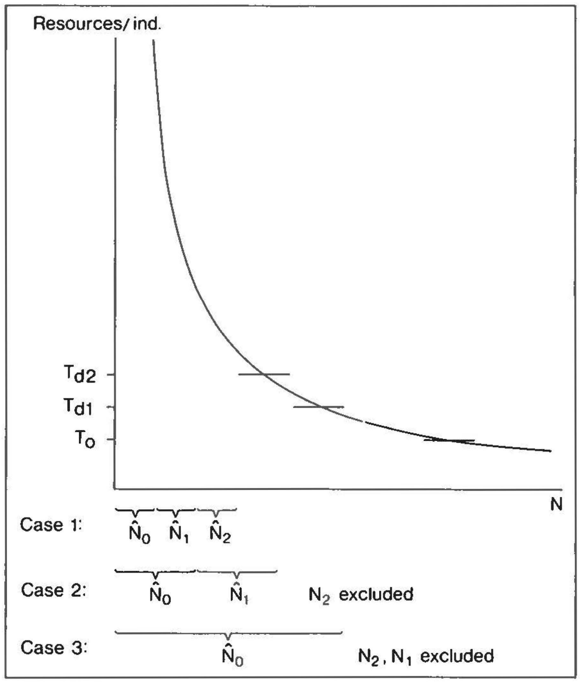


Fig. 19. Effects of competition for limited spring staging resources between individuals from populations with different migration distances from the staging site to breeding areas. Long-distance migrants (distance d_2 for birds of population N_2) have a larger threshold of resource requirements during the resting period (T_{d2}) than medium-distance migrants (T_{d1}) and local breeders (T_0, cf. Fig. 18). With potential equilibrium population sizes (determined by resources other than those at the staging site, e.g. by wintering or breeding resources) as in Case 1, staging resources will have no population limiting effects. With larger potential equilibrium populations of medium-distance migrants and local breeders, staging resources will be reduced below the threshold for accumulation of fat for long-distance migration. As a result, long-distance migrants, or both long- and medium-distance migrants become outcompeted as in Cases 2 and 3, respectively.

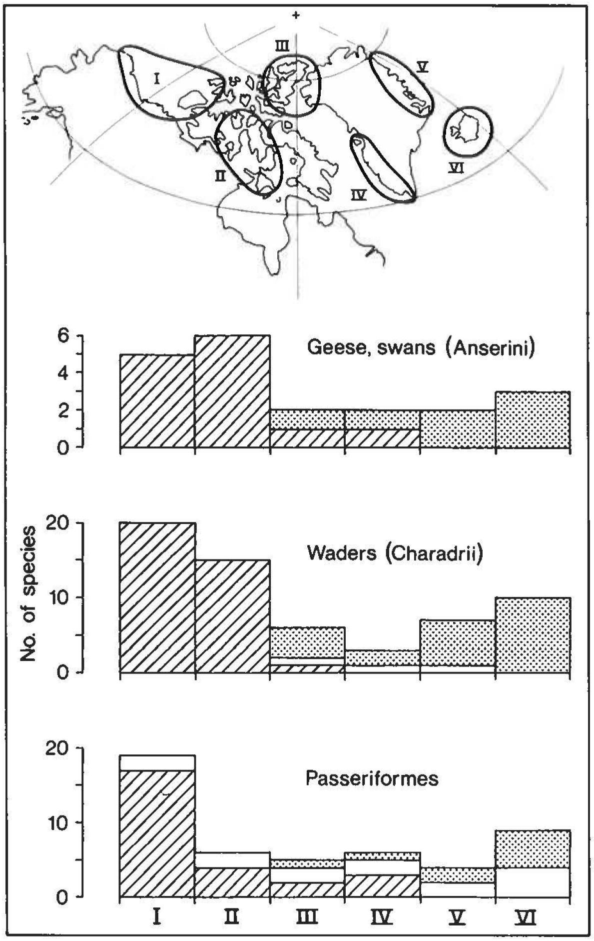


Fig. 20. Number of species of different categories of birds breeding in different regions of the Nearctic and in Iceland. Species taking part in American (or in a few cases Asian) migration systems are indicated by hatching, those taking part in European migration systems by dotting. Blank spaces refer to resident species or species with poorly known migration habits. Mainly based on Armstrong (1980), Godfrey (1966) and Salomonsen (1981).

may be limiting for the use of Iceland as a spring staging site and consequently, for the distribution of these species in the Nearctic. Interestingly, there are indications that the Dunlins of the fairly small NE Greenland population (*Calidris alpina arctica*) are staging only briefly in Iceland, or depart directly for Greenland from Great Britain in late spring, overflying Iceland (Wilson 1981, Meltofte 1985). In this way, competition with the large Icelandic Dunlin population is avoided. A similar overflying of Iceland probably occurs also in populations of other species departing from Great Britain and breeding in NE and E Greenland, like the Ringed Plover and Sanderling.

Fig. 20 illustrates the diversity of arctic geese, waders and passerines in different regions of the Nearctic and in Iceland. Of course, part of the differences in species diversity between regions is due to differences in habitat richness and diversity. Iceland, SW Greenland and N Alaska belong to the low arctic zone, in contrast to the high arctic regions in northern Canada and Greenland. Still, environmental differences between the regions are probably not sufficient to fully account for the faunistic differences. Other crucial factors are the degree of geographical isolation of different breeding regions (determining the migration costs in terms of necessary fat loads, and of risks associated with the long-distance flights), the positions and carrying capacities of staging sites, and the intensity of competition at these sites.

Even if the Greenland Inlandice is no barrier for bird migration, it is probably an important contributary cause, adding to the isolating effects of sea expanses and unproductive land, of the comparatively low diversity of arctic birds breeding in the sector around Greenland.

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