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Populations and breeding schedules of waders, Charadrii, in high arctic Greenland

Hans Meltofte

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To Eigil Knuth in gratitude for his life-long efforts to give young naturalists the chance to work in high arctic Greenland

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Waders are the dominant birds of the high arctic tundra of Greenland, both in terms of population densities and number of species. Of 11 species of waders breeding regularly in Greenland, nine have their main distribution within the high arctic part. *Charadrius hiaticula, Arenaria interpres, Calidris canutus, Calidris alpina, Calidris alba* and *Phalaropus fulicarius* are the most abundant. Living conditions in high arctic Greenland are characterized by extremely low and often sparse vegetation, moderate snow-cover and short cool summers. Large regional, local and annual differences occur, however, and the breeding phenology and population densities of waders are described and analysed in relation to these differences. The annual schedules of the wader populations are reviewed, and the governing factors discussed for each stage, as well as the factors involved in controlling population densities, sizes and changes, and distribution on a larger scale.

A very strong negative correlation was found between start of laying and snow-cover in early June, while breeding densities were best correlated with snow-free vegetation cover at this time. The most important ultimate factors involved are probably feeding conditions early in the season and, in snow-rich areas, also increasing predation risk with increasing snow-cover. Compared to other arctic areas, the waders in high arctic Greenland show moderate or low population densities, but they breed earlier than most other arctic populations. Low productivity, as compared to the extremely productive low arctic tundras of North America and Siberia, is responsible for the lower densities, while the limited spring snow-cover makes it possible for the waders to breed earlier in high arctic Greenland.

Finally an attempt is made to estimate the total population sizes of the waders breeding in high arctic Greenland, using both breeding density estimates and estimates of the same populations during winter in the Old World.

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Fig. 1. Most of high arctic Greenland is mountainous, with lowland areas being restricted to valley floors and a number of more extensive foreland areas. Here the south coast of Hochstetter Forland is seen on 17 June 1976, when the snow-free patches were used as communal feeding areas for waders and a few pairs of turnstones and sanderlings started to nest. Photo by the author.

Introduction

Nine of the 11 species of waders, Charadrii, breeding in Greenland, either breed exclusively in the high arctic part, or at least have their main populations there.

High arctic Greenland, surrounded as it is throughout the year by continuous sea ice, is characterized by long-lasting and extremely cold winters and short cool summers, by little precipitation and consequently limited snow cover and by extremely sparse vegetation. Temperatures above freezing are normally recorded only from late May until early September, and mean temperatures of the warmest month generally do not exceed +5°C (Salomonsen 1950). However, inland areas often have a warmer summer climate. In fact, many favourable inland areas of high arctic Greenland have summer temperatures more typical of the Low Arctic (Meltofte 1976a, 1976b). Winter precipitation is limited and frequent storms clear the snow off large expanses of land, so that extensive areas are relatively snow-free throughout the winter. Such areas are of decisive importance to the fauna. Precipitation ranges from 440 mm annually at Scoresbysund in the south to 132 mm at Danmarkshavn, and even less in the northernmost parts (*i.e.* 44 mm at Eureka, on Canadian Ellesmere Island) (Meteorological Institute of Copenhagen, Nettleship & Maher 1973).

Most of the country is mountainous, lowland areas being restricted to narrow fringes along the coasts and to valley floors apart from a number of more extensive foreland areas, built up of glacial deposits and raised marine sediments (Fig. 1). In most places the vegetation cover is patchy or with much bare ground between the plants. Continuous vegetation occurs only in limited areas. Relatively well vegetated areas generally make up about half of the lowland in the southern and central parts, decreasing to a few per cent in the northernmost parts. The vegetation rarely exceeds a height of a few centimetres.

In contrast to these continental conditions, low arctic Greenland is characterized by a more Atlantic climate with relatively mild winters with high precipitation and warmer summers; the southernmost parts even being subarctic (Salomonsen 1950). Annual precipitation in southern Greenland ranges from 622 mm at Nuuk (Godthåb) to 2391 mm at Prins Christian Sund, and during winter the country is covered by soft snow, which is often continuous and deep. Vegetation is often luxuriant, with meter high shrub of *Salix* and *Betula* species *etc.*, and extensive fertile heath- and herb-fields (Böcher *et al.* 1957, Böcher & Böcher 1975).

Following the earliest scientific ornithological report from high arctic Greenland in 1869–70 (Finsch 1874), expedition activities increased to a peak during the 1930's. These expeditions, whether wintering or visiting the country only during the summer months, provided mainly faunistic and taxonomic data, with only few exact data on phenology and population densities. Modern quantitative field ornithology was not introduced until 1964 (Rosenberg *et al.* 1970).

During seven seasons, 1969–76, I carried out ornithological observations in areas ranging from the southernmost to the northernmost parts of high arctic Greenland, partly during employment at weather stations, and partly as a member of various expeditions. Especially during the latter seasons, the population densities and breeding phenology of waders were studied (Meltofte 1976a, 1979, Meltofte *et al.* 1981, de Korte *et al.* 1981). The present paper is a review of present knowledge about these topics and attempts to trace some of the decisive factors affecting distribution, population densities and breeding phenology of waders in Greenland, both in relation to the differing environmental conditions inside the high arctic part itself, as well as between the high and the low arctic parts. A few abstracts have earlier been published (Meltofte 1981, 1982, 1984).

Material

Census areas

Population estimates from well defined census areas are now available for a series of sites from the south to the north in high arctic Greenland. Furthermore data from Lake Hazen on Canadian Ellesmere Island were included (Fig. 2).

These sites are listed below and in Table 1, together with details of source, size, situation, year of census (and period of census in cases when not all of the breeding season was studied), vegetation cover, and snow cover on 10 June. If snow cover was not stated for this date, it has been estimated from other statements, using snow melt curves presented by Meltofte (1979), de Korte *et al.* (1981) and Meltofte *et al.* (1981). In addition, I have estimated the accuracy of the census. In the analysis all pairs and individuals defending a territory have been considered full members of the populations, whether breeding or not (see Meltofte 1979).

1: Kap Stewart (de Korte *et al.* 1981). 27 km^2 on the southeastern part of Jameson Land at Scoresby Sund were censused in 1974, but the wader populations may well have been underestimated by up to 50%. The habitat is extensive tundra heath slopes with low hills, ridges and river ravines from sea level to an altitude of about 300 m (see Figs 4 and 21).

2: Kærelv (de Korte *et al.* 1981). 7 km^2 at the northeast coast of Hurry Inlet were fairly accurately censused in 1975, although the figures are more likely to be low than high. The area is well vegetated undulating tundra, entirely below 100 m above sea level. In the same area 18.5 km^2 were fairly accurately censused in 1979 (Hansen undated).

3: Ørsted Dal (Ferns & Mudge 1976, Green 1978a). The entire valley (260 km^2) was censused mainly after 12 July 1974, but only the central 25 km^2 were well covered. The habitat is well vegetated, gently undulating terrain up to 200 m altitude. Snow cover, which was less than 10% on 25 June, was estimated to have been about 40% on 10 June.

4: Henrik Møller Dal and Edderfugledal (Ferns & Mudge 1976, Green 1978a). 28 km^2 valley slopes below 200 m above sea level were fairly accurately censused from 20 July to 4 August 1974. Parts of the area are well vegetated, others less so. Snow cover was 60–75% on 25 June, and was estimated to have been more than 95% on 10 June.

5: Antarctic Havn (Green 1978a). 20 km^2 valley slopes and floor were fairly accurately censused 6–20 July 1974. Mainly sparse tundra heath below 100 m above sea level, but with extensive marsh areas. Snow covered 90–95% on 25 June, giving close to complete cover on 10 June.

6: Mestersvig (Green 1978a). 38 km^2 extensive gravel plains and sparse tundra heath mainly below 100 m above sea level were fairly accurately censused after 26 June 1974. Snow covered 90–100% on 25 June.

7: Karupelv (Green 1978a). 22 km^2 valley floor and slopes mainly below 200 m above sea level on Traill Ø were fairly accurately censused after 6 July 1974. The habitat is extensive areas of tundra heath of various densities. Snow cover was less than 10% on 6 July, and was estimated to have been about 80% on 10 June. In July 1979 very similar densities were found in partly the same area (Kempf undated). This year snow covered 5–10% on 29 June (C. Kempf *in litt.*).

8: Vega Sund (C. Kempf *in litt.*). 26 km^2 coastal slopes and lowland below 250 m above sea level on southern Geographical Society Ø were fairly accurately censused 26 June to 27 July 1982. Snow covered about 40% on 1 July.

9: Myggbukta (Elander & Blomqvist *in print*). 6.1 km^2 coastal slopes were censused fairly accurately in 1979. The habitat is barren gravel slopes and well vegetated raised beach ridges with many ponds, all below 100 m above sea level.

10: Daneborg (Rosenberg *et al.* 1970). Ca. 3 km^2 (measured on the map to be 3.7 km^2) on southern Wollaston Forland was censused fairly accurately in 1964. The habitat is sparsely vegetated and barren coastal slopes and plains and rocky hills mainly below 150 m above sea level. Snow covered 30% on 1 July and at least 70–80% around 10 June (Niels Hesselbjerg Christensen *in litt.*), but the snow free areas were mainly barren rock and fell-field.

11: Southern Hochstetter Forland (Meltofte *et al.* 1981). 18.2 km^2 were censused quite accurately in 1976. The habitat is

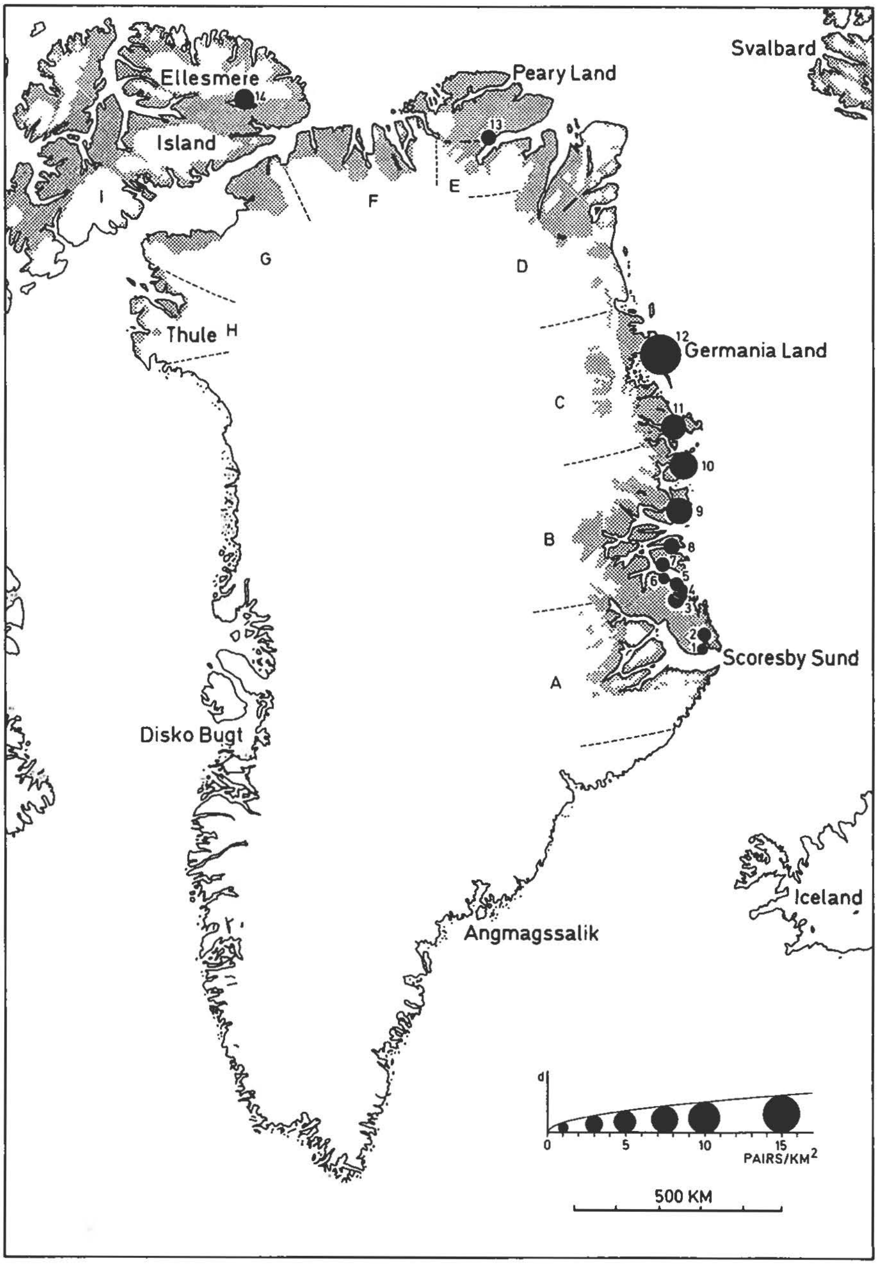

Fig. 2. Map of Greenland showing the high arctic area (shaded) and the population densities of waders (all species grouped) in 14 census areas. When more than one census has been made in an area, only the one covering the largest area is plotted. 1) Kap Stewart, 2 Kærelv, 3) Ørsted Dal, 4) Henrik Møller Dal and Edderfugledal, 5) Antarctic Havn, 6) Mestersvig, 7) Karupelv, 8) Vega Sund, 9) Myggbukta, 10) Daneborg, 11) Southern Hochstetter Forland, 12) Danmark Havn, 13) Jørgen Brønlund Fjord, and 14) Lake Hazen. Sections and letters refer to Table 3.

dominated by extensive well vegetated slopes and luxuriant boggy plains with many ponds and tarns; mainly below 100 m above sea level (see Figs 1 and 13).

12: Danmark Havn (Meltofte 1975, 1977a, 1979). 4.49 km^2 on southeastern Germania Land were censused accurately in 1975. Less reliable censuses were performed in 1969 and 1970. All of the area is below 100 m above sea level (see Fig. 20).

13: Jørgen Brønlund Fjord (Meltofte 1976a). 8.6 km^2 in southern Peary Land were censused accurately in 1973. The area is mainly barren shingle and gravel plains and clay slopes below 100 m above sea level, with only a few per cent vegetation cover concentrated along streams.

14: Lake Hazen (Nettleship & Maher 1973, Nettleship 1973, 1974). 23 km^2 on central Ellesmere Island were fairly accurately censused in 1966. The area is dominated by extensive sparsely vegetated hummock and tundra plains, mainly from 158 m to some hundreds of metres above sea level. From the map I have estimated the vegetation cover to be about 20%. and Nettleship (*in litt.*) estimated the snow cover to about 10% on 10 June 1966. Earlier estimates from the same area were presented by Saville & Oliver (1964).

At Alexandra Fjord, eastern Ellesmere Island, 12 km^2 were censused in 1980 and 1981 (Freedman & Svoboda 1982). Except for Baird's sandpiper *Calidris bairdii*, almost none of the species dealt with in this paper were found in the area, and it was not included in the analysis (see also Witts, undated a).

In general all the census areas are coastal plains or valley slopes and floors, mainly below 200 m above sea level. The vegetation cover varies with the spring snow-cover from only a few per cent at Jørgen Brønlund Fjord to generally about 50% or more in the central and southernmost census areas. All the areas held marshy vegetation on wet slopes and low plains. For more detailed habitat descriptions, see the original sources.

In most of the areas the populations were followed throughout the breeding season, but areas 3–8 were censused so late in the season that most unsuccessful pairs had probably left the territories together with territorial non-breeders (see Meltofte 1976a, 1979). The accuracy of the counts cannot be estimated further, but it probably varies greatly. Waders are not easy to census on the breeding grounds. Very often the birds do not react to the presence of the counter even when close to the nest, and on other occasions they may give alarm calls and perform distraction displays several hundred metres away from their nest or young (see Meltofte 1976a, 1977b, 1979). It is likely that the populations generally have been underestimated in several of the census areas. This may apply to a lesser extent to the ringed plover *Charadrius hiaticula,* due to the more demonstrative behaviour of this particular species (Meltofte 1979).

The sanderling *Calidris alba* poses special problems in relation to censussing of breeding pairs. Parmelee (1970) and Parmelee & Payne (1973) found a double clutch system in this species in high arctic Canada, similar to that known for certain other *Calidris* sandpipers (Pitelka *et al.* 1974). Information from high arctic Greenland is contradictory. Recent studies by Pienkowski & Green (1976) and by Meltofte (1979) showed an ordinary single-clutch system at Mestersvig and Danmark Havn, respectively, while some indications at least of a two-clutch system was found by Meltofte (1976a) in Peary Land. Both Meltofte *et al.* (1981) and de Korte *et al.* (1981) found that both sexes incubate, but no clear evidence was found concerning the strategy. The older literature from Northeast Greenland is even more contradictory. Manniche (1910) stated that only females incubate, and that the males leave the territories and form post-breeding flocks soon after egg-laying. Also Pedersen (1934, 1942) found only females on eggs, and states like Manniche that males have less developed brood patches, and that they form flocks early. Both Løppenthin (1932) and Bird & Bird (1941) present similar evidence, while in accordance with Kolthoff (1903), they state that both mates may attend young. In contrast, Madsen (1925) found exclusively males incubating. A total of seven males were shot on nests while one female was shot attending a brood. All these older statements are based on shot birds. It seems possible that sanderlings differ in their breeding strategy from one geographical area to another, and perhaps even from year to year. In this account, however, I have found it most practical to accept each nest or territory as representing one pair.

Phenology

Most older ornithological reports from the areas in question give information on earliest observation dates, pair formation and territory establishment, departure etc., but very little exact information on breeding phenology. When nests were found, the clutches were usually collected, and thus no hatching dates could be determined. Observations of young are often given, but usually without any indication of age.

Samples of laying or hatching dates are presented only in the papers mentioned in the above section and in Green *et al.* (1977), but additional information on phenology and general occurrence has been found in the following papers and reports: Finsch (1874), Hart (1880), Bay (1894), Kolthoff (1903), Deichmann (1909), Manniche (1910), Freuchen (1915, 1921), Gibson (1922), Pedersen (1926, 1930, 1934, 1942), Løppenthin (1932), Schaanning (1933), Bertram *et al.* (1934), Tcherniakofsky (1939), Bird & Bird (1941), Petersen (1941), Møhl-Hansen (1949), Hylbom (1951), Johnsen (1953), Conradsen (1957), Goodhart & Wright (1958), Marris & Ogilvie (1962), Røen (1965), Hall (1966), Hall & Waddingham (1966), Just (1967), Marris & Webbe (1969), Andersen (1970), Grant (1972), Hjort (1976 and *in litt.:* Observations from North Greenland 1979), Meltofte (1976b), Thing (1976), Ferns (1978a), Greenwood (1978), Håkansson *et al.* (1981), Sellar *et al.* (1981), Madsen & Boertmann (1982 and *in litt.*), Plantema (1983), Hjort *et al.* (1983), Madsen *et al.* (1984 and *in litt.*), Bosman (undated), Campbell (undated), Erskine (undated a, b), Ferdinand (undated), Greenwood *et al.* (undated), Smart (undated a, b), Smart & O'Brian (undated), Witts (undated b), Watson *et al.* (undated), and Jeppe Møhl (*in litt.:* Observations from Hall Land 1965).

Age estimates of pulli from my first reports have been checked with the latest data on growth rate *etc.* (see Meltofte 1979). Similarly, the calculated hatching dates of turnstone *Arenaria interpres* chicks presented by Green *et al.* (1977) have been revised using the original data (G. H. Green *in litt.*) and the growth rates presented by Meltofte (1976a, 1979). Data given by Hansen (undated) have also been revised in this way, and additional more exact hatching data have been provided by J. M. Hansen (*in litt.*).

Transformations from hatching dates to 1st egg dates (and *vice versa*) have been made by using the following number of days for combined egg-laying and incubation: ringed plover 28 days, turnstone *Arenaria interpres* 26 days, knot *Calidris canutus* 28 days, dunlin *Calidris alpina* 26 days, sanderling 28 days, and red phalarope *Phalaropus fulicarius* 21 days (Green *et al.* 1978, Mayfield 1979).

Fig. 3. Dunlin habitat in the Modiolaelv valley in southern Jameson Land, 16 July 1974. The habitat on the ridge behind the three Musk-oxen is typical for sanderling. Photo Ko de Korte.

Special account

Breeding distribution and habitats

Ringed plover, turnstone, knot and sanderling are widely distributed almost all over the high arctic tundra of Greenland. The ringed plover is apparently missing in part of the area between Peary Land and the Thule district, and the sanderling is perhaps missing in the Thule area, where it is replaced by Baird's sandpiper. The dunlin *C.a. arctica* breeds in Northeast Greenland at least as far north as Germania Land, while the southern subspecies *C.a. schinzii* breeds in the Angmagssalik area, Southeast Greenland. The red phalarope breeds largely in the same area of Northeast Greenland as the dunlin, while the golden plover *Pluvialis apricaria* only breeds at Scoresby Sund (de Korte 1975). In the summer of 1982, also the whimbrel *Numenius phaeopus* was found breeding in Jameson Land at Scoresby Sund (Boertmann *et al.* in print).

Whereas turnstone, knot and sanderling breed almost exclusively in the high arctic area, the ringed plover is found widely scattered in low arctic Greenland especially in gravelly river deltas. The red phalarope occurs also in some areas in Northwest Greenland.

Besides the eight high arctic species, the two low arctic breeding waders of Greenland, the purple sandpiper *Calidris maritima* and the red-necked phalarope *Phalaropus lobatus* extend their breeding distribution into the southern part of Northeast Greenland. The purple sandpiper breeds regularly along the outer coast, perhaps even to Germania Land (see Meltofte *et al.* 1981), while the red-necked phalarope probably breeds only locally and occasionally north of the Scoresby Sund/Kong Oscar Fjord area, as well as in the southern part of the Thule district.

In the Canadian High Arctic, the same populations of ringed plover, turnstone, knot and Baird's sandpiper breed on Ellesmere and adjacent islands (e.g. Godfrey 1966), but only turnstone and knot apparently being

Fig. 4. Incubating male turnstone on "frost-boiled" tundra at Kap Stewart on southernmost Jameson Land, 7 July 1974. Photo Ko de Korte.

widespread and common (MacDonald 1953, Parmelee & MacDonald 1960, Nettleship & Maher 1973), though Baird's sandpiper is locally abundant (Freedman & Svoboda 1982, Witts 1981, undated a). Also sanderlings and red phalaropes are found here, but these probably belong at least partly to other populations than those in Northeast and North Greenland (cf. Parmelee 1970).

The waders of high arctic Greenland breed primarily on the coastal plains, valley floors, and slopes formed from raised sea-bed and moraine material. Their main concentrations are found at altitudes from sea-level up to 100–200 metres, but in certain areas, especially on south-facing valley slopes and mountain flats, up to 400–500 metres above sea level. The wader species show a quite clear cline in habitat selection, from the dunlin and red phalarope, which breed in the most fertile and boggy marshland areas, through the turnstone, knot and sanderling, which breed from the immediate surroundings of wet and well vegetated areas to the more extensive and drier arctic heaths and even sparsely vegetated slopes and rolling plains, to the ringed plover, which prefers to nest in gravelly and stony habitats with very poor vegetation. All species, however, most often breed within 50–100 metres of fertile wet or moist sites (Figs 3, 4 and 5).

The ringed plover is probably the most widely distributed wader, found even at the most remote small and moist vegetated sites. It is found at higher altitudes than the other wader species, possibly except for the knot. The highest densities are found where smaller, more arid sites alternate with more fertile, moist patches, and it is missing in areas too well-vegetated and boggy (Meltofte 1976a, 1979, Ferns & Mudge 1976, Ferns 1978b, Meltofte *et al.* 1981, de Korte *et al.* 1981, Håkansson *et al.* 1981, Elander & Blomqvist *in print*).

Turnstones, knots and sanderlings nest in habitats ranging from well-vegetated, moist sites to well-drained clay or gravel slopes and flats with patchy vegetation or hummocks with *Salix arctica, Carex, Cassiope, Saxifraga* or *Dryas,* as well as to dry extensive polygonous or

Fig. 5. Although ringed plovers nest in stony and gravelly habitats, nests are rarely far from moist, well-vegetated sites. Danmark Havn, mid-June 1970. Photo by the author.

frost-cracked areas mainly with lichens and patches of bare clay and gravel (Parmelee & MacDonald 1960, Parmelee 1970, Rosenberg *et al.* 1970, Nettleship 1973, 1974, Meltofte 1976a, 1979, Ferns & Mudge 1976, Ferns 1978b, Meltofte *et al.* 1981, de Korte *et al.* 1981, Håkansson *et al.* 1981, Hansen undated).

Dunlins and phalaropes are normally confined to wet, luxuriant marsh habitats with dense cover of bryophytes and *Carex, Salix* and *Eriophorum*. Such sites are found mainly below large, persistent snow-fans and in boggy areas with streams and ponds. In some areas a large proportion of the dunlin nests are situated in adjacent drier habitats, but nearly always within 30–100 m of wet sites. Phalaropes are even more confined to boggy areas (Fig. 6) (Ferns & Mudge 1976, Meltofte 1979, Meltofte *et al.* 1981, de Korte *et al.* 1981).

In Northeast Greenland the habitat selection patterns lead to a marked difference in the species composition between the cool, foggy and often barren outer coast where low population densities are found, but to where the purple sandpiper is confined; the central, sunnier and better vegetated areas, where the highest densities are found in most species, and the innermost arid areas, where the ringed plover is often the only wader species present (Hjort 1976, Greenwood 1978, Meltofte *et al.* 1981, Håkansson *et al.* 1981).

Besides these more general and merely subjective habitat statements in the literature, Ferns (1978b) has attempted to quantify and analyse statistically a number of components in nesting and territorial habitats of the waders in the southern part of Northeast Greenland. More studies of this kind are needed, including different

Fig. 6. In Northeast Greenland, red phalaropes are confined largely to the most luxuriant marsh habitats with ponds and pools. Here a male at Danmark Havn, mid-July 1969. Photo by the author.

sites throughout the species ranges, as the preferences apparently differ between sites. Thus both turnstones and knots prefer to nest in more moist, well-vegetated, and less stony habitats on Ellesmere Island than in Greenland (cf. Parmelee & MacDonald 1960, Nettleship 1973, 1974). Extensive hummocked slopes and tundra, typical of the lowlands of Ellesmere and adjacent islands in the Canadian Archipelago, are found only locally on late thawing sites in high arctic Greenland. Here stony and gravelly slopes and flats with polygonous or creeping soil areas dominate among the moraine and silt hills and ridges.

Much more extensive habitat selection studies were performed during five years at Point Barrow in Alaska, including changes during the breeding cycle and annual differences (Myers & Pitelka 1980a, b).

Population composition and densities

The densities of wader pairs vary considerably between the 14 high arctic census areas, reaching a peak of 16.6 pairs per km^2 at Danmark Havn (Table 1). However, these census areas are not representative of the high arctic lowlands of Greenland and Ellesmere Island, since they are usually limited to the optimal wader sites within much larger areas. Wet, boggy and well-vegetated areas are thus over-represented, hence over-representing e.g. the dunlin in relation to the other species. Furthermore, the wader density is highly dependent on the extent to which more marginal habitats are included in a given census area. Thus, the largest areas are likely to be the most representative, while those covering only a few km^2 are less so. (See the section on material for evaluation of census accuracy in the individual areas.)

Nevertheless, the available information may be used to attempt analysing the species composition and relationships with factors such as vegetation and snow cover within these census areas (Table 1). The population densities of turnstone and knot and of dunlin and sanderling are highly correlated (Table 2), while they are not significantly correlated with the other species; the ringed plover may be negatively correlated with turnstone and knot. These correlations are likely to be attributable to habitat differences between the areas being reflected in the species composition.

The high correlation between dunlin and sanderling is probably not representative for Northeast Greenland in general, as the dunlin is overrepresented in the census areas, as mentioned above. Sanderlings may simply have a more wide habitat spectrum than the other species, so that the high correlation with the dunlin reflects the higher quality of the "dunlin habitat", and that sanderlings are more attached to boggy areas than turnstones and knots.

There is no significant correlation between the population densities of waders and the vegetation cover in the census areas (Table 1). However, most are better correlated with snow-cover on 10 June and with snow-free vegetated proportions of the areas at the same time, i.e. at the beginning of the breeding season (see section on timing of breeding). The ringed plover behaves in quite the opposite way to all other species in being negatively correlated with vegetation cover and positively correlated with snow-cover (within certain limits – presumably!). When the ringed plover is excluded from the sum of all waders, the correlation between densities and both snow-cover and snow-free vegetated areas increases to give a statistical significance (see further in Discussion).

A few less exact population estimates from Mestersvig (Vibe 1954, Green & Williams undated) and from Stormkap near Danmark Havn (Manniche 1910) are included in Table 1.

Few other wader population counts exist from the High Arctic. From Bathurst Island in the Canadian High Arctic, Parmelee (1970) and Mayfield (1983) gave sanderling densities within the same range as the Greenland figures, while higher densities of red phalaropes were found in most years (Mayfield 1979, 1983). Fair densities of Baird's sandpiper (one pair per km^2) were found on the east coast of Ellesmere Island (Freedman & Svoboda 1982; see also Witts undated a) and of grey plover *Pluvialis squatarola,* white-rumped sandpiper *Calidris fuscicollis,* and Baird's sandpiper from line transects on eastern Devon Island (Pattie 1977). Similar or somewhat higher densities were found of these species and of golden plover *Pluvialis apricaria* on southern Bylot Island (Van Tyne & Drury 1959). From further south in the Canadian High Arctic, Manning *et al.* (1956) and Manning & Macpherson (1961) presented line transect estimates of sanderling densities from Banks and Prince of Wales Island, that are notably higher (more than 6.7 pairs per km^2), than those found by Parmelee (1970) and in this study. On Banks Island, semipalmated sandpipers *Calidris pusilla,* and on Prince of Wales Island red phalaropes, showed similar high densities, whereas turnstones and about ten other wader species showed densities similar to those found in the waders of high arctic Greenland. Even on Melville Peninsula, densities of eight species of waders were similar to those found in high arctic Greenland (Montgomerie *et al.* 1983).

On Svalbard and in low arctic West Greenland, purple sandpipers (together with red-necked phalaropes in W. Greenland) dominate among the waders, with densities similar to wader densities in high arctic Greenland (Longstaff 1932, Joensen & Preuss 1972, Bengtson 1975, Alendal *et al.* 1982, Meltofte *et al.* 1983). Few other waders breed in these areas, however.

From the edge of the High Arctic near Point Barrow in Alaska and from low arctic Canada and Alaska, wader densities have been reported to be much higher than in the High Arctic (e.g. Pitelka 1959, Holmes 1970, 1971a, Salter *et al.* 1980, Myers & Pitelka 1980a). In ad-

Table 1. Wader population densities at 16 counts in 14 different census areas in high arctic Greenland and Ellesmere Island 1964–1982. Three less exact estimates are also presented. 1) Vegetation cover was measured from published maps when not given in the reports.

Locality	1 Kap Stewart	2 Kærelv	2 Kærelv	3 Ørsted Dal	4 H. Møller Dal	5 Antarctic Havn	6 Mestersvig	7 Karupelv	7 Karupelv	8 Vega Sund
Census year	1974	1975	1979	1974	1974	1974	1974	1974	1979	1982
Area (km^2)	27	7	18.5	25	28	20	38	22	25	26
Vegetation cover (%)	70	70[1]	67[1]	40[1]	45[1]	60[1]	45[1]	80[1]	50	60
Snow cover 10 June	>90	40	40	40	>95	~100	~100	80	60	>90
Snow-free vegetation	(7)	(40)	(40)	(25)	(2)	(2)	(1)	(15)	(20)	(5)
Charadrius hiaticula	0.37	0.71	0.38	0.28	1.36	0.80	0.97	0.68	0.76	0.12
Pluvialis apricaria	0.11	0	0.14	0	0	0	0	0	0	0
Arenaria interpres	0.04	2.14	0.43	1.04	0	0	0	0.36	0.24	0.58
Calidris canutus	0.11	0.14	0.30	0.20	0	0	0	0.41	0.28	0.42
Calidris alpina	0.41	1.29	0.59	0.52	0.57	0.75	0.13	0.36	0.28	1.58
Calidris alba	0.07	0.29	0.05	0.39	0.11	0.15	0.08	0.73	0.44	0.15
Phalaropus fulicarius	0	0	0	0	0	0	0	0	0	0
Phalaropus lobatus	0	0	0	0	0	0	0	0	0	0
Waders in total	1.11	4.57	1.89	2.43	2.04	1.70	1.18	2.54	2.00	2.85
Waders excl. *C. hiaticula*										

dition to the fact that many more species breed in these areas, maximum densities per species were *e.g.* 75 pairs of dunlins and more than 500 pairs of western sandpipers *Calidris mauri* per km^2 in certain areas in western Alaska (Holmes 1970, 1971a).

Red phalaropes were also found in high densities on Baffin, Victoria and Jenny Lind Islands (7 to 20 pairs per km^2) (Soper 1940, Parmelee *in* Mayfield 1979). Even higher densities were found at Barrow, Alaska (up to 44 nests per km^2) (Schamel & Tracy 1977).

From northern Siberia, Flint (1976), Kistchinski (1982), and Ryzhanovskii *et al.* (1983) report similar high densities. Maximum densities on the most luxuriant southern tundras reached 300 pairs of waders per km^2, while densities decreased to the north with 80 pairs per km^2 on the Chukotsk Peninsula tundras, 63–71 per km^2 on high arctic northern Taimyr and 22 wader pairs per km^2 on Wrangel Island. On the latter island Dorogoy (1982) found more than six pairs of knots breeding per km^2 in optimal habitat. Of 300 pairs of waders per km^2 in the most favourable southern moss and sedge tundras of the lower Indigirka delta plain, phalaropes make up nearly two thirds of the population, with 100–150 pairs of red phalaropes and 90 pairs of red-necked phalaropes per km^2 (Kistchinski 1975, 1982, Flint 1976).

Table 2. Correlation coefficients (r_s) between densities of five wader species compared pairwise for the 14 census areas in high arctic Greenland and Ellesmere Island. For correlation coefficients (r_s) one asterisk denotes $p \leq 0.05$ ($r_s \geq 0.54$), and two asterisks $p \leq 0.01$ ($r_s \geq 0.71$).

	C. hia.	*A. int.*	*C. can.*	*C. alp.*	*C. alb.*
Charadrius hiaticula	–				
Arenaria interpres	−0.47	–			
Calidris canutus	−0.54	0.76**	–		
Calidris alpina	0.19	0.17	0.25	–	
Calidris alba	0.25	0.35	0.10	0.64*	–

Population fluctuations and changes

No long term studies of population fluctuations have taken place in high arctic Greenland. A few repeated counts exist, however, and the large number of faunistic reports provide an opportunity of comparing relative abundances, *etc.*

Repeated population counts have been performed at Danmark Havn in 1969 and 1975 (Meltofte 1975, 1979), at Kærelv in 1975 and 1979 (de Korte *et al.* 1981, Hansen undated), and at Karupelv in 1974 and 1979 (Green 1978a, Kempf undated). When comparing only numbers estimated within exactly the same areas, most figures are very close to each other during the two census years in each area (±0–3 pairs). Only ringed plovers at Danmark Havn and turnstones at Kærelv vary markedly, but both these and the other smaller differences may at least partly be attributed to differences in census accuracy. Turnstones have been found to breed in the snow-rich areas at Mestersvig and Kap Stewart in some years and not in others (Greenwood 1978, de Korte *et al.* 1981).

Holmes (1966, 1971a) found little year-to-year variation in the population densities of dunlins and western sandpipers in Alaska. Similarly, five years of repeated counts in a number of census areas at Point Barrow in Alaska showed relatively stable populations of most wader species except pectoral sandpiper *Calidris melanotos* and red phalarope (Myers & Pitelka 1980a), as did Montgomerie *et al.* (1983) in most wader species on the Melville Peninsula in the Canadian Arctic in 1981–

Snow-free vegetation on 10 June is given in brackets when simply estimated from vegetation-cover and snow-cover on 10 June. For correlation coefficients (r_s) one asterisk denotes $p \leq 0.05$ ($r_s \geq 0.51$), and two asterisks $p \leq 0.01$ ($r_s \geq 0.67$).

9 Myggbukta	10 Daneborg	11 Hochstetter	12 Danmark Havn	13 Peary Land	14 Lake Hazen	Correlation coefficients (r_s)			Mestersvig	Mestersvig	Stormkap
						Vegetation cover	Snov cover 10 June	Snow-free vegetation on 10 June			
1979	1964	1976	1975	1973	1966				1953	1972	1907–08
6.1	3.7	18.2	4.49	8.6	23				100	40	23
>90	>10[1]	80	37	<5	20[1]						
<10	75	93	40	<10	10						
85	5	3	23	2	(18)						
0.16	4.59	0.36	4.79	0.58	0	−0.31	0.36	−0.31	0.20	0.75	–
0	0	0	0	0	0				0	0	0
1.48	0	2.06	3.79	0.93	3.04	0.07	−0.65*	0.60*	0	0.06	1.74
0.49	0	0.11	0.45	0	1.09	0.26	−0.50	0.72**	0	0	1.30
2.15	1.89	1.21	4.23	0	0	0.28	0.01	0.35	0.10	0.20	1.30
1.95	1.08	1.65	3.12	0.35	0	0.13	−0.20	0.24	0.20	0.13	–
0.16	0	0.55	0.22	0	0				0	0	>0.43
0.33	0	0	0	0	0				0	0	0
6.72	7.57	5.93	16.59	1.86	4.13	0.02	−0.36	0.45	0.50	1.14	–
						0.11	−0.54*	0.58*			

82. Opposite to these relatively "stable" counts, Parmelee (1970) found markedly lower densities of sanderlings on Bathurst Island in 1969 than in 1968. (See also Mayfield 1983 and the Discussion.)

Older reports on occurrence, abundance *etc.* of individual species in certain areas of high arctic Greenland are hard to evaluate owing to their lack of quantitative data. The most definite information is whether a species was found at all. The most interesting species in this respect is probably the knot, which was not mentioned from Northeast Greenland by either Finsch (1874) or Kolthoff (1903), despite the fact that their reports are based on observations throughout the season or on extensive surveys of the region. Bay (1894) reports only one flock, of five juveniles, during one year at Scoresby Sund, whereas Manniche (1910) found knots breeding extensively in Germania Land in 1906–08, and from the 1920s it was found in numbers by several observers (*e.g.* Pedersen 1926, 1930). In southern Peary Land no knots were seen until 1949, when one single juvenile was found during a two year stay (Johnsen 1953). Since then, increasing numbers of knots have been found in the same areas (Meltofte 1976a). The species was found relatively common along the north coast, west of Peary Land, already in 1917, however (Wulff 1934).

The turnstone shows a somewhat similar pattern. Only three individuals were reported by Bay (1894) in one year at Scoresby Sund, and Manniche (1910) reports that no turnstones bred at Danmark Havn in 1906–08, where a dense population is found now (Meltofte 1975, 1979). In Peary Land also, this species seems to have increased since the middle of the century (Meltofte 1976a).

At least for a number of the earliest reports, the lack of experienced field ornithologists may explain the lack of observations. Certain species are lacking in a few other old reports as well, but nevertheless it seems likely that some marked population changes have taken place in these two species.

More recently, extensive counts in western Europe have shown that the Greenland/Canadian population of knots has decreased from more than 600 000 to about 350 000 during the last decade (Prater 1976, 1981a, 1981b, Engelmoer 1982). Annual fluctuations vary in parallel with the breeding success of the Greenland/Canadian population of brent geese *Branta bernicla hrota* wintering in the British Isles, thus indicating that conditions on the breeding grounds may be involved (Prater 1981a). This marked decrease has not been recorded on the breeding grounds – probably due to lack of data.

Byrkjedal & Bernhoft-Osa (1982) found decreasing numbers of juvenile ringed plovers and sanderlings staging during autumn at Revtangen in southwestern Norway during the years 1947–1967. The possible relation of this to the breeding population of high arctic Greenland is unknown.

The recent findings of golden plover and whimbrel breeding at Scoresby Sund may be associated with a general amelioration of the summer climate in East Greenland during this century, as suggested by Hall (1966). These species may already have bred occasionally in East Greenland in the first half of the century (Bertram *et al.* 1934, Salomonsen 1935), and may actually have been present for a long time, but their frequency must have increased to some extent.

Salomonsen (1950) and Rosenberg *et al.* (1970) suspect that the red-necked phalarope has expanded to the north in Northeast Greenland during this century, again owing to the warmer climate. Phalarope populations are known to fluctuate considerably (Mayfield 1979), however, so no definite statements are possible (cf. Elander & Blomqvist in print). See also Salomonsen (1948).

Fig. 7. After having wintered in West Africa, Nearctic ringed plovers, dunlins and sanderlings concentrate during April and May around the Irish Sea for a final fattening, before they migrate more or less directly to the breeding grounds in late May and the first days of June. Here Greenlandic ringed plovers and (mainly Icelandic) dunlins roost during high tide at Solway Firth in Scotland, May 1983. Photo Mike Moser.

From these examples it is clear that significant population fluctuations occur among the waders of high arctic Greenland, but so far too little is known about their magnitude and reasons (see further in Discussion).

Spring migration

Most of the wader populations of high arctic Greenland winter in the Old World. Only the purple sandpiper winters in Greenland although birds from East Greenland winter also in Iceland and perhaps in the British Isles (Salomonsen 1967, R. I. G. Morrison *in litt.*). The phalaropes winter in the tropical and subtropical waters off the west coasts of South America and West and Southwest Africa. Turnstones and knots winter mainly in Northwest Europe, whereas the ringed plovers, dunlins and sanderlings winter mainly in West Africa (Nørrevang 1959, Salomonsen 1967, Prater 1974a, 1980, Morrison 1975, Dick *et al.* 1976, Branson *et al.* 1978, Green 1978b, Taylor 1980, Roselaar 1983; see also Boere *et al.* 1984 for purple sandpipers). It is possible that the small population of turnstones breeding at Disko Bugt in low arctic West Greenland belongs to the North American population (Salomonsen 1967).

The spring migration initially brings all the Old World wintering populations together in northwestern Europe. From there they migrate during late April, May and the first days of June to the breeding grounds with many birds making a stopover in Iceland. Ringed plovers, dunlins and sanderlings stay in West Europe until May, especially around the Irish Sea (Fig. 7) (Eades & Okill 1976, Clapham 1978, Hardy & Minton 1980, Ferns 1980a, 1980b, 1981a, Prater 1981a, Clark *et al.* 1982). About half of the knots leave the British Isles and France as early as March and April for the Wadden Sea, where they concentrate in the Schleswig-Holstein part during late April and early May (Fig. 8) (Prater 1974b, 1980, Boere & Smit 1981). They leave this area for Iceland during the second week of May, when flocks of more than 2000 have been seen heading NW at a high altitude out across the North Sea (Meltofte & Lyngs 1981), and when major arrivals are noted in Iceland (Wilson 1981, Morrison & Wilson undated). On weather ships in the North Atlantic, the migration of turnstones also peaks in the second week of May (Luttik & Wattel 1979).

Fig. 8. About half of the Old World wintering Nearctic knots move east from the British Isles and France during March and April to spend one or two months in the Schleswig-Holstein part of the Wadden Sea before they move on to Iceland during early May. Here a small part of a flock of 40 000 knots are seen together with oystercatchers *Haematopus ostralegus* on a high tide roost on the Danish isle Jordsand just north of the Danish/German border, 20 April 1983. Photo John Frikke.

Ringing data confirm the presence of Nearctic ringed plovers between 30 April and 20 May in Britain (5 records) and Belgium (1), and dunlins between 7 and 22 May in Britain (4). Three sanderlings were recorded on 3 and 20 March and on 8 April, respectively, in the British Isles (Green 1978c, Prater & Davies 1978, and the' Zoological Museum, Copenhagen).

Whereas Greenlandic ringed plovers, dunlins and sanderlings leave Britain during late May more or less directly for the breeding grounds without large concentrations appearing in Iceland, knots and most turnstones stay a few weeks in Iceland for "refuelling" before the onward migration to the high arctic breeding grounds of Greenland and Canada (Morrison 1975, 1977, Branson *et al.* 1979, Clapham 1979, Ferns 1981b, Wilson 1981). During May concentrations of more than 1000 turnstones and 12 000 knots have been found on southwestern Iceland (Wilson 1981, Morrison & Wilson undated). The majority of the populations of the three former (and smaller) species are found in Northeast Greenland, whereas large numbers of turnstones and knots fly the far longer distance to reach the western part of North Greenland and Ellesmere Island. This involves a flight of some 600 km across the Greenland ice cap from around Angmagssalik to the Disko Bugt area in West Greenland (Salomonsen 1967). The migratory divide between birds migrating up the east coast of Greenland and those which cross the ice cap apparently lies somewhere between Thule and Peary Land (Meltofte 1976a). However, Morrison (1975, 1977) suggests that also a part of the Ellesmere Island knots may join the populations passing east and north of Greenland. In spring 1985, studies in northern Norway indicated that 15–30 000 knots staging in Balsfjord were probably Nearctic Birds (Nick Davidson in litt.). Birds were seen departing northwest in the direction of Northeast Greenland.

During the stay in the British Isles and in Iceland, fat reserves ranging from one third to one half of the departure body weight is deposited. This fat enables the birds to undertake the long, non-stop flight and to withstand the often harsh conditions during the first days on the breeding grounds (Prater 1974a, Morrison 1975, Eades & Okill 1976, 1977, Branson *et al.* 1979, Clapham 1979, Pienkowski *et al.* 1979, Ferns 1980b, 1981a, 1981b). Thus, with a lean weight of about 105 g (Pienkowski & Evans 1984), newly arrived turnstones in Northeast Greenland still carried up to 25 g fat (cf. Meltofte 1979). In spite of the different flight distances covered, newly arrived turnstones showed about the same weight in Ellesmere Island as in Northeast Greenland (Morrison 1975, Meltofte 1979). Clapham (1979) found that turnstones leaving the British isles early for Iceland carried less fat than those leaving in late May probably directly for the breeding grounds.

Arrival and immigration

The first individuals of all wader species, except for the phalaropes, appear in Northeast Greenland highly synchronously during the last week of May, at the time when thaw starts in most areas (see Discussion). The majority of initial observations lies around 23–25 May, with knots often a few days later, while some of the other species have been seen as early as 17–20 May (see tables in Meltofte 1975, de Korte *et al.* 1981, Elander & Blomqvist in print, and Pedersen 1934, Salomonsen 1950, Meltofte 1979, Meltofte *et al.* 1981, Hansen undated). Mean dates of first sightings in 9–14 observation year-sites since 1964 are: ringed plover 22.9 May, turnstone 22.7 May, knot 27.6 May, dunlin 22.6 May and sanderling 25.2 May. Initial observation dates for the purple sandpiper ranges from 22 May to 4 June. In extremely late seasons, *e.g.* 1939, the first waders may not appear until well into June (Pedersen 1942). Delayed arrival is possibly local, however, as normal arrival dates were recorded the same year farther south at Myggbukta (Elander & Blomqvist in print). In central Northeast Greenland the first birds are generally seen a few days later than in the southernmost parts, and in North Greenland as well as in the Canadian High Arctic they are seen a few days later still (Hart 1880, Gibson 1922, Parmelee & MacDonald 1960, Parmelee 1970, Nettleship 1973, 1974, Nettleship & Maher 1973, Meltofte 1976a, Witts & Morrison 1980).

In Southeast Greenland a few much earlier arrival dates have been reported, such as a ringed plover on 4 May 1898 (Petersen 1908). Such early arrivals probably involve individuals which have overshot Iceland during their migration from the British Isles.

Dates of initial observation have tended to be earlier during recent decades than around the turn of the century (Rosenberg *et al.* 1970, Meltofte 1975). According to Sigfúsdóttir (1969), spring (April-May) temperatures in Iceland changed very markedly from a cold period lasting from the middle of the 19th century until around 1925 to a subsequent warmer period lasting from then until relatively recently (late 1960s?). Comparing all initial observation dates of ringed plover, turnstone, knot, dunlin and sanderling reported from the period 1892–1933 with those since 1964 (only few and partly unprecise data are available from the intervening period), it appears that the latter are 0.7/5.4 days earlier on average. In ringed plover (4.0 days), in turnstone (2.1 days), and in dunlin (5.4 days) the difference is statistically significant (Mann-Witney U-test: $p \leqslant 0.05$). The data base from the first half of the century is extremely limited, however (only 4–8 observation years before 1933), and the change should be interpreted with caution. It is possible that observers nowadays are more "field-minded" and alert than earlier observers, but similar changes have been noted in the Palearctic (see Discussion).

First observation dates from all of Northeast Greenland 1892–1979 were tested for correlation with spring temperatures in Iceland (means from Stykkishólmur May, April-May, and sum of means January to May), Ireland (Valentia May, April, April-May, and sum January to May), and the Netherlands (Utrecht de Bilt May, April-May, and sum January to May). Only the turnstone showed any significant correlation, and only with the sum of monthly means from Ireland January to May ($p < 0.05$). However, this single correlation may very well be coincidental.

Dates of first observation in Northeast Greenland since 1949 showed better correlations with records from the weather stations in the same areas (the present weather stations were not established until 1946), but only the correlation between the initial observation dates of the ringed plover and the mean temperature for May at Kap Tobin was statistically significant ($p < 0.05$) (tests for May means from Kap Tobin and sum of May means from Kap Tobin, Mestersvig, Daneborg and Danmarkshavn). Best correlations were achieved between arrival dates and records from the nearest weather station, especially with the start of "continuous daily thaw" (redifined by Meltofte (1976a) as the date after which the number of days with positive maximum temperatures exceeds the number of days with negative maximum temperatures). The start of daily thaw is most often very pronounced and often marks an influx of mild weather late in May or early June. This is probably a better measure of the arrival conditions for the waders than the May mean temperature, which is often highly influenced by periods of hard frost in the beginning of May. All species showed highest correlation with this measure, but only in ringed plover and dunlin were the correlations statistically significant ($p < 0.05$).

These correlations do not, however, reflect the decisive factors governing the annual differences in the arrival of the waders on the breeding grounds, but only suggest that the arrival of the pioneers (first stragglers) is somewhat correlated with influx of mild weather in late May near the point of arrival.

Although of interest, the date of initial appearance of the pioneers is clearly not a sound basis for an analysis of the factors influencing the annual variation in the arrival of the waders. Of relevance are data on the main immigration together with observations on mass departures from the final staging areas in northwestern Europe and Iceland.

Prater & Wilson (1972) state that knots in Morecambe Bay on the Irish Sea stayed longer than normally in the spring of 1970 and apparently had difficulty in gaining sufficient fat reserves for the flight to Iceland.

The winter of 1969–70 was very cold in northern Europe, and the effect of such conditions might perhaps be seen on the breeding grounds. Arrivals in Northeast Greenland that year, however, were not significantly delayed, although the spring was late and the waders may have dispersed later than in more favourable years. Individuals of both knots, turnstones and dunlins which had not moulted fully into breeding plumage were seen until 10 June (Meltofte 1975).

After the pioneers have appeared, a few days often elapse before the main influx takes place. In all of the breeding area this happens during the last days of May and the first days of June without significant differences between the species (Fig. 9). Flocks migrating north have been seen until about 7–10 June (Rosenberg *et al.* 1970, Meltofte 1975, 1979, Meltofte *et al.* 1981, de Korte *et al.* 1981).

At Thule (Dundas) Lorenz Ferdinand (in litt.) observed heavy migration of turnstones and knots during the period 29 May until 12 June 1964 (the first knot was seen on 26 May). Flocks mostly of 5–25 individuals (max. 32) came in from the sea at Kap Atholl and continued in a northerly (most of the knots) or an easterly (most of the turnstones) direction. The birds flew low over the sea and on reaching the coast, followed it at an altitude of 20–50 m. Most flocks were entirely or predominantly made up of one or other of the species. The main influx was observed 31 May and 1 June when at least 205 knots and 148 turnstones passed, together with 22 unidentified waders. On 12 June flocks of 25 and 5 knots headed NW-NNW.

Heavy immigration as observed at Thule in 1964 has not been reported from other sites in Greenland. At Kap Tobin (Scoresby Sund), which ought to be one of the first landfalls in East Greenland for waders arriving from Northwest Europe and Iceland, no significant wader migration was observed in 1974 (Meltofte 1976b). In Northeast and North Greenland most migrating birds were observed in small groups, and few flocks exceeded 15 individuals (Rosenberg *et al.* 1970, Meltofte 1975, 1979, Thing 1976, Meltofte *et al.* 1981, de Korte *et al.* 1981, Bosman undated, Elander & Blomqvist in print). The largest migrating flocks reported were 45 and 50 sanderlings at Danmark Havn on 1 and 3 June 1970, respectively (Meltofte 1975).

Observations from Northeast Greenland are perhaps not very representative, however, as flocks may migrate at high altitudes (especially in fine weather), and split up before descent and dispersal. The observations of a flock of 50 ringed plovers roosting in the snow at Kap Tobin during a spell of bad weather on 1 June 1974 and of a flock of 100 together with other wader species at Kap Stewart on the same day (Meltofte 1976b, de Korte *et al.* 1981), may be indicative, as at least those at Kap Tobin could hardly have been congregations of birds which had already arrived, but more likely flocks that had been interrupted by bad weather during migration. Pedersen (1926) reports a "vast" flock of dunlins at Scoresby Sund on 27 May 1925. When descending, they split up into flocks of 6–10, however. Nettleship (1974) gives a mean of 27 (range 6–60) for seven migrating flocks of knots at Lake Hazen.

Observations of (mainly Icelandic) ringed plovers and dunlins departing from Britain in May involve larger flocks. Most depart in groups of 10–150 (mean 110 for 11 dunlin flocks), while two departing flocks of sanderlings on 1 June 1979 numbered 100 each. Most leave on the incoming tide and climb rapidly to high altitudes (Ferns 1979, 1980b). Observations of the departure of knots from the Schleswig-Holstein Wadden Sea gave mean flock sizes ranging from 217 to 413 on days with heavy migration (more than 7 000 birds passing) the largest flock holding 2 300 individuals (Meltofte & Lyngs 1981). This may indicate a massive migration to Iceland, but such large flocks may soon break up into smaller flocks.

Apparently, males are usually the first birds to arrive, and may outnumber females in the early flocks (Parmelee & MacDonald 1960, Holmes 1966, Parmelee 1970, Rosenberg *et al.* 1970, Nettleship 1973, 1974, Meltofte 1979).

The majority of the ringed plovers, knots and dunlins have attained full nuptial plumage well before they arrive on the breeding grounds (cf. Prater & Wilson 1972, Ferns & Green 1979), while turnstones and sanderlings moult later, and some may complete the moult after arrival on the breeding grounds (cf. Ferns 1980b, 1981a, de Korte *et al.* 1981 and Meltofte unpublished). (See also the section on non-breeders.)

Red phalaropes start to arrive on the breeding grounds during the second week of June. Many birds arrive in pairs, but females usually predominate in the first few days (cf. Höhn 1971, Kistchinski 1975, Mayfield 1979, Ridley 1980; see, however, Myers 1981a). Some have been seen as early as about 1 June, and perhaps they spend some time (and mate) at early ice-free leads or polynyas on the outer sea coast in the same way as ducks and divers. Red phalaropes have been observed in such places in late May (Meltofte *et al.* 1981). The main influx takes place in mid-June together with ducks and divers, and when ponds and lakes start to thaw. Red-necked phalaropes arrive somewhat earlier, with most initial observations occurring in the first week of June (Elander & Blomqvist in print). Red-necked phalaropes may also appear at the ice-edge in early June (de Korte *et al.* 1981). (See also Orr *et al.* 1982.)

Pre-breeding concentration and dispersal on breeding grounds

In certain favourable areas flocks may concentrate during the first time after arrival, when congregations of 100 or more individuals have been reported for most species (Figs 9 and 10). Turnstones are among the most gregarious and ringed plovers the least, since the latter may establish feeding territories directly upon arrival (Rosenberg *et al.* 1970).

In most areas studied, the first territories are established from the first days of June, or even the last days of May. Apparently the most favourable sites are occupied early, while many birds initially have to spend some time in early snow-free and relatively food-rich areas before they can disperse following the melt. Large annual differences are observed: In late and snow-rich years (and areas), large concentrations occur and the birds may disperse as late as the second half of June, whereas dispersal occurs directly upon arrival in years of early thaw (*e.g.* Pedersen 1942, Rosenberg *et al.* 1970, Meltofte 1975, 1976a, 1979, Meltofte *et al.* 1981, de Korte *et al.* 1981).

In most areas and seasons unsettled birds are seen until mid-summer, but the situation is complicated by the presence of non-breeding individuals (see section on non-breeders), as well as breeders performing feeding flights to communal feeding areas. Early flocks probably consist largely of breeders which disperse early, while late flocks are made up mainly of non-breeders (Meltofte 1979). Apparently most breeders have dispersed by mid-June.

During the pre-breeding period, large numbers of birds may be found at sites where few or none are found breeding later, and the species composition may differ considerably from that of the breeding populations. Thus, up to 80 turnstones fed daily at Daneborg during late May and early June 1964 (Fig. 10), but none bred there, and few bred on Wollaston Forland at all (Rosenberg *et al.* 1970).

To what extent waders use such pre-breeding feeding areas for staging before further long distance migration is unknown. The only observations of flocks leaving from such areas, were one of 16 knots and one of 31 sanderlings, which departed northwards from the head of Hurry Inlet near Scoresby Sund on 1 and 2 June 1975, respectively (Bosman undated). Otherwise such flocks give the impression of waiting for the surrounding land to thaw, and thus being breeders from say within 100–200 km at the most (see Witts undated a). A few ringed plovers, turnstones and sanderlings, dyed conspicuously at my study area in Peary Land in early June 1973, left after a few days (except for a breeding ringed plover), and were not seen again (Meltofte 1976a). In contrast, at least seven turnstones of 19 dyed at Danmarkshavn Weather Station during the first half of June 1975, apparently established territories in the neighbourhood and reappeared on feeding excursions and during a period of bad weather (Meltofte 1979). These may very well have been non-breeders caught after the main migration, however, as non-breeding turnstones continued to utilize the communal feeding area at the weather station until early July (Meltofte 1979). Similarly, turnstones dyed at the weather station at Alert on northernmost Ellesmere Island in 1975 were subsequently

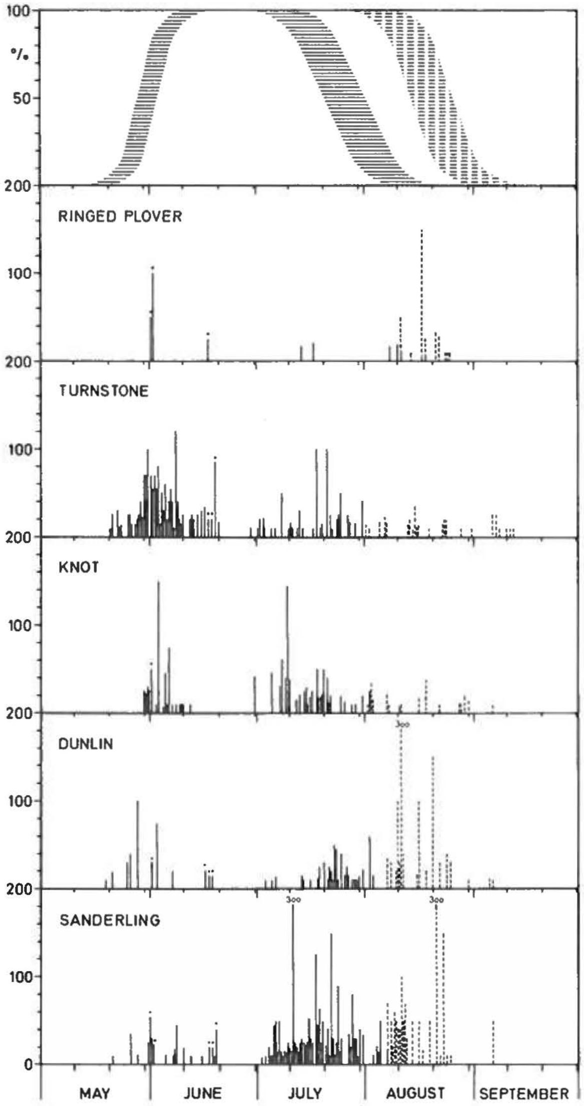

Fig. 9. Flocks or concentrations of more than 10 individuals of adults (full line) and juveniles (dashed) in Northeast Greenland and Peary Land, together with a schematic outline of the migratory seasons in all five species together (above). Concentrations during spells of inclement weather are headed with a dot. Data are taken from the literature, my own original notes, and correspondence with a number of observers. Unfortunately many authors have only stated the first, last or largest flocks, and often even without date etc. In a number of cases, the age of the birds is estimated from date, etc.; this means that the separation in early August must be taken with some caution. In the schematic outline of the im- and emigrations, the slopes of the "curves" denote schematically the spread of the migration within the species, and the width of the "curves" denote the spread between species and years.

Fig. 10. Upon arrival, flocks of waders may stay for one or two weeks to feed in certain favourable snow-free sites until they disperse as the snow melts on the breeding grounds. Here turnstones, knots and a single sanderling are seen at Daneborg in early June 1964. Photo Benny Gensbøl.

found on territories within a 10 km radius of the station (R. I. G. Morrison in litt.).

During spells of bad weather with cold wind and snow-fall, waders may again congregate in favourable areas. This is often seen at huts and weather stations until mid-summer (Fig. 9). Congregations of up to 163 individuals have been reported on such occasions (*e.g.* Manniche 1910, Meltofte 1979, de Korte *et al.* 1981), and flocks have even been observed migrating south during heavy snow-fall in early June (Meltofte *et al.* 1981). Individuals from bad-weather congregations consist of both non-breeders and breeders that have left their territories (Meltofte 1979, de Korte *et al.* 1981).

Most newly-arrived waders still carry fat reserves (Morrison 1975, Melofte 1979), but during periods of adverse weather many birds are clearly emaciated and may die. Freuchen (1921) reported 200 dead knots as well as other dead waders during the extremely unfavourable spring of 1918 in Thule, and Morrison (1975) reported large numbers of knots and turnstones died from starvation at Eureka Weather Station on Ellesmere Island during a period of bad weather in mid-June 1974.

Start of breeding and timing of egg laying

Waders may arrive in pairs or at least pair up immediately upon arrival and prior to occupation of territories (Manniche 1910, Parmelee 1970, Nettleship & Maher 1973, Meltofte 1976a, 1979, Witts undated a; see also Holmes 1966). Pairs, song display and territoriality have been observed among newly arrived birds on snow-free areas as early as the last days of May, but most often the first pairs appear and territorial and courtship display is initiated during the first week of June. In late thawing areas (and years), the main part of the breeding population does not appear until the second week of June, and territories are not occupied until mid or even late June by the latest breeding pairs (Manniche 1910, Pedersen 1926, 1930, 1942, Parmelee & MacDonald 1960, Rosenberg *et al.* 1970, Meltofte 1975, 1976a, 1979, Meltofte *et al.* 1981, de Korte *et al.* 1981, Hansen undated, Elander & Blomqvist in print). During spells of cold weather display may be completely suppressed (Meltofte 1976a).

Studies at Danmark Havn in 1975 showed that most pairs were present on territories about 5–10 days prior to initiation of egg-laying. Song display reaches a peak just prior to and during egg-laying, and decreases as incubation progresses (Meltofte 1979). Depending on the breeding schedule in different areas, song and other display in most species cease during late June and the first half of July. Song flights by ringed plovers, perhaps performed as displacement activities in response to predators or other disturbances, may be heard until late July/early August (Meltofte 1976a).

From Fig. 11 it appears that egg-laying by ringed plover, dunlin and sanderling peaks in mid-June, and that turnstones and knots lay somewhat earlier. In all species, except the phalaropes, the first eggs are laid in the first days of June. In ringed plover and sanderling the first eggs may even have been laid during the very last days of May (cf. de Korte *et al.* 1981). As these extreme first egg dates have been calculated from the age of relatively old pulli, however, they must be treated with some caution.

Besides the data included here, Smart (undated a) and Smart & O'Brien (undated) reported flying ringed plover juveniles on 12 July 1968 and 11 July 1970 in Scoresby Land. This indicates that egg-laying would have started about 23 May, which seems so unrealistic that the observations need further confirmation.

Even though replacement clutches have been partly separated, the laying dates presented in Fig. 11 are biased somewhat by unidentified replacement clutches.

Very few clutches are initiated after the first five-day period of July, *i.e.* at the time when peak hatching commences (Fig. 11). Nearly all young hatch during July, the ringed plover apparently with more late broods than the other species. As in other aspects of the breeding schedule, egg-laying in phalaropes is about two weeks later than in the other waders (Fig. 11).

To what extent the data presented in Fig. 11 are representative for the populations in general is unknown. Even though the samples are highly scattered over high arctic Greenland, there may be a tendency towards collection of more data in favourable, early snow-free areas, and thereby from earlier breeding populations (see below). Furthermore, in a number of reports only the first young *etc.* are stated, but the material probably reflects the general pattern quite well.

Within the individual samples the clutches are much more synchronized than appears from Fig. 11, where data from all of Northeast and North Greenland have been pooled (*cf.* Fig. 12). The highly synchronized laying within the wader populations in high arctic Greenland is in good agreement with the findings by Väisänen (1977), who showed that the "mean laying period" of northern populations is significantly shorter than in southern populations of the same species.

In Finland Soikkeli (1967) found that dunlins breeding for the first time arrived and nested later than the rest of the population, while Holmes (1966) found no such difference in Alaska.

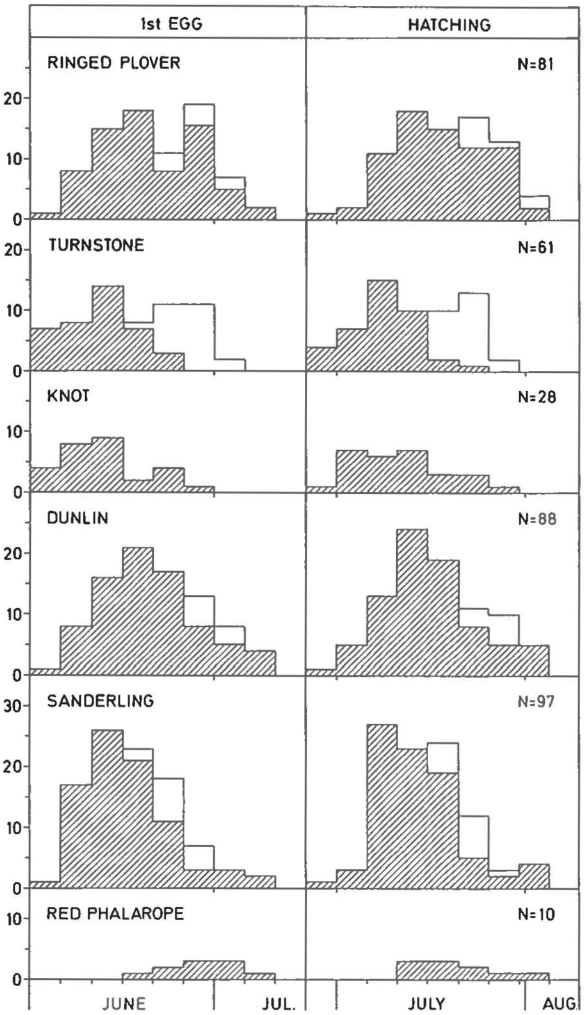

Fig. 11. The distribution in 5-days periods of 1st egg and hatching dates of waders in high arctic Greenland from the literature. Most data are from observed hatching or hatching dates calculated (or estimated) from measurements of pulli. Hatched columns denote initial clutches while open columns denote probable replacement clutches. Apart from clutches estimated by the respective authors to be replacements, I have revised a number of samples in this respect (see text).

Green *et al.* (1977) found that laying extended over a longer period in the early snow-free areas than in the late thawing areas, and attributed this to the longer time available between uncovering of the country and the ultimate last laying possibility in early July set by the minimum time needed for the young to develop before autumn migration. I think that the spread is partly caused by differing snow cover within the single areas sampled, and partly by replacement clutches. In early thawing areas, the birds are able to relay over a longer period compared to late thawing areas where breeding starts later. Apparently at least eight days are needed to pro-

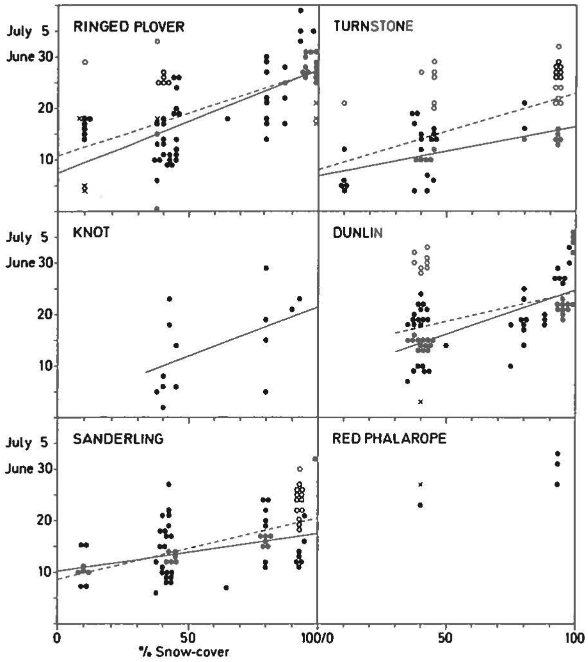

Fig. 12. First egg dates in relation to snow cover on 10 June in all sampled areas in high arctic Greenland. Dots denote initial clutches, open circles probable replacement clutches and crosses denote clutches from other years in the same area as the sample plotted. Regression lines represent initial clutches (unbroken line) and all clutches (broken line), respectively. The material does not allow for an analysis of possible non-linear relationships.

duce a new clutch after the loss of the first (Meltofte 1979), and thus clutches lost after the end of June are hardly replaced (see also Pienkowski 1984a).

The relation between laying and snow cover in the individual areas and years is presented in Fig. 12. In accordance with the conclusions of Meltofte (1976a) and Green *et al.* (1977), it appears that laying date is highly correlated with snow cover in early June. The correlation is statistically significant at the 0.1% level in all species except knot ($p < 0.05$), both with and without inclusion of the supposed replacement clutches. Even here unidentified replacement clutches bias the correlations, especially as replacement clutches may be more successful than initial ones (Meltofte *et al.* 1981), and thus more likely to be found and included in the samples. Moreover, wader populations are small or even lacking in the most snow-rich areas (see section on population densities), and samples from such areas often come from smaller, less snow covered areas within the study areas. Only ringed plovers and dunlins bred in all seven study areas with more than 70% snow cover, while *e.g.* turnstones bred only in two of these. The correlation is thus probably even more pronounced than indicated.

In none of the study areas have systematic studies been continued in successive years, so little is known about year-to-year differences in the breeding schedule in relation to *e.g.* differing snow cover. However, data from Danmark Havn in 1969, 1970 and 1975 suggest differences reflecting the differing snow cover conditions (Meltofte 1975, 1979). Snow cover on 10 June in the three years was 20, 50 and 40% respectively, and the corresponding earliest wader clutches hatched on 29 June (turnstone and dunlin), 5 July (turnstone) and 5–6 July (turnstone and dunlin), respectively. Pronounced delays were reported in the extremely late season of 1939 (Pedersen 1942).

Besides snow cover in early June, it is possible that the start of egg-laying is influenced by weather conditions during the pre-breeding period, but no data are available to test this possibility. Soikkeli (1967) found evidence for a correlation between start of egg-laying in dunlins in Finland and the increase in spring temperatures prior to laying. Start of thaw (daily positive maximum temperatures) is 2–3 weeks earlier in the south of high arctic Greenland than in the northernmost parts (Meltofte 1976a). However, as the waders do not breed earlier in the southern parts than in the northern (the contrary, in fact), this well illustrates that it is the snow cover and not the thaw itself that governs the start of breeding here (see Discussion).

The amounts of snow-fall have apparently decreased during this century in Northeast Greenland (Vibe 1967, Meltofte 1975) but, due to the lack of precise data from the first part of the century, possible changes in the onset of breeding since then cannot be established. Hatching dates from Peary Land in 1912 (Freuchen 1915) are fully as early as found later, but snow cover here is always so limited that it can hardly have any great effect on the start of breeding (*cf.* Meltofte 1976a). Early reports from more southern and snow-rich parts of Northeast Greenland, give a generally later start of egg-laying than the earliest found during the last decade of intensive studies. However, Schaanning (1933) quoted information given by trappers of clutches of 3 and 4 eggs of turnstone and knot, respectively, found at Moskusoksefjord on 1 June 1931. Moskusoksefjord is known to be very rich in snow in spring, and I do not consider these statements fully reliable (*cf.* Meltofte 1976a).

Compared to other high arctic and even low arctic breeding grounds, the waders in high arctic Greenland are among the earliest to breed (cf. Holmes 1966, Parmelee *et al.* 1967, Parmelee 1970, Nettleship 1973, 1974, Montgomerie *et al.* 1983). This is especially true of those populations breeding in the less snow-rich areas, which have provided some of the earliest breeding records in the Arctic (Meltofte 1976a). Turnstones and knots breed relatively late at Lake Hazen (more than 158 m above sea level), but as early on west-central Ellesmere Island as in the earliest areas in high arctic Greenland (*cf.* Parmelee & MacDonald 1960). Most other parts of the Arctic are much richer in snow, which is clearly the reason why waders in more southerly parts of the Arctic do not breed earlier than those in the relatively arid high arctic parts of Greenland and Ellesmere Island (*cf.* Hussell & Holroyd 1974).

Non-breeders and non-breeding years

Most individuals of at least the larger wader species under consideration do not mature and breed until they are two or three years old. Most immatures apparently summer south of the breeding areas, and many of them do not attain full nuptial plumage. In the British Isles about 15 000 knots are present in June (Prater 1981a), and in the Niedersachsen part of the Wadden Sea 32 000 have been counted in this month (Boere & Smit 1981, see also Heldt 1968).

A few hundred turnstones and knots remain in Iceland during the summer (Wilson 1981). No records of one year old knots were made during the spring migration in Iceland, and insignificant numbers of one year old turnstones were found by Morrison & Wilson (undated). During the same study only one sanderling in "winter-plumage" was observed (on 2 June). Branson *et al.* (1979) state that most one year old turnstones do not migrate to the breeding grounds, while Clapham (1979) found that some (possibly Scandinavian) moult into breeding plumage and gain nearly as much weight during May as adults, and presumable migrate to the breeding grounds. Ferns (1980b) states that one year old (Palearctic) sanderlings moult and migrate later to the breeding grounds than the adults. In West Greenland summering ringed plovers with undeveloped gonads have been recorded by Salomonsen (1967).

Few individuals in partial nuptial plumage have been reported from the breeding grounds, but several observations of incompletely moulted birds in late May and early June (Meltofte 1975, 1979, and unpublished, de Korte *et al.* 1981) may have involved immatures. 15 turnstones caught at Danmarkshavn Weather Station between 8 and 22 June 1975 had no or poorly developed brood patches. They weighed on average about 10% less than those adults which had arrived earlier, and were most likely non-breeders (Meltofte 1979). Some individuals collected from post-breeding flocks (see below) at Scoresby Sund during July were non-breeders (de Korte *et al.* 1981). Hence, immature non-breeders apparently make up a minor, but still significant, proportion of the populations. They arrive probably a little later than the breeders and often gather at favourable feeding places until mid-June. Most likely they all disperse and occupy marginal territories (and pair?) during the second half of June at least (Meltofte 1976a, 1979). At Danmark Havn non-breeding turnstones continued to visit the communal feeding areas until early July when hatching commenced and territories started to break down. At this time they probably joined the post-breeding flocks (Meltofte 1979) (see next section).

According to Holmes (1966) and Soikkeli (1967, 1970a), one year old dunlins in both Alaska and Finland may migrate to the nesting grounds and breed, although the proportion of one year old birds in the breeding population differs markedly between the two places, and also between years. Summering flocks of dunlins are well known at lower latitudes in the Old World (*cf.* Boere & Smit 1981, Prater 1981a); *e.g.* 10 000 individuals on the Banc d'Arguin in Mauritania and similar numbers in the Wadden Sea and in the British Isles. It is likely that most of the non-breeding ringed plovers, dunlins and sanderlings which occur in high arctic Greenland are one year old individuals, while most of the immature turnstones and knots are two year old, but this needs further confirmation.

Non-breeding years have only been reported a few times from high arctic Greenland. None of the reports, however, are fully reliable. Bird & Bird (1940) state that 1938 was a non-breeding year for the waders in central Northeast Greenland, but give details of breeding waders at the same time (Bird & Bird 1941, Meltofte 1976a). Freuchen (1921) states that 1918 was a non-breeding year for the waders at Thule. Many died during extremely bad weather in spring, but no details are given about the extent of non-breeding. Late thaw or severe weather may locally prevent waders from breeding in certain years (*cf.* Mayfield 1983), but until now large scale non-breeding has not been documented (see also review by Ferns 1978a). In accordance with this, Bertram *et al.* (1934) concluded that waders are largely unaffected during non-breeding years of other species.

Local non-breeding may take place primarily in marginal, snow-rich areas, and could contribute to whatever population regulation may take place on the breeding grounds (see Discussion). Marginal habitats may be occupied principally by younger individuals, and the variable conditions in such areas may affect the extent to which young age-classes are able to breed.

Post-breeding gatherings and departure of adults

The first small flocks of post-breeders appear during the very last days of June (Fig. 9). In contrast to the often looser flocks observed during the pre-breeding period, post-breeding flocks are easily recognizable by their strong flocking behaviour, which already very much resembles the behaviour seen on the autumn staging areas. The birds appear very often in mixed flocks with several wader species, and roam around at the most favourable feeding sites such as lake and pond margins, marshy areas, and lagoons (Fig. 13) (Manniche 1910, Meltofte 1975, 1976a, 1979, Meltofte *et al.* 1981, de Korte *et al.* 1981).

Numbers increase during early July, and in the northernmost areas peak during the first half of the month (Meltofte 1976a). In the southern half of Northeast

Fig. 13. Pond margins and marshes play an important role as feeding sites, especially in July when peak emergence of flying Diptera takes place. Adults bring their young to such places soon after hatching, and at the same time flocks of post-breeders gather here to feed intensively before their departure during the second half of July and early August. Turnstone on southern Hochstetter Forland, July 1976. Photo Magnus Elander.

Greenland, numbers peak during the second half of July, and rapidly decrease during the last week of the month and the first few days of August (Meltofte *et al.* 1981, de Korte *et al.* 1981) (Fig. 9). At least in the northernmost areas, the peak occurrence of post-breeding flocks is strongly correlated with the peak emergence of adult Diptera (Meltofte 1976a; see also Nettleship 1973, 1974), while in the southernmost areas the appearance of invertebrate food is more level during July and August (Green *et al.* 1977). In addition, the breeding cycle is generally later in the southern areas than further north (see Discussion).

During the first part of this period especially, some of the birds in the flocks appear to be in pairs, and flight pursuits, song and other courtship behaviour may occur (Meltofte 1976a, 1979). Colour-marked and collected individuals from these flocks show that they include both non-breeders and failed breeders, which have left the territories. From around the middle of July individuals which have left the care of the young to their mates join the flocks, and occasionally "off-duty" breeders may join in feeding excursions away from their eggs or young (Manniche 1910, Pienkowski & Green 1976, de Korte *et al.* 1981). In turnstones and dunlins it is the female which leaves early (Holmes 1966, Soikkeli 1967, Nettleship 1973, Meltofte 1976a), while this is not clear in knot and sanderling (*cf.* Parmelee & MacDonald 1960, Parmelee 1970).

Holmes (1966) found that the occurrence and composition of flocks of dunlins early in the season in Alaska reflected the breeding success. In unsuccessful years, early flocks comprised both sexes, while in successful years flocks appeared later comprising mainly females in the beginning and males later on. Immature non-breeders apparently do not occur in this species in Alaska, however.

The appearance of the first post-breeding flocks coincides with the hatching of the first young. In accordance with the fact that very few (replacement) clutches are initiated after the first days of July, it appears that failed breeders, together with non-breeders, leave their territories if their clutches are lost after late June. At this

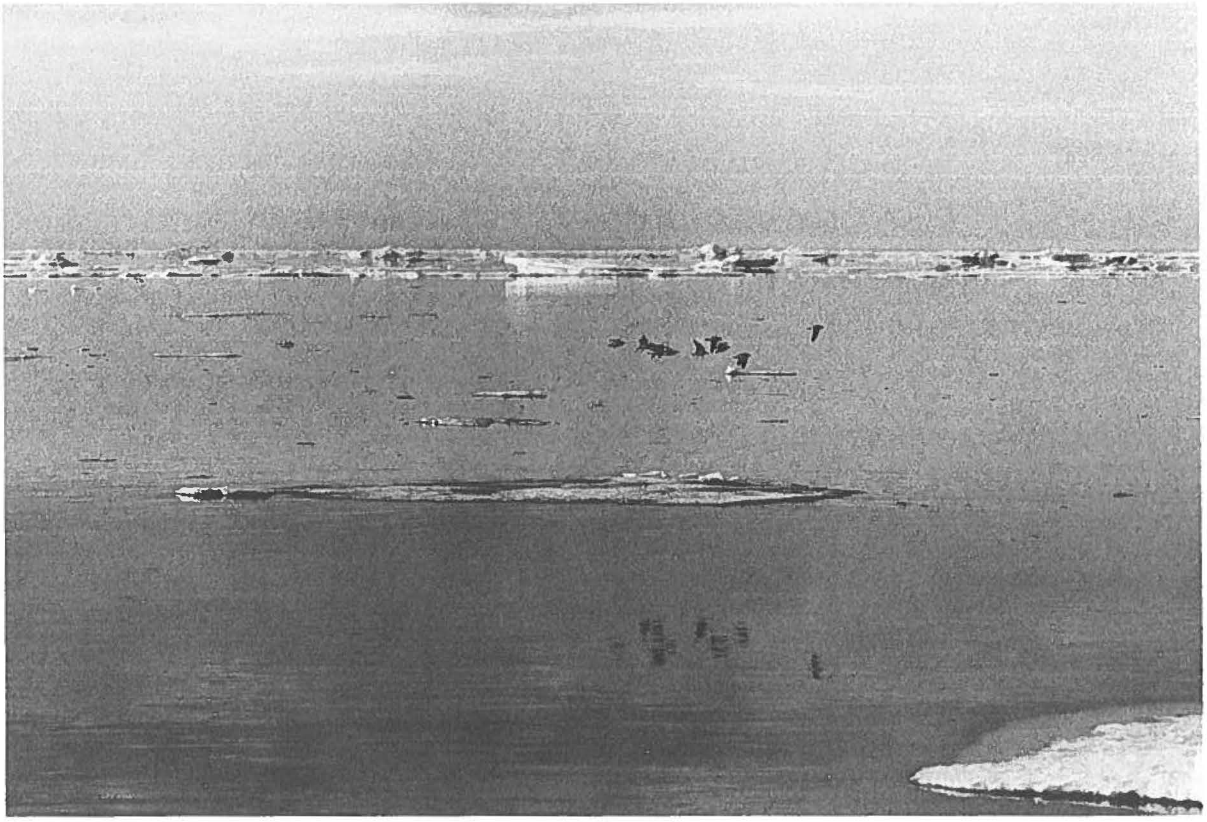

Fig. 14. During early August, when the majority of the adults have left, most juveniles leave the tundra and gather into small flocks along the coasts, which have become ice-free at this time. Juvenile turnstones in Young Sund, 4 August 1978. Photo Magnus Elander.

time the first young hatch, the territories start to break down, and it would anyway be too late to breed successfully (Meltofte 1976a).

In the northernmost areas, post-breeding flocks normally do not exceed 20 individuals. They leave during mid-July when migrating flocks are also seen heading east and south (Meltofte 1976a, C. Hjort in litt.). Further south, mixed species flocks of more than 100 individuals have been encountered from around 10 July (Fig. 9), although most number less than 20 individuals. Already at this time flocks show strong migratory restlessness (Meltofte *et al.* 1981, Elander & Blomqvist in print). Ringed plovers are less gregarious and only small groups are seen.

It is possible that flocks departing early from northerly areas move first to more southern parts of Northeast Greenland, where large favourable feeding areas in deltas and late thawing marshes are available at this time (*cf.* Myers & Pitelka 1980b).

During the last week of July and the first days of August there is an extremely rapid decline in the number of both post-breeders and breeders. By the end of July the great majority of adults attending young leave, apparently more or less directly from the breeding grounds. Only a few late breeders are seen attending young until about 10 August, but single adults may be seen even until early September (Meltofte 1975). In accordance with their breeding schedules turnstones and knots seem to leave a little earlier than the other species. Ringed plovers generally leave latest, both mates normally attending the young until after fledging; the latest adults reported were seen on 27 August, two weeks after fledging of the young (de Korte *et al.* 1981).

Female red phalaropes may gather into small groups and leave by mid-July. The males follow during the second half of July, the last being seen by mid-August (Meltofte *et al.* 1981). Two red phalaropes were recorded in the pack-ice off Scoresby Sund on 28 July 1933 (Bertram *et al.* 1934) (see also Orr *et al.* 1982, Schiemann 1983).

Ferns (1978c) showed that more than 70% of the Northeast Greenland waders (except in dunlins) initiated post-nuptial body moult from about mid-July, and that the start was to some extent related to the breeding schedules between different species and areas. Most adults leave before more extensive moults into winter plumage is conspicuous, but a few late adults showed heavy body moult (Petersen 1908, Meltofte 1976a, Plantema 1983). Red phalaropes regularly show heavy body moult before the departure (Pedersen 1942, Bengtson 1968, Meltofte *et al.* 1981 and unpublished). However, an extremely late female was still in full nuptial plumage on the sea at Danmark Havn on 29 August 1907 (Manniche 1910).

Pre-migratory weight gain was recorded in two adult ringed plovers at Mestersvig on 17 and 21 August 1972, respectively (Green & Williams undated). They weighed about 17 and 25% more than the mean weight of breeders.

Post-fledging movements and departure of juveniles

The first independent juveniles are seen in the last days of July in most areas, the earliest reported being a knot on 24 July 1969 at Danmark Havn (Meltofte 1975). During the first week of August, when the majority of the adults have left, most juveniles leave the tundra and concentrate along the coasts (Fig. 14). By early August the ice disappears from the beaches and large mixed flocks occur at river outlets and deltas especially at low tide. Numbers increase during the first half of August, and peak about the middle of the month (Fig. 9). During the last week of August, numbers rapidly decline and, in most areas and years, the last juveniles are seen around 1 September. Occasionally flocks have been seen in September, and late individuals may be seen until late in the month (Tcherniakofsky 1939, Petersen 1941, Meltofte 1975). Juvenile red phalaropes have been seen swimming among ice floes on the fjords until late September (Pedersen 1930, Meltofte 1975). Relatively few observations are available after mid-August since most observers have left the country by that time.

The phenology of the juvenile migration may be related to some extent to the timing of breeding in different areas and years, and to the onset of winter in different years (*cf.* Meltofte 1975). In most of high arctic Greenland, continuous frost starts in early September, so that juvenile waders leave the country when feeding conditions deteriorate.

Autumn migration

The first flocks of waders migrating southwards have been observed in the first days of July, and intensive southward migration has been reported as early as around 10 July (Meltofte *et al.* 1981). From mid-July until the first week of August, many migrating flocks of adults have been seen (Meltofte 1975, 1976a, Hjort 1976 and in litt., Ferns 1978a, Meltofte *et al.* 1981, Bosman undated, Campbell undated, Witts undated b). Flocks numbered from a few up to 40 individuals; most, however, comprising less than 10, and sometimes containing two or three species together (Hjort 1976).

Many flocks have been seen flying along the fjords and the outer coasts. However, no concentrated migration has been recorded at the southeasternmost point of Northeast Greenland, at Kap Tobin (Meltofte 1976b). Flocks flying along the coasts or over the fjords, fly low, some even just over the water surface (Meltofte 1975). Most observations involve small groups, and it is possible that larger flocks leave at high altitudes, directly southeastwards over the sea. This was suggested by the behaviour of three flocks totalling 300 sanderlings on 11 July 1976. Several times they circled up to an altitude of some hundred metres, before they broke up into smaller flocks and alighted again (Meltofte *et al.* 1981).

Migrating flocks have been reported at all hours of the day, but from early August "nights" start to get darker, and a night maximum is seen, with most "take-offs" at about 18–21 h. local time (Meltofte 1975, Hjort 1976).

The migration route of the populations from west of the migratory divide in North Greenland, *i.e.* the populations from around Thule and Ellesmere Island, is little known. It is most likely that they follow the same way back over the inland ice from central West Greenland to Southeast Greenland as during the spring migration (Salomonsen 1967; see also Morrison 1975, 1977).

From the arctic breeding grounds the migrants head more or less directly towards northwestern Europe, with only part of the populations staging in Iceland. Adults appear in Iceland around mid-July and the great majority have left by mid-August (Morrison 1977, Wilson 1981). Numbers of adult knots peak at the end of July, and during their stay in Iceland they accumulate about 30% fat for the onward migration (Morrison 1977). Turnstone flocks usually do not exceed 100 birds, while flocks of up to 5000 knots have been reported (Wilson 1981, Emms & Elston undated). As in spring, especially turnstones and knots utilize the staging possibilities in Iceland. This is probably due to the large distances covered by large parts of the populations to and from northwestern Greenland and the northernmost Canadian isles, including the passage of the Greenland ice cap.

On Jan Mayen, numbers of ringed plovers, turnstones, dunlins and sanderlings are seen both during spring and autumn migration, while this apparently does not apply to the knot (Schaanning 1933).

Apparently most of the birds head for the British Isles and perhaps France, although some fly directly to the Wadden Sea. In the knot, the latter even applies to half of the population. Significant numbers of ringed plovers, turnstones, knots, and sanderlings pass southwestern Norway and the west coast of Denmark (Fig. 15) (Ferdinand 1953, Nørrevang 1959, Grimeland 1967, Netterstrøm 1970, Prater 1974a, 1981a, Morrison 1977,

Fig. 15. Significant numbers of Nearctic ringed plovers, turnstones, knots and sanderlings pass southwestern Norway and the west coast of Denmark during autumn migration. Here a flock of adult sanderlings is seen during a stop-over at Blåvandshuk, the westernmost point of Denmark, 8 August 1965. Photo Arthur Christiansen.

Meltofte & Rabøl 1977, Andreassen & Råd 1977, Drenckhahn 1979, Smit & Wolff 1981). With westerly or southwesterly winds knots and sanderlings may be seen as far north as central Norway (Folkestad 1975).

The only site where the migration has been recorded systematically is at Blåvandshuk on the west coast of Denmark (Meltofte *et al.* 1972, Meltofte & Rabøl 1977). In accordance with observations of departure from the breeding grounds, the first significant migration at Blåvandshuk starts immediately after 10 July in turnstone, knot, and sanderling, while ringed plovers appear after the middle of the month. The main adult migration passes very distinctly during the last ten days of July and the first ten days of August, again with turnstone and knot peaking earliest. Mean size of migrating flocks of knots at Blåvandshuk is about 8 with about 100 as the largest observed (Netterstrøm 1970). The phenology of the wader migration at Blåvandshuk must, however, be interpreted with some caution regarding the Nearctic populations, since Palearctic populations are also involved (Meltofte & Rabøl 1977). The first turnstones reach Britain in mid-July (Branson *et al.* 1978), while adult "northwestern" ringed plovers apparently do not arrive at the south coast of England until the second half of August (Insley & Young 1981).

Soon after arrival in the Wadden Sea and the British Isles, turnstones and knots undergo post-nuptial moult, which lasts until late October. After the moult, most knots leave the Wadden Sea and move to the British Isles and other West European wintering sites (Boere 1976, Branson *et al.* 1978, 1979, Clapham 1979, Smit & Wolff 1981). Most Nearctic ringed plovers, dunlins and sanderlings stage only briefly in western Europe to replenish their fat reserves for onward migration to wintering sites in West Africa and further south (Fig. 16). They do not moult until they arrive on the wintering grounds (Pienkowski & Dick 1975, Pienkowski *et al.* 1976, 1979, Boere 1976, Eades & Okill 1976, Clapham 1978, Insley & Young 1981). It is possible, however, that a few dunlins and sanderlings stay in Europe during the winter (Prater & Davies 1978 and ringing recoveries mentioned below).

The migration patterns of juveniles are similar. Flocks migrating southwards have been seen in Northeast Greenland from early August (Hjort 1976, Ferns 1978a). Flocks number from a few to about 20 individu-

Fig. 16. The majority of the Old World wintering Nearctic ringed plovers, dunlins and sanderlings winter in West Africa, where Banc d'Arguin in Mauritania is one of the most important wintering sites. Here ringed plovers, dunlins and sanderlings are roosting together with little stints *Calidris minuta* and curlew sandpipers *Calidris ferruginea* at high tide in Banc d'Arguin, January 1980. Photo Berry Stokvis.

als. On 10 and 12 August 1975, a flock of 70 sanderlings flew around at Hurry Inlet for some time, whereupon it broke up into groups of about 20 which left the fjord towards the southeast (Bosman undated).

In contrast to adults, many juveniles are seen further south in both West and East Greenland in autumn (*cf.* Salomonsen 1967). This cannot, however, be attributed to differing migratory pathways, but merely to greater dispersal during the juvenile migration, as is well known in most wader species. The juvenile migration is most pronounced in Greenland during mid and late August (Kolthoff 1903, Hylbom 1951, Johnsen 1953, Håkansson *et al.* 1981, Meltofte *et al.* 1981, Bosman undated, C. Hjort in litt.), and the birds reach western Europe at about the same time (*e.g.* Netterstrøm 1970, Insley & Young 1981).

In Iceland, juvenile Nearctic waders occur from mid-August until mid or late September and numbers peak during late August and early September (Glue 1972, Wilson 1981). On weather ships in the North Atlantic, the migration of juvenile turnstones peaks also in the second half of August: autumn migration (of juveniles) also appears to be more dispersed than the spring migration (Luttik & Wattel 1979). At Blåvandshuk, juvenile knots make up 37% of the total visible autumn migration of the species (Netterstrøm 1970). In autumn juvenile turnstones make up about 15% of the population at the Wash (Branson *et al.* 1978). There is some evidence that some waders may winter farther south during their first year than do adults (*e.g.* Branson *et al.* 1978, Prater 1980, Engelmoer *et al.* 1984).

The migratory patterns of Nearctic knots are well documented by ringing results. The two populations, one of which stages in the Wadden Sea during both spring and autumn, and the other which stays in the British Isles during all of the non-breeding season, are partly separated during the rest of the year as well (Prater 1980). The "Wadden Sea birds" keep east of the other part of the population during most of the year. The two groups may to some extent be made up of Northeast Greenland and Thule area/Ellesmere Island birds, respectively, and thus be related to the two distinct migratory pathways east and west of the Greenland ice cap, as suggested by Morrison (1977). However, as several knots ringed in Norway and the Netherlands have been recovered at Thule and *vice versa,* this separation may only be weak.

Ringing recoveries of the other species are less numerous. Nearctic turnstones have been recovered south as far as Mauritania, but the great majority is found in northwestern Europe during winter, especially in the British Isles (Salomonsen 1967, Branson *et al.* 1978). Records of ringed plovers, dunlins and sanderlings ringed or dyed in Northeast Greenland (Meltofte 1976a, Green 1978c, Green & Williams undated, and the Zoological Museum, Copenhagen) support the general statements. Six adult ringed plovers have been recorded in Britain during the period 18 August to 3 September, three juveniles in Norway, Britain and France during the period 31 August until 25 September, and 11 unaged birds in Britain between 16 August and 12 September. One ringed plover was found in Senegal on 22 October. Three adult dunlins were recorded in Britain on 29 July, 26 and 29 August respectively, and one on 24 August in France and again two years later on 9 August in Portugal. Three juveniles (plus one unaged) were recovered in Britain and France during the period 24 August to 15 September. Very recently a juvenile dunlin was recovered on 20 November in France. An adult dunlin was recovered on 24 April in Morocco, as the first from Africa. However, one adult identified by size as *arctica,* was ringed in England on 17 August and caught in Morocco 13 days later (Pienkowski & Dick 1975). One adult sanderling was recovered on 1 August in France, two juveniles on 2 and 7 September in Norway and France respectively, and 13 unaged birds during the period 1 August to 13 September from Norway and Britain. However, one sanderling ringed in Iceland was recorded in Britain on 23 November, indicating possible wintering there (Prater & Davies 1978). The only other record from Europe in winter of a Greenland marked bird is a juvenile dunlin from France in February, also indicating wintering, but the date is not fully reliable.

Samples of measurements on fresh specimens of high arctic Greenland waders are given by Møhl-Hansen (1949), Meltofte (1976a, 1979), Green (1978d), de Korte *et al.* (1981), and Hansen (undated).

Discussion

Annual cycle

The summer schedule of waders in high arctic Greenland is constrained by the start of thaw in late May, the emergence of midges in early July, and the start of winter in early September. The waders stay at temporate latitudes as long as possible before they leave for the breeding grounds, and they leave again as soon after breeding as possible to be able to complete the postnuptial moult at southern latitudes as early in the season as possible. Young of the year need as long as possible between fledging and the onset of winter in the Arctic for development and to build up sufficiently large fat reserves for the very demanding autumn migration. The margins seem quite narrow, an impression which is further supported by the considerable phenological synchrony between the species.

The Northeast Greenland populations stay in northwestern Europe for a rapid fattening and completion of pre-nuptial body moult during April and May, while the Thule/Ellesmere Island populations especially, utilize southwestern Iceland as a final surplus fattening post before their even longer passage over the Greenland ice cap to the breeding grounds (Wilson 1981).

Feeding on annelid and arthropod prey in May is clearly much better in western Europe than further north, and the smaller wader species apparently most often cover the distance across the North Atlantic in one step to the breeding grounds in high arctic Greenland. The reason why half of the Nearctic population of knots moves from the British Isles to the Wadden Sea, nearly 1 000 km in the opposite direction or at least transversely to their final goal, remains obscure. Is it possible that the food resources on the wintering grounds are so much depleted during winter, that they cannot provide sufficient food for spring pre-migratory fattening for the whole population? P. J. Dugan (cited in Pienkowski & Evans 1984) points out that spring temperatures on the continental side of the North Sea tend to be higher than further west. This may make prey more available to waders in these areas. But what about the same phenomenon in autumn, then? (see also Boere 1976).

Apparently the departure from northwestern Europe and Iceland is little influenced by annual differences in spring temperature *etc.*, but is adapted to the average start of acceptable living and breeding conditions in the High Arctic (*cf.* Holmes 1966). The waders arrive at about the time when thaw starts in most areas, and only a few days before egg-laying begins in the most favourable areas. The start of thaw (more or less daily positive maximum temperatures), however, varies 2–3 weeks from place to place (and from year to year) generally beginning earliest in the southernmost and innermost parts of the country and latest to the north and at the outer coasts (Meltofte 1976a). Yet the arrival of waders is little related to these differences, the main influx lasting less than one week and appearing nearly at the same time all over the range, and with little variation from year to year.

Even though regular positive daily maximum temperatures most often start in late May or early June, the weather remains cold and unstable during the first three or four weeks after arrival. Not until about mid-summer does proper thaw start and living conditions become more favourable for the waders (*cf.* Meltofte 1975, 1979).

Alerstam & Högstedt (1980) argued that the advancement of spring in the Arctic is more regular and predictable than in the temperate regions. This should explain why Arctic wader populations often winter farther south than temperate populations (and thus explains the so-called leap-frog migration). In contrast to temperate populations, they have no advantage in staying close to their breeding grounds to be able to occupy them as soon as sufficiently favourable conditions appear. However, this is not fully in agreement with conditions in high arctic Greenland. Firstly, the advancement of spring is far from predictable (see also Slagsvold 1982). Secondly, high arctic Greenland waders (like those from Iceland) winter both in the "northern" (western Europe) and "southern" (West Africa) main Old World wader wintering areas. However, as also pointed out by Alerstam & Högstedt (1980), the progress of spring in the Arctic cannot be detected by birds staying outside the Arctic zone during spring, and the regularity of their arrival from year to year in the high arctic breeding grounds in Greenland is more likely explained by the fact that the birds have to cross a considerable stretch of open sea, and thus have to "take the chance" every year at the time when conditions on average are acceptable (see further below). Recently, the hypothesis by Alerstam & Högstedt (1980) was seriously qustioned by Pienkowski *et al.* (1985).

Apparently, waders arrive a few days earlier now than at the beginning of the century. Similar earlier spring migration has been recorded in lapwing *Vanellus vanellus,* black-tailed godwit *Limosa limosa* and a number of other early migrants in Sweden (Lundberg & Edholm 1982, Gustavsson undated), together with bar-tailed godwit *Limosa lapponica* and a number of breeding waders in Denmark (Meltofte unpubl.). These changes may be related to the general amelioration of the climate in northern latitudes during this century, and in high arctic Greenland, perhaps to lesser snow cover in spring and thereby earlier appearance of acceptable feeding and breeding conditions (Vibe 1967, 1984, Meltofte 1975). This change may also include an earlier start to breeding, as found in the ringed plover in northwestern Europe during the last one hundred years (Väisänen 1969).

Competition for the earliest snow-free breeding habitats is probably intense. Waders commence breeding in such areas a few days after arrival and some 1–2 weeks ahead of the latest breeding populations. The earliest breeders hatch young when flying Diptera start to appear, and available food on the tundra soon increases manifold. This means that the adults can leave earlier (*cf.* Hildén 1961) and that the young are growing in July when food is plentiful (Holmes 1966, Nettleship 1973, 1974) and have maximum time for development and pre-migratory fattening. The advantages of early breeding may to some extent be counteracted by higher nest losses owing to predation (see below), periods of inclement weather with snow, heavy wind and cold, and flooding. Waders are, however, to some extent able to cope with quite harsh weather conditions and floods (Owen 1927, Lind 1961, Bengtson 1963, Spjøtvoll 1972, Ojanen 1979, Hildén 1979, Meltofte 1979).

The strong relation between start of egg-laying and snow cover on the breeding grounds probably has several reasons. The simple inability of the birds to nest in completely snow covered areas is obvious, and may actually be an ultimate factor in many snow-rich areas (*cf.* Green *et al.* 1977): large areas do not harbour wader populations at all owing to extensive and late thawing snow cover.

Feeding conditions prior to and during egg-laying may be important, as egg-laying is a nutritionally demanding task (*cf.* Perrins 1970), and feeding conditions in early June are very limited in the High Arctic. Dunlins in newly arrived pre-breeding flocks at Myggbukta in early June were found to feed for 91.7% of 24 hours (Elander & Blomqvist in print), and waders have been found to feed on vegetable matter at this time (*e.g.* Manniche 1910, Johnsen 1953, Nettleship 1973, 1974, Witts undated b). A direct correlation between food availability and the duration of the pre-laying period has been found in the lapwing in southern Scandinavia (Högstedt 1974; see also Miller 1983 for further evidence). That feeding conditions in the latest thawing areas are unfavourable is indicated by the fact that such areas are occupied up to at least two weeks later by birds which have spent the intermediate period in more favourable areas. This problem could partly be solved by the birds undertaking feeding excursions to more favourable feeding areas, which, in fact, many waders do after settling in perhaps less favourable areas (*e.g.* Meltofte 1979, de Korte *et al.* 1981, Pienkowski 1984a). It would appear to be advantageous, however, to be able to stay (and defend) the territory from the very beginning (*cf.* Pitelka *et al.* 1974: 194).

Nest predation is clearly a very important factor for ground-nesting birds. Many such species solve the problem more or less effectively by breeding on inaccessible cliffs or islets without mammalian predators (*cf.* Larson 1960, Meltofte 1978). To waders nesting on mainland tundra, often with many highly effective arctic foxes *Alopex lagopus,* the problem must exert high selective pressure. Waders (and other ground-nesters) have evolved a variety of sophisticated adaptations to avoid predation, ranging from spacing of nests, concealed situation of the nest (or just a scrape) and camouflaging egg colouration, through crouching on the nest (including camouflage-colouration of the incubation bird) to a great variety of distraction displays and tactics against predators (*e.g.*Tinbergen *et al.* 1967, Meltofte 1977b). Aggressive tactics may have some effect against avian predators (*e.g.* Göransson *et al.* 1975, Dyrcz *et al.* 1981), but less so against mammalian predators.

Meltofte *et al.* (1981) found that waders and other ground nesting species suffered heavy nest losses early in the season on the snow-rich Hochstetter Forland in 1976, a year with many foxes. The success of later (relaid) clutches was significantly higher, and it was concluded that the extent of snow cover is a decisive factor in determining nest-predation by foxes. When the snow cover is extensive, foxes only have to search the narrow

Fig. 17. Although most wader young hatch and grow up in July, when food normally appears to be super-abundant on the tundra, the timing of breeding seems to be more directly governed by the progress of snow melt at the time of egg-laying. Sanderling with young, southern Jameson Land, 13 July 1974. Photo Ko de Korte.

snow-free patches to find nests. Similarly, experimental studies by Byrkjedal (1980) in the Norwegian mountains indicated that extensive snow cover highly increased the predation rate, in this case by ravens *Corvus corax* and red foxes *Vulpes vulpes*. Byrkjedal concluded that predation is a decisive factor in the relation between start of egg-laying and snow cover (see also Pienkowski 1984a).

The higher hatching success of late clutches found on Hochstetter Forland (Meltofte *et al.* 1981) does not prove that the ultimate success of late breeders was higher, but provides evidence for selection pressure against breeding too early in snow-rich areas. Replacement clutches may be smaller (Meltofte *et al.* 1981) and the delay in schedule and shorter time available for development of late-hatched young may limit their chances of survival both on the breeding grounds owing to decreased availability of food and adverse weather during late July and August, and perhaps especially during the autumn migration across the North Atlantic.

The *variation* in timing of breeding in high arctic Greenland does not appear to be directly related to food for the young. Even though peak emergence of flying Diptera may vary from late June or the beginning of July in the earliest thawing areas (Meltofte 1976a, Elander & Blomqvist in print) to after the middle of July at the latest (Meltofte *et al.* 1981), flying Diptera were present from around 1 July in all areas studied, and are everywhere plentiful by the second five-day period of the month (Meltofte 1976a, 1979, Meltofte *et al.* 1981, de Korte *et al.* 1981, Kempf in litt.; see also Soikkeli 1967).

The timing of breeding in high arctic Greenland is apparently balanced between the availability of snow-free nesting ground, feeding conditions at egg-laying, increased predation risk at early breeding in snow-rich areas, optimal time for development for the young, and the advantages of early departure of adults (see below) (Fig. 17). The importance of the individual factors may vary from place to place and from year to year.

Apparently "all" breeders are prepared to breed soon after arrival (*cf.* Byrkjedal 1978), and in most of the species found in high arctic Greenland, most individuals probably show high site tenacity (see Soikkeli 1970b, Pienkowski 1984b, and also Holmes 1966, Meltofte 1975, and Green 1978c for recoveries). Competition for optimal territories within each area is probably intense, however, and apparently it is advantageous for all of the population to arrive early in order to compete for the best sites, instead of delaying the spring migration in relation to the later thaw in some areas (*cf.* Meltofte 1983 for the snow bunting *Plectrophenax nivalis*). The flexibility of the pre-laying period is then necessary to make it possible to adjust onset of breeding to the varying local and annual conditions (*cf.* Meltofte 1976a).

If the clutch is lost after the end of June, no further breeding attempts are normally made. Time available for development of the young would probably be too short at later attempts (*cf.* Green *et al.* 1977) (juvenile knots arriving in the Dutch Wadden Sea in August are 10–25 g lighter than adults arriving in July, M. Engelmoer in litt.), and perhaps the resulting delay in departure of the adults could also be critical to them. Failed breeders leave their territories and join post-breeding flocks together with non-breeders, which gather in flocks at the same time at favourable feeding sites on the tundra. Feeding conditions on the tundra appear to be optimal at this time, and after a short premigratory fattening period, they start to leave for western Europe. Successful breeders follow shortly after fledging of the young, one of the adults often leaving the mate to care for the young during the fledging period.

In contrast to more southern sites, the littoral zone in high arctic Greenland offers very little or no feeding possibilities in July (*versus* Connors *et al.* 1979 for Alaska), and apparently it is advantageous for the adults to leave as soon as possible for the West European estuaries. Competition for food between adults and young seem unlikely to occur on the tundra in July, when food often appears to be super-abundant (*cf.* Pienkowski 1983). The break-down of territoriality after hatching may also indicate that availability of food for the young is not an important problem: many families gather at favourable feeding sites or wander over the tundra. Later in July and in early August, food decreases in most areas (Nettleship 1973, 1974, Meltofte 1976a, 1979, Meltofte *et al.* 1981, *versus* Green *et al.* 1977). This decrease, together with insufficient quality of the food for adults (*cf.* Pitelka 1959, Holmes 1966), may contribute to the early departure, but more likely the indirect effect on the moult is more important. The limited time available and insufficient food resources later in the season do not generally allow high arctic waders to moult on the breeding grounds (see discussion in Soikkeli 1967 and Holmes 1971b), and the populations discussed here do not initiate primary moult until close to the wintering areas (see also Miller 1983).

At Point Barrow in Alaska MacLean & Pitelka (1971) found that late summer climate (temperatures and rainfall in late July and August) varied markedly from year to year. Due to the consequent unreliable invertebrate food resources at this time (Myers & Pitelka 1979), this might be an ultimate cause of the evolution of early departure of the adults in most of the wader species breeding there, *i.e.* prior to moult (Holmes 1971b). This cannot be the case in Greenland, as August actually showed the lowest standard deviation of monthly mean temperatures of the three summer months; all of them being less than ±1°C (data from 32 years at Danmarkshavn Weather Station).

In northwestern Europe, benthic invertebrate food peaks during July-August (June-September) and rapidly decreases during autumn (Beukema 1974, Drenckhahn 1980), in some areas perhaps partly due to heavy predation by staging waders (*cf.* Schneider & Harrington 1981, Hicklin 1983). Pienkowski *et al.* (1976) point out that earlier in the season not only do food resources peak (and are more available), but also the days are longer and temperatures higher than later in the season. During moult, waders require undisturbed favourable feeding areas, their flying capacity is hampered during replacement of primary feathers, and birds wintering in northwestern Europe must complete the moult before the need for winter fattening starts in early November (*cf.* Boere 1976). Pienkowski et al. (1976) conclude that it is also advantageous for waders to spread the moult over as long a period as possible. All these factors support the conclusion that the sooner the waders of high arctic Greenland can leave the breeding grounds without reducing their breeding success the better (see also discussion by Johnson & Minton 1980, Myers 1981b, Prater 1981c, and Greenwood 1983).

Juvenile waders leave the tundra soon after independence, and start feeding in the littoral zone from early August, probably as a result of better feeding conditions here than on the tundra in August. In the northernmost areas, however, virtually no invertebrate life exists in the littoral zone, and the young waders stay on coastal tundra and chiefly feed on vegetable material (Johnsen 1953, Meltofte 1976a).

Immatures summering south of the breeding grounds benefit from the abundance of food during the summer bloom without suffering competition from adults of higher competitive ability. They enjoy reduced mortality compared with birds migrating to the north (Morrison 1983), and they are able to moult from mid-summer when conditions are optimal (Boere 1976, Pienkowski *et al.* 1976, Branson *et al.* 1979).

The advantage to sub-adults in migrating to the breeding grounds as prospectors, may be to gain experience, and may be even to attempt breeding in favourable years.

As discussed above, the wader populations of high arctic Greenland and northeastern Canada which migrate to the Old World have different wintering strategies. The two larger species winter mainly in northwestern Europe, while the three smaller species winter mainly in West Africa. This pattern is consistent with the observation that smaller waders feeding on intertidal flats go further south than larger species (and subspecies), owing at least partly to the reduced accessibility of invertebrate food in northern areas during winter (*cf.* Smit 1981). Palearctic populations of the same species (ringed plover, dunlin, and sanderling), however, winter in large numbers far north of the populations discussed here (Pienkowski & Dick 1975, Prater & Davies 1978, Taylor 1980), while Palearctic populations of the two larger species (turnstone and knot) on the contrary winter in West Africa (Dick *et al.* 1976, Branson *et al.* 1978). Does this mean that Nearctic turnstones and knots are in some way dominant to the Palearctic birds, and similarly, that Nearctic ringed plovers, dunlins and sanderlings are sub-dominant to the Palearctic birds? (See further below and Alerstam & Högstedt 1982, Pienkowski & Evans 1984.)

Population densities and distribution

Considering the limited sample, the heterogeneity of the census material, and the often rough estimates of snow and vegetation cover (and especially the combination of these) in the individual areas, it is notable that the total population densities are best correlated with snow-free vegetation cover in early June (Table 1). In general, there should be a high correlation between spring snow cover and the vegetation cover, as irrigation from melting snow often provides the main source of water for the vegetation in many high arctic areas. The lower wader population densities found in many well vegetated areas should then be related to the corresponding extensive and long lasting snow cover, while the likewise lower densities found in poorly vegetated, but early snow-free areas should be related to the limited feeding resources in such desert-like areas. In many areas with a relatively luxuriant vegetation, virtually no waders breed, apparently as a result of long lasting snow cover. The higher population densities found in moderately vegetated and relatively early snow-free areas thus seem to represent a balance between the needs for both well vegetated and reasonably early snow-free sites (see further below).

The factors active in determining the relative densities of waders in high arctic Greenland may be the same as discussed in relation to the correlation between start of egg-laying and snow cover. Most likely there is a very strong correlation between vegetation cover and invertebrate food for waders, so that food during the pre-laying and laying periods could regulate dispersal on the breeding habitats. Food supply for the young later in the season could be important too, acting through fledging success and site tenacity of both adults and offspring. The low densities found in highly vegetated but late-thawing areas seem to contradict this, at least for such areas, since food is plentiful here in July during the fledging period. In such areas, however, the delay in breeding due to *e.g.* predation risk, may limit the population density. Nest predation in snow-rich areas is apparently very high (Meltofte *et al.* 1981, de Korte *et al.* 1981, Pienkowski 1984b), but even in such areas production may exceed annual mortality (Pienkowski 1984b). The effects of feeding conditions up to and during egg-laying on potential nesting density may be modified by communal feeding in especially favourable feeding areas. Territoriality, whether operating to secure basic food resources during critical periods (*cf.* MacLean 1969, cited in Pitelka *et al.* 1974: 193), to space nests out as an anti-predator mechanism (*cf.* Tinbergen *et al.* 1967), and/or to provide a rendezvous for pair formation including mate-faithfulness (Soikkeli 1967), prevents all pairs from breeding around such optimal feeding sites.

Fox predation is not only linked to the snow cover *per se,* but naturally also to the density of foxes, and thereby to the lemming cycle. As fox numbers are at a maximum *the year after* a lemming peak, wader (and other ground nesters) breeding success may be low in such years (Meltofte *et al.* 1981).

As with the timing of breeding, different population density regulation factors may be most important in different areas (and species), and apparently the densities are balanced between several decisive factors (see further below).

The majority of the high arctic waders of Greenland display a "conservative" breeding strategy (*cf.* Pitelka *et al.* 1974), which is characterised by a "single-clutch" monogamous pair-bond and a highly territorial system with little fluctuation in populations from year to year. Only phalaropes and perhaps part of the sanderling population may display more "opportunistic" strategies (see p. 7). This may indicate that environmental conditions in high arctic Greenland are harsh but not as variable as apparently is the case in large parts of low arctic Canada, Alaska and eastern Siberia, where the opportunistic strategies are especially common (*cf.* Myers & Pitelka 1979: 140).

The correlation between population densities and food resources in spring, found by Holmes (1970) for the dunlin in Alaska, does not prove that feeding conditions necessarily limit the wader populations concerned. The birds may simply disperse and adjust territory size according to the overall environmental resources available. Even the removal experiments performed by Holmes (1966) at Point Barrow, showing that empty territories in optimal habitats kept being re-occupied until mid-June, could be interpreted to imply that potential breeders waiting for marginal habitats to become accessible took the opportunity to occupy the vacant territories (Holmes 1966, Pitelka *et al.* 1974). In high arctic Greenland, a "floating surplus" of individuals of all species may be present on the breeding grounds, but apparently it consists mainly of immature non-breeders, which occupy "marginal" territories, at least for part of the incubation period. Mainly optimal habitats have been studied in the Arctic, so that very little is known about wader populations in marginal areas, but it is possible that the most important population controlling processes may take place here (*cf.* Soikkeli 1967, Goss-

Custard 1978/79). If snow cover limits the breeding populations in snow-rich areas, year-to-year variations in snow cover should cause a varying proportion of the population to be non-breeding (*cf.* Green et al. 1977). Pienkowski (1984a) actually found evidence of a proportion of the population of ringed plovers being prevented from breeding by extensive long-lasting snow cover at Mestersvig in 1974.

Until more conclusive evidence is available, the following subjective impression concerning saturation or not of high arctic Greenland wader populations may be of some use. Personal experience from several widely scattered areas and faunistic reports from all of the country, suggest that "all" suitable habitats for at least the ringed plover, and probably also for the dunlin and sanderling are occupied. This does not seem to be the case for turnstone, knot and red phalarope. Even though extensive and late-thawing snow cover or, on the other hand, aridity may exclude these species from many areas, there still seems to be many suitable habitats that are unoccupied. Turnstones especially breed densely in certain areas, while others are almost avoided. While no large scale population changes can be documented for the three former species, more changes have been found in turnstone, and especially in knot during this century (see p. 13), as well as in the phalaropes (Elander & Blomqvist in print). Excluding the phalaropes, owing to their different breeding and wintering strategies, it is worth noting that the three apparently "stable" species winter mainly in West Africa, while the two "fluctuating" species winter in northwestern Europe. Populations of turnstone and knot may thus be limited by winter conditions, while breeding habitats of ringed plover, dunlin and sanderling could actually more or less be saturated.

The marked amelioration of the winter climate in northwestern Europe during this century could be important in this respect. Prater (1981a: 111) states that more waders winter in the British Isles nowadays than around the turn of the century (and suggests decreased disturbances from shooting as a possible reason), and Väisänen (1969) suggests that lowered winter mortality, may have been beneficial to North European ringed plovers wintering in western Europe during the last one hundred years of milder winter climate. Hence, the apparent population increase found on the breeding grounds of turnstones and knots could be related to improved conditions on the wintering grounds. Recently, however, the eastern Nearctic population of knots have decreased markedly, and Prater (1981a) suggests poor breeding success and also land reclamation on the wintering grounds as possible reasons. It may be noted that the most marked population changes concern the species with the most narrow "continental" niche among the high arctic waders in Greenland, *i.e.* the turnstone and knot (together with golden plover and whimbrel). Turnstone and knot may have had a low around the turn of the century, when the climate was most Atlantic, while they may have peaked during the 1950s and 1960s, when the continental conditions apparently came to a maximum (*cf.* Vibe 1967). Hence, factors both on the breeding grounds and in the wintering areas may be involved (see discussion by Baker & Baker 1973, Goss-Custard 1978/79, 1983, Evans & Pienkowski 1984). To the extent that population regulation takes place on the breeding grounds, I suspect food conditions during the pre-laying and laying periods to be most important.

Nothing is known about possible competition between wader species in high arctic Greenland. Their summer schedule is highly synchronous, but considerable separation seems to occur in feeding technique and habitat preferences. The six dominant species each represent one major group of feeding technique or available habitat, at least for part of the breeding season (see further in Holmes & Pitelka 1968 and Baker 1977). Far larger niche separation may occur on the wintering grounds, however (Baker & Baker 1973).

If the correlation between population density and snow-free vegetation cover in early June is related to the distribution of the waders in high arctic Greenland, the following model may be useful (Fig. 18). Although large local and regional differences are found, there is a general decrease in the amount of snow cover in early June from close to 100% in the southern parts of Northeast Greenland to less than 10% in certain areas in Peary Land (Figs 19, 20 and 21), and correspondingly a decrease in vegetation cover from about 70% in the south to just a few per cent in the north. Accordingly, the maximum amount of available snow-free vegetated land in early June should be found in the central parts of Northeast Greenland, and thereby the highest wader population densities. This is in good accordance with the conditions found (Fig. 2 and Table 1), and the graph (Fig. 18) may thus be used as a very simplified and the-

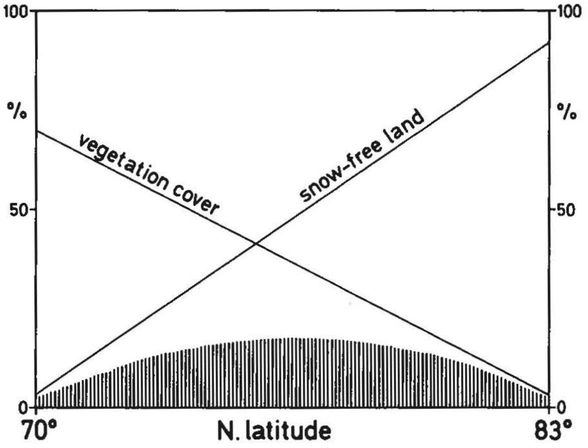

Fig. 18. Theoretical and very schematic outline of the decreasing vegetation cover and the increasing snow-free proportion of the lowland in early June from the south to the north in high arctic Greenland. The resulting proportion of snow-free vegetation cover (hatched) provides an index for potential wader population densities. See further in the text.

Figs 19–21. Three photos illustrating the extreme regional differences in snow cover at the start of nesting of waders in early June. The pictures also show the overall cline in decreasing snow cover from the south to the north in high arctic Greenland.

Fig. 19. At the expedition station "Brønlundhus" at Jørgen Brønlund Fjord in the highly continental inner part of southern Peary Land, snow was restricted to drifts at sheltered places in early/mid June 1973. Photo by the author.

Fig. 20. Moderate snow cover is typical for southern Germania Land. Although Danmark Havn is situated close to the outer coast, the common storms blow the snow from large areas and produce a patchy "semi" snow cover, Danmark Havn 31 May 1975. Photo by the author.

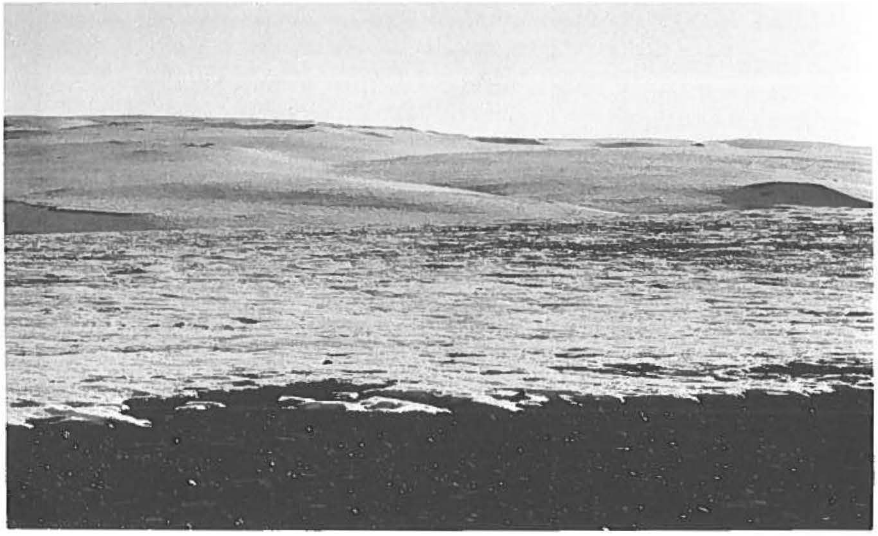

Fig. 21. Extensive and heavy snow cover at Kap Stewart in southernmost Jameson Land, 28 May 1974. Photo Ko de Korte.

oretical index of wader population densities in Northeast and North Greenland. To some extent this index also illustrates the change in conditions occurring from the snow-rich (but food-poor) outer coasts to the arid innermost areas at the edge of the Greenland ice cap. In this case, optimal conditions are also found in the intermediate parts of the country.

As the breeding schedule is highly influenced by snow cover, the principal pattern of wader populations in high arctic Greenland can be summarized as follows: relatively thin but very early breeding populations are found in the northernmost areas; the southernmost parts are populated also by relatively thin but, in contrast, late-breeding populations, while the highest densities are found among relatively early breeding populations in the central parts.

If this pattern is extended to include all of Greenland, it may provide an explanation for the very pronounced restriction of most wader populations to the high arctic part of Greenland. South of Scoresby Sund, which forms the southern limit of a number of species, and of regular occurrence of others, the spring snow cover is heavier and later-thawing than in southern Northeast Greenland and the country more mountainous and glaciated. Hence, these areas may be too snow-rich (and Atlantic even in summer) to be accessible for breeding in most waders. Conversely, the northern limits of dunlin and red phalarope may be determined by conditions which are too arid and which have too few luxuriant marsh habitats.

This pattern does not, however, explain why very few wader species occupy the inner parts of Southwest Greenland, where large well vegetated, and early snow-free areas are found, and where *e.g.* Greenland white-fronted geese *Anser albifrons flavirostris* breed (Salomonsen 1981). Geographical barriers and immigrational history may be involved in the dunlin (Nørrevang 1963), but not in the other species, and they do not explain why North American wader species, several of which breed just west of the Davis Strait and occur regularly during spring migration in West Greenland (Salomonsen 1981), have not extended their breeding range to these apparently suitable areas. The vegetation may be too luxuriant and scrub-like to be suitable to high arctic waders, but what is the difference from the breeding habitat of many New World species breeding in low arctic Canada? Is the climate too Atlantic and variable after all? In certain areas purple sandpipers and red-necked phalaropes breed in densities as high as any wader species in high arctic Greenland (Longstaff 1932, Joensen & Preuss 1972). The low diversity suggests that unstable conditions are involved (*cf.* Stearns 1976).

The theory put forward by Larson (1960) that ecological differences between blue and white arctic foxes could be the main factor limiting the distribution of high arctic waders in Greenland, was refuted by Meltofte *et al.* (1981). Foxes may play an important role in relation to snow cover, but not at all to the extent proposed by Larson.

Compared to the more southern arctic tundras of Canada, Alaska, and eastern Siberia (see pp. 11–12), the population densities of waders in high arctic Greenland are markedly lower, but similar, however, to those found on the northeastern Canadian islands. The tundra of northern Alaska is much more productive than the high arctic Greenland tundra (*cf.* MacLean & Pitelka 1971, Green *et al.* 1977), and the same apply for the extreme densities found in northeastern Siberia (Kistchinski 1982). On nearby Svalbard, however, wader population densities are even lower than in high arctic Greenland, except for the purple sandpiper, which is the only common and widespread wader species. As on the outer coasts of Northeast Greenland, where the purple sandpiper is also found, potential food for waders is poor on Svalbard, and purple sandpipers manage by feeding in the littoral zone (Bengtson & Fjellberg 1975, Meltofte *et al.* 1981, Meltofte *et al.* 1983).

Hence, with population densities varying by a factor of more than one hundred between the poorest high arctic habitats of North Greenland, Svalbard and the northeasternmost Canadian islands, and the most productive low arctic tundras of Canada, Alaska and Siberia, food would clearly appear to be the major overall factor governing wader densities in the Arctic. This principal factor is then modified by long-lasting snow cover, *etc.*

Total population sizes

Sixteen population counts have now been made over a total of some 250 km^2 distributed over most of high arctic Greenland and Ellesmere Island. From these data, one may attempt to calculate the size of the populations involved. Furthermore,estimates from the non-breeding season are available from both Europe and West Africa for comparison.

Land areas below 200 m above sea level were measured for eight sections of high arctic Greenland, and for Ellesmere Island and eastern Axel Heiberg Island in Canada (Table 3). The areas were measured with a Calcomp digitizer and calculated by computer. For Greenland a 1:2 000 000 scale map (Geodetic Institute, Copenhagen 1969) was used and for Canada a map of scale 1:1 000 000 (International map of the World, Ottawa, 1975–77). The 200 m contour is probably a fairly good average limit of suitable lowland wader habitat in most areas. In some areas, waders breed in numbers up to 3—400 m above sea level (*e.g.* at Lake Hazen) but, on the other hand, large lowland areas are far from suitable for breeding waders. The Greenland map especially, is not very accurate, but I think that the areas derived represent a reasonable estimate of the magnitude of lowland areas in these regions.

Table 3. Estimates of numbers of pairs per "section" in high arctic Greenland and Ellesmere Island (plus eastern Axel Heiberg Island) (see Fig. 2). From the total number of pairs, the autumn population is estimated by adding juveniles and one-year-old immatures. These totals are compared with the mid-winter counts from the wintering areas of the respective species (populations) in West Europe

Area	A 69°–72° N. lat.	B 72°–75° N. lat.	C 75°–78° N. lat.	D 78°–81° N. lat.	E 81° N. lat.- 40° W. long.	F 40° W. long.- Peterm. Gl.
Lowland area (km²)	10 100	9800	10 300	6900	13 900	8400
Charadrius hiaticula	3000	6900	7200	2100	4200	–
Arenaria interpres	1000	1000	5000	700	1400	800
Calidris canutus	1000	700	2000	1000	2000	1000
Calidris alpina	2000	1000	2000			
Calidris alba	2000	4000	6000	1000	3000	1000

Total wader populations were estimated within each region using the available counts, line transects and general literature statements on relative abundance. Considering that the census areas often cover the most favourable breeding habitats within each region, the average breeding densities were often estimated to be considerably below the figures found for the census areas. In Northeast Greenland these estimates could benefit from my personal knowledge of much of the country, whereas in the western parts of North Greenland, I have no direct knowledge of the country.

In Canada, the areas for which numbers of waders were estimated include only Ellesmere and eastern Axel Heiberg Island occupied by both turnstones and knots migrating to the Old World (Godfrey 1966), whereas the rest of the breeding range of knots on the islands farther south and west were not included due to lack of information on habitats and breeding densities. Parmelee (1970) states that knots were "only a third to half as abundant" as the sanderling on Bathurst Island in 1968, which should mean that less than one pair was found per 2–4 km², and Savile (1961) "tentatively assumed" two pairs to breed on 15 square miles of "arctic desert" on Ellef Ringnes Island in 1960 (see further below). Old World wintering ringed plovers also breed in low arctic Greenland and on Baffin Island, but compared to the populations breeding in the high arctic areas, numbers are probably low.

The results of the estimates are presented in Table 3, and it appears that the total breeding population vary from 25 000 pairs of ringed plovers and turnstones to 5 000 pairs of dunlins. The numbers of breeding golden plovers, purple sandpipers, red- and red-necked phalaropes should probably only be counted in hundreds of pairs or even less in some of the species. Nothing is known about population densities of Baird's sandpipers in the Thule district.

From these totals of breeding or territorial pairs the total autumn populations were estimated by adding 1.5–2.0 fledged juveniles per pair and at least a further 50–60% of these as survived one-year-old immatures of the two later maturing species, turnstone and knot (Table 3).

These figures may then be compared with the estimates from the mid-winter counts in Europe and the Atlantic coast of Africa (most recent review by Engelmoer 1982, Engelmoer *et al.* 1984). For most of the species, however, the wintering populations are a mixture of Nearctic and Palearctic breeding populations, and only the turnstones and knots wintering in West Europe are known almost entirely to make up the Old World wintering Nearctic populations. Knots stay in very large concentrations in winter, and the counts must be considered quite reliable. Hence, a very large discrepancy appears between the 100 000 individuals estimated from the breeding population and the 350 000 found in Europe in winter. Part of this discrepancy is due to the number of knots breeding on Devon Island, western Axel Heiberg Island and the smaller but low islands west thereof. But even if these populations are estimated to be 15 000 pairs, the total population still only adds up to 165 000 individuals in autumn, less than one half of the winter population.

The most logical explanation for this discrepancy is that my breeding population estimates are too low. This could apply partly to the other species as well. As the population estimates were fitted to the estimated overall relative abundance between the species in the single "blocks", the ratio between my breeding estimate of knots and the mid-winter count could also apply to the other species. This means that the autumn population of ringed plovers should be about 200 000, turnstones 250 000 and sanderlings 130 000. The dunlins were hardly underestimated in the same way, as their breeding habitats are much more local.

These higher estimates agree somewhat better with the winter counts from the Atlantic coast of Europe and Africa (Table 3). Only the turnstones highly exceed the mid-winter total, but this species as well as the ringed plover and sanderling are distributed over far longer stretches of coasts during winter than those counted (*e.g.* Buxton 1982). It is not unlikely, however, that the Nearctic populations of ringed plovers and sanderlings make up the main part of the numbers wintering in West Africa. Prater (1981a) has estimated that possibly more than 100 000 turnstones may winter along the coasts of Norway and Iceland. This is questionable, however, at least for Iceland, since counts indicate that wintering

(E) and along the west coast of Africa (A). Mid-winter counts partly including Palearctic populations are in brackets. The "corrected" totals are then calculated. See the text for further explanation and discussion.

G Peterm. Gl.- 78° N. lat. 5200	H 78° N. lat.- Kap York 2900	I Ellesmere Island (+) 27 400	Total no. of pairs	Total autumn pop.	Mid-winter count	'Corr.' total
–	600	500	25 000	90 000	(200 000) A	200 000
500	300	13 700	25 000	120 000	32 000 E	250 000
1000	1000	10 000	20 000	100 000	350 000 E	350 000
			5 000	18 000	(1 000 000) A	20 000
–		–	17 000	60 000	(150 000) A	130 000

numbers of turnstones there are unlikely to exceed a few thousands (Wilson 1982).

Concerning the dunlin, Pienkowski & Dick (1975) concluded on the basis of bill measurements, *etc.* that the proportion of *arctica* among dunlins wintering in West Africa is extremely small, if present at all. Ringing recoveries have shown that *arctica* dunlins do reach at least Morocco, and from the figures presented by Pienkowski & Dick (1975) it can be estimated that 1–3% of the dunlins in West Africa are *arctica.* Of the 1 000 000 dunlins wintering in West Africa, 10–30 000 should then be *arctica,* a figure close to the 18 000 estimated from the breeding censuses. van Brederode *et al.* (1982) found that 41% of 325 dunlins caught during spring migration in Morocco appeared to be *arctica.* However, this proportion cannot at all be representative for the West African wintering dunlins.

Even the higher estimates may be too low. For one knowing the birds from high arctic Greenland, ringed plover, turnstone and sanderling should all be more numerous than the knot. The reason may be that a very high proportion of the knots breeds in the Canadian Archipelago, but even here the turnstones outnumber knots in parts of Ellesmere Island (Parmelee & MacDonald 1960, Nettleship 1973, 1974; versus Witts 1981, undated b), and it is possible that the Old World wintering Nearctic turnstone population exceeds the number of West European wintering knots.

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Epilogue

One of the first and most dedicated ornithologists working in high arctic Greenland, A. L. V. Manniche, who stayed with the Denmark Expedition at Danmark Havn for two full years 1906–1908, showed how extremely different successive years can be in the Arctic concerning nearly all environmental conditions important to the fauna, such as winter snow-layer, progress of spring, break-up of the fjord ice, and spells of inclement weather during the productive season. He clearly considered the more favourable of the two years to be "normal", whereas the unfavourable year was "abnormal". Since then many studies have documented such variations, but very few long term studies have followed bird populations over a number of years. Far too many studies in the Arctic are made in only one season or even part of the season.

Even larger differences exist between different geographical areas and regions in the Arctic, and recent studies have indicated that the strategies of the individual species may vary markedly in relation to these differences. Very few studies, however, have compared the biology (in its broadest sense) of a species within large and separated parts of its range. A factor, shown to be of decisive importance to the population in one study area, may be completely insignificant in another.

The present paper, based on my own work during seven seasons in four different areas ranging from the southernmost to the northernmost parts of high arctic Greenland, is not a detailed analysis of arctic wader ecology. Much of my work was done in spare time during my work at weather stations, and my qualifications were not those of a professional. Besides a review aimed to be used for comparison with other areas, I have, however, tried to provide a broader basis for future more detailed studies in high arctic Greenland, emphasizing the considerable difference existing even within this "limited" area.

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Biology of the peregrine and gyrfalcon in Greenland

Burnham, William A. and Mattox, William G. 1984. Biology of the peregrine and gyrfalcon in Greenland. – Meddr Grønland, Biosci. 14, 25 pp. Copenhagen 1984-05-30.

A ten year study began in 1972 in West Greenland to investigate the breeding biology of the peregrine falcon. Data on nesting gyrfalcons were also collected. Thirty-four peregrine nesting sites were examined in the 6050 km^2 inland study area near Søndre Strømfjord. Limited research also centered in Disko Bugt and Frederikshåb. Peregrines were found nesting predominantly on high, south-facing cliffs which overlooked large areas. The mean minimum distance between peregrine eyries was 7.7 km for the inland area (1972 and 1973) and 55 km for the coast (1974). Approximately 60 percent of the inland nesting sites were occupied each year. A ten-year average production of 1.90 young per occupied site and 2.78 young per successful site was determined. Lapland longspurs, snow buntings, wheatears, and redpolls comprised 90 percent of the peregrine's diet. Raven nests and prey availability may affect gyrfalcon nesting. Gyrfalcons and peregrines did not breed successfully on the same cliffs as they do in Alaska where prey species number and density is greater. Competition for nest sites probably occurs, but prey availability may be the most significant factor affecting falcon density. Addled peregrine eggs, eggshell fragments, and peregrine prey species were collected. Whole eggs averaged 14.3 ppm wet weight (305 ppm lipid weight) DDE, while eggshell measurements showed a 16 percent thinning compared with pre-1940 eggs from Greenland. Prey species carried low levels of DDE. The peregrine population appears to be at a near critical contamination level, and a small increase in DDE level could contribute to a population decline. No indication of a decline has been observed during the study, and the population appears stable. The project banded 185 peregrines, from which 8 recoveries occurred. The recoveries suggest peregrines migrate south to winter in South America.

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