

**The Greenland White-fronted Goose *Anser albifrons
flavirostris***

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Anser albifrons flavirostris **Greenland White-fronted Goose**

Anser albifrons flavirostris Dalgety and Scott, 1948

Editor's note. In BWP Vol. 1, the Greenland White-fronted Goose was treated as a subspecies of the White-fronted Goose *Anser albifrons*. Since that time, a great deal of ecological and behavioural work has been undertaken on this distinctive taxon, and it was felt that *flavirostris* merited an account of its own. In the light of the emerging data that highlight its distinctive nature, it seems increasingly likely that the Greenland form will be recognized as a species in its own right. Consequently, it has been decided that a separate account of the Greenland White-fronted Goose should be published at this time. Although there is ongoing research into the other forms of *A. albifrons*, it is unlikely that an *Update* of the full species will be available in the near future.

Holotype and paratype both in the British Museum (Natural History) [BM(NH) reg. nos 1954.62.1 and 2]

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Summary. This account provides an updated overview of the Greenland race of the circumpolar White-fronted Geese, which formed only a part of the previous species account. Because of the differences in many features of the nominate and Greenland races, extensive new information is provided on habitats used throughout the annual cycle. The population breeds in west Greenland, migrates through Iceland on autumn and spring passage, and winters in Britain and Ireland. Extensive new information based on regular co-ordinated ground censuses on the wintering grounds, expeditions to staging areas, satellite telemetry studies, and aerial surveys have resulted in new information which has been incorporated into much-revised Movements and Distribution sections. Following declines in the 1950s from between 17 500 and 23 000 birds to perhaps as few as 14 300 by the late 1970s, this population was the focus of conservation concern. The Population section reports the subsequent increase in numbers to c. 33 000 in the late 1990s, under protective legislation on the wintering grounds and site safeguard throughout the breeding and wintering range. New information on conservation is provided for the first time, underlining the effects of hunting mortality on the population, and its susceptibility to disturbance, especially in situations in which geese have few alternative feeding areas in which to seek refuge from disruptions to their feeding activity. Despite protection from hunting on the wintering grounds, small numbers continue to be taken in the breeding areas and 3000–3500 in Iceland in autumn. In spite of the implementation of site safeguard programmes, some wintering flocks have disappeared and numbers at some other resorts continue to decline (especially in southern Ireland). Numbers at the large resorts are generally increasing or stable, especially in Scotland. Much new detail is provided about feeding selection and diet in the Food and feeding section. New information is presented in the Social pattern and behaviour section, most notably relating to the prolonged parent–offspring relationships observed in this race. Based on two major expeditions to the breeding areas and extensive ringing and capture–mark–recapture studies, the sections on Breeding, Survival, Measurements, and Weights have been considerably expanded.

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Field characters. (Updates *BWP* Vol. I, pp. 403–4)

Taxonomy of circumpolar White-fronted Geese is still contested, but is generally agreed that, during last glaciation, all the present (four) taxa were forced south of present breeding range. Ancestral *flaviostris* (isolated from *albifrons* stock of that time) persisted in ice-free tundras of south North Sea and Ireland, gradually moving to present breeding range during subsequent amelioration (Johansen 1956). However, Ploeger (1968) considered that slight morphological differences between *flaviostris* and *albifrons* point to recent common origin, present separation resulting only from use of western and eastern North Sea refugia. More likely that *flaviostris* split off from ancestral *frontalis* during one of its excursions eastwards from Beringian refugia during recent interglacials, since morphological differences between these races are slight (Fox and Stroud 1981*b*). Simple principle components analysis of linear measurements taken from White-fronted Geese around arctic suggests that Greenland birds are distinct from, but resemble, most *frontalis* forms, especially those in Yukon (C R Ely unpublished data). Greenland birds show least affinity (based on measurements) with nearest breeding *albifrons* from Taimyr Peninsula and Lena Delta. Whatever the precise origin of *flaviostris*, it is clear that they represent one of earliest groups to split from ancestral *A. albifrons*, on basis of morphological differences, specialized habitat exploitation, and disjunct breeding range. Clear need to analyse genetic relationships of existing populations of White-fronted Goose to establish their potential ages and inter-relationships. Nevertheless, on basis of morphological, plumage and bill coloration, feeding ecology, and behaviour (e.g. unusually prolonged parent–offspring relationships), this race shows greater differences than those among all other forms of *A. albifrons*.

Habitat. (Updates *BWP* Vol. I, p. 404)

GREENLAND. Following account based mainly on Madsen and Fox (1981), with supplementary unpublished observations from subsequent years. Observed patterns stem largely from one area, Eqalummiut Nunaat (67°30'N 50°30'W), a low, lake-studded, plateau 400–600 m above sea level (a.s.l.) deeply incised by wide glacial valleys (Fox and Stroud 1981*a*). Topography of breeding areas at higher latitudes quite different and this likely to affect breeding and feeding ecology.

Spring. Earliest arriving geese feed on mature sandur flats in Greenland with abundant open water and bare mud substrate, where early thaw enables extraction of subterranean overwintering part of plants. Also feed in pools and around lake margins close to sea level as these thaw (Fox and Madsen 1981, Madsen and Fox 1981,

Glahder 1999*a, b*). Generally, all spring staging areas associated with low snow cover and early thaw, majority being between 66° and 68°N, in precipitation shadow of Sukkertoppen Ice Cap, where spring temperatures in the interior among earliest to rise (Glahder 1999*a, b*).

Summer. Greenland White-fronted Geese generally select range of wetland habitats where favoured food plants occur, as these become freed by spring thaw. Use lakes during flightless moult period (when forage on peripheral wetlands and take to safety of open water when threatened on land), finally resorting to heath communities in late summer to exploit berry crop prior to autumn migration. From pre-nesting period onwards, follow delay in growth of emergent aquatic and marsh vegetation up an altitudinal gradient from sandur marshes to plateau lakes (400–600 m a.s.l.). This is equivalent to temperature gradient that results in delayed phyto-production at successively higher altitudes. During first half of incubation period, feed in flush runnels, streams, lake margins and other wetland areas where *Eriophorum angustifolium* common and easily extracted from substrate (Madsen and Fox 1981). Increasingly into latter part of incubation, above-ground growth of sedges *Carex* consumed, especially *C. rariflora* characteristic of sedge meadows along rivers, margins of lakes, and other open flat areas where water lies for long periods during the melt. Such habitats increasingly favoured by geese and become dominant habitat type used during early moult. During latter part of incubation, large non-breeding element of population moves to high altitude to commence feeding around lake margins of plateau. From hatching, almost all geese present on this plateau, feeding around lake fringes. Sedge meadows fringing upland lakes usually restricted to <20 m from lake edges. After moving from sea level to plateau following thaw, geese also exploit differences in phenology of thaw on plateau lakes. Here, initially exploit flat or south-facing areas that are first to thaw, finally moving to snow patch vegetation on north-facing slopes that are very last areas to initiate young green plant growth in landscape. Hence, even at this altitude, geese follow phenology of plant growth by selecting between habitats. Exploitation of such altitudinal gradient not possible at lowland sites exploited by geese throughout summer, e.g. Naternaq (68°N) where geese moult on lakes containing abundant suspended glacial sediment and so support rich emergent vegetation. Here, use emergent *Equisetum*, *Carex* and *Eriophorum* vegetation around the periphery of pools. Geese in Aqajarua-Sullorsuaq Ramsar site on Disko Island use *Puccinellia phryganodes*-dominated saltmarsh in late August (MacDonald 1993). After moult, when geese confined to lakes with peripheral sedge meadows and

late snow patches, thought to move to heaths, where feed on berries (from *Empetrum* and *Vaccinium* spp.) prior to departure for Iceland. This late summer period, post moult and prior to autumn migration, is least known period of Greenland White-fronted Goose annual cycle.

ICELAND. Spring/autumn. Utilizes natural bogs, fens, and sedge meadows (see Food and feeding), including lakes that have been drained of most of their water, but which often retain dense stands of *Eriophorum angustifolium* (highly attractive to feeding geese). Although such natural wetlands probably traditional staging habitats used by geese prior to agricultural development of landscape, were used by between 9% (in southern lowlands) and 35% (in west, where such habitats more frequent and potatoes/barley rarely grown) of spring staging birds in 1986. Population increasingly uses dry hayfields, both reseeded and low intensity, especially in spring, when 66% of all observations stem from this habitat (Francis and Fox 1987). Greenland White-fronted Geese will exploit other energy-rich habitats (25% use in southern lowlands) such as waste potatoes (especially with Whooper Swans *Cygnus cygnus* in extensive potato fields of Thykkvibær area in Holt, south Iceland) and spilt barley grain (as in Hvolsvöllur area in Hvolhreppur). At Hvanneyri, west Iceland, in spring, also exploits newly sown barley. Generally uses large rivers (especially glacial melt rivers with braided sandur that provides abundant dry or shallow water areas on which to rest), such as Thverá (Rangvellir), Thjórsá (Flói), and Ölfus (Ölfus) in southern lowlands. In west, extensive flats of Borgarfjörður provide roost-sites for extensive feeding areas in farmland and sedge meadows north and south of river. However, in some areas, geese also use lakes and small water bodies as night-time roosts. Include areas such as Frakkavatn and Skúmstaðavatn in southern lowlands (Garðarsson 1976; but apparently not used in recent years) and at Hvanneyri, where lakes and central parts of large peatlands (e.g. Ferjubakkaflói) occasionally used instead of, or as well as, adjacent fjord system.

BRITAIN AND IRELAND. Winter. Traditionally associated with peatlands, especially oceanic blanket mires and raised bogs, characterized by pronounced surface patterning. These biotopes support locally abundant stands of Common Cotton Grass *Eriophorum angustifolium* and White-beaked Sedge *Rhynchospora alba*, favoured food items of geese. Both plants widespread in blanket and raised bog biotopes, but generally exploited only in 'quaking' or permanently wet areas. These are topographically defined and hence not evenly or extensively distributed in bogland landscapes. Underground overwintering organs of both plants extracted from soft *Sphagnum* moss typical of low-lying parts of pool and hummock systems of such

boglands. In arctic, extraction of *Eriophorum* by geese reduces forage availability at exploited sites for 2–4 years (Hupp *et al.* 2000), and similar evidence from Islay indicates a 2- to 3-year recovery for *E. angustifolium* at bog-pools with high extraction of shoots (DAS unpublished data). Despite preference for boglands, and climatic region in which they winter, geese must have always had to move elsewhere when these habitats occasionally frozen. Seems likely that, at such times, flush and spring-line vegetation and possibly alluvial grasslands have been used since pre-agricultural times (Pollard and Walters-Davis 1968, Norriss and Wilson 1993). Bogland-feeding geese traditionally flew to open water to roost at night, and hence may have traditionally used floodplain grasslands as roost-sites. This need to shift from bogland biotopes may explain association of flocks using both raised bogs and river flood plains (known as 'callows' in Ireland) especially in Midlands of Ireland. Throughout range in Ireland, wide range of wetlands, marshes, and wet pasture habitats continue to be used, including turlough habitat (a temporarily flooded basin system reliant on limestone catchment recharge and subject to dramatic changes in water levels), e.g. at Rahasane, Co. Galway (Norriss and Wilson 1993). Greenland White-fronted Geese have increasingly used low-intensity agricultural land in latter half of 20th century (Norriss and Wilson 1993). In Scotland, very few birds now consistently use bogland biotopes for daytime feeding, and numbers that do so in Ireland have also declined recently. In 1980s and 1990s, increasingly began to use reseeded and intensively managed grasslands, notably at two most important wintering resorts of Islay (Inner Hebrides, south-west Scotland) and Wexford Slobs (south-east Ireland). On Islay at least, increased use of reseeded in recent years may simply be result of interaction between strong site fidelity and changing patterns of agriculture: thus, geese continue to visit traditional feeding areas of formerly low agricultural intensity after they have been ploughed and reseeded (Bignal *et al.* 1988, Wilson *et al.* 1991). Generally, Greenland White-fronted Geese feed in autumn on high-energy food such as seeds, grains, and overwintering storage organs, switching to grass as these exhausted and resorting to most digestible and protein-rich foods in spring to accumulate stores for migration and reproduction (Norriss and Wilson 1993).

Islay. On arrival at wintering areas, feeds on stubbles during day, often gathering in large numbers at few suitably harvested grain fields before dispersing throughout island as these are depleted. May feed on potatoes, fodder beet, and turnips where available (post-harvest, gleaning waste). Winter cereals generally not grown on Islay. However, intensive cultivation of high-quality

grassland for dairying has attracted species to nutritious reseeded grasslands since c. 1990 on the 10 or so dairy farms. Islay dairy closed in 2000, although long-term consequences of this for Islay land-use and thus goose populations unclear. During daytime, >80% of all feeding birds in autumn and >90% in spring on pasture, with <3% each on bog, moorland, lochs, mudflats, and saltmarshes (Ridgill *et al.* 1994). Geese select greenest fields with high abundance of *Juncus effusus*, although experiments using different liming and fertilizer treatments failed to affect distribution of geese (Ridgill *et al.* 1994). Most roost-sites were in bogs, often with patterned mire systems, surface pools, and hummock formations, or old, flooded, peat cuttings that represent feeding habitat (McKay 1992) formerly used to greater extent than at present, although roost feeding remains significant. Short vegetation preferred over rank, and quaking mire with open *Sphagnum* lawns often favoured. Sites therefore of low relief, with good visibility but highly exposed. Geese spend night close to small pools and lochans, using edges rather than open water *per se*. Distribution of faecal material (especially conspicuous roost piles) show that geese roost up to 100 m from water, perhaps due to lack of large terrestrial predators. Geese have also been observed roosting on open fields (McKay 1992).

Elsewhere in Britain. Typically feeds on spilt grain in stubbles after harvest (e.g. Kintyre, Caithness, Tiree), but generally confined to grass for majority of winter and especially in spring when almost all use grass. Use of saltmarsh is rare, but Dyfi flock regularly grazes on saltings, taking *Festuca rubra* and *Puccinellia maritima* and also shoots of *Spartina townsendii* (Fox and Stroud 1985). Saltmarsh grazing occurs at Lowlandman's Bay, Jura (and at two Irish sites: Fergus Estuary and Lehinch, Co. Clare). Generally associated with open water night-time roost-sites.

Wexford. Information from Warren (1990), Mayes (1991), and unpublished data. At Wexford, agricultural practices are amongst most intensive in Ireland. In early 1960s, fields predominantly native grasses with invasive *Juncus effusus* but, by 1980s, following intense field drainage and sub-soiling, majority of North Slob was intensively managed grassland, both heavily fertilized and regularly reseeded. During 1980s, substantial amount of stubble and undersown stubble also became available, which affected habitat use of geese. However, most dramatic changes occurred with increase in fodder beet from mid-1980s. In 1990s, increasing tillage substantially reduced amount of grass available, but cultivation of crops such as maize and linseed offered no alternative foods. These changes have inevitably affected habitat use by geese, confining them to smaller feeding areas, but

same patterns generally evident in each winter. Geese tend to feed on stubbles on arrival, but in decreasing numbers through season as this high-energy food is exhausted. In years with efficient harvest (and hence little waste grain), stubble may hardly be used at all and geese move directly to grass. Loss of grassland (to tillage and forestry) led to almost complete abandonment of South Slobs (formerly important feeding area because of stubble and grasslands in 1980s) from mid-1990s. Beet has proved especially attractive to wintering geese, and Mayes (1991) showed that this was highly profitable for geese, especially in mid-winter when grass stops growing in some years. Geese initially fed on beet tops left after cropping but, since early 1990s, sacrificial beet crops have been topped successively throughout season for conservation management purposes (primarily to keep geese off dairy pastures and other sensitive crops elsewhere on Slobs). Hence, increasing numbers of geese using this source of food for progressively longer times through season. Generally, feed increasingly on quality grass as season progresses, such that in spring prior to departure, all utilizing this resource. In earlier years, number using newly sown winter cereal increased from October to January, but numbers were always very small. Increase in number through winter using stubble undersown with grass may reflect that, as grass grows and grain is depleted, probability of finding remaining spilled grain here makes them more profitable than either habitat on its own.

Elsewhere in Ireland. Use of wettest habitats and arable crops predominates in autumn (Norriss and Wilson 1993), presumably because these offer energy-rich foods prior to mid-winter when food scarce, day length short, and thermoregulatory costs greatest. Most feeding on grasslands in winter and dry grasslands in spring (Norriss and Wilson 1993). Despite considerable inter-flock variability in habitat use, consistent patterns apparent within flocks from year to year (Norriss and Wilson 1993). Current habitat use reflects habitat availability within range of each flock; in some areas geese have benefited from local agricultural intensification, whilst other traditional habitats have been lost. Nevertheless, habitat loss and especially disturbance pressure now restricts ranges of most flocks compared with earlier times. Norriss and Wilson (1993) suggested that shifts to farmland have coincided with beneficial changes there, rather than with direct loss of traditional habitats, as proposed by Rutledge and Ogilvie (1979) as cause of declines in Ireland during 1950s–1970s. Hence, rather than geese responding to habitat loss by moving to intensively managed grassland, moved from previously favoured feeding areas to richer agricultural habitats in opportunistic manner. Historically,

population wintered on bogland, but Rutledge and Ogilvie (1979) recorded callows and rough grassland as additional important habitats, with only minor use of marsh, saltmarsh, and arable and root crops. In recent times, geese have increasingly abandoned semi-natural habitats and low-intensity grasslands to feed on more intensively managed grasslands. Seems due to preference for grasslands with improved protection from hunting, agricultural intensification, larger field units, and better grass swards but, nevertheless, Greenland White-fronted Geese still prefer wetter, poorer vegetation than nominate *albifrons* (Norriss and Wilson 1993). Mayes (1991) studied wintering flock of 300–350 birds on Little Brosna River (Cos Offaly and Tipperary), where fed on semi-natural floodplain grasslands (virtually free from reseeding with very little fertilization). Geese highly selective throughout season, especially for *Agrostis stolonifera*/sedge-rich pastures although sedge-dominated grasslands avoided. Higher-lying grasslands used in different combinations throughout season, influenced by flooding and disturbance.

Distribution. (Updates *BWP* Vol. I, p. 404)

BREEDING DISTRIBUTION. Breeds in low-arctic west Greenland mostly between Nuuk (64°N) and Upernavik (73°N; Salomonsen 1950, 1967), most numerous and highest densities between 66° and 68°N (0.28 pairs/km² in 1999; Malecki *et al.* 2000). No records south of Sukkertoppen Ice Cap (65°45'N) to Nuuk since those of Salomonsen. Summering birds now occur as far north as Qanaq (77°N) (Best and Higgs 1990). Information relating to summer distribution comes from historical accounts, expedition reports, and aerial surveys carried out to locate spring staging, breeding, and moulting distributions in recent years (Joensen and Preuss 1972, Stroud 1981a, Glahder 1999a, Malecki *et al.* 2000). Sub-fossil remains from archaeological sites all lie within present breeding range. For example, bones aged from Norse occupation period 1000–1350 AD at 64°07'N (Møhl 1982, McGovern *et al.* 1983), at 67°06'N (Grønnow *et al.* 1983), and at 67°32'N (bones undated; Stroud 1981g). Whitefront feathers also found in bird-skin jackets on Inuit mummies dating from 1475 ± 50 AD at 70°07'N (Hansen and Gulløv 1989). Whitefront remains have not been found in comparable investigations at sites outside current breeding range (e.g. in south Greenland; Vebæk 1992) suggesting that gross extent of breeding range in west Greenland has been substantially unchanged for perhaps last two millennia. Abundance of Whitefront bones (including bones of c. 1- and 2-month-old goslings) compared with other birds found at 67°06'N (Grønnow *et al.* 1983) confirms that south-central region of breeding area (between Kangerlussuaq

and Isortoq) has long been important for geese. Area also origin of oldest detailed written account of Whitefronts in Greenland (Muller 1896).

Recent aerial survey south from Nuuk to 62°N located no birds despite apparently suitable habitat (Malecki *et al.* 2000). Historical records (Salomonsen 1950, 1967) indicate that in 1940s and 1950s southernmost birds nested in interior parts of Godthåbsfjord, closest to ice cap, with relatively few northwards to Sukkertoppen Ice Cap which reaches the sea. Immediately north of Sukkertoppen Ice Cap, relatively high (>800 m a.s.l.) plateau areas, which are late to thaw, are virtually devoid of suitable vegetation and therefore also of geese. Greatest densities occur close to ice cap, north from Kangerlussuaq, with densities declining west to coast, generally because of higher altitudes here. Densest breeding concentrations thought to occur between 66° and 68°N, especially in interior close to ice cap, although breeding geese occur with increasing frequency away from inland areas at low altitudes, reaching coast south of Disko Bay. Favoured interior areas generally characterized by plateaux reaching to 800 m a.s.l., broken by deep glacial valleys with extensive marshes and river systems, but with numerous pools, lakes, and marshes at various elevations. Open expanse of lowland flats known as Naternaq supports at least 2600 breeding and moulting Greenland White-fronted Geese in relatively small area. Geese exploit numerous lakes and wetlands studded throughout flat open plain composed of unstable fine glacial deposits. Further north, important concentrations in Sullorsuaq and Kuusuat areas on Disko Island, where very high mountainous terrain restricts geese to coastal areas, vegetated outwash plains and valley bottoms, and other lowland wetlands. Disko Bay coastal strip north from Naternaq holds appreciable numbers at low densities (mean 0.11 pairs/km² in 1999), but high densities occur only in small pockets further north. Nuussuaq peninsula mostly very high altitude and unsuitable, but valley north of Sarqaq [Sarqaq dalen where Fencker (1950) made first ever studies of breeding Greenland White-fronted Geese] holds high densities (Joensen and Preuss 1972). Further north, terrain very rugged and geese confined to small coastal lowlands with suitable breeding habitat. Only really high densities occur in extensive marshy lowlands of Svartenhuk peninsula. Known to breed as far north as Upernavik, although probably only in small numbers (Joensen and Preuss 1972). In 1940s, Salomonsen (1948) noted considerable increase in numbers in northernmost parts of range (given then as 72°N). North of Upernavik, rugged ice-dominated terrain of Melville Bay unsuitable, although has been recorded recently near Avanersuaq/Thule (Best and Higgs 1990).

MOULTING DISTRIBUTION. Generally thought that non-breeders moult close to breeding pairs, but since brood-rearing parents tend to be dominant over, and highly aggressive towards, non-breeders, at local scale often displaced from favoured brood-rearing habitats. Salomonsen (1950, 1967) reported northwards moult migration of non-breeders, and no doubt that major non-breeding moulting aggregations lie well north of favoured breeding areas where densities highest. Aerial censuses (July 1992 and 1995) between 67° and 72°N (Glahder 1999a) located important concentrations of moulters (figures in parentheses indicate numbers of birds counted from the air) on Svartenhuk (72°N, 820–1348) and Nuussuaq (70°N, 634–1003) peninsulas, Disko Island (70°N, 855–1788), Naternaq (68°N, 2562–2588), Eqalummiut Nunaat (67°N, 611–1163), and Nasuttuup Nunaa (67°N, 1387). Mean flock sizes highest in north of range. Overall densities low (<1 goose/km²) and varied considerably between areas and years. In 1992, cold spring and summer, more appeared to summer in central areas (66–69°N), but 1995 was warmer than normal and geese were more numerous to north and south (Glahder 1999a).

AUTUMN MIGRATION. In autumn, migrates mainly through south and west Iceland (Francis and Fox 1987, Stroud 1992, Fox *et al.* 1999a) to winter exclusively in Ireland and Britain. Concentrate in southern lowland (Árnessýsla, Rangárvallassýsla, and Vestur-Skaftafellssýsla 63°30'–64°N) and western lowlands (Kjósarsýsla, Borgarfjalðarsýsla, Mýrarsýsla, and Snæfellsness-og Hnappadalssýsla 64°10'–64°40'N) in both spring and autumn. Most important site in western lowlands at Hvanneyri, Borgarfjalðarsýsla (64°34'N, 21°46'W), area with extensive *Carex lyngbyei*-dominated wetlands, boglands, and abundant silage and hayfields associated with agricultural university (Fox *et al.* 1999a).

WINTERING DISTRIBUTION. Wintering range restricted to north and west fringes of Britain and Ireland, confined within 3°C January isotherm, which represents climate template for formation of patterned mire systems (Belman 1981, Fox *et al.* 1999b). For full assessment and description of numbers, status, and other information relating to individual flocks, see Fox *et al.* (1994, 1998a). In north Scotland, there are two flocks on Orkney and five discrete areas in Caithness, where geese use cereals (Caithness only), semi-natural grasslands, reseeded and improved pastures, and mire. Regular occurrence at Loch Eye (only flock known on east coast of Scotland) ceased in mid-1980s. On Western Isles, of five former discrete flocks, one has disappeared and North Uist flock is close to extinction; all use machair and other rough wet pasture, marsh, and bog close to sea. Amongst Inner

Hebrides, flocks on Skye (two), Muck, Coll, Tiree, Mull (two), Colonsay/Oransay, and Jura (two) with greatest concentrations on Islay. On adjacent mainland, flocks occur on traditional raised bog around Loch Shiel, with farmland flocks on Benderloch/Lismore, Keills/Danna, and Moine Mhor and two major groups on Mull of Kintyre. Further south, major aggregations occur at Loch Lomond, Stranraer, and Loch Ken; last regular flock in England and Wales continues to winter on Dyfi Estuary in west Wales. In Ireland, flocks concentrated in west and north Midlands (with notable exception of Wexford Slobs) congruent with distribution of former habitats (raised mires and associated callows, or floodlands in juxtaposition). Large concentration associated with land claim on Inch Levels, Loughs Foyle, and Swilly, but in north flocks more often associated with intensive, wet, and unimproved grasslands, with three other flocks in Co. Donegal. Flocks in Cos Sligo, Fermanagh, and Cavan all rely on intensively managed grasslands, but flock in Co. Armagh/Monaghan still uses wet pastures and lake margins. In north-west, about seven flocks continue to use such natural bogland and semi-natural habitat as exists within their ranges in Co. Mayo, as does threatened flock in Connemara, Co. Galway, that subsists almost entirely on boglands. Three flocks in Co. Galway and three in Co. Clare, while four major flocks in Co. Roscommon and another in Co. Westmeath use managed grasslands associated with large lough roosts. Two important flocks associated with extensive Shannon catchment floodplain systems, Rivers Suck and Little Brosna, continue to thrive despite decline in use of associated bog systems. These tributary floodplain systems are well removed from major sources of disturbance along river channel. Despite apparent suitability, central Shannon Valley floodplain no longer extensively used, due to narrow linear nature of available habitat, which makes geese prone to disturbance. Southern flocks (one in Co. Kilkenny, one in Co. Cork, and four in Co. Kerry) all small and declining. Only two flocks occur on east coast of Ireland: new flock established on very intensively managed grasslands in Co. Louth in late 1980s and Wexford flock, which constitutes single most important wintering site. Wexford flock, largest concentration of wintering birds in Ireland, formerly used both North and South Sloblands, former intertidal areas claimed from Wexford Harbour. In last 10 years, afforestation and changes in agricultural use have rendered South Slob less attractive, and most now confined to North Slob. Wintering geese use Wexford Harbour as night-time roost, and may disperse to feed on grassland at Cahore (30 km north of Wexford Slobs) as well as wet grassland around Tacumshin Lake and Lady Island Lake (both within 10 km of South Slobs).

Since 1986, almost annual reports of Greenland White-fronted Geese from Jæren in Rogaland County, Norway (58°5'N, 5°55'E). Up to 300 Whitefronts (both *albifrons* and *flavirostris*) have been reported, including 2 collared at Wexford (one of which was shot on 15 September 1991; Jensen and Mjøs 1998; P Shimmings in litt.). Considered that between 1 and 20 *flavirostris* have wintered (November–April) regularly in Norway since 1988.

Present wintering range of Greenland White-fronted Goose considered to have changed very little in last 50 years but, nevertheless, Ruttledge and Ogilvie (1979) documented 34 deserted sites in Ireland and three in Scotland until 1979, and Fox *et al.* (1998a) reported a further seven (five in Ireland) by 1994/5. Despite recent increase in numbers, a further five flocks remain close to extinction. Marked differences between patterns of change at different wintering sites, relating to differences in breeding success, survival, and annual immigration/emigration. Uneven distribution of family parties among wintering flocks on Islay, with certain areas (especially certain farms) supporting more juveniles over several winters, although habitat did not appear to affect site selection by families (Ridgill *et al.* 1994). Islay and Wexford have higher levels of annual production than other areas and, until early 1990s, Wexford had greater proportions of young in winter than Islay, although this has reversed since mid-1990s.

SPRING MIGRATION. Migrates directly from wintering areas to stage in south and west lowlands of Iceland, using same areas as in autumn (see Autumn Migration). On arrival in west Greenland, lowland areas of early thaw especially important (e.g. Fox and Madsen 1981). Cluster of records from south-east Greenland, especially in Ammassalik area, in spring and autumn suggest that it may be regular visitor, especially on spring migration having successfully crossed from Iceland. Records from further north (including moulting individuals) presumably relate to geese associating with breeding Pink-footed or Barnacle Geese in east Greenland that have summered there (Stroud and Fox 1981). One fitted with satellite radio tag summered in south-east Greenland in 1999, but returned to Wexford next winter. Using satellite imagery to assess snow cover in west Greenland and to derive index of vegetation cover in early May, Glahder (1999a, b) identified 35 potential spring staging areas between 63° and 70°N. Using helicopter searches to determine true importance of these sites, located 28 spring staging areas supporting 1000–1500 geese in all, almost all in Kangerlussuaq area (66°29'N–68°21'N; Glahder 1999a, b).

Population. (Updates *BWP* Vol. I, pp. 404–6)

Regular counts available from Islay since 1962 and Wexford since 1968, as well as from few other sites in Britain and Ireland. Based on literature survey and responses to questionnaires or enquiries, Ruttledge and Ogilvie (1979) suggested that global population of 17 500–23 000 in 1950s had fallen to perhaps as few as 14 300 by late 1970s. Based on Ruttledge and Ogilvie (1979) and further research, and internationally coordinated annual surveys since their time, now more confidently known that population comprises *c.* 35 regularly wintering flocks in Ireland and 33 in Britain. Census of entire population annually since 1982/3, during which time numbers have increased from 16 000–17 000 to *c.* 33 000 (Stroud 1984, Fox *et al.* 1994, 1998a, 1999b). Increases most dramatic at Wexford (where numbers increased from 5000–6000 to just over 10 000 in early 1990s, but numbers have since stabilized and declined slightly) and Islay (where numbers have increased from 3500 to 13 000). At 17 Irish sites, numbers have increased, 10 are stable, and 8 have declined since 1982/3 (Fox *et al.* 1998a). In Scotland, most sites show stability or increase but, numbers continue to decline at five sites. Seven sites totally abandoned in last 18 years (Fox *et al.* 1998a).

Survival. (New section)

Using Haldane (1955) method, Boyd (1958) estimated annual adult survival to be 66.1% (SE = 3.6) based on recoveries of birds ringed during 1946–50. Subsequently, Kampp *et al.* (1988) used similar methods for recoveries from 1946–74 and found survival rates of 76.7% (SE = 3.4). More recently, Bell *et al.* (1993) used resightings of neck-collared birds marked at Wexford during 1984–9 to calculate annual adult survival using SURGE4 (Clobert *et al.* 1987, Pradel *et al.* 1990) to generate maximum likelihood estimates of 78.5% (SE = 1.4). This compares with 72.4% (SE = 7.3) based on same data using BROWNIE (recoveries only; Brownie *et al.* 1985). More recent analysis has been undertaken using combination of recoveries and resightings of collared birds at Wexford using MARK (White and Burnham 1999, using recovery–recapture models of Burnham 1993 and multi-stage models of Hestbeck *et al.* 1991). Selected model of adult survival varied independently with year [weighted mean 78.5%, 95% confidence limits (CL) 76.2–80.5%] and juveniles (67.8%, 63.2–72.0%), with 7% permanent emigration per year (M Fredriksen and A D Fox unpublished data). All but latter of these methods (which incorporates emigration estimate) underestimate true return rates to winter quarters. Crude survival rates based on census data and proportions of young (i.e. survival ± balance of emigration and immigration) varied between 72.8% and 97.7% (mean 85.2%) at Wexford during

1968–99 (unpublished data). Same apparent survival rate varied between 76.2% and 100% (mean 84.3%) on Islay for 1983–94 (Pettifor *et al.* 1999) and was significantly higher after protection than before (Fox *et al.* 1994).

Diseases and parasites. (New section)

Very little known, but cestodes *Drepanidotaenia barrowensis* (Schiller 1952) and *Hymenolepis creplini* (Krabbe, 1869) have been found in faeces and upper small intestine of Greenland White-fronted Geese. Nematode *Heterokis dispar* (Schränk, 1790) also present in caeca of 2 of 24 shot Whitefronts on Islay (Stroud 1981f). In early December 1992, several Greenland White-fronted Geese picked up dead and dying in and around Wexford Harbour. In all, some 36 bodies retrieved, including 4 collared birds (1.6% of marked population that year), and further 80–100 showed severe symptoms of disease. Veterinary examination showed severe haemorrhaging in birds that had died, and isolation of *Pasteurella pneumotropica* from bodies was suggestive of outbreak of septicaemic pasteurellosis (O'Sullivan *et al.* 1992).

Conservation. (New section)

HUNTING LEGISLATION. Following first appraisal of global distribution and abundance in late 1970s, conservation concern was expressed for Greenland White-fronted Goose (Owen 1978, Ruttledge and Ogilvie 1979). Led to enhancement of conservation status throughout its range, especially through protection from hunting and site safeguard (see Stroud 1992 for full protection status over last 50 years). In both Britain and Ireland, national legislation incorporates requirements of EC Directive on Conservation of Wild Birds (EEC/79/409). Directive, which came into effect in 1979, lists Greenland White-fronted Geese in Annex I requiring Member States to take special conservation measures regarding habitat, in particular classification of Special Protection Areas (SPAs) to be given strict legal protection. Consequence was protection of subspecies in Ireland from 1982, when hunting moratorium was declared there (although this was lifted temporarily at Wexford in winters of 1985/6 and 1989/90 under strict bag limitation under Wildlife Act 1976). Greenland White-fronted Geese protected from hunting in Northern Ireland in 1985 [Wildlife (Northern Ireland) Order 1985] and in Scotland since 1982 (Wildlife and Countryside Act 1981). Nevertheless, in Scotland, some 200 geese have been shot on Islay under licences issued by Scottish Office (now Scottish Executive) in response to alleged serious agricultural damage. Remains legal quarry in England and Wales, but last regular site (Dyfi Estuary in Wales) continues to be subject to voluntary shooting ban by local wildfowling in effect since 1972 (Fox and Stroud 1985). In Greenland, protection extended in 1985 from

just nesting period to include most of spring arrival with hunting season shortened to 15 August–30 April. Thought that 100–200 birds killed here annually (P Nielsen). In Iceland, population legal quarry between 1 September and 15 March, which effectively restricts hunting to autumn, since most do not arrive until mid-April (see Movements). Some 3000–3500 shot every year: 3237, 2947, 3185, and 3215 in 1995–8, respectively (Wildlife Management Institute 1999). Age ratios in sample of wings returned by hunters and ringing recoveries suggest that high proportion of young killed at this time (A Sigfusson in litt.). Among recovery sites of geese marked in Greenland, Ireland, and Britain or reported from Iceland, most have provided one (73 sites) or two recoveries (23 sites), but Leirulækjarsel and Bóndhóll (Mýrarssýsla) have provided 8 and 7 recoveries, respectively. Kolviðarnes (Snæfellsness-og Hnappadalssýsla, 8) and Thykkvibær (Rangárvallassýsla, 7) are known popular hunting sites.

SITE SAFEGUARD. Britain and Ireland have special obligations under EC Birds Directive to protect both population and habitats of Greenland White-fronted Geese. More general obligations of Ramsar, Bonn, and Berne Conventions also apply (de Klemm and Shine 1993). Use of Ramsar 1% criterion for site protection has proved effective mechanism to provide site safeguard for larger concentrations, but fails to protect smaller more vulnerable flocks that show most dramatic declines (Fox *et al.* 1998a). Maintenance of current range on very western fringe of European landmass represents important contribution to local biodiversity in these biogeographically unique areas. Given high winter site fidelity of individuals from this population, site safeguard represents important contribution to overall conservation of population. Listed as of high status by recently concluded African–Eurasian Waterbird Agreement, which requires and encourages range of co-ordinated international conservation actions. Throughout wintering areas, conservation has concentrated on protection of most important natural and semi-natural habitats, as well as safe roost-sites that have been used for many years. Geese may sometimes switch feeding areas in response to local management at sites where dependent on cropping regimes, hence 'wider countryside' conservation measures may often be appropriate to support site safeguards. In these circumstances, especially in Republic of Ireland, local management agreements have been adopted to maintain agricultural conditions suitable for geese. Only in relative few situations in Ireland have major state land acquisitions resulted in reserves specifically for White-fronted Geese. This is the case at Wexford Slob Wildfowl Reserve in south-east Ireland, where 470 ha of farmland have been

acquired primarily for Greenland White-fronted Geese during winter and provide increased public awareness through visitor observation and interpretation facilities (Wilson 1996).

Site protection in UK is based on designation of EC Birds Directive SPAs and Ramsar Wetlands of International Importance (which protect or are proposed to protect 17 sites supporting Greenland White-fronted Geese), National Nature Reserves (NNRs), and Sites of Special Scientific Interest (SSSIs) or, in Northern Ireland, Areas of Special Scientific Interest (ASSIs). These cover, in whole or in part, 22 sites used by geese. UK SPA network anticipated to hold *c.* 8240 geese at 12 SPAs specifically classified for Greenland Whitefronts (59% of British total and 28% of international population in mid-1990s; Stroud *et al.* 2001.). SPA suite includes state-owned NNR, Eilean na Muice Dubh/Duich Moss on Islay, most important single roost-site in UK acquired following major threat from commercial peat-cutting in 1980s (Nature Conservancy Council 1985, Stroud 1985, Greenland White-fronted Goose Study 1986). Statutory protection measures supplemented by nature reserves established by NGOs such as RSPB (five reserves: on Islay, Colonsay, Coll, Loch Ken, and Dyfi Estuary).

In Republic of Ireland, site protection now founded on designation of Natural Heritage Areas (NHAs), formerly Areas of Scientific Interest (ASIs). Fifteen actual or proposed SPAs and/or Ramsar sites, 31 NHAs, and 4 additional areas covered by management agreements protect areas used by Greenland White-fronted Geese in Ireland, although in some localities area protected is less than total used.

In Iceland, currently only one site with formal protection that supports migrant Greenland White-fronted Geese, namely Pollengi, Biskuptungur, in south-west Iceland. Six sites known to be used by Whitefronts mentioned in Nature Conservation Register of Iceland (which lists sites of national importance) and these also feature in Important Bird Areas list compiled by BirdLife International partner for Iceland. Five of these are in southern lowlands, sixth in west, but none has statutory protection, management, or monitoring. Most important staging area, Hvanneyri Agricultural University in west of Iceland, recently (2002) declared a reserve for the staging geese. Voluntary ban on shooting at the site has made this the single most important staging area in Iceland, with up to 1600 staging in spring and more than 2000 in autumn 2001.

In 1989, Greenland Home Rule Authority announced five major Ramsar wetlands of international importance covering some 700 000 hectares of goose summering areas (for full details, see Jones 1993 and Fox *et al.* 1994).

In 1992, aerial surveys indicated that protected areas north of Kangerlussuaq (including Eqaalummiut Nunaat), Naternaq, and three important areas on Disko Island (Aqajarua-Sullosuaq, Qinguata-Kuussuaq, and Kuanersuit kuussuat) held approximately one-fifth of summering population. Very important wetlands of Svarthuk peninsula have also been considered for future designation as Ramsar site.

DISTURBANCE. Disturbance plays pronounced role in winter ecology of Greenland White-fronted Geese because of extensive fragmentation of traditional feeding ranges. Recent changes in individual flock sizes in Ireland were correlated with number and size of feeding sites and with disturbance rate, and use of individual feeding sites may relate to relative levels of disturbance (Norriss and Wilson 1988, Fox *et al.* 1989, 1998a). Agricultural disturbance was single most important source of disruption in Ireland and overall rates of disturbance were highest on most intensively managed farmland (Norriss and Wilson 1988). However, some suggestion that geese using dry and improved grassland had greater tolerance to disturbance than those on wet pastures, although sample sizes were small (Norriss and Wilson 1988). Even on traditional bogland, may be disturbed by large numbers of Sika Deer *Cervus nippon* which actively forage amongst geese (apparently for goose droppings). Originally thought that geese obtained some vigilance benefit from association with deer (Carruthers 1988), but now thought that deer initiate contact, to detriment of geese at high deer densities (T Carruthers in litt.).

In late 1980s, model aircraft tested as technique to displace geese from most sensitive grassland areas on Wexford Slobbs (Walsh 1993). Flying at low altitude (<25 m), these had devastating effect on geese, invariably flushing 80% of all geese within 500 m. Flying at greater heights (up to 60 m), all geese were flushed from area of 500–800 m and none returned within 2 h, although individually marked birds did return to their original feeding site later in day (Walsh 1993). Geese took off low and flew at speed directly away from model aircraft and, on one occasion, some were killed in collisions with overhead power cables. During same period, numbers using 80 ha of large low-lying grassland fields close to coast at Cahore (*c.* 30 km north of Wexford Slobbs) increased in response to disturbance on their regular feeding areas. Model aircraft flying took place from February to April in 1988/9 and 1989/90, and goose numbers increased at Cahore in spring. However, spring build-up in numbers took place 3 weeks before flying commenced and geese actually returned from Cahore to Wexford in 1988/9 during late March/early April when aircraft scaring was still taking place. Of seven collared

birds seen at Cahore, two regularly resighted back at Slobs after 20 March. Hence, despite appearances, seems unlikely that flying model aircraft alone was responsible for shifts in wintering area (Walsh 1993).

Detailed studies also showed that wintering Greenland White-fronted Geese tended to avoid strip of grassland within 75 m of busy access road, but fed right up to sea wall embankment (subject to very low levels of public access; Walsh 1993). Effects of such disturbance were detectable up to 150 m from field margins bounding copse showing that geese also avoided wooded fringes of fields (Walsh 1993).

EFFECTS OF CONSERVATION ACTIONS. After protection from hunting on wintering range in 1982/3, population increased from 16 500 (1983) to 33 000 (1999), although rate has slowed in recent years. Despite overall increase, seven flocks have become extinct and 18 more have declined under protection: indeed, only 20 sites show increases (Fox *et al.* 1998a). Analysis suggests that size, number, and quality of feeding sites, disturbance levels, flock size, and latitude all influence flock status—small, most southerly flocks on poorest and most limited feeding ranges show most serious declines (Fox *et al.* 1998a). Hunting mortality appears to be largely additive, so effects of hunting bans on wintering grounds probably directly responsible for subsequent increases under protection at major resorts of Islay and Wexford. Recent policy document from Scottish Office, stated that 'given the potential vulnerability of this sub-species from quite small changes in additional mortality, it is not recommended that the population be returned to the quarry list' and '... it is not recommended that an enhanced level of licensed hunting be resumed on this population' (Scottish Executive 2000).

POTENTIAL INTER-SPECIFIC COMPETITION. Since mid-1980s, Canada Geese *Branta canadensis interior* have become established as common breeding bird in areas of west Greenland previously exploited only by Greenland White-fronted Geese (Fox *et al.* 1996). Ringing has shown that these Canada Geese winter in eastern USA, from Massachusetts and Connecticut south to Delaware, and probably originate from the Ungava Bay population (Kristiansen *et al.* 1999a). Canada Geese arrive in late May and commence nesting close to open water, so little competition in time and space for nesting habitat between this species and Greenland Whitefront. However, during moult, both species use same habitats and areas to regrow flight feathers. At this time, both largely confined to areas within 50 m of open water and, during this critical phase in life cycle, there is potential for competition (Kristiansen and Jarrett 2002). In sympatry, diet of Greenland White-fronted Geese included higher levels of poor-quality bryophytes compared with sites from which

Canada Geese were absent (Jarrett 1999, Kristiansen 2001). Faecal analysis suggested that Canada Geese had broad dietary range that changed little between sympatric and allopatric sites; in contrast, allopatric Whitefronts showed very narrow niche breadth, suggesting that this species is specialist grazer (Jarrett 1999, Kristiansen 1997, 2001). Appears that co-existing with Canada Geese results in switch to more generalized diet, perhaps due to competition for favoured food items with Canada Geese. Two species appeared to segregate where they co-exist and, in 45 agonistic interactions, Canada Geese always won, even when outnumbered (Kristiansen and Jarrett 2002). As consequence, Whitefronts stop feeding and adopt alert posture when Canada Geese approach within 3 m (Jarrett 1999, Kristiansen 2001). In study area in Isúngua, numbers of both species increased from 1988 but, in mid-1990s, Greenland Whitefronts began to decline and have disappeared as moulting birds from many lakes in this area where Canada Geese now predominate. Implications from this study of small area are that Whitefronts forced to moult with Canada Geese may be subject to exploitative competition as favoured plants are eaten out and interference competition when dominant species physically prevents access to potential feeding areas. Data from 1999 aerial survey suggest that, although both species showed highest densities in same Kangerlussuaq region, at local scale were less likely to co-exist than expected by chance (Malecki *et al.* 2000).

Movements. (Updates *BWP* Vol. I, p. 406)

Data come from metal ring banding carried out by Copenhagen Museum during 1940s and 1950s, from small-scale ringing with plastic tarsus bands in Greenland in 1979 and 1984, and from extensive colour marking (principally using neck collars) in Ireland (mainly at Wexford Slobs) since 1983. More recently, geese also collared in Scotland, Iceland, and Greenland as part of continuing international marking programme. Analysis of recoveries and resightings of individually marked birds confirms that birds from south of wintering range tend to breed in north of breeding quarters (Salomonsen 1967, Fox *et al.* 1983, Kampp *et al.* 1988). However, this is at best only a trend, since geese ringed together in moulting non-breeding aggregations in Greenland have dispersed throughout entire wintering range (Fox *et al.* 1983, Wilson *et al.* 1991). Although birds tagged with satellite-transmitters from Wexford tended to return to north of breeding range, two individuals summered near Kangerlussuaq in centre and several staged in south Greenland in 1998 and 1999 before moving northwards (Glahder *et al.* 1999; unpublished data).

Literature review (Stroud and Fox 1981), radar studies (Alerstam *et al.* 1986), and use of satellite telemetry

(Glahder *et al.* 1999) provide basic information about migration patterns. These confirm migration directly from wintering areas between 6 and 25 April (extremes 1 April and 3 May; Francis and Fox 1987) to south and west Iceland, although final departures most frequent 15–22 April. Based on satellite telemetry, spring departure from Wexford occurs between 7 April (1997) and 14–19 April (1998 and 1999), with arrival in Iceland between 17 and 22 April in all three years (birds stopped off elsewhere in Ireland in 1997). In many years, geese depart during calm anticyclonic conditions or wait for assisting tail winds before departure (O J Merne, A J Walsh). In 1997 and 1998, geese initiated migration shortly after wind had changed to southerly direction, maintaining ground speeds between 50 and 90 km/h, following narrow migration corridor only 100 km wide (Glahder *et al.* 1999).

Satellite-tagged individuals staged in Iceland for mean of 18.2 days (range 12–21 days), with onward migration between 2 and 10 May. Observations of collared birds show that these may remain at same site in Iceland for up to 3 weeks, although overall migration period ranges from *c.* 10 April until *c.* 12 May (Fox *et al.* 1999b, Glahder *et al.* 1999). Generally, geese using southern and western staging areas (see Distribution) show very high degree of site loyalty with few records of individuals moving between staging areas within or between migration episodes (unpublished data). Eight geese fitted with satellite transmitters in Wexford staged in Hvanneyri or Mýrar areas of west Iceland, four in south-west Iceland, although one moved from latter to west after 1 week (Glahder *et al.* 1999). Owen *et al.* (1986) stated that the stopover in Iceland is too short 'to make a substantial contribution to feeding requirements on migration'. However, it is apparent from increase in abdominal profiles that this refuelling stop is important for rapid accumulation of fat (Boyd *et al.* 1999). Indeed, changes in abdominal profile and sequential capture of geese through spring of 1999 suggested that adult males may accumulate 500 g and adult females 400 g of body mass during 3-week staging period in Iceland (Nyegaard 2001).

All three tagged geese left Iceland on 7 May 1998 when winds swung to south-east and major departures were observed (Glahder *et al.* 1999). All arrived in west Greenland during 8–10 May, possibly after resting in east Greenland for up to 2 days, one south of Ammassalik (65°N) and the others further north (66°15'N). In 1999, average departure date was 8 May (range 2–10 May), all flew along similar migration corridor, spread over some 300 km at its widest. Flight speeds similar over open sea and ice, but took longer to climb over east coast of

Greenland. Average arrival was 9 May 1998 (range 9–10 May) and 11 May 1999 (range 3–17 May), which corresponds to general observations of first arrivals in first week of May (Fox and Madsen 1981, Fox and Ridgill 1985, Glahder 1999a). Arrived in different initial areas between Kangerlussuaq Fjord (66°30'N) and northern Disko Bay (69°50'N) and most remained in same general area, as if exploiting specific staging areas from point of arrival. Two tagged geese briefly explored summering area during staging period before settling for summer. Geese staged to varying degrees (mean 9 days in 1998 when little snow cover, 16 days in 1999 when spring melt delayed) before continuing to ultimate summering areas (Glahder *et al.* 1999). Some summered relatively close to staging area, others continued as far north as Svartehuk (72°N) and Upernavik (74°N), but all remained in same general area for most of summer (Glahder *et al.* 1999).

Autumn departure of satellite-tagged birds from west Greenland took place 11–23 September in 1998 and 1999. Goose that summered on Svartehuk moved south between 15 and 21 September 1998, last recorded position before transmitter failure was over ice cap 100 km east of Ilulissat ice fjord (Glahder *et al.* 1999). Recoveries and resightings of individually marked birds show that staging period in Iceland extends from *c.* 30 August to *c.* 31 October, but much less known about return migration (Fox *et al.* 1999b). Birds staged for variable periods in Iceland before arrival in Wexford 2–27 October (unpublished data). We still know lamentably little about autumn migration.

Site fidelity between winters generally high (80% Islay; Ridgill *et al.* 1994; 85% Wexford), with no apparent difference between sexes (Wilson *et al.* 1991, Warren *et al.* 1992a). Most changes (67%) between years involved birds in their second or third years, so may be associated with pairing and break-up of family bonds (Wilson *et al.* 1991, Warren *et al.* 1992a). Most changes between years associated with pairing (Warren *et al.* 1992a). Site fidelity within winters also high, but geese wintering on Wexford Slob stage on Islay or nearby Kintyre in autumn en route (Wilson *et al.* 1991, Warren *et al.* 1992a). Some site interchange occurs between Irish sites, especially birds staging briefly in Irish Midlands in autumn en route to Wexford, and, in former times, some moved off Slob to other resorts in February. One satellite-tagged bird departed from Wexford as early as 7–9 April 1997 (when large number also left site) and spent from 10 April in Lough Foyle area of Northern Ireland before departing for Iceland *c.* midnight on 16 April (Glahder *et al.* 1999).

Despite extensive areas of uninterrupted agricultural habitat at Wexford Slob and on Islay, shows very high

fidelity to same set of fields between and within years (Wilson *et al.* 1991, Glahder *et al.* 1999). At Wexford, resightings in successive years show individual ranges generally 700–800 ha, but majority of positions represent excursive activity and 80% of reports from core range of <200 ha (Bell 1990). Intensive analysis of few individuals revealed discrete home-ranges for two groups of related birds centred on three and four grass fields, respectively, with excursive use of stubble and beet outside these core areas at appropriate times of year (Bell 1990). On Islay, maximum home-ranges varied between 42 and 1444 hectares, although many fields within home-range never used (Ridgill *et al.* 1994). More realistically, 80% of resightings were in areas of 13–20 ha in extent and individuals tended to use very small number of favoured fields both within and between winters (Ridgill *et al.* 1994). Geese concentrated in smaller number of fields early in season on Islay, but dispersed into smaller flocks using larger number of fields as winter progressed.

Food and feeding. (Updates BWP Vol. I, pp. 406–7)

GREENLAND. Based heavily on observations from Eqaalummiut Nunaat, hence not necessarily representative of entire range (Madsen and Fox 1981). Exploits below-ground storage organs of overwintering plant parts during May–July, but increases use of developing fresh green shoots and leaves, which displace below-ground parts in mid-July. Geese in Eqaalummiut Nunaat tended to move uphill, foraging especially on below-ground stem-bases of *Eriophorum angustifolium* as released by permafrost thaw at higher altitudes. Stem-bases are rich in protein and carbohydrates and are main over-wintering storage organ for this species of cotton grass (Phillips 1954, Shaver and Billings 1976), dominating diet during most of summer, therefore some detail given below regarding growth form and exploitation.

Overall size of *Eriophorum* shoot and stem-base decreases with altitude. At lowest altitudes (40–80 m a.s.l.), typical of areas used on first arrival, *Eriophorum* shoots very large (average 2.35–3.35 g wet weight, $n = 136$). In mid-altitude (270 m) marshes, close to nesting areas used in June, shoots smaller (average 1.85 g, $n = 108$), although *c.* 40% of shoot weight comprises stem-base (average wet weight 0.68 g) compared with *c.* 10–20% at lower altitudes. *E. angustifolium* plants at high altitudes, in areas used during moult, much smaller (average shoot weights 0.78–0.85 g; $n = 185$), whereas in high-altitude snow-patches (615 m) shoots are dwarfed (0.3 g/shoot; $n = 21$). On plateaux, stem-bases small in absolute terms (0.25 g at 485 m, 0.2 g at 545 m, 0.09 g at 610 m).

Given dietary preference for carbohydrate-rich stem-base and lower shoot, these data suggest that grazing *Eriophorum* shoots at low or mid-altitudes (<300 m a.s.l.)

is more cost effective (in terms of total nutrient intake related to energetic costs of extraction and handling) than higher up. Indeed, shoot bases rarely eaten in mid-summer (July and August) in plateau areas. Probably not only consequence of limited quantity (extraction costs of eating small shoots) but also declining quality as nutrients are translocated to leaves and flowers (Shaver and Billings 1976, Chapin *et al.* 1980).

Selection of *Eriophorum* shoots was not random. At lowest altitudes (<100 m a.s.l.), significant selection for smaller size classes. Here, shoot growth vigorous and few of the very largest shoots (>4.0 g) taken, probably because older, larger shoots more firmly rooted (Shaver and Billings 1976). At all altitudes, geese selected shoots of 0.5–1.5 g wet weight, irrespective of sizes available. On plateau areas (>400 m), overall smaller shoots result in apparent lack of selection between size classes available and taken.

Nutritional consequences of choices made have yet to be studied. Alaskan research (Shaver and Billings 1976), however, has shown that in arctic spring (June), stem-bases of *E. angustifolium* contain *c.* 20% by weight of sugars as well as significant quantities of storage polysaccharides. ‘Young’ small shoots, of size and age selected by Whitefronts in Greenland, have higher proportions of sugars and total non-structural carbohydrates (TNCs) than older, larger *Eriophorum* shoots. In absolute terms, *E. angustifolium* with its long-lived stem-bases stores more carbohydrate than other arctic graminoids (Shaver and Billings 1976).

Combining Alaskan data on *Eriophorum* nutrient quality with Greenlandic information of stem-base and shoot consumption indicates that, at low altitudes (<100 m a.s.l.), geese consume *c.* 18 mg dry weight TNCs per shoot extracted. At mid-altitude (100–300 m), this amounts to *c.* 11 mg TNCs/shoot, but on high plateaux (525–560 m) falls to *c.* 4 mg TNCs/shoot. Given very large numbers of shoots extracted by Greenland Whitefronts from wetlands at low and mid-altitudes through May and June, *Eriophorum* stem-bases clearly represent major source of easily metabolizable nutrients at time when other forage options limited.

Greenland pre-breeding. On arrival in spring, few observations show feeds initially on below-ground, overwintering parts of two cyperacean species, lower stem-base of *E. angustifolium* and bulbils of *Triglochin palustris*. Latter associated with lowland wetlands along fringes of fjords with sandy or muddy substrate that are amongst earliest areas to thaw. Both food items obtained by probing and rooting in substrate, even though above-ground visual cues for finding *Triglochin* are few (dead parts from previous years often absent). *Puccinellia*

deschampsoides, characteristic of these wetlands, also taken at this time, also rhizomes and developing shoots of *Hippuris vulgaris*. Much grit in faeces at this time, characteristic of foraging in minerotrophic wetlands (rather than peatlands), unlike other periods in summer. On arrival in Greenland spends 51–68% of total diurnal activity feeding (12.2–16.4 h/day), roosting only during sub-zero temperatures (Fox and Madsen 1981, Fox and Ridgill 1985). Attendant vigilant ganders in solitary-feeding (presumably pre-breeding) pairs enable females to feed for maximal uninterrupted periods, without risk of extra-pair copulations threatening ganders' paternity. Staging birds apparently spent less time feeding and twice as much time roosting compared with local breeding birds, although males still spent more time alert and less time feeding (Fox and Ridgill 1985). These males gain some advantage from joining groups of other geese, spending less time alert and more time feeding, although seemed no benefit to females from such social feeding (Fox and Madsen 1981).

Greenland incubation. Dominant food during early part of incubation is *E. angustifolium*. Stem-base and lower stem extracted from thawed substrates and consumed, leaving rest of above-ground parts, rhizome, and roots uneaten. Commonly root for below-ground storage organs of *Polygonum viviparum*, species also eaten in late summer when bulbils become available on lower part of flowering stem. However, as incubation progresses, more above-ground parts appear in diet, as growth gets under way and storage organs decline in quality. Hence, epidermal fragments of leaves from grasses and sedges appear more frequently in faecal material as season progresses, especially favoured *Carex rariflora*, although this may be linked to local relative abundance (Madsen and Fox 1981). Parental males fed for 24% of time on feeding marshes while female incubated, and showed most feeding activity between 23.00 and 06.00 hours (Stroud 1981*d*).

Greenland post-incubation. During latter part of incubation, most non-breeders move up to plateau lakes, where forage around margins. Here, feed on waterside vegetation, similar to that at lower altitudes, but with more *Equisetum*, grasses, and sedges and less *Eriophorum*. Dominant component is now *Carex rariflora*, major element of waterside vegetation. From hatch, goslings move to plateau where associate with marshes and open water. At this stage all family members graze fresh shoots and leaves; roots, rhizomes, and other subterranean parts totally absent from diet. Adult diet more varied at this time and differs considerably between sites, but nevertheless green parts of grasses and sedge predominate (Madsen and Fox 1981). Variety of grasses taken, including *Calamagrostis langsdorfi* and *C. neglecta*, as well as

various cyperaceans (e.g. *Juncus arcticus*, *Luzula multiflora*; Kristiansen 1997). Later, *Trisetum spicatum* and *Poa pratensis* taken increasingly until late in moult, when most important. These two species were especially common on late snow patches that are last areas to thaw close to plateau lakes. Immediately after hatch, gosling diet dominated by *Equisetum* although increasingly diet resembles that of parents until, in late July, food items functionally the same. *Equisetum* frequent in diet at several times throughout summer, but never dominant in adult diet because of small size and relatively low abundance. High in protein and energy, which may explain why seems favoured by females during recesses from nest and forms dominant part of gosling diet in early stages (Madsen and Fox 1981, Kristiansen 1997). Herbs (such as *Stellaria longipes* and *Euphrasia frigida*) and bryophytes taken in small amounts by adults, perhaps ingested with more favoured items, but tend to be more common in faeces of young goslings. Under normal circumstances, mosses taken in small amounts by moulting geese, but perhaps highly significant that, in presence of Canada Geese, level of moss remains in faecal material much higher than in similar habitats where moult alone (Jarrett 1999, Kristiansen 2001). Brood-rearing parents fed for c. 35% of time, non-breeders c. 33%, and goslings c. 62% (Madsen 1981).

ICELAND. Thought to traditionally exploit bogs and wetlands of lowland Iceland, feeding on lower stems of two cyperacean species extracted with bills from soft substrates. To this day, many still use natural boglands where extract *E. angustifolium* (e.g. Garðarsson 1974, 1976). This species especially abundant in numerous drained lakes of south and west Iceland created by drainage schemes, but which frequently retain large stands of *Eriophorum* in peaty sediments and remaining shallow water. *Carex lyngbyei* also eaten, large robust sedge, widespread on coasts of north America, but known only in Iceland in Europe. Has stem structure very similar to *E. angustifolium* and an extremely nutritious lower stem which geese extract, deftly nipping off more fibrous and energy-poor parts of plant which, like *Eriophorum*, remain floating as conspicuous evidence of feeding activity. Rhizomes have high metabolizable energy in spring (McKelvey 1985). *C. lyngbyei* was grown as hay crop during much of 20th century, by flooding of large areas (Ingvason 1969). Grows naturally in saltmarshes, along river and glacial melt river floodplains, and in bogs and fens, and was successfully cultivated by creating shallow water conditions by artificial flooding in southern Iceland. From 1950s, this practice gradually abandoned as new varieties of grass became available (especially Timothy *Phleum pratense* from Norway) and maintenance

declined drastically. Now, only areas with abundant *C. lyngbyei* still extensively exploited by geese on passage are around Borgarfjörður, especially below farm of Bönðhöll and at Hvanneyri, where sedge meadows still harvested for their haycrop. New lateral shoots extracted and eaten in spring as these grow from parent plants of previous year (D Stroud *et al.* in prep.). Geese select areas with highest abundance of such shoots, which often exhibit relatively low plant densities. Feeding areas selected on basis of plant size and softness of substrate, areas which are earliest to thaw and which remain waterlogged (e.g. runnels and flush lines) being favoured over drier firmer substrates where extraction more difficult (D Stroud *et al.* in prep.). As in Greenland, *Triglochin palustre* taken, especially along glacial melt river flats where may be locally abundant on sandy and muddy substrates (e.g. in Biskuptungur). In some areas, geese can be found in heathy areas and species-rich pastures where take *Equisetum* and rhizomes of *Polygonum viviparum* (especially in autumn; Garðarsson and Sigurðsson 1972). However, in most frequented areas, most choose agricultural fields, and especially select Timothy grass *Phleum pratense*. This non-native species has become commonly grown for hay and silage, and exhibits earlier growth than native species such as *Poa pratensis* and *Deschampsia caespitosa*. Geese take only youngest leaves, which stand erect, whilst leaving two prostrate leaves that continue to provide photosynthetic products to growing plant. *Phleum* responds to such defoliation by rapid nutritious regrowth of youngest leaf, a feature exploited by Whitefronts (Fox *et al.* 1998b). These youngest leaves selected only to minimum threshold size, presumably below which nutrient gain does not merit harvest (Kristiansen *et al.* 2000b). Hence, when all suitable leaves of *Phleum* eaten, geese abandon fields to forage elsewhere, leading to sequential use of individual fields (Fox *et al.* 1998b). In early season, when *Phleum* offers the only green forage, its relative abundance is major determinant of distribution of geese between fields (J Kristiansen *et al.* unpublished). Other common hayfield grasses also taken, especially once first flush of *Phleum* removed. Despite tussocky nature, *D. caespitosa* can yield high protein content. Its leaves grow more rapidly, in greater abundance, and have higher protein content on south-facing side of tussocks, feature exploited by geese, which tend to forage more on southern side (Kristiansen *et al.* 1998). On Icelandic hayfields in spring, geese fed for 80–90% of the 15–18 h of daylight, feeding least and roosting most in early morning after flight from roost (Nyegaard 2001).

BRITAIN AND IRELAND. Winter. Feeds by grazing green leaves and probing for rhizomes, stems, and stolons

throughout winter (Pollard and Walters-Davis 1968, Ruttledge and Ogilvie 1979, Fox *et al.* 1990). Excavates submerged vegetation (Mayes 1991) and will even occasionally strip seeds in autumn (*BWP* Vol. I; Fox and Stroud 1985). Traditionally, fed predominantly, but not exclusively, on boglands where probed for, uprooted, and ate storage organs of *Eriophorum angustifolium* and *Rhynchospora alba* (which overwinters as small bulbils in substrate). Ruttledge (1929) first described feeding on *E. angustifolium* with distinctive bitten-off parts of plant left on surface (Cadman 1953, 1956, 1957, Pollard and Walters-Davis 1968, Fox *et al.* 1990).

Islay. Feeds for 51–77% of daylight on variety of grasses. Those selected above their abundance in sward include *Lolium perenne*, *Alopecurus geniculatus*, *Festuca rubra*, *Agrostis stolonifera*, *Poa trivialis*, and *Anthoxanthum odoratum*. *Holcus lanatus* has been recorded from faecal material. *Trifolium repens* and *Ranunculus repens* taken, probably in mid-winter when geese spend more time probing and tugging at roots and stolons. From mid-February, almost all feeding is by pecking, maintaining high intake rates from grass sward (Ridgill *et al.* 1994).

On arrival in October, extensive feeding at peatland roosts on *Juncus bulbosus* stands (which are rapidly depleted) and on stalks and stems of *Menyanthes trifoliata* and *Nymphaea alba*, then dying back at end of growing season. By mid-November, these are exhausted and for rest of winter roost feeding focuses on stem-base and lower shoots of uprooted *E. angustifolium*. While *E. angustifolium* widespread in peatlands on Islay, solely taken from softest areas of peatland, flushes, or *Sphagnum cuspidatum*-dominated pools (Bignal and Curtis 1981; the M3 *E. angustifolium* bog pool community and M2 *S. cuspidatum/recurvum* bog pool community of Rodwell 1991). In these habitats, shoots easily extracted without leafy shoot breaking off from base. Ease of extraction of whole (i.e. including complete stem-bases) *E. angustifolium* shoots on winter peatland feeding areas strongly correlated with substrate softness. Investigated on Islay with shoots extracted by hand mimicking geese with substrate softness measured by soil penetrometer (DAS unpublished data). Average weight of extractable stem-base at softest locations was 0.53 g/shoot (95% of shoots extracted with whole stem bases); at locations with firmest peat only 0.042 g/shoot (21% of stem bases extracted whole)—a 12-fold difference. At randomly chosen locations within peatland roost, substrate significantly softer at locations used by feeding geese than elsewhere ($P < 0.001$, comparison of softness at 18 sites each measured at 20 locations). Local selection of feeding pools appears to vary between years as *Eriophorum* shoots recolonize soft substrates (DAS unpublished data). At

peatland pool complex on Islay, use of pools closely linked to water level, local extraction of *Eriophorum* shoots being higher at high water levels (DAS unpublished data). Based on grazed remains of *E. angustifolium*, original ungrazed size and weight of shoot stem-base before extraction could be calculated (and thus amount of tissue eaten; DAS unpublished data). On Islay in 1981/2 all grazed shoots on peatland pool complex collected weekly. Wet weight of stem-base and lower shoot eaten varied between 0.11 and 0.36 g/shoot, amounting to 20–40% of total wet weight of the *Eriophorum* shoots extracted (Phillips 1953, 1954). More *Eriophorum* shoots taken later in winter. Strong correlation between bite size and plant weight, hence more of shoot eaten from larger plants in all winter months. Some evidence for selection of rhizomes, remains of which often found amongst extracted leafy shoots (DAS unpublished data).

Wexford. Stubble grain invariably first source of food on arrival from Iceland in autumn. *L. perenne* dominant grass taken in reseeded; fodder and sugar beet taken when available (Mayes 1991). Also feeds on carrots and potatoes when available.

Elsewhere in Ireland. Mayes (1985, 1991) reported geese using *L. perenne* and *Glyceria fluitans* in floodplain grasslands, where *Agrostis stolonifera* also taken, but (despite its abundance) never dominant in diet. *F. rubra*, *Agrostis* spp., *Anthoxanthum odoratum*, *Equisetum* spp., *T. repens*, *F. ovina*, *H. lanatus*, and *Alopecurus geniculatus* also taken. Diet in late autumn and April includes much non-leaf material, such as grass roots, stolons of *T. repens* and *Agrostis stolonifera*, subterranean parts of *J. articulatus*, and *R. repens* roots. Bogland birds in Killarney Valley spent 65–88% of time feeding, mostly on *Rhynchospora alba* (Carruthers 1991, 1992). On blanket bog in Co. Kerry, Mayes (1985) found *R. alba* main food (58–85% of droppings), with *Trichophorum caespitosum* (6–38%) and *Eriophorum angustifolium* (0–16%) taken to lesser extents. One sample contained 9% *Narthecium ossifragum*, a dietary item unknown elsewhere. *E. angustifolium* taken appeared to be leaves rather than shoot base. Some faecal samples from Midland raised bog were composed entirely of *R. alba*, while others consisted wholly or in part of grasses (principally *A. tenuis*), reflecting use of raised bogs both as feeding sites and as roosts for birds feeding in surrounding farmland (Mayes 1985). High utilization of *R. alba* and low use of *E. angustifolium* on Irish peatlands contrasts with Scotland where reverse appears to hold.

Social pattern and behaviour. (Updates *BWP* Vol. I, p. 407)

BREEDING DISPERSAL. Not markedly territorial, nests widely dispersed in open tundra: mean inter-nest distance from nearest neighbours was 2.08 km in 1979 and

1.98 km in 1984 (Fox and Stroud 1988). See Breeding for nesting densities throughout range.

ROOSTING. In winter, tends to use discrete night-time roosts away from daytime feeding areas. At Wexford, geese fly out to intertidal sand and mud flats off Raven Point and in Wexford Harbour to roost at night. Feeding group using Cahore Marshes (35 km north of Wexford Slobs) flies back to these roosts at night. Flock feeding around Stranraer also roosts on intertidal flats, but majority of flocks roost on lakes or pools within bog landscapes. On Islay, over 60 different roost-sites used by more than 100 birds, although use varied through winter (McKay 1992). Some changes appeared associated with state of moon, major core roosts being used during new moon, but 'satellite' roosts being utilized during full moon, especially in mid-winter (McKay 1992). At Wexford, night-time feeding at full moon is commoner in mid-winter than autumn or March/April (A J Walsh). Hence at two major wintering sites, may return from roost to feed under full moon, especially when day length is minimal. On Islay, most geese left feeding areas 25–70 min after sunset (mean 49.4, SE = 23.05, range 0–112 min), although this varied with season. In December/January when day length is shortest, earliest departures occurred at least 30 min after sunset, with further departures spread over following hour. In March, earliest departures at or very soon after sunset with significant negative correlation between sunset–departure interval and time of sunset, suggesting that geese are less able to attain food intake requirements during shortest day length (Mayes 1991, McKay 1992).

FLOCKING. Size of winter flocks, defined as discrete group of socially interacting geese at least 100 m distant from other birds, recorded during systematic surveys on Islay between 1984/5 and 1987/8 (unpublished NCC reports 1984–8; Easterbee *et al.* 1990). Combining all data for all months in all years indicates average flock size very small compared with other species of geese. Of 3162 flocks, 52.9% held 29 or fewer geese, while only 7.5% of flocks held >140 birds. Pronounced seasonal differences in flock size, however.

In all years, flock sizes greatest in autumn (October and November) when birds fed on stubbles in large groups after autumn arrival. Few large flocks (maximally 400–700, median *c.* 40) fragmented into many smaller flocks. In all years, median sizes were smallest in January (22–32). In two years, flocks continued to decline into April (e.g. April 1986, median of 308 flocks = 17), while in another two years small, mid-winter flocks started to aggregate in March into larger spring groupings (e.g. late March 1985, median of 175 flocks = 34). Latter situation probably represents the norm. Changes

in flock size not associated with gross distributional changes on Islay (Bignal *et al.* 1988). Rather, following collective feeding in autumn, in mid-winter smaller groups (presumably of extended families; Warren *et al.* 1993) feed separately within shared home-ranges or functional units (Wilson *et al.* 1991).

RELATIONS WITHIN FAMILY GROUP. Individually marked birds observed at Wexford Slobs in south-east Ireland allow study of long-term parent-offspring bonds. In first winter, juveniles associated with one or both parents in 94% of 188 occasions (Warren *et al.* 1992b). Generally, young remain close to parents through winter, although in rich feeding opportunities (e.g. fodder beet or stubble) inter-bird distances may become extended, and familial relationships become difficult to detect. Regular observations (3–4 times per week, September–April) established that family cohesion was consistent through first winter, and the residual 6% probably reflects temporary separation or failure to observe or read collars. Subsequently, 68% seen with one or both parents in second winter, 49% in third, 33% in fourth, 31% in fifth, and 2 birds (25%) remained with single parent for six winters (Warren *et al.* 1992b). Mean age of leaving family was 1.65 (males) and 2.00 (females) years, although these not significantly different (Warren *et al.* 1992b). No suggestion that offspring left families when parents bred again; indeed, of five collared pairs that bred in consecutive years, four offspring from previous year associated with parents and new brood in following year. Even if parent-offspring bond had weakened, 14% of birds associated with one or more siblings after having left their parents, 11% paired, and 14% associated with other unmarked geese on leaving parents. Evidence exists that subadults associate with breeding birds during breeding season (Stroud 1981a, d) as observed in other Whitefronts (e.g. Ely 1993, Fox *et al.* 1995). Warren *et al.* (1992b) suggested that large body size, discrete nature of traditional peatland feeding habitat, and suggestion of alloparental care (Ely 1979, Stroud 1981d, Fox *et al.* 1995) may partly explain extreme persistence of parent-offspring associations in this population.

Voice. (Updates *BWP* Vol. I, pp. 407–8)

Voice of males more highly pitched than that of females.

Breeding. (Updates *BWP* Vol. I, p. 408)

SEASON. Generally arrive on breeding grounds between 28 April and 5 May, with considerable movement northwards during early May. In Eqaalummiut Nunaat, first arrivals recorded on 7 May 1979 and 6 May 1984, but peak passage occurred on 12 and 8 May, respectively. Nest-site altitude in Eqaalummiut Nunaat influenced by availability of forage, determined by extent of snow

cover and phenology of thaw. In 1984, very late thaw commenced rapidly on 2 June when warm föhn wind spectacularly thawed snow at all altitudes simultaneously. This was in considerable contrast to 1979, when there was little snow cover, but thaw of substrate progressed slowly up altitudinal gradient. As a consequence, nesting occurred earlier (mean clutch initiation 22 May, 15 days after arrival, range 19–27 May) in 1979 mostly at low altitude (below 300 m). In 1984, nesting occurred later (mean 11 June, 34 days after arrival, range 6–17 June) and more often above 400 m (Fox and Madsen 1981, Stroud 1981b, Fox and Ridgill 1985, Fox and Stroud 1988).

NEST-SITE. In Eqaalummiut Nunaat, nests predominantly (1) on slopes above marshes; (2) on, or adjacent to, marshes; and (3) among hummocks adjacent to lakes (Stroud 1981b, Fox and Stroud 1988). Nests almost exclusively near (usually overlooking) *Eriophorum angustifolium*-dominated marshes that formed feeding area of attendant gander and female during her recess (Madsen and Fox 1981, Stroud 1981b, 1982, Fox and Stroud 1988). Nests generally in hollow top of hummock, or tucked between hummocks. Fencker (1950) described nests as made of dried grass with down lining, and all nests in Eqaalummiut Nunaat were of similar construction, incorporating bryophytes, herb litter, and small twigs gathered from *c.* 30 cm around nest. Amount of down varies among nests. In some, eggs buried in deep down, but others simply lined nest cup. Most down plucking occurred during first 6 days of incubation (Fox and Stroud 1988). Altitude of site varied with nature of spring thaw. In 1979, most nests at mid-altitude but, in 1984, when there was late but simultaneous thaw, nest-sites were at higher elevations close to brood-rearing areas used in both seasons (Stroud 1981b, Fox and Ridgill 1985, Fox and Stroud 1988). Differences in nesting patterns between contrasting seasons and highly specific nature of nest-sites make it difficult to compare nest densities, but consistent both years in Eqaalummiut Nunaat. Aerial survey in 1999 found mean densities of 0.28/km², compared with 0.25/km² for Canada Geese in same area (Malecki *et al.* 2000). Highest densities found in Kangerlussuaq area (66°55'N–67°30'N), declining to 0.11/km² northwards to Disko Island (68°40'N), with very few further north. However, late spring conditions (with complete snow cover in early June) north of Kangerlussuaq probably resulted in complete non-breeding in some areas to north in that year.

Eggs. Mean 52.5 × 79.2 mm (*n* = 38), mean mass 120.3 g (range 101–156), with wide range of total clutch mass (clutches of six were 641, 691, 728, and 815 g in 1979; Stroud 1981c, Fox and Stroud 1988). Clutch 3–6, mean 4.59 (1979, *n* = 8) and 4.17 (1984, *n* = 6).

INCUBATION. 25–27 days, by female only. Males feed on nearby marshes, both sexes show strong diurnal rhythms in alertness, feeding, and roosting (Stroud 1981*d*, 1982, Fox and Stroud 1988). In 1979, incubating female spent most time vigilant during middle part of day, sleeping early morning; in 1984, female slept at midday and was most alert in early morning. In 1979, four of seven active nests were unsuccessful and ultimately predated by Raven *Corvus corax* and/or Arctic Fox *Alopex lagopus* (Fowles 1981). Foxes predated five of the six nests located in 1984, although such high rate could relate to human observers (Fox and Stroud 1988). Eggs, especially of relatively early-nesting species such as Greenland White-fronted Geese, form important element in diet of Arctic Foxes in Eqaqummiut Nunaat, where may sometimes take incubating females (Fowles 1981, Birks and Penford 1990). Goose eggs common at unearched caches, suggesting that they may not always be consumed immediately (Birks and Penford 1990). Fox predation greater in 1984 (83% predated, when no Caribou *Rangifer tarandus* die-off) than 1979 (43% when abundant Caribou carcasses). Thus, tempting to speculate that spring predation on goose clutches related to quantity of Caribou carrion from previous winter (Birks and Penford 1990).

Recesses in 1979 lasted average 24 min, majority between 19.00 and 01.00 hours; on 20 June, female left nest twice in 24 h but not again until 22 June when clutch hatched (Stroud 1981*d*). Daily recess increased from <20 to 80 min/day as incubation progressed (Stroud 1981*d*), but time spent incubating still high (>97%). Female would leave and fly towards male, who would join her within seconds, two birds flying to feeding area. Male would stand alert close by female while she drank and fed intensively; followed by bout of washing and preening before returning directly to nest-site. Male would stand within 20 m of nest for following 10–15 min before flying back to marsh. Female spent some 20 min adjusting nest, rolling eggs, and preening before settling to incubate (Stroud 1981*d*).

HATCHING TO FLEDGING. Mean brood size declined from 3.70 ($n = 10$) in late July to 3.46 ($n = 5$) by fledging in early August in 1979, and from 4.25 ($n = 12$) to 3.65 ($n = 20$) in 1984. Parents highly attentive to goslings at all times, while they concentrate on feeding. Parents observed brooding on regular basis up to c. 14 days after hatching, especially early on, for between 2 and 45 min, especially if weather cold or wet (Madsen 1981). Goslings observed to run and seek shelter under parents in first days after hatch when Raven *Corvus corax* flew over but, when larger, would take to safety of open water like their parents. Parents nesting at mid-altitude

in 1979 escorted offspring on to plateau 1 or 2 days after hatching. In 1984, when nests constructed at higher altitudes, broods had shorter journeys to get to ultimate nursery areas around edge of plateau lakes. During brood rearing, parents fed for 35% of time (females 42%, males 26%), goslings for average of 62%, although proportion spent feeding decreased during period to fledging (Madsen 1981). One gosling observed for 3 h without ever adopting extreme head-up posture typical of alertness. Parents with large broods spent proportionally more time vigilant than those of small broods or single goslings (Madsen 1981). Non-breeders, which often moulted on same lakes as breeders, much less alert (although associated in larger groups) and fed less than parents with young, which preened and rested less than non-breeders. Non-breeders not tolerated as close to broods as other families (mean inter-distances 22 and 10 m, respectively) and flying non-breeders were seen off from brood-rearing areas by parents. Attacks by breeders on non-breeder groups more frequent than on other broods, and attacking parents always won agonistic interactions even when non-breeding groups were larger than family flocks (Madsen 1981). On three occasions, associating non-breeders tolerated in very close proximity to broods (Madsen 1981).

FLEDGING TO MATURITY. Relatively little known about period from fledging until departure from summering areas. One pair observed throughout incubation in 1979 raised five goslings from six eggs, of which four survived to reach Kintyre in Scotland (one gosling shot in Iceland). In 1984, another pair raised six young from six eggs and, although all were ringed, none has been subsequently recorded. Mean brood size post fledging in Greenland in 1979 and 1984 fell from 3.46 and 3.65, respectively, to 2.84 on wintering areas in both years (based on mean brood size on Islay in November, $n = 68$ and 80 for 1979 and 1984, respectively; Fox and Stroud 1988). Overall, 7% of goslings ringed in Greenland have been shot in Iceland on autumn passage. Annual survival in first year (59.6%, 95% CL 29.8–89.5%) significantly less than older birds (72.4%, CL 58.3–86.6% for 1984–9; Bell *et al.* 1993), despite close association with parents in first year (see Relationships in Families). More recent analysis using combination of ringing recoveries and capture–recapture analysis using resightings of collared birds gives similar relationship (first-year weighted mean survival 67.8% CL 63.2–72.0%, versus 78.5%, CL 76.2–80.5%, for adults; M Frederiksen and A D Fox unpublished data). Mean age at first pairing was 2.46 years (SE = 0.08), age at first successful breeding 3.15 (SE = 0.17) with no difference between sexes (Warren *et al.* 1992*b*).

BREEDING SUCCESS. Densities of families on breeding grounds vary with general levels of breeding success. Hence, in 1992 (late cold spring, with <10% young in following autumn), 24 families encountered during 2538 km of flown transects, compared with 83 during 3298 km of aerial survey in 1995 (mild spring followed by warm summer, with very high production of young recorded in Scotland) (Glahder 1999a).

Proportion of young in autumn population generally lower than for most other White-fronted Goose populations. At Wexford, mean proportion for 1968–99 inclusive was 15.77% (SE = 0.986; range 5.5% in 1999 to 32.5% in 1969; O Merne, D Norriss, A Walsh, National Parks and Wildlife, Ireland). On Islay, for 1962–99 inclusive proportion was 14.74% (SE = 0.945; range 6.7% in 1992 to 27.3% in 1985 (M Ogilvie, Greenland White-fronted Goose Study, Wildfowl and Wetlands Trust, Scottish Natural Heritage). Generally, flocks at Wexford consistently contain more young than other resorts, and same is true for Islay birds compared with rest of Britain (Fox *et al.* 1999b). Overall, annual patterns of breeding success are correlated among winter resorts. Poor seasons associated with late spring thaw where thick snow cover in northern areas led to abandonment of breeding (e.g. 5.5% young at Wexford in 1999) or early snow in July which may affect gosling survival (e.g. 6.4% at Wexford in 1996). Between 1962 and 1995, significant correlation between June temperatures in west Greenland and average productivity recorded at Islay and Wexford in following winter (Zöckler and Lysenko 2000). While in 1970s and 1980s productivity of Wexford birds nearly always greater than on Islay, in 1990s this difference diminished, and Islay productivity in several recent years has exceeded that at Wexford. Evidence for any density-dependent relationship for productivity amongst Scottish wintering flocks weak (Pettifor *et al.* 1999).

Mean brood size relatively high and varied between 2.4 and 4.2 at both Wexford (mean 3.4, SE = 0.07) and Islay (mean 3.1, SE = 0.07) during 1968–99. Mean brood size at Wexford significantly correlated with proportion of young in winter, but no such relationship on Islay. Tendency for larger broods with increasing age of first breeding (Warren *et al.* 1992b).

Plumages. (Updates *BWP* Vol. I, p. 408)

ADULT. White-fronted Geese show most pronounced belly bars of all *Anser* species and *flavirostris* has more extensive barring than other taxa (*BWP* Vol. 1, p. 403; Kristiansen *et al.* 1999b). Extent and pattern of black variable between individuals, sufficient to enable identification of individuals (Stroud 1981e, Kristiansen *et al.* 1999b). However, detailed study showed no consistent

difference between sexes, no marked change with age after second winter when most barring is attained, and no clear pattern variation among years (Kristiansen *et al.* 1999b). There is, however, highly significant seasonal variation, since individual birds consistently become darker in late winter (Kristiansen *et al.* 1999b).

Bare Parts. See *BWP* Vol. I, pp. 408–9.

Moult. See *BWP* Vol. I, p. 409.

Measurements. (Updates *BWP* Vol. I, p. 409) All are given in millimetres.

No significant differences between skull and tarsus measurements for birds caught in Iceland, Scotland, and Ireland, hence these measurements presented combined (A J Walsh).

		SEX	MEAN	SD	NO.	RANGE
ADULT	WING	♂	435.3	0.61	340	387–463
	SKULL		113.4	0.19	398	104–126
	TARSUS		92.6	0.17	334	78–98
JUVENILE	WING		413.9	0.60	377	370–450
	SKULL		111.8	0.20	373	101–123
	TARSUS		91.8	0.17	359	84–100
ADULT	WING	♀	416.2	0.61	306	386–445
	SKULL		107.2	0.19	366	93–121
	TARSUS		87.4	0.17	366	85–106
JUVENILE	WING		398.0	0.63	337	355–428
	SKULL		106.5	0.21	327	98–119
	TARSUS		87.3	0.18	318	78–101

Significant differences between all age and sex classes for each linear measurement summarized above, except for tarsus of adult and juvenile females ($t_{650} = 0.66$, $P = 0.26$). Hence, males larger than females and adults larger than juveniles for all categories except this one.

Weights. (Updates *BWP* Vol. I, p. 409) All are given in grams.

Winter data (all months combined) from Wexford (A J Walsh).

		SEX	MEAN	SD	NO.	RANGE
ADULT	'WINTER'	♂	2738.4	14.92	294	2050–3650
	OCTOBER		2717.3	40.73	45	
	NOVEMBER		2713.2	19.28	135	
	DECEMBER		2703.4	37.58	44	
	JANUARY		2718.8	53.63	17	
	FEBRUARY		2688.9	82.82	9	
	MARCH		3005.6	58.96	25	
	APRIL		2812.5	31.46	4	
JUVENILE	'WINTER'	♂	2522.7	13.09	352	1900–3510
	OCTOBER		2533.3	41.11	45	
	NOVEMBER		2473.7	16.78	167	
	DECEMBER		2518.8	28.38	64	
	JANUARY		2500.3	38.86	34	
	FEBRUARY		2612.5	71.54	12	
	MARCH		2785.2	45.98	31	
	APRIL		2400.0	73.60	4	
ADULT	'WINTER'	♀	2436.8	13.49	270	1800–2900
	OCTOBER		2470.3	31.50	45	
	NOVEMBER		2377.3	17.01	136	
	DECEMBER		2390.6	34.64	40	
	JANUARY		2405	45.61	10	
	FEBRUARY		2550	90.91	9	
	MARCH		2700	27.54	25	
	APRIL		2726.7	89.69	3	

		SEX	MEAN	SD	NO.	RANGE
JUVENILE	'WINTER'	♀	2286.0	12.44	312	1700-315
	OCTOBER		2274.9	29.55	42	
	NOVEMBER		2259.1	18.20	128	
	DECEMBER		2241.5	24.18	76	
	JANUARY		2225	29.52	26	
	FEBRUARY		2427	78.43	10	
	MARCH		2555.6	41.03	27	
	APRIL		2400.0	0	2	

Spring data from Iceland, data from Hvanneyri, west Iceland 1997 and 1999.

		SEX	MEAN	SD	NO.
ADULT	APRIL	♂	2886.8	50.52	22
	MAY		3166.7	77.73	9
JUVENILE	APRIL		2625	65.51	6
	MAY		2900.0	0	2
ADULT	APRIL	♀	2647.1	46.47	17
	MAY		2850.0	111.05	6
JUVENILE	APRIL		2561.1	97.54	17

Moult data from west Greenland (Eqalummiut Nunaat 1979, 1984, Isúngua 1989, 1992, 1997; Greenland White-fronted Goose Study). Little evidence of weight change during moult (Belman 1981, Fox *et al.* 1999c).

	SEX	MEAN	SD	NO.	SEX	MEAN	SD	NO.
ADULT	♂	2600.9	18.12	108	♀	2270.6	16.18	112

Geographical variation.

None known.

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