Mortality and movements of the Greenland White-fronted Goose *Anser albifrons flavirostris*

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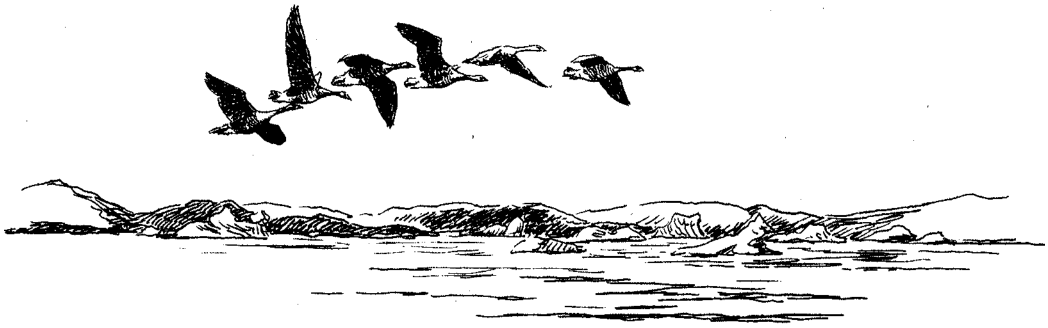
KAJ KAMPP, A. D. FOX and DAVID A. STROUD



(Med et dansk resumé: Dødelighed, træk og vinteropholdssteder hos den Grønlandske Blisgås Anser albifrons flavirostris*)*

Introduction

The Greenland White-fronted Goose *Anser albifrons flavirostris* breeds in West Greenland from Godthåb (Nuuk) (64°N) to Upernavik district (73°N) and winters in Ireland, Scotland and Wales (Salomonsen 1950, 1967). The population size in the late 1970s was estimated between 14,300 and 16,600 birds, a decline from 17,500-23,000 in the 1950s (Ruttledge & Ogilvie 1979). Concern about the decline and the factors responsible have been discussed by Owen (1978), Ruttledge & Ogilvie (1979) and Fox et al. (1983).

Counts in the British Isles show Greenland Whitefronts have consistently lower productivity but larger brood sizes than either Siberian (*A. a. albifrons*) or American (*A. a. frontalis, A. a. elgasi*) races (Ogilvie 1978, Ruttledge & Ogilvie 1979, Timm et al. 1982, Stroud 1984). This feature may result from high predation/desertion rates on the breeding grounds (Stroud in Fox & Stroud 1981: 78-81), with many pairs attempting to breed but few being ultimately successful.

The population in very recent years has increased slightly during a period of mild winters and protection over much of the wintering range. The vulnerability of the geese to severe winters is well illustrated by the virtual elimination of a flock of 600 in central Wales after the severe 1962/63 winter (Fox & Stroud 1985). This was thought largely due to the feeding method adopted by the geese of probing soft peatland vegetation for subterranean perenniating plant material (Cadman 1953). Such fedding technique is restricted during periods of prolonged frost.

Small population size, restricted geographic distribution, low productivity and loss of traditional habitats make the Greenland White-fronted Goose an unsuitable quarry species. In spite of this, it is still legitimate quarry in Iceland, England and Wales, while in Ireland and Greenland there are but temporary bans on shooting.

White-fronted Geese were protected in Scotland under the Wildlife and Countryside Act (1981) which effectively gave protection to the vast majority of British-wintering Greenland Whitefronts. Complete protection was given to Greenland Whitefronts in Ireland from winter 1982/83 until 1984/85. A limited open season was introduced at Wexford in 1985/86 and this will be reviewed on an annual basis. Landstinget (the Home Rule Parliament) in Greenland gave the geese full protection there from spring 1985, with revision in 1988. Protection has also been

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given in Northern Ireland since February 1985, leaving only Iceland and the two Welsh flocks without any legal protection. (A voluntary ban on shooting operates at the major Welsh site at the Dyfi National Nature Reserve.)

In view of the problems associated with this race of geese, it is clearly imperative to understand the dynamics of the population and identify the factors affecting survivorship and fecundity. The present paper develops and updates Boyd's (1958) work on the mortality and survival of the subspecies.

Additionally, site fidelity and patterns of movement between summer and wintering areas are investigated using data from the København ringing scheme (1946-present) and a darvic ringing programme (1979-present).

Material

Since 1946, 1,504 Greenland White-fronted Geese have been ringed in West Greenland (Fig. 1, Tab.1). Effort was greatest in the 1940s and 1950s at the Sarqaq valley (70°6' N, 52°8' W). Ringing was directed by the Zoologisk Museum, København, organised by the late Professor Finn Salomonsen. Early ringing was stimulated by Salomonsen under a bounty scheme encouraging Greenlanders to catch geese to ring and release for financial incentive rather than to eat. The involvement of untrained ringers was a necessary prerequisite if any ringing should be achieved in the country, but has meant that a number of sites have not been precisely designated. This fact precludes breakdown of ringing effort by more than coarse geographical subdivision and age.

All recoveries have been handled via the ringing scheme at the Zoologisk Museum; unpublished data supplement the accounts of recoveries outside Greenland published by Salomonsen (Dansk Orn. Foren. Tidsskr. 41: 141-143 (1947); 42: 100-108 (1948); 43: 251-255 (1949); 44: 168-170 (1950); 46: 110-117 (1952); 49: 130-135 (1955); 51: 33-39 (1957); 53: 31-39 (1959); 55: 197-208 (1961); 59: 92-103 (1965); 61: 151-164 (1967); 65: 11-19 (1971); 73: 191-206 (1979)).

During 1979, 96 (67 adults and 29 pulli) were caught and ringed in Eqalummiut Nunaat (67°30' N), additionally marked with white darvic leg rings to identify individuals on the wintering grounds (Belman in Fox & Stroud 1981: 123-138; Fox et al. 1983). A further 88 were caught in the same area during the summer of 1984 and ringed in the same way (Davies unpubl.). Initial sightings of these birds on the wintering grounds were discussed by Belman (l.c.) and Fox et al. (l.c.). In the present paper, use is made of resightings of these ringed birds to analyse site fidelity, but no attempt made to use this information in the analysis of survivorship, other than in cases of birds killed and Museum rings returned.

In addition, 350 geese have been ringed in Ireland by the Forest and Wildlife Service at Wexford Slobs during winters 1983/84, 1984/85 and 1985/86. These carry both darvic neck-collars and leg rings as well as standard metal rings. Two have been recovered in West Greenland, otherwise these birds are not included in the present analysis.

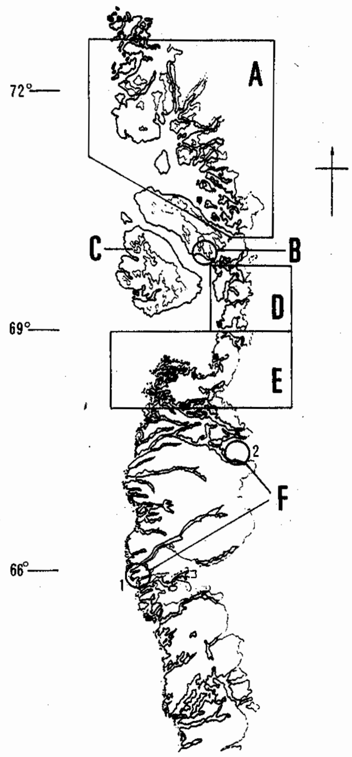

Fig. 1. Map of West Greenland showing the distribution of ringing sites of Greenland White-fronted Geese (cf. Tab. 1). A) Umanaq and southern Upernavik districts. B) Sarqaq valley. C) Disko Island. D) Northern Disko Bay. E) Southern Disko Bay. F) Kangaamiut (1) and Eqalummiut Nunaat (2).
Kort over Vestgrønland, med angivelse af de områder, hvor der er ringmærket Blisgæs (jvf. Tab. 1). A) Uummannaq og sydlige Upernavik. B) Sarqaq-dalen. C) Disko. D) Nordlige Disko Bugt. E) Sydlige Disko Bugt. F) Kangaamiut (1) og Eqalummiut Nunaat (2).

Tab. 1. Ringing of White-fronted Geese in Greenland 1946-84. The ringing areas (see Fig. 1) are: A) Umanaq and southern Upernavik districts. B) Sarqaq valley. C) Disko Island. D) Northern Disko Bay. E) Southern Disko Bay. F) Kangaamiut (1940s) and Eqalummiut Nunaat (1979, 1984).
Ringmærkede Blisgæs i Grønland 1946-84. Ringmærkningsområderne fremgår af Fig. 1.

	age	ringing area *område*						Total
	alder	A	B	C	D	E	F	
1946-50	adults	12	131	0	2	6	2	153
	young	49	238	0	5	152	28	472
	unknown	1	5	0	17	11	0	34
1951-60	adults	6	15	0	76	2	0	99
	young	27	124	0	12	47	0	210
	unknown	18	1	18	17	63	0	117
1961-70	adults	5	27	31	12	0	0	75
	young	17	77	22	0	0	0	116
	unknown	0	0	14	6	0	0	20
1971-74	adults	19	0	0	0	0	0	19
	young	4	0	0	0	0	0	4
1979	adults	0	0	1	0	0	67	68
	young	0	0	0	0	0	29	29
1984	adults	0	0	0	0	0	58	58
	young	0	0	0	0	0	30	30

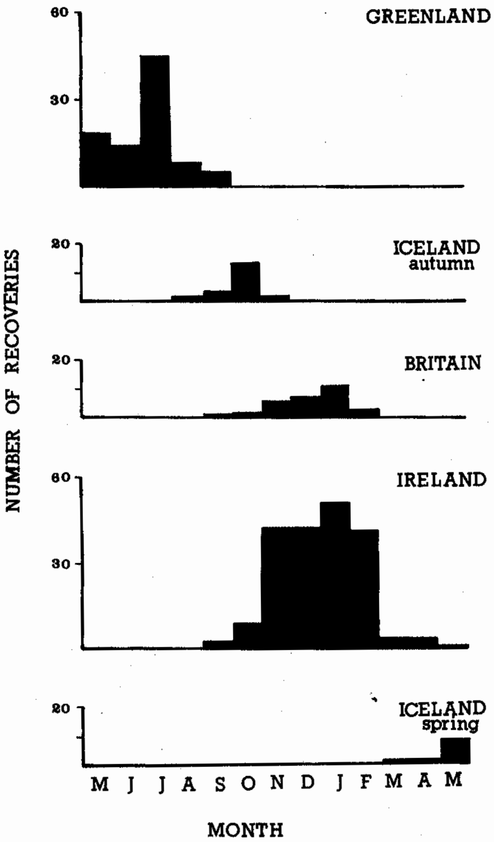

Fig. 2. Monthly distribution of ringing recoveries of Greenland White-fronted Geese throughout their regular world range.
Månedsvis fordeling af genmeldte Grønlandske Blisgæs.

Results

Distribution of annual losses

Recoveries of ringed geese throughout the range reflect the geographical distribution discussed by Salomonsen (1950), with summer recoveries in Greenland, passage occurrence in Iceland and winter recoveries in the British Isles (Fig. 2). The bi-modal distribution of ring recoveries in Greenland highlights the two periods when these dispersed nesting geese are gregarious. On arrival in May birds are concentrated by limited forage availability (Fox & Madsen 1981, Fox & Ridgill 1985), whilst from mid-July, breeding and non-breeding birds become flightless during moult, aggregating in open-water habitats with abundant local feeding (Stroud in Fox & Stroud 1981: 51-62; Fox et al. 1983). Intensive shooting of arriving geese occurs around Søndre Strømfjord in spring (K. Vægter, S. Malmquist pers. comm.) and also at favoured spring staging areas at Tasersuaq (67°00' N, 52°20' W) near Sisimiut (P. Grossmann pers. comm.). Such practices probably also occur elsewhere.

Tab. 2. Distribution of recoveries of Greenland White-fronted Geese ringed in West Greenland.
Genmeldinger af Blisgæs ringmærkede i Vestgrønland.

	Shot *Skudt*	Other[a] *Andet*	Total *Ialt*
Greenland	79	18	97
Ireland	180	13	193
Scotland	23	10	33
England	1	2	3
Wales	1	0	1
Iceland	26	5	31
Canada	3	0	3
Norway	0	1	1
Total	313	49	362

a: includes 10 with unknown cause of recovery

In July, some Greenlanders used to round up flightless geese during the moult period, but this is currently illegal and the practice is now thought rare. However, in the 1940s and 1950s this was the time of year when many geese were ringed and recoveries at this time were increased by this and thus may increase the proportions of birds showing extreme site loyalty.

The decline in Greenland recoveries towards the end of the summer corresponds to increasing movement in autumn to Iceland on passage south. Little is known of past or present Icelandic shooting pressure, but numbers shot compared to recoveries in Greenland and the British Isles are relatively minor. However, of 18 recoveries of geese ringed in Eqalummiut Nunaat in 1979 and 1984, six have been shot in Iceland, four in their first year. This represents a 7% known loss from a sample of 59 goslings. There is no information on the total bag of Greenland Whitefronts taken annually in Iceland.

Fig. 2 shows the vast majority of recoveries came from Ireland, but the inference that this country »is by far the most important wintering place of this population...« (Boyd 1958) was perhaps more a function of bias in ringing sites in Greenland than a real feature of importance of Ireland. The majority of birds ringed have been from the north of the breeding range where predominantly Irish wintering geese breed (below) (Salomonsen 1950). Recent census data (Stroud 1984, 1985; Wilson & Norriss 1985) suggest numbers in Scotland and Ireland are of approximately equal importance.

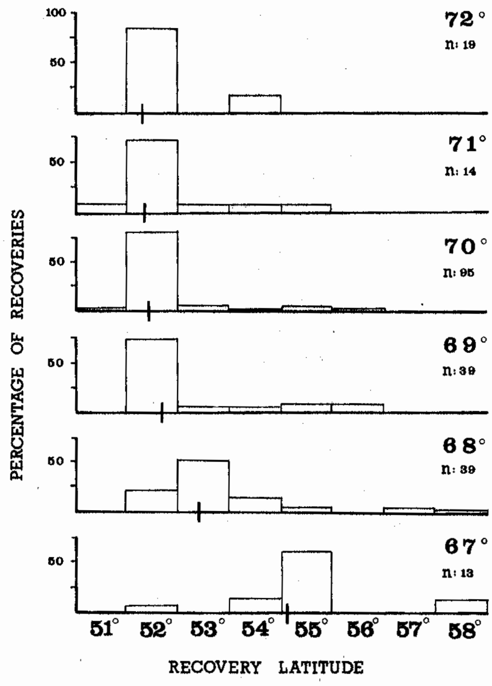

Fig. 3. Percentage frequency of ringing recoveries of Greenland White-fronted Geese by degrees of latitude in the British Isles, segregated by degrees of latitude of ringing sites in Greenland. Vertical bar indicates »mean« recovery latitude for each data set. Data for 66°N (n=5) and 65°N (n=8) omitted due to small sample size. Data from 1946-1984.
Genmeldingerne af Grønlandske Blisgæs fra de Britiske Øer, fordelt efter breddegraden for genfundsstedet. Genmeldingerne er opdelt efter mærkningsstedets breddegrad og er angivet som procenter af hver gruppe. Trods en uheldig geografisk fordeling af mærkningerne (Fig. 1, Tab. 1) kan der spores en tydelig tendens til, at de synlige bestande overvintrer længere mod nord end de nordlige.

The vast majority of the recoveries were shot (Tab. 2). This is the case irrespective of the place of recovery. The true percentage of recoveries killed by man is even larger than appearing in Tab. 2 (86%), because most of the 34 birds reported found dead or wounded, or with unknown cause of death, should undoubtedly be applied to this category as well.

Segregation of birds ringed in Greenland

It has long been proposed that Greenland White-fronted Geese exhibit classic leapfrog migration, with birds breeding furthest north in Greenland wintering further south in the British Isles and vice versa (Salomonsen 1950, 1967; Boyd 1958). This is borne out by analysis of ringing recoveries to the present day (Fig. 3).

The majority of birds ringed in the extreme northern Upernavik district were recovered in Wexford, whilst the majority ringed in Eqalummiut Nunaat towards the southern half of the range have been recovered in Scotland. Unfortunately too few birds have been ringed and recovered from the extreme south of the range to offer any meaningful interpretation from this area.

However, the leapfrog pattern is only a tendency, as geese so far recovered show a remarkable range of recovery sites from any one ringing site (see Fig. 6 in Fox et al. 1983). Clearly more information is required regarding this segregation. Give that birds in winter tend to be highly site loyal (below), this pattern represents widespread segregation of flocks from one Greenland site to different wintering grounds rather than birds wandering between different sites during winter or on migration.

Movements within Greenland

In analysing movements within Greenland, it is important to realise that recorded sites of capture and recovery were often rather general, referring to the ringing group area rather than a specific location.

Of 97 geese recovered within Greenland (excluding an additional two birds recovered in Greenland which were ringed in Wexford in winter 1983/84), 79 (81%) were recovered at the site of original marking, 8 birds in the season of capture (Tab. 3). This total includes 3 birds ringed in Eqalummiut Nunaat in 1979 retrapped in the same area in 1984. Of the other birds recovered in Greenland away from the original ringing site, 12 were recovered in May/early June and August/September when birds were likely to be on migration to or from summering areas.

This leaves 6 birds (6% of the recoveries in Greenland) recovered in July away from the original ringing site, presumably in areas where they would have spent most of the summer. These represent genuine movements between areas which are not attributable to migration movements. The movements include 3 juveniles from Sarqaq ringed in 1947; 2 recovered in Niaqornarsuk (Egedesminde district) in July 1949, the third in Jakobshavn in 1953. Two birds of unknown age moved from Ikamiut to Sarqarleq (Egedesminde district), and Sarqaq to Ritenbenk (Jakobshavn district), after two and four years respectively.

Given the inaccurancy of site description in some cases, and that ringers could conceivably move up to 50 km (e.g. geese ascribed to Ikamiut are known to have been ringed in the Lersletten or Naternaq area 50 km south of the settlement), it is clear that the site loyalty described above is perhaps not as spectacular as first appears. However, given the extremely low summer densities of the birds over a large breeding range, the results suggest little gross movement between different nesting areas.

Further evidence for summer site fidelity comes from up to 10 of a maximum of 77 surviving darvic-ringed geese seen again in Eqalummiut Nunaat five years after ringing.

Movement within the British Isles

Darvic ringed birds have been seen throughout the winter range (Fig. 4) although search effort has not been constant (Belman in Fox & Stroud 1981: 123-138). Some sites were checked more than once a month, others only once or twice in six years. A 'site' is defined as the regular winter range of a flock of Greenland Whitefronts, including daytime feeding and night-time roost areas. On Islay, flocks usually have traditional ranges of about 12 km² but extent and use of sites is variable (Stroud unpubl.).

Tab. 3. Greenland White-fronted Geese ringed and recovered in Greenland 1946-84.
Blisgæs ringmærket og genmeldt i Grønland 1946-84.

Recovery area *Genmeldingsområde*	Age at ringing *Alder* Young	Adult	Unknown
Ringing area *Ringmærkningsområdet*			
Total *Ialt*	27	15	37
Recovered same year *Genm. samme år*	3	0	5
Elsewhere *Andetsteds*			
Total *Ialt*	7	2	9
Probably on migration *Genm. i trœktiden*	4	1	7

Tab. 4. Within-winter resightings of Greenland White-fronted Geese darvic ringed in Eqalummiut Nunaat in 1979.
Gentagne kontroller inden for samme vinter af Blisgæs farveringmærket i Eqalummiut Nunaat 1979.

	Adults	Juveniles
Goose sightings at same locality as last sighting *Fundet på samme lokalitet som ved forrige aflæsning*	306	46
Goose sightings at different locality to last sighting *Fundet på anden lokalitet end ved forrige aflæsning*	9	2

Tab. 5. Between-winter resightings of Greenland White-fronted Geese darvic ringed in Eqalummiut Nunaat in 1979.
Gentagne kontroller i forskellige vintre af Blisgæs farveringmærket i Eqalummiut Nunaat 1979.

	Adults	Juveniles
Number of geese seen in more than one winter *Antal gæs kontrolleret i mere end én vinter*	32	10
Number of goose/winters at same site *Antal gåse-vintre på samme lokalitet*	128	26
Number of goose/winters at site different to previous winter *Antal gåse-vintre på anden lokalitet end foregående vinter*	9	1

The following results are based on two methods: estimation of the probability of a bird moving between wintering sites (i) between years, and (ii) between successive sightings based on records from the years 1979/80 up to and including 1985/86.

Moves between sightings
Fourteen of the 69 birds sighted on the wintering grounds were recovered dead or seen only once. These are excluded from further analysis since they cannot provide information on site fidelity or movements. Of 55 remaining birds, there are 363 sightings/recoveries, broken down by age in Tab. 4 (1979 pulli separated from birds ringed as probable yearlings or adults). Repeat sightings of known age birds show 96% were at the same wintering sites as the previous observation. The corresponding figure for birds of unknown age is 97%, indicating considerable site loyalty. There were only eleven between-wintering-site moves (by 10 different birds) amongst all birds over seven winters.

Of these, 3 birds were male and 5 female. Three of the five moves made by females were known to have involved loss of the mate and re-pairing to a different bird. Although the sample size is small, this process may prove an important factor in initiating between-site movement, with birds re-pairing to mates of differing winter provenance on the breeding grounds or whilst staging in Iceland.

Recent information from the Irish Greenland Whitefront colour ringing scheme has shown a small degree of within-winter movement (H. J. Wilson pers. comm.). Although this involves only a very small proportion of birds, clearly further observations are required to establish the full extent of site loyalty.

Moves between winters
Some birds were repeatedly seen within winters, whilst others were seen only when sites were checked once or twice a year. The method above may be biased by inclusion of many within-winter sightings at well-watched sites. The alternative approach here assumes complete site loyalty *within* winters. This assumption seems valid. Of twelve recorded moves, only one occurred within a winter: from Scotland to the Netherlands well outside the normal wintering range. This occurrence can be regarded as highly atypical. Using this assumption, sightings of birds seen only once become equivalent records to those seen regularly, and a probability of movement between winters can be calculated (Tab. 5). Thus, 96% of known age birds and 93% of unknown age birds wintered at the same site as the previous winter, again exhibiting little difference in the behaviour of juveniles and

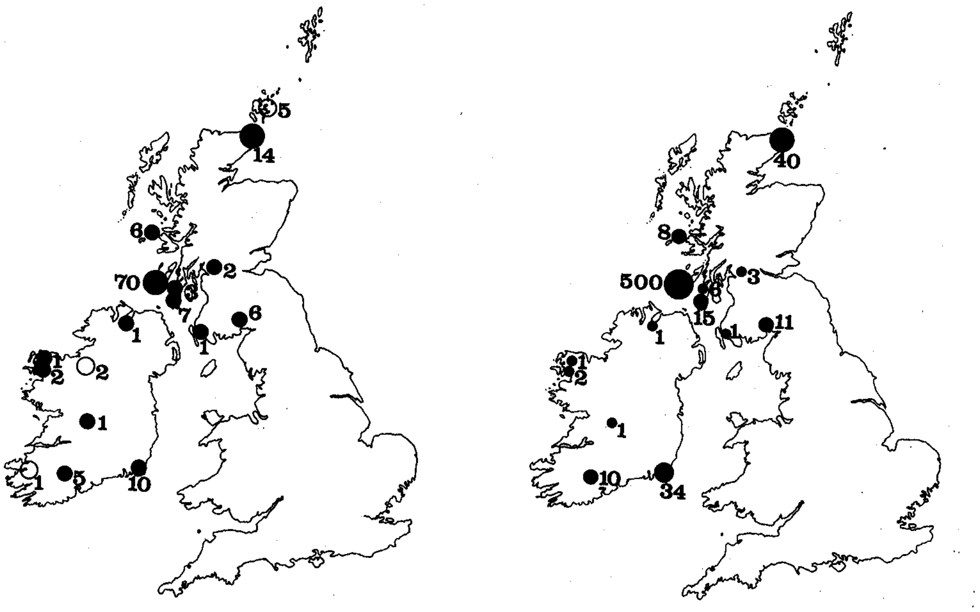

Fig. 4. Distribution and number of sightings of Greenland White-fronted Geese in the British Isles ringed with darvic leg rings in Eqalummiut Nunaat (67°30'N 50°30'W) during summer 1979 and 1984. The left figure shows the distribution of sightings of different birds. The numbers indicate the number of individual birds seen at each site; open symbols indicate unread rings. The right figure shows the total number of sightings at each wintering site from 1979 - 1987.
Kontroller på de Britiske Øer af Grønlandske Blisgæs mærket i Eqalummiut Nunaat 1979 og 1984. Til venstre er vist fordelingen af aflæsningerne af forskellige fugle; tallene angiver antallet af forskellige fugle set hvert sted (åbne symboler angiver tilfælde, hvor ringenes numre ikke med sikkerhed blev fastslået). Til højre er vist det totale antal aflæsninger ved hver overvintringslokalitet i årene 1979-87.

older birds of unknown age. Although the majority of darvic sightings were from Islay, there was no significant difference in site fidelity between Islay wintering geese and those from elsewhere in Scotland.

Annual survival rates

In calculating annual survival rates a complication arises because not all ringed geese were aged in the 1940s and 1950s. The number differentiated into birds of the year and full grown improves in later years (Tab. 1).

Haldane's (1955) method was modified to treat 'truncated' data, so as to avoid bias caused by ring loss. 'Years' ran from 15 September which separated Greenlandic from Icelandic and other recoveries, and only shot birds were included in the analysis. Recoveries of 1979 and 1984 birds are excluded. The data set is given in Tab. 6.

Clearly, survival of birds in their first year is lower than in later years, and recoveries from the first 1-2 years must be excluded (Haldane's method assumes age- and year-independent survival and recovery rates). Calculating survival for young from 3-10 years gives s = 0.798 (s.e. = 0.048, $\chi^2_7 = 2.3$, P = 0.94). Survival for adults from 1-10 years gives s = 0.762 (s.e. = 0.039, $\chi^2_9 = 5.8$, P = 0.76), whilst Combination 2 (of Tab. 6: young + unknown aged birds with adults 1-8 years) gives survival of s = 0.767 (s.e. = 0.034, $\chi^2_7 = 3.2$, P = 0.86). Thus the ringing data indicate that annual survival after the second year of life is 76.7 ± 3.4%.

Calculating survival of young from 2-10 years, both alone and in combination with adults, gives poorer fit to the model and a lower survival (72.9 ± 2.5%), suggesting that higher mortality of young extends into their second year also. This is perhaps not surprising.

An approximate attempt to calculate first year survival rate can be made using 'smoothed' recovery numbers. This uses the survival values for young from 3-10 years and for adults from

1-10 years (above), and ringing totals of N_a = 343 and N_j = 801 for adults and juveniles respectively. In this way the survival through the first two years is given by:

$$s_1s_2 = N_aR^*{}_3 / N_jR_1 = 0.39$$

where R and R* are smoothed recoveries for adults and juveniles respectively (R^*_3 = 15.2; R_1 = 16.6).

Using this value, it is possible to calculate recovery rates as a proportion of all adult birds alive at the beginning of the year-class: $f = R_1 / N_a = 0.048$. This 4.8% is a very minimum hunting pressure, since not all discovered rings are returned, and since not all shot birds are re-

Tab. 6. Data set used to calculate mortality, using only recoveries from shot birds.
Genmeldingsmateriale (kun skudte fugle) som er anvendt til beregning af den årlige dødelighed.

Status	Year *År*									
	1	2	3	4	5	6	7	8	9	10
Banded as young	77	35	14	12	10	9	6	6	5	1
Unknown age	22	8	6	5	0	1	1	0	0	0
Adults	18	11	13	6	2	4	3	4	3	1
Combined 1)	61	31	30	16	12	11	9	9	4	
Combined 2)	38	28	23	16	9	10	8	5		

Combined 1): young + unknown: year 2-10; and adults: year 1-9
Combined 2): young + unknown: year 3-10: and adults: year 1-8

Tab. 7. Adult and juvenile Greenland White-fronted Geese shot in Islay, Scotland, and Wexford, Ireland. Analysis of bag samples against percentage of juveniles in field samples shows significantly more juveniles are shot than would be expected by chance (chi^2_9 = 131.6, $p \ll 0.001$ excluding data in years marked * when sample sizes are small).
Førsteårs-fugle er overrepræsenteret blandt de nedlagte fugle, hvilket almindeligvis er tilfældet hos jagtbare arter. Det er her demonstreret ved stikprøver fra Islay (Skotland) og Wexford (Eire); i begge tilfælde er ungfuglene knap 2 gange hyppigere blandt de skudte fugle, end de er i bestanden.

	Sample of shot birds *Stikprøve, skudte fugle*		Percentage of juveniles *Procentdel af ungfugle*		Differential vulnerability of juveniles
	Adult	Juvenile	bag sample *nedlagte*	field sample *bestand*	*Overrepræsentation af ungfugle i jagtudbytte*
Islay[a]					
1979/80	3	1	16.7*	11.9	-
1980/81	54	32	37.2	23.3	1.6
1981/82	36	8	18.2	14.3	1.3
Total	93	41	30.6	16.5	1.9
Wexford[b]					
1969/70	198	77	28.0	32.5*	-
1970/71	230	104	31.1	15.1	2.1
1971/72	260	69	21.0	14.8	1.4
1972/73	67	27	28.7	12.7	2.7
1973/74	94	44	31.9	15.8	2.2
1974/75	28	12	30.0	17.7	1.7
1975/76	149	73	32.9	25.3	1.3
1978/79	10	10	50.0*	13.2	-
1980/81	30	18	37.5	13.2	2.8
1981/82	49	23	31.9	18.4	1.7
Total	1115	457	29.1	16.3	1.8

a: Data for 1979/80 courtesy of P. J. Belman
b: Data for all years courtesy of O. Merne, D. Norriss and H. J. Wilson

trieved by the hunter. The first year recovery rate can be estimated from the actual number returned, i.e. $f = 77/N_j = 0.096$. This is precisely twice the proportion of that for older birds.

The higher vulnerability to hunting of first-year birds is borne out also by analysis of bag age ratios from sites where Greenland White-fronts have been shot in the past. The proportion of juvenile birds amongst bag totals at Wexford and Islay is consistently higher (mean of 1.8 times greater than expected by chance) than the proportion of juvenile birds in wintering flocks (Tab. 7). Such high mortality amongst shot birds in their first year is a feature of all goose and other quarry species (e.g. Miller et al. 1968, Wright & Boyd 1983) and relates to the experience of an individual and ability to avoid its human predator. Timm & Dau (1979) found differential vulnerability of birds of the year ranged from 1.2-5.0 times the proportion of young in the winter flocks of Pacific White-fronted Geese between 1962 and 1977.

The mean productivity of Greenland White-fronted Geese wintering at Wexford Slobs and Islay since 1971 are 17.2% and 14.5% respectively (Tab. 8). Clearly this level of productivity and an overall survival of 0.77 (and hence mortality of 23%) would lead to a halving of the population within about 10 years. Since this is not occurring, there can be little doubt that this survivorship estimate based solely on ringing returns is incorrect.

As an alternative, a crude 'direct' estimate of overall mortality (all age-classes) is available if it is assumed that the populations on Wexford Slobs and the Isle of Islay are closed. If this is the case, a value for 'compensatory mortality' can be derived by difference (Ogilvie 1983): annual recruitment ($Y_t = jN_t$) and losses ($L_t = N_t - N_{t+1} + Y_{t+1}$) can be obtained from Tab. 8, to give a crude mortality rate $d_t = L_t / N_t$.

The results are rather discouraging, however. The Wexford data show mean mortality of 16% during the period when shooting occurred at the Slobs (before 1982/83), 12% after the cessation of shooting. But the figures vary widely from year to year, much more than one would expect. There are few mortality studies on geese based on high quality data, but in one such study on the Svalbard Barnacle Goose *Branta leucopsis*, Owen (1984) found that adult mortality varied only between 9% and 14% through 7 consecutive years. – The Islay data show no trend, and calculated losses are in fact negative in several years. The assumption of closed populations seems not to be valid, and at least for Islay difficulties in ensuring complete and accurate census counts in the past may well add substantially to the error.

Tab. 8. Winter counts N and percentage juveniles j of Greenland White-fronted Geese. Data for Wexford Slobs (mean winter counts) from Wilson & Norriss (1985) and O. Merne (unpubl.). Data for Islay (maximum November counts) from Ogilvie (1983), Ogilvie (in litt.) and Stroud (1984, 1985, unpubl.).
Gennemsnitlige vintertal (Wexford) henholdsvis maksimale november-tal (Islay) (N), og procentdel af ungfugle (j).

	Wexford		Islay	
	N	j	N	j
1970	–	–	2000	12.5
1971	5252	14.8	3400	7.4
1972	5001	12.7	2580	4.6
1973	4836	15.8	4180	15.1
1974	5141	17.7	3430	18.4
1975	5058	25.8	4150	21.4
1976	5417	19.6	4210	20.8
1977	5632	12.1	3300	10.2
1978	5074	13.2	3380	9.7
1979	5191	11.7	2900	11.9
1980	4598	13.2	4200	23.3
1981	5158	18.4	3588	14.3
1982	5550	18.8	3879	12.9
1983	6004	12.2	4592	9.9
1984	6881	17.2	5256	12.1
1985	7930	34.4	6346	27.3
Mean		17.2		14.5

Discussion

Segregation

The trend of leapfrog migration does indeed seem to apply to Greenland White-fronted Geese, with the caveat that birds from any one ringing site can segregate throughout the wintering range. Most show a tendency towards this phenomenon. The extreme site fidelity of birds ringed in Greenland to their ringing/natal regions (based on ringing recoveries) and in Britain (based on darvic ring sightings) clearly suggests that segregation occurs on migration either in Iceland or during departure from Greenland. Hunting in restricted areas of either Greenland or the British Isles would manifest itself as loss of geese in restricted areas of breeding or wintering areas although the loss could potentially have wider effects throughout the population (cf. Abraham 1981, Fox et al. 1983).

It has previously been considered that the race of Greenland White-fronted Geese consists of just one population. Clearly though, the situation at a sub-population level is complex. Much further darvic ringing is required to investigate mortality and movements at this lower, sub-population level. In the absence of ringing in the extreme southern part of the breeding range, nothing can be concluded about migration patterns of these birds. It should be a priority to investigate the movements of these birds.

The segregation of birds within the population implies that different population segments (whether on the breeding, migration or wintering areas) may experience different mortality rates reflecting a variety of different risks. Such heterogeneity within the population will add to the problems of calculation of mortality/survivorship from pooled ringing recoveries (see below).

Mortality

The ringing analysis indicated an adult mortality rate of 23%. Hunting alone caused a mortality of at least 4.8% annually (9.6% in 1st-year birds), but these estimates are certainly too low since not all shot geese are retrieved, and not all recovered rings are reported. The true harvest could well be twice as high; the relative values, implying a two times higher risk of being shot in 1st-year Whitefronts compared with older birds, may be quite accurate, however.

An adult mortality rate of 23% appears rather high for a bird like the Whitefront, but does in fact seem quite 'normal' for (hunted) grey geese – see reviews in Cramp & Simmons (1977). Most estimates have been based on ringing, using more or less adequate techniques, and as in the present case the data sets have often been rather small.

Haldane's method was chosen by necessity, since the data did not allow calculation of age- and year-specific survival rates. The validity of the result depends on how well the assumptions of constant mortality and recovery rates are fulfilled – they will, of course, never be perfectly true. The obtained result will at best be a reasonable, though somewhat vaguely defined mean value. How good Haldane estimates are in actual cases is difficult to ascertain, however. The method is robust and a good fit of recovery data to the model is no guarantee of a good estimate.

In the present case the calculated mortality seems to exceed recruitment. The latter is based on age composition of wintering flocks, and at least for later years the figures should be rather accurate. The population has in fact experienced some decline in the past, but not at the predicted rate. It may therefore be that mortality actually is over-estimated. This appears quite often to be the case when calculations are based on general ringing, though the reasons for this are rather obscure. Ring loss is probably not the cause in the actual case. Varying mortality rates between sub-populations, combined with a bias in recoveries in favour of the high-mortality population segments may well be involved, however; this would be the case if hunting was an important mortality factor (as it certainly must be here), and if different sub-populations experienced different hunting pressures (see Pollock & Raveling 1982).

It should also be remembered that the present mortality and productivity data refer to different periods, with most of the ringing recoveries stemming from the fifties and early sixties, when the subspecies was legitimate quarry in most of its world range. In view of the considerable recent change in its protected status, it is vital that ringing, both conventional and darvic, is undertaken more intensively over the next few years. Ringing is needed on both wintering and breeding areas, in order that the effects of this legislative change on Greenland White-fronted Goose mortality can be assessed with a view to future population management.

To conclude, our present understanding of the population dynamics of the Greenland White-fronted Goose is poor. More detailed studies in the future, and the accumulating controls of birds now carrying individually recognizable darvics, may alter this situation. Until then, the gaps in our knowledge should urge caution in the management of the subspecies. The impact of hunting on the population processes of other arctic-nesting geese has been well documented (e.g. Ebbinge 1985). The combination of low productivity and normal (rather than low) mortality in the Greenland Whitefront is no cause for contentment, the less so because the population, by its limited size, will necessarily be vulnerable.

Greenland White-fronted Geese. Photo: Hans Meiniche.

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Resumé

Dødelighed, træk og vinteropholdssteder hos den Grønlandske Blisgås *Anser albifrons flavirostris*

Den vestgrønlandske bestand af Blisgåsen omfatter hele verdensbestanden af underarten *flavirostris*. Bestanden er ret lille, og de ca 15.000 fugle anslået sidst i 1970erne synes at angive en tilbagegang siden 1950erne med omkring 25%. Faktorer bag denne tilbagegang er sandsynligvis både jagt og habitatødelæggelser på de Britiske Øer, hvor hele bestanden overvintrer. I løbet af 1980erne er underarten blevet helt eller delvist fredet i størstedelen af det område, hvor den forekommer, med Island som den vigtigste undtagelse.

Med henblik på forvaltning af denne sårbare gåsebestand er vinteropholdsstederne blevet overvåget regelmæssigt, og oplysninger om dødelighed, opholdssteder for forskellige delbestande og stedtrohed søgt fremskaffet v.h.a. ringmærkningsdata. Disse omfatter dels det generelle grønlandske ringmærkningsmateriale, opbevaret på Zoologisk Museum i København, dels kontroller på de Britiske Øer af fugle, der blev forsynet med farveringe under to ekspeditioner til Eqalummiut Nunaat (Fig. 1) i 1979 og 1984.

Genmeldingerne (hovedsageligt skudte fugle, Tab. 2) antyder, at størstedelen af bestanden overvintrer i Irland. I virkeligheden er fordelingen mellem Irland og Skotland nok mere lige; men ringmærkningerne har været koncentreret til den nordlige del af yngleområdet, og der synes at være nogen forskel på hvor de forskellige delbestande overvintrer (Fig. 3). Også på de grønlandske ynglepladser er der tendenser til opsplitning i delbestande i den forstand, at fuglene gennemgående er meget stedtro (Tab. 3).

Dødelighedsberegninger på basis af almindelig ringmærkning er noget usikre. Med brug af den såkaldte Haldane-metode fås her en årlig dødelighed for de voksne fugle på 23%. Det er ret normalt for jagtligt udnyttede bestande af grå gæs. Men ungeproduktionen hos den Grønlandske Blisgås er ringe (Tab. 8), og vil med den beregnede dødelighed ikke kunne erstatte tabene. Da bestanden gennem de senere år har været ret stabil, er den beregnede dødelighed muligvis for stor. Det kunne dels skyldes, at genmeldingerne i hovedsagen stammer fra 1950erne og ikke repræsenterer den nuværende situation, dels den nævnte tendens til opsplitning i delbestande. Hvis nemlig jagt er en væsentlig dødelighedsfaktor (som det her er tilfældet), og hvis forskellige delbestande jages i forskellig grad og derfor udviser forskellige årlige dødeligheder, vil delbestanden med højst dødelighed blive overrepræsenteret i genmeldingerne.

I øjeblikket er underartens populationsdynamik altså ikke særlig godt klarlagt. Men kombinationen af lav ungeproduktion og tilsyneladende normal (ikke lav) dødelighed i en så lille og sårbar bestand gør, at stor forsigtighed i forvaltningen af bestanden må anbefales.

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