

**The breeding biology of the Greenland White-fronted
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The breeding biology of the Greenland White-fronted Goose (*Anser albifrons flavirostris*) was studied during two expeditions to Eqaqunmiut nunat, West Greenland (67°N) during 1979 and 1984. Nest sites were situated close to or overlooking wetlands which constituted the feeding area of the attendant ganders during incubation. Mean date of clutch initiation in 1984 (11 June) was delayed due to the late spring thaw compared with 22 May in 1979 when spring conditions were more typical of most years. Nesting occurred significantly more often above 400 m in 1984 than in 1979 when most nesting attempts were below 200 m and the significance of this is discussed. Productivity in terms of brood size and percentage young amongst winter flocks did not differ between 1979 and 1984. Greenland Whitefronts are solitary nesting with nest densities lower than recorded for other races of Whitefront. Modal clutch size of six is typical for the species and there are no apparent differences in egg size compared with other races. During incubation, both parents show strong diurnal rhythms of alertness, feeding and roosting activity which may be correlated with the activity of the most important predator of eggs, the Arctic Fox *Alopex lagopus*. Discussion of this and other studies of the Greenland Whitefront suggest that the pre-nesting feeding may reduce the impact of poor spring weather on productivity, but that the high percentage of time spent by the female incubating and the dramatic observed predation rates may explain the characteristically low productivity of the race compared to other grey geese.

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Introduction

The Greenland White-fronted Goose *Anser albifrons flavirostris* breeds in west Greenland and winters exclusively in Ireland, Scotland and Wales. The world population declined from 17 500-23 000 in the 1950's to 14 300-16 600 in the late 1970's (Ruttledge & Ogilvie 1979). Following conservation measures in the winter range and several successful breeding seasons, the population in April 1986 was thought to number c. 22 000 (Norriss & Wilson 1986). However, small population size and low productivity of the race (Fox *et al.* 1983), coupled with habitat loss (Ryan & Cross 1984), high mortality (Kampp *et al.* in press) and disturbance on the wintering grounds give cause for concern for this population (Owen 1978). The conservation problem is

more acute since mean brood size (e.g. 2.9-3.0 in 1982 considered typical of recent years, Stroud 1984a) is high compared to many arctic nesting geese, indicating that only a very small proportion of the population breeds successfully. In 1982, when count coverage was good and the percentage young amongst wintering flocks close to the mean value over the previous fifteen years, it was estimated that from a world population of 16 600 only 723 pairs returned with young to the wintering grounds.

The breeding range of Whitefronts extends from 64° to 72° N in West Greenland, but low breeding densities and inaccessible terrain have resulted in little published information on summer biology. Until recently, most of the scant information on Greenland Whitefront breeding biology derived from Fencker (1950) and Salomonson (1950), with anecdotal information from visiting

ornithologists (e.g. Beer *et al.* 1956, Joensen & Preuss 1972, Plantema & Groesz 1978, Bohemen 1978, N. Thingvad *in litt.* and unpublished data).

In response to the observed declines in the population, an area of inland West Greenland was visited in 1979 and 1984 to study the summer ecology of the Greenland White-fronted Goose. Results of the 1979 studies were published in Fox & Stroud (1981) and summarised in Fox *et al.* (1983); some results from the 1984 expedition are presented here. The present paper draws on information from these two four-month expeditions supplemented by information from a variety of sources.

Study area

Eqalungmiut nunât (67° 50'N) is a discrete area of 750 km² of low arctic tundra in the southern central part of the range of the Whitefront in Greenland. It lies close to the ice-cap and experiences a continental climate with low precipitation, low humidity and high insolation. The area is gneissic plateau 450-630 m above sea level with a few large lowland valleys extending to sea level and is dotted with lakes and marshes. Details of the topography, geology, climate and vegetation of the area are given in Fox & Stroud (1981).

There is no information concerning the quality of breeding habitat in Eqalungmiut nunât compared to other parts of West Greenland, but densities here are slightly higher than to the south and west (Holthe in Stroud 1981a). From maps and photographic evidence, it would seem that the habitats were typical of large areas further north at least as far as Disko Bugt.

Methods

Fieldwork was conducted during 5 May – 20 August 1979 and 2 May – 14 August 1984. Pairs were watched back to nests during egg-laying and incubation, and other suitable habitat searched up to 8 km from Base Camp (see Fox & Stroud 1981). Nest records were compiled for the two years; one nest in both years was subject to continuous observation from the date of discovery until hatching and the disappearance of the family group from the nest area, whilst other nests were checked as frequently as possible without causing disturbance to incubating females. 'Continuous observation' of nesting geese involved regular recording of goose behaviour at five minute (1979) and two minute (1984) intervals, together with all records of calling foxes or other predator activity in the vicinity of the nest site to give an index of predator activity and abundance. Details of clutch size; egg morphometrics, nest construction, site and habitat, predation (where appropri-

ate) and other features of interest were recorded on standard cards (Stroud 1981b). Clutch initiation was defined as the date when the first egg was laid, determined by (i) direct observation, (ii) dates of subsequent eggs, based on one egg laid per day (Owen 1980) or (iii) hatching date, assuming an incubation period of 26 days (unpublished data).

To relate timing and success of breeding to weather conditions, meteorological data were collected in the two years. In 1984, snow depth was recorded by measuring snow surface level against ten 1.5 m stakes at Base Camp (200 m a.s.l.). Since there was no appreciable snow-lie in 1979, there are no equivalent measurements for 1979. Comparison of maximum daily temperatures for the two years from the Meteorologisk Institut using data from the station at Søndre Strømfjord, some 60 km south of Eqalungmiut nunât. This area has a similarly continental climate to Eqalungmiut nunât and it was thus considered valid to use data from the more southerly meteorological station to highlight differences in weather conditions in 1979 and 1984.

Results

Meteorological conditions

Snow depths were substantially greater in 1984 than 1979 (Fig. 1). Winter 1983/84 was one of the coldest on record, resulting in a very late spring. This meant particularly late snow-lie in West Greenland during 1984 (Figs 2 and 3). Depths of 80 cm were usual on flat areas in Eqalungmiut nunât on 3 May, and drifts were considerably deeper. Deep snow persisted well into June, the gradual thaw accelerating with a warm föhn wind on 2 June (Fig. 4). This was in considerable contrast to 1979. On arrival on 5 May, there was only c. 15% snow cover,

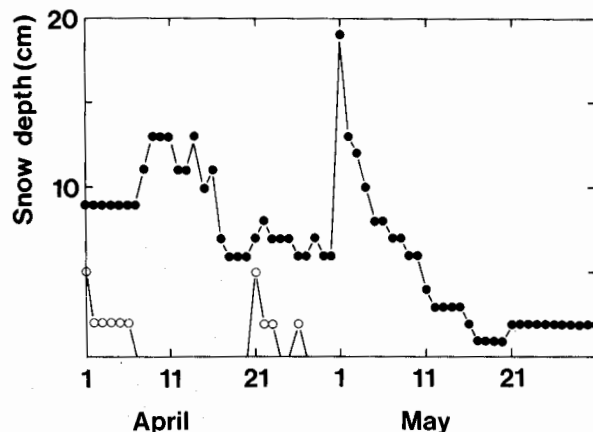


Fig. 1. Recorded daily snow depth (cm) at Søndre Strømfjord Meteorological Station, West Greenland (66°20'N, 51°00'W) for April/May 1979 (○) and 1984 (●). Data courtesy of Meteorologisk Institut, København.



Fig. 2. Snow cover in Eqalungmiut nunât, looking south from 67°34'N, 50°29'W, 15th May 1979.

restricted to patches on north-facing slopes. Thus in terms of snow cover, the 1984 season lagged almost exactly two months behind the 1979 thaw (Fig. 1), although after the thaw summer rainfall and temperature differed little between years (Fig. 5).

Nest site selection

On Nûgssuaq (70°6'N, 52°8'W), Fencker (1950) found nests placed on a small heather or grass hummock on small hills and gently sloping hillsides in the vicinity of lakes or marshy valleys, never on lake-shores or in moist valleys. He thought sites were selected on the basis of good all-round visibility to ensure early predator detection. In Eqalungmiut nunât, nests were pre-

dominantly 1) on slopes above marshes, 2) on or adjacent to marshes and 3) amongst hummocks adjacent to lakes (Table 1). Nests were almost exclusively near *Eriophorum angustifolium* dominated marshes which invariably formed the feeding area of the attendant gander (Fig. 6, Stroud 1982, Madsen & Fox 1981). Sites chosen were generally raised above the general water table of the surrounding wetlands (Fig. 7). The lakeside nests were close to similar transition mire vegetation, while slope nests were on large open slopes dominated by *Salix glauca/Calamagrostis lapponica* vegetation overlooking the feeding area of the gander. The exceptional low altitude sites of 1979 (Table 1) were both near *Eriophorum angustifolium* marshes.



Fig. 3. Snow cover in Eqalungmiut nunât, 12th May 1984, almost the same view as in Fig. 2.

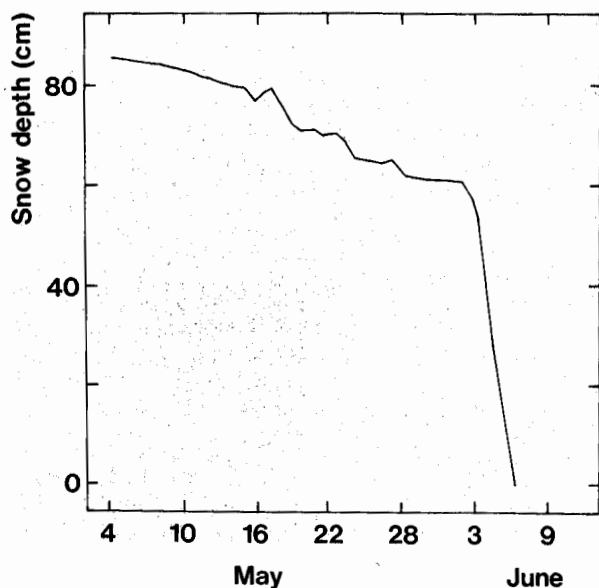


Fig. 4. Mean progressive snow-melt measured at Base Camp, Eqalungmiut nunât, West Greenland (67°34'N, 50°29'W) for May/June 1984. There was no snow lying in this area during the equivalent period in 1979.

Nests

Fencker (1950) described nests as made of dried grass with down lining and all nests in Eqalungmiut nunât were of similar construction. During clutch initiation most nests were rudimentary with the body of the nest being rapidly constructed from dead vegetation (primarily dried grass litter) from the immediate vicinity. Indeed, stripping of this litter from the immediate nest vicinity caused an obvious green circle of enhanced plant growth c. 30 cm around the nest by the end of incubation. Where available, bryophytes (especially the ubiquitous *Aulacomnium turgidum*) were also included

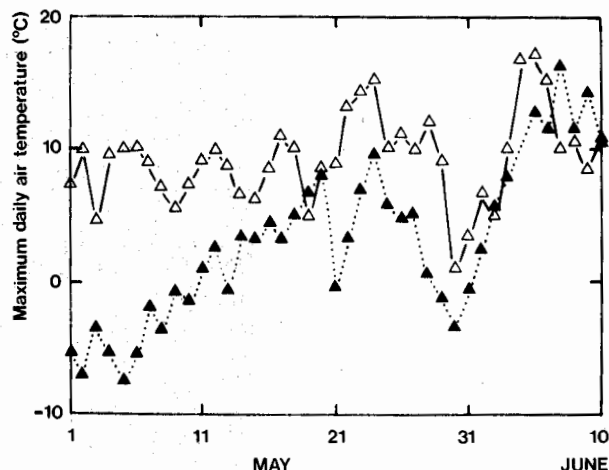


Fig. 5. Maximum daily air temperature recorded at Søndre Strømfjord Meteorological Station, West Greenland for May/June 1979 (Δ) and 1984 (\blacktriangle).

in the structure, but other material such as herb litter, *Salix glauca* and *Betula nana* twigs, etc. made up low proportions of the structural material and varied according to availability.

Nests were all lined with down, the amount varying between nests. The nest subject to special investigation in 1984 was particularly densely lined, the eggs buried in thick down, separated by feathers and leaving only the very tops in contact with the female. Down was progressively added to the nest by the incubating female with most down plucking being observed during the first six days of incubation.

Nesting altitude and phenology

Patterns of feeding of breeding geese in Eqalungmiut nunât in both years were influenced by state of the thaw

Table 1. Environmental details of goose nests found in Eqalungmiut nunât 1979 and 1984.

Year	Site	Location	Vegetation of immediate nest site	Approximate distance to open water (m)	Approximate altitude (m)
1979	1	Slope	<i>Calamagrostis</i> steppe	400+	300
	2	Slope	<i>Empetrum nigrum</i> moss mat	50	100
	3	Slope	Marsh/grassland	40	250
	4	Slope	<i>Calamagrostis</i> steppe	300	250
	5	Slope	<i>Calamagrostis</i> steppe	50	250
	6	Lake shore	<i>Salix/Calamagrostis</i>	3	50
	7	Sandur	Sand and Boulders	20	50
	8	Marsh	<i>Empetrum/Vaccinium</i> hummock	0.2	450
1984	1	Marsh	<i>Betula/Salix</i> hummock	4	550
	2	Lake shore	<i>Betula/V. vitis-idaea</i> hummock	8	400
	3	Marsh	<i>V. uliginosum/Ledum</i> hummock	2	450
	4	Lake shore	<i>Betula</i> hummock	6	550
	5	Slope	<i>V. uliginosum/Ledum</i> hummock	400	150
	6	Marsh	<i>V. uliginosum/Ledum</i> hummock	4	550

Fig. 6. Typical nesting marsh of Greenland White-fronted Geese, 67°34'N 50°36'W, Eqalungmiut nunât, June 1979.



and snow cover which affected availability of forage: the seasons 1979 and 1984 were radically different in this respect. The föhn wind of 2 June 1984 brought about rapid thaw, with spectacular reduction of snow cover and sudden growth of forage plants at all altitudes simultaneously. This was in considerable contrast to 1979 when thaw progressed up an altitudinal gradient. As a consequence, nesting occurred earlier in 1979 mostly close to low to mid-altitude marshes (Table 1) after pre-nesting feeding had occurred at the lowest altitudes; mean date of clutch initiation that year was 22 May (range 19-27 May; Stroud 1981a). With no difference between patterns of search between years to bias nest detection, nesting in 1984 occurred significantly more above 400m compared to 1979 (Fig. 8, Fisher Exact

Probability Test $p=0.016$, Table 1). Mean clutch initiation was 11 June (range 6-17 June) in 1984. Hence in 1979, peak nesting initiation commenced fifteen days after first sighting of geese on the breeding area and ten days after peak passage numbers (Fox & Madsen 1981), compared to thirty-four and fifteen days respectively in 1984 (Fox & Ridgill 1985).

Nesting density

Change in nesting pattern observed in contrasting seasons together with the highly specific nature of the nest sites makes comparison of nesting density difficult. There is some evidence of gregariousness in nesting of

Fig. 7. Typical Greenland White-fronted Goose nest, 67°34'N 50°36'W, Eqalungmiut nunât, June 1979.



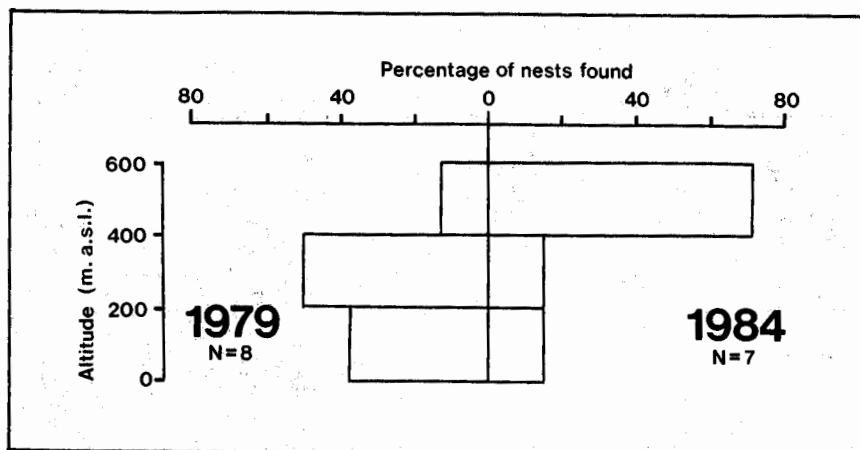


Fig. 8. Percentage frequency of Greenland White-fronted Goose nests with altitude in Eqalungmiut nunât, West Greenland, 1979 and 1984.

Whitefronts and considerable variation in local breeding densities (e.g. Gabrielson & Lincoln 1959, Dall in Nelson 1887, Snyder 1957 and discussion in Ely 1979), but Whitefronts undoubtedly nest at considerably lower densities in Eqalungmiut nunât and West Greenland generally than in other parts of the species' range (Table 2). Mean inter-nest distances from nearest neighbour measurements were 2.08 km in 1979 and 1.98 km in 1984, with similar distribution of distance classes in both years.

Egg characteristics

Mean breadth of 32 eggs was 52.47 mm and mean length 79.19 mm (Fig. 9), mean mass 120.3 g. A wide range of total clutch weights (clutches of six of 641 g, 691 g, 728 g, 815 g in 1979) was noted. There were no significant differences between egg weights between years. Cramp & Simmons (1977) state there is no difference between eggs of *albifrons* and *flavirostris* (see Table 3).

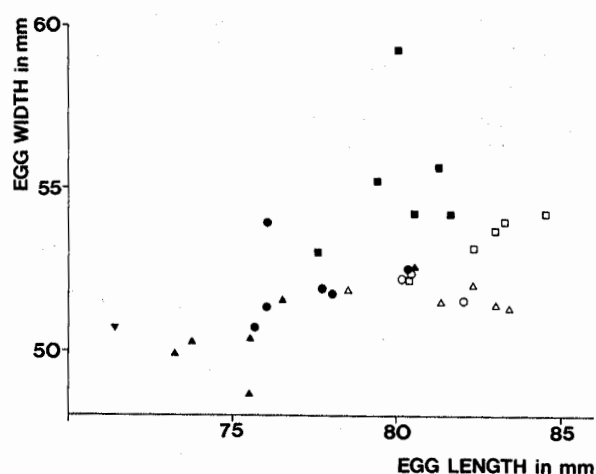


Fig. 9. Egg measurements from Greenland White-fronted Goose clutches, Eqalungmiut nunât, in 1979 (solid symbols) and 1984 (open symbols). Each different symbol denotes eggs from different clutches.

Table 2. Nesting densities of White-fronted Geese from differing breeding populations.

Density (pr/km ²)	Area (km ²)	Region or Site	Literature Reference
<i>A. a. frontalis</i>			
0.4	51800	Alaska	Dzubin <i>et al.</i> (1964)
14.0	1.3	Yukon-Kuskokwim Delta Alaska	Mickelson (1975)
2.0	10.4	Yukon-Kuskokwim Delta Alaska	Mickelson (1975)
2.9	9.8	Yukon-Kuskokwim Delta Alaska	Ely & Raveling (1984)
4.6	9.8	Yukon-Kuskokwim Delta Alaska	Ely & Raveling (1984)
2.7	9.8	Yukon-Kuskokwim Delta Alaska	Ely & Raveling (1984)
5.7	?	Old Crow Flats Alaska	Dzubin <i>et al.</i> (1964)
23-30	?	Point Barrow Alaska	Dzubin <i>et al.</i> (1964)
<i>A. a. flavirostris</i>			
"not colonial"	?	West Greenland	Fencker (1950)
"20 goslings"	c. 30	Sarqaqdaalen	Joensen & Preuss (1972)
<0.5	10	Eqalungmiut nunât	This study (1979)
<0.5	10	Eqalungmiut nunât	This study (1984)

Table 3. Comparative egg morphometrics of different races of White-fronted Geese.

Race	Weight (g)		Length (mm)		Breadth (mm)		Sample size
	mean	range	mean	range	mean	range	
<i>A. a. albifrons</i> Schönwetter (1967)			79	72-89	53	47-59	51
Kear (pers. comm.)	114	97-126					20
Alpheraky (1905)	110	100-125	81	76-88	54	49-58	24
<i>A. a. frontalis</i> Ely (1979)	127.8±2.65se		80	71-87	54	49-58	373
<i>A. a. flavirostris</i> Schjøler (1925)			79.5		52.3		17
Kear (pers. comm.)	124	108-137					100
This study	120	101-156					38

Clutch size

The mean clutch size of 4.59 (n=8, 1979) and 4.17 (n=6, 1984) compares with a mean of 4.53 from 77 broods over four years for *A. a. frontalis* (Mickleston 1975) and 4.91 from 99 clutches during 1977-1979 in-

clusive (Ely & Raveling 1984). However, in the present study, clutches from both years were predated before completion, such that the modal class of six eggs per nest (observed in six nests in the two years) is perhaps a more meaningful statistic.

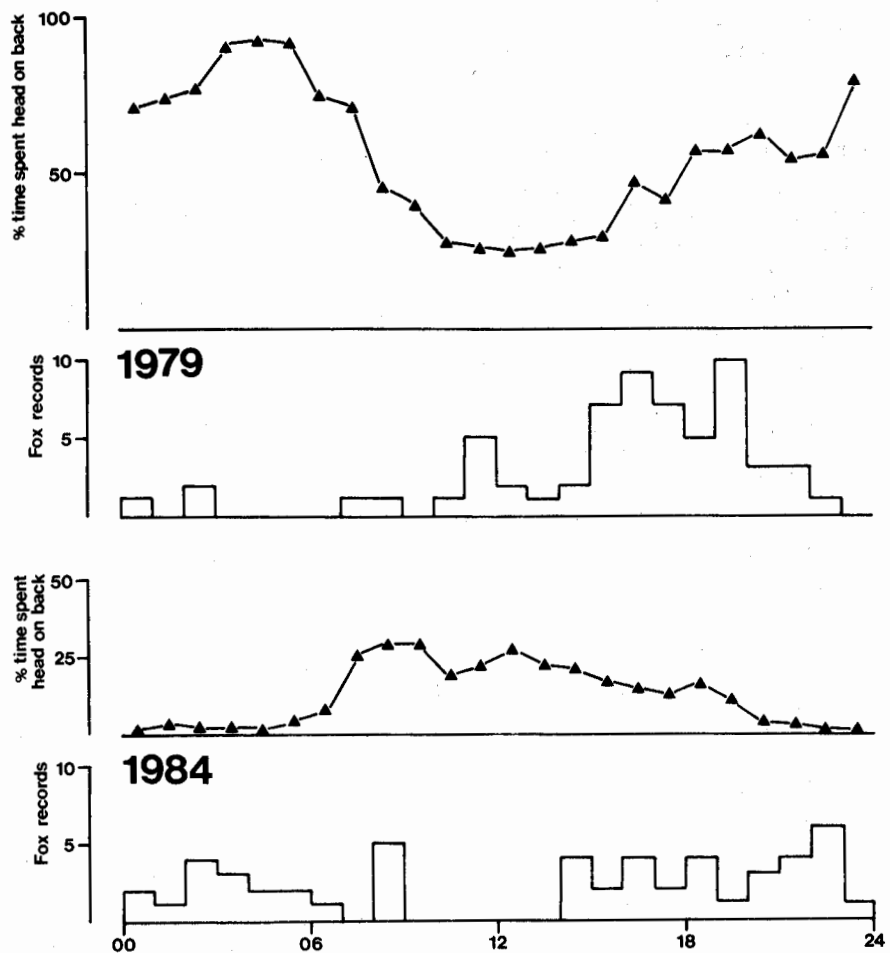


Fig. 10. Comparison of the diurnal pattern of percentage time spent by incubating female Greenland White-fronted Geese asleep (head-on-back posture) in 1979 (upper) and 1984 (lower). For each year, the diurnal patterns of fox barks and sightings are given as a representation of their activity patterns.

Incubation

At the study nests, incubation was carried out by the female alone for 25 days in 1979 and 27 days in 1984. Ganders fed in both cases on nearby marshes, and both birds of both pairs showed a strong diurnal rhythm in alertness, feeding and roosting activity (Stroud 1982). However, continuous observations of nests in the two seasons gave contrasting results. In 1979, the incubating female spent most time vigilant during the middle part of the day, sleeping in early morning (these being the two predominant activities and consequently inversely correlated – see Stroud 1982); in 1984, the female slept at midday and was most alert in the early morning (Fig. 10). Stroud (1982) proposed that the 1979 pattern related to peak of predator activity at midday, and despite the change in diurnal pattern between years, this explanation also holds in 1984, with peak Arctic Fox (*Alopex lagopus*) activity at “dawn” and “dusk” periods (Fig. 10). This feature underlines the significance of predation during incubation, a factor which may be responsible for the low productivity of the race, with only a relatively small proportion of pairs breeding successfully in Greenland in any one year.

Nest predation

In 1979, of seven active located nests, four were unsuccessful and ultimately predated; Foxes were implicated at two of these, Ravens (*Corvus corax*) at one and both Ravens and Foxes at another (Fowles 1981). In 1984, six nests were discovered, five of which were predated by foxes. This extremely high fox predation

rate of 77% in the present study (n=13 from two years data) compares with only 5% in Alaska (Ely & Raveling 1984), where the overall success rate of nests was 62% (n=63 from three years data). Such a high predation rate in the course of the present study may relate more to the presence of the researchers (despite considerable attempts to minimise disturbance) than to “normal” levels of predation in the population. This has also been found by MacInnes & Misra (1972) in a population of Canada Geese *Branta canadensis*. Although Iceland Gulls (*Larus glaucoides*) and Glaucous Gulls (*Larus hyperboreus*) were present on the coastal part of the study area, they were not serious predators due to the fact that they foraged away from goose breeding areas. Indeed, they were seen only thrice in two years anywhere near nesting geese during incubation. Arctic skuas (*Stercorarius parasiticus*) are totally absent from inland areas of West Greenland such as Eqaqungmiut nunât, but are known to be serious predators of goose nests at coastal nest sites (Plantema & Groesz 1978, Plantema *in litt.*).

Brood survival to wintering grounds

In 1979, the pair subject to continuous observation hatched five young from six eggs of which four survived to reach Machrihanish, Argyll Scotland in the autumn (one gosling was shot on passage in Iceland). In 1984, another observed pair raised six young from six eggs and although all were ringed, none have been subsequently recorded in the British Isles. Mean brood survival is shown in Fig. 11 for the two seasons under review.

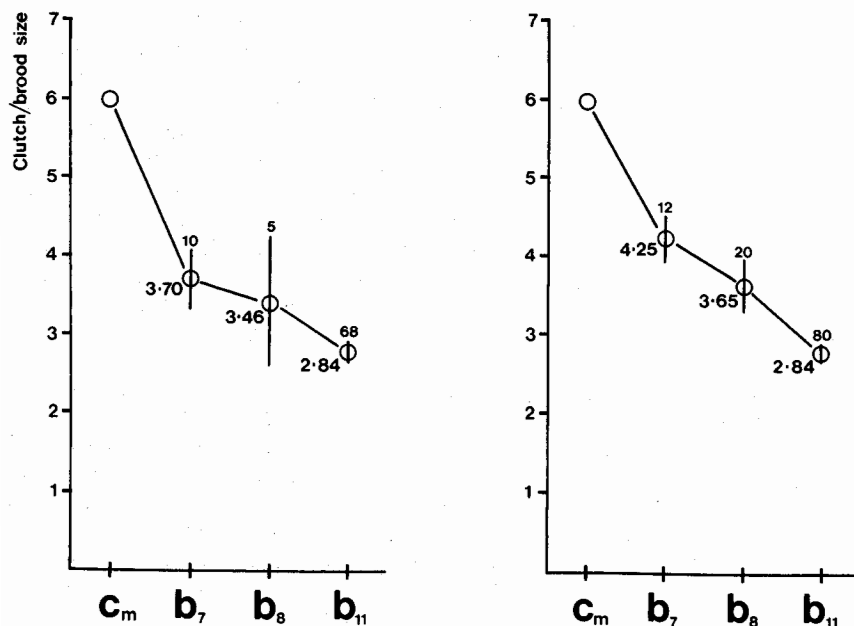


Fig. 11. Mean brood survival of Greenland White-fronted Geese in Eqaqungmiut nunât, West Greenland in 1979 (left) and 1984 (right), with subsequent brood size the following autumn of Islay (where most resightings of ringed birds have occurred, Fox *et al.* 1983). c_m = modal clutch size; b_7 = mean brood size 14-31 July; b_8 = mean brood size 1-14 August; b_{11} = mean brood size on Islay during November. Values indicate mean, digits sample size and bars standard error.

Discussion

The arrival of Whitefronts in Eqalungmiut nunât in 1984 when the area was frozen and still covered in snow was a day earlier than in the milder spring of 1979 and suggests arrival was dependent on factors other than weather on the breeding range. This is a feature of arctic-nesting geese (Cooch 1958, Barry 1962, Raveling & Lumsden 1977) including Whitefronts (Ely & Raveling 1984). In 1979, Greenland Whitefronts settled to a period of pre-nesting feeding even though nest-sites were physically free from snow and ice during this time (Fox & Madsen 1981). This probably contributed to the maintenance or improvement in the condition of females prior to laying. By contrast, arriving geese in 1984 overflowed Eqalungmiut nunât, since the area was covered by deep snow. Geese returned to the study area as forage became available some 10-15 days later and it became apparent that at least some birds were staging in the study area before moving further north (Fox & Ridgill 1985).

Despite the fortnight delay enforced by snow cover, in 1984, geese fed for approximately two weeks prior to nesting as observed in 1979. Raveling (1978) found that a similar delay of 12-13 days in nest initiation corresponded to the period of rapid yolk development in female Canada geese and suggested that the cue for rapid oocyte growth was coincidental with their departure from final spring staging areas or arrival on nesting grounds. Fox & Ridgill (1985) suggested that the Greenland Whitefront does not have a series of spring staging areas but relies on pre-breeding feeding within the breeding range to supplement reserves in preparation for egg-laying. Hence, irrespective of the widely contrasting seasons in West Greenland in 1979 and 1984, clutch-initiation followed about 10-15 days after maximum numbers of geese were reported in Eqalungmiut nunât. This corresponds well to the time of rapid yolk formation in Whitefronts (C.R. Crau – reported in Ely & Raveling 1984).

The long spring flight to the nesting grounds of the Greenland Whitefront is in sharp contrast to the northward movement between staging areas typical of the continental geese of Europe and America (Owen 1980, Thomas 1983). It was considered somewhat surprising that in spite of the lack of a prolonged migration stop-over en route to breeding areas, the race exhibits a large clutch size. It is known that substantial numbers stop in Iceland on passage in spring, although it is still not known if this represents true staging for breeding birds in the population (Francis & Fox 1987). In this respect, it would appear that Greenland Whitefronts are not that unusual, but rather stage in West Greenland as they move north to their ultimate summering areas. This being so, it may be that cues for rapid oocyte development coincide with arrival at favoured staging areas within West Greenland which contain food resources which are available (subject to thaw). Such a strategy of

staging and pre-breeding feeding close to eventual nesting areas might allow a greater degree of flexibility in ensuring an appropriate and rapid follicular response to varying year-to-year weather conditions. Ely & Raveling (1984) suggested that in years with late spring thaw, lack of nest sites prevented laying and led to resorption of follicles reducing clutch size in *A. a. frontalis* in severe seasons as reported in Brants (*Branta bernicla nigricans*) by Barry (1962). Such decline in clutch size with time and in severe seasons is a feature of many other arctic nesting goose populations (e.g. Cooch 1958, Ryder 1967, 1972, Raveling & Lumsden 1977) as a response to the diversion of stored body reserves from potential clutch production to body maintenance. Small sample sizes in Eqalungmiut nunât in both years preclude any such conclusion yet for *A. a. flavirostris* but brood sizes later in the season were no smaller in 1984 than 1979 and brood size on the wintering grounds were identical in the two seasons (Ogilvie 1983, Stroud 1985).

Boyd (1966) showed a negative correlation for *A. a. albifrons* between rainfall on the nesting grounds at times when small goslings might be susceptible to chilling and mortality by soaking, and productivity as measured on the wintering grounds, and it may be that severe weather and resulting gosling mortality in mid-summer has a greater effect on subsequent numbers of surviving goslings than clutch size of nesting females. It is worth noting in this context that the summers of 1979 and 1984 were both equally dry and relatively mild in contrast to the very wet summer of 1983 when productivity was poor (K. Vægter & N. Thingvad *in litt.*, Stroud 1984b, 1985) and the warm dry summer of 1985 when the proportion of young in flocks returning to Britain were the largest ever recorded (Norriss & Wilson 1986). Neither Salomonsen (1950, 1967) nor Fencker (1950) mention a depressing effect on brood size in severe seasons, both recording brood size as five to seven, generally six. Much more information is required to substantiate the effects of weather on clutch size in Greenland Whitefronts, and the effects of female pre-nesting condition on brood size and clutch survival.

Greenland White-fronted Geese are a highly dispersed nesting goose species (see review in Stroud 1981c), making census and study difficult and resulting in a paucity of past information. Whilst the advantages of social nesting as a strategy for arctic nesting geese have been investigated for Snow and Ross' goose (Ryder 1969a, 1969b, 1975) and Pink-footed goose (Inglis 1976, 1977; Lazarus & Inglis 1978), there is little ethological literature concerned with the determinants of solitary nesting as an alternative strategy. However, Newton's studies of Pink-footed Geese in East Greenland (Cabot *et al.* 1984) have shown that where these geese nest at a range of densities, solitary nesting birds lay significantly larger clutches and probably raise bigger broods than more gregarious breeders. This was considered to be possibly due to one or both of the

following reasons: solitary breeders may be less easily detected than colony nests and thus less likely to lose eggs to predators, alternatively more experienced birds are known in some geese to lay larger clutch sizes (Raveling 1981) and thus colonial birds may be less experienced than solitary ones.

In the case of Whitefronts in continental West Greenland, it is clear that feeding marshes adjacent to the actual nest site play some part in nest site selection. Lowland nests near marshes elsewhere in West Greenland have been previously found by Thingvad (*in litt.*) and Beer *et al.* (1956). In the two years when nesting pairs were studied, the attendant gander was able to feed within 1 km of the incubating female and, whilst not constantly close to the nest site, is within sufficient proximity to offer some protective vigilant function in the vicinity of the nest. Plantema (*in litt.*) witnessed this further north on Disko where both adults of a pair would remain at the nest when large numbers of skuas were present. The feeding area for the gander enables him to confer some protection whilst he is able to maintain his body reserves in readiness for the still greater investment in vigilant behaviour which is incumbent on ganders during the development of young after leaving the nest (Stroud 1982, Madsen 1981). The marshes where ganders fed are invariably the feeding sites of the incubating females during her brief recesses from the nest (Stroud 1982).

Nest sites were generally well concealed, but the use of hummocks 20-35 cm above the surrounding vegetation in areas with otherwise little relief was conspicuous, both in the present study and in literature references. This presumably gives incubating females elevation to assist in early predator detection as well as affording protection from flooding during periods of thaw. The exceptional lowland sites of 1979 were both near *Eriophorum angustifolium* marshes, but the unusual nest positions (on a vegetated promontary on a lake and amongst open sand amidst boulders) may be due to protection from higher densities of foxes at low altitude during the period of clutch initiation.

These marshes are, by their very nature in continental West Greenland, discrete and contrast with the large expanses of suitable nesting habitat which are the dominant vegetation types over much of the Yukon-Kuskokwim Delta, where *A. a. frontalis* breed at much greater densities (Ely 1979, Ely & Raveling 1984). Since much of the hypothesised advantage of colonial nesting relates to predator awareness and the reduction of the impact of predators by a swamping effect (see discussion in Owen 1980), it may be that the strategy imposed by the discrete breeding sites results in the high predation rates witnessed in Eqaungmiut nunât during both seasons, or that the highly dispersed habit is a strategy to avoid yet higher predation. The probabilities of predator encounter within the nesting area was lower in Eqaungmiut nunât in 1979 than in studies of Pink-foot colonies (Stroud 1981c); however, this is an area with-

out skuas and it may be presumed to be much greater in more coastal areas. Other factors such as human hunting, quality of feeding areas and spacial distribution of feeding marshes may have been important in the evolution of a solitary breeding strategy. It is also possible that inland Eqaungmiut nunât is not a typical area in all these respects. In historical terms, such a strategy could have evolved in more coastal or other areas where conditions (e.g. human hunting patterns, extent of wetlands) were different to those witnessed in Eqaungmiut nunât.

The larger clutch size compared to high-arctic nesting geese would be expected to place a correspondingly greater reliance on feeding by the female during incubation, yet the two studies of incubating females in Eqaungmiut nunât have shown the period spent incubating each day (>99.99%) is greater than in *A. a. frontalis* (97.3%, Ely 1979), *A. canagicus* (99.5%, Thompson *in litt.*) and *A. brachyrhynchus* (96.2%, Inglis 1977). The latter may to some extent reflect the protective function of the colony. The possibility remains, however, that dispersed nesting is not adaptive and available suitable nest sites fall far short of saturation levels in West Greenland.

In addition to the date of the thaw, the nature of thaw clearly has considerable implications for the summer ecology of the geese. In 1979, the absence of snow cover did not necessarily equate to availability of forage, since many of the marshes of importance for feeding geese did not become available until the substrate had thawed. This is particularly relevant in the case of the most important food item, *Eriophorum angustifolium*, since it is the overwintering lower stem and stem-base living below the surface which is eaten. The thaw of the substrate also determines the onset of growth of *Carex rariflora*, the other important species which dominates the diet later in the season (Madsen & Fox 1981). Thaw was progressively delayed at higher altitudes in 1979 and goose distribution was determined by availability of forage released from the thaw. This factor applied as much to nesting geese as non-breeding birds. The altitudinal distribution of located nest sites reflected this. In 1984, melt was not merely delayed, but when it came was dramatic and rapid at all altitudes, largely eliminating altitudinal progression in availability of forage.

The important moulting and brood rearing areas for the entire population are predominantly the high plateau lakes where there is abundant food and safety of open water for predator avoidance at a time of vulnerability. This feature was common to both years. In view of the established relationship between distance from nest to water and duckling mortality (e.g. Dzubin & Gollop 1972) and heavy gosling predation in terrestrial situations in other arctic nesting goose populations (e.g. Cabot *et al.* 1984), the risk of brood predation would be reduced if the distance to plateau moulting areas were reduced. Hence altitude and location of nest sites may well be selected within the constraints of

(i) degree of thaw of forage and (ii) the need to be close to the ultimate nursery areas. The interaction of these two factors is reflected in the difference in nesting altitudes in the two years.

The lack of difference in the mean reproductive success (measured by percentage young and mean brood size on the wintering grounds) in two seasons of contrasting spring severity underlies the flexibility of the Greenland White-fronted Goose breeding strategy, whilst highlighting our lack of understanding relating to proximate factors acting upon breeding biology.

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