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A. D. FOX and S. C. RIDGILL

Introduction

The Greenland White-fronted Goose *Anser albifrons flavirostris* is unusual amongst arctic-nesting geese in its migration and staging behaviour. The race winters exclusively in the western British Isles and migrates to its West Greenland breeding grounds with but a short stop-over in Iceland (Salomonsen 1950; Fox *et al.* 1983). The long oceanic spring flight to the nesting range 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 is thus surprising that, in spite of the lack of apparent migration stop-over, the race also exhibits large clutch size in the absence of nutrient supplements to reserves by feeding on migration (Ogilvie 1978). Observations suggest Greenland Whitefronts are in fact not that unusual, and the present paper describes staging within the breeding range in West Greenland as they move northwards to their ultimate summering areas.

During 1984, Greenland White-fronted Geese were studied in Eqaungmiut Nunaat, West Greenland (67°32' N, 50°30' W) (see Fox & Stroud 1981). Previous investigations in 1979 found arriving pairs feeding for up to ten days before clutch initiation (Fox & Madsen 1981a, 1981b). This pattern of pre-breeding feeding contrasts with most arctic-nesting geese which nest soon after arrival on their breeding areas, having fed in more southerly staging areas en route (Ryder 1970; Raveling 1978; Thomas 1983).

Greenland White-fronted Geese breed in low arctic West Greenland between 64° and 73° N (Salomonsen 1950), so that Eqaungmiut Nunaat is moderately central in the breeding range. In 'typical' years, the geese arrive from their wintering grounds in early May and commence laying between 20–28 May (Fencker 1950; Stroud 1982; Fox *et al.* 1983). In 1979, thought to be a 'typical' year, geese were seen in the study area on 7 May, with numbers of lowland feeding birds peaking on 12 May and passage through the area largely complete by 17 May. Peak nest

initiation occurred on 22 May (range 19–27 May).

In contrast, winter 1983–4 was one of the coldest on record in West Greenland, and this considerably delayed the spring thaw. Although on 7 May 1979 there was only 15% snow cover (mainly snow patches in deep shade) and abundant running water, on 7 May 1984 there was up to 50 cm of snow on wind-blown surfaces, with deep drifting elsewhere. The first running water was not seen until 13 May. Thus in early May 1984, lowland areas with abundant *Triglochin palustris* and *Puccinellia deschampsoides* considered so important for arriving geese (Stroud 1981; Fox *et al.* 1983) were covered in deep snow. With these and all other feeding areas unavailable during the first half of May, patterns of goose behaviour and feeding were very different from those recorded in 1979.

Timing and status of arriving geese

In 1984, the first geese were heard on 6 May (a day earlier than 1979) and on 8 May, six skeins totalling 150 birds flew over strongly northwards. With no feeding available in Eqaungmiut Nunaat, geese did not land and were not seen in numbers until 20 May. Fox *et al.* (1983) suggested that the earlier arriving birds were breeding in pairs, and, if correct, these early skeins were probably potentially breeding geese. The first substantial area to thaw was an area called 'Ridgeway Marshes' (described below), and by 22 May geese were congregating here, increasing to a peak of 180 birds on 26–27 May.

While it is impossible to state that some of these birds seen on Ridgeway Marshes did not breed, it is reasonable to assume that these geese were (a) only passage migrants staging in the area, and (b) were not breeding either in Eqaungmiut Nunaat or elsewhere in the range. When numbers declined at this site after the peak on 26–27 May, there was no increase in numbers seen elsewhere in Eqaungmiut Nunaat. This suggests these birds were dispersing else-

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where. Two birds neck-banded as non-breeders at Wexford, Ireland, in February 1984 were present amongst the feeding birds at Ridgeway Marshes from 27 to 31 May and one was later shot further north in early June. Some pairs had already dispersed to smaller marsh areas and were showing site-loyalty typical of breeding pairs whilst numbers at Ridgeway Marshes were still increasing. Observations showed that these birds appeared almost immediately at potential nesting areas on their arrival in Eqalungmiut Nunaat. These potential breeding pairs remained at these sites after the aggregation at Ridgeway Marshes had dispersed.

Our proposition is that the birds observed at Ridgeway Marshes were thus migrating birds, temporarily feeding in Eqalungmiut Nunaat, until conditions improved further north in the range. Whilst most of the pairs studied in 1979 were thought to have been potential breeders (Fox & Madsen 1981a, 1981b), maximising food intake prior to clutch initiation, we here contrast the feeding and behaviour of what seemed to be non-breeding geese in a spring of greater climatic severity.

Study area

Ridgeway Marshes is an alluvial flood plain marsh at about 100 m a.s.l. The commencement of river surface flow in mid-May flooded peripheral wetland areas and progressively freed the area of snow.

The marshes were of a very different character to Kûk Marshes where birds commenced feeding in 1979 (Fox 1981). The flood-plain marshland contains tussocky *Carex stans*, *Eriophorum angustifolium* and *E. scheuchzeri* over-lying a thick moss-mat of *Sphagnum squarrosum* and *Calliergon cuspidatum*, mixed with a complex of runnels and pools.

Initially the removal of snow exposed *E. angustifolium* which constitutes the most important dietary item of the geese during the early part of the summer (Madsen & Fox 1981). In winter and early spring the lower stem and stem-base of this plant contains high levels of carbohydrates (Phillips 1954; Shaver & Billings 1976) and are selected for by Greenland Whitefronts (D. Stroud, per com.). Faecal analysis and direct observation showed the geese to be feeding on the lowest plant parts during the study period,

although with the initially frozen substrate, the most nutritious below-ground stem-base section probably remained inaccessible. Thus, early in the period their forage quality would have been poorer than under conditions of advanced thaw.

Methods

The marshes could be watched from a ridge some 200 m to the north, with a concealed approach and extensive views. Observations using 20–45x telescopes from a hide commenced on 22 May and continued until 4 June. An intensive period of continuous observation occurred during the period 25–27 May when numbers reached a peak of 180 birds.

Two methods of data collection were used:

- (1) At 15-minute intervals, the marsh was scanned and the location and activity of all geese present were noted. Behavioural classes followed Inglis (1977) and Stroud (1982) as follows. Activities: sit, stand, walk, run, swim, fly, float on water; and postures: head on back, head low, head up, extreme head up, graze, preen, drink, threat, bathe.
- (2) Concurrently, pairs of birds were watched continuously, and for each bird, activity, posture, inter-distance and distance to the nearest other goose were scored at minute intervals. Birds lost from sight or which flew off were abandoned and the same technique transferred to adjacent pairs. The same activity states were used as in the quarter hourly scans.

Times given are Greenland local time, i.e. GMT + 3 hours.

Results

Total marsh scans

Hourly maxima through the period 15.00 hrs on 25 May, to 16.00 hrs on 27 May, are presented as Figure 1. A strong diurnal pattern of attendance at the marsh is conspicuous, with maximum daily numbers occurring just before midnight and declining rapidly to minimum numbers at 08.00 hrs. Despite fewer observations, this pattern occurred on other dates before and after the period of intensive observation.

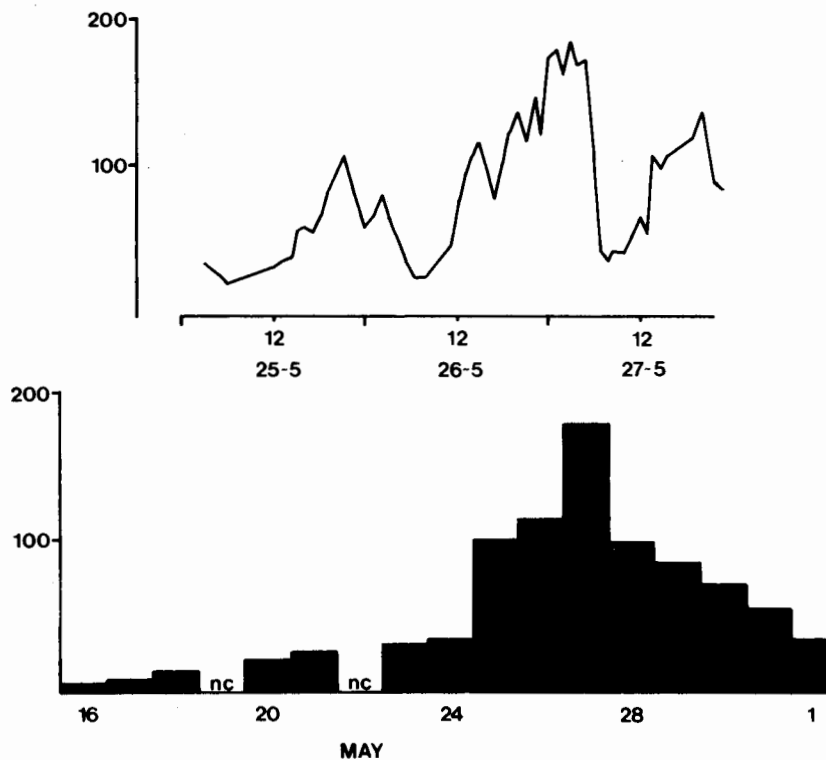


Figure 1. Maximum numbers of Greenland White-fronted Geese counted during daily observations, 16 May – 1 June 1984, except 19 and 22 May when no counts carried out (lower). Note the diurnal pattern in numbers present during hourly maximum 25–27 May 1984 at the same site (upper).

This cycle was mainly due to birds from elsewhere flying to the marshes to roost communally with those present there all day. The main river and marsh area was also probably ice-free for longer than the smaller wetlands nearby used by the birds flying in at night. Severe heat-haze during the middle of the day may also have had the effect of artificially lowering the midday counts.

Behaviour throughout the day also shows a strong diurnal element and patterns of selected activities are shown in Figure 2. The migrating birds at Ridgeway Marshes tended to alternate between low levels of grazing between midnight and 09.00 hrs during which period most roosted, and high grazing levels with little roosting through the rest of the day. Alertness similarly followed this pattern, but preening and general plumage care continued throughout the day. This contrasted with the potentially breeding birds of 1979 which preened most during the night.

- (i) *Feeding*: 51% of total daily activity was spent feeding (a mean of 12.2 hours per day), significantly less than observed on Kùk Marshes amongst potentially breeding pairs (68%, $X^2 = 4.17$, $p < 0.05$) (Figure 3). Feeding took up a mean of $64.5\% \pm \text{SE } 0.6$ throughout the period 10.00–24.00 hrs, falling to 10–40% of all activity during the remaining 'night' period. This also contrasts with the potentially breeding pairs observed in 1979 where time spent feeding only dropped below 50% during the extreme cold period of 01.00 and 05.00 hrs when roosting occurred. The conspicuous increase in feeding rate towards the onset of roosting observed in 1979 and during the winter studies of Owen (1972) was absent in 1984 amongst staging birds.
- (ii) *Roosting*: 22% of daily activity was spent roosting (5.2 hr/day), exactly twice that observed in 1979 ($X^2 =$

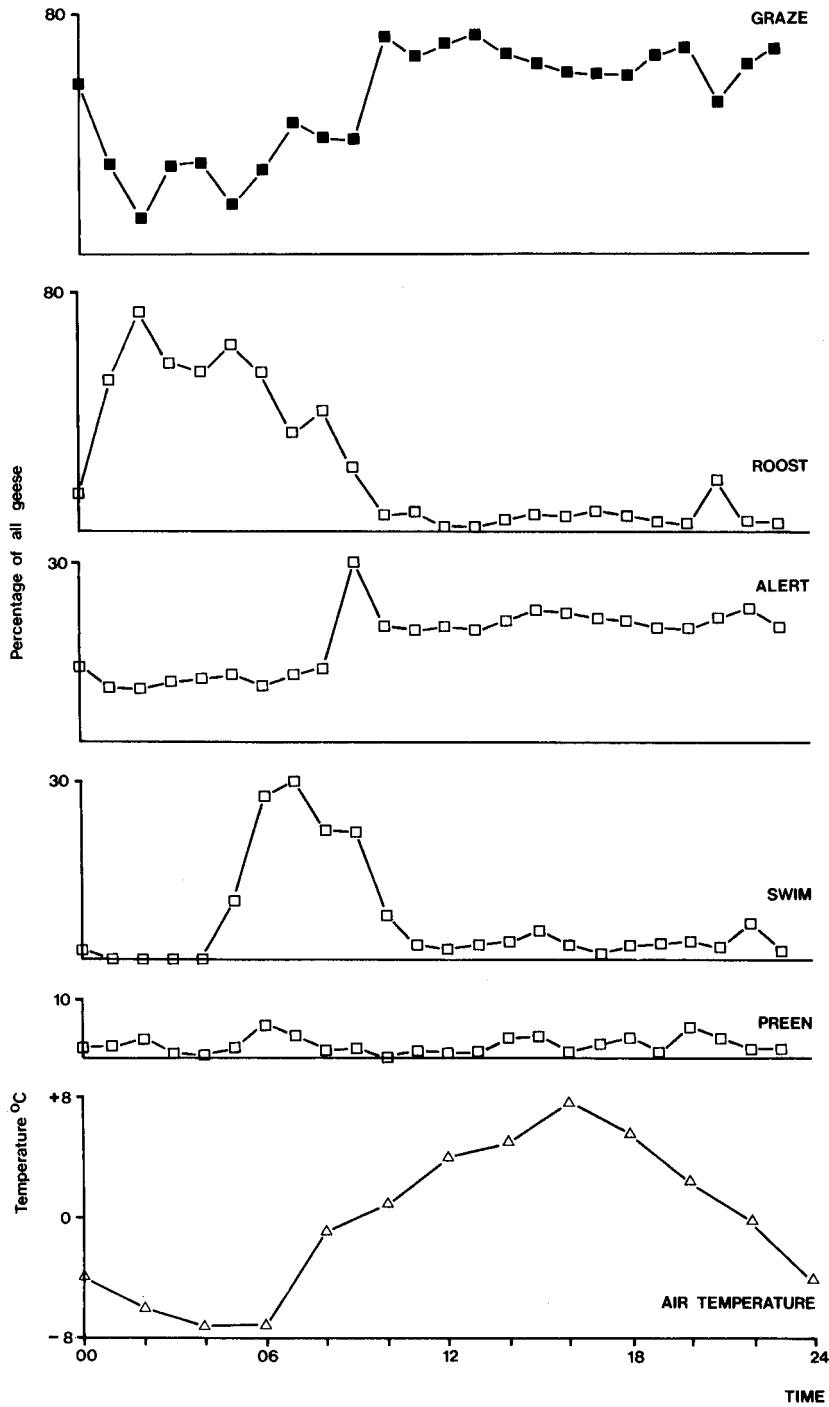


Figure 2. Percentage activity of all geese on Ridgeway Marshes, 25-27 May 1984. Each point is the mean of quarter-hourly scans of the entire marsh from each of these three days. The lowest graph shows the two-hour air screen temperature readings for comparison.

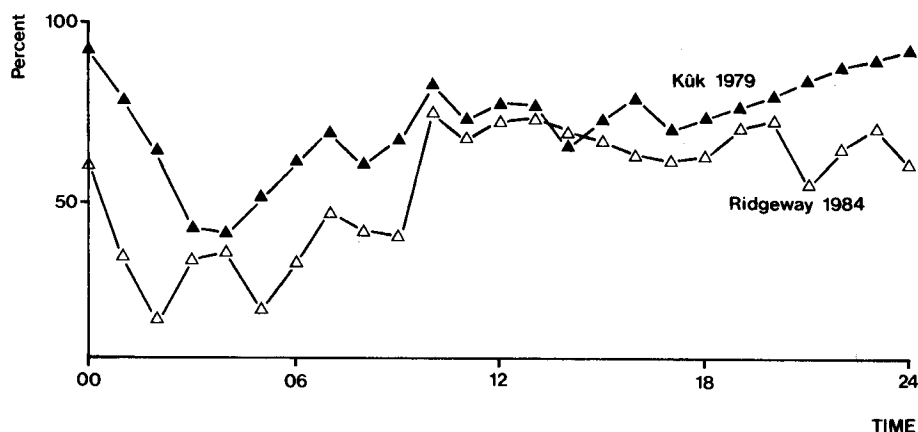


Figure 3. Mean percentage hourly grazing activity on Ridgeway Marshes 25–27 May 1984 and Kûk Marshes 10–12 May 1979. Both sets represent hourly means from quarter-hourly scans of the two sites.

11.45, $p < 0.001$), with more than 20% of all activity during the hours 01.00 to 09.00 hrs coinciding with periods of lowest temperature.

- (iii) **Alert:** 17.3% of daily activity was spent alert (4.1 hr/day) significantly more than the Kûk study of 1979 (10%, $X^2 = 5.27$, $p < 0.05$). Whilst a relatively constant proportion of birds were alert throughout the twenty-four hour period in 1979, the Ridgeway Marshes birds were generally more alert during the period of maximal feeding compared to the 'night-time' roosting hours.
- (iv) **Preening:** Most preening activity occurred during the main roosting period in 1979, contrasting with the continuous background preening of all birds evenly spread throughout the day in 1984. This activity amounted to the same proportion of daily activity (2% in 1984 against 3% in 1979, $X^2 = 0.28$, $p > 0.05$, not significant).
- (v) All other activities constitute the remaining 8% of daily activities and show few trends of interest. The pattern of swimming/floating postures, however, is of interest, since this shows a strong diurnal pattern, being most prominent during the hours 05.00 to 11.00, at a time when substrates become most frozen, and forage in shallow flowing water most accessible and cost-effective, a feature suspected in the Kûk Marshes study of 1979 (Fox & Madsen 1981b).

Behavioural studies of individual pairs

With such a substantial diurnal pattern in numbers present on Ridgeway Marshes, it was clearly necessary to test patterns of activity derived from the activity patterns of the entire population on the marshes against the activity patterns of individual birds. Clearly if birds were fighting in to roost during the night-time period, the relative proportion of birds feeding at the time would diminish as a percentage whilst remaining unchanged in the absolute sense. To this end, individual pairs were observed, their activity scored each minute throughout the day, and their diurnal activity summarised hourly as a mean of the individual observations. In this way, percentage activity patterns were obtained from individual pairs for comparison with data derived from the 15-minute scans described above. These are shown in Table 1, including a separation of the sexes by the latter method. This shows there is no significant difference in the two methods in determining the gross activity budgets for the four major constituents of the goose diurnal activity ($X^2 = 0.201$, $p > 0.05$). Intriguingly, there were again significant differences between the activity patterns of male and female geese (Fox and Madsen 1981a). Males spent more time alert than females ($F_{47} = 27.2$, $p < 0.001$), which in turn spent a greater part of their time grazing than the males (Figure 4; $F_{47} = 178.31$, $p < 0.001$), although there are no

Table 1. Comparison of the gross activities of Greenland White-fronted Geese, Ridgeway Marshes, May 1984, from two methods of data collection. Budgets evaluated from data collection by scores of the individual activity of paired birds recorded at minute intervals and total scans of the entire marshes scoring all birds present every quarter of an hour. Both represent data from more than one 24 hour period for the four most significant activity classes.

	Graze	Alert	Roost	Preen
Male scores	44.0	26.6	21.4	2.0
Female scores	63.0	5.8	23.1	1.6
Mean of male and female scores	53.5	16.2	22.3	1.8
Fifteen minute scans	51.2	17.3	22.2	2.0

significant differences between the sexes in time spent roosting or preening. No attempt was made to separate the vigilance schedules of birds between those pairs in flocks and those feeding away from other birds, but generally the proximity of other feeding birds on Ridgeway Marshes meant that rarely were observed pairs solitary in the sense of the Kùk birds of 1979. Unfortunately, the differing methods of data collection in 1979 and 1984 precludes the statistical comparison of the relative feeding and vigilance schedules of ganders and females between years.

Discussion

Behaviourally, there are many differences in the diurnal activity patterns of birds staging at Ridgeway Marshes in late May 1984 compared to arriving, potentially breeding pairs observed in early May 1979. It is tempting to speculate that these differ-

ences are due to the differing status of the birds involved. Non-breeding birds, which make up a large proportion of this population (Ruttledge & Ogilvie 1979), having arrived on the summering grounds and following the thaw slowly northwards, might be expected to be concentrated by the atypically late spring into a few lowland feeding areas.

Thomas (1983) has presented a generalised model of body reserve build-up and loss through the migration-staging-breeding period of arctic nesting geese. This indicates that for breeding birds, feeding at staging areas and on arrival on the nesting grounds can be crucial in maximising reproductive output. Ankney and MacInnes (1978) showed that protein intake at Lesser Snow Goose staging areas approximated to a potential extra egg. However, for later migrating birds, non-breeding either by reason of physiological condition or inexperience, there is less imperative to maximise body condition. This is certainly

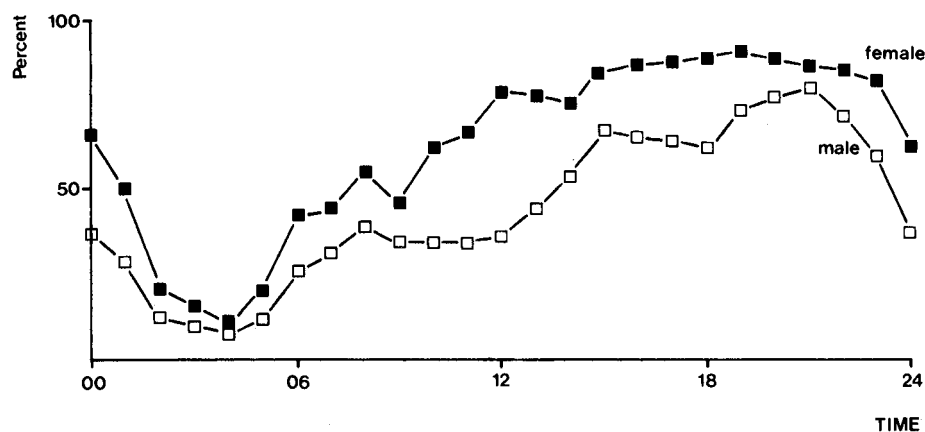


Figure 4. Plot of three-hour running mean percentage feeding activity of male and female paired Greenland White-fronted Geese from Ridgeway Marshes, May 1984.

borne out by the present observations, where both sexes fed for less time, ganders spent far less time as an alert sentinel guarding females, and both sexes spent up to twice the time roosting compared to potentially breeding pairs observed in 1979. With the improvement (as contrasted with maintenance) of female body condition at less of a premium for non-breeding birds, the gander was able to spend proportionately more time feeding and roosting, whilst investing less time in a protective alert posture.

Despite the differences in behaviour, it is difficult to make meaningful comparisons when the food items involved were different: *Triglochin palustris* bulbils and *Puccinellia deschampsoides* roots in 1979 taken by potentially breeding birds, and mainly *Eriophorum angustifolium* stem-bases amongst putatively non-breeding, staging birds in 1984. However, it was clear from general observations that peck-rate and therefore food intake by females in 1979 was considerably higher and more urgent than in 1984. Hence, not only did the Ridgeway Marshes birds spend less time feeding in absolute terms, but the amount taken in was probably also less than in 1979 per unit time spent feeding.

Evidence thus continues to support the assertion that the breeding and non-breeding elements of the population of Greenland White-fronted Geese behave differently in patterns of migration, arrival on the breeding grounds, and use of feeding marshes within the summering areas, while the differences in behaviour of the two partners amongst breeding pairs maximise the improvement of condition in pre-nesting breeding females. All these differences in patterns of activity relate to the status of the birds, but clearly further work is required to verify these differences, particularly concentrating on the specific identification of subsequently successfully breeding and non-breeding geese and the differences in nutritional intake of these contrasting groups on arrival in Greenland.

It would thus appear that Greenland Whitefronts have evolved a strategy appropriate to their long spring migration in the absence of staging areas and the long narrow breeding corridor straddling 9° of latitude. Without the facility of a migration stop-over en route to the nesting grounds, the geese are able to top-up reserves immediately before breeding. The low-

arctic nature of their nesting area ensures that there is a food resource freed by the spring thaw, even if this is restricted to southern fringes of the range on arrival at the start of the season. Birds nesting locally in these areas can thus derive forage immediately prior to clutch initiation (Fox & Madsen 1981b), while birds breeding further north in the range can stage in such areas prior to movement to their ultimate summering area. In addition, it would appear that a higher proportion of reserves is put into eggs than, for example, by the high-arctic Lesser Snow Goose *Anser caerulescens caerulescens*, with a consequent greater reliance on feeding by the female Whitefront during the incubation. Having dispersed throughout the breeding range, locally nesting birds are then able to exploit the progressive altitudinal thaw in forage to provide sufficient fresh growth during the stress of moult in adults and the main growth phase of young birds of the year (Madsen & Fox 1981).

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Summary

Greenland White-fronted Geese *Anser albifrons flavirostris* typically produce large clutches without nutrient supplement at spring migration staging areas. Observations of geese in an area central to their breeding range suggest a large