Activity budgets of Greenland White-fronted Geese *Anser albifrons flavirostris* spring staging on Icelandic hayfields

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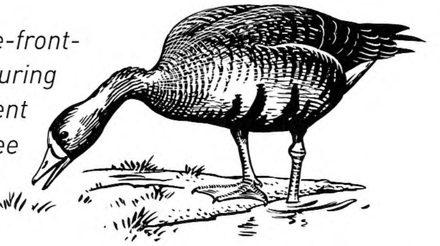

The activity budgets of Greenland White-fronted Geese Anser albifrons flavirostris *during spring staging were studied in different Icelandic hayfields dominated by three grass species:* Poa pratensis, Deschampsia caespitosa *and* Phleum pratense. *Geese spent 70-90% of the daylight period (12.5-14.5 hours a day) feeding, consistent with the need to build up body reserves during the short staging period before the onward flight to West Greenland summering areas. Feeding activity showed a strong diurnal rhythm, being least (70%) on arrival in fields from the roost, increasing steadily during the day, with a corresponding drop in resting activities, to reach 90% feeding in the evening. Possible explanations for this unusual pattern are discussed. There were small but significant differences in the time spent feeding in fields of different sward types. Geese were foraging in* Phleum *fields, thought to be the most nutritious grass species compared to the two native ones, for 81% of daylight hours compared with 83% in the two other sward types. The conservation implications of the high percentage time spent feeding are discussed.*

Key Words: *Anser albifrons flavirostris*, activity budget, feeding ecology.

Long distance migratory birds such as arctic breeding geese rely upon spring staging sites en route to their breeding grounds in order to refuel and accumulate sufficient energy and nutrient stores for their onward migration and investment in subsequent breeding attempts (Krapu & Reinecke 1992). Geese are herbivores but are considered to have inefficient digestive systems, which necessitate high food intake rates of relatively poor quality forage (Owen 1980). It would therefore be expected that these birds spend much of their time feeding during spring staging, at the cost of other activities.

The total population of Greenland White-fronted Goose *Anser albifrons flavirostris* numbers 33,000 geese, which winter in Ireland and Britain, and breed in west Greenland. During spring they migrate for c.1,500 km before reaching Iceland where the geese stage in the southern and western regions for about three weeks (Fox *et al.* 1999). Here they rapidly accumulate body stores for the onward flight of another 1,500 km over the Denmark Strait and the Greenland Ice Cap to their summer quarters (Boyd *et al.* 1998). The aim of this study is to assess the behavioural activities (with particular emphasis on feeding) of the Greenland White-fronted Geese during their spring staging in Iceland, and to compare whether these activity patterns differ between the three dominant hayfield sward types upon which the geese feed.

Methods

The study was carried out at Hvanneyri Agricultural College, Borgafjórdur, in west Iceland (64°34'N, 21°46'W) from 17 April to 8 May 1999, a total of 22 days. The area is the most important spring staging site known for Greenland White-fronted Geese (Francis & Fox 1987; Fox *et al.* 1994, 1999). It comprises some 85 ha of relatively undisturbed hayfields in close proximity to safe roost sites (the adjacent intertidal Borgafjórdur and a lake on the farm). The numbers of geese quickly reached a maximum of 1100 geese on 21 April, but after a few days levelled off to 400-600 geese, until departure (Fox *et al.* 1999). The geese used 64 different fields in the area during the study. The fields are dominated by three species of grass, all of which are eaten by the geese: *Poa pratensis, Deschampsia caespitosa* and *Phleum pratense* (Kristiansen *et al.* 1998b). The two former species are native to Iceland, whereas *Phleum* is an important haygrass introduced from Norway during the last 50 years. *Phleum* requires reseeding to maintain its presence in the sward, as it becomes out-competed by the two native species, *Poa* through tiller invasion and *Deschampsia* by its tussock growth (Fox 1993; Kristiansen *et al.* 1998b).

Daily activity budget data were compiled by scan-sampling (Altman 1974). The behaviour of each individual was assigned to one of the following categories: feed, alert (head-up), aggression, rest (sleep, sit), walk, drink and comfort (preen, wing stretch, wing-flapping). Scans of flocks were of geese within individual fields made from a car using telescope or binoculars and included all individuals of a given flock. Flocks of geese obviously affected by our presence were not scan-sampled. Scans were carried out every day during the staging period and overall the data covered the whole feeding day of the geese, ie approximately from sunrise to sunset. There is an unavoidable inter-dependence between samples when scans were carried out of the same fields on the same day. To minimise this effect, at least 30 minutes separated any two scans of the same field, and in most cases this period exceeded an hour.

Each major behavioural category size was related to the following variables: sward type, time of day, date and flock size. Logistic regression (PROC GENMOD with CONTRAST, SAS Inst. 1985) was used for statistical analysis. To correct for overdispersion the PSCALE operator was applied when Pearsons χ^2 value exceeded one. The *P* value of each model was calculated by comparing the deviances of the model with (D_m) and without (D_0) variables, using methods described by Manly (1990). ΔD was calculated as $(D_0-D_m)/D_0$ to express the degree of explanation of each model (Hosmer & Lemeshow 1989). Flock size was related to sward type, time of day and date using multiple regression (PROC GLM, SAS Inst. 1985). The effect of time of day and date on time spent flying was also analysed with multiple regression (PROC GLM, SAS Inst. 1985). To avoid type one errors, sequential Bonferroni corrections were made using the Dunn-Sidák method in all tests (Sokal & Rohlf 1995).

Sward composition was determined for each field unit (defined by ditches or fence boundaries) by sampling 25 random 10 x 10 cm quadrats sampled from each field during the night time, when the geese were roosting on the nearby fjord and lake, to avoid disturbance of feeding patterns. In each quadrat, the percentage cover of green material of each plant species was estimated. Fields were then assigned to the following categories: *Phleum, Poa* or *Deschampsia* dominated, when cover of the most abundant species exceeded that of the next most abundant species by more than 20%. Using this criterion, 41 fields were classified as being dominated by a single grass species. Observations from the remaining fields were excluded in the present study since those fields consisted of mixed swards.

The average times of arrival and departure of the geese to and from the fields were obtained by observations of the times of roost flights. These showed that the feeding day started, on average, 10 minutes before sunrise and ended 30 minutes after sunset. Due to the increase in day length of almost three hours from 17 April to 8 May in Iceland, time of day was normalised by dividing each day into 10 periods of equal length, and each scan assigned to one of these periods. There was no systematic recording of behaviour when the geese were at the roost sites, but no positive signs of night time feeding was obtained.

To estimate the amount of time spent flying during the day, flight surveys were carried out from the first floor of one of the college buildings, a vantage point that offered a simultaneous view over almost all the fields. In all, a total of 14 surveys were evenly distributed throughout the feeding day and the whole staging period, each survey lasted 30 minutes. All flocks taking to the air were counted and the flight duration timed, so that the time an average goose spent flying per hour could be calculated based on the total number of geese present in all the visible fields during each observation period. The time spent flying to and from roost sites were recorded separately.

Daily maximum and minimum temperatures were obtained from the Hvanneyri automatic weather station.

Results

The overall time allocation of the geese calculated by field sward type is presented in **Table 1** and the results of the statistical analysis of behavioural data are shown in **Table 2**.

Time spent feeding increased significantly during the day, while resting activities decreased significantly during the day (**Figure 1**). Aggressive behaviour increased during the day. Drinking and aggressive behaviour significantly decreased with date, while alertness increased. Flock size showed positive correlation with comfort, but a negative effect on aggressive behaviour and alertness. Furthermore the flock size decreased with date (multiple regression, *P*=0.0001).

There were significant differences in the time spent feeding on different sward types, with differences between *Phleum* and *Poa* (logistic regression, *P* =0.0172) and *Phleum* and *Deschampsia* (logistic regression, *P*=0.0074). Geese spent least time feeding on *Phleum* dominated fields. Drinking occurred more often on *Phleum* than on *Poa*

Table 1 Activity budgets of Greenland White-fronted Geese feeding on three different sward types during spring staging in Iceland 1999. N=number of scans.

		Time expenditure (% ± SE)							
	n	Feed	Alert	Rest	Walk	Comfort	Flight[a]	Aggression	Drink
Poa	272	83.0 ± 1.1	9.9 ± 0.8	5.3 ± 0.8	1.0 ± 0.3	0.7 ± 0.2	0.5 ± 0.1	0.1 ± 0.1	0
Phleum	163	81.3 ± 1.4	9.7 ± 0.9	6.1 ± 1.1	1.7 ± 0.3	1.0 ± 0.2	0 .5 ± 0.1	0	0.1 ± 0.1
Deschampsia	122	82.9 ± 1.9	7.7 ± 1.0	6.8 ± 1.5	1.7 ± 0.6	0.6 ± 0.3	0.5 ± 0.	0.3 ± 0.3	0

[a]Time spent flying was assessed for all sward types together.

Table 2 Logistic regression of the relationship between time spent by Greenland White-fronted Geese on each behavioural category and four variables (n=557). The variables are (with range): time of day (1-10), date 17 April-8 May), sward type (*Poa, Phleum* and *Deschampsia*) and flock size (2-305; mean = 18.8). Sequential Bonferroni was made on the *P* values of the seven models.

Behaviour class (No of geese obs.) *P* value of model		Intercept	Time of Day	Date	Sward Type	Flock Size
Feed (8815)	Estimate± SE	1.804±0.961	0.097±0.017	-0.005±0.008	Poa: -0.110±0.123 Phl: -0.352±0.132 Des: 0.000±0.000	0.002±0.002
<0.0001***	*P*	0.0605	0.0001***	0.5313	0.0123*	0.2371
Alert (770)	Estimate ± SE	-4.368±1.068	-0.020±0.018	0.018±0.009	Poa: 0.189±0.137 Phl: 0.286±0.146 Des: 0.000±0.000	-0.012±0.003
<0.0001***	*P*	0.0001***	0.2691	0.0418*	0.1396	0.0001***
Rest (594)	Estimate ± SE	-2.184±1.713	-0.236±0.032	0.003±0.015	Poa: 0.114±0.227 Phl: 0.296±0.240 Des: 0.000±0.000	0.003±0.003
<0.0001***	*P*	0.2024	0.0001***	0.8434	0.4163	0.3684
Walk (181)	Estimate ± SE	-0.346±2.438	0.008±0.042	-0.034±0.021	Poa: -0.239±0.326 Phl: 0.343±0.322 Des: 0.000±0.000	0.002±0.004
0.0006***	*P*	0.8872	0.8494	0.1058	0.0738	0.6792
Comfort (97)	Estimate ± SE	-8.657±2.667	-0.006±0.044	0.029±0.022	Poa: 0.159±0.383 Phl: 0.638±0.384 Des: 0.000±0.000	0.009±0.004
0.0004***	*P*	00.12**	0.8987	0.1870	0.1135	0.0268*
Aggression (15)	Estimate ± SE	20.23±6.934	0.306±0.119	-0.246±0.062	Poa: -0.384±0.575 Phl: -2.095±1.104 Des: 0.000±0.000	-0.033±0.015
<0.0001***	*P*	0.0035**	0.0098**	0.0001***	0.0568	0.0337*
Drink (9)	Estimate ± SE	12.87±8.561	0.040±0.143	-0.183±0.076	Poa: -24.4±123547 Phl: 1.489±1.077 Des: 0.000±0.000	-0.008±0.010
<0.0001***	*P*	0.1328	0.7794	0.0162*	0.0010**	0.3955

**P*<0.05, ***P*<0.01, ****P*<0.001.

(logistic regression, P=0.0002).

There was no effect of date and time of day on the time the birds spent flying when present at the feeding grounds (multiple regression, P=0.3117 and P=0.5222, respectively). Therefore, the mean value of all observations were used (mean 19.0 ± 4.3 SE seconds flying per hour per goose).

During the study period minimum temperatures ranged from -12.3°C to 7.7°C and maximum temperatures ranged from -0.7°C to 13.8°C. Temperatures dropped below 0°C during the first eight days of spring staging and again on 2 May. There was no correlation between minimum temperature and feeding activity in the morning (linear regression, n=128, P=0.2380).

Discussion

After a sea crossing of some 1,500 km from Britain to Iceland, Greenland White-fronted Geese stage for only three weeks in Iceland before a journey of similar length (which includes flying over the Greenland Ice Cap, Glahder 1999). The geese are therefore expected to allocate more time to feeding than on the wintering grounds, where they have several months to accumulate body stores in late winter and spring. Given the short period of time available, it is expected that the geese would potentially feed for as much of the available time as possible, constrained by essential activities such as drinking, plumage care and social interactions. Overall the geese spent 70-90% of the daylight hours feeding in

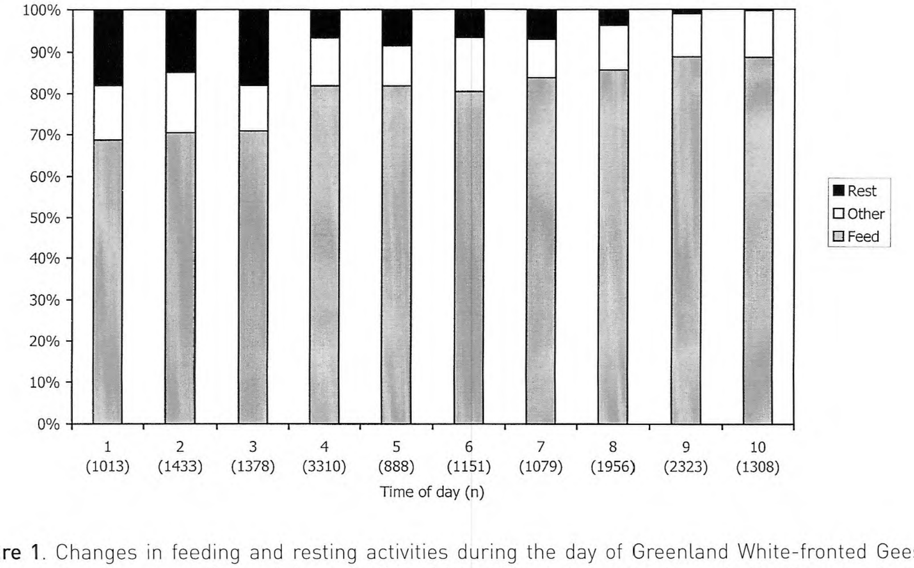

Figure 1. Changes in feeding and resting activities during the day of Greenland White-fronted Geese spring staging in Iceland. Time of day was divided into 10 periods of equal length, the first starting 10 minutes before sunrise and the last ending 30 minutes after sunset. (n) = number of birds observed.

Iceland, which was generally more than on the wintering grounds, eg 51-77% on Islay, southwest Scotland (Ridgill *et al.* 1994) and 65-88% in Killarney Valley, western Ireland (Carruthers 1991, 1992). When the differences in day length are taken into account, this represents a considerable longer daily feeding time in absolute terms. European White-fronted Geese *A. a. albifrons* wintering at Slimbridge, southwest England spent 89-95% of the day feeding, which results in 8.5-10.5 hours of feeding per day during late winter (Owen 1972). In Iceland, the Greenland White-fronted Geese spent 12.5-14.5 hours a day feeding during spring staging. This increase in feeding intensity from wintering grounds to spring staging sites has also been described for Barnacle Geese *Branta leucopsis* spring staging in northern Iceland, and reflects the need to increase body stores during spring staging (Percival & Percival 1997).

Lesser Snow Geese *A. caerulescens caerulescens* feeding on waste grains spent less time feeding compared to geese feeding on grasslands (Burton & Hudson 1978; Davis *et al.* 1989; **Table 3**), suggesting that the chemical composition and digestibility of the food can influence feeding time considerably (see also Madsen 1985; Amat *et al.* 1991). Greater feeding activity of geese in Iceland could therefore also be a response to the reduced nutritious quality of grasslands in Iceland compared to grasslands in Western Europe. However, the geese increased their body mass much faster during spring staging than on the wintering grounds and during the pre-nesting period in Greenland (Nyegaard *et al.* in prep.). The increased feeding activity in Iceland could therefore represent both (1) compensation for feeding on less profitable food, and (2) a response to the demand for gaining weight rapidly in preparation for the flight to the breeding grounds.

Time of day

Feeding activity increased during the day throughout the staging period, and was inversely related to the amount of time allocated for resting by the geese (**Figure 1**). This differs from the observed feeding patterns described in other studies. Two patterns of diurnal feeding have generally been observed. One involves the greatest levels of feeding activity in the morning and evening, with a reduction at midday (eg Owen 1972; Ely 1992; Mooij 1992; Zhang & Lu 1999). The midday reduction in feeding is normally related to movements to sites to drink, but also to preen and rest, which often take place in sites separated from the feeding grounds (Owen 1980). Secondly, geese have been observed to feed in discrete bouts (punctuated by short rest periods) through the full 24 hour period when exposed to continuous light either artificially in captivity (Boudewijn 1984) or during the 24 hours of daylight in the arctic summer (Madsen & Mortensen 1987; Kristiansen & Jarrett unpubl.). This

Table 3 Daylight and diurnal feeding activity of different goose species. Activity of geese during dark hours were only recorded in the study by Mooij (1992).

Species	Feeding (% of daylight activities)	Feeding (% of diurnal activities)	Feeding source	Season	Author
Greenland White-fronted Goose *Anser albifrons flavirostris*	70-90	52-60	Grasslands	Spring	Present study
Greenland White-fronted Goose Anser albifrons flavirostris	51-77		Grasslands	Winter	Ridgill *et al.* 1994
Greenland White-fronted Goose *Anser albifrons flavirostris*	65-88		Grasslands	Winter	Carruthers 1991, 1992
Greenland White-fronted Goose *Anser albifrons flavirostris*	c. 68		Grasslands	Pre-nesting	Fox & Madsen 1981
European White fronted Goose *Anser albifrons albifrons*	89-95	c. 40	Grasslands	Winter	Owen 1972
European White-fronted Goose *Anser albifrons albifrons*	c. 75	c. 55	Grasslands	Winter	Mooij 1992
Greater Snowgoose *Anser caerulescens atlanticus*	c. 75	c. 55	Grasslands	Spring	Gauthier *et al.* 1988
Lesser Snowgoose *Anser caerulescens caerulescens*	c. 80	c. 30	Grasslands	Winter	Burton & Hudson 1978
Lesser Snowgoose *Anser caerulescens caerulescens*		c. 20	Waste grains	Winter/Spring	Davis *et al.* 1989
Barnacle Goose *Branta leucopsis*	c. 80	c. 30	Grasslands	Winter	Ebbinge *et al.* 1975
Barnacle Goose *Branta leucopsis*		50-70	Grasslands	Spring	Black *et al.* 1991

type of feeding pattern slows down the through put time of food considerably, and most likely enhances digestion efficiency (Ebbinge & Ebbinge-Dallmeijer 1976; Boudewijn 1984). This feeding pattern is probably the most cost effective for geese, but maximum efficiency demands nearly permanent daylight, a feature not available in Iceland during the spring migration period of the Greenland White-fronted Geese. Geese may however adopt a mixed strategy combining elements of both foraging patterns. For example, European White-fronted Geese wintering in the Lower Rhine, Germany, had a typical morning and evening peak in feeding activity, and during the night they fed in discrete bouts punctuated by short periods of rest (Mooij 1992).

The elevated levels of feeding activity in the evening have been explained in terms of the advantage gained by a goose from filling the gut just before the flight to the roost so that the food can be digested thoroughly during the night (eg Owen 1972). This advantage may also be enhanced by increasing the peck rate toward the end of the feeding period (Owen 1980). However, the reduced feeding activity during the early hours of daylight consistently found in this study is unusual. One explanation could be that geese arriving in the fields defrost the grass in the morning by resting on it before feeding, a phenomenon seen before (H. Boyd, pers. comm.). There could be several advantages to this behaviour: (1) Geese are highly selective for grass species, leaf type and leaf length during feeding (eg. Fox *et al*. 1998; Kristiansen *et al*. 1998, 2000) and it may be difficult to differentiate between green and dead leaves when the grass is covered by hoar. (2) Valuable heat energy may be lost when filling the gut with frozen grass. It is unlikely that this phenomenon is the only explanation for the feeding patterns presented here though, since there was no correlation between minimum temperature and feeding activity in the morning. However, the temperature at ground level was probably lower than the air temperature in the morning, so that frost or heavy dewfall on the grass every morning during staging still cannot be excluded. (3) The food quality of the grass leaves may be lowest in the morning. It has been shown in a study of *Puccinellia* in Denmark that the content of sucrose fluctuates during the day. Sucrose content reached a diurnal maximum of about 8.5% of dry weight during 17.00-21.00 hours and fell to a minimum of about 5% of dry weight between 07.00-11.00 in the morning, probably due to the processes of photosynthesis and respiration linked to light and temperature levels (A.D. Fox & J. Kahlert unpubl. data). (4) It is possible that the geese have been feeding during the night. Night time feeding would reduce the immediate demand for the geese to commence feeding in the morning on arrival on the fields, which could also explain the low feeding activity during the early hours of daylight.

Trends in behaviour over time

There was a decline in aggressive behaviour during the staging period, which could be due to a change in food supply availability. When the geese arrived, the growth season of the grass had barely begun, and they had to compete for a restricted food supply. The increase in alertness is most likely a function of decrease in flock size through the period (see Flock size).

Flock size

The very strong negative correlation between flock size and date (P=0.0001) may be at least partly due to the phenology of the geese in the area. The numbers increased very rapidly in mid April to more than 1,000 birds, but decreased after a few days to a level of about 500 birds, which remained until their departure in early May (Fox *et al.* 1999). With more birds in the area, larger flocks were more likely. Furthermore low temperatures and low food abundance concentrated in few available patches due to snow cover could have caused more aggregation in the first part of the staging period.

The very strong negative correlation between flock size and alertness is consistent with results from many other studies (eg Caraco 1979; Bertram 1980), including Greenland White-fronted Geese at this site (Kristiansen *et al.* 1998a). An advantage of increasing flock size is the reduction in time each individual needs to spend being alert to maintain the overall level of alertness in the flock. This gives more time to invest in other activities, which might explain the positive correlation between flock size and comfort.

Aggressive behaviour occurred most often among geese in smaller flocks. A possible explanation could be that smaller flocks have to feed on less abundant and nutritious food than larger flocks. This could lead to a higher competitive level in the small flock and therefore result in more conflicts. It should be noted that surprisingly few conflicts were observed (n=15, <0.3%).

Sward type

The geese spent less time feeding when foraging on *Phleum* fields. This may reflect the higher nutritious value of *Phleum* compared with the two native grasses *Poa* and *Deschampsia* in combination with a higher intake rate on *Phleum* fields (Nyegaard *et al.*, in prep.). Hence, the geese need to spend more time eating when feeding on *Deschampsia* or *Poa* in order to gain the same amount of energy as obtained on *Phleum* fields.

Management implications

The geese spent most of the daylight hours feeding, except in the early morning when relatively much time was used for resting, but this activity is probably also part of the feeding process. Less than 13% of the time budget is allocated to other activities, so disturbance to the geese (ie agricultural activities, hunting, aircraft, etc.)

reduce feeding time and increase energy expenditure. The geese are not likely to be able to compensate for lost feeding time due to disturbances, because the time investment in foraging is probably already maximised. Undisturbed feeding grounds are therefore especially important during spring staging.

Food quality is most likely a determining factor. When choosing the most profitable swards the geese can afford to spend less time on feeding, and more time on other activities. A more comprehensive analysis of the energetic consequences of feeding on the three different sward types is the topic of a future paper (Nyegaard *et al.*, in prep.).

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