Feeding ecology of Black Brant on the north slope of Alaska

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1. Abstract

The feeding ecology of Black Brant (*Branta bernicla nigricans*) in their summer habitat was studied on the North Slope of Alaska from May to September 1978. The birds began arriving on the North Slope in late May. Breeding adults set up nesting territories on islands in coastal lakes and rivers. During nesting, males spent 22% and females 9% of the time feeding, primarily on *Carex aquatilis*, *Dupontia fischeri*, and mosses (sp. unknown). Non-breeders spent the early summer in arctic salt marshes where they fed on *Carex subspathacea* and *Puccinellia phryganodes*. In mid August, migrating brant frequented salt marshes where they spent 77% of the average 16-h daylight period in foraging at an average rate of 83 pecks/min. By the use of three different methods, food intake was estimated at an average of 305 g dry weight/day. Grazing pressure on arctic salt marshes was calculated at 374 brant-days/ha.

2. Résumé

De mai à septembre 1978, nous avons étudié l'écologie alimentaire de la Bernache noire (*Branta bernicla nigricans*) dans son habitat estival sur le versant nord de l'Alaska. Les oiseaux ont commencé à arriver en cet endroit à la fin de mai. Les adultes reproducteurs ont établi leurs territoires de nidification sur les îles parsemant les lacs et les rivières côtiers. Durant la nidification, les mâles passaient 22 % et les femelles 9 % de leur temps à se nourrir surtout de *Carex aquatilis*, de *Dupontia fischeri* et de mousses (espèces inconnues). Les oiseaux non reproducteurs ont séjourné au début de l'été dans les marais salants arctiques où ils se nourrissaient de *Carex subspathacea* et de *Puccinellia phryganodes*. À la mi-août, les bernaches en migration fréquentaient les marais salants où elles consacraient 77 % de la période diurne moyenne de 16 h à fouiller à un rythme moyen de 83 coups de becs par minute. À l'aide de trois méthodes différentes, nous avons estimé la consommation alimentaire à une moyenne de 305 g de poids sec par jour. La pression de broutage sur les marais salants arctiques a été calculée à 374 bernaches-jours par hectare.

3. Introduction

Oil exploration and development along the North Slope of Alaska pose a potential threat to coastal habitats and the animal populations they support. Thousands of Black Brant annually migrate to lakes and rivers there to nest, raise their young, and undergo an annual moult of body feathers (Owen 1980). Equally large numbers of non-breeding brant also moult along the North Slope (Derksen *et al.* 1979). Coastal salt marshes in the area serve as foraging sites for non-breeding brant during spring migration and for breeding birds, young, and non-breeders in the fall. In the event of an oil spill, brant using the marshes could be severely disrupted during critical foraging periods in their yearly cycle.

Geese, as grazers, must process large amounts of vegetation daily; however, they lack the complex digestive tract of ruminants, and little more than cell solutes may be absorbed by the intestines (Mattocks 1971). Geese, therefore, may exhibit adaptive behaviour which allows for the selection of plants of high nutritional quality.

Black Brant experience further constraints. As specialized feeders they select only a few plant species that are highly localized along the Pacific coast of North America. In addition, they are considered to be relatively inflexible in their feeding habits (Gabrielson and Lincoln 1959).

Several investigators (Harwood 1975, Owen 1972*a*, Owen *et al.* 1977, Lieff *et al.* 1970) have studied food selection by geese. To my knowledge, however, food intake has never been estimated for wild geese during the summer or while migrating. In order to obtain information on the threat that oil development on the North Slope might pose to the coastal habitats of Black Brant, a study of the birds was conducted from late May to September 1978. The objectives were to determine consumption and foraging routines, food selection, and grazing pressure in arctic salt marshes.

4. Study sites

Studies were conducted at two principal sites (Fig. 1). The first was at Anachlik Island, one of a few tundra-bearing islands in the aggrading Colville River delta (150° 24′ N, 70° 26′ W), which reaches Harrison Bay in the Beaufort Sea. The study site was a wetland habitat of about 300 m^2 on the northwest shore of the island where a series of drowned polygonal ridges becomes part of a complex lake. Within the lake, humps of exposed ridges form a system of small islands. One or two pairs of brant nested on each of these islands, making a total of 26 pairs at the site. *Carex aquatilis*, *Dupontia fischeri*, and moss (sp. unknown) were the dominant plants in the region.

The second site was a salt marsh along the mouth of the Putuligayuk River (148° 30′ N, 70° 19′ W). *Puccinellia phryganodes* and *Carex subspathacea* were the dominant plants in the marsh which lined the eastern and western shores

and covered a small island in the mouth of the river. Total area of vegetated salt marsh was about 1 km^2 (Fig. 1). Flocks of up to 250 migrating brant fed here for periods of from several hours to 2 days in the late summer.

In addition, counts of brant droppings were made at four other salt marshes on two occasions. Two of these marshes were in the Colville River delta, another was along the mouth of the Kalubik River, and the fourth was due west of West Dock, Prudhoe Bay, Alaska (Fig. 1). Dropping counts were also made at the Putuligayuk River salt marsh.

5. Methods and materials

5.1. Consumption and foraging routines

The first of three methods used in determining food intake consisted of five feeding trials with two 38-day-old brant carried out every 2–4 days from 16 to 26 August. At the time of capture the goslings weighed 60.8 g and 62.3 g, respectively. They were reared on local vegetation until they reached adult weights of 1335 g and 1420 g, respectively, on 20 August. The brant were held in 1-m by 2-m by 1-m wire pens where they remained for 24 h. Known quantities of saltmarsh vegetation were given the captive birds, along with water and a weighed pan of gravel. At the end of the 24-h period the vegetation and grit remaining in the pen and the feces were collected and weighed. The weight of food left in the pens was subracted from the weight of food supplied to the birds to give a measure of consumption during the experiment. Brant weight was recorded before and after each trial.

The second method involved observing the percent of time spent in foraging, the feeding rate (in pecks per min), and the amount of vegetation taken per bite by migrating and captive brant.

At the nesting colony on Anachlik Island, Black Brant were observed with a 20–60X zoom spotting scope at a distance of about 50 m. The population was scanned every 15 min, and the activity of each bird was recorded as outlined by Henry (1980) and Altman (1974). Observations were made from the time the brant arrived on the nesting ground on 1 June until they left the nesting area on 12 July.

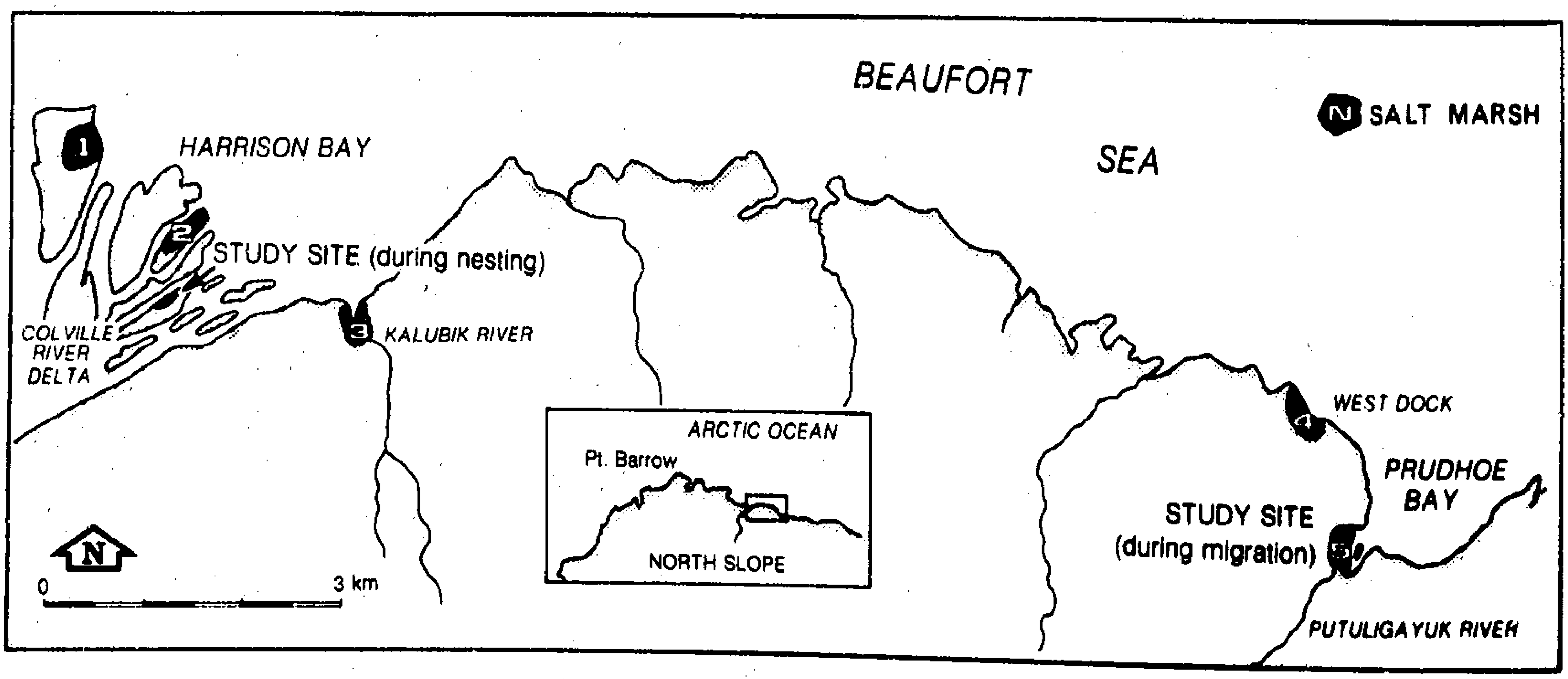
From 17 August until 7 September similar observations were carried out on flocks of geese at the Putuligayuk salt marsh. Because the distance from the flocks (200 m) and the number of individuals were large, feeding was the only behaviour that was generally noted. The population was scanned every 5 min with the telescope. Birds whose heads were lowered were counted as feeding; and those that were swimming, flying, or had their heads up were listed under the general category of other behaviour. The time taken for 50 pecks was measured in between scans for feeding behaviour.

Observations were also made on the feeding behaviour of the imprinted brant in the Putuligayuk marsh between 18 August and 1 September on days other than when the feeding trials were conducted. Bite size was estimated by watching one of the imprinted birds feed and by counting the number of bites taken. After feeding, the number of graminoid blades clipped by the bird was counted, and the lengths of unclipped as well as clipped blades were measured with a centimetre ruler. This gave a value for number and length of blades taken in each bite. Dry weight per unit length of graminoids was also measured. Graminoid vegetation refers to both grasses and sedges.

Multiplying the percent of foraging time by feeding rate and this value by the size of bite gave an estimate of consumption for wild birds and a second value for the imprinted brant.

The third method for estimating consumption is outlined by Ebbinge *et al.* (1975). Physiological studies indicate that cellulose digestion is quantitatively insignificant in geese (Mattocks 1971). Therefore, the relative content of cellulose in the food and in the droppings can be used as an indicator of digestibility. By knowing the daily fecal output,

Figure 1
North Slope of Alaska showing study sites during nesting and migration. Numbers in salt marshes designate areas used in the grazing pressure study



and the proportion of crude fibre in the food and that rejected in the feces, the rate of use of the food on a dry-weight basis can be calculated.

Fecal output was measured by weighing the droppings produced by the imprinted brant in the 24-h consumption trials. In the field,the feces produced in an hour by the imprinted birds were collected and weighed. Goose droppings from areas where wild geese had fed for a known amount of time were counted, collected, and weighed to give a third estimate of fecal output. Rate of food use was calculated by the formula of Ebbinge *et al.* (1975):

$$\% \text{ use (dry weight)} = 1 - \frac{M_r}{M_d} 100\%$$

where M_r = grams of marker substance (crude fibre) per 100 g food (dry weight), and M_d = grams of marker substance per 100 g of droppings (dry weight). Food intake was then calculated by using the following formula:

$$\text{Food intake} = \frac{DW}{1 - \frac{\% \text{ use}}{100\%}}$$

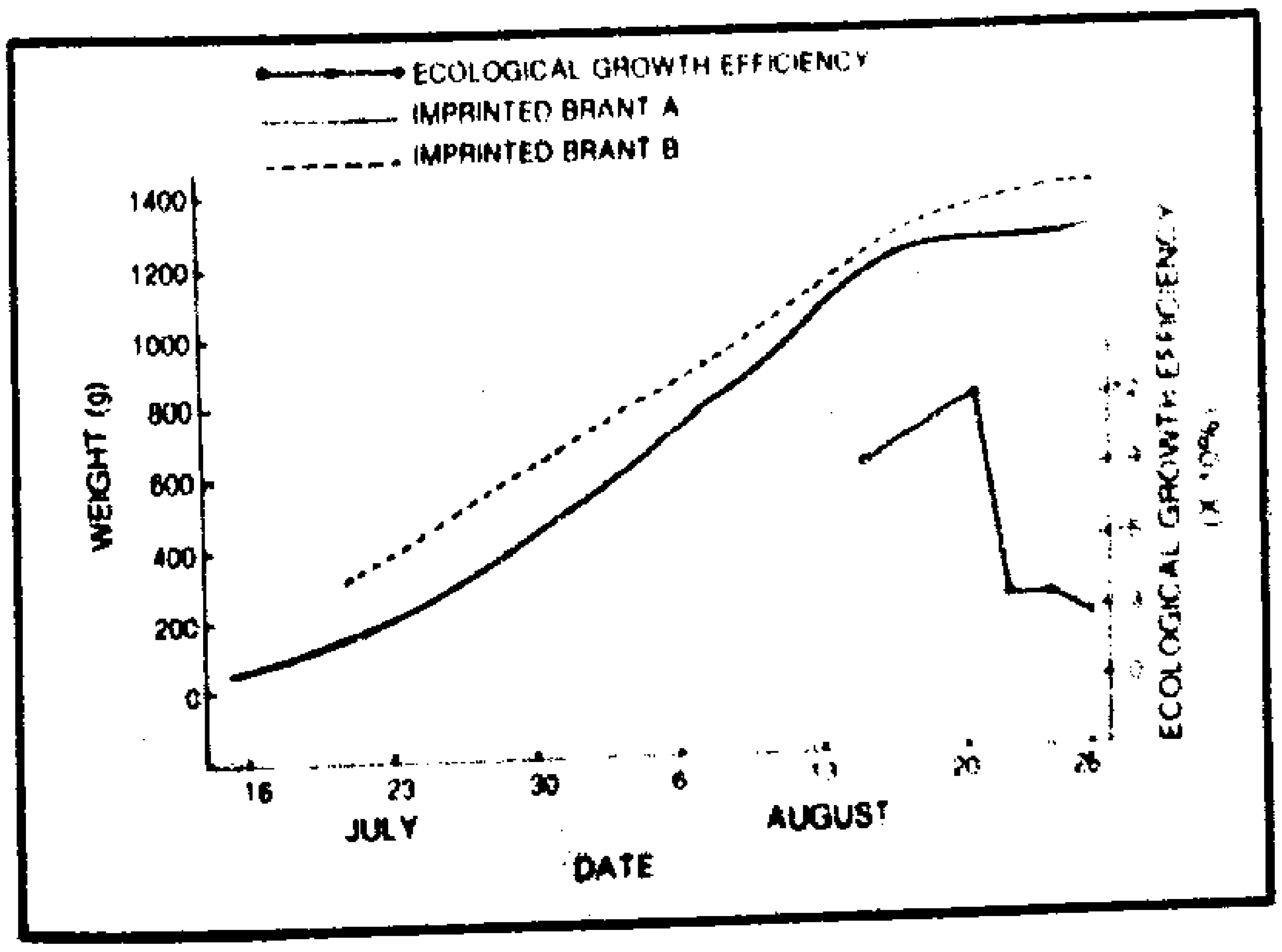
where DW = grams dry weight of droppings produced per day.

The three methods used for measuring consumption were applied only to fall-migrating brant and the imprinted geese feeding on saltmarsh vegetation. All values for food intake in the tables and throughout the text are given in grams dry weight of vegetation per day.

5.2. Food selection

Plants collected during the field season were identified according to Hulten (1968). During the feeding trials, *Carex subspathacea* and *Puccinellia phryganodes*, the main foods of migrating brant in this study, were provided to each of the captive goslings in separate food boxes and the relative proportion of each species eaten was determined. In addition, *C. subspathacea* and *P. phryganodes* were collected from areas where brant rarely grazed throughout the season.

Figure 2
Growth (in grams gained per day) of imprinted Black Brant, and ecological growth efficiency during the feeding trials



Samples were weighed, dried at 60°C for 24 h, and reweighed. Calculations for percent water content were made on these data. The dry samples were brought back from the Arctic for protein, fat, ash, and crude fibre determinations.

5.3. Grazing pressure

Five salt marshes (Fig. 1) were visited on 18 July before brant began migrating and on 7 September after the major migration was over. Counts of brant droppings were made with a 0.25-m^2 quadrat dropped randomly throughout the salt marsh. Total area of each salt marsh was obtained by means of a 50-m tape and maps. Knowing the average number of droppings per 0.25 m^2, the size of the marshes, and daily fecal output by brant, I calculated brant-days per marsh and grazing pressure in brant-days/ha. (Brant-days are the total number of brant visiting a marsh times the days they spent there.)

5.4. Laboratory methods

Samples were ashed according to the methods of the Association of Official Analytical Chemists (Horwitz 1975).

Crude fibre was measured by means of the acid-detergent method (Van Soest 1962). Birds with gizzards consume quantities of sand and gravel regularly. Wild geese are no exception. Because no commonly used crude-fibre method extracts other ashable components and grit and because brant droppings contained large and varying percentages of grit, I ashed the crude-fibre extract to obtain an ash-free determination as well as to measure the unashed crude-fibre extract.

Fecal and vegetation samples were analysed for nitrogen by means of the micro-Kjeldahl method (Joslyn 1970). Protein was calculated by multiplying nitrogen by 6.25.

Calorimetric measurements of *Carex aquatilis*, *Carex subspathacea*, and *Puccinellia phryganodes* were obtained by means of a Parr bomb calorimeter (Schoemaker *et al.* 1974). Kilocalories were determined for the green blades of *Zostera marina* collected on 20 June 1979 in Puget Sound, Washington. Caloric values of *Zostera* do not vary significantly throughout the year or in different localities, and thus these values are comparable to those obtained for arctic graminoids eaten in the summer by brant (McRoy 1970).

6. Results

6.1. Consumption and foraging routines

The results of the five feeding trials are shown in Table 1. The amount of food consumed by the birds increased by more than 1.5 times during the trials, although the geese had reached adult weight of 1.25 kg and 1.35 kg (Morehouse 1974, Boyd and Maltby 1980), respectively, by the second trial and further weight changes were minimal (Fig. 2). By the third feeding trial the weight gain per weight of food eaten (ecological growth efficiency) decreased. The goslings mastered flying by 20 August.

The values on wild birds in Tables 2 and 3, and in Figure 3 were derived from data collected prior to and during nesting, and during migration. They could not be used to estimate consumption quantitatively as I was unable to measure the size of a bite taken by nesting brant (method 2) or collect feces in the lake region where they nested

(method 3). The figures, however, are useful in that they allow a comparison of activity patterns and foraging routines during different times in the summer season when the birds were engaged in different activities (arrival on nesting grounds, nesting, and migrating).

Upon arrival at the nesting grounds, brant fed 28% (SD = 15.4, N = 67) of the 24 h of daylight (Table 2). More time was devoted to resting, alert behaviour, and aggressive intraspecific interactions than at other times in the summer. They fed less between 00:00 and 06:00 (16% of the time, SD = 11.8, N = 5). Feeding increased throughout the morning and reached a peak in late afternoon between 14:00 and 17:00 (Fig. 3).

During nesting the percentage of time spent feeding dropped to 22% for males and the occasional female off the nest (see note in Table 2). All other activities except nesting also decreased. During the migration period the imprinted brant spent 64% (SD = 14.9, N = 52) of the time feeding, whereas wild birds fed significantly more of the time (77%, SD = 22.4, N = 148, F-test, $P<0.05$) (Table 3).

During nesting, females fed 9.4% of the time (Table 3). Other observations I made indicate they left the nest an average of eight times a day and fed for an average of 18 min each day. Seventy-four percent of their feeding took place between 08:00 and 11:00 and 14:00 and 17:00. They took an average of 100 pecks per min. Males plus females off their nest during the nesting season fed 22% of the time at a rate significantly slower than that of nesting females, 75 pecks per min (F-test, $P<0.05$). They fed sporadically throughout the day, with a slight increase of feeding activity between 10:00 and 12:00 (Fig. 3).

Brant observed during the migration period spent 77% of the average 16 h of daylight in foraging during late August and early September. Adults fed at an average rate of 83 pecks/min whereas juveniles pecked significantly faster, taking 103 pecks/min (Table 3). I was unable to definitely distinguish between adults and juveniles while scanning the flock for percent foraging time. When counting pecks/min in between scans, I located isolated family groups in which the age differences were readily visible and based my data for juveniles on these observations. The wild birds fed most heavily in the morning and significantly less as the day passed (F-test, $P<0.05$) (Fig. 3). In late August the imprinted brant fed an average of 64% of the time, taking 91 pecks/min. The amount of time they spent feeding did not decrease significantly throughout the day (F-test, $P>0.05$).

Based on pecks/h, males (see note on Table 3) fed almost twice as much as females during nesting. During the migration period, brant fed about 3.5 times as much as birds off the nest during the nesting period, with the imprinted geese averaging slightly less than the wild birds (Table 3).

The length of a graminoid blade that brant ate depended upon the height of the plant. *Carex aquatilis* by the

Table 1
Amount of vegetation (g dry weight/day) consumed by two imprinted Black Brant in feeding trials in August 1978

Date	Brant A	Brant B
16 August	266	281
20 August	235	235
22 August	275	337
24 August	355	492
26 August	473	465
$\bar{x}$ food intake	341.4	
SD	101.0	
N	10	

Table 2
Time budget (percent time spent in different behaviours) of wild Black Brant before and during nesting*, and of imprinted Black Brant in the late summer

	Pre-nesting	Nesting	Imprinted brant
Dates	1 – 12 June	13 June – 12 July	18 Aug. – 1 Sept.
Hours observed	**20**	**24**	**26**
Foraging	28	22	64
Alert	19	12	—
Nesting	0	40	0
Resting	28	14	11
Preening	7	4	11
Interaction	10	2	—
Swimming	4	2	—
Flight	3	1	—
Other	1	3	14
Totals, %	100	100	100

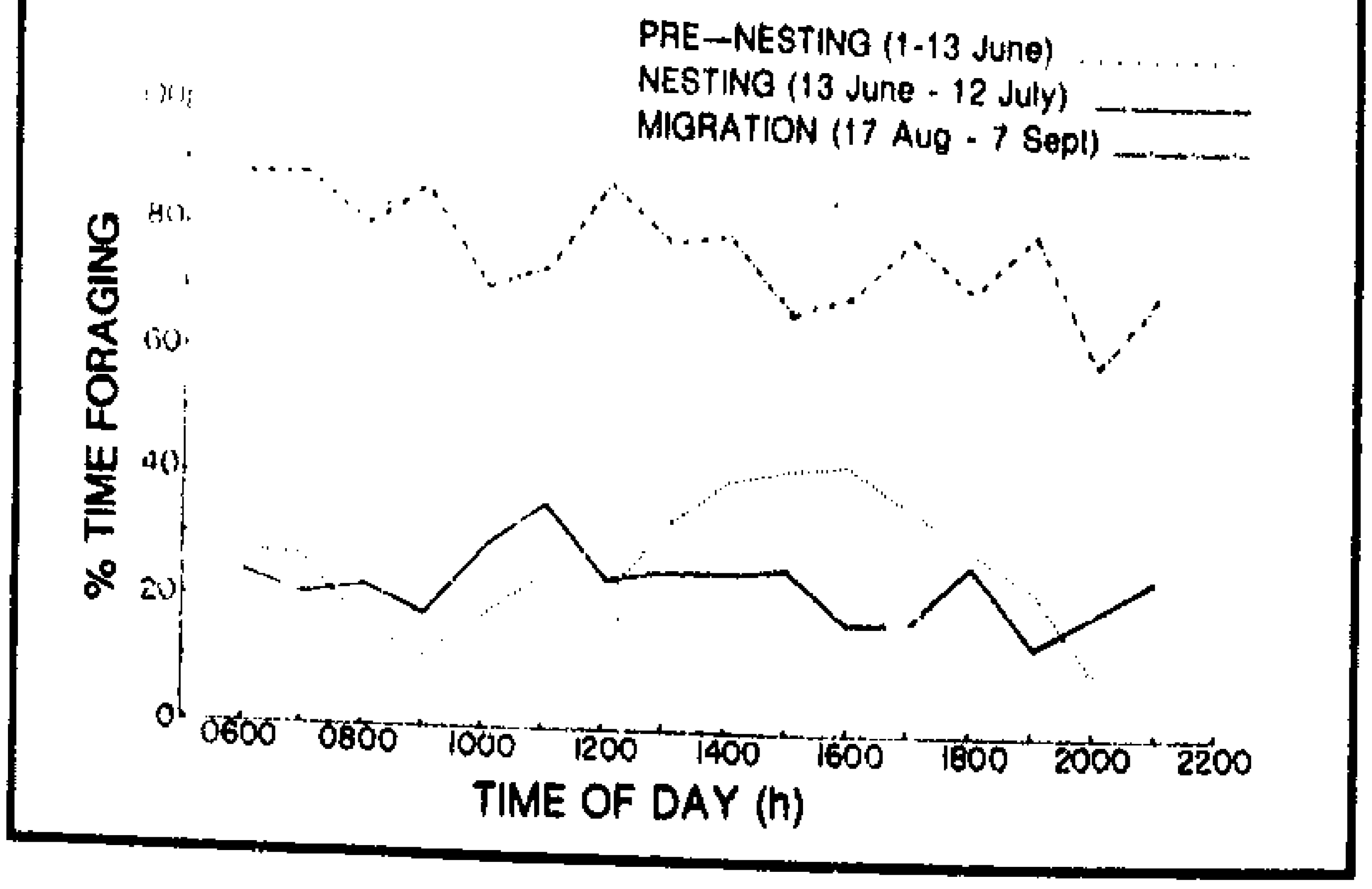
*Counts before nesting based on both males and females: Counts during nesting based on all birds except six nesting females, but could have included some females off their nests.

Table 3
Feeding rate of Black Brant at several times during the summer season

	Nesting, 13 June – 12 July		Migrating, 17 Aug. – 7 Sept.		Imprinted brant, 18 Aug. – 1 Sept.	
	Females*	Males†	Adults and juveniles	Juv.	A	B
% time foraging	9.4	21.7	77.3	‡	66.8	60.8
Pecks/min	100§	75§	83§	103§	85	97
SD	18.0	17.2	7.0	13.5	10.5	12.7
N	109	79	489	29	93	88
Pecks/h¶ (effective)	564	977	3850	—	3407	3540

*Based on six nesting females.
†Based on all birds except the six nesting females. Counts could have included some females off their nests.
‡Data incomplete as juveniles within flock were not always distinguishable from adults.
§$P<0.05$, F-test.
¶Pecks/h = pecks/min × 60 min × percent time foraging.

Figure 3
Daily foraging pattern exhibited by Black Brant at three different times in the summer season



end of nesting season had attained a height of about 60 mm. The geese broke off an average of 35 mm (SD = 10.3, N = 148) of the blade in a bite.

Saltmarsh vegetation is much shorter than that found in the tundra. The brant took bites of blades of *Carex subspathacea* and *Puccinellia phryganodes* that were an average of 19 mm (SD = 6.6, N = 93) and 13 mm (SD = 5.3, N = 95) in length, respectively. In many places in salt marshes, vegetation was clipped to within 15 mm of the ground. On the average, the geese ate 2.9 (SD = 0.85, N = 21) blades in each bite of *C. subspathacea* and 2.5 (SD = 0.92, N = 21) blades of *P. phryganodes*. The dry weight of saltmarsh graminoids, averaged over the season, that was taken in one bite was 3.1 mg (SD = 0.6 mg, N = 6). Multiplying the weight of vegetation taken in one bite by the feeding rate and percent time spent foraging, I estimated consumption by the migrating birds at 283 g/day and by the imprinted brant at 250 g/day (Table 4). These values were calculated on an assumed 24-h feeding period. It is generally believed that most geese do not feed at night unless there is a full moon (Ranwell and Downing 1959, Owen 1972*a*, Ebbinge *et al.* 1975, Henry 1980). Burton and Hudson (1978), however, have reported that the feeding activity of Lesser Snow Geese is dependent on tidal fluctuations, and night-time feeding is common in winter during low tides, regardless of light intensity. I based my calculations on the fact that the imprinted brant fed at night at the same rate as during the day. Geese, when they do feed in the dark (Owen 1976), probably forage at a slower rate than during the day becaus of a necessary increased alertness for predators. I had no way, however, of estimating a night-time feeding rate. Therefore, my values should be considered as maximum estimates of food intake.

The crude fibre method as outlined by Ebbinge *et al.* (1975) gave a consumption of 375 g/day for birds on the North Slope (Table 4). The crude fibre extract from both the fecal and graminoid samples, however, contained large and varying amounts of grit and other refractory components. Although the data obtained from the crude fibre analysis appeared reasonable when compared with the other estimates of consumption, they had to be discounted because of the presence of grit. To correct for this error, I ashed the crude fibre extract and calculated a new estimate of consumption of 352 g/day and 299 g/day for the imprinted brant and wild brant, respectively.

Table 4
Amounts of vegetation consumed by imprinted and wild Black Brant as estimated by three different methods (standard deviation and number of samples in parentheses)

	$\bar{x}$ consumption of vegetation, g dry-wt/day	
	Imprinted brant	**Wild brant**
Method 1 (feeding trials)	341 (104, 10)	—
Method 2 (field observations)	250	283
Method 3 (ash-free crude fibre)	352 (36, 4)	299 (60, 4)
(crude fibre)	374 (17, 4)	376 (82, 6)
$\bar{x}$	305.5*	
SD	42.98	
N	5	

*Method 3 (crude fibre) not averaged in with other values because of presence of grit in samples.

The caloric value for several arctic graminoids are given in Table 5. They are somewhat higher than the value of 3.3 kcal/g that I determined for *Zostera marina*, the principal winter food of Black Brant (Cottam *et al.* 1944, Henry 1980).

C. subspathacea and *P. phryganodes* were of a comparable nutritional quality. *C. aquatilis* had a consistently higher protein content than either of the saltmarsh graminoids. Both *C. subspathacea* and *P. phryganodes*, however, had a significantly higher moisture content than *C. aquatilis* (F-test, $P<0.05$) (Table 5).

Analyses of *C. subspathacea* collected at different times during the summer indicated that nitrogen content increased from mid June to mid August and declined thereafter (Table 6). Samples of *P. phryganodes* showed a gradual, although not consistent, decline in nitrogen content. The mean values for nitrogen content in *C. subspathacea* was 1.73 (SD = 0.26, N = 5) and in *P. phryganodes*, 1.86 (SD = 0.28, N = 4). Water content in *C. subspathacea* increased from August to September, whereas in *P. phryganodes*, water content increased until 22 August and thereafter remained the same (Table 6). Fat content in *C. subspathacea* generally decreased throughout the season.

Table 5
Proximate analysis of three plants and of Black Brant droppings (All values are based on dry weights and are averages for the summer. Standard deviation and number of observations are given in parentheses. Superscripts denote significant differences where letters are paired (t test $P<0.05$))

	Carex aquatilis	*Carex subspathacea*	*Puccinellia phryganodes*	**Brant droppings**
% water content	[illegible] (15.9, 10)	73^{a} (7.8, 4)	72^{b} (4.8, 4)	82 (6.4, 9)
% ash	$9.0^{c,d}$ (6.7, 8)	10.5 (4.0, 5)	11.3^{d} (2.0, 4)	15.5 (6.4, 26)
% fat		5.28 (1.0, 5)		3.78 (1.2, 3)
% nitrogen	3.2^{e} (1.1, 5)	1.7^{e} (0.26, 5)	1.9 (0.28, 4)	1.6 (0.30, 15)
% protein (nitrogen × 6.25)	20.2	10.6	11.9	9.7
kcal/g	4.3	3.7	3.6	
% crude fibre	21.5^{f} (1.0, 4)	16.5^{f} (0.71, 4)	19.4 (1.2, 4)	25.5 (3.7, 21)
% ash-free crude fibre	18.3^{g} (4.9, 6)	13.8^{g} (1.0, 4)	10.1 (7.2, 4)	19.2 (5.4, 16)

Table 6
Variation in nutritional characteristics of *Carex subspathacea* through the summer and of *Puccinellia phryganodes** in late summer 1978. (All values are given as percentages based on dry-weight measurements. Standard deviation and number of observations are given in parentheses. Superscripts denote significant differences where letters are paired [t-test, $P<0.05$])

	Water content		Nitrogen		Fat	
Dates	***C. sub.***	***P. phr.***	***C. sub.***	***P. phr.***	***C. sub.***	***P. phr.*** †
15 June	†	†	1.65^{a} (0.21, 2)	—	6.27^{g} (0.08, 2)	—
14 Aug.	65	65	$2.17^{a,b,c}$ (0.08, 2)	2.15^{c} (0.05, 2)	4.75 (2.53, 4)	
22 Aug.	76	76	1.50 (0.71, 2)	1.67 (0.21, 2)	5.0 (1.72, 4)	—
26 Aug.	69	74	$1.69^{b,d}$ (0.02, 2)	$2.06^{d,f}$ (0.13, 2)	5.75 (1.77, 2)	—
1 Sept.	83	73	1.62^{e} (0.08, 2)	$1.58^{e,f}$ (0.13, 2)	4.13^{g} (0.39, 2)	—

**Puccinellia phryganodes* was not collected on 15 June, when it was covered with water from the Putaligayuk River during spring thaw.
† Analysis not performed.

Table 7
Brant-days and grazing pressure in several arctic salt marshes

Salt marsh no.	Droppings/m^2 18 July – 5 Sept.		Brant-days/marsh	Brant-days/ha
1	2.56	13.6	109,975	425
2	0	9.2	3,539	354
3	2.72	*	—	—
4	0	12.4	768	379
5	4.4	14.4	19,231	385
$\bar{x}$ brant-days/ha				385.75
SD				29.40
N				4

* Droppings washed away when river flooded.

6.2. Food selection

When brant first arrived at the nesting area, the ground was still partially covered by snow, and little green vegetation was available. During this time I observed them feeding on mosses (sp. unknown), fresh water algae (sp. unknown), *Equisetum variegatum*, and old seed heads of *C. aquatilis*.

During nesting I observed the brant feeding predominantly on *C. aquatilis* and *Dupontia fischeri*. The vegetation around the nesting area was clipped level with the ground. On the islands where the nests were located, graminoids were sparse and here a lush ground cover of moss grew. On warm days when many adult insects were emerging, I observed brant apparently feeding on chironomids (*Chironomus* spp.) which were in windrows along the lake's edge. The birds skimmed the water's surface with their opened bills, seemingly collecting hundreds of the insects.

The imprinted brant frequently accompanied me out in the field where they were free to select any vegetation available. In the salt marsh along the Putuligayuk River they invariably ate *C. subspathacea* and *P. phryganodes* in the salt marshes. To see if they preferred one of these graminoids over the other, I measured the amount of each that the imprinted brant ate in the feeding trials. The two birds ate an average of 707 g (SD = 600, N = 5) and 550 g (SD = 172, N = 5) of *P. phryganodes*, and 530 g (SD = 135, N = 5) and 658 g (SD = 104, N = 5) of *C. subspathacea*. A t-test on the results showed that the brant did not significantly choose either *C. subspathacea* or *P. phryganodes* over the other ($P>0.05$).

6.3. Grazing pressure

Between 13 and 18 June, 10–20 non-breeding brant fed along the Putuligayuk River (Fig. 1, salt marsh #5). From 19 to 24 June, 60 non-breeding brant were seen feeding in a salt marsh in the Colville River delta (Fig. 1, salt marsh #2). These geese were probably second- or third-year birds that had migrated to the North Slope to moult. By the beginning of July, non-breeders had left the salt marshes, presumably for inland lakes where they moult. Thirty-two thousand non-breeders spent from July to early August in the Lake Teshepuk region, 120 km west of Prudhoe Bay, on the western shores of Harrison Bay. By early August, moult was completed and the brant moved to coastal habitats (Derksen *et al.* 1979).

The brant nesting on Anachlik Island left the area as soon as the young were hatched. They were seen occasionally in the Colville River delta for about 1 month (Jim Helmerick, pers. commun.). Paired brant and family groups were seen infrequently in salt marshes near Prudhoe Bay from mid July to mid August. At this time of year they were moulting and, therefore, flightless, and swam out of sight before I could observe them feeding. On 27 July I flew an aerial survey from Flaxman Island to the Kuparuk River and counted 200 brant in small groups at the mouths of rivers.

The first flock of adults and young of the year was seen on 17 August when 1300 birds flew west past Oliktok, 35 km northwest of Prudhoe Bay (Katie Hirsch, pers. commun.). On 18 August a small flock of 25 brant landed in the Putuligayuk salt marsh and fed for several hours. From then until 7 September, when I left the North Slope, flocks of up to 250 brant stopped and fed along the Putuligayuk River for as long as 2 days. The peak migration in 1978 passed Simpson Lagoon, 30 km west of Prudhoe Bay, on 17 – 31 August, and in 1977, on 22 August – 6 September. The total number of brant migrating west past Simpson Lagoon was estimated to be 4638 in 1977 and 11 000 in 1978 (Johnson 1979).

Over a 19-day period, I observed 861 brant feeding in the Putuligayuk salt marsh. This resulted in a grazing pressure of 327 brant-days/ha. The imprinted and migrating birds produced an average of 237 droppings/day (SD = 54.7, N = 16). From the area of the salt marshes, the average number of droppings/m^2, and the number of droppings produced in a day, I calculated an average grazing pressure of 386 brant-days/ha (Table 7), SD = 29, N = 4). Based on this value and the 19-day observations, the average brant-days/ha was 374 (SD = 36.6, N = 5). By converting hectares to square metres and dividing by the average number of brant-days, one brant would feed from 26.7 m^2 in a day. A brant consuming about 305 g/day (Table 4) would take 11.4 g dry weight of vegetation per square metre.

7. Discussion

7.1. Feeding ecology

Barry (1956) noted brant feeding on *Equisetum* sp. and unidentified grass shoots before nesting in the Canadian Arctic. He reported that during nesting they fed on *Puccinellia phryganodes* around the nests. After the young had hatched, the adults led them to coastal mudflats where the flock fed on small crustaceans and small invertebrates. I observed brant prior to nesting, feeding on mosses (sp. unknown), freshwater algae (sp. unknown), *Equisetum variegatum*, and old seed heads of *Carex aquatilis*. During nesting, however, they fed primarily on shoots of *C. aquatilis* and *Dupontia fischeri*. Chironomids were taken on days of peak emergence. Derksen *et al.* (in press) reported that, based on examination of the droppings, non-breeding brant in the Lake Teshekpuk area fed primarily on mosses and to a lesser extent on *Deschampsia caespitosa* and *C. aquatilis*. Mosses grew lushly around brant nests on Anachlik Island, and it was quite likely that they fed on them, although I was not close enough to the nests to make direct observations.

In late summer, brant fed on *Carex subspathacea* and *Puccinellia phryganodes* in salt marshes along the arctic coastline (this study, David Mason, pers. commun.). The movement of brant to marshes from a tundra habitat can be theoretically associated with the need to maximize the quantity or the nutritional quality of the forage they are consuming (Krebs and Cowrie 1978).

Results of the nutritional analyses show the saltmarsh species, *C. subspathacea* and *P. phryganodes*, to have a significantly higher moisture content than the tundra species, *C. aquatilis*, and *C. subspathacea* to have a significantly lower fibre content than *C. aquatilis*. This suggests that saltmarsh plants are more easily ground up in the gizzard and, therefore, have a higher digestibility and greater nutrient availability. In addition, more food may be processed per unit time. Charman and Macy (1978) suggested the degree to which a plant could be ground up in the gizzard as a factor in food selection by brant wintering in England. Owen *et al.* (1977) reported that Barnacle Geese respond adversely to the brittleness of vegetation and thus selected, on a mechanical basis, the more tender plants with higher percentage of moisture.

Owen *et al.* (1977) also noted that the plants selected by geese had a higher nitrogen content than those not selected. Other investigators have also suggested that geese select foods to optimize nitrogen intake. Harwood (1975) reported that the blue race of Lesser Snow Geese fed most heavily in plots where vegetation had a significantly higher protein content than in other areas. Owen (1975) reported that Eurasian Greater White-fronted Geese selected fertilized vegetation with a 10% higher nitrogen content rather than vegetation in unfertilized plots. On the other hand, Lieff *et al.* (1970), in grazing trials with captive Lesser Snow Geese and Canada Geese, found no relationship between goose preference and the nutritional characteristics of the plants they chose. Owen (1972*b*, 1976) found a high rate of food intake by Eurasian Great White-fronted Geese to be more important than the nutritional qualities of the vegetation they selected. My results show that *C. aquatilis* had a significantly higher nitrogen content (3.2%) than *C. subspathacea* (1.7%, t-test, $P<0.05$). There was no significant difference between *C. aquatilis* and *P. phryganodes* (1.9%, t-test, $P>0.05$). Ulrich and Gersper (1978) reported nitrogen values in *C. aquatilis* of 2.9% in 1972 and 3.3% in 1973. Cargill (1981) found nitrogen content in ungrazed *P. phryganodes* to be 0.8 and 2.1% during August 1979 and 1980, respectively. For the same sampling periods she reported 1.3 and 3.0% nitrogen, respectively, in ungrazed *C. subspathacea*. These studies indicate that nitrogen content in arctic graminoids varies greatly from year to year and that the tundra species, *C. aquatilis*, generally has a higher nitrogen content than ungrazed saltmarsh vegetation. Cargill (1981), however, showed that grazing by Lesser Snow Geese increased the average total nitrogen content in saltmarsh vegetation. In samples collected in August she found grazed *P. phryganodes* to have a nitrogen content of 2.5% in 1979 and 2.8% in 1980, and grazed *C. subspathacea*, 3.0% in 1979 and 3.9% in 1980. I collected samples of vegetation from areas where grazing by brant was infrequent. The results, therefore, must be interpreted in this light, and no definitive statement can be made whether or not brant moved to salt marshes to maximize nitrogen intake. It is apparent, however, that saltmarsh graminoids had a higher moisture content and a lower fibre content than tundra vegetation, and brant may have been exploiting these characteristics in the plants they selected.

The results I obtained for food intake indicate that brant were maximizing the quantity of forage consumed during late summer. A mean value for consumption of 305 g/day (dry weight) was obtained from the three methods of estimating food intake. Based upon my caloric determination of food, this amounts to 1100 kcal/brant/day. This value for food intake varies from those of other investigators (expressed in grams dry weight/day). Simcock (1965) estimated food intake by wintering Atlantic Brant at 10% of body weight, or 150–180 g/day. Ogilvie (1978) gave an estimate of 135–158 g/day for Barnacle Geese wintering in England. Captive brant during the summer were estimated to use 306–367 kcal/bird/day (85–100 g/day) while feeding on commercial feed with a caloric value of 3.65 kcal/g (Morehouse 1974). The values given by Morehouse are not strictly comparable to values I obtained for unrestrained birds at normal field temperatures feeding on native vegetation, but they are of interest as the only values of food intake I have found for geese during the summer. Ebbinge *et al.* (1975), using the crude fibre method, estimated consumption by wintering Barnacle Geese at 135–160 g/day. In the same study, he compared grazed vegetation to ungrazed vegetation within an exclosure, and estimated a maximum food intake of 255–340 g/day. Since food intake varies with body weight of the bird, and since brant and Barnacle Geese both weigh approximately 1.3 kg, the values reported in the literature for these two species are likely to be similar. My results show that Black Brant during summer 1978 were consuming about twice as much food as brant and Barnacle Geese do in winter.

The values I obtained for droppings produced by a goose per day were similarly high compared to values reported elsewhere. Ebbinge *et al.* (1975) gave a value of 160 droppings, or 106 g dry weight, produced by wintering Barnacle Geese per day. Kear (1965) reported that geese excreted between 58 and 175 g dry weight of droppings per day, depending on the size of the goose. Owen (1972*a*) calculated that Eurasian Greater White-fronted Geese produced 150 droppings, or 110 g dry weight, in a day in which 9 h were spent actively feeding. Adult Lesser Snow Geese summering in the Arctic, produced 231 droppings in a day (Susan Cargill, pers. commun.). My imprinted brant and

those that were migrating produced 237 droppings (SD = 54.7, N = 16) with a mean dry weight of 1 g each. It is to be expected that if brant in the late summer are consuming more vegetation than in the winter, they would also be producing more droppings.

Behavioural traits of brant appear to be adapted to allow them to maximize food intake in the late summer when they are recouping the energy losses of summer and preparing for migration. The birds at the Putuligayuk salt marsh spent 77% of the average 16 daylight hours feeding. Although the number of daylight hours available to geese for foraging varies from season to season and place to place, several investigators have reported geese spending about three-fourths of the daylight period feeding. Kramer (1976), studying Black Brant wintering in Baja California, and Harwood (1977), working with Lesser Snow Geese in the Canadian Arctic, reported the birds feeding 77% of the daylight hours. In Humboldt Bay, California, brant fed 63.8% of the daylight period over the winter, and 80.4% during April prior to spring migration (Henry 1980). Owen (1972*a*), however, reported Eurasian Greater White-fronted Geese fed up to 90% of the daylight hours on their wintering grounds in England in a year when food was not plentiful. During moult, Black Brant on Alaska's North Slope fed 89–95% of the time (Derksen *et al.* 1982). Thus, in the long hours of arctic daylight, brant are able to maximize food intake by spending a high proportion of time in foraging.

Food intake may also be maximized by an increased rate of pecking. Females during nesting fed significantly faster than males. During the migration period, juveniles pecked at a significantly higher rate than adults. At both of these times, maximizing consumption within a given time period may be adaptive behaviour. Harwood (1975) found that Lesser Snow Geese spent more time feeding and pecked significantly faster in grazed areas than in ungrazed areas. Grazed vegetation had a higher protein content, and, thus, geese maximized both protein and food intake per time spent foraging, provided the take per peck in the two situations was comparable.

7.2. Grazing pressure and carrying capacity

Average grazing pressure by brant in four salt marshes along the central coast of the North Slope was 374 brant-days/ha. Based on this value and values for food intake, the birds consumed approximately 11.4 g dry weight of saltmarsh vegetation per square metre. Annual above-ground productivity of *C. subspathacea* in the Putuligayuk salt marsh has been measured at 33 g/m^2 in 1977 and 29 g/m^2 in 1978 (David Mason, pers. commun.). Geese were seen grazing in the area in which the measurements were taken, but grazing was light during the 2 years of the study. Brant would consume under these circumstances about one-third of the vegetation available in salt marshes, if it is assumed that grazing does not significantly increase productivity.

Several investigators have reported values for grazing pressure by wintering geese in lower latitudes. These values varied from 630 to 1500 goose-days/ha (Kuyken 1969, Owen 1972*b*, Ebbinge *et al.* 1975). Carrying capacity of grass pastures in the Netherlands was estimated by Ebbinge *et al.* (1975) at 2600 goose-days/ha and by Owen (1972*b*) in England at 1750 goose-days/ha, values two to three times higher than those of grazing pressure reported by the same investigators. In the Netherlands pastures Barnacle Geese would remove 40% of the standing crop of subarctic tundra vegetation. Kuyken (1969) noted a 34% decrease in standing crop from grazing by geese wintering in Belgium. During May on the Dutch island, Schiermonnikoog, brant removed 30% of *Plantago maritima* and *Puccinellia maritima* leaves. Clipping experiments showed a 30% removal of leaf material to result in the highest regrowth of new plant tissues (Prins *et al.* 1981). These values reported in the literature correspond well with those for brant in the Arctic and possibly represent the maximum vegetative removal without resulting in the overgrazing of an area. Cargill (1981), however, reported that Lesser Snow Geese removed 80% of the standing crop in low-latitude arctic salt marshes with no evidence of overgrazing. Nevertheless, grazing pressure at four salt marshes along the North Slope were amazingly consistent, indicating that brant were spacing their foraging in a manner that avoided overexploiting the vegetation.

8. Conclusions

Migration data from fall 1978 show 11 000 brant passing Simpson Lagoon (Johnson 1979). Thirty-two thousand brant migrated west from the Lake Teshekpuk area after moult in 1978, a number which has more than doubled since 1976 (Derksen *et al.* 1979). Thus, at least 42 000 birds are using salt marshes along the North Slope during fall migration.

Oil development is continually expanding along Alaska's northern shores. With development comes the constant threat of habitat destruction by oil spills, and of disturbance of foraging brant by human activity. Brant depend on arctic salt marshes during the season when their metabolic reserves are low and the energetic demands of migration high. This study shows that if the present number of birds are to continue to use the North Slope, oil development should proceed in a way such that salt marshes are protected from proximity to development and, in the case of an oil spill, every effort should be made to prevent oil from washing into salt marshes.

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