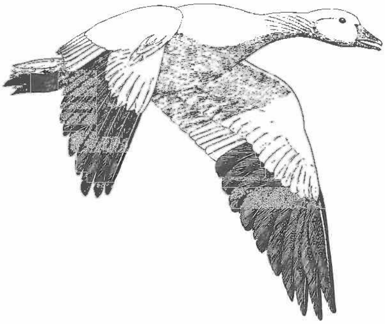
Summer habitat use and behaviour of Greater Snow Geese *Anser caerulescens*



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We studied habitat use by Greater Snow Geese in a glacial valley on Bylot Island, Northwest Territories, the most important breeding site for this population. The valley contains a mosaic of polygon wetlands surrounded by upland tundra. Twelve habitat types were identified based on physical features, and the floristic characteristics of each was sampled and described. Daily visual surveys were conducted from 11 July to 16 August 1990 in a 14 km^2 area. Habitat used, group size and behaviour were recorded for all adult-plumaged geese. Wetland habitats were grouped into two classes, pond/lake and wet meadow, and all other habitat types were classified as upland. Plant species composition was similar in the two wetland classes with a dominance of graminaceous plants (Dupontia fisheri, Carex aquatilis and Eriophorum spp.). Both families and non-parental geese significantly preferred all habitats with ponds and lakes throughout the summer, probably because of the high quality food and the protection from predators conferred by these habitats. However, there was a shift toward greater use of wet meadow habitats in the latter half of the season. Although upland habitat was avoided, it was used at a low level throughout the summer by families. Because both families and non-parental geese shifted simultaneously, the shift is probably related to reduced food availability in the preferred habitats rather than changes in gosling size or physiology. Time spent foraging was relatively constant across habitat types and was approximately double (60%) for non-parental compared to parental adults (30%). Adults with young were alert approximately 20% of the time compared to less than 3% for non-parental birds.

Keywords: Arctic Grassland, Breeding Behaviour, Feeding, Rearing, Nutrition, Snow Goose

Arctic nesting geese take advantage of long days and rapidly growing, highly nutritive plants while rearing their young (Owen 1980). Nevertheless, growing seasons are short so young geese must assimilate nutrients rapidly to maximize growth rate and to ensure the accumulation of adequate energy stores for the fall migration. Food choice is therefore critical at this time of year. The nutritive quality and available biomass of plants depend upon species, time in the growing season, and habitat-specific growing conditions (Sedinger & Raveling 1984, Manseau & Gauthier 1993). Forage quality, however, may not be the sole determinant of habitat use. Because both young goslings and moulting adults are flightless during much of the summer, they are vulnerable to terrestrial predators. Their preferred habitats at this time of year often include some form of refuge such as open water (eg. Mickelson 1975, Prop *et al.* 1978, Giroux *et al.* 1984, Sedinger & Raveling 1986).

Geese themselves may influence the quantity or quality of available food by reducing the standing crop (Cargill & Jefferies 1984, Sedinger & Raveling 1986) or by maintaining high nutrient levels longer into the growing season through regular, moderate grazing (Ydenberg & Prins 1981, Cargill & Jefferies 1984, Hik & Jefferies 1990). Habitats with plants which respond best to grazing may therefore have very high value for geese. However, if feeding areas with the greatest foraging value are used by broods first, later hatched goslings may be faced with a lower availability of high quality food plants and forced to move to new feeding locations (Prop *et al.* 1978, Sedinger & Raveling 1986, Cooch *et al.* 1991a) to maintain a sufficient rate of food intake. The negative impact of grazing by geese may be particularly important when population density is high (Kerbes *et al.* 1990, Cooch *et al.* 1991b).

The Greater Snow Goose *Anser caerulescens atlanticus* is a High Arctic nesting species. Within the breeding range (latitudes above 70°N), climatic conditions limit the distribution of many plants and the growing season lasts only about 6 weeks. Based on a description of habitats used during the latter half of the brood-rearing period at Jungersen Bay, northern Baffin Island, Northwest Territories (N.W.T.) and a series of rough calculations, Giroux *et al.* (1984) suggested that there was a twenty-fold excess of suitable habitat within the breeding range of the Greater Snow Goose. Because of the possibility of seasonal changes in habitat use, observations made during only part of the brood-rearing period should not be used to evaluate optimal habitats. Further-more, their calculations were based on 1980 population estimates when the springtime population (180 000 adults, Anon. 1981), was less than half the size it is now (434 500 in 1992, A. Reed, unpubl. data).

With the continuing rapid growth of this population, there is a need to evaluate the extent of available brood-rearing habitats and to understand the relationships between the geese and their habitats. Our objectives were to identify preferred brood-rearing habitats in an important breeding area and to determine if there are temporal differences in habitat use during brood-rearing. We also examined the potential impact of non-parental geese on habitat use by broods.

Study area

The study was conducted in a 14-km^2 portion of a glacial valley with a total area of 50 km^2 (**Figure 1**) located on the southwest plain of Bylot Island, N.W.T. (73° 08'N - 80° 00'W). Bylot Island is the single most important nesting area for the Greater Snow Goose with 13-15 % of the total breeding population located there during 1983 and 1988 surveys (Reed *et al.* 1992). The valley is bounded to the west by the sea, and to the north, east and southeast by low mountains up to 600 m high. To the southwest, the mountains give way to rolling hills of dry tundra. Central portions of the valley consist of large areas of mostly concave tundra polygons (Zoltai *et al.* 1983) forming a mosaic of wetland habitats. These include numerous small lakes and aggrega-

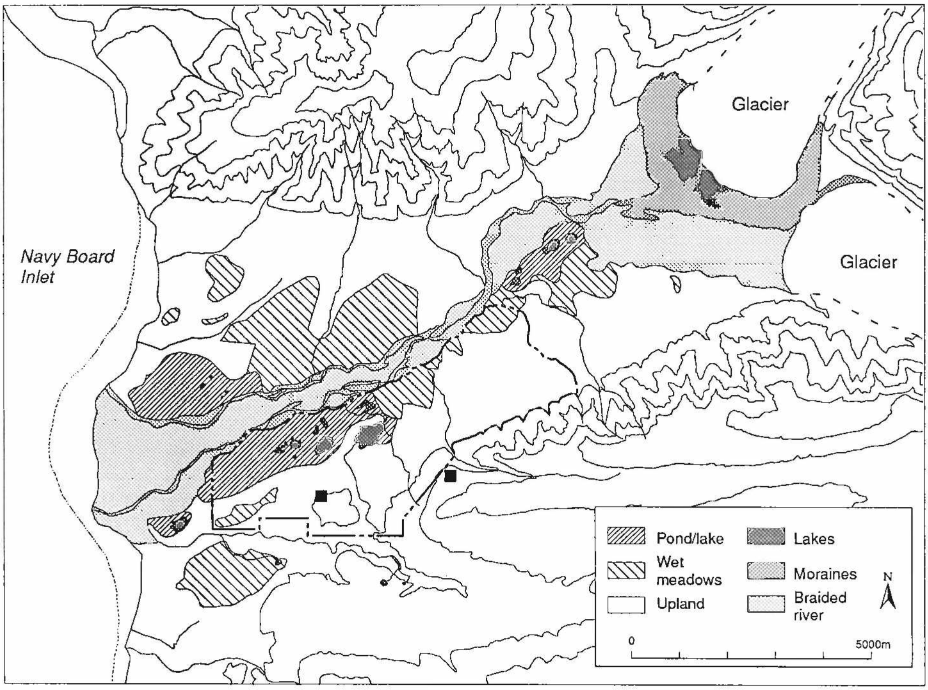


Figure 1. Map of the study valley showing the three major habitat classes and other geographical features. Broken line shows the 14 km^2 study area for daily visual surveys. The positions of the two observation sites are shown as solid squares.

tions of ponds with mossy margins dominated by graminaceous plants. A second major class of wetlands consists of multiple broad, shallow polygons forming extensive wet, moss-covered meadows also dominated by graminaceous plants. Although our study area contained one of the largest contiguous expanses of wetlands on Bylot Island, habitat types occurring there do not necessarily represent all of those used by brood-rearing Greater Snow Geese on the island.

Climatic conditions during brood-rearing, from early July to late August, are generally stable with temperatures ranging from about -2 to +15 °C and little precipitation. Days consist of 24 hour daylight with temperature and visibility being slightly lower during late evening to early morning hours. In August, a few hours of twilight occur around 2400 h. The growing season lasts from late June until mid-August when most plant species have begun to senesce.

Potential predators of Greater Snow Goose goslings include arctic fox *Alopex lagopus*, Glaucous Gull *Larus hyperboreus*, Long-tailed Jaeger *Stercorarius longicaudus*, Parasitic Jaeger *Stercorarius parasiticus* and Common Raven *Corvus corax*.

Methods

Habitat delimitation and sampling

We identified 12 habitat types (**Table 1a,b,c**) according to physical characteristics visible on 1:13000 black and white aerial photographs and each was verified by ground level observation. Presence or absence of polygon structure, size and density of ponds, water depth or wetness and elevation were important factors determining habitat classifications. Pond density was determined by placing a grid (squares equal to 200 m X 200 m) over aerial photographs of the study area and counting all ponds in squares more than half covered by the habitat type in question. Dimensions of lakes were measured directly on aerial photographs and those of ponds and polygons were estimated at randomly selected locations. The availability of each habitat type was determined by direct measurement on the study area map (1:13000) with a Koizumi digital planimeter.

The floristic composition of each habitat was determined using transects. To sample vegetation, a 0.5 m wide by 0.25 m long frame was moved parallel along the transect for a total of four (0.5 m X 0.25 m) quadrats per metre of transect. All species of vascular plants present in each quadrat were noted (moss and lichen were almost always present and were not included in analyses). Within transects, the abundance of each species was determined by counting the number of quadrats in which it was present and the five most abundant species were scored from one to five (5 being the most abundant). Scores were averaged across all transects within each of the 12 habitat types to produce mean ranks for the five most abundant species. Botanical nomenclature follows Porsild & Cody (1980).

For each habitat type, two 'patches' (individual patches were isolated from other areas of the same habitat type) were randomly selected. In uniform habitats, starting-points and directions were determined randomly for two independent 10 m transects. In habitats characterized by polygons (e.g. wet meadows or ponds), transects were run from the centre (wet meadows) or water edge (ponds), of randomly chosen polygons, to the outer limit (e.g. the summit of the ridge separating it from an adjacent polygon). The same method was employed for streams and lakeshores with transects running toward dry ground (generally 5-10 m) from a random point located in the stream or on the shoreline. As polygons and streams were often small, two or more transects were run until a minimum of 20 m of transect was sampled.

Visual Surveys

Daily visual surveys were conducted, using spotting scopes (X20-60), from two observation points, 100 m and 300 m above the valley bottom, together providing an unobstructed view of a 14 km^2 portion of the valley (**Figure 1**). A total of 28 surveys was conducted from 11 July to 16 August 1990. The day was divided into six 4 h blocks and survey start times were systematically distributed over the diurnal cycle on successive days. Surveys lasted from one to four hours depending on the number and distribution of geese in the study area. Habitat type used was determined by plotting goose positions on a 1:6500 habitat map of the study area. Group size, and instantaneous behaviour were recorded for all

Table 1a. Physical characteristics of Greater Snow Goose brood rearing habitats associated with permanent ponds or lakes (PL) at Bylot Island.

Habitat type	pond/lake shape[1] (range)	pond/lake size (ha) (range)	depth (m) (range)	description
Large polygon ponds	irregular	0.2-1.5	1-3	50-80 % of habitat water covered, <3 pond/ha ($\bar{x}$= 2.4 ± 0.91, n=22)
Small polygon ponds	regular	<0.2	0.5-1	25-50 % of habitat water covered, 2.5-13 pond/ha ($\bar{x}$= 7.3 ± 2.3, n=21)
Wet moss flats	none	N.A.	N.A.	flat, wet land within 50 m of polygon ponds
Broad lakeshore	regular	1.5-25	3+	flat, wet ground within 100 m of shoreline

[1] Shape distinguishes between those ponds having high shore length/area ratios (irregular), and those with low shore length/area ratios (regular).

Table 1b. Physical characteristics of Greater Snow Goose brood-rearing habitats characterised by regular-shaped moss covered, shallow, concave polygons or wet meadows (WM) separated by raised ridges at Bylot Island.

Habitat type	polygon size (ha) (range)	ridge height(m) (range)	ridge width(m) (range)	moisture regime in polygon centre
Wet moss meadows	0.01-0.5	0.1-1.5	1-15	saturated, from 0 to 10 cm standing water depending on snow melt and weather
Irregular ponds	0.005-0.2	0.1-1.5	1-15	dry or with 0 to 10 cm standing water (highly variable)

Table 1c. Physical characteristics of Greater Snow Goose brood-rearing habitats dominated by relatively featureless, dry upland (UP) terrain at Bylot Island.

Habitat type	Description
Dry valley bottom	extending from wetlands in the central part of the valley to the base of the surrounding hills; dry, flat moss and lichen covered ground
Dry hills	dry hillsides and elevated plateaus in and around the valley up to about 200 m above sea level; ground surface covered by densely vegetated frost boils
Isolated wet patches	includes isolated ponds and small lakes (<1.5 ha), streams flowing across otherwise dry land, or simply wet depressions in upland areas; distance from large expanses of wetlands ranges from several hundred metersto a few kilometers
Sparsely vegetated mud	open, low-lying areas of mud lacking a moss layer due to winter exposure to high winds and extreme cold; becomes very dry early in the summer
Deep canal polygons	raised convex polygons (diameter from 5 to 20 m) separated by narrow canals (width from 0.5 to 2 m; depth from 0.5 to 1.5 m; water depth around 0.5 m); abrupt margins sparsely vegetated by graminaceous plants
Dry moss meadows	concave polygons similar to wet moss meadows but drier (dry to very wet, highly variable) and height of ridges lower (0.1-0.5 m); vegetation typical of upland sites

adult-plumaged birds. Parental and non-parental (non-breeders and failed breeders) adults were distinguished by the presence or absence of goslings. No attempt was made to distinguish between male and female parents. Because of their small size and dull colour, gosling behaviour could not be determined. Behaviour of adults was classified as alert if a goose was stationary with the head held high. Geese were considered to be grazing whether stationary or moving slowly as long as the head was low, and there was no evidence of other behaviour such as aggression toward other geese. Resting geese were sitting and not feeding and include those sleeping, brooding young or preening. The fourth category recognized was walk, which was characterised by geese moving with head up (includes swimming).

Data Analysis

All survey data were pooled and analyses conducted on the actual number of geese observed. Habitat use was compared to availability using a Chi-squared test and Bonferroni simultaneous confidence intervals (Neu *et al.* 1974) using families (or pairs) as the sampling unit. We assumed observations of habitat use for individual families of geese to be independent even though they often foraged in flocks because: 1) flocks were not stable throughout the brood season and 2) the fine scale heterogeneity of the habitat enabled individual families within flocks to occupy different habitat types. The use of the terms *preference* and *avoidance* is restricted to indicate situations whereby a habitat is used in greater or lesser proportion, respectively, than it's availability; no conscious choice by geese is implied. The brood-rearing period was divided into early, mid and late periods to detect seasonal changes in habitat use. The relationships of time of day and association with other families with habitat use, for parental geese, and the relationship between behaviour and habitat use by both parental and non-parental geese were evaluated using 2-way contingency tables (SAS Institute Inc. 1985) in both early and late seasons. Time of day was classified into periods when the sun was high (0800-2000 h) or low (2000-0800 h) above the horizon. The effect of flocking was evaluated by comparing habitat use by single

Table 2. Dominant plant species[1] of Greater Snow Goose brood rearing habitats at Bylot Island. The five most abundant plants in each habitat and their mean ranks (0-5.0) are given.

Pond/lake habitats					
Large polygon ponds		Small polygon ponds		Broad lakeshores	
Dupontia fisheri	(4.6)	*Dupontia fisheri*	(4.6)	*Salix arctica*	(4.3)
Salix arctica	(3.6)	*Salix arctica*	(4.0)	*Dupontia fisheri*	(4.0)
Carex aquatilis var.*stans*	(1.6)	*Carex aquatilis* var.*stans*	(2.4)	*Arctagrostis latifolia*	(2.3)
Equisetum arvense	(1.4)	*Eriophorum scheuchzeri*	(1.6)	*Saxifraga* spp.	(1.6)
Astragalus alpinus	(1.2)	*Arctagrostis latifolia*	(1.6)	*Carex aquatilis* var.*stans*	(1.0)
Wet moss flats					
Dupontia fisheri	(5.0)				
Eriophorum angustifolium	(3.8)				
Carex aquatilis var.*stans*	(3.5)				
Salix arctica	(1.3)				
Eriophorum scheuchzeri	(0.8)				
Wet meadow habitats					
Wet moss meadows		Irregular ponds			
Dupontia fisheri	(4.8)	*Salix arctica*	(3.8)		
Carex aquatilis var.*stans*	(3.0)	*Arctagrostis latifolia*	(3.3)		
Eriophorum scheuchzeri	(2.0)	*Luzula confusa*	(2.0)		
Salix arctica	(1.5)	*Stellaria longipes*	(1.5)		
Eriophorum angustifolium	(1.3)	*Dupontia fisheri*	(1.3)		
Upland habitats					
Isolated wet patches		Sparsely vegetated mud		Deep canal polygons	
Salix arctica	(3.5)	*Salix arctica*	(4.8)	*Salix arctica*	(4.8)
Arctagrostis latifolia	(2.5)	*Poa arctica*	(2.5)	*Luzula confusa*	(3.8)
Equisetum arvense	(2.1)	*Dupontia fisheri*	(1.8)	*Carex aquatilis* var. *stans*	(2.8)
Saxifraga spp.	(1.3)	*Stellaria longipes*	(1.3)	*Poa arctica*	(1.8)
Carex aquatilis var.*stans*	(1.1)	*Astragalus alpinus*	(0.8)	*Polygonum viviparum*	(0.5)
Dry moss meadows		Dry valley bottom		Dry hills	
Salix arctica	(4.8)	*Salix arctica*	(4.8)	*Salix arctica*	(4.8)
Arctagrostis latifolia	(3.5)	*Dryas integrifolia*	(2.8)	*Arctagrostis latifolia*	(3.5)
Carex aquatilis var.*stans*	(2.3)	*Salix reticulata*	(2.5)	*Cassiope tetragona*	(2.5)
Stellaria longipes	(2.3)	*Arctagrostis latifolia*	(2.3)	*Luzula nivalis*	(2.3)
Luzula nivalis	(1.8)	*Alopecurus alpinus*	(1.5)	*Luzula confusa*	(1.4)

[1] Not all plants were identified to the species level. Some which were identified were subsequently grouped together under a common genus (eg. *Saxifraga*).

families *v* families in flocks (aggregations of 2-50+ families).

Results

Habitats

Three broad habitat classes were recognized: pond/lake (PL), wet meadow (WM), and upland (UP), comprising a total of 12 distinct habitat types (**Table 1a, b, c**). Pond/lake (PL) habitats (**Table 1a**) at Bylot Island are characterised by abundant, permanent water bodies of various sizes providing excellent refuges for geese threatened by terrestrial predators. Polygon ponds have wet mossy margins one to three metres wide and are separated by dry raised ridges with upland vegetation and small patches of bare ground or (less often) by low wet moss covered ground (contiguous margins of adjacent ponds) dominated by graminaceous plants (*Dupontia* > *Carex* > *Eriophorum* > *Arctagrostis*, **Table 2**).

Wet meadow (WM) (**Table 1b**) habitats consist mostly of large, shallow polygons covered by wet mossy ground dominated by graminaceous plants (*Dupontia* > *Carex* > *Arctagrostis* > *Eriophorum*, **Table 2**). The water level in these polygons varies depending upon snow-melt and summer rain. Because of the large size of these meadows, the area available for grazing, and hence food availability, is high. The moss covering the ground in these meadows is thicker and less compact than that found in other areas. Vegetation on ridges separating polygons resembles that in dry, valley-bottom tundra. Occasionally, small, elongated ponds, that are remnants of deep canals which once separated convex polygons (Table 1c) are present (Irregular Ponds, Table 1b). The vegetation associated with these ponds differs slightly from that found in the surrounding polygons (**Table 2**). Due to their small size (< 2 m in width), these ponds offered geese little protection from terrestrial predators.

Upland (UP) habitats are much more heterogeneous than the other two major habitat classes, both in their physical characteristics and in the plant species present (**Tables 1c** and **2**). These habitats are dominated by Arctic Willow *Salix arctica* and lack both an abundance of ponds and the grasses and sedges typical of the two wetland habitat classes. Included in this class of habitats are small isolated wet patches (ponds, stream beds, or wet depressions) surrounded by extensive dry tundra. Although far (from several hundred metres to more than 1 km) from other wetlands, these areas often appeared to have highly productive plant communities.

Above ground shoots of grasses and sedges were the foods most often consumed by broods based on evidence of grazing and casual observations of foraging geese. In wetland habitats, the two most common plant communities were *Dupontia fisheri*/*Eriophorum* spp. or *Carex aquatilis*/ *Dupontia fisheri* (**Table 2**., Manseau & Gauthier 1993). In PL habitats, graminaceous plants were typically from 1-10 cm high and above ground biomass reached 25-35 $g.m^{-2}$ (dry weight) at peak of growth (in areas protected from grazing, Gauthier unpubl. data). The same species of graminaceous plants growing in WM were from 5-20+ cm high and peak above ground biomass varied from 30-40 $g.m^{-2}$ in *Dupontia*/*Eriophorum* dominated areas to 60+ $g.m^{-2}$ in *Carex*/*Dupontia* communities (Manseau & Gauthier 1993). In UP habitats, seeds of *Luzula* spp. and *Alopecurus alpinus*, and seeds and flowering parts of *Oxytropis maydelliana* were also consumed.

Habitat Use

We estimated that a minimum of 1200 pairs of geese nested in the valley in 1990. Peak hatch occurred on 9 July and nesting success was 82 % (Gauthier, unpubl. data). On average, 221 (range: 65-349) families and 86 (range: 0-294) non-parental geese were present in the study area during surveys. Mean brood size declined significantly from 3.17 ± 0.06 [SE] (n = 414) early in the season to 2.70 ± 0.04 [SE] (n = 1060) late in the brood-rearing period (ANOVA, $P < 0.0001$).

Greater Snow Goose families significantly preferred all PL habitats throughout brood-rearing ($P < 0.01$ for all tests, **Table 3**). More than 50 % of goose observations were in these habitats during the entire season even though they represented only 26 % of the area surveyed. Early in the rearing period, goose families used mainly areas of large polygon ponds separated by narrow strips of ground, but gradually shifted to areas with smaller ponds and more available grazing area (pond margins

Table 3. Comparison of habitat use to availability for Greater Snow Goose families at Bylot Island, 1990 using a Chi-squared test and Bonferroni simultaneous confidence intervals (Neu *et al.* 1974). Signs following numbers (+,-) indicate habitats which are used in significantly greater or lower proportion than their availability ($P \leq 0.01$). An '=' sign indicates no significant preference or avoidance ($P > 0.05$). Early: 11-19 July, Mid: 20 July - 1 August, Late: 2-16 August.

Habitat	% Avail.		% Use	
		Early	Mid	Late
Pond/lake habitats				
Large polygon ponds	6.9	20.3+	15.0+	10.4+
Small polygon ponds	8.5	13.6+	18.4+	20.3+
Broad lakeshores	5.0	11.5+	7.6+	10.8+
Wet moss flats	5.8	15.9+	12.4+	13.5+
Wet meadow habitats				
Wet moss meadows	5.0	1.5-	11.9+	12.0+
Irregular ponds	6.6	3.0-	7.6=	16.9+
Upland habitats				
Isolated wet patches	8.5	10.8=	5.8-	2.3-
Sparsely vegetated mud	6.3	5.4=	1.7-	1.4-
Deep canal polygons	9.9	6.9-	5.9-	4.5-
Dry moss meadows	7.6	4.3-	3.7-	3.6-
Dry valley bottom	29.8	6.8-	9.9-	4.3-
	100 %			
Dry hills	40.5[1]	N.A.-	N.A.-	N.A.-
n (families)		1794	2108	2293

[1] Dry slopes and hilltops represented over 40 % of the study area, but less than 5 % of the observations were made in this habitat. If included in the analysis, it would cause many little-used habitats to appear preferred, it has therefore been excluded.

Table 4. Comparison of habitat use to availability for non-parental Greater Snow Geese at Bylot Island, 1990 using a Chi-squared test and Bonferroni simultaneous confidence intervals (Neu *et al.* 1974). Signs following numbers (+,-) indicate habitats which are used in significantly greater or lower proportion than their availability ($P \leq 0.01$). An '=' sign indicates no significant preference or avoidance ($P > 0.05$). Early: 11-19 July, Mid: 20 July - 1 August, Late: 2-16 August.

Habitat	% Avail.		% Use	
		Early	Mid	Late
Pond/lake habitats				
Large polygon ponds	6.9	43.4 +	25.1 +	22.9 +
Small polygon ponds	8.5	5.5 =	28.8 +	28.3 +
Broad lakeshores	5.0	25.6 +	2.5 -	5.1 =
Wet moss flats	5.8	21.9 +	24.3 +	11.0 +
Wet meadow habitats				
Wet moss meadows	5.0	0.0 -	6.6 =	10.2 +
Irregular ponds	6.6	1.4 -	0.5 -	1.8 -
Upland habitats				
Isolated wet patches	8.5	0.0 -	0.9 -	0.0 -
Sparsely vegetated mud	6.3	0.0 -	0.0 -	0.0 -
Deep canal polygons	9.9	1.4 -	10.8 =	2.6 -
Dry moss meadows	7.6	0.9 -	0.0 -	9.3 =
Dry valley bottom	29.8	0.0 -	0.4 -	8.8 -
	100 %			
Dry hills	40.5[1]	N.A.-	N.A.-	N.A.-
n (geese)		219	1092	1091

[1] Dry slopes and hilltops represented over 40 % of the study area, but less than 5 % of the observations were made in this habitat. If included in the analysis, it would cause many little-used habitats to appear preferred, it has therefore been excluded.

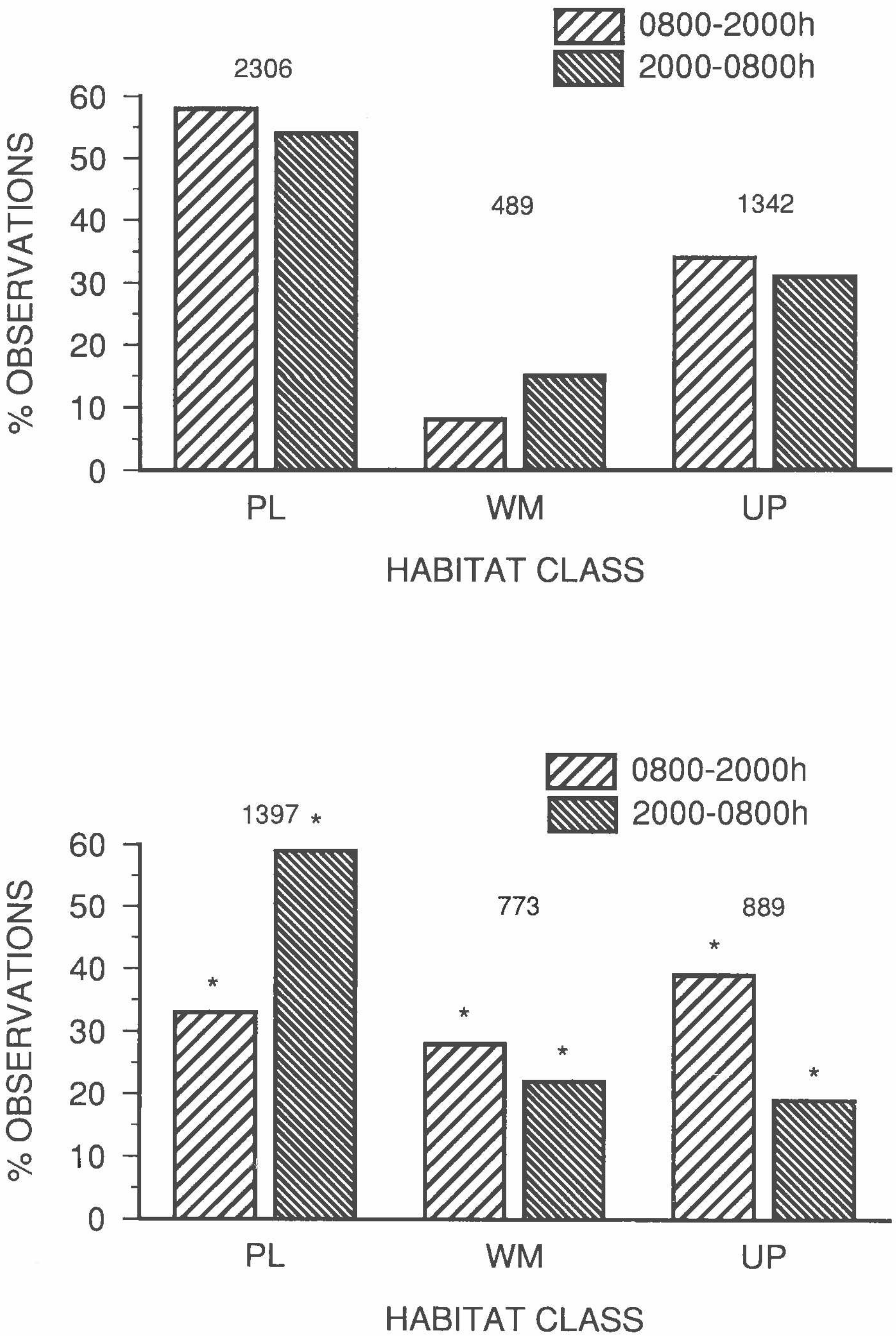


Figure 2. Effect of time of day on habitat use by Greater Snow Goose families at Bylot Island. Asterisks indicate significant differences from expected proportions, (X^2 test, $P \leq 0.05$). For 0800-2000 h and 2000-0800 h, n =1901 and 2236 (early) and n = 1593 and 1466 (late).

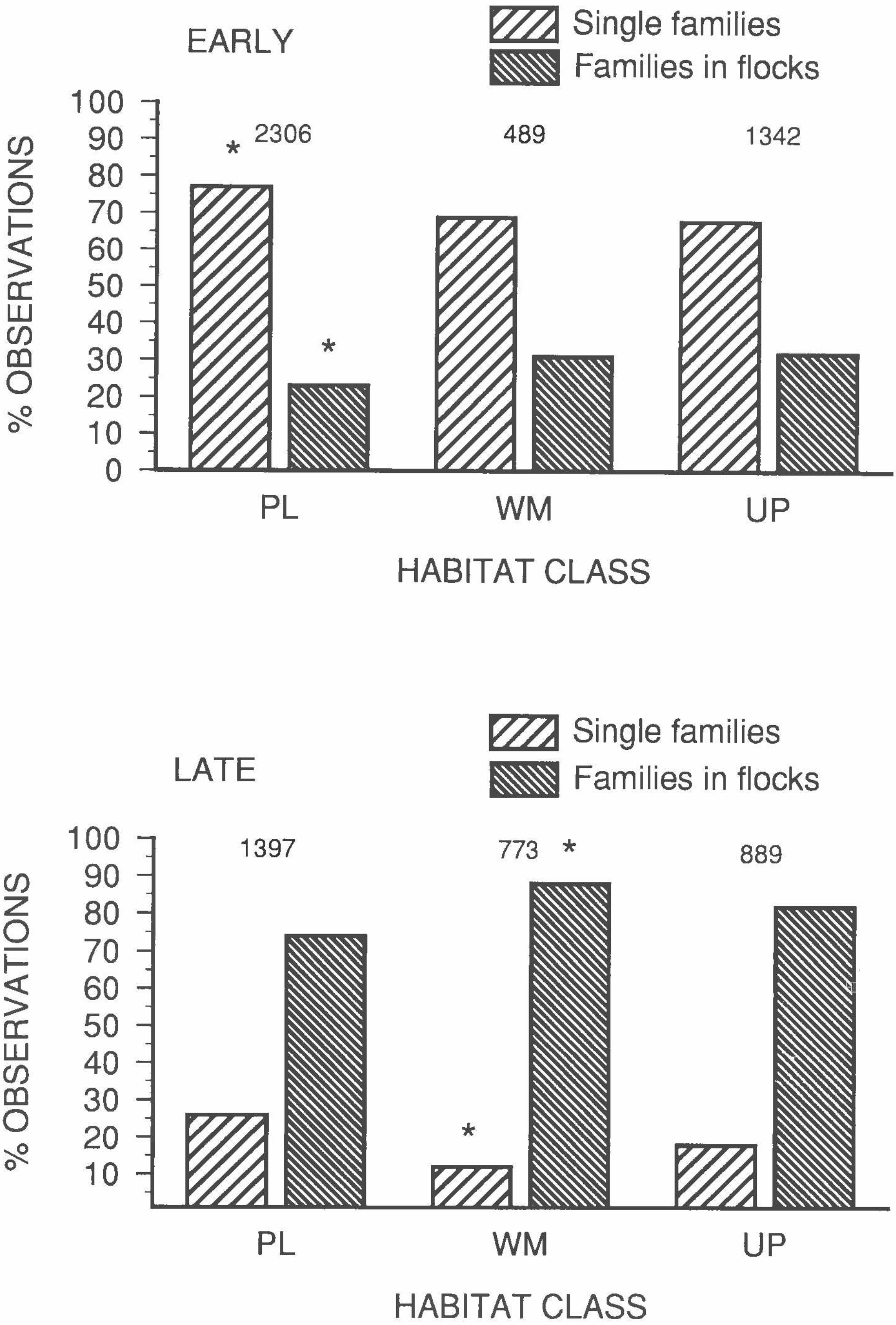


Figure 3. Relation between group size and habitat use by Snow Goose families at Bylot Island. Asterisks indicate significant differences from expected proportions, (X^2 test, $P \leq 0.05$). For single families and families in flocks , n = 3042 and 1095 (early) and n = 624 and 2435 (late) respectively.

and small wet polygons with no standing water). Use of large wet moss flats associated with lakes and ponds remained relatively constant (Table 3). WM habitats were initially avoided by brood-rearing geese, but in the latter part of the summer these areas were preferred as much or more strongly than some PL habitats (**Table 3**).

Upland habitats accounted for approximately 3/4 of the study area but only about 1/4 of all goose observations. Although no UP habitat type was ever significantly preferred by geese with young, all were nevertheless used to some extent throughout the brood-rearing period (**Table 3**). Use of these habitats was not uniform, as most observations of feeding geese were associated with isolated wet patches, particularly early in brood-rearing. Sparsely vegetated mud was also used in proportion to its availability early in the season but became very dry after the first week of brood-rearing and potential food plants, such as *Carex aquatilis*, became severely desiccated. Included within this habitat type were a few small patches of *Puccinellia phryganodes* which may have been exploited by geese early in the season.

Non-parental Greater Snow Geese also significantly preferred PL habitats and similarly used small polygon pond habitat more intensively later in the summer (**Table 4**). Non-parental birds avoided WM early in the season and showed a preference for it later, but the change in habitat use was not as great as that for families (**Table 4**). In contrast to families, non-parental geese almost entirely avoided all UP habitats.

Although the data cannot be directly compared between years, similar observations made in the same period and location in 1989 revealed a highly similar pattern of habitat use by both brood-rearing and non-parental geese.

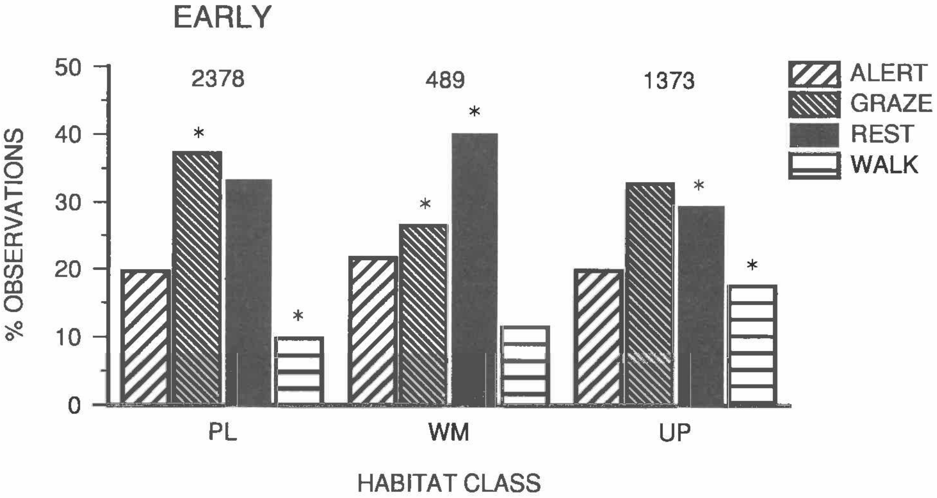
The effect of time of day on habitat use by Greater Snow Goose families was relatively weak early in the brood-rearing season. However, later in the season, a significantly greater proportion of geese used PL habitats between 2000 h and 0800 h compared to 0800-2000 h while the proportion of geese in both WM and UP habitats was significantly lower between 2000 h and 0800 h (**Figure 2**).

A greater proportion of the parental geese observed in PL habitats consisted of single families in both early and late seasons compared to other habitat classes despite a general tendancy for geese to form flocks later in the brood-rearing period. In early summer, the proportion of single families was similar in WM and UP habitats whereas later on the proportion of single families in UP was intermediate between that in PL and WM (**Figure 3**).

Behaviour

The behaviour of parental Greater Snow Geese was not uniform across habitat types in both the first (X^2=71.45, P<0.0001) and second (X^2=163.23, P<0.0001) halves of the brood-rearing period. Early in the season (**Figure 4**), geese in PL grazed more (P<0.05) than expected whereas geese in WM grazed less (P<0.01) than expected. Geese in WM rested more (P<0.01), and geese in UP less (P<0.05) than expected, geese in UP walked more (P<0.001), and in PL less (P<0.001) than expected. There was no difference in the proportion of geese in the alert posture among habitat classes. During the latter half of brood-rearing (**Figure 4**), both grazing and alert were constant across habitat classes. More geese in WM (P<0.05) and in PL (P<0.001) were resting than expected whereas less in UP were resting than expected (P<0.001). Geese walked more (P<0.001) than expected in UP and less (P<0.001) in PL. In all habitat/season combinations (except UP-late), grazing and resting were the dominant behaviours of breeding adults accounting for 26.6-37.2 % and 21.2-40.3 % respectively of all observations.

The behaviour of non-parental Greater Snow Geese was also not uniform across habitats in both the first (X^2=34.21, P<0.0001) and second (X^2=82.85, P<0.0001) halves of the brood-rearing season. Early in the season, non-parental birds in WM rested more than expected (P<0.001) and those in UP both walked and were alert more than expected (P<0.001) (**Figure 5**). Later in the summer, non-parental birds in WM grazed less and rested more than expected (P<0.001). In UP, they rested less and walked more than expected (P<0.001) and in both PL and WM they walked less than expected (P<0.001).



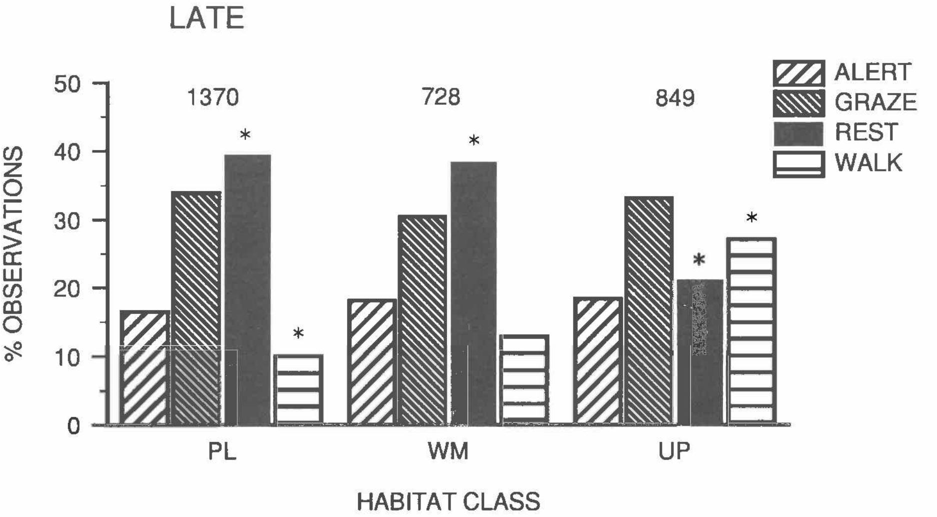


Figure 4. Behaviour of parental adult Greater Snow Geese by habitat class in early and late seasons at Bylot Island, 1990. The number of total observations is shown above the columns for each habitat class. Asterisks indicate significant differences from expected proportions, (X^2 test, $P \leq 0.05$).

Discussion

Habitat Use

Young of arctic nesting geese require high quality food for optimal growth and development during the short growing season. The diet of goslings consists mainly of above-ground parts of graminaceous plants (Harwood 1977, Giroux *et al.* 1984, Sedinger & Raveling 1986, Manseau & Gauthier 1993). However, the nutritive quality of graminaceous plants varies considerably among species and even within a species depending upon specific growing conditions (Sedinger & Raveling 1984, Manseau & Gauthier 1993). Moreover, plant nutrient content declines steadily through-

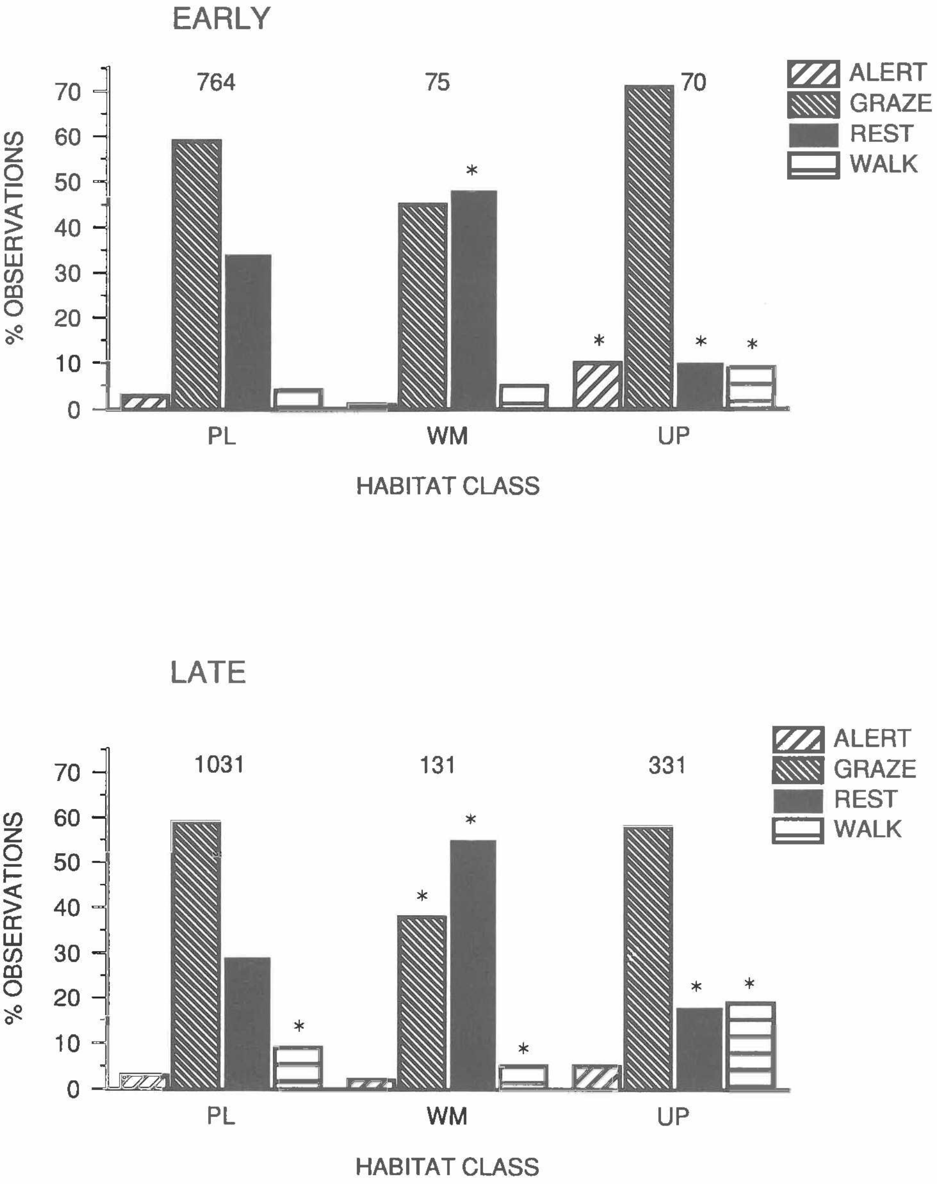


Figure 5. Behaviour of non-parental adult Greater Snow Geese by habitat class in early and late seasons at Bylot Island, 1990. The number of total observations is shown above the columns for each habitat class. Asterisks indicate significant differences from expected proportions, (X^2 test, $P \leq 0.05$).

out brood-rearing (Harwood 1977, Cargill & Jefferies 1984, Sedinger & Raveling 1986, Manseau & Gauthier 1993). Habitat choice can therefore be an important determinant of diet quality, even among habitats with the same plant species.

At Bylot Island, brood-rearing geese concentrated their activities at first in a few small areas characterised by large ponds and lush graminaceous vegetation but with limited grazing surface. This may occur because of the protection conferred by ponds against terrestrial predators. Predation is an important source of gosling mortality and adult geese are also vulnerable to attacks by terrestrial predators while moulting. Thus, proximity to open water is an important component of brood-rearing habitat (eg. Mickelson 1975, Prop *et al.* 1984). As goslings become stronger and more mobile with increasing size, their dependence upon proximity to water bodies as a defence against predators may be reduced permitting families to exploit other habitats (Prop *et al.* 1978, Reed *et al.* 1992). This may explain why we observed a habitat shift from areas with large ponds separated by narrow strips of land to those with smaller ponds and more land surface area. Presence of certain mineral rich plants such as *Equisetum arvense* (*sensu* Thomas & Prevett 1982), which may be of particular importance to post-incubating females or newly hatched goslings, could also influence which habitats are used initially.

The continued use of pond/lake habitats throughout the summer may merely be a consequence of their early-season use. Regular, moderate grazing by geese can delay the seasonal decline in plant quality by keeping plants at an early stage of growth and maintain high nutrient levels longer into the growing season (Ydenberg & Prins 1981, Hik & Jefferies 1990). Hence, except at the onset of growth, ungrazed plants would always have a lower quality at any given time than grazed ones. The most common graminaceous plant in wetland habitats in our study area, *Dupontia fisheri*, is well adapted to grazing and rapidly replaces grazed leaves with young, nutrient rich foliage (Mattheis *et al.* 1976).

Even though pond/lake habitats were preferred throughout the summer, Wet meadows were used increasingly in late season. Differences in plant phenology among habitats could have promoted this shift in habitat use. Alternatively, it may reflect a depletion of food resources in the most heavily grazed habitats (Sedinger & Raveling 1986). Gauthier (unpubl. data) found that, at Bylot Island, the above-ground biomass of grasses and sedges was negatively related to grazing intensity. Regrowth of plants following grazing diminishes as the season advances (Hik & Jefferies 1990) and at some point previously grazed habitat may no longer be able to support large numbers of geese. As goslings approach adult size, their nutrient requirements increase, further exacerbating the situation.

Considerable numbers of non-parental geese were observed in the study area. Although these birds may have included some non-breeders most were probably failed breeders as the ratio of the average number of parental to non-parental adults observed (442:86) corresponds closely to the proportion of successful nests in 1990 (82%). These birds often formed large flocks distinct from those of parental geese and used pond/lake habitats heavily, particularly early in the season. The presence of non-parental birds in the most preferred habitats may have accelerated the depletion of resources and forced families to look elsewhere to find less heavily exploited food patches. Further evidence that resources in these heavily used areas were becoming depleted was the sharp decline in numbers of non-parental birds in the study area during the last week of the study (7-14 August), the period when adult geese were first observed flying (9 August) after the moult (Madsen & Mortensen 1985). Parental birds were not observed in flight until 16 August when families were herded into nets for banding.

Habitat shifts by families could also be related to developmental changes such as increasing digestive tract size or improved digestive efficiency which allow older goslings to tolerate coarser/lower quality food plants elsewhere. However, because similar shifts in habitat use occur for moulting, non-parental geese whose size and digestive tract presumably do not change, resource depletion seems to be a more plausible explanation.

General avoidance of upland habitats at Bylot Island is probably related to their lack of ponds and abundant graminaceous plants. Use of these habitats may largely be attributed to travel between wetland patches. However, geese may have been occasionally attracted to these areas to exploit small patches of lush vegetation (especially in early summer), or by the presence of particular plants such as *Polygonum viviparum* (an important food of pre-nesting geese at Bylot Island, Lemieux 1959, Gauthier 1993) or *Equisetum arvense*. This suggests that exploring may be an important means of locating small patches of under-exploited, high quality resources, a phenomena which may be particularly true in the High Arctic where the rapid sequence of growth and seed production of diverse species produces many temporary and unpredictable food sources (Prop *et al.* 1978). In some years an increase in the use of upland habitats by large multifamily groups has been noted late in brood-rearing at Bylot Island (A. Reed & H. Boyd unpubl. data).

In summary, seasonal shifts in habitat use are important to consider when one is attempting to evaluate availability of suitable brood-rearing habitats for Arctic-breeding geese.

The greatest proportion of goose families occurring in flocks was noted in WM habitats in the latter half of the brood-rearing season when their use of these habitats had nearly doubled compared to early in the season. Flocking may therefore be partly related to a change in feeding strategy with changing habitat use. Many geese observed late in the season were in groups of up to 60 families moving slowly and cohesively across wet meadows, or occasionally to wet areas on hillsides (UP), probably reflecting a high available biomass of food plants compared to previously grazed areas. Also, at this time, goslings began eating basal stems (shoot pulling) of *Carex aquatilis* and *Eriophorum* spp., probably because, as plants senesce, they transfer resources from leaves to below-ground storage structures (Haag 1974, Chapin *et al.* 1975).

Brood-rearing geese used PL habitats proportionally more between 2000-0800 h in the latter half of the summer when low light levels may have increased the risk of predation and low temperatures increased the brooding requirements of young goslings. In Alaska, Sedinger & Raveling (1984) reported for Canada geese, a clear pattern of use of ponds at night and other areas during the day. However, at Bylot Island the effect of time of day on habitat use was weak, particularly early in the summer, probably because there is never a period of total darkness during brood-rearing.

Behaviour

Because food availability and risk of predation differ among habitat types, we may expect corresponding differences in the behaviour of geese. Indeed, the high incidence of resting in pond/lake compared to upland may be related to the protection that proximity to large water bodies offered from terrestrial predation during this activity. In wet meadow habitats, geese may have rested more than expected because in areas of high food availability, passage rate of food in the gut limits the rate of food intake, thus forcing goslings to rest more often (Sedinger & Raveling 1988, Manseau & Gauthier 1993). In upland habitat, the high incidence of walking is consistent with the hypothesis that these habitats were mostly crossed while moving from one wetland area to another.

In all habitats, brood-rearing geese were alert approximately 20% of the time. Even though pond/lake habitats may be safer from terrestrial predators, they apparently do not relieve parents from the necessity to be vigilant against avian predators. However, in situations where the risk of predation by Arctic Fox is greater than at Bylot Island, alert behaviour may be more prevalent. Giroux *et al.* (1986) reported that brood-rearing Greater Snow Geese at Jungersen Bay, N.W.T., were alert 40 % of the time, but they also observed 10 incidences of harassment by foxes in only 49 hours of observation compared to four in over 150 hours in our study.

Non-parental moulting geese were typically alert less than 3 % of the time (maximum 10 %) compared to an average of 20 % for adults raising young. As with parents, non-parental birds at Bylot Island were alert less often than reported by Giroux *et al.* (1980). Their tendency to form large flocks and to use pond/lake habitats almost exclusively presumably reduced the risk of predation so that fewer individuals needed to be watchful. Non-parental birds also walked less than adults with young (4-19 % *v* 10-27 % of the time) a result consistent with their more concentrated use of some habitats. These differences in behaviour allowed non-parental birds to devote more time to grazing than adults raising young (38-71 % *v* 27-37 %). However, since sexes could not be distinguished, differences must be interpreted with caution, especially in parental birds (Sedinger & Raveling 1990).

Our results show that when estimating the total availability of suitable feeding habitat for brood-rearing geese (e.g. Giroux *et al.* 1984), it is important to consider: 1) all habitats used over the course of the season (because habitat use changes over time), and 2) the portion of each habitat actually used for feeding (areas with many large ponds have much less potential grazing surface per hectare than large wet meadows). Moreover, large numbers of non-parental birds present in important brood-rearing habitats increases intraspecific competition and may reduce the availability of resources for families.

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