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**MILIEUX MÉSIQUES ET SECS
DE L'ÎLE BYLOT, NUNAVUT (CANADA):
CARACTÉRISATION ET UTILISATION PAR
LA GRANDE OIE DES NEIGES**

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Résumé

La densité de familles de la Grande Oie des neiges a augmenté récemment dans les milieux mésiques et secs de l'île Bylot, Nunavut (Canada). Ces milieux qui représentent environ 90% de la plaine sud de l'île sont aussi utilisés, parfois intensément, par les lemmings. Cette étude est la première à caractériser la végétation de ces milieux et à quantifier l'utilisation faite par ces principaux herbivores. L'utilisation et la sélection des habitats humides et mésiques par les familles d'oies ont également été étudiées *via* des décomptes d'oies.

Dix communautés végétales ont été identifiées en 2000 et 2001. Leur couvert total de végétation était élevé (>95%), à l'exception de deux communautés végétales xériques. Les différentes communautés végétales étaient liées à l'hétérogénéité topographique du paysage et reflétaient un gradient d'humidité et de perturbation. Par son couvert total de végétation, sa diversité de communautés végétales et sa richesse spécifique, l'île Bylot est considérée comme étant une oasis polaire. Les oies et les lemmings utilisaient la majorité des communautés végétales. Les plantes latifoliées et graminoides étaient sous une forte pression de broutement, particulièrement pour leurs inflorescences.

Tout au cours de la l'été 2001, les familles d'oies ont intensivement utilisé les habitats humides. Une forte pression de prédation pourrait être la cause de la faible utilisation des habitats mésiques. Toutefois, la proportion de familles dans ces habitats avait tendance à augmenter à la fin de la saison ce qui serait lié à la grande disponibilité de graines, fruits et rhizomes, structures riches en lipides et en hydrates de carbones. Les résultats obtenus suggèrent qu'à la fin de la saison, afin de subvenir à leurs besoins énergétiques, les oies doivent faire un compromis entre la disponibilité et la qualité de la nourriture et leur protection contre les prédateurs.

Avant-Propos

Ce mémoire de maîtrise comprend 3 chapitres. Le premier chapitre est un résumé substantiel du mémoire en français qui inclut une introduction générale et se termine par une conclusion générale. Suit ensuite les deuxième et troisième chapitres rédigés en anglais et sous la forme d'articles scientifiques. Dans tous les cas, je suis l'auteure principale de ces articles. Le deuxième chapitre amène de nouvelles connaissances sur les milieux mésiques et secs de l'île Bylot en ce qui a trait à leur composition en espèces mais aussi à leur utilisation par différents herbivores de l'île. Pour sa part, le troisième chapitre contribue à la compréhension de l'utilisation des milieux mésiques par les familles de la Grande Oie des neiges pendant la période d'élevage des oisons. Comme il a été convenu avec ma directrice de recherche, Dre Esther Lévesque, les deux articles issus de mon projet de recherche seront soumis à des revues scientifiques (chapitres 2 et 3).

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Chapitre I

Résumé substantiel

Ce chapitre débute avec une introduction générale où je vais présenter des grandes caractéristiques de la végétation arctique et l'utilisation des habitats et des ressources alimentaires par les oies. Ensuite, suit un résumé long des deux principaux chapitres de ma thèse. Une conclusion générale, reprenant les points importants de l'étude, termine finalement cette partie.

Introduction générale

L'environnement extrême de l'Arctique impose des contraintes particulières tant à la végétation qu'aux animaux. Cet environnement influence entre autres l'abondance et la distribution des espèces végétales pouvant être consommées par les herbivores. La sélection d'habitat est donc vitale pour un animal car elle influence son histoire de vie et ses stratégies écologiques. La façon dont un animal choisit un habitat a un impact direct sur l'abondance et la qualité de sa nourriture, en plus d'affecter son accès à un partenaire, sa vulnérabilité aux prédateurs et à des stress environnementaux.

Caractéristiques de l'Arctique

L'Arctique de l'Amérique du Nord est divisé en deux grandes zones selon leurs caractéristiques physiques et biologiques : le Bas- et le Haut-Arctique (Figure 1). L'été, le Haut-Arctique se distingue par une courte saison de croissance (1,5 à 2,5 mois), de basses températures (juillet : 3 à 8°C) et de faibles précipitations (25 à 100 mm), tandis que la lumière est disponible près de 24 heures sur 24 (Pielou 1994, Bliss 1997). Le sol arctique est gelé en permanence (pergélisol). Seule la portion supérieure (entre 20-60 cm), appelée mollisol, dégèle annuellement au cours de l'été (Bliss 1997). L'ensemble de ces conditions influence à la fois la distribution des plantes et les activités des animaux et limite la richesse spécifique végétale et animale (Bliss 1981, Bliss 1997, Tableau 1).



Figure 1. Carte de l'Arctique circumpolaire montrant les limites sud du Haut- et du Bas-Arctique (ligne en gras pointillée et pleine respectivement). Modifié de Bliss et Matveyeva (1992).

Tableau 1. Les trois classes de végétation retrouvées dans le Haut-Arctique canadien. Modifié de Bliss (1997).

Haut-Arctique			
Classes de végétation	<i>Toundra</i>	<i>Semi-Désert Polaire</i>	<i>Désert Polaire</i>
Proportion du paysage	6%	45%	41%
Couvert végétal total	80-100%	20-80%, dominé par les mousses et lichens (~15% de plantes vasculaires)	< 5% (~0,75% par les plantes vasculaires)
Richesse spécifique	10-40 ^{1,2,7}	7-40 ^{3,4,5}	1-20 ^{3,4,5,6}
Productivité végétale g/m²/an	85-165 ⁸	35 ⁶	1 ⁶
Types de végétation	-Prairie de plantes graminoides -Arbustales basses -Bruyère à arbustes nains	-Plantes en forme de coussin avec des cryptogames - Cryptogames et latifoliées	-Couvert clairsemé de latifoliées et de cryptogames
Utilisation par les herbivores	-Boeuf musqué (<i>Ovibos moschatus</i>) -Caribou (<i>Rangifer tarandus</i>) -Lemming brun (<i>Lemmus sibiricus</i>) -Lemming variable (<i>Dicrostonyx groenlandicus</i>) -Certaines espèces d'oies et de bernaches -Plusieurs oiseaux de rivages	- Boeuf musqué -Caribou -Lièvre arctique (<i>Lepus arcticus</i>) -Lagopède des rochers (<i>Lagopus mutus</i>) -Lemming variable -Plusieurs passereaux	Utilisation peu fréquente par les même animaux qu'en semi-désert (sauf les lemmings) mais surtout fréquenté par le lièvre arctique, le boeuf musqué et le lagopède des rochers

¹ Nams et Freedman 1994; ² Muc et al. 1989; ³ Bliss et al. 1984; ⁴ Bliss et Svoboda 1984; ⁵ Bliss et al. 1994; ⁶ Bliss et Matveyeva 1992; ⁷ Reznicek et Svoboda 1982; ⁸ Muc 1977.

Le paysage du Haut-Arctique se subdivise en trois grandes classes de végétation qui sont la toundra, qui couvre une faible superficie (6%), les semi-déserts polaires et les déserts polaires qui représentent une grande proportion du paysage (45% et 41% respectivement), les glaciers couvrant le reste du territoire (8%; Figure 2, Tableau 1). Le couvert végétal, la composition en espèce végétale, la structure des communautés végétales et la diversité des animaux distinguent les trois classes de végétation (Tableau 1; Bliss 1981, Bliss 1997). Le couvert végétal, la richesse spécifique et la productivité sont plus élevés en toundra et sont à leurs plus bas dans les déserts polaires (Tableau 1). La majorité des herbivores fréquentent les types de végétation ayant un couvert végétal supérieur à 20% (Bliss 1997).

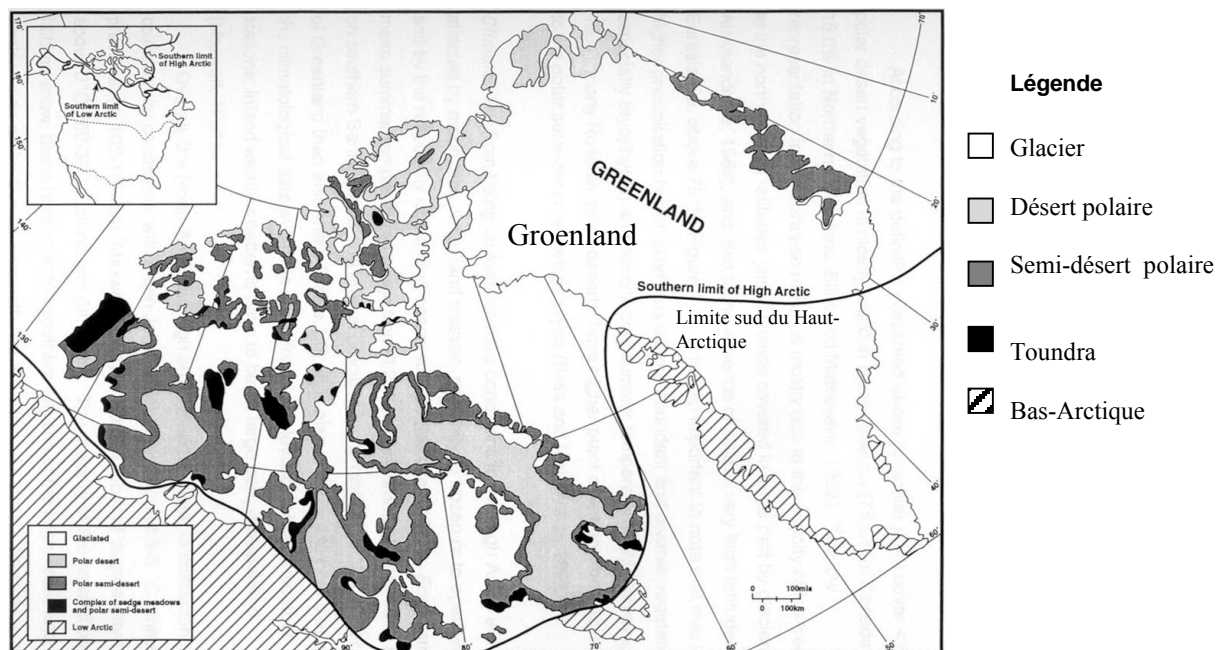


Figure 2. Limites géographiques du Haut-Arctique canadien montrant les principaux types de végétation. Modifié de Bliss (1977).

Végétation arctique

La végétation du Haut-Arctique est dominée par des plantes de basse stature (rosettes, arbustes nains) adaptées à l'exposition au vent, à de basses températures du sol et de l'air, et à des extrêmes d'humidité du sol (Billings 1987, Bliss 1997). Certaines espèces comme *Salix arctica* (saule arctique), *Dryas integrifolia* et *Cassiope tetragona* sont omniprésentes dans le Haut-Arctique et prédominent à l'intérieur d'un large éventail d'habitats.

Le tableau 2 résume différentes communautés végétales décrites dans l'Arctique canadien au cours des vingt dernières années. La majorité des études portant sur la végétation dans l'Arctique canadien ont eu lieu dans la partie nord des îles arctiques, dans le Haut Arctique. Toutes ces études soulignent l'importance majeure de l'humidité du sol dans la distribution des espèces et des communautés végétales. La topographie, les matériaux de surface, les caractéristiques du sol et l'accumulation de neige influencent aussi la distribution des communautés dans le Haut Arctique.

Présentement, il n'existe aucun consensus clair sur la nomenclature des communautés végétales dans cette région. C'est ainsi que plusieurs communautés semblables ont été nommées différemment par les auteurs. Nous avons donc regroupé les communautés végétales semblables en suivant la composition floristique et les conditions d'humidité (xérique, mésique, humide).

Communautés végétales xériques

Ces communautés végétales sont typiques dans les déserts et semi-déserts polaires (Tableau 2). Balayés par le vent durant l'hiver, ces sites retiennent peu de neige et sont donc libérés tôt au printemps, ce qui entraîne une faible disponibilité en eau (Bliss et al. 1984). Les basses températures et une plus courte saison de croissance limitent aussi la croissance des plantes sur ces sites (Bliss et Matveyeva 1992, Lévesque et al. 1997). Dans les déserts polaires, le couvert végétal est faible (~5-10%) et est principalement composé de plantes latifoliées (herbacées à feuilles larges), dont principalement *Saxifraga oppositifolia*, *Papaver radicum* et *Draba* sp., ou de graminoides. Dans les semi-déserts polaires, ce couvert varie entre 5-73% et est dominé par *D. integrifolia* ou les latifoliées. Le couvert de mousses et de lichens peut aussi être très élevé (jusqu'à 50%). Généralement, aucune essence ligneuse ne croît dans les déserts polaires tandis que *S. arctica* et *D. integrifolia* sont fréquents dans les semi-déserts polaires.

Communautés végétales mésiques

On retrouve quatre grands types de végétation dans cette catégorie hétérogène en terme de composition végétale (Tableau 2). 1) Les **steppes polaires** sont dominées par les luzules, *Luzula confusa* et *L. nivalis*, et sont parfois classées parmi les semi-déserts polaires à cause de leur couvert élevé de sol nu (jusqu'à 80%) ou de cryptogames (mousses-lichens, jusqu'à 75%; Bliss et Svoboda 1984). 2) La **toundra arbustive** est composée de trois sous-types dont chacun diffère par la dominance de *S. arctica*, *D. integrifolia* ou *C. tetragona*. Le couvert total de plantes vasculaires et de cryptogames est très variable, entre 20-60% et 0-50% respectivement. La toundra arbustive contient des types de végétation ayant la plus haute richesse spécifique (e.g. Muc et Bliss 1977, Bergeron 1988). 3) La **prairie mésique** a un important couvert de mousses, jusqu'à 80%, et un couvert abondant de plantes graminoides. Le saule arctique et les latifoliées sont les plantes vasculaires ayant également un couvert élevé. 4) Les **combes à neige** sont dominées par les mousses, les lichens et les latifoliées. La fonte d'un banc de neige à proximité alimente ces communautés en eau une bonne partie de la saison de croissance. Le sol peut donc être saturé en eau une partie de l'été (Thompson 1980).

Communautés végétales humides

- eau douce

Les plantes graminoides sont généralement abondantes dans ces communautés où leur couvert peut atteindre jusqu'à 70% (Bergeron 1988), et les mousses sont souvent dominantes au détriment des lichens (près de 100%; Tableau 2). Le couvert végétal est ainsi presque continu. Le saule arctique, *D. integrifolia*, *C. tetragona* et les latifoliées poussent sur le sommet des hummocks et les marges de polygones. Ces communautés sont les plus productives (Muc 1977, Webber 1978, Sheard et Geale 1983) et les plus homogènes en terme de composition en espèces (Bergeron 1988, Muc et al. 1989).

- eau salée

Les marais salés sont situés le long des côtes et sont dominés par quelques espèces de plantes halophytes, principalement *Puccinellia phryganodes* (Tableau 2). Le couvert total de végétation varie entre 15-25% (Bliss 1977) et les mousses et lichens sont peu abondants. La salinité, l'érosion des plages par les glaces, les marées et les faibles températures du sol limitent le développement des marais et l'établissement des espèces végétales (Bliss 1997).

Classe de végétation	Type de végétation	Muc and Bliss 1977 Devon Island 75°N, 84°W	Thompson 1980 Boothia Peninsula 68°N, 95°W	Edlund 1980 Loughheed Island QEI 78°N, 105°W	Sheard and Geale 1983 Bathurst Island- QEI 75°N, 98°W	1-Bliss et al. 1984 2-Bliss and Svoboda 1984 QEI 76°N, 93°W	Batten and Svoboda 1994 Alexandra Fiord Ellesmere Island 78°N, 75°W	Muc et al. 1989 Alexandra Fiord Ellesmere Island QEI 78°N, 75°W	Bergeron 1988 Sverdrup Pass, Ellesmere Island QEI 79°N, 80°W	Schaefer and Messier 1994 Victoria Island 69°N, 106°W
XÉRIQUE à XÉRIQUE-MÉSIQUE										
DÉSERTS POLAIRES	HERB or GRAMINOID BARRENS	<u>Moss-Herb</u> <i>S. opp.</i> Latifoliées <i>Phippsia</i> spp CT : 2-7%		<u>Saxifraga-barrens</u> <i>S. opp.</i> qqes graminées <u>Alopecurus-Poa</u> <u>barrens</u>	<u>Ridge (#1)</u> <i>S. opp.</i> Latifoliées Lichens qqes graminées	<u>1-Polar barrens</u> <i>S. opp.</i> Latifoliées K : 0,7% CV : 2-3% CT: 2,5 % <u>2-Graminoid and herb barrens</u> <i>Phippsia</i> spp <i>Puccinellia</i> spp <i>A. alpinus</i> B : <2 % L : <3% CV: 7 % CT: ~10%	<u>Saxifraga opp.-</u> <u>Luzula spp</u> <i>S. opp.</i> <i>Luzula nivalis</i> <i>Luzula confusa</i> B : 8 % L : 8% CV: 9 % CT: 25%		<u>Herb-Barrens (G)</u> <i>Poa abbreviata</i> <i>Draba</i> spp <i>Potentilla nivea</i> CT : trace	
SEMI-DÉSERTS POLAIRES	DRYAS or HERB based communities	<u>Unvegetated scree slopes</u> <i>S. opp.</i> Latifoliées <i>Salix arctica</i> qqes bryophytes <u>Cushion plant-lichen</u> <i>D. integrifolia</i> <i>S. opp.</i> <i>Carex nardina</i> <i>Salix arctica</i> K : 40-45% CV: 20 % CT: 60-65%	<u>Rock barrens</u> sol à nu <i>D. integrifolia</i> <i>C. tetragona</i> Latifoliées Pl. graminoides B : 9 % L : 24% CV: 13 % CT: 51% <u>Purple-saxifraga</u> <i>S. opp.</i> Latifoliées B : 17 % L : 10% CV: 38% CT: 71%	<u>Cryptogamic community</u> Mousses et lichens	<u>Polar desert (#2)</u> <i>D. integrifolia</i> <i>S. opp.</i> Lichens qqes graminées	<u>1-Cushion-plant community</u> <i>D. integrifolia</i> <i>Salix arctica</i> , <i>S. opp.</i> Latifoliées B : 0.5 % L : 3% CV: 4 % CT: 7% <u>2-Cryptogam-herb</u> Lichens <i>A. alpinus</i> <i>Luzula</i> spp. <i>S. opp.</i> Latifoliées B : 13 % L : 33% CV: 16 % CT: 62%	<u>Dryas barrens community</u> <i>D. integrifolia</i> <i>S. opp.</i> <i>Salix arctica</i> <i>Draba alpina</i> B : 1.5 % L : 6% CV: 16 % CT: 23%	<u>Lichen-cushion plant-dwarf shrub</u> <i>D. integrifolia</i> <i>C. tetragona</i> . <i>Salix arctica</i> <i>S. opp.</i> B : 9% L : 41% CV : 23% CT : 73%	<u>Dwarf shrub-bryophyte (E)</u> <i>D. integrifolia</i> <i>Salix arctica</i> , <i>Poa abb.</i> <i>S. tricuspidata</i> B : 9% CV: 18% CT: 30%	<u>Raised beaches (#5)</u> Roches <i>D. integrifolia</i> <i>Carex rupestris</i> <i>S. opp.</i> Lichens K : <2 % CV: 3% CT: 5% <u>Dryas based communities (#4, 7)</u> <i>D. integrifolia</i> <i>Carex</i> spp. <i>Kobresia</i> spp. B : <4% L : <4% CV: 27-31% CT: 31-36%

Classe de végétation	Type de végétation	Muc and Bliss 1977 Devon Island 75°N, 84°W	Thompson 1980 Boothia Peninsula 68°N, 95°W	Edlund 1980 Lougheed Island QEI 78°N, 105°W	Sheard and Geale 1983 Bathurst Island-QEI 75°N, 98°W	1-Bliss et al. 1984 2-Bliss and Svoboda 1984 QEI 76°N, 93°W	Batten and Svoboda 1994 Alexandra Fiord Ellesmere Island 78°N, 75°W	Muc et al. 1989 Alexandra Fiord Ellesmere Island QEI 78°N, 75°W	Bergeron 1988 Sverdrup Pass, Ellesmere Island QEI 79°N, 80°W	Schaefer and Messier 1994 Victoria Island 69°N, 106°W
XÉRIQUE-MÉSIQUE À MÉSIQUE-XÉRIQUE										
TOUNDRA	STEPPE POLAIRE			<u>Luzula-based communities</u> <i>Luzula confusa</i> <i>Luzula nivalis</i> <i>A. alpinus</i>		<u>2-Graminoid steppe</u> <i>Luzula confusa</i> <i>A. alpinus</i> B : 22 % L : 6,7% CV: 12,5 % CT: 41,2%.	<u>Luzula-dominated</u> <i>Luzula nivalis</i> <i>Salix arctica</i> <i>S. oppositifolia</i> <i>Festuca spp</i>			
MÉSIQUE (mésique-xérique à mésique à mésique-humide)										
TOUNDRA	TOUNDRA ARBUSTIVE 1. dominé par <i>Salix arctica</i>	<u>Ice-wedge polygons</u> <i>D. integrifolia</i> <i>Salix arctica</i> <i>A. alpinus</i> <i>Carex misandra</i>	<u>Willow Hummocks</u> <i>Salix spp</i> <i>Carex spp</i> Mousses <i>A. latifolia</i> <i>Dupontia fisheri</i> <i>P. sabinei</i> B : 22 % L : 7% CV: 37% CT: 75%		<u>Willow-lichen meadow (#7)</u> Mousses <i>Salix arctica</i> Lichens <i>A. alpinus</i> <i>Dupontia fisheri</i> <i>A. latifolia</i> Latifoliées B : ~45%		<u><i>Salix arctica-Cassiope dwarf-shrub</i></u> <i>Salix arctica</i> <i>C. tetragona</i> <i>D. integrifolia</i> B : 8,6 % L : 13% CV: 28 % CT: 50%	<u>Deciduous dwarf shrub-graminoid</u> <i>Salix arctica,</i> <i>Luzula confusa</i> <i>Poa arctica</i> <i>F. brachyphylla</i> B : 17% L : 23% CV: 49% CT: 89%	<u><i>Salix arctica-grass</i> (C)</u> <i>Salix arctica</i> <i>A. alpinus</i> <i>Poa arctica</i> <i>E. arvense</i> <u><i>Salix arctica-dominated</i> (F)</u> <i>Salix arctica</i> <i>D. integrifolia</i> Latifoliées CV: 21% CT: 21%	
	TOUNDRA ARBUSTIVE 2. dominé par <i>Dryas integrifolia</i>	<u>Cushion plant-moss</u> <i>D. integrifolia</i> <i>Carex rupestris</i> <i>S. oppositifolia</i> <i>C. tetragona</i> <i>Salix arctica</i> K : 30-50% CT : 100%	<u>Lichen-Dryas Plateaus</u> <i>D. integrifolia</i> Lichens <i>Salix arctica</i> B : 8 % L : 15% CV: 49 % CT: 78%			<u><i>Dryas-Carex complex</i></u> <i>D. integrifolia</i> <i>Carex misandra</i> <i>Salix arctica,</i> <i>C. tetragona</i> <i>P. viviparum</i> <i>Luzula nivalis</i> B : 3% L : 16% CV: 29% CT: 48%	<u>Lichen-cushion plant-dwarf shrub</u> <i>D. integrifolia</i> <i>C. tetragona.</i> <i>Salix arctica</i> <i>S. opp.</i> B : 9% L : 41% CV : 23% CT : 73% <u>Dwarf shrub-cushion plant</u> <i>D. integrifolia</i> <i>C. tetragona</i> <i>Salix arctica</i> B : 19%, L : 31% CV: 58% CT: 108%	<u><i>Dryas integrifolia-dominated</i> (D)</u> <i>D. integrifolia</i> <i>C. tetragona</i> <i>Salix arctica,</i> <i>Carex spp</i> CV: 30% CT: 34%	<u><i>Dryas based communities</i> (# 6, 8)</u> <i>D. integrifolia</i> <i>Carex spp.</i> <i>Kobresia spp.</i> B : <3% L : 1% CV: 37-42% CT: 40-46%	

Classe de végétation	Type de végétation	Muc and Bliss 1977 Devon Island 75°N, 84°W	Thompson 1980 Boothia Peninsula 68°N, 95°W	Edlund 1980 Lougheed Island QEI 78°N, 105°W	Sheard and Geale 1983 Bathurst Island-QEI 75°N, 98°W	1-Bliss et al. 1984 2-Bliss and Svoboda 1984 QEI 76°N, 93°W	Batten and Svoboda 1994 Alexandra Fiord Ellesmere Island 78°N, 75°W	Muc et al. 1989 Alexandra Fiord Ellesmere Island QEI 78°N, 75°W	Bergeron 1988 Sverdrup Pass, Ellesmere Island QEI 79°N, 80°W	Schaefer and Messier 1994 Victoria Island 69°N, 106°W
TOUNDRAS	TOUNDRAS ARBUSTIVES 3. dominé par <i>Cassiope tetragona</i> (Bruyère)	<u>Dwarf shrub heath-moss</u> <i>C. tetragona</i> , <i>D. integrifolia</i> <i>S. oppositifolia</i> <i>Salix arctica</i> <i>Carex misandra</i> B : 14% L : 21% CV : 37%					<u>Cassiope-dominated</u> <i>C. tetragona</i> <i>S. oppositifolia</i> <i>Poa arctica</i> <i>Luzula nivalis</i> <i>Luzula confusa</i> <i>Salix arctica</i> B : 2% L : 3-22% CV: 21% CT: 17-56%	<u>Dwarf shrub-cushion plant</u> <i>C. tetragona</i> <i>D. integrifolia</i> <i>Salix arctica</i> <i>S. oppositifolia</i> <i>Luzula nivalis</i> B : 19% L : 31% CV: 58% CT: 108%		
	PRAIRIE MÉSIQUE	<u>Graminoid-moss meadow</u> <i>A. latifolia</i> <i>Carex spp</i> <i>E. triste</i> <i>P. viviparum</i> <i>Salix arctica</i> , <i>D. integrifolia</i>		<u>Grass-based communities</u> <i>Alopecurus-Caryophyllaceae</i> <i>Alopecurus meadow</i>	<u>Mesic grass meadow (#10)</u> Mousses <i>A. latifolia</i> <i>E. triste</i> Latifoliées Joncacée <i>Dupontia fisheri</i> <u>Grass-forb meadow (#11)</u> Mousses Latifoliées <i>Dupontia fisheri</i> <i>A. latifolia</i> <i>Salix arctica</i> <i>Luzula nivalis</i>	<u>2-Moss-graminoid meadow</u> Mousses <i>A. alpinus</i> <i>Luzula nivalis</i> <i>Luzula confusa</i> Latifoliées B : 50-80% L : 14% CV: 12 % CT: 78%			<u><i>E. angustifolium-C. tetragona</i> (# 3)</u> <i>E. angustifolium</i> <i>C. tetragona</i> <i>Carex spp</i> K : <6% CV: 39% CT: 45% <u>Willow-sedge meadows (# 2)</u> <i>Salix spp</i> <i>Kobresia spp</i> <i>Carex spp</i> <i>A. latifolia</i> K : <6% CV: 51% CT: 57%	
	COMBE À NEIGE	<u>Herb-moss snowbed</u> Mousses <i>Phippsia spp</i> Latifoliées <i>Luzula nivalis</i> <i>R. sulphureus</i> B > CV	<u>Seepage slopes</u> Cryptogames Latifoliées B : 15% L : 12% CV: 22% CT: 76% <u>Moss Tundra</u> Mousses Latifoliées B : 32%; L: 11%; CV: 21% CT: 73%			<u>Hummock seepage slope (#4, 5, 8, 14, 15)</u> Lichens Mousses Latifoliées Graminées Joncacées	<u>1-Snowflush communities</u> Mousses <i>E. triste</i> <i>A. alpinus</i> <i>A. latifolia</i> <i>Luzula nivalis</i> <i>S. oppositifolia</i> B : 19 % L : 8% CV: 10 % CT: 37%			

Mesic and dry habitats of Bylot Island:
characterisation and use by herbivores

I. Duclos 2002

Classe de végétation	Type de végétation	Muc and Bliss 1977 Devon Island 75°N, 84°W	Thompson 1980 Boothia Peninsula 68°N, 95°W	Edlund 1980 Lougheed Island QEI 78°N, 105°W	Sheard and Geale 1983 Bathurst Island- QEI 75°N, 98°W	1-Bliss et al. 1984 2-Bliss and Svoboda 1984 QEI 76°N, 93°W	Batten and Svoboda 1994 Alexandra Fiord Ellesmere Island 78°N, 75°W	Muc et al. 1989 Alexandra Fiord Ellesmere Island QEI 78°N, 75°W	Bergeron 1988 Sverdrup Pass, Ellesmere Island QEI 79°N, 80°W	Schaefer and Messier 1994 Victoria Island 69°N, 106°W	
HUMIDE											
TOUNDRAS	PRAIRIE ou TOUNDRAS HUMIDE	<u>Hummocky Sedge-moss meadow</u> Mousses <i>Carex spp</i> <i>E. angustifolium</i> <i>Salix arctica</i> <i>A. latifolia</i> <u>Frost-boil Sedge-moss meadow</u> Mousses <i>E. triste</i> <i>Carex spp</i> <i>Salix arctica</i> <i>A. latifolia</i> <u>Wet sed-moss meadow</u> Mousses <i>Carex stans</i>	<u>Sedge meadows</u> <i>Carex spp</i> , <i>Eriophorum spp</i> Mousses <i>A. latifolia</i> <i>P. sabinei</i> <i>Dupontia fisheri</i> B : 21 % L : 2% CV: 52 % CT: 84%	<i>Alopecurus-Puccinellia bruggemanni</i> <i>Alopecurus-Dupontia</i> (wet meadows)	<u>Sedge meadow (#6)</u> Mousses <i>Carex stans</i> <i>Salix arctica</i> <i>Dupontia fisheri</i> <i>E. triste</i> B : 75% L: ~4% <u>Emergent meadow (#9)</u> Mousses <i>Carex stans</i> <i>Dupontia fisheri</i> <i>Arenaria rubella</i> <i>Salix arctica</i> <i>E. scheuchzeri</i>	<u>2-Wet graminoid-moss meadow</u> Mousses <i>Dupontia fisheri</i> <i>E. triste</i> <i>Carex stans</i> <i>E. scheuchzeri</i> <i>P. sabinei</i> B : 44% L : 1,3% CV : 27% CT : 100%	<u>Carex-meadow</u> <i>Carex aquatilis</i> Mousses <i>Salix arctica</i> , <i>C. tetragona</i> <i>D. integrifolia</i> <i>V. uliginosum</i> <i>E. angustifolium</i> B : 15% L : 0,3% CV: 59% CT: 74%	<u>Sedge-cushion plant-dwarf shrub</u> <i>E. angustifolium</i> <i>Carex spp</i> Mousses <i>D. integrifolia</i> <i>C. tetragon</i> <i>Salix arctica</i> B : 23% L : 12% CV: 67% CT: 109%	<u>Carex aquatilis-Eriophorum triste meadow (A)</u> <i>Carex aquatilis</i> <i>E. triste</i> Mousses B : 20% CV: 46% CT: 67% <u>Carex aquatilis meadow (B)</u> <i>Carex aquatilis</i> Mousses B : 33% CV: 45% CT: 79%	<u>Graminoid-dominated meadow (#1)</u> <i>Carex spp</i> <i>E. angustifolium</i> K : <3% CV: 47% CT: 50%	
	PRAIRIE HUMIDE	<u>Hummocky graminoid meadow</u> Mousses <i>A. latifolia</i> <i>Dupontia fisheri</i>			<u>Grass-moss meadow (#12)</u> Mousses <i>Dupontia fisheri</i> B : 90%						
	MARAIS SALÉS	<u>Tidal salt marsh</u> <i>Puccinellia phryganodes</i> <u>Unvegetated coastal shoreline</u> <i>Cochlearia officinalis</i>		<u>1- Halophytic community</u> <i>Puccinellia phryganodes</i> <u>2- Halophytic community</u> <i>P. phryganodes</i> <i>S. humifusa</i> <i>C. officinalis</i>				<u>Salt marsh</u> <i>Puccinellia phryganodes</i> <i>S. humifusa</i> B : 0% L : 0% Algues: 10% CV: 6% CT: 16%			

Sélection et utilisation des ressources

En plus des conditions environnementales rigoureuses, la croissance et la distribution de la végétation arctique sont aussi affectées par les animaux. En retour, la composition, la structure et l'abondance de végétation influencent en partie le comportement des animaux dans l'utilisation de leur environnement. En effet, la végétation est une des nombreuses ressources faisant partie intégrante de l'habitat d'un animal.

Terminologie

Johnson (1980) ainsi que Hall et al. (1997) ont tenté de définir la terminologie liée à l'utilisation et la sélection d'une ressource alimentaire ou d'un habitat. Cette terminologie est ici décrite brièvement et sera utilisée dans ce document.

L'**abondance** d'une ressource représente son importance à l'échelle du paysage ou dans l'aire d'étude alors que sa **disponibilité** est la proportion qui est accessible à l'animal. L'**utilisation** est la proportion d'une ressource disponible qu'un animal utilise à une période donnée. La **sélection** est le processus hiérarchique par lequel un animal choisit la ressource qu'il utilisera (voir plus bas). L'utilisation d'une ressource est dite sélective (ressource **sélectionnée**) lorsque celle-ci est utilisée de manière disproportionnée à sa disponibilité. Finalement, la **préférence** d'une ressource reflète la probabilité qu'elle soit choisit par l'animal si elle était offerte sur une base équivalente aux autres ressources (Johnson 1980).

Sélection: processus hiérarchique

La sélection d'un habitat par un animal serait un processus hiérarchique qui s'insérerait à l'intérieur de plusieurs échelles spatiales (Owen 1972, Johnson 1980, Owen 1980, Wiens 1985, Hupp et Robertson 1998). La variation temporelle influence aussi le processus à différents niveaux (Wiens 1985). La sélection ou l'occupation d'une aire de répartition géographique ou physique par une espèce donnée constitue une sélection de premier ordre. À l'intérieur de cette aire de répartition, la sélection de deuxième ordre définit le domaine vital d'un individu ou d'un groupe d'animaux. L'utilisation des différents habitats composant le domaine vital représente la sélection du troisième ordre tandis que la sélection du quatrième ordre constitue l'utilisation de ressources spécifiques (alimentaires) disponibles dans un habitat (Johnson 1980). Notons que la disponibilité d'une ressource à une plus petite échelle de résolution peut influencer les choix à une plus grande échelle (Johnson 1980).

Sélection au niveau de l'habitat (troisième ordre)

Hall et al. (1997) définit un habitat comme étant l'ensemble des ressources et des conditions d'un environnement qui amène un animal à occuper ce lieu en particulier dans un but de survie ou de reproduction. L'habitat implique plus que la végétation ou la structure de la végétation, c'est aussi la somme des ressources spécifiques dont un organisme a besoin tel que la présence de plan d'eau ou d'abris.

Plusieurs facteurs peuvent influencer la sélection d'habitat à l'intérieur des domaines vitaux. Par exemple, la structure et la disponibilité de ressources intrinsèques (Cody 1985) affectent directement l'utilisation d'un habitat. Pour sa part, la disponibilité des ressources ou d'un habitat est influencée par des facteurs biotiques (e.g. présence de prédateur, compétition inter/intra-

spécifique; Wiens 1985) et abiotiques (*e.g.* fonte de la neige; Prop et al. 1984, Carrière et al. 1999). La densité d'une population (Fretwell et Lucas 1970), la philopatrie natale (Cooke et Abraham 1980) ou le sexe de l'animal (Cody 1985) peuvent aussi influencer les choix d'habitats.

Sélection d'habitat chez les oies

Dans les régions arctiques et sub-arctiques, les oies sélectionnent habituellement les milieux humides comme aire d'alimentation. L'abondance élevée de plantes graminoides de bonne qualité dans ces milieux leur permet de minimiser leur effort de récolte et de maximiser leur apport en nourriture. De plus, comparativement aux autres types de végétation dans l'Arctique, la production primaire des terres humides est élevée, et ce, principalement à cause de la grande disponibilité en eau (Muc 1977, Webber 1978). Finalement, la proximité d'étendue d'eau (lacs, étangs) permet aux oies d'échapper aux prédateurs terrestres (Buchsbaum et Valiela 1987, Laing et Raveling 1993, Hughes et al. 1994).

En milieu naturel, les oies choisissent les types de végétation où la qualité des plantes est plus élevée, et ce, même entre des types de végétation très similaire (Manseau et Gauthier 1993, Gadallah et Jefferies 1995, Wilson et Jefferies 1996). La digestibilité de la végétation expliquerait aussi la sélection d'un type particulier de végétation plutôt qu'un autre (Boudewijn 1984). Il a été démontré que les Bernaches nonnettes (*Branta leucopsis*) sélectionnaient les sites d'alimentation où la productivité des plantes fourragères était plus élevée (Ydenberg et Prins 1981). Par contre, les oies étaient en partie responsables de la productivité élevée des plantes par leur pression de broutement. Cependant, la Bernache du Canada (*Branta canadensis minima*) sélectionnerait les types de végétation en fonction de la qualité nutritive des plantes plutôt que de leur productivité (Sedinger et Raveling 1986).

La variabilité dans la phénologie des plantes peut aussi amener les oies à se déplacer et à utiliser des types de végétation similaires ou différents de ceux utilisés précédemment (Boudewijn 1984, Prop et al. 1984, Prins et Ydenberg 1985). Au Groenland, l'Oie à bec court et la Bernache du Canada quittent partiellement les marais au mois d'août pour se disperser dans la toundra où elles se nourrissent entre autre d'*Equisetum* spp., de latifoliées et de divers petits fruits (Madsen et Mortensen 1987).

Sélection alimentaire (quatrième ordre)

Les graminées et les cypéracées qui dominent dans les milieux humides sont faciles à digérer pour les oies à cause de leur faible concentration en fibres. Elles sont aussi nutritives de par leur concentration élevée en azote, leur contenu élevé en eau et en minéraux et leur faible concentration en composés phénoliques (Sedinger et Raveling 1984, Buchsbaum et Valiela 1987, Manseau et Gauthier 1993, Gadallah et Jefferies 1995).

Toutefois, certaines espèces, qui peuvent être peu abondantes, sont fréquemment consommées à cause de leur qualité nutritive ou énergétique particulière. Par exemple, la récurrence d'*Equisetum* spp. dans la diète de la Bernache du Canada (Prevett et al. 1985) s'expliquerait par son contenu élevé en protéines et en minéraux (Thomas et Prevett 1982). La plante latifoliées *Triglochin palustris* (joncaginacée) est sélectionnée pour son contenu très élevé en protéines et en hydrates de carbone et son faible contenu en fibres (Sedinger et Raveling 1984, Summers et al. 1993, Thomas

et Preveit 1980, Preveit et al. 1985). Certaines espèces ou parties végétales sont par contre évitées à cause de leur faible digestibilité. Plusieurs facteurs affectent la digestibilité des plantes: une concentration élevée en métabolites secondaires (Buchsbaum et Valiela 1987, Summers et al. 1993), un ratio phénols : protéines élevé (Gauthier et Hughes 1995) ainsi qu'un contenu élevé en fibres et faible en nutriments (*e.g.* mousse ; Madsen et Mortensen 1987, *Elymus arenarius* ; Laing et Raveling 1993).

Plusieurs tactiques sont utilisées par les oies pour augmenter leur apport en azote ou en énergie. Par exemple, pour une espèce végétale donnée, les oies seraient capables de sélectionner les plantes ou parties de plantes les plus nutritives (Sedinger et Raveling 1984, Buchsbaum 1985, Laing et Raveling 1993, Manseau et Gauthier 1993, Piedboeuf et Gauthier 1999). La consommation de fruits, de graines ou de parties souterraines des plantes au printemps et à l'automne permettrait aux oies de maintenir une diète de bonne qualité et de subvenir à leurs besoins énergétiques qui changent au cours de la saison (Thomas et Preveit 1980, Sedinger et Raveling 1984, Preveit et al. 1985, Gauthier 1993). Tous ces exemples démontrent comment les oies peuvent exercer une forte sélection sur certaines espèces ou parties végétales.

Problématique

Depuis les années '70, les populations d'oies à travers le monde ont considérablement augmenté (Madsen 1991, Owen et Black 1991, Ankney 1996, Abraham et Jefferies 1997). Ces changements récents dans la taille des populations seraient directement ou indirectement liés aux activités humaines tels que l'expansion de l'agriculture et l'établissement de refuges et d'aires de repos tout au long des routes migratoires. Ces facteurs ont eu comme impact d'abaisser le taux de mortalité des oies (Owen 1990, Owen et Black 1991, Ankney 1996, Abraham et Jefferies 1997).

Cette augmentation dans le nombre d'oies n'est pas sans conséquence sur la végétation de leur aire d'alimentation (Giroux et Bédard 1987, Esselink et al. 1997, Filion et al. 1998, Giroux et al. 1998). Dans la région de la Baie d'Hudson au Canada, le cas de la Petite Oie des neiges (*Chen caerulescens caerulescens*) est un exemple bien documenté où le sur-broutement suite à l'augmentation rapide de la population a eu un impact sur la végétation (Kerbes et al. 1990, Iacobelli et Jefferies 1991). Entre 1973 et 1993, 2 454 hectares de marais salés ont été détruits (Jano et al. 1998), soit environ 65% de la superficie total des marais (Abraham et Jefferies 1997). La recolonisation des marais salés par les communautés végétales originales est restreinte par l'apparition d'une rétroaction positive qui crée des conditions de sols hypersalines hostiles à la croissance des plantes graminoides ou pouvant être létales pour les saules (Iacobelli et Jefferies 1991, Srivastava et Jefferies 1996). La dégradation de la qualité des marais a donc amené les oies à se déplacer vers d'autres sites d'alimentation et dans certains cas, à utiliser des habitats plus secs, inhabituels pour leur alimentation (Kerbes et al. 1990, Gadallah and Jefferies 1995). La consommation de plantes alternatives dans les marais a eu comme effet de diminuer la taille corporelle des oisons et des adultes (Cooch et al. 1991ab), de diminuer la condition corporelle des oisons et d'augmenter la mortalité des oisons (Francis et al. 1992, Cooch et al. 1993, Williams et al. 1993).

Cas de la Grande Oie des neiges

Tout comme les autres populations d'oies, la population mondiale de la Grande Oie des neiges (*Chen caerulescens atlantica*) a considérablement augmenté, passant de 150 000 oiseaux en 1975 à 740 000 en 1998 (Reed et al. 1998). À l'île Bylot au Nunavut, où 15% de la population se rassemble pour nicher (Reed et al. 1992), le nombre total d'oies a triplé entre 1983 et 1993, passant de 52 000 à 155 900 oiseaux (Reed et al. 1998). Après l'éclosion des oisons, les familles utilisent préférentiellement comme site d'alimentation les milieux humides dominés par les graminées et les cypéracées (Hughes et al. 1994). En plus de leur abondance en nourriture, ces milieux ont une densité élevée de lacs et d'étangs qui servent de refuges aux familles contre les prédateurs terrestres. Massé et al. (2001) ont estimé que les milieux humides de la plaine sud de l'île Bylot étaient utilisés à $46 \pm 10\%$ de leur capacité de support. Par contre, cette valeur peut considérablement varier sur une base annuelle suite aux fluctuations annuelles du nombre d'oies ou de la productivité des plantes selon les conditions environnementales. De plus, à long terme, avec l'accroissement de la population d'oies, la capacité de support pourrait rapidement être atteinte ce qui entraînerait une détérioration de l'habitat.

Jusqu'à présent, aucun dommage comparable à celui de La Pérouse Bay n'a été noté à l'île Bylot. Cependant, le broutement par les oies a un impact sur la végétation des milieux humides. Gauthier et al. (1995) ont estimé que les oies pouvaient consommer jusqu'à 78% de la production aérienne annuelle de *Dupontia fisheri* et jusqu'à 100% de la production aérienne annuelle d'*Eriophorum scheuchzeri*. Beaulieu et al. (1996) ont aussi remarqué que l'accumulation d'hydrates de carbone solubles dans les rhizomes était moins élevée dans les plantes broutées ce qui aurait éventuellement comme conséquence de diminuer la productivité des plantes. En effet, le suivi d'exclos permanents sur une période de 5 ans a permis de constater que le broutement modifiait la composition végétale des communautés et diminuait la densité et la production des plantes broutées (Gauthier et al. 1996).

Même si les estimés de Massé et al. (2001) indiquent que la capacité de support des milieux humides à l'île Bylot ne serait pas atteinte, plusieurs indices suggèrent par contre que la disponibilité de nourriture dans ces milieux diminue. En effet, certains effets dépendants de la densité ont déjà été détectés chez la Grande Oie des neiges. Par exemple, un déclin de la condition des jeunes (poids et taille) et de leur taux de croissance a été mesuré (Reed et Plante 1997). Ce déclin serait attribuable à une diminution de la disponibilité des ressources végétales *per capita* sur les sites d'élevage suite à l'augmentation de la population (sur-broutement). De plus, des mouvements entre différents habitats notés chez les familles d'oies suggèrent aussi que la disponibilité des ressources végétales dans les milieux humides diminue au cours de la saison dû à une sur-utilisation (Hughes et al. 1994). Finalement, les milieux mésiques et secs, ou hautes-terres, sont davantage utilisés par les familles d'oies. Entre 1983 et 1993, la densité des familles a augmenté de plus de 10 fois dans ces milieux considérés de pauvre qualité pour les oies (Reed et al. 1998).

À l'île Bylot, les milieux humides de la plaine sud ne représentent qu'une petite proportion du territoire tandis que les milieux mésiques et secs (les hautes-terres) couvrent environ 90% du paysage (Massé et al. 2001). Même si elles sont moins préférées par les oies, les hautes-terres sont utilisées périodiquement lors de la fonte des neiges, de migrations locales pendant la période

d'élevage des oisons ainsi qu'à la fin de la saison pour la disponibilité de graines (Hughes et al. 1994, Gauthier 1993, Chapitre 2 et 3). L'utilisation des milieux mésiques et secs par les familles d'oies a considérablement augmenté au cours des dernières années (Reed et al. 1998). Par contre, on ne connaît pas l'importance de ces milieux pour l'alimentation des oies. De plus, ces milieux sont aussi utilisés par les lemmings (*Lemmus sibiricus*, *Dicrostonyx groenlandicus*) dont leur densité augmente de façon cyclique aux 3 ou 4 ans (Bêty et al. 2002).

Comme le nombre d'oies continue d'augmenter (Reed et al. 1998) et que les lemmings peuvent atteindre de fortes densités certaines années, le broutement de ces deux herbivores peut potentiellement affecter la structure des communautés végétales. Toutefois, malgré leur grande superficie, nous avons peu d'informations à propos des milieux mésiques et secs. Ainsi, afin de déterminer si ces milieux contribuent à la capacité de support de la plaine sud et de bien évaluer l'impact des herbivores sur ces milieux, il était crucial de les caractériser et d'évaluer leur utilisation par les oies.

Mes objectifs spécifiques étaient de :

- 1) Caractériser et cartographier la végétation présente dans les milieux mésiques et secs (hautes-terres) dans le but de déterminer les communautés végétales;
- 2) Déterminer les variables environnementales qui influencent la distribution de ces communautés à l'échelle du paysage;
- 3) Estimer l'utilisation de ces communautés par les principaux herbivores de l'île (décomptes de fèces);
- 4) Identifier les espèces et les parties végétales broutées par les oies et les lemmings, et évaluer l'intensité de broutement sur ces parties de plantes broutées;
- 5) Décrire l'utilisation et la sélection par les familles d'oies des différents habitats humides et mésiques au cours de la saison (décomptes d'oies);
- 6) Décrire plus spécifiquement l'utilisation et la sélection des milieux mésiques par les familles d'oies au cours de la saison.

Méthodologie

Site d'étude

L'étude a eu lieu à l'île Bylot au Nunavut, Canada (73°N, 80°O). La plaine sud de l'île est un sanctuaire d'oiseaux et accueille entre autre la plus grande colonie de Grande Oie des neiges au monde (Reed et al. 1992). La plaine sud est vaste (ca 1600 km²) et est entrecoupée de plusieurs vallées où les plateaux ont une altitude généralement inférieure à 350 m au-dessus du niveau de la mer. Les milieux humides représentent une faible proportion du paysage tandis que les milieux mésiques et secs (hautes-terres) couvrent environ 90% de la plaine sud (Massé et al. 2001).

Les données ont été récoltées dans une vallée (ca 50 km²), et à proximité, se situant dans la partie nord-ouest de la plaine sud. Cette vallée est un des principaux sites d'élevage des oisons pendant l'été, certaines familles marchent jusqu'à 30 km pour avoir accès à ce site. L'abondance de milieux humides dominés par les plantes graminoides (*Dupontia fisheri*, *Carex* spp. et *Eriophorum* spp.) particularise cette vallée (Hughes et al 1994). Les hautes-terres prennent la forme de collines, de fonds de vallée, de terrasses et de montagnes abruptes dont le couvert de végétation est supérieur à 95%, à l'exception des sommets et crêtes des montagnes (Chapitre 2). Les plantes vasculaires communes dans ces habitats sont *Salix arctica* et un riche assortiment de plantes latifoliées et graminoides (Zoltai et al. 1983, Chapitre 2).

Caractérisation des milieux mésiques et secs (Chapitre 2)

Treize grandes zones homogènes de végétation ont été délimitées à partir de photos aériennes et de cartes topographiques. À l'intérieur de ces zones, des parcelles de 5 m x 20 m ont été établies en fonction de la superficie de la zone (minimum de 3 par zone). En tout, 94 parcelles ont été échantillonnées à l'aide de 10 quadrats aléatoires (0,5 m x 0,5 m). Le couvert total des espèces de plantes vasculaires, de mousses, de lichens et de croûte cryptogamique était évalué. Les fèces de tous les herbivores étaient dénombrés. Pour les fèces d'oies, seulement les vieilles étaient retenues (>1 an). Le broutement sur les feuilles, les inflorescences et les parties souterraines était noté (été 2000). Le broutement incluait celui des oies et des lemmings. Au niveau des variables environnementales, le couvert au sol (litière, sol nu, sable, pierres, roches), la microtopographie, l'altitude, l'exposition et l'angle de la pente étaient évalués. Les dépôts de surface ont été déterminés à partir d'une carte géologique (Klassen 1993).

Utilisation et sélection des habitats (Chapitre 3)

Au cours de l'été 2001, des décomptes journaliers ont été fait dans une aire d'étude de 14 km² contenant deux habitats humides, Étang/Lac et Prairie humide, et trois habitats mésiques, Collines à *Cassiope*, Polygones mésiques et Prairie mésique. Les deux habitats humides avaient une forte densité d'étangs pouvant servir de refuges aux oies contre les prédateurs terrestres. La composition végétale, dominée par les plantes graminoides (*D. fisheri*, *Eriophorum* spp. et *Carex* spp.), était aussi similaire entre ces deux habitats. Par contre, le couvert total de plantes graminoides était supérieur dans l'habitat Étang/Lac que dans la Prairie humide. Les Collines à *Cassiope* étaient dominées par l'éricacée *Cassiope tetragona*, les Polygones mésiques par les saules (*Salix* spp.) et les plantes graminoides, tandis que la Prairie mésique avait une plus grande abondance de plantes graminoides. Ces trois habitats mésiques avaient peu d'étangs et la Prairie humide était éloignée

des deux habitats humides pouvant servir d'habitat-refuge aux familles. L'utilisation des habitats par les familles d'oies et le comportement des couples possédant des oisons ont été noté à partir de deux caches en montagnes. La disponibilité des habitats a été mesurée directement sur des photos aériennes à l'aide d'un planimètre ou d'un curvimètre digital.

Approches analytiques

Dans le deuxième chapitre, une classification divisive de la végétation a été effectuée (Twinspan; Hill 1979) pour décrire la structure des communautés végétales. Une ordination directe (analyse canonique de correspondance; ter Braak 1995) a ensuite été appliquée afin d'identifier les variables environnementales influençant le plus la distribution des communautés. L'intensité de broutement a été déterminée grâce aux ratios de sélection, W_i , qui est le ratio entre la proportion (%) broutée et la proportion (%) disponible (Manly et al. 1993).

Dans le troisième chapitre, afin de déterminer si le patron d'utilisation des habitats changeait au cours de la journée ou au cours de la saison, les jours ont été divisés en deux grands blocs (jour : 6h-18h00, et soir : 18h-2h00), et la saison en trois périodes (début, mi- et fin). L'effet de l'habitat, de la période de l'été, du moment de la journée et du comportement sur le nombre de familles a été analysé avec un modèle linéaire généralisé (distribution de Poisson, contrastes de Type 3). La sélection de modèle s'est faite de manière hiérarchique. Pour la sélection des habitats, l'utilisation des habitats a été comparée à leur disponibilité à l'aide d'un test de chi-carré et des intervalles de confiance de Bonferroni ont ensuite été calculés (Manly et al. 1993). La sélectivité des habitats entre eux a été mesurée en utilisant un ratio de sélection, W_i , qui est le ratio entre la proportion (%) utilisée et la proportion (%) disponible (Manly et al. 1993).

Résultats

Chapitre 2: Caractérisation des milieux mésiques et secs

En tout, 81 espèces de plantes vasculaires ont été identifiées à l'intérieur des 94 parcelles échantillonnées. La majorité des espèces était des latifoliées (65%), suivi des plantes graminoides (26%), et d'une faible proportion d'arbustes (9%). Toutefois, les arbustes, particulièrement *Salix arctica* (saule arctique), dominaient en terme de couvert dans l'aire d'étude. Le premier et deuxième axe de l'analyse directe de gradient (ACC) expliquaient 61,1% de la variance de la relation entre les espèces et l'environnement. Parmi les facteurs mesurés, la pente, l'altitude, l'exposition, le couvert de litière et de sol nu, et les dépôts de surface (littoral et éolien) étaient les variables environnementales qui influençaient le plus la distribution et le couvert de la végétation.

La classification de la végétation a mené à la formation de 10 communautés végétales qui suivaient principalement un gradient d'humidité (allant de mésique à xérique) et de perturbation (allant de stable à instable). Les communautés poussant dans les milieux plus secs avaient tendance à avoir une faible abondance de mousses, de lichens, de croûte cryptogamique, de plantes graminoides et de plantes vasculaires. Ces communautés avaient également tendance à être plus perturbées. De plus, les espèces de graminées et de cypéracées typiques des milieux plus humides étaient absentes des communautés poussant dans les milieux plus secs (*e.g. Arctagrostis latifolia*, *Carex bigelowii*, *Eriophorum* spp.) alors qu'elles étaient communes en milieux mésiques.

Six communautés végétales mésiques ont été identifiées. La première communauté était une bruyère dominée par l'éricacée *Cassiope tetragona* (25%) qui poussait sur des pentes douces de collines faisant face au nord ($10 \pm 1^\circ$). Les terrasses étaient couvertes par deux types de prairies mésiques dominées par les plantes graminoides (17 à 20%; *A. latifolia* et *Luzula* spp.). Les trois dernières communautés étaient toutes dominées par les arbustes, principalement le saule arctique (*Salix arctica*; 10 à 26%). Deux d'entre elles, la toundra *Salix*-graminoïde-latifoliée et *Salix*-graminoïde avaient aussi un couvert élevé de *Salix reticulata* (9%). La toundra *Salix*-graminoïde-latifoliée se distinguait par son abondance de légumineuse *Oxytropis maydelliana* (5%), de *Dryas integrifolia* (4%) et de latifoliées (9%), et poussait sur des pentes modérées ($14 \pm 1^\circ$) en montagnes ou sur des collines. Pour sa part, la toundra *Salix*-graminoïde poussait strictement sur des dépôts éoliens, en terrain plat, dans le fond de la vallée. Finalement, la toundra *Salix*-cryptogame avait un couvert élevé de croûte cryptogamique (13%) et de sol nu (11%), et ne se retrouvait qu'à des hautes élevées (225 ± 22 m) sur les versants ouest des montagnes longeant la mer.

Deux communautés végétales mésiques-xériques ont aussi été caractérisées en montagnes. La toundra *Salix*-légume-graminoïde et *Salix*-mousse-légume avaient un couvert très élevé de plantes vasculaires, particulièrement de saule arctique (41 à 76%) et de légumineuses (7 à 24%) contribuant ainsi au couvert élevé de litière (21 à 82%). La toundra *Salix*-mousse-légume avait un couvert élevé de cryptogames (54%) contrairement à la toundra *Salix*-légume-graminoïde qui en avait pratiquement pas (<2%). Ces deux communautés étaient typiques des pentes abruptes mais stables (22 - 23°) à de hautes altitudes (jusqu'à 400 m). Ces pentes faisaient face au sud, à l'ouest ou à l'est.

Finalement, deux communautés végétales xériques ont aussi été identifiées. Ces deux communautés avaient un couvert clairsemé: 1) de latifoliées et de saule arctique ou 2) de plantes graminoides. Ces communautés se distinguaient des précédentes par leur couvert élevé de sol nu (25 à 88%) et leur faible abondance de plantes vasculaires ($\leq 18\%$), de cryptogames ($\leq 2\%$) et de litière ($\leq 2\%$). La communauté caractérisée par les latifoliées et le saule arctique poussait sur les versants de montagnes abruptes et instables ($30 \pm 2^\circ$) à des altitudes intermédiaires (188 ± 33 m) tandis que celle caractérisée par les plantes graminoides poussait sur la plage couvert de sable (dépôt littoral).

Nous avons compté des fèces d'oies dans toutes les parcelles échantillonnées sauf une dans la communauté xérique de plage. Les lemmings utilisaient aussi la plupart des communautés, par contre, aucune fèces n'a été comptée dans les deux communautés xériques. Les oies avaient tendance à utiliser davantage les communautés dominées par les plantes graminoides ($2,7 \pm 0,6$ fèces m^{-2}) et à moins utiliser celles en montagnes (< 1 fèces m^{-2}). Parmi les communautés utilisées par les lemmings, aucune différence d'utilisation n'a été notée. Les lièvres et les lagopèdes utilisaient davantage les communautés en montagnes et peu de fèces de caribou ont été comptées dans l'aire d'étude.

À l'été 2000, 60% des taxa dans l'ensemble des milieux mésiques et secs échantillonnés avaient été broutés, dont 40% fréquemment. Parmi les taxa disponibles, 41% étaient broutées pour leurs feuilles et 71% pour leurs inflorescences. Les latifoliées et les plantes graminoides étaient sous une forte pression de broutement et leurs inflorescences étaient fréquemment broutées de manière

sélective. Au printemps et à l'automne, *O. maydelliana* et *Polygonum viviparum* étaient aussi fréquemment broutés pour leurs rhizomes et leurs bulbes respectivement.

Chapitre 3: Utilisation et sélection des habitats

L'habitat, la période de l'été, le moment de la journée, le comportement et certaines de leurs interactions influençaient le nombre de familles d'oies. À l'été 2001, une faible proportion des familles ont utilisé les habitats mésiques (14% des observations). En effet, la majorité des familles utilisaient intensivement les deux habitats humides, particulièrement l'habitat Étang/Lac. Par contre, la sélectivité de l'habitat Étang/Lac avait tendance à diminuer à la fin de la saison. Inversement, l'utilisation et la sélectivité de la Prairie humide a augmenté au cours de la saison ainsi que dans deux habitats mésiques, les Collines à *Cassiope* et les Polygones mésiques. L'effet du moment de la journée sur l'utilisation des habitats était faible en début et à la mi-saison. Par contre, à la fin de la saison, les différences étaient plus fortes. Plus de familles utilisaient la Prairie humide le soir comparativement au jour et les habitats mésiques n'étaient pratiquement pas utilisés le soir. Enfin, le soir à la fin de la saison, les familles avaient tendances à s'alimenter et à marcher davantage et à moins se reposer comparativement aux deux premières périodes de l'été.

Discussion

La région de la vallée étudiée est une oasis en terme de couvert total de végétation, de diversité de communautés végétales et de richesse spécifique. En fait, tout la plaine sud de l'île Bylot est une oasis polaire qui accueille une grande diversité d'oiseaux et de mammifère (Zoltai et al. 1983, Lepage et al. 1998). Combiné aux espèces vasculaires des milieux humides, la région de la vallée étudiée contient au moins 100 espèces ce qui est comparable aux autres oasis polaires de l'Arctique. Les communautés de l'île Bylot étaient semblables à celles décrites dans les oasis polaires du Sud de l'Archipel de la Reine Élisabeth (île Devon, Muc et Bliss 1977 ; île de Bathurst, Sheard and Geale 1983).

Caractérisation des milieux mésiques et secs

La topographie affecte la disponibilité en eau et le régime de perturbation (Webber 1978, Thompson 1980, Washburn 1980, Miller et Alpert 1984). L'hétérogénéité topographique du paysage explique donc en parti la grande diversité de communautés dans les hautes-terres à l'île Bylot. Même si la disponibilité en eau des sols n'a pas été mesurée dans notre étude, la pente est très représentative des conditions de drainage, et nos résultats reflètent un gradient d'humidité. Du fond de la vallée vers les pentes abruptes des montagnes, nous avons observé une diminution dans le couvert total de cryptogames associé avec une augmentation de la valeur de la pente. Cette relation entre le couvert de cryptogames et l'humidité du sol a fréquemment été observée dans l'Arctique (Vitt et Pakarinen 1977, Bliss et Svoboda 1984, Bliss et al. 1984, Miller et Alpert 1984). En général, le couvert des plantes vasculaires répondait aussi à l'humidité du sol, leur couvert diminuait des sites mésiques à xériques, particulièrement celui des espèces typiques des milieux humides qui étaient absentes des sites à forte pente.

L'exposition de la pente est un autre facteur qui influençait la distribution de la végétation dans notre aire d'étude. Les communautés végétales mésiques-xériques avaient le couvert total de plantes vasculaires le plus élevé. Poussant sur des versants sud, ouest et est des montagnes, ces

communautés recevaient de plus fortes radiations solaires. L'exposition de ces sites au soleil réchauffe la température de l'air et du sol ce qui favorise la croissance de la végétation (Reznicek et Svoboda 1982, Muc et al. 1994b). De plus, en étant déneigés tôt au printemps, ces sites ont une plus grande saison de croissance. Le contenu en nutriment des sols pourrait aussi contribuer au couvert élevé de la végétation.

L'exposition aux vents dominants a aussi un impact sur la végétation (Reznicek et Svoboda 1982). Dans notre étude, les toundras *Salix*-graminoïde-latifoliée et *Salix*-cryptogame poussaient à de plus hautes altitudes et étaient exposées aux vents dominants. Elles avaient un couvert plus élevé de *D. integrifolia* qui est un arbuste bien adapté aux conditions environnementales difficiles (Reznicek et Svoboda 1982, Bliss 1997). De plus, la forte abondance de *Salix arctica* (saule arctique) et de latifoliées comme *Saxifraga oppositifolia*, ainsi que la présence de figures périglaciaires dans la toundra *Salix*-cryptogame témoignent des conditions environnementales rigoureuses sur ce site.

Plusieurs études ont démontré l'importance des caractéristiques du sol dans la distribution des communautés végétales dans l'Arctique (e.g. Bergeron et Svoboda 1989, Batten et Svoboda 1994, Muc et al. 1994a). Dans notre étude, les dépôts éoliens et littoraux affectaient le drainage des sols qui influençait à son tour la distribution des communautés végétales (Zoltai et al. 1983, Klassen 1993). De plus, l'instabilité du sol dans les deux communautés végétales xériques expliquerait en partie leur faible couvert végétal.

Utilisation par les herbivores

Les oies avaient tendance à utiliser davantage les habitats plats dominés par les plantes graminoides, type de plantes préférées des oies. Les communautés en montagnes semblaient moins utilisées. Par contre, celles-ci sont très utilisées par les oies au printemps où elles se nourrissent entre autres des rhizomes et des bulbes de certaines plantes (Gauthier 1993). Le nombre de fèces a possiblement été sous-estimé dans ces communautés à cause du couvert élevé de végétation et de litière.

Au moment de l'échantillonnage, à l'été 2000, les densités de lemmings étaient élevées, et il semblerait que les deux espèces de lemmings utilisent les milieux mésiques, particulièrement les années de fortes densités (Pitelka 1973, Krebs 1964, Batzli et Jung 1980, G. Gauthier, données non-publiées). L'absence de refuges, comme les 'hummocks', ou l'impossibilité de creuser à cause de l'instabilité du sol expliqueraient l'absence des lemmings dans les deux communautés végétales xériques.

Les fèces de lièvres arctiques et de lagopèdes étaient plus fréquentes dans les habitats plus secs et à de plus hautes altitudes, où leur nourriture préférée (saules et latifoliées) était abondante et disponible durant toute la saison (Parker 1977, Smith et Wang 1977, Williams et al. 1980, Klein et Bay 1991, Larter 1999).

Broutement

Nous connaissons peu de choses à propos de l'alimentation des oies dans les hautes-terres. Plusieurs études, dont une à l'île Bylot, rapportent tout de même la présence de latifoliées, de graines, de racines ou de rhizomes dans la diète des oies, incluant certaines espèces typiques de milieux plus secs (e.g. Prevett et al. 1979, 1985, Sedinger et Raveling 1984, Bazely et Jefferies

1986, Madsen et Mortensen 1987, Gauthier 1993). De plus, contrairement aux lemmings, les oies peuvent manger une grande variété de plantes ainsi que différentes parties de celles-ci.

La diète des lemmings bruns est dominée par les plantes graminoides tandis que celle des lemmings variables est composée d'arbustes, comme le saule ou *Dryas*, et de quelques latifoliées (Batzli et Jung 1980, Batzli et Pitelka 1983, Rodgers et Lewis 1986). Leur diète estivale est composé de peu de genres, entre 2 et 5, et principalement de tiges et de feuilles. Les parties souterraines et les inflorescences ne se seraient donc pas une composante importante de leur diète (Batzli et Jung 1980, Batzli et Pitelka 1983, Rodgers et Lewis 1986) et seraient principalement consommés par les oies. Pour leur part, les latifoliées auraient été broutées à la fois par les oies et les lemmings variables.

Certaines espèces de latifoliées sont très nutritives et faciles à digérer, et peuvent être préférées par plusieurs herbivores dont les oies (White et Trudell 1980a, Williams et al. 1980, Sedinger et Raveling 1984, Rodgers et Lewis 1985, Larter 1999). Pour leur part, les fleurs, les graines, les fruits et les parties souterraines sont hautement digestibles et ont un contenu élevé en azote, lipides et hydrates de carbones (Thomas et Pevett 1980, White et Trudell 1980b, Sedinger et Raveling 1984, Klein 1990). Cette abondance de nourriture de bonne qualité tout au cours de la saison expliquerait le broutement sélectif de plusieurs latifoliées ainsi que de leurs inflorescences. La sélection des fruits, graines et des parties souterraines par les oies à la fin de l'été serait possiblement en réponse au besoin d'accumuler des graisses pour la migration automnale (Pevett et al. 1979, Sedinger et Raveling 1984).

Utilisation et sélection des habitats

La forte utilisation et sélectivité des milieux humides, particulièrement de l'habitat Étang/Lac, s'expliqueraient par l'abondance de plantes graminoides et la densité élevée d'étangs et lacs. Après l'éclosion, les parents et les oisons recherchent de la nourriture de haute qualité et en grande disponibilité pour s'alimenter. De plus, les jeunes oisons et les parents en mus sont vulnérables aux prédateurs terrestres, d'où l'importance des étangs et des lacs qui servent de refuge aux oies (Prop et al. 1984, Madsen et Mortensen 1987, Laing et Raveling 1993).

Plus les oisons sont gros, plus leur dépendance face aux refuges diminue. Ainsi, au cours de la saison, les familles sont plus mobiles et peuvent se permettre d'exploiter d'autres habitats (Prop et al. 1980, Reed et al. 1992, Hughes et al. 1994). Ceci expliquerait l'augmentation de l'utilisation et de la sélectivité des Prairies humides au cours de la saison. La présence d'étangs, la proximité d'une grande rivière et la disponibilité élevée de plantes graminoides auraient pu attirer les familles d'oies dans cet habitat. La diminution de la disponibilité de nourriture, comme de l'espèce préférée *Eriophorum* spp., dans l'habitat Étang/Lac pourrait aussi expliquer l'augmentation de l'utilisation des Prairies humides à la fin de la saison. *Eriophorum* spp. est préférée par les oies à cause de son contenu élevé en protéines et en fibres (Manseau et Gauthier 1993, Gauthier et al. 1995).

À la fin de la saison, de plus en plus de familles utilisaient les milieux mésiques où elles se nourrissaient dans les collines à *Cassiope* et les Polygones mésiques. L'augmentation de l'utilisation de ces deux habitats pourrait être lié à la consommation de graines, de fruits et de parties souterraines riches en azote, hydrates de carbones et lipides (Thomas et Pevett 1980,

White et Trudell 1980b, Sedinger et Raveling 1984, Klein 1990). Ceci reflèterait un changement dans leurs besoins énergétiques afin d'accumuler des graisses pour la migration automnale (Prevett et al. 1979, Sedinger et Raveling 1984). La présence d'espèces nutritives comme *Equisetum* spp. aurait pu aussi attirer les familles vers les hautes-terres (Gardarsson et Sigurdsson 1972, Prevett et al. 1979, Brackney et Hupp 1993). Finalement, le déclin saisonnier de la qualité des plantes graminoides dans les milieux humides pourrait aussi expliquer le mouvement des oies vers les milieux mésiques.

Toutefois, la dispersion des familles vers d'autres habitats semblait être restreinte par la proximité de refuges. À l'été 2001, la pression de prédation sur les oies par les renards arctiques (*Alopex lagopus*) était possiblement élevée puisque l'abondance de lemmings était faible (G. Gauthier, données non-publiées). Cette forte pression de prédation pourrait expliquer la faible utilisation de la Prairie mésique malgré l'abondance de plantes graminoides, ainsi que des milieux mésiques en général. La diminution de l'intensité lumineuse le soir en août augmenterait la vulnérabilité des familles à la prédation (Hughes et al. 1994) et expliquerait ainsi la faible utilisation des milieux mésiques le soir à la fin de la saison. De plus, exceptionnellement, nous avons observé des attaques de loup sur les familles d'oies dans notre aire d'étude en août.

Le soir, à la fin de la saison, les familles étaient plus actives, passant davantage de temps à s'alimenter et à marcher. Ces comportements pourraient être liés aux besoins des oies d'accumuler des graisses pour la migration automnale ou à l'augmentation du gésier et de la taille corporelle des oisons (Lesage and Gauthier 1997). Toutefois, ces comportements pourraient aussi refléter la diminution de la disponibilité de nourriture dans les milieux humides (Sedinger et Raveling 1988, Percival et Evans 1997, Hupp et Robertson 1998).

Conclusion générale

À l'île Bylot, le broutement des oies a un impact sur la végétation des milieux humides (Gauthier et al. 1995, Beaulieu et al. 1996, Gauthier et al. 1996). Puisque le sur-broutement peut conduire à la destruction des habitats de nidification dans l'Arctique (Kerbes et al. 1990, Iacobelli et Jefferies 1991, Srivastava et Jefferies 1996, Kotanen et Jefferies 1997), il devenait crucial d'évaluer l'impact que les oies ont sur leur environnement. Une des premières étapes fut de déterminer la capacité de support des milieux humides de la plaine sud de l'île Bylot (Massé et al. 2001). L'étape suivante sera d'intégrer les hautes-terres dans cette évaluation. Toutefois, il est d'abord essentiel de caractériser ces milieux et d'identifier les facteurs limitant ou incitant leur utilisation par les oies.

Les milieux mésiques et secs, ou les hautes-terres, étaient diversifiés en terme d'espèces vasculaires et de communautés végétales. Cette diversité était liée à l'hétérogénéité topographique du paysage et aux caractéristiques des sols qui influencent la disponibilité en eau. Le couvert de végétation était généralement très abondant (>95%) sur l'ensemble de l'aire d'étude (90% du paysage), et ceci est représentatif de l'ensemble de la plaine sud de l'île Bylot. Tous ces facteurs font donc de l'île une oasis polaire. Cette diversité d'habitats et l'abondance de végétation alimentent plusieurs espèces d'herbivores dont les oies, les lemmings, les lièvres arctiques, les lagopèdes et les caribous, ainsi que plusieurs espèces de sauvagines. L'utilisation des milieux mésiques par les familles d'oies semble être limitée par le risque de prédation. Toutefois, leur utilisation augmente au cours de la saison et serait liée à la grande disponibilité de fleurs, de graines, de fruits et de parties souterraines riches en azote, lipides et hydrates de carbone.

Étonnamment, nous avons compté des fèces d'oies dans toutes les parcelles échantillonnées, sauf une, ce qui suggère que les oies utilisent une grande variété d'habitats au cours de leur séjour sur l'île, l'intensité d'utilisation varie cependant d'une communauté à l'autre. Les lemmings semblent aussi utiliser plusieurs communautés végétales, du moins lors des années de forte densité. Notre étude a aussi démontré qu'une grande variété de plantes dans les hautes-terres était broutée, et que certaines étaient consommées de manière sélective, particulièrement leurs inflorescences. Ainsi, les années de forte abondance d'oies et de lemmings, le broutement de ces deux herbivores pourrait avoir un impact sur plusieurs communautés végétales. De plus, la compétition pour les ressources végétales entre ces herbivores pourrait augmenter au cours de telles années, particulièrement si la population d'oies continue à augmenter.

Certaines études démontrent en effet que le broutement aurait un impact négatif sur les dicotylédones. Par contre, peu d'études portent sur la tolérance des plantes des milieux mésiques et secs à différents types ou intensité de broutement. Comme la population de la Grande Oie des neiges augmente à l'île Bylot, l'utilisation des hautes-terres par les oies pourrait rapidement augmenter. Par conséquent, l'impact du broutement des oies et des lemmings sur la structure des communautés pourrait être accentué, surtout les années de forte densité de lemmings. L'établissement d'exclos permanents dans les milieux mésiques à l'été 2001, dans le cadre d'un nouveau projet de recherche, permettra de mieux comprendre l'effet de ces herbivores sur leurs habitats, et d'amener possiblement des éléments de réponse face à la tolérance de ces plantes à la défoliation.

À partir de la littérature, nous déduisons que les inflorescences et les parties souterraines sont principalement broutées par les oies, et non par les lemmings. Toutefois, l'utilisation accrue des milieux plus secs par les oies pour leur alimentation n'est pas abondamment documentée. De plus, seules quelques études décrivent la diète des lemmings à l'espèce, les autres se limitant seulement aux grands groupes de végétation (*i.e.* arbustes, latifoliées, plantes graminoides). Finalement, on connaît peu l'utilisation des milieux mésiques par les lemmings bruns et les lemmings variables.

Afin de mieux déterminer l'impact de chacun de ces herbivores sur la dynamique des communautés végétales, il est crucial de déterminer la diète, de manière plus spécifique, de tous ces herbivores dans les milieux mésiques et d'approfondir l'utilisation de ces milieux par les deux espèces de lemmings. De plus, l'intégration de l'échelle temporelle dans la variation de la diète et de l'utilisation des habitats me semble essentielle pour mieux comprendre cet écosystème.

Grâce à l'analyse du broutement et de l'utilisation des habitats par les oies, il semble que l'utilisation des milieux mésiques à la fin de la saison soit influencée en partie par la qualité des plantes et de leurs différentes structures. Par contre, la plupart des études portant sur la qualité nutritive des plantes fourragères portent habituellement sur les plantes poussant en milieux humides (*e.g.* Cargill et Jefferies 1984, Sedinger et Raveling 1984, Manseau et Gauthier 1993) ou se limitent seulement aux feuilles. Il serait donc important de déterminer la qualité nutritive saisonnière des espèces et des structures végétales intensément ou fréquemment broutées puisque certaines jouent un rôle important dans l'accumulation des graisses chez les oies en préparation pour la migration automnale.

Puisque les oies utilisent de manière plus intensive les hautes-terres à la fin de la saison malgré leur vulnérabilité à la prédation, ceci suggère que la consommation de certaines plantes dans ces milieux est importante à ce moment de leur cycle vital et que ces milieux jouent un rôle dans l'alimentation des oies. Les années de forte densité d'oies, où la disponibilité de nourriture diminuerait rapidement dans les milieux humides, les milieux mésiques pourraient être particulièrement importants pour l'accumulation des graisses en vu de la migration.

En conclusion, ce travail a permis, d'une part, d'identifier les communautés végétales qui poussaient dans les milieux mésiques et secs et d'en déterminer leur utilisation par les principaux herbivores de l'île et d'autre part, de mieux comprendre l'utilisation d'habitats inhabituels pour l'alimentation des oies. Il met en évidence la nécessité de caractériser les communautés végétales en tenant compte des différents utilisateurs et souligne les différents facteurs limitant et incitant les oies à utiliser des milieux plus secs. Il ouvre la voie à des études futures qui pourront évaluer plus en détail la diète des différents herbivores et l'utilisation des habitats par ceux-ci. Ce mémoire servira de point de départ à l'évaluation de la capacité de support des habitats mésiques et de l'impact du broutement par les oies et les lemmings sur ces habitats.

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Chapitre II

**Upland plant communities on Bylot Island, Nunavut:
characterisation and use by geese and lemmings**

RÉSUMÉ

À l'île Bylot, Nunavut (Canada), les familles de la Grande Oie des neiges (*Chen caerulescens atlantica*) utilisent préférentiellement les milieux humides pour s'alimenter. Par contre, entre 1983 et 1993, la densité de familles a augmenté de plus de 10 fois dans les milieux mésiques et secs qui couvrent environ 90% de la plaine sud de l'île Bylot. Comme la densité de lemmings (*Lemmus sibiricus*, *Dicrostonyx groenlandicus*) peut aussi être très élevée dans ces milieux certaines années, ces rongeurs et les oies pourraient avoir un impact sur la structure des communautés végétales. Le lièvre arctique (*Lepus arcticus*), le lagopède des roches (*Lagopus mutus*) et le caribou (*Rangifer tarandus*) utilisent aussi les milieux mésiques et secs pour s'alimenter mais leur densité est moins élevée comparativement aux oies et aux lemmings. Afin d'évaluer l'impact des oies et des lemmings sur les milieux mésiques et secs, il était essentiel de caractériser les communautés végétales et d'en déterminer leur utilisation par les cinq principaux herbivores de l'île. Pour chaque espèce vasculaire, nous avons évalué la fréquence et l'intensité de broutement sur différentes parties comme les feuilles, les inflorescences et les parties souterraines.

Quatre-vingt-une (81) espèces vasculaires ont été identifiées dans l'aire d'étude. Suite à la classification de la végétation, dix communautés végétales ont été retenues. Leur couvert total de végétation était élevé (>95%), à l'exception de deux communautés végétales xériques, et *Salix arctica* dominait ou co-dominait dans toutes les communautés. Les communautés végétales poussant dans les milieux plus secs avaient tendances à avoir une abondance plus faible de plantes graminoides, de mousses, de lichens et de croûte cryptogamique. La diversité de communautés végétales était lié à l'hétérogénéité topographique du paysage et reflète un gradient d'humidité et de perturbation. D'après une analyse directe de gradient, la pente, l'altitude, l'exposition, le couvert de litière et de sol nu, et les dépôts de surface (littoral et éolien) influençaient le plus la distribution et le couvert de la végétation. Par son couvert total de végétation, sa diversité de communautés végétales et sa richesse spécifique, l'île Bylot est considérée comme étant une oasis polaire.

Les oies et les lemmings utilisaient la majorité des communautés végétales. Les oies avaient tendance à utiliser davantage les communautés dominées par les plantes graminoides ($2,7 \pm 0,6$ fèces m^{-2}) et à moins utiliser celles en montagnes (<1 fèces m^{-2}). Aucune fèces de lemmings n'a été comptée dans les deux communautés végétales xériques et parmi celles utilisées par les lemmings, aucune différence d'utilisation n'a été détectée. Les lièvres et les lagopèdes utilisaient davantage les communautés en montagnes et peu de fèces de caribou ont été comptées dans l'aire d'étude. Les latifoliées et les plantes graminoides étaient sous une forte pression de broutement, particulièrement pour leurs inflorescences. Au printemps et à l'automne, *Oxytropis maydelliana* et *Polygonum viviparum* étaient aussi fréquemment broutés pour leur rhizome et leur bulbe respectivement. Étant donné les caractéristiques des principaux herbivores, les oies seraient responsables du broutement des inflorescences et des parties souterraines des plantes et ceci serait lié à leur qualité nutritive.

ABSTRACT

On Bylot Island (73°N, Nunavut, Canada), wetlands are intensively used by Greater Snow Goose families (*Chen caerulescens atlantica*). However, density of families has increased more than 10 times in upland habitats, which cover 90% of the south plain of Bylot Island. Since lemmings (*Lemmus sibiricus*, *Dicrostonyx groenlandicus*) can also reach high densities in these habitats, both lemmings and geese can potentially impact plant community structure. As a first step towards the evaluation of the impact of geese and lemmings on upland habitats, we characterised dominant plant communities, determined their use by the five main herbivores and evaluated species specific foraging intensity on different plant structures. Excluding wetland communities, classification analysis of 85 taxa led to ten distinct upland plant communities. Bylot Island is a polar oasis, the vegetation cover being >95%, except in two xeric plant communities, and *Salix arctica* dominated or co-dominated in all communities. Diversity of plant communities was linked to the heterogeneous topography and reflected moisture and disturbance gradients. According to a direct gradient analysis, slope, altitude, exposition, cover of litter and bare ground, and surficial deposits influenced most the distribution and cover of vegetation. Geese and lemmings used most of the communities while arctic hares and ptarmigans fed mostly in mountainous areas. Caribou faeces were seldom seen in our study area. In these communities, forbs and graminoids were under a high grazing pressure, particularly for their inflorescences. Grubbing was frequent in spring and fall on *Oxytropis maydelliana* and *Polygonum viviparum*. Foraging on inflorescences and below-ground parts was most likely done by geese and can be linked to their high nutritive quality.

Key words: Arctic, uplands, plant communities, ordination, classification, herbivores, foraging, polar oasis.

INTRODUCTION

Herbivory can significantly affect plant community dynamics by changing vegetation composition (Batzli et al. 1980, McKendrick et al. 1980, Bazely and Jefferies 1986, Hik et al. 1992, Moen et al. 1993), plant productivity (Cargill and Jefferies 1984, Bazely and Jefferies 1985, Pastor et al. 1993, Ford and Grace 1998) and competition among species (Louda et al. 1990, Oksanen and Moen 1994, Mulder and Ruess 1998a, Virtanen 1998). Plant community composition, the type and intensity of herbivory, and intrinsic plant ability to regrow after damage will determine impacts of herbivory on the plant community (Archer and Tieszen 1980, Chapin 1980, Mulder and Ruess 1998a, Iacobelli and Jefferies 1991). Occasionally a rapid increase in herbivore population can lead to the destruction of vegetation at the landscape level (Klein 1968, Kerbes et al. 1990, Manseau et al. 1996, Jano et al. 1998).

On Bylot Island, the Greater Snow Goose population (*Chen caerulescens atlantica*), representing 15% of the breeding population (Reed et al. 1992), tripled between 1983 and 1993 (Reed et al. 1998). These authors estimated that the population, including non-breeders and goslings, reached 156 000 birds in 1993. Goose families use wetlands intensively for feeding during brood-rearing (Hughes et al. 1994), where they consume between 30% and 100% of the net above-ground primary production of the dominant graminoid species, *Dupontia fisheri* and *Eriophorum* spp (Gauthier et al. 1995). Goose grazing may thus affect vegetation in wetland areas. A long-term study using goose exclosures for 5 consecutive years, showed that goose grazing modified species composition and decreased plant density and plant production. These results suggest that chronic grazing may lead to a low-level production equilibrium between geese and plants (Gauthier et al. 1996). Those impacts could be partly linked to a decrease in accumulation of soluble carbohydrate in *Dupontia* and *Eriophorum*'s rhizomes during the summer (Beaulieu et al. 1996).

Geese feeding in dryer habitats, which are dominant on higher grounds (referred to as upland habitats), have been reported for Lesser Snow Geese (*C. caerulescens caerulescens*) at La Pérouse Bay, and this was linked to reduced availability of preferred salt-marsh species following rapid population growth (Gadallah and Jefferies 1995). Newly used communities are dominated by willows (*Salix* spp.), *Calamagrostis deschampsoides* and *Festuca rubra* swards growing in proximity of tidal flats. At Bylot Island, the density of goose families has increased more than 10

times in upland habitats between 1983 and 1993 (Reed et al. 1998). It is not clear if this increase represents a shift in habitat use related to decreasing food availability in wetlands (Reed and Plante 1997) or simply a parallel increase of goose densities over all habitats.

Two species of lemmings are also important herbivores at Bylot Island: brown lemmings (*Lemmus sibiricus*), which occur in wet habitats, and collared lemmings (*Dicrostonyx groenlandicus*), which use preferentially upland habitats (Gauthier et al. 1996). Lemming populations are cyclical, typically reaching high density every 3 - 4 years on Bylot Island (Bêty et al. 2002). Other herbivores, such as rock ptarmigan (*Lagopus mutus*), arctic hare (*Lepus arcticus*) and caribou (*Rangifer tarandus*) are present at low density on the island (Zoltai et al. 1983).

Increasing numbers of geese in upland habitats may have resulted in increased grazing pressure. Lemmings can also reach high densities in some years, and thus both groups can potentially impact plant community structure. However, despite their importance in the landscape (90% of Bylot Island's south plain; Massé et al. 2001), little is known about upland habitats. Thus, in order to properly evaluate the impact of herbivores on upland habitats, it is essential to characterise the dominant plant communities and to evaluate factors such as foraging intensity and selectivity on different species and plant parts grazed. Our specific objectives were to 1) characterise and map upland plant communities in an area used by goose families and lemmings on Bylot Island; 2) identify environmental parameters influencing the distribution of these communities at the landscape level; 3) identify plant communities used by the main herbivores of the island; 4) identify plant species and plant parts that were grazed by geese and lemmings and evaluate the grazing intensity.

METHODS

Study area

The study was conducted in the northwest part of Bylot Island's south plain, Nunavut Territory, Canada (73°08'N, 80° 00'W). Lowlands and upland plateaus (generally below 350 m above sea level) intersected by numerous valleys characterised the south plain. Uplands cover approximately 90% of the landscape (Massé et al. 2001). Poorly consolidated sedimentary rock such as

sandstone, mudstone and coal form the bedrock whereas the main deposits are glacial, glaciofluvial and marine in origin (Zoltai et al. 1983, Klassen 1993).

The valley studied and its immediate surroundings are one of the most important brood-rearing area for Greater Snow Geese on the island (Reed et al. 1992). Uplands are characterised by rolling hills, valley bottom, terraces and steep hills covered by mesic plant communities (vegetation cover >95%), except for mountain tops and ridges (this chapter). Common plants of these habitats include dwarf shrubs (*Salix* spp., *Dryas integrifolia*, *Cassiope tetragona*) and a rich assortment of forbs (*Saxifraga* spp., *Potentilla* spp., *Ranunculus* spp., *Pedicularis* spp.) and graminoids (*Arctagrostis latifolia*, *Alopecurus alpinus*, *Poa* spp., *Luzula* spp.; Zoltai et al. 1983). Though less preferred by geese, uplands are used periodically and may contribute to the Island total carrying capacity. At snow melt, geese feed in mountains and in snow free patches for specific species such as legumes and *Polygonum viviparum* (Gauthier 1993). Later in the brood-rearing period, geese graze on seeds, fruits and below-ground structures in upland habitats (this study, Chapter 3). Uplands are also used at low densities throughout the brood-rearing period (Hughes et al. 1994). Surficial deposits and bedrock of the study area are illustrated in Figure 1.

Plant community characterisation

Prior to sampling, we mapped homogenous vegetation zones in uplands using black and white aerial photographs (1:13 000 approx.) and topographic maps (1:50 000). To be considered homogenous, a vegetation zone had to have a uniform grain on the photo on a surface > 1 km². In the field, studied areas were surveyed by foot or helicopter to validate each vegetation zone. Some of the zones were subdivided or grouped together based on the visual estimate of their vegetation composition. Thirteen vegetation zones were identified, covering a territory of 70 km² (Figure 1). Sampling was carried out in summer 2000 and 2001.

Three plots (minimum) of 5 x 20 m size were established in an homogeneous and representative portion of the zone. All measured variables at the plot or quadrat level are summarized in Table 1. Microtopography, altitude (m a.s.l.), slope angle (°) and exposition (°) were evaluated for each plot. The frequency of occurrence of rocks (diameter >25 cm) was evaluated in the vicinity of the plot on a scale from 1 (non rocky) to 6 (excessively rocky). Surficial materials were determined based on the map of Klassen (1993). Vegetation inside each plot was quantified within 10 random

quadrats (50 x 50 cm). Cover (%) of each vascular plant species, total cover of mosses, lichens, cryptogamic crust (mix of lichen and algae fixing air nitrogen), litter and bare ground were visually estimated using cover classes: 1% for the lower cover classes (0-5%), 5% for the mid cover classes (5-30%) and 10% classes above 30%. Mean cover per plot was calculated using mid class values for each quadrat. Total cover may exceed 100% since more than one strata of vegetation was present. Occurrence of stones (<25 cm) and rocks (>25 cm; included stone slabs) were also noted. A complete list of vascular plant species was established for the 20 m x 5 m plot. Taxonomic names follow the nomenclature of Porsild (1957) and Porsild and Cody (1980).

Herbivore use and grazed species

To estimate habitat use by geese, we surveyed old goose faeces in two transects (1 x 10 m each), one inside the plot and the other outside but near the plot. Only old goose faeces, excluding <1 year old faeces, were counted because their number did not vary over the course of the season. Lemming faeces, which could not be classified as fresh or old, were estimated in each quadrat using an abundance index (logarithmic scale: 1-10; 10-100; 100-1000 faeces). Occurrence of winter nests of lemmings were also noted as well as occurrence of arctic hare, caribou and rock ptarmigan faeces in plots. In summer 2000, the number of grazed leaves, and grazed and ungrazed inflorescences were noted for each species in sampled quadrats. The term inflorescence includes flowers, seeds and fruits. During that same summer, there was a lemming peak thus it was impossible to distinguish marks left by goose from those of lemming grazing. All plant communities were surveyed for grazing in 2000 except one, Graminoids barrens #10 surveyed in 2001, and sampling was conducted from 6 July to 15 August.

Data Analysis

Vegetation data matrix contained 94 plots and 85 taxa (mean % cover). In order to determine upland plant communities, we classified the data using a two-way indicator species analysis (Twinspan, default settings; Hill 1979, PC-ORD v4). Three species with low frequency (≤ 2 plots) were removed from the analysis (*Androsace septentrionalis*, *Melandrium triflorum*, *Erysimum pallasii*). Environmental parameters influencing plant community distribution were identified using a canonical correspondence analysis for all 85 taxa (CCA; ter Braak 1995). Considering the large number of environmental parameters (Table 1), a manual forward selection was used to

retain parameters that influenced plant community distribution (CANACO v4). To reduce the risk of making a type II error (*i.e.* falsely rejecting variables that have an important contribution), we used an α level of 0.1. Prior to analysis, some variables (Table 1) were transformed (log or square root) to minimise effects of outliers on results. Because slope exposition was directly linked to slope value, two variables were generated, EW and NS, in order to interpret exposition ecologically:

$$EW = \sin(\text{exposition}) * \sin(\text{slope})$$

$$NS = \cos(\text{exposition}) * \sin(\text{slope}).$$

EW represents east-west exposition while NS is the north-south exposition. Plots on flat terrain or on gentle slope have no particular exposition (small value of EW and NS) while plots on steep slopes have gradually higher values of EW (positive values for East, negative for West) or NS (positive values for North, negative for South).

We used an ANOVA to determine which plant communities were mostly used by geese and lemmings, based on faeces abundance. Mean values for lemming faeces were calculated from the geometric mean of the quadrats ($n=10$). Faeces data were $\log(n+1)$ transformed to meet the homogeneity of variances and normality requirements. Since sampling in 2001 complemented that of 2000 and that we counted, for geese, faeces deposited over many years (excluding < 1 year old faeces), we combined data from both years to estimate the overall use by herbivores. Also, since we were not able to distinguish fresh lemming faeces from old ones, plots surveyed late in the summer could contain more faeces due to accumulation. Thus, we tested whether day of sampling had an effect on the number of faeces counted with an ANOVA for unbalanced designs, using only five communities that were sampled throughout the summer and including year as a covariate. Species specific grazing intensity was calculated for upland habitats, without distinction among plant communities. Frequency of grazing for specific taxa was calculated using only plots where it was present. Because leaves were available throughout the summer, frequency of grazed leaves was counted using all plots, whereas for inflorescences, only plots sampled during and after the last week of July were used. In order to evaluate the intensity of utilisation of grazed species, a selection ratio W_i was calculated (Manly et al. 1993) as follows:

$$W_i = G_i / A_i.$$

Where: G_i = % of grazed leaves or inflorescences of species i ; and A_i = % of availability (cover or inflorescences count) of species i . When $W_i = 1$, species i was grazed proportionally to its availability; when $W_i < 1$, species i was sparsely grazed; and when $W_i > 1$, species i was selected or heavily grazed. Plots were only sampled once in the season. Thus, our estimate of grazing is minimal because plots that we sampled in early season could have been grazed later in the season such that frequency of grazing and selection of some species may be higher than what we evaluated.

RESULTS

Plant communities

In the 94 plots sampled, we identified a total of 81 vascular plant species, the majority being forbs (65%), followed by graminoids (26%) and shrubs (9%), although shrubs were dominant in term of cover in almost all plant communities (Table 2). In our study, *Salix arctica* (arctic willow) dominated or co-dominated all plant communities and 13 species had a low cover but were present in 90% or all communities (underlined species in Table 3).

The divisive classification analysis (Twinspan) at the fourth level of division (Figure 2) identified most of the vegetation zones mapped prior to sampling. In addition, subsequent divisions had eigenvalues inferior to 0.1. From the 12 clusters obtained, two contained only one plot. After comparing the vegetation composition using the ordination analysis (CCA) these plots were pooled with their most similar community type. Thus, we distinguished a total of 10 plant communities. For five of the vegetation zones identified from aerial photos (Figure 1), all plots belonged only to one plant community. The remainder eight zones belonged to two plant communities with one clearly dominant (Table 4).

The first division of the classification (accounting for 30% of the variance) separated mesic (#1-6) from mesic-xeric to xeric plant communities (#7-10; Figure 2). Other divisions within mesic communities were relatively weak, explaining less than 20% of the variance whereas divisions within mesic-xeric to xeric communities were stronger (>20% of the variance). Similarly, the first axis of the ordination performed on the same data separated mesic communities to the left from

dryer ones on the right (CCA; Figure 3). Axes 1 and 2 explained respectively 43.3% and 17.8% of the variance of the relation between distribution of the species and their environment (Table 5, Figure 3). Only the first and second axes were significant (Monte Carlo permutation test $p < 0.05$). Of all the environmental parameters measured, nine influenced distribution of plant communities (Figure 3). North-South exposition, slope, litter cover, altitude and bare ground had the strongest influence on axis 1 whereas bare ground, litter cover, altitude and East-West exposition influenced the distribution on axis 2. Two types of deposits (littoral and eolian) and the absence of microtopography (flat) were retained in the analysis and affected plant communities mostly on axis 2.

The number of shrub species and the cover of graminoids diminished from mesic to xeric communities (Table 2). With the exception of community #8, we also observed a decrease in total moss, lichen and cryptogamic crust cover along this gradient. In addition, none of the species characteristic of wetter habitats (*e.g. Arctagrostis latifolia, Carex bigelowii, Eriophorum* spp.) were found on mesic-xeric and xeric communities (Table 3). This reflected a decrease in moisture availability from flat habitats at low altitude (*e.g. communities #2 and #3*) to abrupt slopes in mountains (*e.g. communities # 7-9; Table 3, Figure 3*). The plant communities identified with these analyses were mapped and their relative area calculated over the study area (Figure 4).

1. Mesic plant communities

These communities can be distinguished from dryer ones by their high cover of cryptogams and by their distribution on flat terrain and gentle slopes (Table 2). Species diversity ranged from 32 to 48 species. Despite different origin of the surficial deposits, hummocks were the predominant microtopography. Mesic communities covered 79% of the study area (Figure 4).

1.1 Heath tundra

Cassiope heath tundra (#1)

Moss and lichen cover was extensive (76%; Table 2) and the ericaceous species *Cassiope tetragona* was the dominant vascular plant with 25% cover (Table 3). The Heath tundra covered about 6% of the study area and was prominent at low altitude on north facing hummocky gentle slopes (Figure 4, Table 2). This community grew mostly on glacial deposit but also on

sedimentary rocks (Figures 1 and 4). Species composition of the Heath tundra was similar to the two mesic meadows (communities #2 and #3) except for the abundance of *C. tetragona* (Table 3) and its presence only on gentle slopes. Accordingly, the distribution of these three communities overlapped in the CCA (Figure 3).

1.2 Mesic meadows

Arctagrostis meadow (#2) and *Salix-Arctagrostis* meadow (#3)

Terraces (60-160 m a.s.l.) were covered with a mosaic of both types of mesic meadows dominated by cryptogams (77-84%) and graminoids (*A. latifolia*: 8-13%; *Luzula* spp.: 5-7%; Table 2). Compared to the *Arctagrostis* meadow, the *Salix-Arctagrostis* meadow had a higher cover of arctic willow (9% vs. 13%) and cryptogamic crust (8% vs. 14%) and a higher frequency of *Festuca brachyphylla* (13% vs. 74%) and forbs, especially *Cerastium alpinum* and *Papaver radicum* (25% vs. 78% and 25% vs. 74% respectively; Table 3). *Salix-Arctagrostis* meadow had the highest vascular species richness of all communities studied (Table 2). As for the Heath tundra, surficial deposits were glacial in both meadows and hummocks were the predominant microtopography (Figure 1 and 4). Mud-boils were also observed in 22% of the plots of *Salix-Arctagrostis* meadow. *Arctagrostis* meadow was confined to terraces whereas *Salix-Arctagrostis* meadow were more widely distributed, growing also as patches on north facing hills and in the valley bottom (Table 4). Mesic meadows were extensive in the uplands covering 53% of the area (Figure 4).

1.3 Dwarf-shrub tundra

Salix-graminoid-forb tundra (#4) and *Salix*-graminoid tundra (#5)

In these communities, the vascular cover was dominated by *Salix* spp. (19-34%; Table 3). *Salix reticulata* reached its highest abundance (cover greater than 5%; Table 3) and was an indicator species (Figure 2). Graminoid cover was relatively high (11-12%) and hummocks were dominant (Table 2). *Salix*-graminoid-forb tundra was characterised by a high abundance of the legume *Oxytropis maydelliana* (5%; Figure 2) and by a higher cover of arctic willow (25 % vs. 10%), *Dryas integrifolia* (4% vs. 1%) and forbs (9% vs. 2%) than in the *Salix*-graminoid tundra (Table 3). *Salix*-graminoid-forb tundra covered south facing hills (60-90 m a.s.l., glacial deposits) and

west facing mountains (160-200 m a.s.l., sedimentary rock) on $14 \pm 1^\circ$ slope (Table 2, Figure 4). This community was not prominent in the studied area covering only 3% (Figure 4).

Compared to the former, *Salix*-graminoid tundra was on flat terrain in the valley bottom (Table 2) and was characterised by large, more or less defined polygons with exceptionally large rims (5-30 m). This habitat included few small scattered wet patches (polygon center) dominated by graminoids typical of wetter sites (*Dupontia fisheri*, *Carex* spp.). The *Salix*-graminoid tundra covered about 10% of the terrain (Figure 4) and was strictly established on eolian deposits (Figure 1).

Salix-cryptogam tundra (#6)

Compared to the other Dwarf-shrub tundra communities (#4 and 5), this one had a lower cover of *S. reticulata* and of graminoids but a higher cover of cryptogamic crust and bare ground (Table 2 and 3). *Salix*-cryptogam tundra had also a high cover of *D. integrifolia* (4%). This tundra covered about 7% of the area of the studied uplands and was only found on west facing slopes of mountains near the sea at high altitude (Table 2, Figure 4). Stones were frequently observed in sampling plots (86%) and bare ground formed stripes and mud-boils (Table 2).

2. Mesic-Xeric plant communities

Compared to the mesic communities, mesic-xeric ones had a lower cover of cryptogams (except mosses in community #8) and was characterised by the absence of *C. tetragona* and of species from mesic to wetter habitats (e.g. *A. latifolia*, *C. bigelowii*, *Eriophorum* spp.; Table 2 and 3). High cover of vascular plants contributed to the high cover of litter (Table 2). Typical of abrupt but stable slopes at high altitude (up to 400 m a.s.l.), mesic-xeric communities occupied grounds with sedimentary rock (Table 2, Figures 1). Microtopography was heterogeneous, with the principal one being undulating, gelifluction lobes and flat (Table 2).

2.1 *Salix*-legume tundra

Salix-legume-graminoid tundra (#7) and *Salix*-moss-legume tundra (#8)

These two communities had a large cover of arctic willow (76% and 41% respectively) and legumes such as *Astragalus alpinus* (24% vs. 7%) and *O. maydelliana* (16% vs. 8%; Table 3).

Typical of south facing mountains, cryptogams were practically absent of the *Salix*-legume-graminoid tundra that also had a high cover of *Polygonum viviparum* (5%) and graminoids such as *Alopecurus alpinus* (7%) and *Poa arctica* (4%; Table 2 and 3). *Salix*-legume-graminoid tundra covered about 8% of the study area (Figure 4).

Contrary to the former, *Salix*-moss-legume tundra had a high moss cover (44%; Figure 2, Table 2), and was not restricted to one topographic zone. This community was found on west and east facing slopes of mountains and as small areas on south facing slopes of hills and mountains (Table 4). *Salix*-moss-legume tundra covered only 3% of the landscape (Figure 4).

3. Xeric communities

Distinct from other communities by the dominance of bare ground and low abundance of vascular plants, cryptogams and litter, these communities had no particular microtopography (Table 2).

3.1 Barrens

Forb-*Salix* barrens (#9)

This community grew on the steepest unstable slopes (scree slopes) on north and east facing mountains (above the *Salix*-moss-legume tundra on east slopes; Table 2, Figure 4). Vegetation cover was dominated by forbs including *Epilobium latifolium*, *Cerastium alpinum* and *Oxyria digyna* (Table 3). Stone slabs were consistently present in plots (100%; Table 2). Forb-*Salix* barrens were a relatively minor community covering about 3% of the studied uplands (Figure 4).

Graminoid barrens (#10)

This community was found only on sandy beaches which covered 7% of the area (Figure 4). Plant cover was sparse with grasses and sedges like *Alopecurus alpinus* (2%), *Luzula confusa* (2%), *Carex maritima* (1%), *F. brachyphylla* (1%) and *P. arctica* (1%), and by many forb species (Table 3). There was a very low abundance of bryophytes, lichens and crust, the dominant cover being sand (88%; Table 2).

Herbivore use

Signs of herbivore activity were common throughout the uplands. Goose faeces were present in all sampled plots except one from the Graminoid barrens (Table 6). Generally, mean density of goose faeces varied across plant communities ($F=6.16$, $df=9$, $p<0.001$) and was highest in the *Salix-Arctagrostis* meadow (2.7 ± 0.6 faeces m^{-2}) and lowest in mountainous plant communities (*Salix*-graminoid-forb, *Salix*-cryptogam, *Salix*-legume-graminoid and *Salix*-moss-legume tundra: <1 faeces m^{-2} ; Table 6).

Day of sampling did not affect lemming faeces counts ($F=1.75$, $df=1$, $p=0.191$), indicating that accumulation of faeces throughout the summer was not important in either year. As for geese, lemmings did not use all plant communities equally ($F=5.47$, $df=9$, $p<0.001$), mostly because of the absence of faeces in xeric communities (Table 6). Within plant communities used by lemmings, density of faeces was variable. Winter nests of lemmings were not frequent but were almost exclusively in mesic habitats (Table 6). Arctic hare and rock ptarmigan faeces were more common in mountains (*Salix*-cryptogam, *Salix*-legume-graminoid and *Salix*-moss-legume tundra, and Forb-*Salix* barrens; Table 6). Very few faeces of caribou were noted on the study area.

Grazing

Grazed taxa

In summer 2000, 40% of the 64 vascular taxa were frequently grazed as defined by frequency of grazing in $> 30\%$ of the plots (Table 7), 20% were sparsely to moderately grazed (2 to 30% of the plots) and 40% of the vascular taxa showed no signs of grazing (Appendix 1). However the low density of flowering shoots for some of these taxa (*e.g.* *Carex* spp. and many forbs) did not allow to assess if they were grazed or not in the sampled quadrats (*i.e.* there were no inflorescence in the quadrats; Appendix 1).

In the studied vegetation, 41% of available vascular taxa had their leaves grazed while 71% of those that produced inflorescences were grazed. Out of 17, 11 graminoid species were grazed (nine of them were frequently) compared to 22 forbs grazed (16 frequently grazed) from a total of 40 species of forbs. Five of the 7 shrubs were grazed but none of them frequently.

Selection and frequency of grazing/grubbing

In general, occurrence of grazing was higher for forbs than for the graminoids and shrubs. In addition, selection of forbs (measured with the selection ratio W_i) was higher for inflorescences than leaves, whereas it was higher for leaves than inflorescences in graminoids (Table 7). Two groups of taxa had their inflorescences grazed frequently (>32% of plots). In the first group, which frequently produced inflorescences (>40% of the plots; Table 7), there was a selection for inflorescences of *L. confusa* whereas those of *Astragalus alpinus* and *Draba* spp. were generally grazed in proportion to their availability (Table 7). In the second group, which rarely produced inflorescences (<30% of the plots; Table 7), those of *Ranunculus nivalis* were consistently selected. On the other hand, those of *Ranunculus pedatifidus*, *Saxifraga cernua*, *P. radicum*, *Eutrema edwardsii*, *Saxifraga hieracifolia*, *Melandrium* spp., and *Arnica alpina* ssp. *angustifolia* were selected in some plots as indicated by the high variance. Selection for leaves of *P. radicum*, *Melandrium* spp. and *Eriophorum triste* was also high but highly variable.

Three grasses (*A. latifolia*, *Alopecurus alpinus*, *P. arctica*), the rush *Luzula nivalis*, the legume *O. maydelliana* and the forb *P. viviparum* all had both their inflorescences and leaves frequently grazed (Table 7). Selection for these inflorescences was generally high. Leaves of the three grass species were also highly selected and those of the rush *L. nivalis* were selected in some plots only. Leaves of *Equisetum* spp., *Eriophorum scheuchzeri*, *Ranunculus sabinei*, *O. digyna* were frequently grazed (>40% of the plots; Table 7). Except for *O. digyna*, these species were not frequent in upland habitats (frequency $\leq 5\%$) and were not seen with inflorescences. However, there was a strong selection on the leaves of *Equisetum* spp. and *O. digyna*.

Only two taxa were frequently grubbed across the uplands: *O. maydelliana* and *P. viviparum* (82% and 46% of the plots respectively). We also frequently observed fresh grubbing on those two species later in the season (43% and 47% frequency). Shoot pulling was also observed on *E. triste* at the end of the season (33% frequency).

DISCUSSION

Six mesic, two mesic-xeric and two xeric plant communities were identified in an area used by goose families and lemmings on Bylot Island. *Salix arctica* (arctic willow) dominated or co-

dominated all plant communities. The vegetation in mesic and mesic-xeric communities was abundant with more than 95% total plant cover and these communities dominated the entire study area (90% of the landscape). As in many other arctic locations (*e.g.* Bathurst Island, Ellesmere Island), topography (Thompson 1980, Miller and Alpert 1984) and soil characteristics (Sheard and Geale 1983a, Bergeron and Svoboda 1989, Batten and Svoboda 1994) explained a large part of the plant community distribution in our study area. The heterogeneous topography of the landscape is associated with the diversity in plant communities in the uplands. Geese and lemmings used a wide variety of these plant communities and grazed a large proportion of the vascular plant taxa, mostly for their inflorescences. Forbs were under a particularly high grazing pressure.

Polar oasis

The studied valley and its surroundings are an oasis in terms of total plant cover, diversity of plant communities, and floristic richness. Compared to other oases in the Arctic, which are surrounded by polar deserts, the south plain of Bylot Island including the studied area is a large green landscape. Great diversity of birds and mammals (Zoltai et al. 1983, Lepage et al. 1998) take advantage of these diverse habitats. Sampled uplands were relatively rich with 81 vascular plant species. Combined to previous studies in wetland and upland habitats, the total vascular species richness of the studied valley is 100 species which is comparable with other polar oases in the Arctic (Table 8).

Legumes were absent in other oasis since this family is not present north of Lancaster sound (Porsild and Cody 1980). Tidal salt marshes dominated by *Puccinellia phryganodes*, present in Truelove Lowland and Alexandra Fiord, are uncommon on Bylot Island where sandy beaches dominated by *Alopecurus alpinus* and few sedges are characteristic of coastal communities. Mesic plant communities on Bylot Island were characterised by a high cover of bryophytes whereas in the other oasis, high cover of bryophytes were confined to wetlands. Wetlands dominated by sedges are present in all polar oasis whereas those dominated by grasses seemed to be confined to southern oasis (Bylot Island, Truelove Lowland and Polar Bear Pass; Table 8). Similarly, mesic meadows dominated by grasses were absent in northern oasis where they were mostly dominated by sedges (Bergeron 1988, Gould 1985). *Dryas* based communities were common in the northern oases (Sheard and Geale 1983b, Gould 1985, Bergeron 1988, Muc et al. 1989). This community

type was not sampled in our area but are present on the island (Zoltai et al. 1983). Finally, Bylot Island plant communities were most comparable to the southern oases at Devon and Bathurst Island.

Plant communities

Topography affects mostly moisture availability and disturbance regime (Webber 1978, Thompson 1980, Washburn 1980, Miller and Alpert 1984). Moisture strongly influences shifts in plant communities in the Arctic as shown by previous studies (e.g. Reznicek and Svoboda 1982, Sheard and Geale 1983a, Bliss et al. 1984, Bergeron and Svoboda 1989, Batten and Svoboda 1994). Although moisture was not measured directly in our study, slope is a surrogate variable indicative of drainage conditions especially in substrate with comparable texture. On the first axis of the ordination, the communities were oriented along an obvious moisture gradient (i.e. slope surrogate). From flat terrain to steeper slopes in the mountains, we observed a decrease in total cover of cryptogams associated with an increase in slope angle. The only exception was the *Salix*-moss-legume tundra, which had a high cover of mosses despite relatively steep slopes. This relation between cryptogamic cover and soil humidity had been frequently noted in the Arctic (Vitt and Pakarinen 1977, Bliss and Svoboda 1984, Bliss et al. 1984, Miller and Alpert 1984). High cover of cryptogams on flat terrain at low altitude could also be attributed to the persistence of snow cover in spring and to the supply in melt water from neighbouring slopes in early summer. High moss cover in *Salix*-moss-legume tundra was typical of slope bottom. In general, vascular plants also responded to soil moisture as their total cover decreased from mesic to xeric sites.

Exposition is another key factor influencing plant distribution in our study area. Mesic-xeric sites had the largest overall vascular plant covers due, mostly, to the abundance of arctic willow (*Salix arctica*) and legumes, contributing to the high litter cover. Their high biomass on south, east (bottom slope) and west facing slopes can partly be associated with higher air and soil temperatures (Reznicek and Svoboda 1982, Muc et al. 1994b) because of their exposition to higher solar radiations. Moreover, these habitats have a longer growth season being first to be snow free in spring because of lower snow accumulation (steep slopes) and exposition to the sun. They are also protected from dominant winds coming from the north-west which contribute to the warming of those slopes in the course of the season. Although not measured, nutrient content

could contribute to the high vegetation cover. Some species like *Poa glauca*, *Trisetum spicatum*, *Erigeron eriocephalus*, *Arnica alpina* ssp. *angustifolia* and *Potentilla nivea* were only recorded in mountain communities. These species are characteristic of drier sites but also of sunny and nutrient rich places such as bird cliffs, dens and burrows (Porsild 1957).

Altitude, independently of its correlation with slope angle, influenced the distribution of plant communities. Sites at higher altitude are exposed to dominant winds diminishing moisture availability and temperature at the soil level during the summer and damaging unprotected vegetation in winter (Reznicek and Svoboda 1982). Communities most exposed to dominant winds were two of the Dwarf-shrub tundra, *Salix*-graminoid-forb and *Salix*-cryptogam-forb tundra which both had the highest *Dryas integrifolia* cover. This shrub is well adapted to harsh environmental conditions (Reznicek and Svoboda 1982, Bliss 1997). *Salix*-cryptogam-forb tundra was probably more exposed to dominant winds than *Salix*-graminoid-forb due to its proximity to the sea and its high altitude. Abundance of arctic willow, *D. integrifolia* and forbs like *Saxifraga oppositifolia* as well as the presence of patterned grounds like stripes and mub-boils, indicate the harsh environmental conditions on this site.

Many studies showed the influence of soil characteristics on distribution of plant communities in the Arctic (Edlund 1982, Bliss and Svoboda 1984, Bergeron and Svoboda 1989, Batten and Svoboda 1994, Muc et al. 1994a). In our study, high drainage (steep slope and generally associated high active layer depth), weak soil development, and soil instability partly explained low abundance of vegetation in Forb-Salix barrens where many pioneer species grew. Similarly, high drainage and instability of the sandy soil (littoral deposits) of the Graminoid barrens could explain its low biomass. In the valley bottom, eolian deposits influencing polygonal formation was observed in *Salix*-graminoid tundra. Alternating layers of organic matter and sand contributed to the weak soil drainage favouring the formation of these polygonal structures (Zoltai et al. 1983, Klassen 1993).

Herbivore use

Geese and lemmings used a wide variety of plant communities in uplands while arctic hare, rock ptarmigan and caribou were confined to four or fewer plant communities. Geese used

predominantly flatter habitats dominated by graminoids whereas mountain slopes were used to a lesser degree. However, mean faeces density was probably under-estimated in mountain communities because of the high vegetation and litter cover. First to be snow free in spring, mountain communities are intensively used by geese at that time of the season where they graze *Alopecurus alpinus* and *Poa spp.* and grubb *Polygonum viviparum* bulbs and *Oxytropis maydelliana* rhizomes (Gauthier 1993, authors' pers. obs).

Habitat use by lemmings coincided with the distribution of their preferred foods; brown lemmings occur in wet habitats where they feed on monocotyledons and mosses whereas collared lemmings feed on dicotyledon leaves in uplands (Fuller et al. 1975, Batzli et al. 1983, Rodgers and Lewis 1986b). However, many studies have suggested that both species may occur in the same habitat. In year of great abundance brown lemmings may be commonly found in drier upland habitats (Krebs 1964, Pitelka 1973). Conversely, Batzli and Jung (1980) noted the presence of collared lemmings in wet habitats where willows were available. On Bylot Island, brown lemmings exhibit a 3-4 years cycle whereas abundance of collared lemmings varies little (Bêty et al. 2002). In years of high abundance, brown lemmings also use uplands where they can be more abundant than collared lemmings in some habitats (G. Gauthier, unpublished data). Thus, it is likely that the two species have used upland communities especially the *Salix*-graminoid tundra since this habitat is in the valley bottom and is interspersed with wet patches and streams dominated by plants typical of wet sites (*Dupontia*, *Carex*). In the field, we observed many heavily grazed patches in *Salix*-graminoid tundra but we avoided sampling these patches because of the disturbance. This may have negatively biased our estimate of mean faeces density, although faeces count tended to be high in that community.

High variability of lemming faeces density within plant community could reflect their small home range (Rodgers and Lewis 1986b, Predavec and Krebs 2000). Thus, sampling was probably too coarse and did not reach the level of discrimination or perception shown by lemmings in their selection of feeding sites. Finally, absence of refuges, like hummocks, the high soil instability which prevent digging and the sparse vegetation cover possibly explain the absence of lemming in both xeric communities, Forb-Salix and Graminoid barrens.

Faeces of arctic hare and rock ptarmigan were found on drier and more elevated habitats, where their preferred food (willows and forbs) were abundant and available at all seasons (Parker 1977, Smith and Wang 1977, Williams et al. 1980, Klein and Bay 1991, Larter 1999).

Grazing

In uplands, a large proportion (60%) of the taxa were grazed, mostly forbs and graminoids. Inflorescences were more frequently grazed and selected than leaves, especially those of forbs. Below-ground feeding was present in upland habitats where *O. maydelliana* and *P. viviparum* were frequently grubbed in spring and late season. Shoot pulling was also observed on *Eriophorum spp.* Our estimate of grazing is minimal, as some observations were done early in the season; thus frequency of grazing and selection of some plant parts may be higher than what we evaluated. The intend here is to present a general indication of forage use and selectivity in upland habitats on Bylot Island.

Little is known about goose feeding in upland habitats during the summer, but many studies have reported forbs, seeds and roots/rhizomes in their diet, including some species typical of dryer habitats (e.g. Prevett et al. 1979, 1985, Sedinger and Raveling 1984, Bazely and Jefferies 1986, Madsen and Mortensen 1987, Hupp and Robertson 1998). In spring, at Bylot Island, Gauthier (1993) reported forbs and below-ground parts typical of upland habitats in the diet of geese. Compared to lemmings, geese can eat a wide variety of plant species and select different plant parts (e.g. Prevett et al. 1979, 1985, Madsen and Mortensen 1987, Gauthier 1993).

We compared our grazed species list with oesophagus contents of wild gosling collected in summer 1993 on Bylot Island (G. Gauthier, unpublished data; Annexe 2). All species were found in oesophagus of wild goslings, except for *Melandrium spp.*, *Hierochloe alpina*, *A. alpina ssp. angustifolia* and *Potentilla hyparctica*.

Diet of collared lemmings is dominated by shrubs (*Salix spp.* or *D. integrifolia*) and a few forbs (Fuller et al. 1975, Batzli and Jung 1980, Batzli and Pitelka 1983, Klein and Bay 1991, Rodgers and Lewis 1986a). Their summer diet is composed of very few genera (between 3 and 5) and mainly stems or leaves, suggesting that other plant structures such as rhizomes or inflorescences are of little importance (<5%) to lemmings (Batzli and Jung 1980, Batzli and Pitelka 1983,

Rodgers and Lewis 1986a). Thus, grubbed rhizomes or bulbs and most of the grazed inflorescences were likely consumed by geese at our study site. In contrast, leaves of shrubs in our study area were infrequently grazed, suggesting that the abundance of collared lemmings was relatively low. In addition to geese, brown lemmings might have contributed to the observed grazing of graminoids, but in an unknown proportion.

Early in the season, new growth of deciduous shrubs and forbs generally has higher nitrogen (or protein), phosphorus and carbohydrate levels, and equal or higher digestibility than graminoids (Klein 1990, Gauthier 1993). As the season progresses, nitrogen and carbohydrate levels diminish in forbs but increase in graminoids, and digestibility is comparable between these two forage types (Klein 1990). Some forbs, such as *Triglochin palustris* and *Pedicularis* spp., can be highly nutritive and digestible during all summer and they are highly preferred by many herbivores, including geese (White and Trudell 1980a, Williams et al. 1980, Sedinger and Raveling 1984, Rodgers and Lewis 1985, Larter 1999). Flowers of *Salix* spp. and forbs have higher nitrogen, phosphorus and carbohydrate levels than corresponding leaf material and also have higher digestibility levels (White and Trudell 1980b, Klein 1990). Later in the season, seeds and below-ground parts are rich in carbohydrates, lipids and proteins, and can be highly digestible (Thomas and Prevett 1980, Sedinger and Raveling 1984). High proteins and minerals content of *Equisetum* spp. may explain its high selectivity (Thomas and Prevett 1982). *Equisetum* spp. can be a prominent component of the diet of geese in spring and fall (Gardarsson and Sigurdsson 1972, Prevett et al. 1979, 1985, Prop et al. 1984, Brackney and Hupp 1993).

This high food quality available throughout the season, justifies the selective foraging of many forbs and of different plant parts that we observed in uplands. Soon after hatch, we regularly saw goose families feeding in uplands. Selection of seeds and below-ground parts by geese was possibly a response to increased energy requirements for pre-migratory fat deposition and to a decreased growth demand (Prevett et al. 1979, Sedinger and Raveling 1984).

It has generally been thought that geese and lemmings had little impact on plant community structure on the uplands of Bylot Island because grazing pressure was assumed to be light and spatially variable among years. However, little is known about the tolerance of upland plants or their response to different type and intensity of herbivory. Despite their low biomass, forbs may

form a large component of the diet of geese (Prevett et al. 1979, 1985, Sedinger and Raveling 1984) or other herbivores (Klein and Bay 1991). In our study, some forbs were under a high grazing pressure. The few studies that have addressed the effects of herbivory on forbs suggest that they are negatively affected by defoliation. Grazing on *Oxytropis viscida* by muskox reduced plant diameter, probability of flowering, number of inflorescences, reproductive biomass and below-ground biomass (Mulder and Harmsen 1995). Many other studies reported a decrease in the probability of flowering or in seed production in forbs following herbivory. This appears to be due to the removal of inflorescences (Bishop and Davy 1984, Bazely and Jefferies 1986, Mulder and Harmsen 1995, Mulder and Ruess 1998a) and decreased allocation to reproduction following defoliation (Crawley 1983, Mulder and Harmsen 1995, Ehrlén 1997, Mulder and Ruess 1998b). Below-ground tissues or leaves lost from direct or indirect herbivory on forbs resulted in lower standing crop biomass and plant density or diversity (Bazely and Jefferies 1986, Crawley 1990, Loonen and Solheim 1998, Zacheis et al. 2001). Thus grazing can lower the potential recruitment of the population of dicotyledons. Finally, faeces deposits in upland habitats at Bylot Island may be too small to have a fertilizing effect on plant growth.

Although density of geese and lemmings tended to be low in uplands (Hughes et al. 1994, Chapter 3, G. Gauthier, unpublished data), they could affect plant community dynamics. Reduced plant density or recruitment *via* selective feeding by generalist herbivores may alter competitive interactions within plant populations (Crawley 1983, Louda et al. 1990), and competition should be greatest when the environment limits opportunities for compensatory re-growth (Louda et al. 1990). Under such circumstances, even low levels of herbivory may have large effects on plant communities by changing competitive interactions (see Virtanen et al. 1997). Moreover, low level of herbivory (or little tissue loss) may seem insignificant over a short period of time (short term) but can have major impacts over the life time of a long-lived perennial (Doak 1992). As the goose population on Bylot Island is increasing (Reed et al. 1998), the impact of goose grazing on vegetation could, in time, be accentuated.

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Table 1. Environmental parameters measured at quadrat (50cm x 50cm) and plot level (5m x 20m) at Bylot Island. *: Variable log or square root transformed; Oc: occurrence.

Environmental parameters	
Quadrat level	Plot level
Litter cover (%)*	Microtopography :
Bare ground or sand cover (%)*	-Hummocks: hummocks of various sizes
Stones (≤ 25 cm; OC) ^a	-Stripes : alternative stripes of vegetation and bare ground
Rocks (> 25 cm) ^a and stone slabs (OC)	-Mud-boils : round surfaces of bare ground ~30-50cm
Lemming faeces (mean density : n/m^2) *	-Small-sized gelifluction lobe (vegetated)
	-Undulating : heterogeneous pattern including mound, fissures and flat surface
	-Flat: no pattern
	Altitude (m a.s.l. –above sea level) *
	Slope ($^{\circ}$) (sin transformed)
	Exposition EW: East-West; NS : North-South (see methods)
	Surficial deposits and bedrock ^b (Figure 1):
	-Eolian: sand deposited by wind and interbedded with organic material, characterised by polygonal patterned ground
	-Colluvial: sand, gravel and boulders deposited as talus and fans at the base of slopes
	-Littoral: coarse sand, gravel and boulders forming flights of beaches
	-Glacial: sediments (debris and marine shells) transported by foreign glacier ice
	-Sedimentary rock (bedrock poorly consolidated to unconsolidated): sandstone, mudstone, and coal of Cretaceous and Tertiary age
	Stoniness (1- low to 6- high) *
	Animal activity (faeces):
	-Old goose faeces (mean density : n/m^2) *
	-Hare (OC)
	-Caribou (OC)
	-Rock ptarmigan (OC)
	Lemming winter nests

^a From The Canadian system of soils classification.

^b From Klassen (1993), see also Figure 1.

Table 2. Species richness, plant abundance (% cover) and environmental characteristics of the 10 plant communities identified by Twinspan classification, Bylot Island, Nunavut, 2000 and 2001.*: Indicator taxa identified by Twinspan classification.

Communities	1	2	3	4	5	6	7	8	9	10
Vascular species richness (#)										
Graminoids	11	11	14	8	18	9	8	8	5	9
Forbs	22	16	29	24	21	26	23	30	23	23
Shrubs	5	5	5	5	4	4	2	3	2	1
Total	38	32	48	37	35	39	33	44	30	33
Plant cover (%)										
Graminoids	12	20	17	12	11	6	16	6	3	8
Forbs	2	2	3	9	2	8	52	18	9	2
Shrubs	35	20	19	39	20	33	76	42	6	2
Total vascular plants	49	42	39	60	33	47	144	66	18	12
Mosses	53	57	47	34	41	34	+	*44	2	+
Lichens	23	19	16	10	25	11	1	6	+	0
Cryptogamic crust	5	8	*14	6	6	13	1	4	0	3
Environmental characteristics										
Litter cover (%)	5	5	7	15	8	13	82	21	2	+
Bare ground cover (%)	+	1	2	+	6	11	6	3	25	88
Stones frequency occurrence (%)	25	38	61	14	0	86	40	27	0	33
Rocks frequency occurrence (%)	6	0	13	14	0	17	20	36	100	0
Altitude (m a.s.l.; $\bar{x} \pm SE$)	72±5	104±12	113±11	133±20	39±2	225±22	166±27	134±5	188±33	28±5
Slope (°; $\bar{x} \pm SE$)	10±1	3±0.6	4±0.6	14±1	1±0.2	12±2	23±4	22±1	30±2	2±0.3
Microtopography	HK	HK	HK mub-boils	HK	HK	stripes mub-boils	flat lobes	flat lobes, undulating	flat	flat

Note: +, cover <0.5%

HK: hummocky

Table 3. Vegetation cover and frequency of occurrence (%) in 10 upland plant communities as identified by Twinspan classification for 40 species with frequency > 75% in at least one plant community, Bylot Island, Nunavut, 2000 and 2001. Low cover species with high constancy are underlined.

*: Indicator species identified by Twinspan classification; C: cover%; F: frequency%.

Communities	1	2	3	4	5	6	7	8	9	10
Species	C F	C F	C F	C F	C F	C F	C F	C F	C F	C F
Graminoids										
(21 species in total)										
<i>Arctagrostis latifolia</i>	5 100	13 100	8 91	3 86	5 100	2 86				
<i>Carex bigelowii</i>	T 19	+ 100	+ 100		T 13					
<i>Luzula nivalis</i>	4 100	4 100	5 100	1 100	1 100	1 100		+ 45		+ 50
<u><i>Luzula confusa</i></u>	3 100	1 88	2 87	3 100	2 100	1 71	+ 40	+ 91	T 33	2 100
<u><i>Festuca brachyphylla</i></u>	T 6	T 13	*+ 74	+ 71	+ 100	+ 100	3 100	1 91	+ 33	1 100
<u><i>Alopecurus alpinus</i></u>	T 19	+ 63	+ 78	2 71	2 100	1 100	7 100	2 100	1 100	2 100
<u><i>Poa arctica</i></u>	+ 75	+ 75	+ 91	2 100	1 100	1 100	4 80	3 100		1 100
<i>Poa glauca</i>							2 100	+ 100		
<i>Trisetum spicatum</i>							+ 100	T 18	+ 100	
Forbs (53 species in total)										
<i>Draba corymbosa</i>	+ 63	T 50	+ 78	+ 86	+ 100	+ 100		T 9	T 33	
<i>Draba lactea</i>	T 81	+ 100	+ 100	T 86	T 88	+ 100		T 27		T 50
<i>Eutrema edwardsii</i>	T 63	+ 75	+ 61	+ 100	T 63	T 14		T 36	T 33	
<i>Saxifraga hieracifolia</i>	T 75	T 50	T 74	T 71	T 88	T 43		+ 36		
<i>Cardamine belidifolia</i>	+ 100		T 4	T 43	T 38	T 14	T 20	T 18		T 50
<u><i>Oxyria digyna</i></u>	1 94	+ 88	+ 74	+ 43		+ 71	+ 20	T 18	1 100	T 17
<u><i>Pedicularis arctica/hirsuta</i></u>	T 50	T 100	T 48	+ 86	T 50	+ 86	T 20	*+ 82		T 17
<i>Potentilla hyparctica</i>	T 19	T 38	+ 74	T 29		T 43		T 18		+ 83
<u><i>Saxifraga nivalis</i></u>	T 56	T 63	+ 78	+ 71	T 50	+ 100	T 20	+ 73	T 67	T 50
<i>Saxifraga caespitosa</i>	T 6		T 39	+ 71	T 75	+ 86		T 45	+ 67	
<u><i>Saxifraga oppositifolia</i></u>	+ 38	T 38	+ 78	+ 86	1 88	1 86		+ 64	T 33	1 50
<u><i>Cerastium alpinum</i></u>	T 19	T 25	*+ 78	+ 71	+ 100	+ 100	+ 100	+ 91	1 100	
<u><i>Papaver radicum</i></u>	T 25	T 25	*T 74	+ 100	T 13	1 100	T 20	+ 64	+ 100	+ 67
<u><i>Polygonum viviparum</i></u>	+ 88	1 88	1 83	1 86	+ 88	1 100	5 100	1 100	T 33	T 33
<u><i>Saxifraga cernua</i></u>	T 44	T 50	+ 74	T 86	T 63	+ 100	T 80	T 91	+ 67	
<u><i>Stellaria longipes</i></u>	+ 94	+ 100	+ 100	+ 100	+ 100	+ 100	1 100	+ 100	+ 100	1 100
<i>Draba cinera/nivalis</i>				T 29		T 29	T 20	T 36	+ 100	T 50
<i>Arnica alpina ssp. angustifolia</i>							3 100	T 18	T 33	
<i>Astragalus alpinus</i>			+ 9	1 86	1 100	2 71	24 100	7 100	4 100	
<i>Draba glabella</i>				T 14	T 25		+ 100	+ 82		
<i>Epilobium latifolium</i>									*1 100	
<i>Melandrium affine</i>				T 14	T 13	T 14	+ 100	T 64		
<i>Oxytropis maydelliana</i>			+ 13	*5 100		1 71	16 100	8 100	T 67	
<i>Saxifraga tricuspidata</i>	T 6			+ 14	T 13	T 14	+ 80	+ 91	1 67	T 17
<i>Taraxacum phymatocarpum</i>						T 14	T 40	T 18	+ 100	T 50
<i>Cerastium arcticum</i>			T 9						T 33	+ 100
Shrubs (7 species in total)										
<i>Cassiope tetragona</i>	*25 100	4 100	2 61	+ 14		T 14				
<i>Salix herbacea</i>	+ 63	5 88	1 52							
<i>Salix reticulata</i>	+ 31	2 38	1 57	*9 100	*9 100	T 14		+ 36	T 33	
<i>Dryas integrifolia</i>	1 31	T 13	2 57	4 86	1 100	4 86	T 20	1 73		
<u><i>Salix arctica</i></u>	9 100	9 100	13 100	25 100	10 100	29 100	76 100	41 100	6 100	2 67

Note: +, cover <0.5%; T, cover <0.05%

Table 4. Number of plots sampled in each vegetation zone (A to M) and proportion of plots corresponding to the plant communities identified by Twinspan classification (#1-10, see text), Bylot Island.

Vegetation zone and # of sampled plots	# of plots per vegetation zone in each corresponding plant community identified by Twinspan										
	1	2	3	4	5	6	7	8	9	10	
A- Mountain bottoms facing North	6	6									
B- North facing hills	11	9	2								
C- Inland terrace	11		5	6							
D- Next to sea terrace	14		3	11							
E- Intermediate zone between beach (M) and terrace (D)	3	1	2								
F- South facing hills	4			3				1			
G- Mesic polygons- valley bottom	10		2		8						
H- West facing mountains -inland	4			4							
-by the sea	6					6					
I- South facing slopes in mountains	5						5				
J- Lower east facing slopes in mountains	5					1		4			
K- West facing slopes in mountains	6							6			
L- Sparsely vegetated slopes ^a	3								3		
M- Beach	6									6	
Total number of plots	94	16	8	23	7	8	7	5	11	3	6

^a Included North and upper East facing slopes in mountains.

Table 5. Summary of the CCA performed on 94 plots containing 85 taxa and the environmental parameters of Table 1. Only first two axes were significant.

	Axis 1	Axis 2	All axes	Total inertia
Eigenvalues	0.329	0.136	0.760	2.475
Species-environment correlations	0.933	0.633	0.778	
Cumulative percentage variance				
of species data	13.3	18.8	24.7	
of species-environment relation	43.3	61.1	80.5	
Monte Carlo permutation test p value	<0.05	<0.05	0.001	

Table 6. Mean density and frequency of occurrence of goose and lemming faeces and frequency of occurrence of lemming winter nests and Arctic hare, Rock ptarmigan and Caribou faeces in each plant community. Calculated from plots sampled in summer 2000 and 2001 (n=94).

Plant communities	n plot	Goose faeces ^a		Lemming faeces ^a		Lemming winter nests frequency (%)	Hare faeces frequency (%)	Ptarmigan faeces frequency (%)	Caribou faeces frequency (%)
		density (n/m ² ± SE)	frequency (%)	density (n/m ² ± SE) ^b	frequency (%)				
Heath tundra	16	1.3 ± 0.1 AB	100	32 ± 10 B	100	6	-	-	6
<i>Arctagrostis</i> meadow	8	1.6 ± 0.3 AB	100	23 ± 8 B	100	38	-	-	-
<i>Salix-Arctagrostis</i> meadow	23	2.7 ± 0.6 B	100	11 ± 2 AB	83	4	4	4	26
<i>Salix</i> -graminoid-forb tundra	7	0.7 ± 0.2 A	100	20 ± 6 B	86	29	14	-	-
<i>Salix</i> -graminoid tundra	8	1.4 ± 0.3 AB	100	34 ± 7 B	100	-	-	-	-
<i>Salix</i> -cryptogam tundra	7	0.4 ± 0.1 A	100	33 ± 27 AB	100	-	29	29	-
<i>Salix</i> -legume-graminoid tundra	5	0.4 ± 0.1 A	100	9 ± 3 AB	100	20	40	-	-
<i>Salix</i> -moss-legume tundra	11	0.8 ± 0.1 A	100	18 ± 5 B	100	-	45	36	9
Forb- <i>Salix</i> barrens	3	0.7 ± 0.1 AB	100	0 A	-	-	67	67	-
Graminoid barrens	6	1.0 ± 0.3 AB	83	0 A	-	-	17	-	-

^a Means with the same letter within each column do not differ (P>0.05); Tukey's test.

^b Faeces density was calculated using the geometric mean at the quadrat level.

Table 7. Specific taxa frequency of grazing (%) on inflorescences (GI) and leaves (GL), taxa frequency of occurrence (%fo) in the study area and mean selection ratio ($W_i \pm SE$). Calculated from plots sampled in summer 2000 and include all plant communities^a.

TAXA	Inflorescences			Leaves		
	Frequency		Selection	Frequency		Selection
	GI	%fo	$W_i^b \pm SE$	GL	%fo	$W_i^b \pm SE$
Frequently grazed on inflorescences						
A. Taxa with high (>40%) flowering density						
<i>Astragalus alpinus</i>	81	44	0.9 ± 0.2	28	48	0.3 ± 0.2
<i>Luzula confusa</i>	71	58	2.5 ± 0.6	22	88	0.4 ± 0.2
<i>Draba</i> spp.	32	69	1.0 ± 0.4	0	92	0 ± 0
B. Taxa with low (<30%) flowering density						
<i>Ranunculus nivalis</i>	100	8	2.6 ± 0.2	33	9	0.4 ± 0.3
<i>Ranunculus pedatifidus</i>	100	3	3.7 ± 0	0	5	0 ± 0
<i>Saxifraga cernua</i>	75	21	3.3 ± 1.4	0	68	0 ± 0
<i>Papaver radicatatum</i>	71	19	15.1 ± 7.9	11	53	6.1 ± 4.2
<i>Poa glauca</i>	70	28	1.1 ± 0.4	0	24	0 ± 0
<i>Eutrema edwardsii</i>	67	25	2.5 ± 1.0	0	56	0 ± 0
<i>Saxifraga hieracifolia</i>	67	17	3.1 ± 1.3	3	56	0.2 ± 0.2
<i>Melandrium</i> spp.	57	19	7.2 ± 3.4	10	30	5.4 ± 4.9
<i>Eriophorum triste</i>	50	6	0.3 ± 0.3	38	24	5.6 ± 3.4
<i>Hierochloa alpina</i>	50	6	1.2 ± 1.2	10	15	0.9 ± 0.9
<i>Arnica alpina</i> ssp. <i>angustifolia</i>	50	6	2.1 ± 2.1	25	12	1.1 ± 0.8
<i>Potentilla hyparctica</i>	33	8	0.5 ± 0.5	0	38	0 ± 0
Frequently grazed on leaves and inflorescences						
<i>Arctagrostis latifolia</i>	100	56	3.5 ± 0.6	90	64	5.3 ± 0.8
<i>Oxytropis maydelliana</i>	93	39	1.5 ± 0.4	50	42	1.3 ± 0.3
<i>Luzula nivalis</i>	88	69	4.3 ± 0.6	69	74	10.2 ± 6.6
<i>Poa arctica</i>	67	67	2.0 ± 0.8	53	89	4.8 ± 1.3
<i>Polygonum viviparum</i>	64	69	2.8 ± 0.8	33	86	1.5 ± 0.6
<i>Alopecurus alpinus</i>	47	49	1.6 ± 0.7	64	76	9.4 ± 1.8
Frequently grazed on leaves						
<i>Equisetum</i> spp.	-	0	- -	100	5	30.0 ± 7.8
<i>Eriophorum scheuchzeri</i>	-	0	- -	50	3	35.6 ± 35.6
<i>Ranunculus sabinei</i>	-	0	- -	50	3	0.8 ± 0.8
<i>Oxyria digyna</i>	27	31	0.8 ± 0.4	42	58	3.1 ± 1.0

^a Graminoid barrens (#10) was sampled in summer 2001.

^b Selection ratio W_i (%grazed / %available); 1: species grazed proportionally to its availability, <1: species sparsely grazed, >1: selection of the species or heavily grazed (Manly et al. 1993).

Table 8. Comparison of previously described vegetation types of oases in the Canadian High Arctic with those at Bylot Island. *Salix*-legume-graminoid and *Salix*-moss-legume tundra (this study), Shrub-Sedge tundra and Lichen barren (Zoltai et al. 1983) were not included since no equivalent was found.

Bylot Island, studied area: wetland, mesic and dry communities	Bylot Island, whole Island, Zoltai et al. (1983)	Truelove Lowland, Devon Island, Muc and Bliss (1977)	Polar Bear Pass, Bathurst Island, Sheard and Geale (1983b)	Alexandra Fiord, Ellesmere Island, Muc et al. (1989)	Sverdrup Pass, Ellesmere Island, Bergeron (1988)	Lake Hazen, Ellesmere Island, Gould (1985)
73°08'N, 80° 00'W	73°08'N, 80° 00'W	75°33'N, 84° 40'W	75°44'N, 98° 25'W	78°53'N, 75° 55'W	79°08'N, 80° 30'W	81°49'N, 71° 18'W
100 vascular species	130 taxa ^a	97 v. species	125 v. species	85 v. species	75 v. species	98 v. species
12 communities	7 types/sub-types	14 community types	15 clusters	6 communities	7 nota	12 communities
Heath tundra (#1)		Dwarf shrub heath-moss		Dwarf shrub-cushion plant		<i>Cassiope</i> hummocks
Mesic meadows (#2 and #3)		Graminoid-moss meadow	Mesic grass meadow (#10)			
Dwarf-shrub tundra (#4-5-6)	Willow-Grass tundra	Ice-wedge polygons	Willow-lichen meadow (#7)	Deciduous dwarf shrub-graminoid	<i>Salix arctica</i> -dominated (F)	
Forb-Salix barrens (#9)	<i>Saxifraga-Papaver</i> barrens	Unvegetated scree slopes	Ridge (#1)	Herb-dominated	Herb barrens (G)	Scree
Not sampled	<i>Dryas</i> barrens	Cushion plant-lichen	Polar desert (#2)	Lichen-cushion plant-dwarf shrub	<i>Dryas integrifolia</i> -dominated (D)	<i>Dryas</i> -sedge meadow, <i>Dryas-Salix</i> tundra
Grass/cottongrass meadow ^b		Hummocky graminoid meadow	Grass-moss meadow (#12)			
Sedge/grass meadow ^b	Sedge-Moss and <i>Eriophorum</i> -Grass wet meadow	Sedge-moss meadow	Sedge meadow (#6) Emergent meadow (#9)	Sedge-cushion plant-dwarf shrub	<i>Carex aquatilis</i> meadow (B)	Wet sedge meadow

^a May include species only found in the Cape Hatt region, Baffin Island.

^b Gauthier et al. 1995

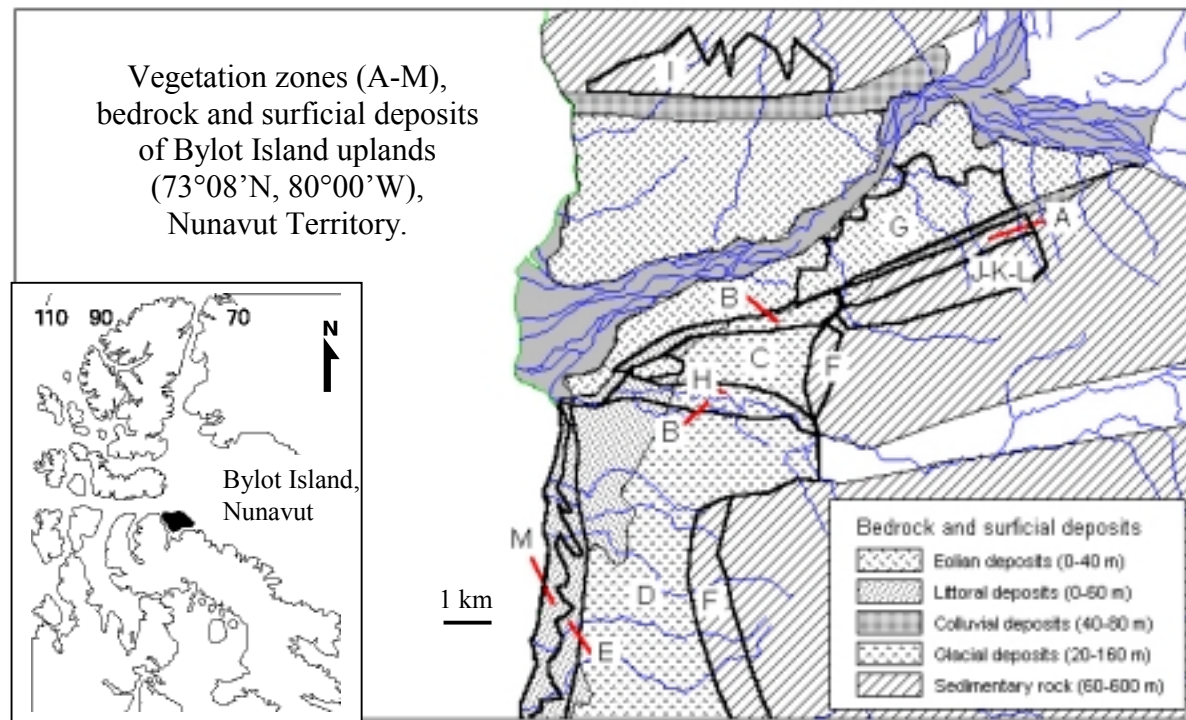


Figure 1. Localisation of the thirteen vegetation zones (letters) representing homogenous vegetation in the study area. Fill patterns identify surficial material and bedrock as modified from Klassen (1993; see Table 1 for description), Bylot Island, Nunavut Territory. A– Mountain bottoms facing North; B– North facing hills; C– Inland terrace; D– Next to sea terrace; E– Intermediate zone between beach (M) and terrace (D); F– West facing mountains: inland and by the sea; G– Mesic polygons- valley bottom; H– South facing hills; I– South facing slopes in mountains; J– Lower east facing slopes in mountains; K– West facing slopes in mountains; L– Sparsely vegetated slopes; M– Beach.

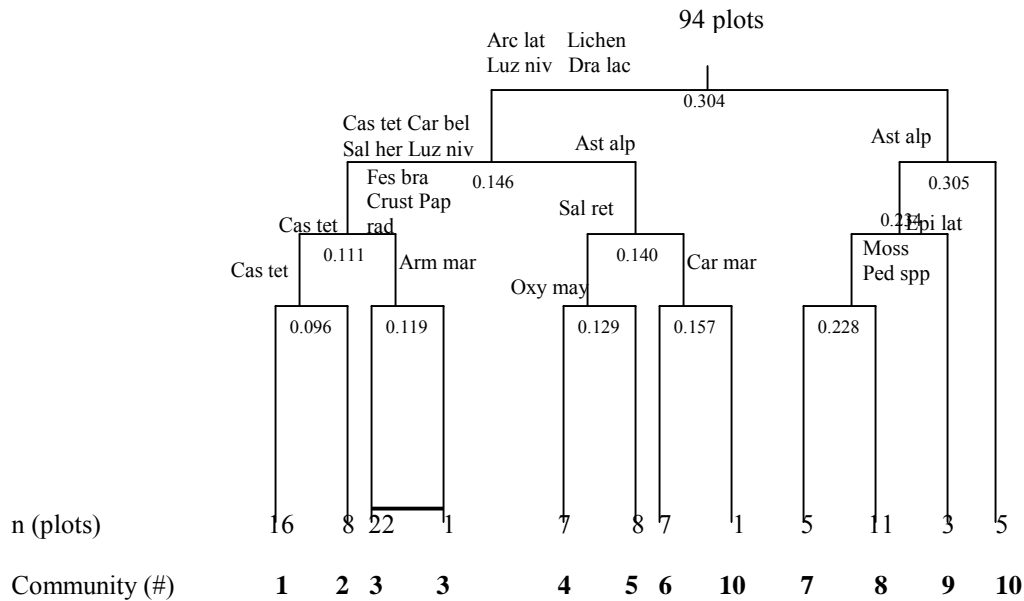


Figure 2. Twinspan classification dendrogram of upland vegetation of the 94 plots on Bylot Island, Nunavut Territory, using the cover of 81 vascular taxa, mosses and lichens. Eigenvalue and indicator species for each division are indicated at the dichotomy; n: the number of plots in the cluster; #1 to 10: plant community number (see text for description). Arc lat: *Arctagrostis latifolia*; Luz niv: *Luzula nivalis*; Dra lac: *Draba lactea*; Ast alp: *Astragalus alpinus*; Cas tet: *Cassiope tetragona*; Car bel: *Cardamine bellidifolia*; Sal her: *Salix herbacea*; Fes bra: *Festuca brachyphylla*; Crust: organic crust; Pap rad: *Papaver radicum*; Cer alp: *Cerastium alpinum*; Sal ret: *Salix reticulata*; Epi lat: *Epilobium latifolium*; Arm mar: *Armeria maritima*; Oxy may: *Oxytropis maydelliana*; Car mar: *Carex maritima*; Ped spp: *Pedicularis arctica/hirsuta*.

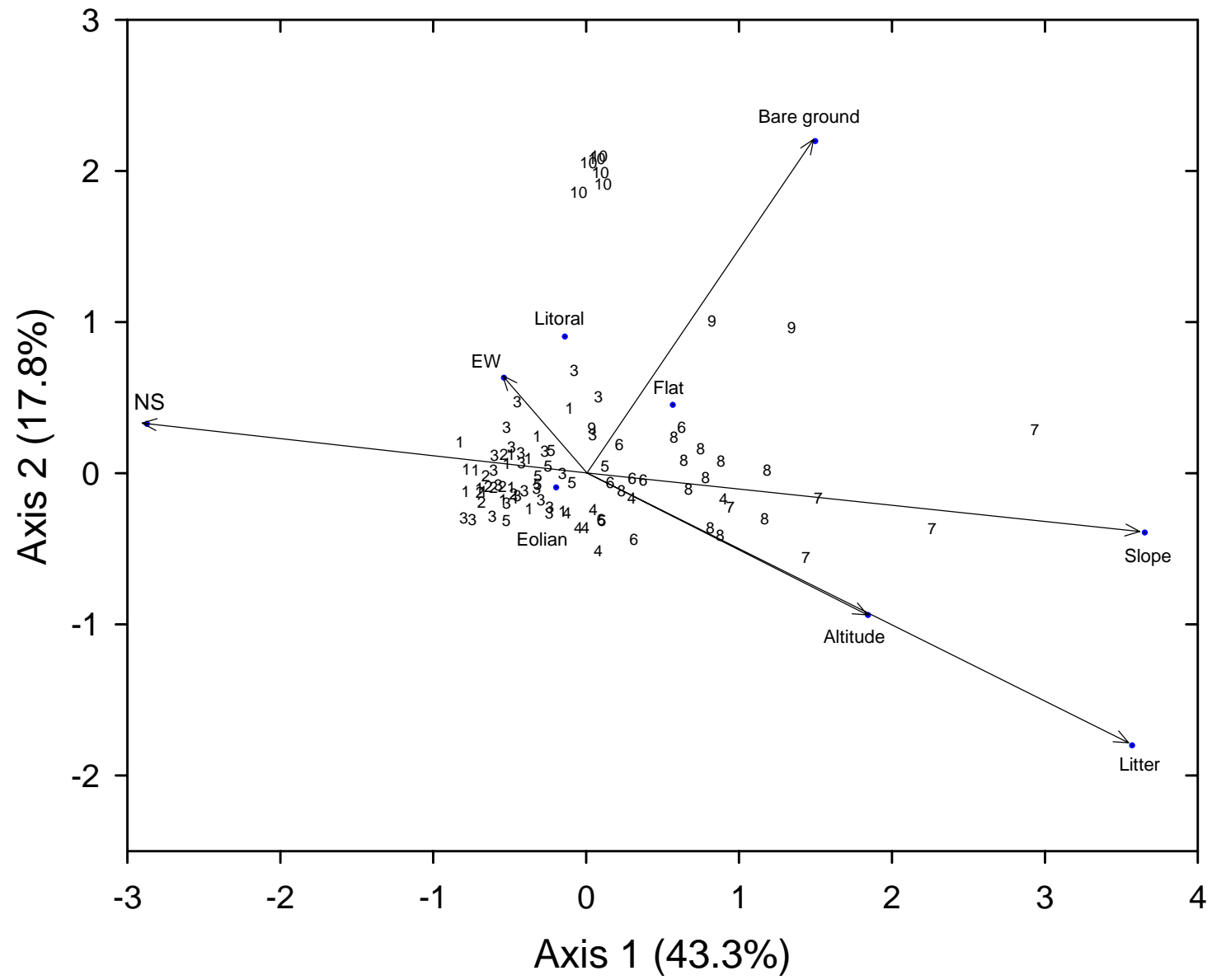


Figure 3. Sampled plots of the canonical correspondence analysis (CCA) of the upland vegetation of Bylot Island (85 taxa and nine environmental variables). Numbers (1-10) represent the ten plant communities identified by Twinspan classification. 1- Cryptogam-heath tundra; 2- *Arctagrostis* meadow; 3- *Salix-Arctagrostis* meadow; 4- *Salix*-graminoid-forb tundra; 5- *Salix*-graminoid tundra; 6- *Salix*-cryptogam-forb tundra; 7- *Salix*-legume-graminoid tundra; 8- *Salix*-moss-legume tundra; 9 Forb-*Salix* barrens; 10- Graminoids tundra. Arrows indicate continuous environmental variables. See Table 1 for description of environmental parameters.

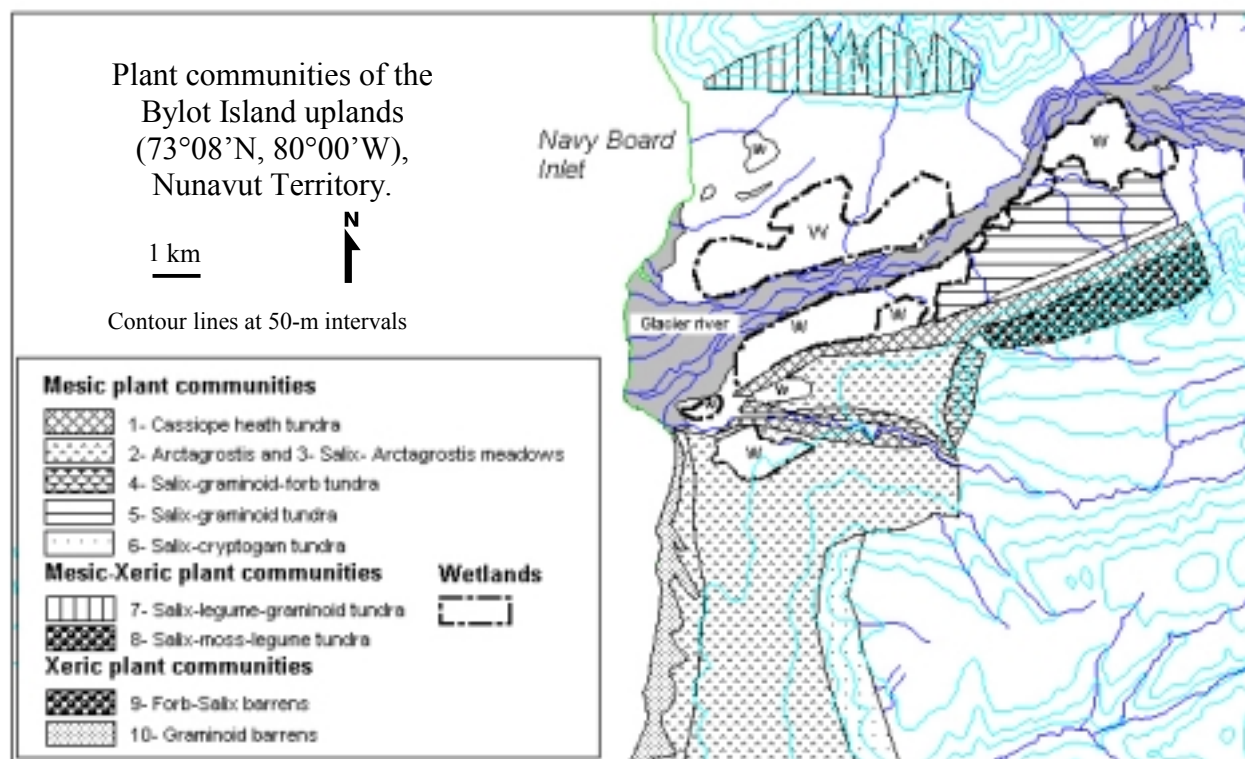


Figure 4. Distribution of the ten plant communities in Bylot Island uplands, Nunavut Territory (#1-10). W: wetlands, as in Hughes et al. 1994.

Appendix 1. List of ungrazed and low frequency grazed taxa. Specific taxa frequency of grazing (%) on inflorescences (GI) and leaves (GL), taxa frequency of occurrence (%fo) in the study area, mean selection ratio ($Wi \pm SE$), and frequency of old grubbing (OGB) and fresh grubbing or shoot pulling (FGS). Calculated from plots sampled in summer 2000 and include all plant communities^a.

Taxa	Inflorescences			Leaves			Below-ground	
	Frequency		Selection	Frequency		Selection	OGB	FGS
	GI	%fo	$Wi^b \pm SE$	GL	%fo	$Wi^b \pm SE$		
Graminoids								
<i>Carex aquatilis</i> var. <i>stans</i>	-	0	-	0	2	0	-	-
<i>Carex bigelowii</i>	0	3	0	0	5	0	-	-
<i>Juncus biglumis</i>	25	11	0.9 ± 0.9	17	18	2.6 ± 2.6	-	-
<i>Festuca</i> spp.	19	44	0.4 ± 0.3	2	71	0.001 ± 0.001	-	-
<i>Poa alpigena</i> var. <i>colpodea</i>	-	0	-	0	8	0	-	-
<i>Deschampsia brevifolia</i>	-	0	-	0	3	0	-	-
<i>Elymus arenarius</i> ssp. <i>mollis</i>	0	3	0	0	5	0	-	-
<i>Trisetum spicatum</i>	0	3	0	0	15	0	-	-
Forbs								
<i>Potentilla vahliana</i>	-	0	-	0	2	0	-	-
<i>Saxifraga hirculus</i>	-	0	-	0	3	0	-	-
<i>Pyrola grandiflora</i>	-	0	-	0	6	0	-	-
<i>Ranunculus sulphureus</i>	-	0	-	0	6	0	-	-
<i>Saxifraga foliolosa</i>	0	6	0	0	15	0	-	-
<i>Cardamine belidifolia</i>	14	39	0.2 ± 0.2	0	61	0	-	-
<i>Saxifraga flagellaris</i>	-	3	-	0	11	0	-	-
<i>Pedicularis arctica/hirsuta</i>	-	0	-	5	65	2.0 ± 1.8	-	10
<i>Sagina intermedia</i>	0	3	0	0	12	0	-	-
<i>Saxifraga nivalis</i>	0	19	0	5	64	1.3 ± 1.1	-	-
<i>Saxifraga caespitosa</i>	0	14	0	0	33	0	-	-
<i>Saxifraga oppositifolia</i>	0	44	0	0	59	0	-	-
<i>Cerastium alpinum</i>	9	31	1.2 ± 1.2	0	76	0	-	-
<i>Stellaria longipes</i>	6	97	0.03 ± 0.02	0	98	0	-	-
<i>Minuartia rubella</i>	-	0	-	0	8	0	-	-
<i>Epilobium latifolium</i>	0	3	0	0	5	0	-	-
<i>Erigeron eriocephalus</i>	-	0	-	0	8	0	-	-
<i>Potentilla nivea</i>	0	6	0	0	3	0	-	-
<i>Saxifraga tricuspida</i>	17	17	0.06 ± 0.06	0	29	0	-	-
<i>Taraxacum phymatocarpum</i>	0	3	0	0	15	0	-	-
<i>Cerastium arcticum</i>	-	0	-	0	2	0	-	-
<i>Saxifraga rivularis</i>	-	0	-	0	6	0	-	-
<i>Androsace septentrionalis</i>	0	3	0	0	2	0	-	-
<i>Erysimum pallasii</i>	-	0	-	0	3	0	-	-
Shrubs								
<i>Salix lanata</i>	-	0	-	0	3	0	-	-
<i>Vaccinium uliginosum</i>	-	0	-	0	5	0	-	-
<i>Cassiope tetragona</i>	14	39	0.02 ± 0.02	0	42	0	-	-
<i>Salix herbacea</i>	0	-	0	13	36	0.2 ± 0.2	-	-
<i>Salix reticulata</i>	11	25	0.01 ± 0.01	3	45	0.003 ± 0.003	-	-
<i>Dryas integrifolia</i>	11	25	0.02 ± 0.02	0	48	0	-	-
<i>Salix arctica</i>	27	97	0.09 ± 0.06	17	97	0.04 ± 0.02	-	-

^a Graminoid barrens (#10) was sampled in summer 2001; ^b Selection ratio Wi (%grazed / %available). 1 = species grazed proportionally to its availability, <1 = species sparsely grazed, >1 = selection of the species or heavily grazed (Manly et al. 1993).

Appendix 2. Species identified in oesophagus of wild gosling killed between 5 July and 6 August 1993 on Bylot Island.

Species	Leaves	Flowers or seeds
Graminoïds		
<i>Arctagrostis latifolia</i>	X	X
<i>Alopecurus alpinus</i> ^a	X	X
<i>Poa arctica</i> ^a	X	X
<i>Poa glauca</i> ^a	X	X
<i>Luzula</i> spp.	X	X
<i>Eriophorum</i> spp.	X	
<i>Festuca</i> spp.		X
<i>Dupontia fisheri</i> ^b	X	
<i>Pleuropogon sabinet</i> ^b	X	
Unknown Gramineae		
Forbs		
<i>Polygonum viviparum</i> ^a	X	X
<i>Draba</i> spp.	X	X
<i>Eutrema edwardsii</i>	X	X
<i>Oxyria digyna</i>	X	
<i>Ranunculus</i> spp.	X	
<i>Pedicularis</i> spp.	X	
<i>Saxifraga</i> spp. ^a	X	
<i>Legumes</i> ^{a c}	X	
<i>Papaver radicatum</i>	X	Floral stems
<i>Equisetum</i> spp. ^a	X	
<i>Stellaria</i> spp. ^a	X	
Dicotyledons spp.	X	
Shrubs		
<i>Salix</i> spp. ^a	X	X
Others		
Moss spp. ^a	X	
Diptera		

^a Also noted by Gauthier (1993), included also *Carex* spp., *Cerastium alpinum*.

^b Can only be found in wetlands.

^c Also include rhizome.

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Chapitre III

**Use and selection of lowland and upland habitats by Greater
Snow Goose families on Bylot Island, Nunavut**

RÉSUMÉ

L'utilisation et la sélection des habitats humides et mésiques par les familles de la Grande Oie des neiges (*Chen caerulescens atlantica*) au cours de la période d'élevage des oisons a été étudiée à l'île Bylot, Nunavut (73°N). Des décomptes journaliers ont été fait dans une aire d'étude de 14 km² contenant deux habitats humides (Étang/Lac et Prairie humide) et trois habitats mésiques (Collines à *Cassiope*, Polygones mésiques et Prairie mésique). Les deux habitats humides avaient une forte densité d'étangs pouvant servir de refuges aux oies contre les prédateurs, et avaient une composition végétale similaire dominée par les plantes graminoides (*Dupontia fisheri*, *Eriophorum* spp. et *Carex* spp.). Les Collines à *Cassiope* étaient dominées par l'éricacée *Cassiope tetragona*, les Polygones mésiques par les saules (*Salix* spp.) et les plantes graminoides, tandis que la Prairie mésique avait une plus grande abondance de plantes graminoides. Ces trois habitats mésiques avaient peu d'étangs. L'utilisation des habitats par les familles et le comportement des parents ont été noté à partir de deux caches surplombant l'aire d'étude.

À l'été 2001, une faible proportion des familles ont utilisé les habitats mésiques (14% des observations), peut-être à cause d'une forte pression de prédation. Toutefois, la proportion de familles dans ces habitats avait tendance à augmenter à la fin de la saison. Tout au cours de la l'été, les familles ont intensivement utilisé les deux habitats humides, qui ont une disponibilité élevée de plantes graminoides et offrent une bonne protection contre les prédateurs terrestres. Par contre, la sélectivité de l'habitat Étang/Lac avait tendance à diminuer à la fin de la saison et serait lié à une diminution de la disponibilité de nourriture. Inversement, l'utilisation et la sélectivité de la Prairie humide a augmenté au cours de la saison ainsi que dans deux habitats mésiques, les Collines à *Cassiope* et les Polygones mésiques. Plus la migration vers le sud approche, plus les oies ont besoin de bâtir leur réserve d'énergie. L'augmentation de l'utilisation des habitats mésiques pourrait ainsi être lié à leur grande disponibilité de graines, fruits et rhizomes, structures riches en lipides et en hydrates de carbones. À la fin de la saison, les oies consacraient plus de temps à s'alimenter à la fin de la journée. Ce comportement pourrait être lié au besoin d'accumuler des graisses mais pourrait aussi être en réponse à la diminution de la quantité de nourriture dans les habitats humides. À la fin de la saison, afin de subvenir à leurs besoins énergétiques, il semblerait que les oies doivent faire un compromis entre la disponibilité et la qualité de la nourriture et leur protection contre les prédateurs.

ABSTRACT

We studied the use and selection of lowland and upland habitats by Greater Snow Goose families (*Chen caerulescens atlantica*) over the course of the brood-rearing period in 2001, on Bylot Island, Nunavut (73°N). Daily visual surveys were conducted in a 14 km² area containing two wetland habitats (Pond/Lake and Wet meadow) and three upland habitats (*Cassiope* hill, Mesic polygon and Mesic meadow). Habitat use and behaviour were recorded for all pairs with goslings. In summer 2001, a small proportion of families use uplands (14% of observations), perhaps because of a high predation pressure. Families intensively used the two wetland habitats throughout the summer. These habitats had a high availability of graminoids and density of ponds that could serve as refuges for families against terrestrial predators. However, selectivity of the Pond/Lake habitat tended to decrease at the end of the season, likely because of food depletion in this habitat. Conversely, as the season progressed, use and selectivity of the Wet meadow increased as well as in two upland habitats, *Cassiope* hill and Mesic polygon. As the southward migration approaches, geese need to build energy reserves. Thus, increased use of uplands may also be linked to their high availability of seeds, fruits and rhizomes, which are rich in lipids and carbohydrates. At the end of the season, families spent more time feeding in evenings. This behaviour may reflect the need to build their energy reserve, but could also be due to the decreasing food supply in wetlands.

Key-words: Arctic, wetlands, uplands, rearing, behaviour, feeding, food depletion, Snow Goose

INTRODUCTION

In the Arctic, the short growing season, low plant diversity and low plant productivity impose particular constraints on herbivores. Selection of feeding habitats is therefore critical to ensure high food and nutrient intake. Low productivity and biomass, as well as patchy distribution of the vegetation may force herbivores to range widely over the landscape in search for food (Klein and Bay 1991). Thus, to maximize food intake, northern herbivores have developed different strategies, such as diet adjustments to take advantage of plant phenology (White and Trudell 1980, Prop et al. 1984, Klein and Bay 1994), high mobility to exploit food pulses in space and time (Jefferies et al. 1994), and selective but opportunistic foraging (White 1983, Klein and Bay 1990, 1994). Finally, through regular and moderate grazing, herbivores can maintain high nutrient and/or productivity levels longer into the growing season (Cargill et Jefferies 1984, Hik et Jefferies 1990, Gauthier et al. 1995, Raillard and Svoboda 1999).

Forage quality may not be the sole determinant of habitat use. Habitat characteristics can also influence habitat use through the amount of predator refugia available (Hughes et al. 1994a, Prevade and Krebs 2000) or varying patterns of snowmelt or snow depth (Adamczewski et al. 1988, Prop and de Vries 1993, Carrière et al. 1999). Factors such as interspecific competition (Parker 1977, Madsen and Mortensen 1987, Laing and Raveling 1993) and herbivore density (Sedinger and Raveling 1984, 1986) may also affect habitat use. In particular, high densities of herbivores may lead to dispersion towards sub-optimal habitats (Fretwell and Lucas 1970, Sutherland 1983) or to damage to the vegetation at the landscape level (Klein 1968, Kerbes et al. 1990, Manseau et al. 1996).

At La Pérouse Bay, Hudson Bay, Canada, the Lesser Snow Goose (*Chen caerulescens caerulescens*) is a well documented example of destruction of the vegetation due to overgrazing. Following rapid increase of the population, 2 454 hectares of salt marsh have been completely destroyed between 1973 and 1993 (Jano et al. 1998), representing approximately 65% of the landscape (Abraham et Jefferies 1997). Habitat degradation forced geese towards drier habitats, an unusual feeding habitat for them (Gadallah and Jefferies 1995).

On Bylot Island (73°N, Nunavut, Canada), the Greater Snow Goose population (*C. caerulescens atlantica*) tripled between 1983 and 1993 (Reed et al. 1998), reaching 156 000 birds in 1993. Goose families use wetlands intensively for feeding during brood-rearing (Hughes et al. 1994a) and they can consume up to 100% of the net above-ground primary production of their preferred plant *Eriophorum* spp. (Gauthier et al. 1995). Consequently, goose grazing affects plant production, decreases below-ground nutrient reserves and modifies vegetation composition of wetlands (Beaulieu et al. 1996, Gauthier et al. 1996). Concurrently to the general population increase on Bylot Island, there has been a 10-fold increase in the density of goose families in upland habitats between 1983 and 1993 (Reed et al. 1998). It is not yet clear if this increase represents a shift in habitat use related to decreasing food availability in wetlands (Reed and Plante 1997) or simply a parallel increase of goose densities over all habitats.

Habitat selection during the brood-rearing period is critical for geese. After hatching, goslings require high quality food to sustain a rapid growth rate and parents need to replenish fat and protein reserves depleted during incubation (Ankney and MacInnes 1978, Raveling 1979, Lesage and Gauthier 1997, Lepage et al. 1998). In addition, both adults and goslings need to be in good condition for the fall migration. Uplands, considered as being of poor quality for geese, cover a large proportion of the south plain of Bylot Island, approximately 90% of the landscape (Massé et al. 2001), and are characterised by a variety of plant communities (Chapter 2). Because little is known about use of uplands by families, our objective was to evaluate the importance of these habitats for geese on Bylot Island. We compared habitat use and selection of several wetland and upland habitats during the brood-rearing period and identified factors that could limit or incite families to use upland habitats.

METHODS

Study area

The study was conducted at the Bylot Island bird sanctuary, Nunavut Territory, Canada (73°08'N, 80° 00'W). The south plain of Bylot Island (ca 1600 km²) is the site of the largest Greater Snow Goose breeding colony (Reed et al. 1998) and is characterised by lowlands and upland plateaus intersected by numerous valleys (see Lepage et al. 1996 for details). Data were collected within a large glacial valley (ca 50 km²) on the northwest part of the south plain of Bylot Island. The valley is one of the most important brood-rearing area on the island.

Lowlands are characterised by an abundance of wetlands dominated by bryophytes and graminoids (Hughes et al. 1994a) whereas cryptogams, shrubs, graminoids and forbs are most abundant in uplands (Chapter 2). Uplands are characterised by rolling hills, valley bottom, terraces and steep hills covered by mesic plant communities (vegetation cover >95%), except for mountain tops and ridges (Chapter 2). Though less preferred by geese, uplands are used periodically and may contribute to the Island total carrying capacity for geese. At snow melt, geese feed in mountains and in snow free patches for species such as legumes and *Polygonum viviparum* (Gauthier 1993). Later in the brood-rearing period, geese graze on seeds, fruits and below-ground structures in upland habitats (Chapter 2). Uplands are also used at low densities throughout the brood rearing period (Hughes et al. 1994a).

Lemmings (*Lemmus sibiricus*, *Dicrostonyx groenlandicus*), arctic hare (*Lepus arcticus*), ptarmigan (*Lagopus mutus*) and caribou (*Rangifer tarandus*) are, with geese, the main herbivores of the island. Apart from lemmings, their density is low relative to snow geese. Our study was conducted in summer 2001, a year of moderate lemming abundance. During the brood-rearing period, foxes (*Alopex lagopus* and *Vulpes vulpes*) are the main predators of geese.

Habitat characteristics

Wetlands included two habitats: Pond/Lake and Wet meadow (Hughes et al. 1994a). A greater abundance of ponds and lakes was found in the Pond/Lake habitat than in the Wet meadow habitat (170.5 vs. 65.3 ponds or lakes m⁻²; Table 1). Vegetation available as forage for geese in the Pond/Lake habitat was mainly strips along the shore of ponds and lakes, and patches in the centre of wet polygons (Hughes et al. 1994a, Massé et al. 2001). Wet meadows were dominated by wet low-centre polygons surrounded by dry elevated rims (Hughes et al. 1994a, Massé et al. 2001). Proportion of available forage plants for geese was higher in Wet meadow than in Pond/Lake habitat (Table 1). Vegetation stands in the Pond/Lake and Wet meadow habitats were homogeneous, dominated by sedges such as *Carex aquatilis* var. *stans*, *Eriophorum scheuchzeri*, and *E. angustifolium*, and grasses such as *Dupontia fisheri*, *Pleuropogon sabinei*, and *Arctagrostis latifolia* (Zoltai et al. 1983, Gauthier et al. 1995). Geese feed on all these species (Gauthier et al. 1996).

Upland plant communities were more heterogeneous than wetlands and had relatively low abundance of graminoids and lakes or ponds typical of the two wetland habitats. Mesic polygon habitat was located in the valley bottom and was characterised by large, more or less defined polygons with exceptionally large rims (5-30 m). This habitat had few shallow ponds (Table 1) and was covered by mosses and lichens (72%), *Salix* spp. (19%) and graminoids (11%, *Arctagrostis latifolia*, *Alopecurus alpinus*, *Luzula* spp. and *Poa arctica*; Chapter 2). Mesic polygons also included few small scattered patches (polygon centre) dominated by graminoids typical of wetter sites (*Dupontia*, *Carex*). Pond/Lake habitat was bordered to the south by gentle north facing slopes dominated by mosses and lichens (81%), the ericaceous species *Cassiope tetragona* (25%), and graminoids (12%, *A. latifolia*, and *Luzula* spp.; Chapter 2). This habitat was named *Cassiope* hills and had only one small pond (Table 1). On the top of the hills, there was an elevated terrace (60-120 m a.s.l.) also covered by cryptogams (78%) and *Salix* spp. (15%) but with a high cover of graminoids (17-20%, Chapter 2). In this Mesic meadow, a few small ponds could serve as refuges (Table 1).

Within the three mesic habitats, there were isolated wet patches dominated by graminoids typical of wetter sites (*C. aquatilis* var. *stans*, *Eriophorum* spp., *D. fisheri*, *P. sabinei*, and *A. latifolia*; Table 1). Streams and gullies running through mesic habitats were also dominated by graminoids. For some analyses, we considered those Wet patches and the Stream/Gully habitats separate from the mesic ones (see below); the wet patches in the Mesic polygon habitat were too small and scattered to be distinguish from the blind (see above), thus were not considered.

Habitat delimitation

A 14 km² study area was delimited in the central portion of the studied valley (Figure 1). Examination of aerial photographs and ground observations showed that transition between habitats were typically abrupt. There were five main habitats in the study area: Pond/Lake and Wet meadow (wetlands), and *Cassiope* hill, Mesic polygon and Mesic meadow (uplands).

Habitats were mapped on black and white 1:13 000 or 1:16 000 (approx.) aerial photos. In order to validate habitat delimitation and to map sections that were not visible from the blinds (e.g. stream and gully sections), a person with colour flag around the knees (~goose height) walked along the border of each habitat while another person observed it with a telescope inside one of the blinds.

We determined visible areas of Mesic polygon, *Cassiope* hill, Mesic meadow and Wet patches on aerial photos using a PLANIX7 digital planimeter (estimated error = 6.5%). Streams and gullies' area that was visible from the blinds was estimated by measuring their width in the field and their length on aerial photos with a curvimeter. Density of ponds and lakes in each habitat was quantified by counting all open water surface with >10 m of diameter. Average distance from an area that could serve as a predator refugia (Pond/Lake habitat or glacier river) was also determined from aerial photos for each habitat. Since habitats had an elongated form, an axis was drawn in the middle of the habitat and a minimum of 4 perpendicular distances were taken along this axis to the border of the nearest refuge. We used the average of the perpendicular distances as an index of the distance between a given habitat and its nearest refuge.

Goose counts

A total of 26 goose counts were conducted between 12 July and 17 August 2001. The day was divided into four 6h blocks (6h-12h00, 12h-18h00, 18h-00h00, 00h-6h00), but we only made one count per day. Survey start times were systematically distributed over the daily cycle on successive days.

Scan samplings (Martin and Bateson 1993) were conducted from two elevated blinds, 100m and 300m above the valley bottom, providing an unobstructed view of the study area. Using a telescope (20-60X), goose families (a pair with young) were counted in each habitat and instantaneous behaviour was recorded. Because behaviours of the male and female are strongly dependant, they were noted at the pair level. Pair behaviour was classified as feeding if at least one of the adults had the head low, whether stationary or moving slowly. Feeding behaviour had precedence over other behaviours. To be considered in alert, both adults had to be stationary with their heads held high. Resting was recorded if one of the adults was sitting but not feeding, including those sleeping, brooding young or preening. Goose pairs moving with heads up were considered walking (includes swimming). Gosling behaviour was not determined because of their small size and dull colour making them difficult to observe.

Data analysis

To detect seasonal changes in habitat use, the brood-rearing period was divided into early, mid and late season (9-22 July; 23 July-4 August; 5-17 August 2001 respectively). Early season started at the median date of hatching in 2001 (9 July; G. Gauthier, unpublished data) and each period had 13 or 14 days. Because of small sample size, observations were combined in two blocks: day from 6h-18h00 and evening 18h-2h00.

Two analyses were made. The first one (landscape analysis) was performed to compare habitat use and selection between wetland and upland habitats (five major habitats; Table 1). The second (upland analysis) only included upland habitats but further recognized Wet patch and Stream/Gully within the upland (Table 1) as distinct habitats in order to understand which factors limit habitat use and selection of uplands by families. Effects of habitat, season, time of day and behaviour on the number of goose families were analysed using Generalized Linear Models with a log-link function and Poisson error term (Genmod procedure of SAS Institute Inc. 1999). Behaviour was included in the model because some habitats were known to be used by geese for resting (Hughes et al. 1994a). Log-linear models are appropriate for data that follow a Poisson distribution, i.e. for non-negative data where the variance increases with the mean (Agresti 1996). Overdispersion is common in the modelling of Poisson counts, as was the case here (predicted variability is greater than predicted by the random component of the model; Agresti 1996). Thus, the Pearson scale option was used in the model to correct for overdispersion.

Type 3 contrasts using the likelihood ratio statistics were used to test the significance of a variable in models with other variables already included. Non-significant interactions were removed, one at a time from higher to lower levels, until only significant interactions remained (Christensen 1990). Because of many zero count cells in the upland habitats analysis, we added a 1×10^{-4} constant to each cell count in order to estimate model parameters (Agresti 1996). We assumed no autocorrelation in data because time between two observations was long enough to enable goose families to move within the study area. Even though goose families tended to forage in groups, we assumed independence between families in habitat use because flocks were not stable throughout the brood-rearing period and families of a same group could use different habitats.

To evaluate selective use of habitats in each period, we compared habitat use with availability using a Chi-square test and Bonferroni simultaneous confidence intervals, with families as the sampling unit (Manly et al. 1993). To compare selection within and between habitats, we calculated a selection ratio \hat{W}_i :

$$\hat{W}_i = o_i / \pi_i$$

where o_i is the proportion of families that are in habitat i , and π_i is the availability of habitat i expressed as a proportion (Manly et al. 1993). Availability was defined as the surface area of each habitat relative to that of the study area. We use descriptive terms that pertain to density of use (e.g. “intensively used,” “under-used”) and avoid the terms “preference” and “avoidance” (Johnson 1980).

The term ‘habitat use’ refers to the usage of a habitat by a consumer whereas use is said to be selective when the habitat are exploited disproportionately to its availability ($\hat{W}_i > 1$, Johnson 1980). According to Johnson (1980), habitat selection at the home range scale corresponds to the third-order selection.

RESULTS

Landscape analysis

Behaviour, habitat, season and time of day, either alone or in combination, affected the number of goose counted (n=26 surveys; Table 2). On average, 389 ± 26 [SE] goose families (range: 132 to 710) were present in the study area during surveys (Figure 2a). Overall, families mostly used wetlands (86% of observations) compared to uplands (14% of observations). However, the proportion of families using wetlands during the day (6h-18h00) tended to decline later in the season whereas it increased in uplands (Figure 2b) but not at night.

Selection varied among habitats within each period of the season (early: $\chi_4^2 = 3327$, $p < 0.001$; mid-: $\chi_4^2 = 2175$, $p < 0.001$; late: $\chi_4^2 = 2035$, $p < 0.001$). The Pond/Lake habitat was intensively used and selected throughout the summer whereas all upland habitats were under-used (Figure 3). However, selection of the Pond/Lake habitat gradually decreased over the course of the brood-rearing period and selection of the Wet meadows increased to a level comparable to the Pond/Lake

habitat later in the season. Use, and thus selectivity, of *Cassiope* hills and Mesic polygons also increased later in the season. The Mesic meadows were under-used throughout the brood-rearing period. Variation in the number of families across surveys was greater in almost all habitats during the late season.

Effect of time of day on habitat use by goose families was weak in early and mid-season (Figure 4). However, later in the brood-rearing period, more families used the Wet meadows during the evening compared to the day. Very few geese were seen in upland habitats in the evenings during this part of the season except for one observation in Mesic polygons with 144 families. Pattern of use over the season between the day and evening block was variable. In early and mid-season, fewer families were counted in the evening than in the day, whereas the pattern was reversed in late season.

Most of the time, goose families were grazing when observed in the study area (65% of observations). Resting was the second most frequent behaviour (23%) while walking and alert posture were relatively minor (8% and 4% respectively). During the evening, mean number of families grazing and walking increased later in the season while resting declined (Figure 5). Excepted for the slight increase in grazing behaviour, no general trends were observed in the behaviour of geese over the course of the season during the daytime.

Uplands analysis

Again, behaviour, habitat, season and time of day, either alone or in combination, affected the number of goose counted in the upland habitats (n=26 surveys; Table 3). Between 0 and 219 goose families (mean: 55 ± 13) were counted in upland habitats during surveys. More families used uplands at the end of the season (85 ± 37) than in early and mid-season (47 ± 16 and 41 ± 15 respectively). Overall, more families used *Cassiope* hill and Mesic polygon habitats (439 and 566 families in total) compared to Mesic meadow, Wet patch and Stream/Gully habitats (116, 125 and 193 families respectively).

In early and mid-season, goose families were more evenly distributed among the different habitats while later in the summer families were concentrated in both *Cassiope* hill and Mesic polygon habitats (Figure 6a). Selection varied among habitats within each period of the season (early: $\chi^2_4 =$

922, $p < 0.001$; mid-: $\chi^2_4 = 422$, $p < 0.001$; late: $\chi^2_4 = 239$, $p < 0.001$). During the two first periods, the Wet patch and Stream/Gully habitats were strongly selected within the upland (Figure 6b). Mesic polygons were also used in proportion of their availability early in the season but less in mid-summer. At the end of the season, the Wet patch habitat was still selected but its selectivity, as that of the Stream/Gully habitat, abruptly decreased. In contrast, *Cassiope* hills and Mesic polygons were used selectively at the last period. Mesic meadows were sparsely used at all time.

In early season, families used upland habitats more during the day than in the evening, except for the Wet patch habitat (Figure 7). In contrast, at the end of the season, more families used the Mesic polygon habitat in evening than in daytime, but sample size is low.

As in the landscape analysis, grazing was the dominant behaviour (64% of observations) followed by resting (23%), walking (8%) and alert posture (5%). Mean number of families in each behaviour class varied among habitats (Figure 8). While families used Streams/Gullies, *Cassiope* hills, Mesic polygons and Mesic meadows mainly for feeding, Wet patches were predominantly used for resting.

DISCUSSION

Wetland habitats, especially Pond/Lake, were used intensively and were highly selected by Greater Snow Goose families throughout the season. After hatching, in order to meet the demands of rapidly growing goslings and to replenish fat and protein reserves of parents, goose families seek abundant, high-quality food, such as graminoids in wetlands, and spent most of their time feeding (Harwood 1977). Moreover, both flightless goslings and moulting parents are vulnerable to attacks by terrestrial predators. Thus, high density of refuges such as ponds and lakes, and high availability of graminoids explain the selective use of the Pond/Lake habitat (Hughes et al. 1994a). The importance of open water as refuges for geese during brood-rearing has also been observed in other studies (e.g. Prop et al. 1984, Laing and Raveling 1993).

As goslings become larger and more mobile, their dependence on refuges likely decreases, permitting families to exploit other habitats (Prop et al. 1980, Reed et al. 1992, Hughes et al. 1994a). This may explain the increasing use and selectivity of Wet meadows as the season progressed. The presence of some ponds, though less than in the Pond/Lake habitat, the proximity

of a large river, and the high availability of graminoids in this habitat can make it attractive to goose families (Table 1). Food depletion of the preferred plant species *Eriophorum* spp. in the Pond/Lake habitat may also explain the increased use of the Wet meadows later in the season. *Eriophorum* is a high quality food for geese because of its high protein and low fiber content (Manseau and Gauthier 1993, Gauthier et al. 1995).

By mid-august 2001, geese had consumed a greater proportion (56%) of *Eriophorum* biomass than of *Dupontia* (35%) in the Pond/Lake habitat (Gauthier et al. 2001). Since graminoids do not show overcompensation after grazing on Bylot Island (Gauthier et al. 1995), biomass of *Eriophorum* may have rapidly decreased over the season. Moreover, regrowth of plants following grazing diminishes as the season advances (Hik and Jefferies 1990). Consequently, as the season progresses, it may have become advantageous for families to use the abundant graminoids in Wet meadow habitat to maximize their rate of nitrogen intake. Seasonal declines in the use of the preferred foraging area, in response to lower availability, have been observed in other locations and resulted, in some cases, in diet and/or habitat use shifts (Sedinger and Raveling 1984, 1986, Vickery et al. 1995, Percival and Evans 1997). Differences in plant quality or phenology among habitats could have also promoted the use of the Wet meadows.

Social factors such as brood-size, dominance, aggressiveness and experience of parents (Black and Owen 1989, Hughes et al. 1994b, Mulder et al. 1995, Hupp and al. 1996) may also influence habitat use. As forage was reduced in the preferred feeding habitat (Pond/Lake), dominant families may have pushed subdominant ones to feed in the Wet meadows where density of ponds are lower.

At the end of the season, more families used upland habitats and large groups of geese fed in *Cassiope* hill and in Mesic polygon habitats. This behaviour was sporadic, as shown by the high variance, but was more frequent during the last surveys, and even more frequent after the surveys had stopped (pers. obs.). On Bylot Island, geese selected floral parts and seeds of many forb and graminoid species, and, late in the season, frequently grubbed rhizomes of *Oxytropis maydelliana* and bulbs of *Polygonum viviparum* (Chapter 2). These plant structures are rich in carbohydrates, lipids, proteins and phosphorus, and can be highly digestible (Thomas and Pevett 1980, Sedinger and Raveling 1984, Klein 1990). An increased use of upland habitats may reflect a shift in energy

requirements by geese for pre-migratory fat deposition, especially for goslings whose demand for proteins is reduced near the end of growth (Prevett et al. 1979, Sedinger and Raveling 1984, Lesage and Gauthier 1997).

Nutritive species like *Equisetum* spp., present in the Mesic polygon habitat and in the mountains, can also be a prominent component of the diet in fall and could have attracted families towards upland habitats (Gardarsson and Sigurdsson 1972, Prevett et al. 1979, Brackney and Hupp 1993). Finally, seasonal decline in quality of graminoids in wetlands may also explain this movement of geese toward uplands (Manseau and Gauthier 1993). Observations from Gauthier et al. (1995) suggested that graminoids were rapidly senescencing by mid-august, with 10 to 15% of the above-ground biomass already turning brown, especially *Eriophorum*. Combined to the reduced biomass of *Eriophorum*, goose families may thus increase their use of uplands where there is a diversity of some high-quality food (seeds, fruits and below-ground structures).

As the season progressed, geese were more mobile and used more habitats. However, this behaviour seemed to be restricted by the proximity of refuges, as the Mesic meadows were almost always avoided during summer even though they had a high availability of graminoids. Predation pressure was probably high in summer 2001 because there was a lemming peak the previous year. Breeding success of arctic foxes increases in years of high lemming abundance (Bêty et al. 2002), and thus the number of foxes are usually high in the year following a peak. High predation pressure by foxes could explain the relatively low use of upland habitats during the summer 2001, particularly for the Mesic meadows which had few ponds and were far from refuges. Declining light intensity during the evening in August may increase the risk of predation, explaining why geese did not stay in uplands during evening at that time, but concentrated in habitats with refuges such as ponds (Hughes et al. 1994a). Exceptionally, in 2001, we witnessed wolf attacks on goose families in August in our study area.

At the end of the summer, families were as much or more active, spending more time grazing and walking, at the end of the day as during the daytime. These behaviours may be linked with a requirement for pre-migratory fat deposition or with the increasing gut capacity and body size of goslings (Sedinger 1986, Lesage and Gauthier 1997). However, this may also reflect the declining availability of graminoids, especially of *Eriophorum* spp. as the season progressed. Brent Geese

(*Branta bernicla*) responded to the decreasing food supply by spending more time feeding, and by extending the time that they spent feeding at night (Percival and Evans 1997). Cackling Canada Goose goslings and Lesser Snow Geese in Alaska also increased foraging time under conditions of reduced food availability later in the brood-rearing period or during fall staging (*Branta canadensis minima*: Sedinger and Raveling 1988; *Chen caerulescens caerulescens*: Hupp and Robertson 1998, see also Vickery et al. 1995). Reduced food availability and quality at the end of the season in wetlands may have forced families to modify their feeding behaviour by spending more time searching for food, and in some cases, exploring for new forage opportunities in uplands.

High selectivity for Wet patches and Streams/Gullies within the upland could be linked to their high availability of graminoids and water, especially in the Wet patches where families could rest by the ponds (Table 1). However, as the season progressed, their selectivity declined even though upland habitats are increasingly used. Goose use of these habitats may decrease at the end of the summer due to an increase of foraging on seeds and fruits in mesic habitats, which Wet patch and the Stream/Gully habitats generally lack.

After hatching, many families migrated into the study area for the brood-rearing period. Thus, early in the season, high selection of the Stream/Gully habitat by the families could also be associated to their gentle microtopography which facilitated the movement of geese across upland habitat, especially for goslings who have short legs. Similarly, the occasional large number of families in the Mesic polygon habitat early in the season may reflect the arrival of geese in the study area on their way to large wetland areas. Families may also be attracted to this habitat by the presence of *Equisetum variegatum* which has a high protein and mineral content, and thus may be of particular interest to post-incubating emaciated females and growing goslings (Prevett et al. 1979, Thomas and Prevett 1982, Prop et al. 1984).

Conclusion

Use and selection of habitats by Greater Snow Goose families reflected a trade-off between food quality and abundance, refuge availability, and energetic demands. Abundance of high-quality food such as graminoids, and availability of refuges influenced the most use and selection of habitats by goose families. As the season progressed, decreasing food availability and quality of

the preferred feeding habitats, as well as increased need for fat deposit in preparation for the fall migration, likely explain modification by geese of their feeding behaviour and strategy of habitat use and selection.

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Table 1. Characteristics of Greater Snow Goose brood-rearing habitats at the landscape level (14 km² study area) and in more details within the Upland (7 km²), at Bylot Island, Nunavut Territory.

Habitats	Landscape analysis				Upland analysis			
	Habitat availability (% of total area)	Graminoids available (% cover ^a)	Pond/Lake density (n/km ²)	Distance from refuge ^g (m)	Habitat availability (% of total area)	Graminoids available (% cover ^a)	Pond/Lake density (n/km ²)	Distance from refuge ^g (m)
Pond/Lake	32.0	42 ^b	170.5	0	-	-	-	-
Wet meadow	14.4	59 ^c	65.3	227	-	-	-	-
<i>Cassiope</i> hill	15.3	13 ^d	0.5	494	28.2	12	0.5	494
Mesic polygon	21.1	17 ^d	6.5	799	38.6	16 ^d	4.5	799
Mesic meadow	17.2	21 ^d	10.3	1376	30.9	19	10.5	1376
Wet patch	-	-	-	-	1.4	90 ^e	51.8	880
Stream/Gully	-	-	-	-	0.9	93 ^f	0	485

^a % cover of the whole habitat area.

^b Calculated from Hughes et al. 1994a and Massé 1998.

^c Calculated from Massé 1998.

^d Calculated from Chapter 2 and includes wet patches dominated by graminoids, see methods.

^e Calculated from Massé 1998 and based on aerial photos.

^f Calculated from Massé 1998.

^g See methods.

Table 2. Regression model estimating the effects of behaviour, habitat, season and time of day on goose family abundance at the landscape level during the brood-rearing period, Bylot Island, Nunavut Territory, summer 2001. Overdispersion value= 9.8.

Source	DF	F value	Pr>F
Behaviour	3	236.2	<.001
Habitat	4	215.3	<.001
Season	2	0.46	0.633
Time of day	1	1.51	0.220
Behaviour*Season	6	5.86	<.001
Habitat*Season	8	2.96	0.003
Habitat*Time of day	4	3.03	0.017
Season*Time of day	2	3.99	0.019
Behaviour*Season*Time of day	9	2.71	0.004
Habitat*Season* Time of day	8	2.49	0.012

Table 3. Regression model estimating the effects of behaviour, habitat, season and time of day on goose family abundance in upland habitats during the brood-rearing period, Bylot Island, Nunavut Territory, summer 2001. Overdispersion value= 4.1.

Source	DF	F value	Pr>F
Behaviour	3	40.0	<.001
Habitat	4	15.6	<.001
Season	2	8.21	<.001
Time of day	1	0.00	0.947
Behaviour*Habitat	12	2.36	0.006
Habitat*Season	8	5.72	<.001
Habitat*Time of day	4	4.96	<.001
Habitat*Season* Time of day	10	3.01	0.001

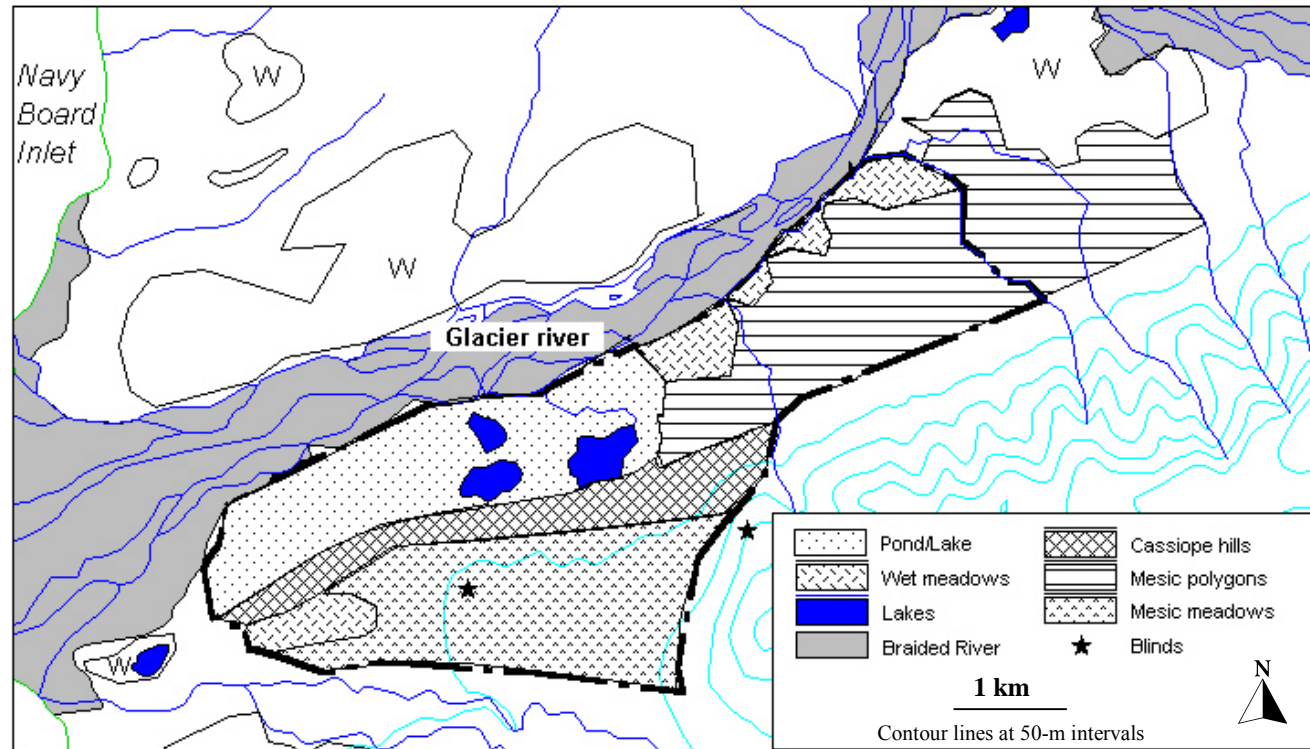


Figure 1. Map of the study area showing the five major habitats on Bylot Island, Nunavut. The broken line shows the limits of the 14 km² study area. The two observation sites are shown by stars. W: wetlands outside the study area, as in Hughes et al. 1994a.

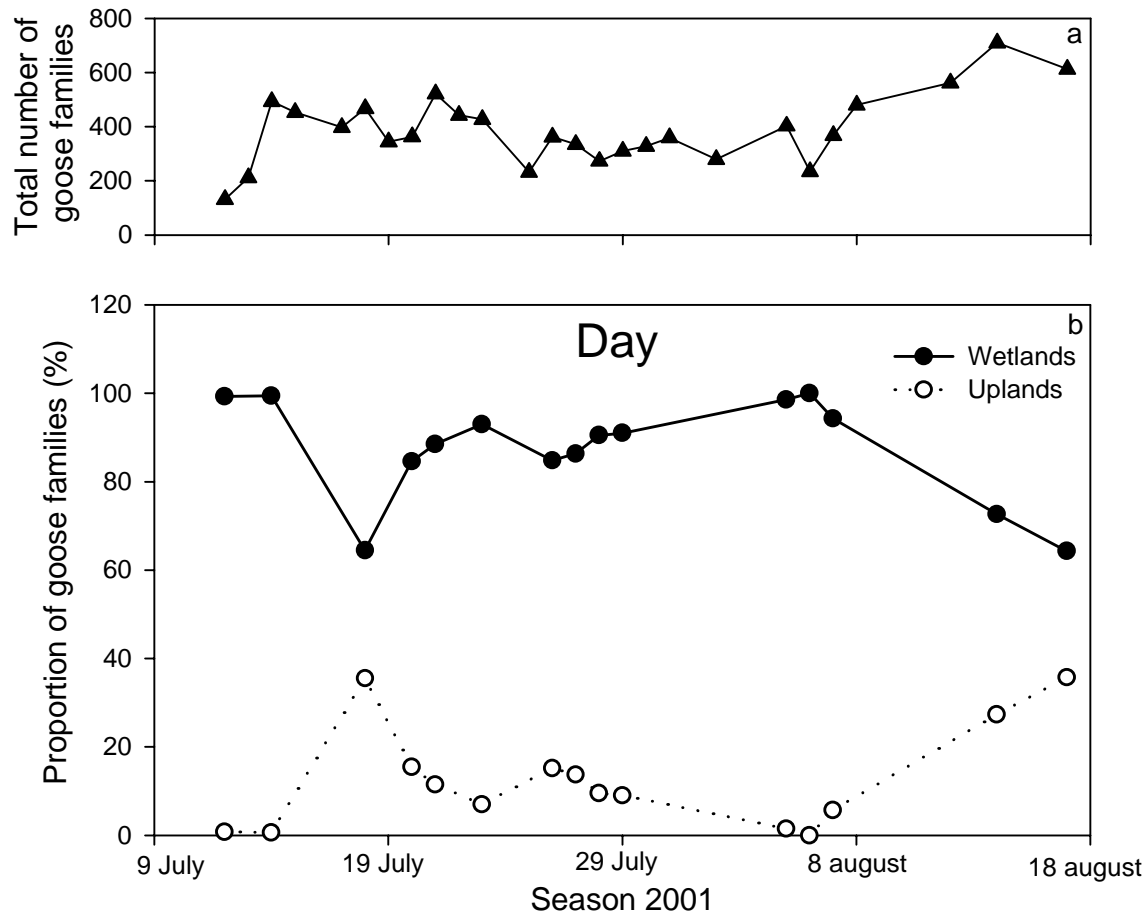


Figure 2. (a) Total number of Greater Snow Goose families counted at each of the 26 surveys and (b) proportion of families in wetland and upland habitats over the course of the season during the day only ($n = 15$), Bylot Island, 2001.

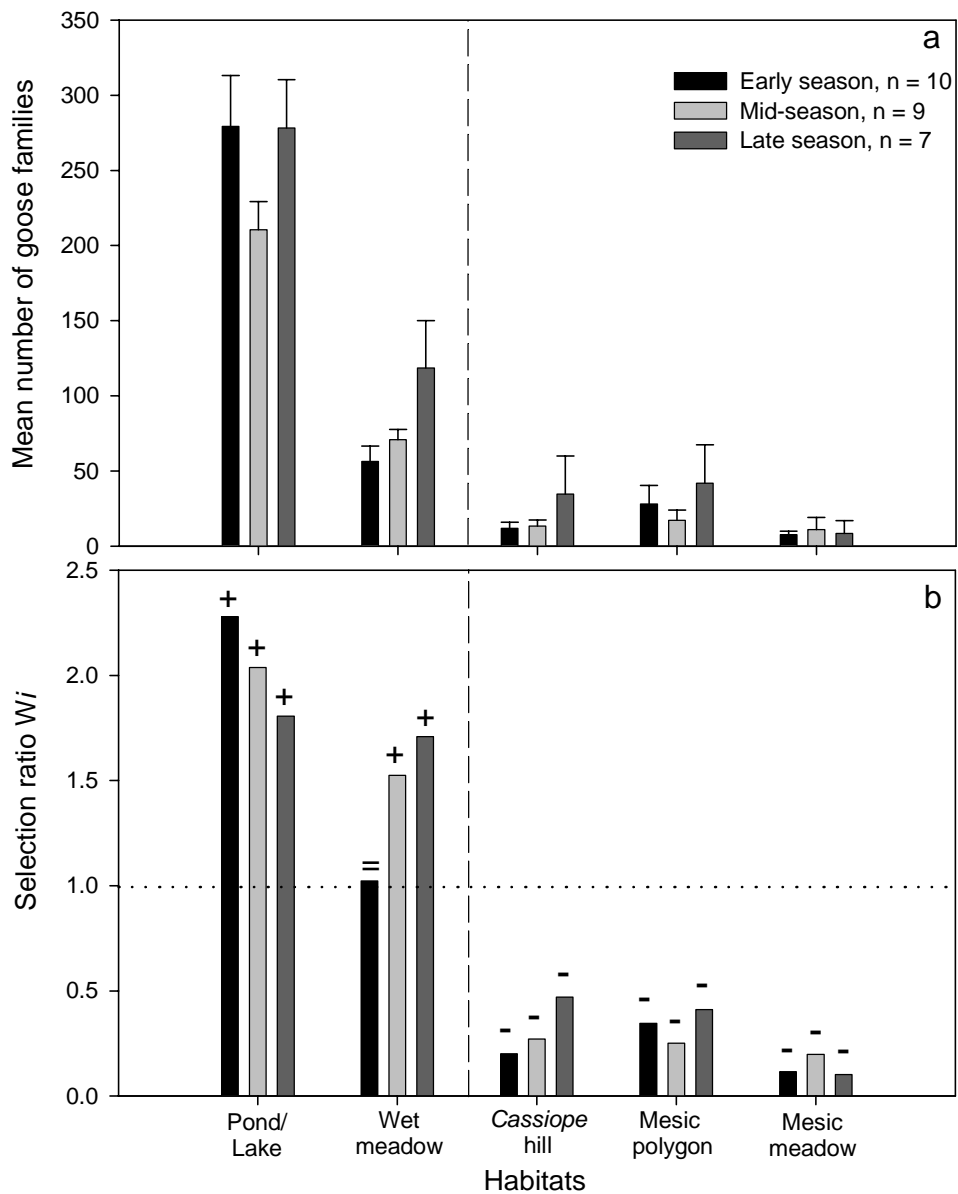


Figure 3. (a) Habitat use and (b) selection by goose families at the landscape level over the course of the season 2001 on Bylot Island. Signs above bars indicate result of selection. "=" indicates the habitat is used in proportion to its availability; "+" indicates the habitat is selectively used; and "-" stands for an habitat that is under-used. Wetlands are on of the left side of the dash line and uplands on the right side. n: number of surveys.

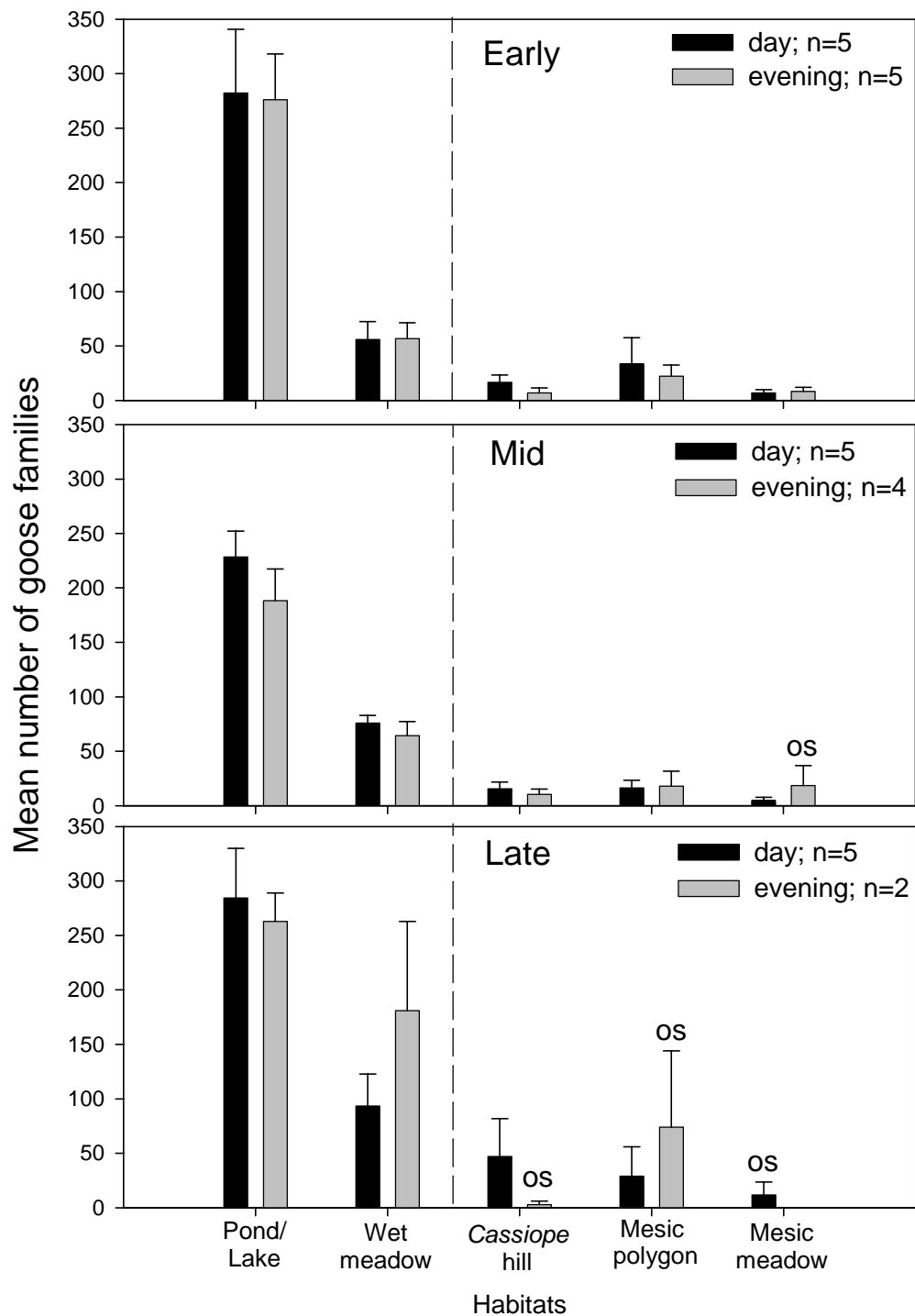


Figure 4. Effect of time of day on habitat use by goose families over the course of the season 2001 at the landscape level on Bylot Island. Wetlands are on the left side of the dash line and uplands on the right side. n: number of surveys; OS: indicates observation of geese in only one survey within the period.

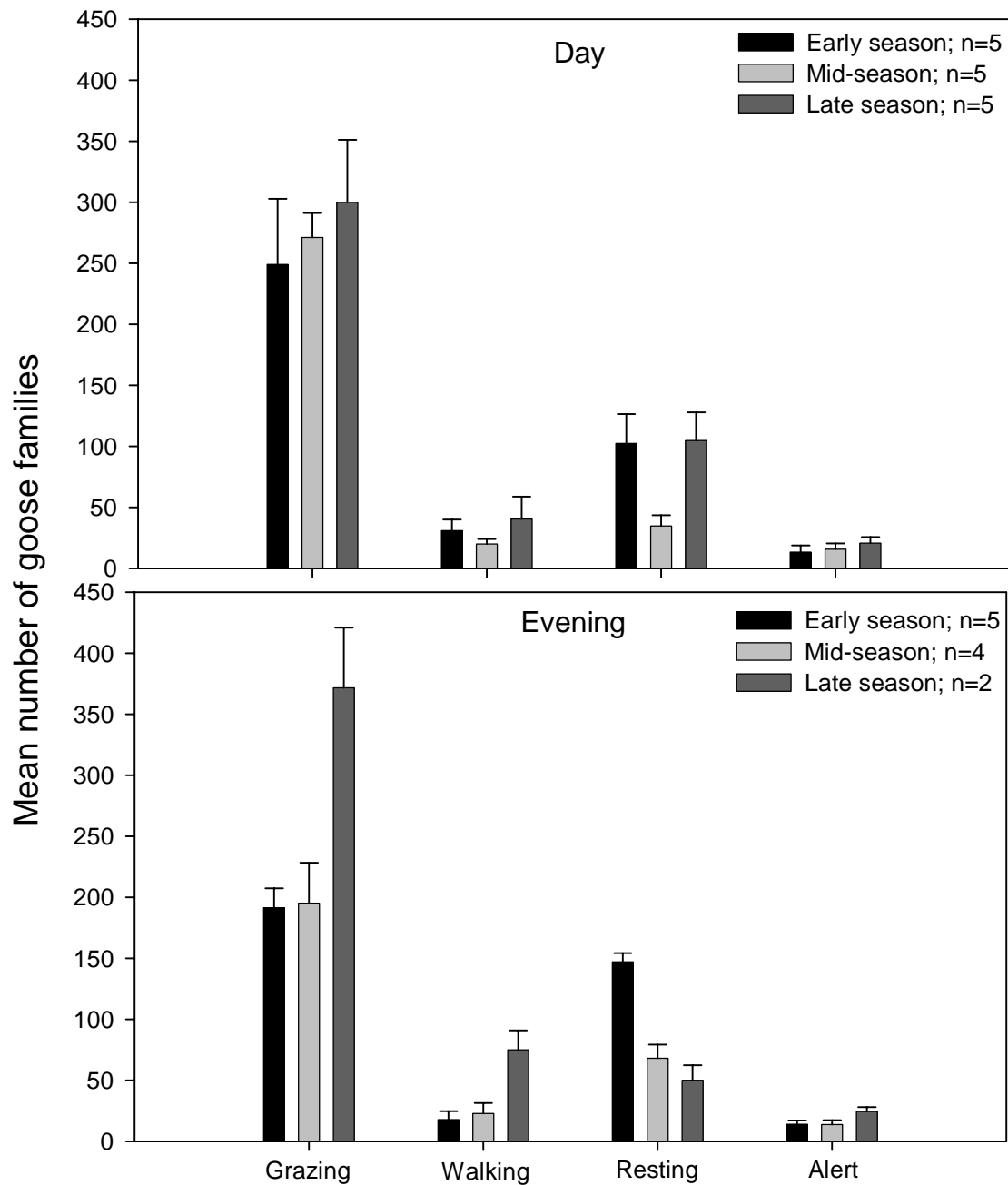


Figure 5. Effect of behaviour, period of the summer and time of day on number of goose families counted, Bylot Island, 2001. n: number of surveys.

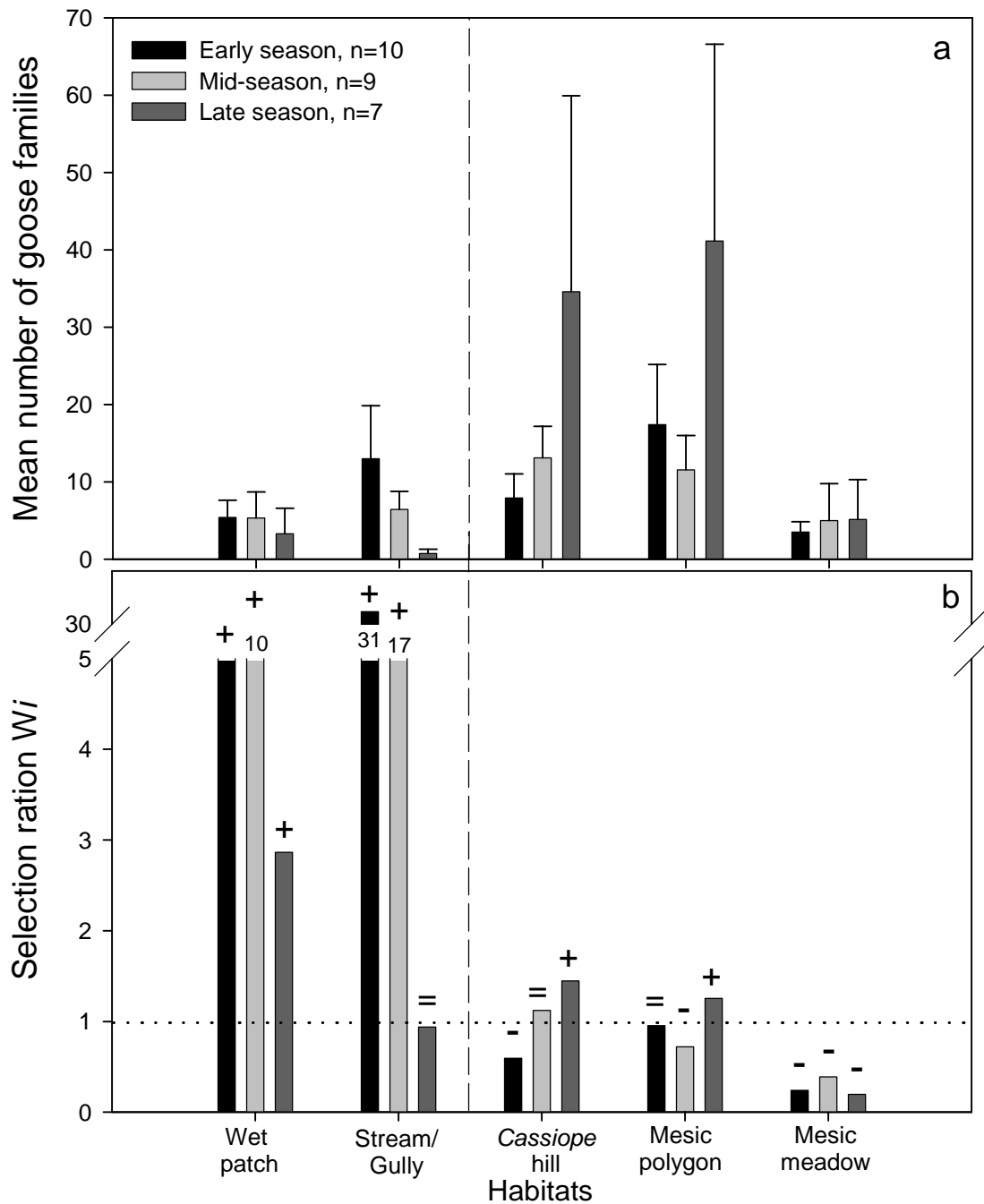


Figure 6. (a) Habitat use and (b) selection of upland habitats by goose families over the course of the season 2001 on Bylot Island. Signs above bars indicate result of selection. "=" indicates the habitat is used in proportion to its availability; "+" indicates the habitat is selectively used; and "-" stands for an habitat that is under-used. Wet habitats are on of the left side of the dash line and mesic habitats on the right side. n: number of surveys.

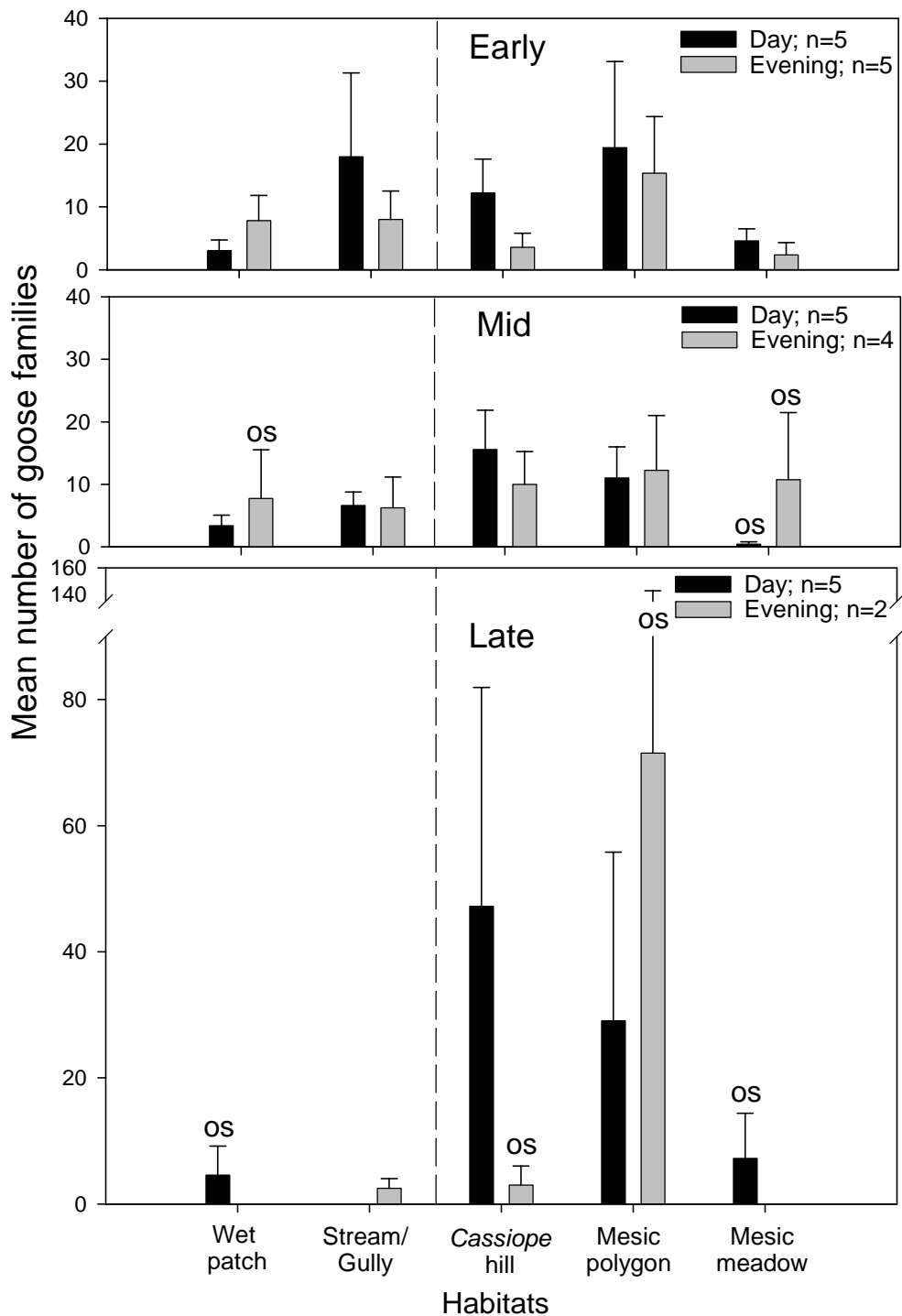


Figure 7. Effect of time of day on habitat use by goose families over the course of the season 2001 at the landscape level on Bylot Island. Wet habitats are on the left side of the dash line and mesic habitats on the right side. n: number of surveys; OS: indicates observation of geese in only one survey within the period.

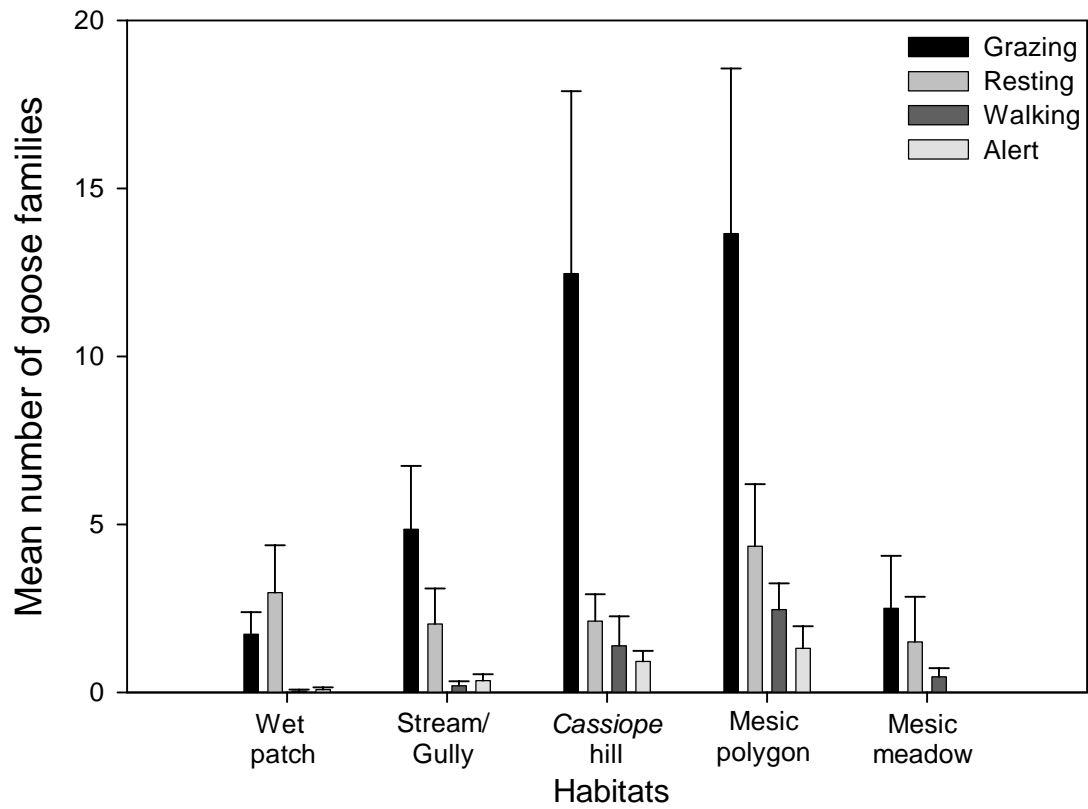


Figure 8. Effect of behaviour on habitat use by goose families during the summer 2001 on Bylot Island. n = 26 surveys.

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Annexes supplémentaires

Appendix 1. Vegetation cover and frequency (%) in the 10 plant communities identified by Twinspan classification, Bylot Island, Nunavut, 2000 and 2001.

* Indicator species identified by Twinspan classification; C = cover%; F = frequency%.

Communities	1		2		3		4		5		6		7		8		9		10	
Species	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
Graminoids																				
<i>Carex aquatilis</i> var. <i>stans</i>					T	17			+	25										
<i>Arctagrostis latifolia</i>	5	100	13	100	8	91	3	86	5	100	2	86								
<i>Carex bigelowii</i>	T	19	+	100	+	100			T	13										
<i>Carex misandra</i>	+	6			T	4														
<i>Carex rupestris</i>					+	4														
<i>Eriophorum scheuchzeri</i>			T	13	T	4														
<i>Eriophorum triste</i>	1	44	1	50	1	61	T	14												
<i>Juncus biglumis</i>	T	6	T	25	+	43			T	13	T	57								
<i>Luzula nivalis</i>	4	100	4	100	5	100	1	100	1	100	1	100			+	45			+	50
<i>Hierochloa alpina</i>	T	6	+	13	+	30	+	29							+	9			T	17
<i>Luzula confusa</i>	3	100	1	88	2	87	3	100	2	100	1	71	+	40	+	91	T	33	2	100
<i>Festuca brachyphylla</i>	T	6	T	13	*+	74	+	71	+	100	+	100	3	100	1	91	+	33	1	100
<i>Alopecurus alpinus</i>	T	19	+	63	+	78	2	71	2	100	1	100	7	100	2	100	1	100	2	100
<i>Poa alpigena</i> var. <i>colpodea</i>											T	29			T	18			T	17
<i>Poa arctica</i>	+	75	+	75	+	91	2	100	1	100	1	100	4	80	3	100			1	100
<i>Deschampsia brevifolia</i>									T	13					T	18				
<i>Elymus arenarius</i> ssp. <i>mollis</i>													+	40					+	33
<i>Festuca baffinensis</i>											+	29	+	40	+	27	1	67		
<i>Poa glauca</i>													2	100	+	100				
<i>Trisetum spicatum</i>													+	100	T	18	+	100		
<i>Carex maritima</i>																			1	50
Total	12		20		17		12		11		6		16		6		3		8	
Forbs																				
<i>Equisetum variegatum</i>									T	13										
<i>Potentilla vahliana</i>							T	14												
<i>Saxifraga hirculus</i>									T	38										
<i>Lycopodium selago</i>	T	6																		
<i>Pyrola grandiflora</i>	+	25					T	14												
<i>Ranunculus nivalis</i>	T	25	T	13	T	13														
<i>Ranunculus sulphureus</i>					T	39														
<i>Saxifraga foliolosa</i>	T	6	T	38	T	52														
<i>Silene acaulis</i>					T	4														
<i>Draba corymbosa</i>	+	63	T	50	+	78	+	86	+	100	+	100			T	9	T	33		
<i>Draba lactea</i>	T	81	+	100	+	100	T	86	T	88	+	100			T	27			T	50
<i>Eutrema edwardsii</i>	T	63	+	75	+	61	+	100	T	63	T	14			T	36	T	33		
<i>Melandrium apetalum</i>					T	26					+	71			T	9				
<i>Saxifraga hieracifolia</i>	T	75	T	50	T	74	T	71	T	88	T	43			+	36				
<i>Cardamine belidifolia</i>	+	100			T	4	T	43	T	38	T	14	T	20	T	18			T	50
<i>Oxyria digyna</i>	1	94	+	88	+	74	+	43			+	71	+	20	T	18	1	100	T	17
<i>Saxifraga flagellaris</i>					T	22			T	13	+	71			T	9				
<i>Pedicularis arctica/hirsuta</i>	T	50	T	100	T	48	+	86	T	50	+	86	T	20	*+	82			T	17
<i>Potentilla hyparctica</i>	T	19	T	38	+	74	T	29			T	43			T	18			+	83

Communities	1		2		3		4		5		6		7		8		9		10			
Species (continued)	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F		
<i>Sagina intermedia</i>					T	43					T	43								+	50	
<i>Saxifraga nivalis</i>	T	56	T	63	+	78	+	71	T	50	+	100	T	20	+	73	T	67	T	50		
<i>Saxifraga caespitosa</i>	T	6			T	39	+	71	T	75	+	86			T	45	+	67				
<i>Saxifraga oppositifolia</i>	+	38	T	38	+	78	+	86	1	88	1	86			+	64	T	33	1	50		
<i>Armeria maritima</i>	T	6			T	4														T	33	
<i>Cerastium alpinum</i>	T	19	T	25	*+	78	+	71	+	100	+	100	+	100	+	91	1	100				
<i>Papaver radicum</i>	T	25	T	25	*T	74	+	100	T	13	1	100	T	20	+	64	+	100	+	67		
<i>Polygonum viviparum</i>	+	88	1	88	1	83	1	86	+	88	1	100	5	100	1	100	T	33	T	33		
<i>Saxifraga cernua</i>	T	44	T	50	+	74	T	86	T	63	+	100	T	80	T	91	+	67				
<i>Stellaria longipes</i>	+	94	+	100	+	100	+	100	+	100	+	100	1	100	+	100	+	100	+	100	1	100
<i>Draba cinera/nivalis</i>							T	29				T	29	T	20	T	36	+	100	T	50	
<i>Minuartia rubella</i>											+	71				T	18	T	33			
<i>Arnica alpina ssp. angustifolia</i>														3	100	T	18	T	33			
<i>Astragalus alpinus</i>					+	9	1	86	1	100	2	71	24	100	7	100	4	100				
<i>Draba glabella</i>							T	14	T	25			+	100	+	82						
<i>Draba subcapitata</i>					T	9									T	9	+	67	T	17		
<i>Androsace septentrionalis</i>														T	20							
<i>Melandium triflorum</i>														T	20							
<i>Epilobium latifolium</i>																			*1	100		
<i>Erysimum pallasii</i>																			T	67		
<i>Equisetum arvense</i>													1	40	T	9						
<i>Erigeron eriocephalus</i>													+	60			+	67				
<i>Melandrium affine</i>							T	14	T	13	T	14	+	100	T	64						
<i>Oxytropis maydelliana</i>					+	13	*5	100			1	71	16	100	8	100	T	67				
<i>Potentilla nivea</i>													+	60							T	33
<i>Ranunculus pedatifidus</i>													+	20	T	18						
<i>Saxifraga tricuspidata</i>	T	6					+	14	T	13	T	14	+	80	+	91	1	67	T	17		
<i>Taraxacum phymatocarpum</i>												T	14	T	40	T	18	+	100	T	50	
<i>Cerastium arcticum</i>					T	9												T	33	+	100	
<i>Cochlearia officinalis</i>																					T	17
<i>Honckenya peploides</i>																					+	17
<i>Melandrium sp</i>																					T	17
<i>Ranunculus sabinei</i>																					T	50
<i>Saxifraga rivularis</i>					T	4															T	50
Total	2		2		3		9		2		8		52		18		9		2			
Shrubs																						
<i>Salix lanata</i>									+	63												
<i>Vaccinium uliginosum</i>							+	29														
<i>Cassiope tetragona</i>	*25	100	4	100	2	61	+	14			T	14										
<i>Salix herbacea</i>	+	63	5	88	1	52																
<i>Salix reticulata</i>	+	31	2	38	1	57	*9	100	*9	100	T	14			+	36	T	33				
<i>Dryas integrifolia</i>	1	31	T	13	2	57	4	86	1	100	4	86	T	20	1	73						
<i>Salix arctica</i>	9	100	9	100	13	100	25	100	10	100	29	100	76	100	41	100	6	100	2	67		
Total	35		20		19		39		20		33		76		42		6		2			

Note: +, cover <0,5%; T, cover <0,05%

Appendix 2. Vascular plants of the studied valley, including uplands and lowlands. Underlined species are from Hughes 1992 (include species from lowlands and uplands).

- Alopecurus alpinus* J.E. Smith
Androsace septentrionalis L.
Arctagrostis latifolia R. Br.
Armeria maritima (Mill.) Willd.
Arnica alpina ssp. angustifolia (J. Vahl) Maguire
Astragalus alpinus L.
Cardamine belidifolia L.
Cardamine pratensis L. s. lat.
Carex aquatilis var. stans (Drej.) Boott
Carex bigelowii Torr.
Carex glacialis Mack.
Carex maritima Gunn.
Carex membranacea Hook.
Carex misandra R. Br.
Carex rupestris All.
Cassiope tetragona (L.) D. Don
Cerastium alpinum L. s. lat.
Cerastium arcticum Lange s.l.
Chrysoplenium tetandrum (Lund) Fries
Cochlearia officinalis L. s. lat.
Colpodium vahlianum (Liebm.) Nevski
Deschampsia brevifolia R. Br.
Deschampsia pumila (Trin.) Ostenf.
Draba cinerea Adams /*nivalis* Liljebl. *
Draba corymbosa R. Br.
Draba glabella Pursh
Draba lactea Adams
Draba subcapitata Simm.
Dryas integrifolia M. Vahl
Dupontia fisheri R. Br.
Elymus arenarius ssp. mollis (Trin.) Hultén
Epilobium latifolium L.
Equisetum arvense L.
Equisetum variegatum Schleich.
Erigeron eriocephalus J. Vahl
Eriophorum angustifolium Honck.
Eriophorum scheuchzeri Hoppe
Eriophorum triste (Th. Fr.) Hadac & Löve
Erysimum pallasii (Pursh) Fern.
Eutrema edwardsii R. Br.
Festuca baffinensis Polunin
Festuca brachyphylla Schultes
Melandrium affine J. Vahl
Melandrium apetalum (L.) Fenzl
Melandrium triflorum R. Br.
Melandrium sp**
Minuartia biflora (L.) Schinzl. & Thell.
Minuartia stricta (Sw.) Hiern.
Minuartia rubella (Wahlenb.) Hiern.
Oxyria digyna (L.) Hill
Oxytropis maydelliana Trautv.
Papaver radicans Rottb. s. lat.
Pedicularis arctica R. Br. /*hirsuta* L. ***
Pedicularis lanata Cham. & Schlecht.
Pedicularis sudetica Willd.
Pleuropogon sabinei R. Br.
Poa alpigena var. colpodea (Fr.) Schol.
Poa arctica R. Br.
Poa glauca M. Vahl
Polygonum viviparum L.
Potentilla hyparctica Malte
Potentilla nivea L. s. lat.
Potentilla vahlia Lehm.
Pyrola grandiflora Radius
Ranunculus hyperboreus Rottb.
Ranunculus nivalis L.
Ranunculus pedatifidus Sm.
Ranunculus sabinei R. Br.
Ranunculus sulphureus Sol.
Sagina caespitosa (J. Vahl) Lange
Sagina intermedia Fenzl
Salix arctica Pall. s. lat.
Salix herbacea L.
Salix lanata L.
Salix reticulata L.
Saxifraga caespitosa L. s. lat.
Saxifraga cernua L.
Saxifraga flagellaris Willd.
Saxifraga foliolosa R. Br.
Saxifraga hieracifolia Waldst. & Kit.
Saxifraga hirculus L.
Saxifraga nivalis L.
Saxifraga oppositifolia L.
Saxifraga rivularis L. s. lat.

Hierochloe alpina (Sw.) R. & S.
Hierochloe pauciflora R. Br.
Honckenya peploides (L.) Ehrh.
Juncus albescens (Lange) Fern.
Juncus biglumis L.

Luzula confusa Lindebl.
Luzula nivalis (Laest.) Beurl.
Lycopodium selago L.

Saxifraga tricuspidata Rottb.
Senecio congestus (R. Br.) DC.
Silene acaulis L.
Stellaria crassipes Hult.
Stellaria longipes Goldie s. str.
Taraxacum phymatocarpum J. Vahl. s. lat.****
Trisetum spicatum (L.) Richt.
Vaccinium uliginosum L. s. lat.

* *Draba cinerea/nivalis* was counted as one species.

** *Melandrium* sp. was not counted as a distinct species because it is probably one of the three species already mentioned.

*** *Pedicularis arctica* and *P. hirsuta* were both identified by Lynn J. Gillespie (Canadian Museum of Nature), thus they were counted as two distinct species.

**** *Taraxacum phymatocarpum* : includes *T. alaskanum*, *T. hyparcticum*, *T. arcticum*, *T. lateritium*, *T. mackenziense* and *T. pumilum* (pers. comm. Laurie L. Consaul, Canadian Museum of Nature)