

ArcticWOLVES

Arctic Wildlife Observatories Linking Vulnerable EcoSystems



Final synthesis report



An International Polar Year project

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TABLE OF CONTENTS

Foreword	iii
In memoriam	v
Executive summary	vii
Research team	xi
Acknowledgments	xxi
Field sites	xxiii
Chapter 1. Introduction	1
<i>Gauthier et Berteaux</i>	
Chapter 2. The human dimension	9
<i>Berteaux et al.</i>	
Chapter 3. Small mammals	14
<i>Reid et al.</i>	
Chapter 4. Geese	28
<i>Gauthier et al.</i>	
Chapter 5. Arthropods	40
<i>McKinnon et al.</i>	
Chapter 6. Shorebirds	50
<i>McKinnon et al.</i>	
Chapter 7. Birds of prey	62
<i>Gauthier et al.</i>	
Chapter 8. Arctic and red foxes	76
<i>Berteaux et al.</i>	
Chapter 9. Tundra food webs	88
<i>Legagneux, Lecomte et al.</i>	
Chapter 10. Integrating scientific and traditional ecological knowledge	100
<i>Berteaux et al.</i>	
Chapter 11. General conclusion	111
<i>Gauthier et Berteaux</i>	
References	117

IN MEMORIAM



Robert L. Jefferies (1936-2009)

Bob Jefferies was a significant person in the lives of many of those involved in the ArcticWOLVES collaboration. During his long career in ecology and plant biology, he was teacher, mentor, colleague and great friend, and stood out as an exemplary gentleman scientist and academic. He provided a model for all of us to emulate both in work ethic and integrity, and in his caring approach to people. His fundamental contributions to the study of northern ecosystems have stimulated and challenged our undertakings. His plant-herbivore studies of geese set standards of investigative procedure and problem solving in the field which we have sought to maintain. He was involved with all aspects of ArcticWOLVES including development of protocols, field work, reporting and administration. He was particularly emphatic about the value of the ArcticWOLVES comparative approach across multiple sites and multiple years and the value of the collaborative approach to synthesis and reporting. His untimely passing has robbed us of the opportunity to benefit from his unique experience and insight, but we trust his legacy of learning will carry us through the tasks that lie ahead.

Kenneth F. Abraham

EXECUTIVE SUMMARY

The International Polar Year project ArcticWOLVES (www.cen.ulaval.ca/arcticwolves/) is a study of tundra ecosystems aimed at understanding food webs and associated ecosystem processes, and assessing current and future impacts of climate change on tundra wildlife. The project involved a coordinated effort by an international team of over 150 researchers, students and collaborators at 15 field sites across the circumpolar regions of Canada, Fennoscandia, Russia and Greenland. Our project focused on the small to mid-size tundra wildlife, primarily small mammals, geese, shorebirds, birds of prey, foxes, weasels, and insects. ArcticWOLVES was highly successful in fostering collaborations among researchers from many institutions spread over 9 countries and in developing strong partnerships with northern organizations and communities.

A new pattern emerging from our study is that, when large mammalian herbivores are absent, the tundra food web appears more likely to be dominated by predator-prey than by plant-herbivore interactions. However, we encountered large variations among sites in this pattern, depending of local features. The combined predation rate of several species appears an important regulating factor of small mammal populations at several Canadian sites but certain snow conditions also seem necessary for the occurrence of peak lemming populations during the summer. Geese are another important summer herbivore at many sites and several populations have increased considerably in recent decades due to events occurring on their wintering ground. At very high goose density, predator limitation weakens and the system becomes dominated by herbivore-plant interactions, with potentially strong negative impact on tundra vegetation. Arctic arthropods play essential ecological roles in the functioning of the tundra, for instance as the main prey of many birds. As temperatures increase, diversity and overall biomass of arthropods in the Arctic should increase and peaks in abundance may shift or broaden. These changes in resource availability may have a negative impact on the reproduction of insectivorous birds. However, shorebird populations may even be more affected by change in predator abundance. We found a large variation in nest predation risk across the Canadian Arctic as predation risk for shorebird eggs decreased considerably at higher latitudes. Shorebird predator-prey relationships could be altered via changes in the abundance of predators or of alternative prey for predators. Another key conclusion is that the functioning of an ecosystem cannot be understood in isolation as subsidies from adjacent ecosystems can shape the structure and dynamic of food webs. This is most evident for top predators such as the arctic fox and several avian predators, for which the marine ecosystem may provide essential foraging ground during the winter. Therefore, a broader, cross-ecosystem perspective may be required when assessing the status or threats faced by these predators. Competition between predators is also an important issue as the northward expansion of some species may pose a significant threat to native tundra predators. Traditional ecological knowledge collected at several sites also allowed us to corroborate, complement or find contrasts with the scientific results that we gathered at those sites for a few key tundra species.

Besides the new scientific findings presented in this report, our project also provided other significant legacies. These include (1) a full database of most of the information that we collected on the abundance, distribution, reproduction and ecology of a large number of wildlife species; (2) the development of durable international collaborations that will extend well beyond the International Polar Year and will increase our scientific capacity in the North; and finally, (3) upgraded research facilities along with new scientific equipment at some of our field sites that will allow a continuation of several of the objectives of our project beyond the International Polar Year.

RÉSUMÉ

Le projet de l'Année Polaire Internationale ArcticWOLVES (www.cen.ulaval.ca/arcticwolves/) est une étude de l'écosystème de la toundra visant à mieux comprendre les réseaux trophiques et les processus qui y sont associés, et à évaluer les impacts actuels et futurs du changement climatique sur la faune arctique. Le projet a été l'œuvre d'un effort coordonné par une équipe internationale de plus de 150 chercheurs, étudiants et collaborateurs mené à 15 sites de terrain dispersés à travers le monde circumpolaire au Canada, en Scandinavie, en Russie et au Groenland. Notre projet s'est concentré sur la faune de petite et moyenne taille de la toundra, principalement les petits mammifères, les oies, les oiseaux de rivage, les oiseaux de proies, les renards, l'hermine et les insectes. Le projet ArcticWOLVES a réussi à mettre en place des collaborations fructueuses entre les chercheurs de nombreuses institutions provenant de 9 pays différents et à développer des partenariats solides avec les organisations et les communautés nordiques.

Un nouveau patron émergeant de notre étude est que, en l'absence de gros mammifères herbivores, le réseau trophique de la toundra semble davantage dominé par les interactions prédateur-proie que plante-herbivore. Nous avons néanmoins observé de fortes variations dans ce patron entre les sites dépendant des conditions locales. La pression de prédation combinée de plusieurs espèces ressort comme un facteur de régulation important des populations de petits mammifères à plusieurs sites au Canada quoique des conditions spécifiques d'enneigement semblent aussi nécessaires pour qu'un pic d'abondance de lemmings survienne durant l'été. Les oies sont un autre herbivore important à plusieurs sites pendant l'été et de nombreuses populations ont considérablement augmenté au cours des dernières décennies, principalement à cause d'événements qui se sont produits sur leurs sites d'hivernage. Lorsque les densités d'oies deviennent très élevées, la limitation par les prédateurs s'atténue et le système devient dominé par les interactions plante-herbivore, avec potentiellement un fort impact négatif sur les plantes de la toundra. Les arthropodes arctiques jouent un rôle écologique essentiel dans le fonctionnement de l'écosystème de la toundra, notamment en étant la proie principale de nombreuses espèces d'oiseaux. Avec l'augmentation de la température, la diversité et la biomasse totale d'arthropodes devraient augmenter dans l'Arctique et le pic d'abondance devrait se déplacer ou s'élargir. Ces changements dans la disponibilité des ressources pourraient avoir un impact négatif sur la reproduction des oiseaux insectivores. Toutefois, les populations d'oiseaux de rivage pourraient être encore plus affectées par le changement dans l'abondance des prédateurs. En effet, nous avons trouvé une forte variation spatiale dans le risque de prédation de leurs nids à travers l'Arctique canadien avec une diminution importante de ce risque aux latitudes les plus hautes. Les relations prédateur-proie des oiseaux de rivage devraient être altérées par des changements dans l'abondance des prédateurs ou de leurs proies alternatives. Une autre conclusion clé est que le fonctionnement d'un écosystème ne peut pas être compris de façon isolée car les subsides d'écosystèmes voisins peuvent affecter la structure et la dynamique des réseaux trophiques. Ceci est le plus évident pour les prédateurs au sommet du réseau comme le renard arctique et plusieurs oiseaux de proies pour qui l'écosystème marin peut fournir une aire d'alimentation essentielle pendant l'hiver. Conséquemment, l'évaluation du statut et des menaces qui pèsent sur ces prédateurs va nécessiter une perspective plus large et qui transcende les écosystèmes. La compétition entre les prédateurs est aussi une préoccupation importante parce que l'expansion vers le nord de certaines espèces peut poser une menace significative pour les prédateurs indigènes de la toundra. Le Savoir Traditionnel autochtone nous a aussi permis de corroborer, compléter ou parfois de trouver quelques différences avec les résultats

scientifiques que nous avons récoltés à plusieurs sites pour certaines espèces clés de la toundra.

En plus des nouvelles découvertes scientifiques présentées dans ce rapport, notre projet a généré plusieurs autres réalisations significatives. Celles-ci incluent une base de données complète regroupant la grande majorité des informations recueillies sur l'abondance, la distribution, la reproduction et l'écologie d'un grand nombre d'espèces fauniques; le développement de collaborations internationales durables qui vont se poursuivre dans le futur et qui vont augmenter notre capacité scientifique dans le nord; finalement, des infrastructures de recherche améliorées incluant plusieurs nouveaux équipements scientifiques à certains de nos sites d'étude, lesquelles vont permettre la poursuite de plusieurs des objectifs de notre projet au-delà de l'Année Polaire Internationale.

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ArcticWOLVES final synthesis report



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ArcticWOLVES final synthesis report



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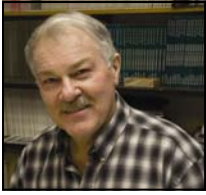


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ArcticWOLVES final synthesis report



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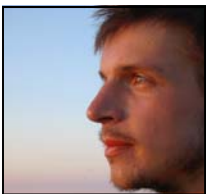
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ArcticWOLVES final synthesis report



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ArcticWOLVES final synthesis report

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ArcticWOLVES final synthesis report

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FIELD SITES



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CHAPTER 1. INTRODUCTION

Gilles Gauthier and Dominique Berteaux

The arctic tundra biome spans over 3 continents and 8 countries. It extends over more than 3,500 km from the tree-line to the northernmost land masses of the planet. Harsh climatic conditions prevail in the arctic tundra, as average annual temperature ranges from about -2°C at its southern limit to -18°C at its northern limit and the ground is covered by snow during 6 to 9 months. Despite these extreme conditions, there is a rich diversity of habitats, from dense shrubs to wetlands and polar semi-deserts. The tundra also harbours a surprising animal biodiversity, especially during summer when many migratory birds come to nest. The need to feed links species through complex food webs. The tundra food web remains one of the least known, largely due to the logistic difficulties involved in conducting scientific studies in the Arctic. The environmental knowledge gained by people inhabiting the North, through their use and observation of wildlife and the land, is sometimes considerable (Gagnon and Berteaux 2006). But most of it is not written, and ecological relations are sometimes too complex to be understood without experiments or the help of sophisticated equipment.

This lack of scientific knowledge is especially worrying because the tundra could change very quickly in the near future. The exploitation of minerals and energy, and the increasing exchanges between the Arctic and the rest of the planet are threatening the environment in several ways. However, human-induced climate warming is probably the most important source of future changes in this region. No other place on the planet is currently warming faster than the Arctic, and the Intergovernmental Panel on Climate Change (IPCC 2007) projects for the area a 3°C to 6°C increase in annual average surface air temperatures during this century.

Studying the impact of climate change on wildlife is difficult (Berteaux et al. 2006). Physical systems such as the permafrost or the oceans should respond to temperature increases in a predictable manner, following well-known physical laws. But the situation is

different for living systems. Although plants and cold-blooded animals such as insects can sometimes respond in straight ways to temperature change, the response of warm-blooded animals is generally more complex. These animals have indeed evolved an ability to regulate their body temperature, which partly buffers them from short-term temperature variations. In many situations, indirect effects brought about by climate change may have a greater impact on animal populations than direct ones. For instance, if climate warming changes the timing at which plants are most nutritive more quickly than it changes the timing at which the energy demand of herbivores is greatest, this may lead to a loss of synchrony (a trophic mismatch) between the two groups of organisms, with negative consequences for herbivore populations (Durant et al. 2007, Post and Forchhammer 2008). Similarly, invasion of the food web by new competitors or predators moving up north may disrupt the food web and cause the demise of some species (Post et al. 2009). In this case, a single, difficult-to-predict event such as the arrival of a new species can have dramatic effects on the ecosystem. The food web may also respond very differently depending on whether it is primarily regulated by predators (top down control) or by plants (bottom up control). For instance, invasion of the system by a new predator would have a much greater impact in a food web with a top-down control than in one with a bottom-up control. In the former case, the effects could trickle down the food chain, leading to a so-called trophic cascade (Bazely and Jefferies 1996, Ims et al. 2007). The control of the tundra food web remains a controversial issue (Gauthier et al. 2009, Krebs 2011), in part due to the lack of empirical evidence.

It is in this context that we developed the International Polar Year (IPY) project Arctic Wildlife Observatories Linking Vulnerable Ecosystems (ArcticWOLVES). The major aims are to improve our understanding of the tundra food web and to assess current and future impacts of climate change on wildlife. The pro-

ArcticWOLVES final synthesis report

ject involves a coordinated effort by an international team of over 150 researchers, students and collaborators at 16 primary field sites and several secondary sites across the circumpolar regions of Canada, Norway, Russia and Greenland (Fig. 1). The component of the project that took place in Eurasia is also referred to as the Arctic Predators project. ArcticWOLVES is primarily a field-based project involving intensive data collection primarily over the period 2007-2009. Using common and standardized methodologies at most field sites we applied a comparative approach to work at a very large spatial scale. Moreover, many of the sites used for the project already had a history of wildlife-related studies, which added a temporal perspective in several cases. In some instances, we conducted manipulative experiments to address more thoroughly some specific questions. In other instances, we used innovative methods such as satellite-tracking to study animal movement

or stable isotopes (proportion of primary elements [i.e. atoms] that make up all living and inert matter) to measure trophic relationships.

Wildlife is closely linked to the culture and health of northern people across the Arctic. These people thus have a vested interest in the changes that are currently occurring or will occur in the tundra food web because these changes will undoubtedly affect their way of life. Northern people also have an intimate knowledge of wildlife species surrounding them. Therefore, our project has attempted to merge western scientific methodology with the traditional knowledge of northern inhabitants whenever possible. One advantage of this approach is that it can provide information that allows us to expand our temporal and spatial resolution of wildlife population studies (Gagnon and Berteaux 2009).

Our project is focused on the small to mid-size wildlife species of the tundra food webs, and on their food resources. This mainly

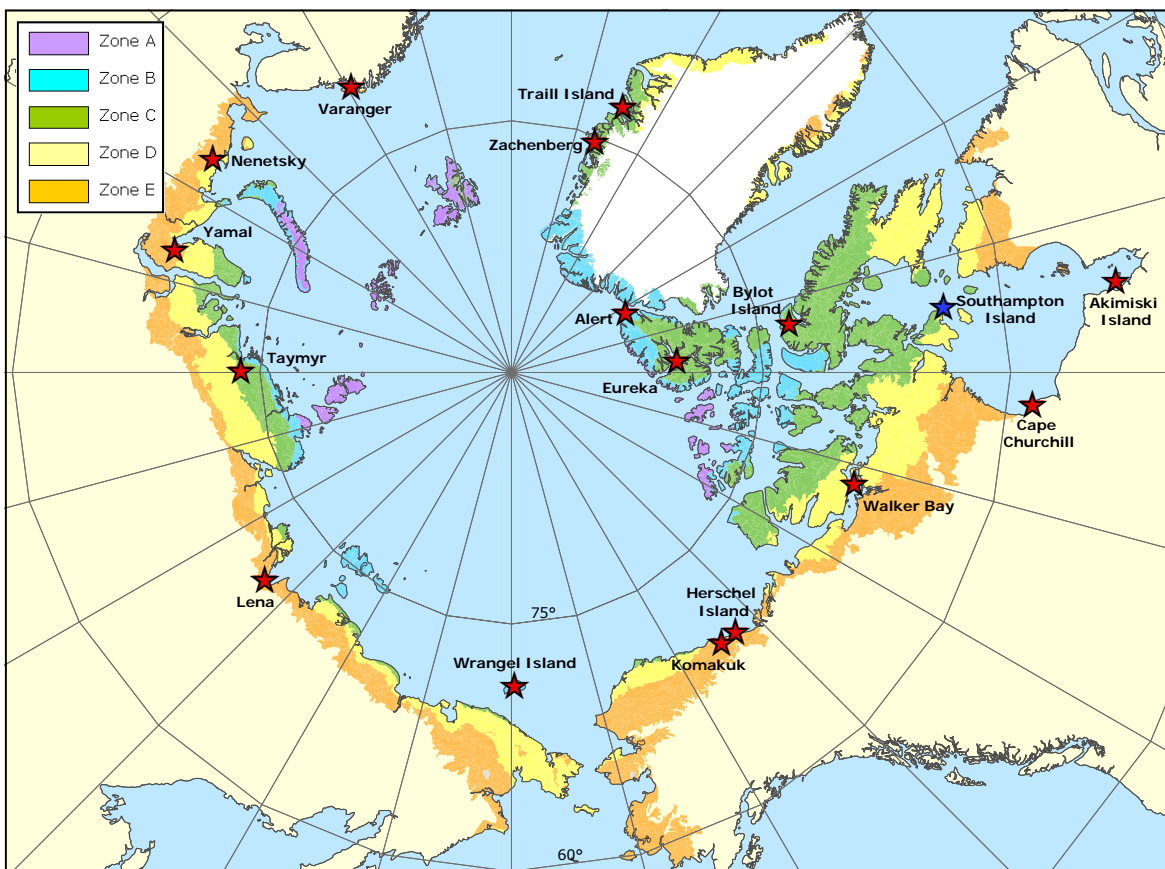


Figure 1. ArcticWOLVES and Arctic Predators study sites (red star) located on a circumpolar Arctic map of bioclimate sub-zones. Blue star indicates secondary study sites. Sub-zone A (herb barrens) is the coldest, and sub-zone E (erect low shrub tundra) is the warmest. Common descriptions for other zones are: B – prostrate dwarf shrub; C – hemi-prostrate dwarf shrub; D – erect dwarf shrub (modified from Walker et al. 2005).

includes small mammals, geese, shorebirds, birds of prey, foxes, weasels and insects. Large mammals like caribou, muskox and wolves were not among the species of prime interest in this project but incidental information on these species was gathered at field sites where they were a significant component of the food web. Even though the project was structured into sub-components often focusing on specific species or groups of closely-related species, we strived to study the interactions among species and how each species or functional group affect each other in the food web.

The goal of this report is to present a synthesis of the key findings of our project and their implications. More specifically, our objectives are to: (1) provide up to date information on the status and trend of the wildlife species that we studied, (2) provide new information on the dynamics of the tundra food web, and (3) identify vulnerabilities to climate change and other perturbations in our focus species and discuss the implications for their future. The report is structured into 10 core chapters in addition of this introductory chap-

ter. Chapter 2 presents the human dimension and the challenges associated with the completion of such a large scale project in some of the most remote parts of the planet. Chapters 3 to 8 focus on the key taxonomic groups that we studied (small mammals, geese, insects, shorebirds, birds of prey and foxes). Chapter 9 presents a global food web perspective and examines how trophic interactions will likely be impacted by a changing environment. Chapter 10 addresses the interface between wildlife and people and relies primarily on traditional knowledge information. Finally, we present the key conclusions of the project in Chapter 11.

We tried to present our science in a language as simple as possible, so that the report becomes accessible to a wide audience. It is our hope that the information presented here will be of interest to decision-makers, governmental and private organizations and northern communities. We included references to the scientific literature to allow those interested into the details of our work to track the scientific facts and data analyses supporting our conclusions.

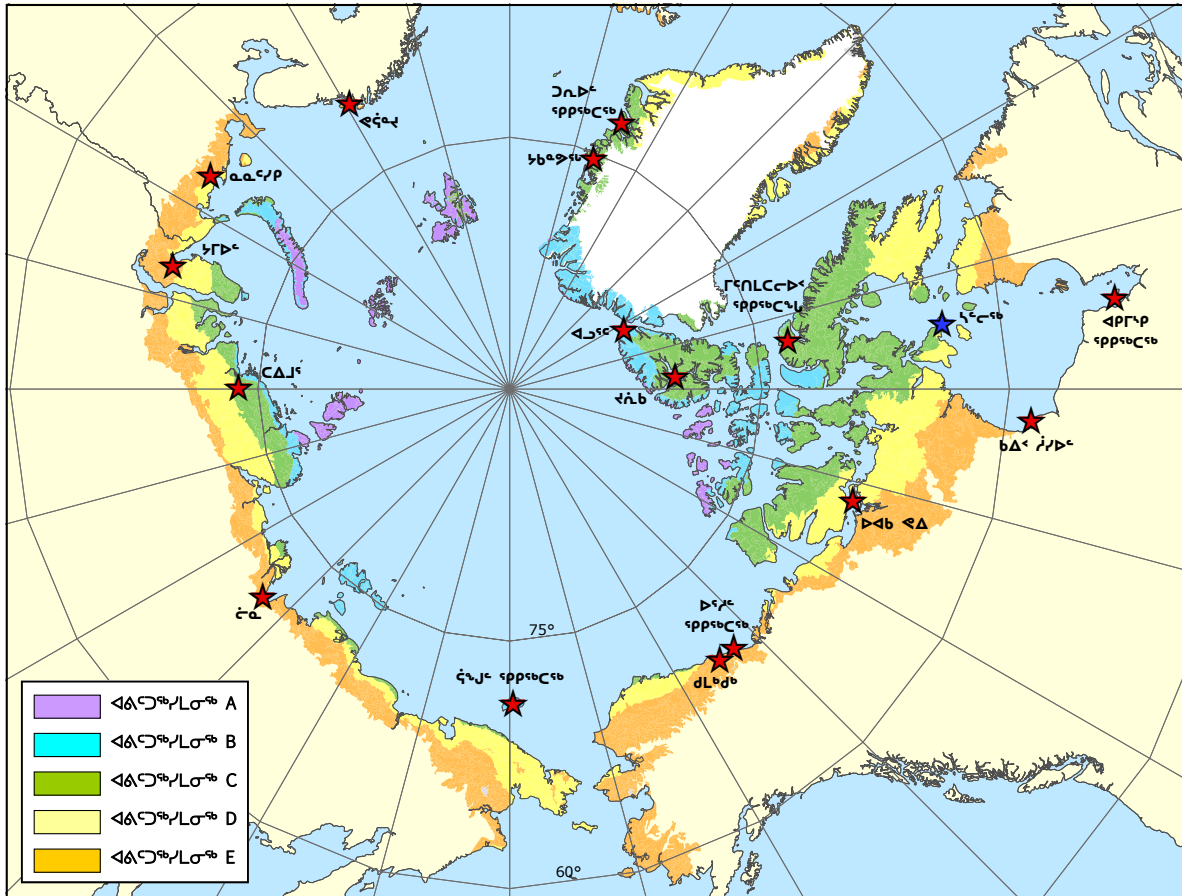
ArcticWOLVES final synthesis report

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A helicopter pilot is refueling his aircraft. Conducting ecological research in the wide expanses of the Arctic involves meticulous logistical planning and cooperation between experts of all kinds, from skilled pilots to vigilant polar bear watchers.

የደህንነቱን ለማስጠበቅ በአርክቲክ ክልል ላይ ምርመራዎችን ለማድረግ የሚያስፈልጉት ማለፊያዎችን በትኩረት ለማግለገል ማስፈጸም የሚገባዎት ነው። ለዚህም ማስፈጸም የሚያስፈልጉትን የሰው ኃይል ለማስጠበቅ እና ለማረጋገጥ በጥንቃቄ ማስፈጸም ያስፈልጋል።

ArcticWOLVES participants met once a year during the IPY program (April 2007 in this case). Field work is done in small teams and data analysis and report writing are solitary exercises. In contrast, scientific meetings are highly social events that are of tremendous importance to share good ideas, avoid repetition of mistakes, and build motivation and team spirit.

ArcticWOLVES ለመግባቱ በሰነድ ላይ ለመገናኛት ያሳለፍላችኋል። በዓለም አቀፍ ደረጃ ላይ ለሚደረግ ዓለም አቀፍ የጥናት ሰነድ አሰጣጥ (የሰነድ አሰጣጥ) ላይ ለማሳተፍ ለሚያስፈልጉት ማስፈጸም የሚያስፈልጉትን የሰው ኃይል ለማስጠበቅ እና ለማረጋገጥ በጥንቃቄ ማስፈጸም ያስፈልጋል።



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- 1 - Eurasian collared lemming © Nicolas Lecomte
- 2 - Norwegian lemming © Rolf A. Ims
- 3 - red-backed vole © Alice J. Kenney
- 4 - tundra vole © Nicolas Lecomte
- 5 - North American collared lemming © Keith Hubert
- 6 - singing vole © Alice J. Kenney
- 7 - Siberian lemming © Arnaud Tarroux
- 8 - brown lemming © Alice J. Kenney

CHAPTER 3. SMALL MAMMALS

Lead author: Donald G. Reid

Co-authors: Frédéric Bilodeau, Angélique Dupuch, Dorothee Ehrich, Gilles Gauthier, Scott Gilbert, Alice J. Kenney, Charles J. Krebs, Douglas W. Morris, Niels Martin Schmidt, Benoit Sittler and Eeva Soininen

Abstract

Small mammals (lemmings and voles) are a very important animal group of the tundra as they are the primary food source for a large number of tundra predators. We studied small mammals in northern Norway, Russia, Canada, and Greenland. The species at our study sites were not substantially different from previous records, but patterns of change in abundance over time have changed, and show substantial variability. In eastern Greenland, high abundance of collared lemmings occurred every 4 or 5 years until 1998, but abundance has remained low since then at several sites. At Varanger, Norway, we noted a high abundance of Norwegian lemmings in 2006-07, something rarely observed since the 1970s. The frequency of high abundance populations at the Russian sites varied from 3 to 5 years. On Bylot Island, Nunavut, high abundance occurred every 2 to 4 years over the last two decades. In northern Yukon, populations have been low at Komakuk Beach (mainland) for a few years, but we observed much greater range in lemming abundance across years on nearby Herschel Island. At most sites with more than one species, high abundance occurred for all species in the same year. Population fluctuations in brown lemmings are wider than those in collared lemmings where the two species live together. Where collared lemmings are the only species, they fluctuate more widely in abundance, suggesting that brown lemmings out-compete collared lemmings. We investigated the winter ecology of small mammals, and found that certain snow conditions are likely necessary for strong winter population growth. We used snow fencing to make snow deeper at three Canadian sites. The animals preferred areas where the fencing created deeper snow with resulting warmer ground temperatures, but there were no clear effects of deeper snow on winter reproduction. Models of winter population growth coupled with data on snow conditions showed that populations could grow at greater rates under deeper and less dense snow. In Greenland, the time at which winter snow starts, and the length of winter, appear to affect lemming population growth. We investigated the summer diet of lemmings and voles at Varanger, Norway, and found no strong influence of animal abundance on the range of foods in the diet, and no evidence that summer food availability could slow down the animals' population growth. We investigated the competitive interactions between brown and collared lemmings at two Canadian sites, and found that the strength of competition varied between sites and sometimes between years. Collared lemmings were more stable in their choice of drier upland habitats. Brown lemmings appeared more flexible in their habitat choice, which was influenced by predation risk. Our collective observations indicate that the patterns of change in population abundance of lemmings and voles are even more variable than previously recognized. No single reason can apparently explain their impressive, periodic changes in abundance. The variability is largely found in the length of the period of low abundance between irruptions, and the range of abundance from lowest to highest. These sources of variation require more focussed research.

Species ranges

The small mammals of the circumpolar arctic tundra are mainly rodents (lemmings, voles and ground squirrels), but also include lagomorphs (hares) and insectivores (shrews).

In Eurasia there are five species of lemmings belonging to two genera (Jarrell and Fredga 1993). Brown lemmings (genus *Lemmus*) are represented by three geographically disjunct species. The North American brown lemming (*Lemmus trimucronatus*) occurs in Siberia, east of the River Kolyma. The Siberian lemming (*L. sibiricus*) is distributed from the Kolyma River west to the White Sea. It occurs as a morphologically and genetically distinct subspecies (*L. s. portenkoi*) on Wrangel Island (Fedorov et al. 1999). The Norwegian lemming (*L. lemmus*) is the only mammal endemic to Fennoscandia, where it inhabits arctic and subarctic tundra, but also alpine tundra further south. The Eurasian collared lemming (*Dicrostonyx torquatus*) occurs from the Bering Sea to the White Sea, but collared lemmings on Wrangel Island (sometimes named *D. vinogradovi*) belong to the North American species, *D. groenlandicus*.

In the shrub tundra zone of the Eurasian Arctic, several species of voles are common, often more so than lemmings. The tundra or root vole (*Microtus oeconomus*) is widespread from Fennoscandia to the Bering Strait and into western North America. In the southern Russian Arctic there are two other *Microtus* voles. The narrow-skulled vole (*M. gregalis*) has a patchy distribution and also inhabits steppes further south in Asia. The Middendorff's vole (*M. middendorffi*) is ecologically distinct but morphologically very similar to the narrow-skulled vole. The grey-sided vole (*Myodes rufocanus*) is common in Fennoscandian tundra, but extends only marginally into the tundra zone in Russia.

In Arctic North America, *Dicrostonyx groenlandicus* is the most widespread species, occupying tundra from western Alaska to east Greenland, but is replaced by the closely related species, *D. hudsonius*, on the Ungava peninsula (northern Quebec and Labrador). The North American brown lemming (*Lemmus trimucronatus*) has a similar distribution but is absent from Ungava, the northern Canadian archipelago (Queen Elizabeth Islands) and Greenland. In North America the tundra vole

occupies true tundra habitats from the coastal plain of Alaska through the mainland west of Hudson Bay. This species also occupies the shrub tundra where it is joined in the west by the tundra red-backed vole (*Myodes rutilus*). The singing vole (*Microtus miurus*) lives primarily in montane tundra and taiga forests of the Yukon and Alaskan cordillera.

Ground squirrels (genus *Urocitellus*, formerly *Spermophilus*; Helgen et al. 2009) only occupy mainland arctic tundra habitats, and only in Siberia and North America west of Hudson Bay. Hares are found on tundra in Eurasia (*Lepus timidus*), western Alaska (*L. othus*), and Greenland and North America east of the Mackenzie River (*L. arcticus*). Finally, various shrew species of the genus *Sorex* inhabit southern arctic tundra, including mainland Fennoscandia, Russia, and North America west of Hudson Bay. They are absent from Greenland, Ungava and most of the arctic islands (Nowak 1991).

ArcticWOLVES project researchers working in the shrub tundra of southern Yamal (western Siberia) have noted that Siberian lemmings, abundant until the 1990s, have almost disappeared in the last decade. Further north on Yamal, they are still common (Sokolov et al. 2010). At Nenetsky we caught several birch mice (*Sicista betulina*) and water voles (*Arvicola amphibious*), neither a typical tundra species, in an area where no small mammal trapping had previously occurred.

On the north Yukon coastal plain (Komakuk), we caught northern red-backed vole and found evidence of singing vole, indicating possible new distributions for these species as this region becomes increasingly shrub tundra in a warming climate. We found that *M. oeconomus* reproduces under the snow in spring (probably April) (see also Krebs et al. 1995). In north Yukon we documented a metapopulation dynamic for *U. parryii* with a currently extinct population at Komakuk (2006-2010) despite previous presence (1950s and 1960s), and long-distance male spring breeding dispersal (mainland to Herschel Island, >10 km) but apparent inability to establish a population on the Island probably because of sex-biased dispersal when sea ice is present. Our small mammal live-trapping in north Yukon provided new documentation for the distribution of both bar-

ArcticWOLVES final synthesis report

ren-ground shrew (*S. ugyunak*) and tundra shrew (*S. tundrensis*) on the coastal plain, and the latter species on Herschel Island.

Patterns of population fluctuation and synchrony

Arctic lemmings and voles vary substantially in population density over time. These fluctuations often have remarkably constant period (3 to 5 years between peak densities), and wide amplitude (25 to 200 fold differences between low and peak phases), and are termed cycles (Stenseth and Ims 1993). Various demographic and behavioural parameters are associated with the phases of the cycles (Stenseth and Ims 1993). Reproductive rates are highest in the increase phase and decrease rapidly at the peak. The increase phase is often associated with winter reproduction. Body mass for various age and sex classes is highest during late increase and peak phases. Animals are more aggressive at higher densities.

Historically, cyclic dynamics have been reported for tundra lemmings and voles, especially towards the northerly portions of species' ranges and in species distributed at higher latitudes (Stenseth 1999). However, it is also clear that such cycles are heavily dampened or non-existent in certain regions (e.g. Krebs et al. 1995, Krebs et al. 2002), and have exhibited less regularity in period and dampening amplitudes in recent years, possibly as a result of a changing climate (Ims et al. 2008, Kausrud et al. 2008, Schmidt et al. 2008, Gilg et al. 2009).

Where strong peaks occur they are generally synchronous among species at one site and often over fairly large regions, though certainly not over all arctic regions (Erlinge et al. 1999, Krebs et al. 2002, Gruyer et al. 2008). The dominant explanation for synchrony is concurrent heavy predation pressure on all species brought about by strong aggregative numerical response of nomadic and migratory predators, and strong breeding numerical response of all predators (Ims and Steen 1990, Krebs et al. 2002).

During the ArcticWOLVES project we documented patterns of lemming abundance at many circumpolar sites, and expanded previously available time series. In Greenland, cyclic lemming populations with peaks every 4

to 5 years have been reported since the early 20th century (Pedersen 1942), and documented more thoroughly by long term studies on Traill Island (Karupelv Valley) since 1988 and Zackenberg since 1996, where densities ranged from <0.1 to >15 lemmings per hectare (Sittler 1995, Gilg 2002, Schmidt et al. 2008). However the last strong peak occurred in 1998 and since then the cycle seems to have dampened at relatively low densities with no clear peak during IPY (Fig. 1A).

In Eurasia we studied small mammal dynamics in detail at six sites during IPY. On the Varanger Peninsula in northern Norway, voles typically fluctuate with a period of five years whereas Norwegian lemmings reach high population densities only in some vole peak years. Previous to IPY, lemmings peaked only 1 or 2 times since the 1970s, but in 2006-2007 they reached peak densities in Varanger (Fig. 1B). Lemming populations started to grow later than the sympatric voles and followed a steeper increase, but all species crashed simultaneously in 2008. Lemming populations grew more quickly at higher altitudes, and this effect was strongest for winter population growth rates, supporting previous findings about the importance of winter climate and snow properties for Norwegian lemmings (Ims et al. 2011). Interestingly lemming populations in northern Norway started to grow again in late summer 2010.

In Nenetsky, tundra voles were the most abundant small mammal, along with low numbers of collared lemmings, birch mice and water voles. The last peak previous to IPY occurred in 2004 and our data showed a peak in 2008 (Fig. 1C), suggesting a period of four years and rather low amplitude of tundra vole fluctuations. Collared lemmings were trapped only in the peak years, 2004 and 2008, and occurred at low frequency in raptor pellets, indicating that they are regularly present but at low densities.

In the shrub tundra of southern Yamal, five species of small mammals were caught, with Middendorff's and narrow-skulled voles being the most common. Their density increased considerably over summer 2009 and possibly reached a peak in 2010 (Fig. 1D). The previous significant small mammal peak in the area had been recorded in 1999 (Sokolov 2002). Densities have been low since

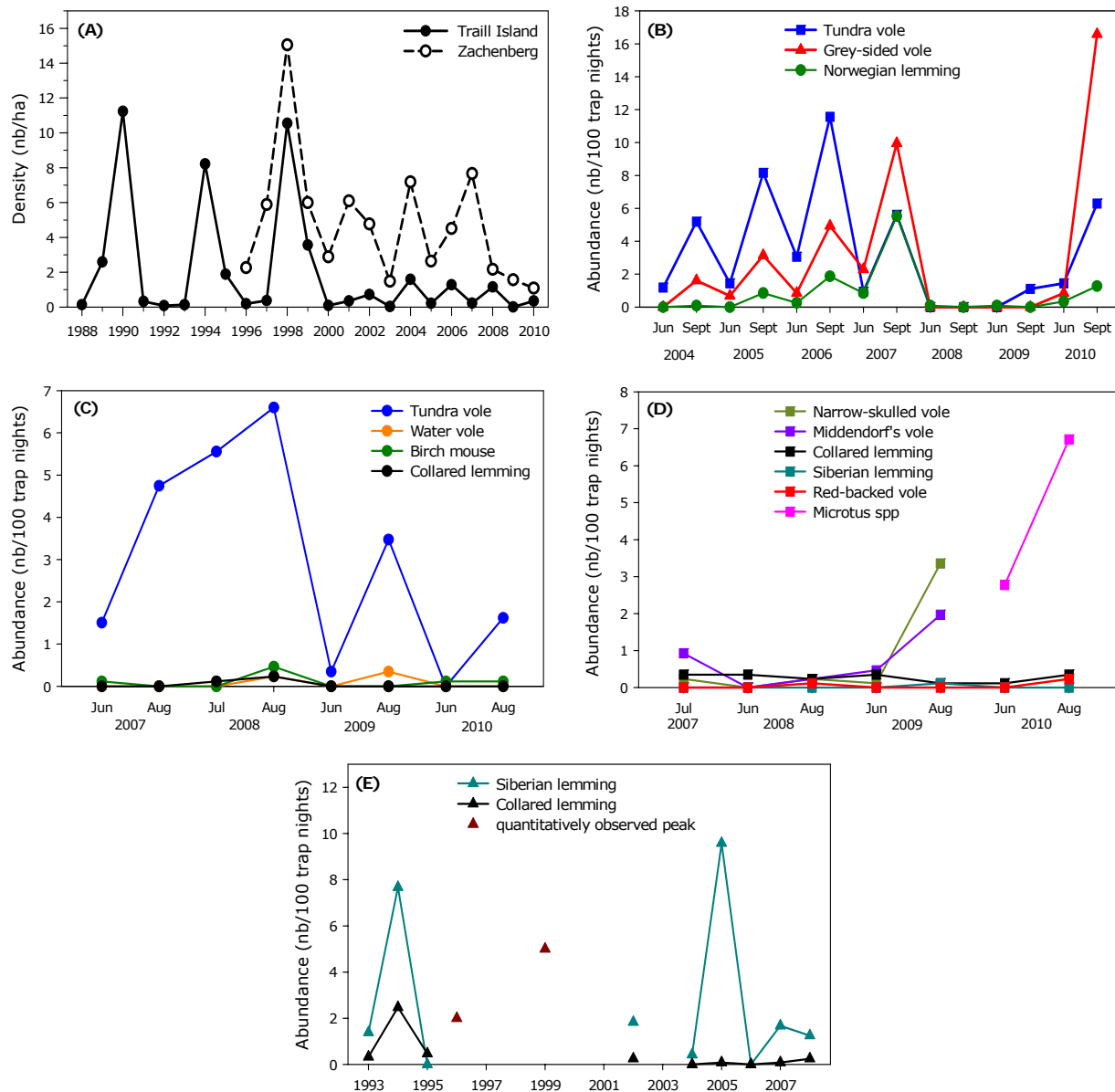


Figure 1. Time series of (A) collared lemming density estimates from two sites in eastern Greenland, Traill Island (Karupelv Valley) and Zackenbergl, (B) vole and lemming abundance in Varanger Peninsula, northern Norway, estimated with snap-traps (data courtesy of projects Ecosystem Finnmark, Arctic fox in Finnmark and Arctic Predators (IPY)), and small mammal abundance in the Russian Arctic estimated using snap-traps at (C) Nenetsky, (D) Yamal and (E) Taymyr. For Yamal 2010, voles have not been identified to species yet, so only total *Microtus* numbers are shown. At Taymyr, the qualitatively observed peak is based on general observations, not trapping data. For Nenetsky and Yamal, data are courtesy of IPY project Arctic Predators. For Taymyr, data are courtesy of Igor Popov and Dutch Taymyr expeditions led by Bart Ebbinge.

then, though somewhat higher in 2002 and 2005, suggesting low amplitude dynamics interspersed with peaks at long, possibly erratic, intervals (Sokolov et al. pers. comm.). Collared lemmings were trapped in the area every year, but numbers did not fluctuate

much.

On the coastal tundra of western Taymyr, lemming cycles were somewhat irregular since the 1990's and occurred at longer intervals than the typical three to four year period described for the area (Kokorev and Kukson

ArcticWOLVES final synthesis report

2002), but they did not fade out (Fig. 1E). A large peak of Siberian lemmings was observed in 2005 (Ebbinge and Mazurov 2005). Densities started to increase again towards the end of summer 2007 and winter nests and grazing indicated that lemmings were very numerous during winter 2007-2008. The population crashed however before or at snow melt and densities in summer 2008 were low (Popov 2009).

In the Lena Delta general observations and sign indices indicate that lemming cycles have a dominant period of three years (Pozdnyakov 2004). The last two cycles were however longer with Siberian lemming peaks in 2001, 2005, and unusually high densities in 2010 (V. Pozdnyakov, A. Sokolov, V. Sokolov, pers. comm.). On Wrangel Island collared and Siberian lemmings are about equally abundant. Recent analysis of a long-term time series indicates that the period of their population fluctuations has lengthened from 4-5 year in the 1970s to 7-8 years in the 1990s and 2000s (Chernyavskii and Tkachev 1982, Menyushina 2007a). Only in very deep crash years do snowy owls not reproduce there (Menyushina 1997), which suggests that the low phase of lemming population fluctuations is generally at higher densities on Wrangel Island than the low phase in other regions.

During the ArcticWOLVES project we extended the time series of lemming density estimates from Bylot Island, a high arctic site, where collared and brown lemmings have shown relatively synchronous cyclic dynamics with a period of 3 to 4 years, and brown lemmings have reached considerably higher densities than collared lemmings (Gruyer et al. 2008). During IPY, densities exhibited wide amplitude but shorter period, with peaks in both 2008 and 2010 (the previous peak being in 2004) (Fig. 2A and 2B). Fluctuations of brown lemmings continued to exhibit wider amplitude than those of collared lemmings. Snap-trapping conducted opportunistically in north and central Baffin Island in July 2008 indicated that the lemming peak that year was widespread across the island. On Herschel Island, occasional snowy owl nesting during past decades and snap-trapping for lemmings in the 1980s indicated relatively abundant lemming populations in some years (Slough 1987), but there are no long term population

data. Changes in density and body mass indicated a peak population of brown lemmings in 2008 and collared lemmings in 2007 and 2010, with brown lemmings having wider amplitude of density change (Fig. 2C and 2D; Krebs et al. 2011). This lack of synchrony is unusual, and may indicate different intensities of predation pressure on each lemming species within a year. Snowy owls only nested in 2008. On the coastal plain of Yukon, previous inventories have failed to identify a peak population or much amplitude in lemming densities (Krebs et al. 2002), but there are no long term data from Komakuk Beach. Our data indicate a persistent low density population of both brown lemmings and tundra voles at Komakuk, with the 2006 data being questionable because of lack of precision (Fig. 2E).

Our ability to compare data from different studies (specifically the amplitude of the cycle) is limited because many studies are based solely on relative abundance indices (e.g. snap trapping; counts of winter nests) rather than absolute density estimation. Nonetheless, our results indicate the following overall patterns:

- Brown lemmings undergo much wider amplitude population fluctuations than collared lemmings when the two species are sympatric; collared lemmings living without brown lemmings (e.g. east Greenland) appear to be able to reach substantially higher densities at the peak than when sympatric with brown lemmings.
- Vole fluctuations appear to have a strongly repeated annual pattern of summer population growth and winter decline, which is superimposed on any longer-period cyclic fluctuations.
- The periods of cycles in full tundra habitats are quite diverse, both within and among sites, with most variation being in the length of the low phase. This suggests variable attenuation of possible delayed density-dependent factors influencing the decline and persistence of the low (e.g. stress and maternal effects; induced plant defence chemicals; diet width of specialist predators), or inter-annual variability in the co-occurrence of necessary conditions for winter population growth (collapse of intense preda-

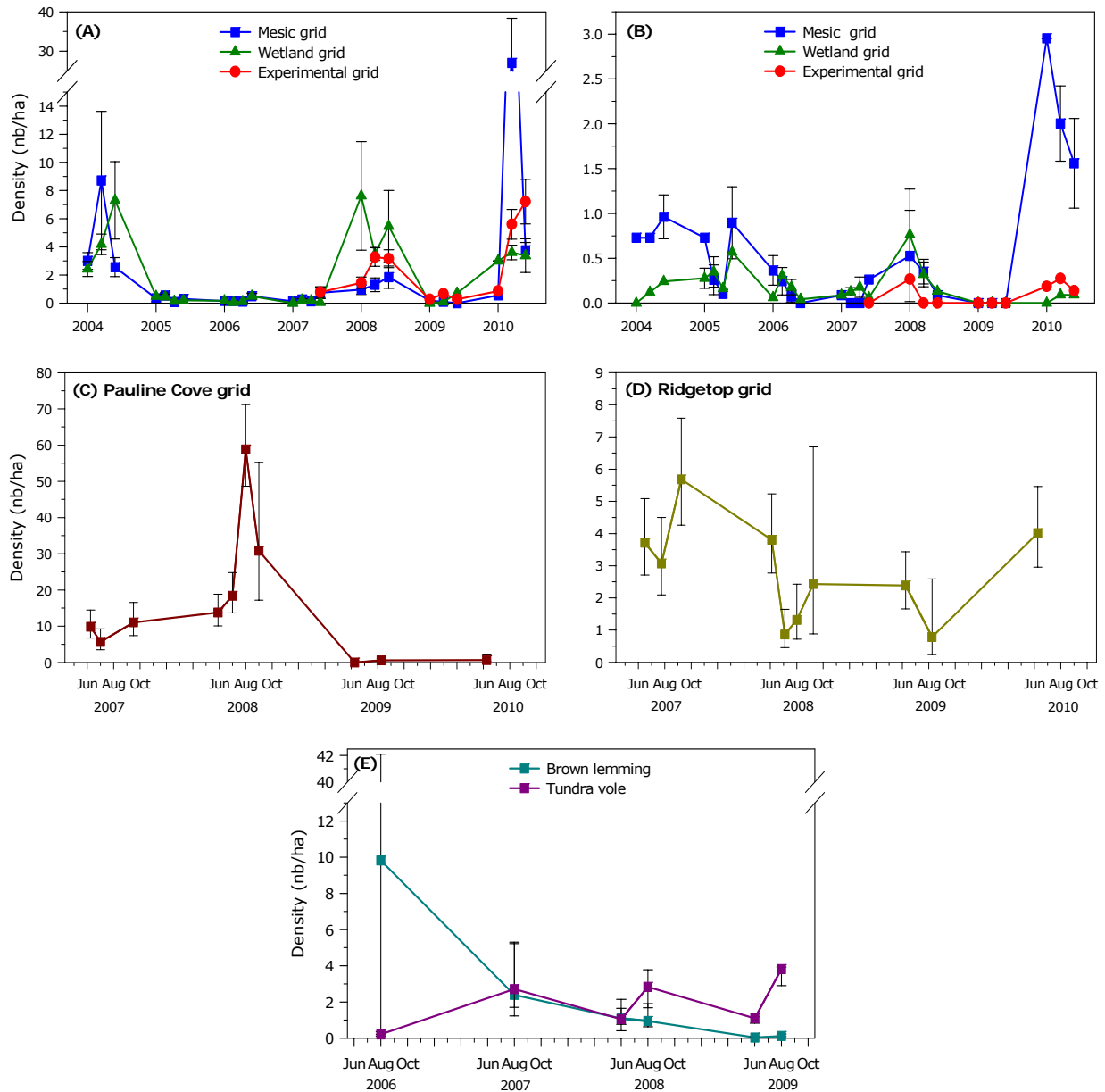


Figure 2. Time series of (A) brown and (B) collared lemming density on Bylot Island, NU, Canada, based on mark-recapture, and of (C) brown and (D) collared lemming density on Herschel Island, Yukon, Canada, based on mark-recapture (Pauline Cove is a mesic erect willow-sedge tundra on an alluvial fan, and Ridgetop is an upland tundra with mix of tussock cotton-grass and dwarf shrub heath; modified from Krebs et al. 2011), and of (E) brown lemming and tundra vole densities in tussock tundra habitat at Komakuk Beach, Yukon, Canada, based on mark-recapture.

- tion; sufficient snow cover).
- Inter-specific synchrony in density fluctuations is the norm, and the odd exception (e.g. Herschel Island) requires specific explanation, perhaps different intensities of predation on individual species in the same year.
- The documented fading of small mammal

cycles in some regions is not necessarily persistent (Brommer et al. 2010). If related to climate change, there should be some changing weather or snow signal that may have limited population increases only for the duration of the dampened dynamics.

Factors limiting population growth

The cyclic dynamics of many populations have stimulated a long history of explanatory hypotheses, with single factors initially aimed at explaining the entire dynamic (Stenseth and Ims 1993). Factors have often been classed as intrinsic (e.g., behavioural or genetic) or extrinsic (trophic or abiotic interactions) (Stenseth and Ims 1993), but these can be intimately inter-related (e.g. Boonstra et al. 2007), and both appear necessary to explain cyclic dynamics (Stenseth et al. 1996). Our project tested only a few hypothesized factors influencing small mammal population dynamics, with a special emphasis on climatic factors.

The increase phase of small mammals populations cycles is almost always driven by reproduction under the snow at least in spring, but also in winter, and such winter reproduction may also be necessary to make up for summer declines independent of any strong cycle (Stenseth and Ims 1993, Krebs et al. 1995, Gruyer et al. 2010). Lemmings clearly choose particular sites under the snow as a focus for their winter activities, as the distribution of their winter nests (mapped in spring) shows strong association with deeper snow, and the greatest probability of occurrence at snow depths from about 60 – 120 cm (Reid and Krebs 1996, Duchesne et al. 2011b). Many parts of the Arctic do receive less than 40 cm of snowfall during a winter, and this is often redistributed heavily by wind, creating a mosaic of habitat patches differing substantially in snow depth as snow is trapped by topography and vegetation. Through a manipulation of the snow cover, we showed that increasing the snow depth in marginal winter habitat increased the habitat's use by small mammals in winter, as expected, but did not affect their demography (reproductive rate, or mortality due to predation) (see Box 1).

We also examined to what extent annual variation in snow depth and quality could affect the amplitude and periodicity of lemming cycles. We used snow models developed by hydrologists, such as SNOWPACK© (Bartel and Lehning 2002, Lehning and al. 2002a, Lehning and al. 2002b), to simulate snow conditions from meteorological data inputs. We validated these models by comparing their



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Lemming winter nest found after snowmelt at Koomakuk, Yukon, Canada.

outputs with data from snow profiles in the field. Using a 16-year time series of brown lemming abundance on Bylot Island, we modelled the cyclic dynamics by imposing a term for cyclicity (either a sinusoidal or an autoregressive function) and adding snow parameters (subnivean temperatures, snow depth and density). Adding the snow parameters greatly improved the model fit for either function, and showed that greater snow depth, lower snow density and higher subnivean temperatures, thus higher snow quality, all had a significant positive effect on the amplitude of the cycle (F. Bilodeau, in prep.). In Zackenberg, Greenland, there is evidence that both the timing of the onset of winter and the length of winter affect lemming population growth, and these are weather parameters currently undergoing directional change (Berg et al. 2008). These results strongly suggest that certain features of the timing, quantity and quality of snow can be considered as necessary condition(s) for a population irruption in the high Arctic.

Food and Habitat

We lack the data to thoroughly assess the role of small mammal-vegetation interactions on their population dynamics. In general, when animal population densities increase, the range of resources they use increases as well (i.e. their niche width increases) (Bolnick et al. 2003). If small mammals at high densi-

ties compete for food, fewer individuals can gain access to an optimal diet. This might have implications for the population reproduction rate through reduced individual body condition, and thus it may limit population growth at peak densities. Such food limitation should increase the range of food items in the diet at peak densities compared to low density years. Using various techniques we examined the summer diet of small mammals at several sites. Our results indicate that variation in diets between individuals was large in all species and that density has no impact on the populations' diet diversities (Soininen et al., in prep.). Thus, it seems unlikely that summer food availability could limit small mammal population growth, in spite of the low primary productivity in the Arctic.

Small mammals are known to have specific habitat preferences. Collared lemmings generally inhabit upland, mesic to xeric, high arctic barrens, prostrate shrub and graminoid tundras (classification system of CAVM Team 2003), where they feed on dwarf woody shrubs (often *Dryas* and *Salix*) and numerous forbs. In the southern Arctic they prefer drier upland habitat with dwarf shrubs such as dwarf birch (*Betula nana*). Brown lemmings occupy more productive mesic to hygic sites with high cover of graminoids (often grasses, sedges and cotton-grasses) and mosses. These are frequently sites without erect shrubs, but Norwegian lemmings prefer wet tundra with erect shrubs such as *B. nana*. The tundra vole occupies both graminoid and erect shrub tundras, preferring wetter sites with graminoid foods amongst the shrub (often willow) thickets. Other northern voles occupy erect shrub and wetland tundras. All species occupy a greater variety of habitats when their densities are very high, or when potential competitor species are at very low densities or absent.

Inter-specific competition among coexisting small mammal species alters their population dynamics. Moreover, because each species has specific habitat preferences, change in habitats caused by climate variation can greatly affect the abundance and distribution of these species. We conducted, therefore, a series of small scale experiments aimed at testing habitat selection in coexisting collared and brown lemmings (see Box 2).

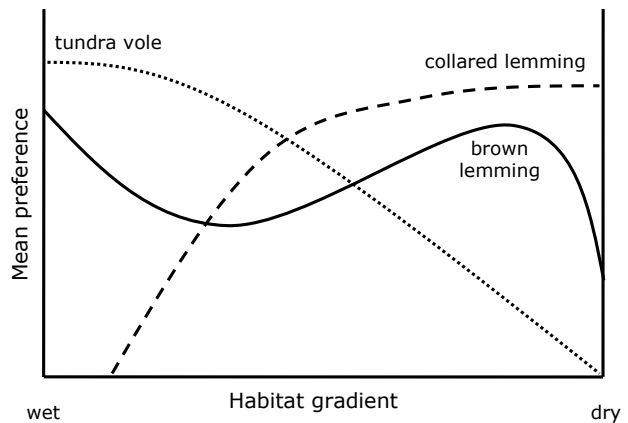


Figure 3. An illustration of the habitat preferences (that also corresponds to their fitness contours) by three species of small mammals at Herschel Island in the western Canadian Arctic. An increase in the proportion of dry habitat will favour further specialization by xeric specialist the collared lemming but will provide less opportunities for divergence between the tundra vole and the brown lemming at the mesic end of the gradient (after Ale et al., 2011).

Our analyses revealed that strength of competition among lemming species varied across sites. For instance, on Herschel Island, brown lemming abundance depended only upon its own density and was little affected by the presence of other species. In contrast, at Walker Bay, both brown and collared lemmings were influenced by interactions with their lemming competitor. The interactions also vary through time. The temporal variation in competition corresponds with habitat change in a warming climate. We expanded our analysis of habitat selection at Herschel Island by assuming a climate-induced increase in the frequency of xeric upland habitat. Based on their habitat preferences (Fig. 3; Morris et al. 2011, Ale et al. 2011), our models predict, with future climate change, that the two wet habitat specialists (brown lemmings and tundra voles) will compete in converging specialist niches while collared lemmings will avoid competition by selecting primarily xeric habitat.

We assessed the joint effects of predators and climate change at Walker Bay where we have an intermittent temporal record of lemming habitat selection beginning in 1996 (Morris et al. 2000). Collared lemmings dominated the lemming community during most years (Fig. 4; Krebs et al. 2002). Our analy-

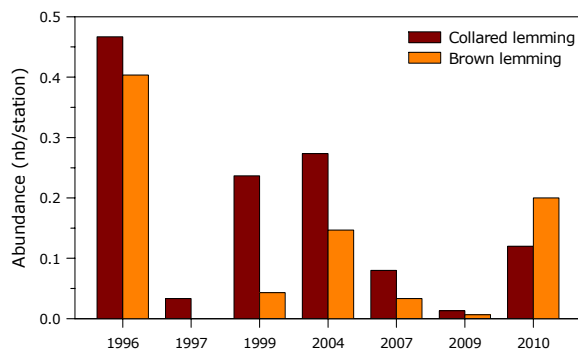


Figure 4. An illustration of changing summer abundances of two lemming species living in mesic versus xeric tundra on 12 study plots at Walker Bay in the central Canadian Arctic.

ses documented a partial replacement of dry habitat by wet habitat at Walker Bay, and a dramatic shift in habitat selection by brown lemmings during 2010 when, for the first time, brown lemmings were more numerous on our permanent plots than collared lemmings (Fig. 4).

Unlike brown lemmings, the strategy of habitat selection by collared lemmings has been constant through time in all of our study plots despite varying predation pressure. Indeed, 1996 was a year when predators such as snowy owls and arctic foxes were abundant on control plots but almost absent from plots inside a predator enclosure, whereas in all subsequent years migratory predators have been conspicuously absent. Temporal stability of the collared lemming habitat selection strategy demonstrates that predation risk had no effect on their selection of dry and wet tundra. These fundamental analyses of potential habitat and spatial responses by lemmings to predators provide rigorous tests of the assumptions of our food-web models. The analyses are also crucial to future assessments of changing food webs such as those at Walker Bay where grizzly bears now appear to be a common and previously ignored summer-time predator on lemmings.

Our research thus documents significant temporal and spatial dynamics in habitat, habitat selection, and trophic structure of terrestrial ecosystems in Canada's Arctic. The research points towards the potential of rather simple predictive models to forecast the future of habitat selection in these rapidly changing

systems.

Conclusion

The observation that brown lemmings undergo much wider amplitude population fluctuations than collared lemmings when the two species are sympatric even though collared lemmings can reach substantially higher densities in absence of brown lemmings requires further attention. This pattern fits the notion that inter-specific competition for access to preferred winter habitats limits collared lemming population growth in sympatry. However, recent evidence from Bylot Island suggests that predator mediated apparent competition, whereby one prey item influences the abundance of another prey item via the response of their shared predator to their respective abundance (Holt 1977), may be involved (J.-F. Therrien, unpubl. data; see BIRDS OF PREY chapter). Indeed, due to their preference for collared lemmings, avian predators may maintain their populations to low levels in presence of brown lemmings as alternative prey. Possible explanations requiring further research include some combination of: (a) brown lemming winter habitat having better insulative snow cover; (b) competitive dominance of brown lemmings with resulting ability to occupy a wider range of habitats especially in winter; (c) higher mortality rates for collared lemmings in summer, and when in areas of shallower snow in winter, due to predation; (d) higher metabolizable energy content of brown lemming foods supporting larger litters and better litter growth rates.

Our increasing knowledge of the patterns of small mammal population fluctuation, both within and between sites, indicates that: (i) no single factor is likely to explain the entire cyclic dynamic (i.e. a number of necessary conditions must be met for a cyclic population increase (irruption); changes in the same, or perhaps other, conditions may explain the decrease phase); (ii) interactions of extrinsic and intrinsic factors are likely involved in the complex demographic and behavioural changes observed; (iii) the insulative properties of snow are a key component of winter habitat, and further energetic studies are required to investigate the relationship to demography; (iv) models of habitat selection can elucidate the influences of habitat struc-

Small mammals

ture and trophic interactions on habitat choice, and can be used to derive forecasts of future conditions; (v) climate change may provide insights because some changes in vegetative and abiotic conditions resulting from a changed climate are accompanied by changes in lemming behaviour and demogra-

phy; (vi) we must be cautious about inferring that climate warming is causing changing patterns of demography based on a general correlation through a time series (see Brommer et al. 2010); it is crucial that we test hypothesized mechanisms of weather-induced effects.



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Siberian lemming.

Box 1. Impact of winter snow cover on lemming and vole habitat use and population dynamics.

To test the hypothesis that snow depth influences lemming habitat use and demography we undertook a snow-fencing experiment at Bylot Island (NU), Herschel Island (YT) and Komakuk Beach (YT). We erected parallel rows of snow fencing, perpendicular to the wind, on substantial portions (4.5 to 7.9 ha) of a small mammal live-trapping grid at each site. The fencing strongly increased snow depths, especially within 10 m of the fence lines. The density of lemming winter nests increased noticeably on the treated areas when compared to concurrent control areas, and the treatment effect was reversed when the fencing was withdrawn from Herschel (Fig. B1.1). The distribution of nests within 10 m of the fence rows showed no association with the fence before or after the treatment, but a significant association with the fence during most treatment winters. Although the fencing experiment showed that greater snow depth influences habitat choice by lemmings, it did not have any effect on their rates of reproduction (Bylot; inferred from winter nests, Duchesne et al. 2011a), or rates of predation by mustelids (Bylot and Herschel), judged by evidence in the winter nests. Subnivean temperatures were on average about 1.9°C warmer on the experimental grids, but this difference might not have been enough to significantly affect the lemmings' energy balance, especially given the high insulative capacity of their winter nests (Casey 1981). Lemming demographic parameters in spring did not differ markedly between control and treatment grids, probably because some individuals move between winter and summer habitats so

the animals in spring are not necessarily the same as those occupying the space in winter.



Snow fence section in the spring of 2008 at Herschel Island, Yukon, Canada.

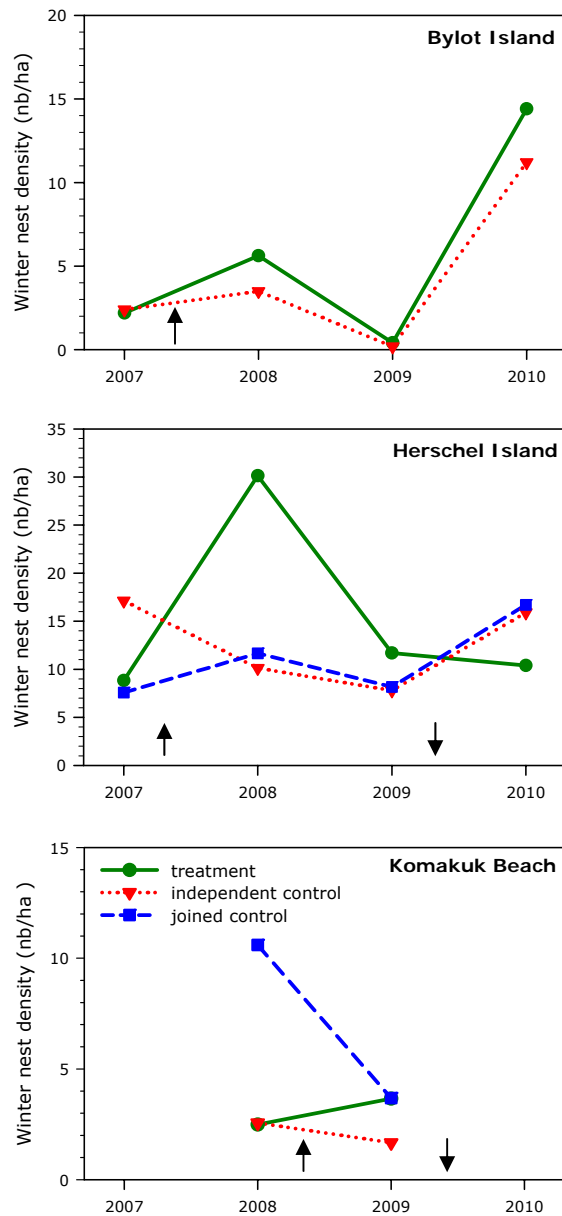


Figure B1.1. Time series of small mammal winter nest counts in June on areas treated with snow fencing, joined control areas immediately adjacent to the treated areas and independent control areas, at our three study sites. Fencing was installed (arrow up) in late summer 2007 at Herschel and Bylot Islands, and 2008 at Komakuk. The fencing was removed (arrow down) from Herschel Island in summer 2009, providing one winter of post-treatment monitoring (Reid et al. 2011).

Box 2. Patterns of habitat use by lemmings.

Habitat quality determines local birth and death schedules while the differences between habitats determine probabilities of dispersal and subsequent gene flow. Habitat-selection models based on “isodars” are built on these facts and investigate density-dependent strategies of habitat selection (e.g. Morris 1988, Morris and MacEachern 2010). An isodar emerges directly from logistic population growth models and includes complex intra and interspecific interactions (Morris 1988, 2003). Isodars are particularly relevant to issues of climate change (Morris et al. 2011) because they represent both ecological and evolutionary strategies of habitat selection. Isodars are also well suited to studying the abundances of northern small mammals because lemming habitat preferences correlate with the extremes of habitat along a single mesic or moist (brown lemming) to xeric or dry (collared lemming) gradient.

We ordinated vegetation along the dominant wet-dry tundra gradient, then used the ordination scores to create the two habitats required to infer density-dependent habitat selection. At Herschel Island, Yukon, brown lemming habitat selection at the mesic-xeric scale depends only on its own density (Fig. B2.1). Neither the collared lemming nor the tundra vole alters its xeric-mesic preference with changes in density. In contrast, at Walker Bay, Nunavut, where the two lemming species periodically irrupt to high densities (Wilson et al. 1999), both are density-dependent habitat selectors, and each is influenced, at some times, by interactions with its inter-specific competitor (Fig. B2.2).



Brown lemming.

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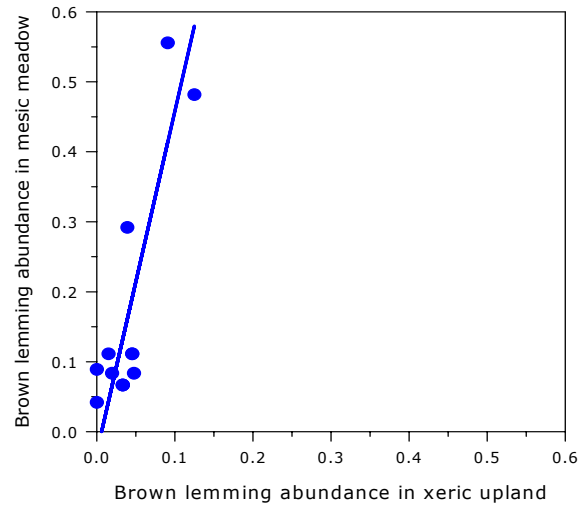


Figure B2.1. Relationship between brown lemming abundance (number of individuals per station per trapping session) in wet (mesic meadow) and dry (xeric upland) habitats at Herschel Island, Yukon, Canada (after Ale et al., 2011). Brown lemmings are approximately five times more abundant in ‘wet’ habitat than ‘dry’ habitat.

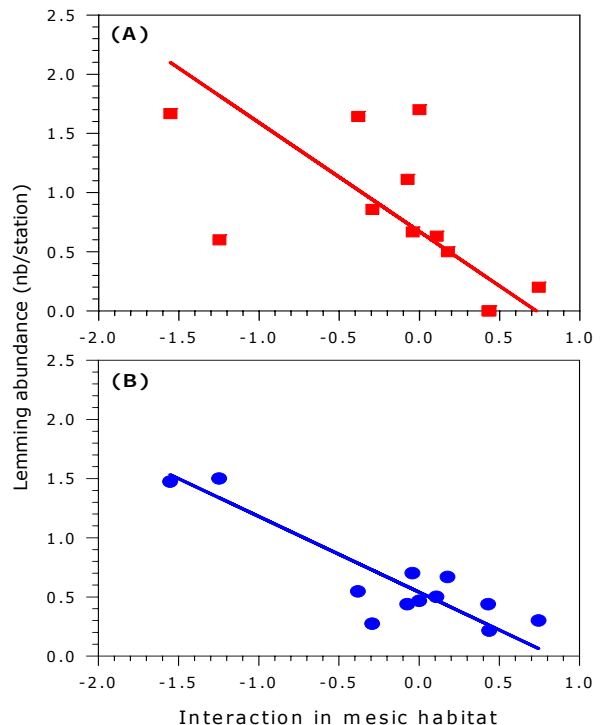


Figure B2.2. Relationships between the abundance of (A) collared lemmings in dry (xeric) habitat, and (B) brown lemmings in wet (mesic) habitat with the strength of competitive interaction between the two species in the wet habitat, at Walker Bay, Nunavut, Canada, as revealed by isodar analysis.



1 - Ross's Goose © Jean Iron
2 - Canada Goose © Kenneth F. Abraham
3 - barnacle geese © Jean Iron
4 - cackling goose © Jean Iron
5 - greater snow geese © Jean Iron
6 - brant geese © Jean Iron
7 - white-fronted goose © Maria Leung
8 - blue phase lesser snow goose © Kenneth F. Abraham

CHAPTER 4. GEESE

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gan, Esther Lévesque, Maarten J.J.E. Loonen and Robert F. Rockwell

Abstract

Geese are a diverse group of migratory birds that breed in several areas throughout the Arctic and winter mainly in temperate regions. They are important herbivores of tundra wetlands. Many goose populations worldwide have experienced large population increases at the end of the 20th century. In North America, of 28 populations with sufficient data, 11 are increasing, 16 are stable and only one is declining. In northern Europe and western Russia, of 21 populations with known long-term trends, 16 are showing increases, 4 are stable and one is declining. For most populations, the high-quality food that geese obtain from agricultural lands in winter and during migration, away from the Arctic, appears to be the primary factor responsible for population expansions. The large increases in the abundance of snow geese in many parts of the Arctic have considerable impacts on the tundra. Some of the strongest impacts have been documented in sub-arctic snow goose colonies of North America (southern/western Hudson and the Queen Maud Gulf). In several areas, goose density apparently largely exceeded the local capacity of the ecosystem, leading to habitat degradation, especially in coastal salt marshes. This provides a prime example of how changes due to human activities occurring thousands of kilometres away from the Arctic may have strong impacts on the tundra due to migratory connectivity in bird populations. It appears that at very high goose density, predator limitation weakens considerably and the system becomes dominated by goose-plant interactions. Detailed analysis of the timing and magnitude of peak in soil nutrients in marshes heavily grazed by geese along the Hudson Bay revealed that winter precipitation and warming events exert considerable control over the availability of plant nutrients in these systems, which in turn affects plant growth. In the High Arctic, goose reproduction is strongly affected by weather conditions, especially in spring. Predictive models previously suggested that anticipated increase in summer temperature should lead to an expansion in goose distribution, and thus higher abundance for some populations. Our findings, however, indicate that other factors may mitigate these positive effects of climate warming on goose populations. First, we found that in years when the spring is earliest and warmest, the growth of goslings is reduced because they hatch too late in the summer to benefit from the period of highest nutritive quality in plants (i.e. there is a lack of synchrony between plant growth and goose reproduction). Second, along west Hudson Bay and in Svalbard, a climate-driven increased overlap between nesting geese and polar bears coming ashore after ice breakup now allows bears to forage on goose eggs, which sometimes result in widespread failure of goose nests. Third, we found that thermal erosion of the permafrost increasingly lead to the draining of low-center polygon wetlands in some areas, which result in the loss of grasses and sedges, the preferred foraging plants of geese. Thus, as the climate warms, we can expect that all these phenomena will intensify, which could lead to a reduction of recruitment in goose populations.

Geese are a diverse group of migratory birds that breed in several areas throughout the circumpolar Arctic and winter in temperate or sub-Arctic regions. Eleven species nest in the arctic tundra. The most widespread and numerous species in North America are the snow goose (*Chen caerulescens*), Ross's goose (*Chen rossii*), white-fronted goose (*Anser albifrons*), Canada goose (*Branta canadensis*), Cackling goose (*Branta hutchinsii*) and brant goose (*Branta bernicla*) and in Eurasia they are the white-fronted goose, pink-footed goose (*Anser brachyrhynchus*), bean goose (*Anser fabalis*), barnacle goose (*Branta leucopsis*) and brant goose. All goose species are strict herbivores year-round and many of them nest colonially or semi-colonially. Snow and Ross's goose are the most strictly colonial species and the density of nesting geese can often exceed 20 individuals/ha in colonies numbering several tens of thousands of individuals. Most goose populations are harvested, either by recreational hunters on their temperate wintering grounds or by subsistence hunters in the Arctic, sub-Arctic and boreal breeding or migration areas. Although geese can use a variety of tundra habitats, their preferred feeding habitats are typically either coastal salt marshes or inland freshwater wetlands where various grasses and sedges form the bulk of their diet.

Population status

Many goose populations worldwide have experienced large population increases in the past century with the most rapid increase generally occurring during the second half of the 20th century (Abraham and Jefferies 1997, Reed et al. 1998, Madsen et al. 1999).

In North America, of 28 populations with sufficient data, 11 are increasing, 16 are stable and only one is declining (NAWMPC 2004). The colonially-nesting snow and Ross's geese are the species that showed the strongest increase. The mid-continent population of lesser snow geese (*Chen c. caerulescens*) has been growing at an annual rate of 3 to 5% over the last decades and may be as high as 20,000,000 birds despite efforts to stop its growth and to decrease population size through increased harvest (Alisauskas et al. 2011). However, there is evidence that growth has stopped at some southern colonies such as along the southwest coast of Hudson Bay due to habitat degradation caused by goose overgrazing and/or increased harvest. The population breeding in western Canada and eastern Russia (Wrangel Island) has also been increasing at a rate close to 5% during the past two decades (S. Boyd, pers. comm.). Population increases in snow geese resulted in an increase in the nesting density or in local expansion of existing colonies but also in the establishment of entirely new colonies such as the West Pen Island colony in Ontario, and the Air Force Island colony in Fox Basin (Abraham and Jefferies 1997, Reed et al. 1998). The population of greater snow geese (*Chen c. atlantica*) breeding in the High Arctic was increasing at a rate of 9% until the end of the 20th century but increased harvest over the last decade has stabilised the population around 800,000 birds (Calvert et al. 2007). The same dynamic has been reported for the Ross's goose (Alisauskas and Rockwell 2001). In this case, an eastward expansion was also noted as the species now breed in large numbers in areas such as west Hudson Bay or



Greater snow goose nesting colony on Bylot Island, NU, Canada.

ArcticWOLVES final synthesis report

south Baffin Island where only snow geese used to breed (Kelley et al. 2001, Kerbes et al. 2006). Brant geese, in contrast to white goose populations, have been either relatively stable in western North America (*Branta bernicla nigricans*, black brant) or increasing slowly in the eastern part (*B. b. hrota*, light-bellied brant; Ward et al. 2005).

In northern Europe and western Russia, of 21 populations with known long-term trends, 16 are showing significant increases, 4 are stable and only one declining, the threatened lesser white-fronted goose (*Anser erythropus*) breeding in northern Scandinavia (Fox et al. 2010). There is evidence, however, that population growth rates may be slowing down in several populations in very recent years, possibly due to density-dependent declines in productivity. Nonetheless, only two populations numbered less than 10,000 birds. Eighteen populations numbered 10,000–100,000, eight 100,000–1,000,000 and the largest 1.2 million individuals. Range expansion or shifts in use of staging areas during migration have been reported in some species over the last decade or so. For instance, the Russian/Baltic sea population of barnacle geese, which has been growing at about 8% per year recently, has expanded its breeding range in the Russian Arctic but also by colonising temperate areas as the species now breeds on its wintering range in the Netherlands (van der Jeugd et al. 2009). Furthermore, birds that are still migratory now delay their departure from the wintering grounds, skip traditional stopovers and are still able to breed successfully in the Arctic (Eichhorn et al. 2009; M.J.J.E. Loonen, unpubl. data). Similar changes in the use of spring staging

area has been noted in the pink-footed geese that migrate along the coastal area of Norway en route to their breeding ground in Svalbard (Bauer et al. 2008, Tombre et al. 2008).

There is a consensus that, for most goose populations, anthropogenic effects during the non-breeding season, away from the Arctic, are primarily responsible for population expansions. Although decreased harvest by recreational hunters may be a factor in some cases, the food subsidy that geese now obtain from agricultural lands in winter and during migration appears to be the major driving factor (Jefferies et al. 2003, Abraham et al. 2005, Fox et al. 2005, Gauthier et al. 2005). The intensification of agriculture due to an increase in the use of fertilizers and the expansion of some crops such as corn, rice and pulse crops (e.g., peas, lentils) now provide geese with highly nutritive food during the non-breeding season, which improves their survival and increases their body condition in spring when they prepare for breeding (Van Eerden et al. 2005, Gauthier et al. 2005).

Goose-plant interactions

The large increase in goose density had considerable impacts on the tundra in many parts of the Arctic. Some of these strongest impacts have been documented in sub-arctic goose colonies along southern Hudson Bay (Jefferies et al. 2003), west Hudson Bay (Kerbes et al. 1990) and the Queen Maud Gulf bird sanctuary (Didiuk and Ferguson 2005). In several areas, goose density apparently largely exceeded the local carrying capacity of the habitat, leading to significant habitat degradation. Habitat destruction due to goose overabundance appears most severe in



Houston Point area, Akimiski Island, NU, Canada before (1976) and after (1996) the salt marshes degradation by goose overabundance.

coastal salt marshes but has also expanded to contiguous freshwater marsh and fen (see Box 1). The use of several sub-arctic coastal areas by spring staging birds en route to more northern breeding colonies has also contributed significantly to the habitat degradation at some southern colonies (Jefferies et al. 2006) as staging birds often dig for underground rhizomes and roots (a feeding technique called grubbing), which is especially damaging for the plants (Gauthier et al. 2006). This situation provides a prime example of how changes due to human activities occurring thousands of kilometres away from the Arctic may have strong impacts on the tundra due to migratory connectivity in bird populations. In the High Arctic, even though snow goose populations have also increased considerably over the past 3 decades, such as on Bylot Island (Reed et al. 2002), the population apparently has not yet reached the carrying capacity of the habitat. Although goose grazing has had an impact on the primary production and specific composition of wetlands (Gauthier et al. 1995, 2004, Valéry et al. 2010), there is no sign of habitat degradation yet. When goose grazing is prevented by fencing off some plots permanently, production increases and species composition changes over a few years (Gauthier et al.



Evidence of grubbing on a vegetation mound on Akimiski Island, NU, Canada.

2004).

At very high goose density, predator limitation weakens considerably and the system becomes dominated by goose-plant interactions. In the spring, prior to extensive above-ground shoot growth, snow geese largely feed on the swollen shoot bases of inland freshwater sedges (this is called "shoot-pulling"), particularly *Carex aquatilis*, which are rich in



Evidence of shoot-pulling of *Carex aquatilis* by geese at Cape Churchill, MB, Canada.

soluble carbohydrates and total nitrogen (Gadallah and Jefferies 1995, Kotanen and Jefferies 1997). In some areas, especially those immediately inland from the coastal marshes of West Hudson Bay, intensive shoot-pulling has led to the replacement of sedge communities by moss carpets, exposed peat or standing water (Kotanen and Jefferies 1997). At High Arctic sites such as Bylot Island, shoot-pulling in the spring also affects other graminoids such as the grass *Dupontia fisheri* and the sedge *Eriophorum scheuchzeri*. To better understand how different species of forage plants respond to shoot-pulling events, and the threshold at which vegetation can recover from this type of herbivory, we measured the impact of different intensities of shoot removal (0, 20, and 50%) on shoot density near Churchill, MB and on Bylot Island, NU over several years. The density of *C. aquatilis* shoots was depressed at both levels of shoot pulling in most years at a dry site but not at a wet site, which suggests that the absence of high water levels in dry sedge meadows limits the recovery of *C. aquatilis*. *E. scheuchzeri* showed no decline in shoot density by the end of the third summer of shoot-pulling but *D. fisheri* density declined in all years in the high removal treatment. Differences in the physiology of these three species coupled with annual fluctuations in abiotic conditions (i.e. timing of snow melt, and the availability of water and nutrients) likely have the most influential role on the observed growth responses to herbivory.

Snow geese that stage and breed on the western coast of Hudson Bay are relying increasingly on fresh-water forage species dur-

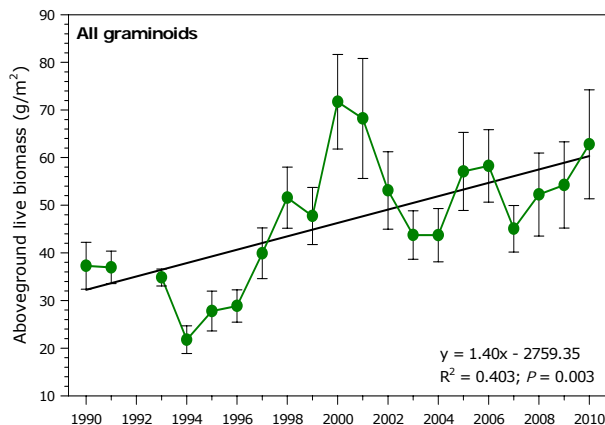


Figure 1. Temporal trend in primary production in the wetland of Bylot Island, NU, Canada, 1990-2010 (from Gauthier et al. 2011).

ing the summer, including the sedge *C. aquatilis*, following the destruction of traditional salt-marsh habitat. A full understanding of the ecological constraints on plant production and nutritional quality of *C. aquatilis* for geese requires knowledge of when and how soil resources, including nitrogen, become available to these plants and what strategies are employed by plants to maximize access to nitrogen in this low-nutrient environment. Controlled experiments conducted near Churchill (MB), revealed that plant-available nutrients were most abundant in late winter, when soils are still frozen, coincident with annual peaks of soil microbial biomass (Edwards et al. 2006). Decompositional processes continue throughout winter months, with the products of decomposition being available for plant growth in early spring. We further demonstrated that *C. aquatilis* is able to take up inorganic nitrogen during or just after soil thaw, at a time of temporary abundance, and prior to the commencement of shoot growth (Edwards and Jefferies 2010). The seasonal processes that govern nitrogen mineralization (i.e. the process by which organic nitrogen is converted to inorganic forms available to plants) and retention in late winter along with the physical processes of soil thaw are thus important for nitrogen acquisition by *C. aquatilis* and subsequent growth of biomass (Jefferies et al. 2010). We observed that inter-annual differences in the timing and magnitude of nutrient peaks were consistent across the landscape in both wet and dry

sedge meadows, revealing that climatic drivers, such as winter precipitation and warming events, exert considerable control over the availability of nutrients in these systems (Edwards 2010). Changes in these climate features will thus impact the timing and magnitude of soil nitrogen availability in early spring and could have deleterious effects on the growth and/or nutritional quality of *C. aquatilis* in these sedge meadows. This in turn could affect the reliability of this food source for snow geese and other wildlife that currently exploit *C. aquatilis* throughout the Hudson Bay Lowlands.

In the western Palearctic, the effect of increased goose grazing on the tundra vegetation depends on habitat type (Sjögersten et al. 2008). In the preferred wet sedge habitat there is a strong decrease in carbon dioxide (CO₂) assimilation and foraging conditions rapidly decline with increasing grazing pressure due to depletion of high quality food plants (Kuiper et al. 2009). After excluding heavily grazed vegetation, these plots showed a rapid recovery of the above ground biomass and CO₂ fluxes. This demonstrates the plasticity of the high arctic ecosystem in response to changing herbivore grazing pressure (Sjögersten et al. 2011). A brief period of early season grubbing by pink-footed geese is sufficient to strongly reduce carbon sink strength and soil carbon stocks. Repeated grubbing opens the soil organic layer to erosion and will thus lead to progressive carbon loss of arctic tundra (Van der Wal et al. 2007).

Climate change and goose populations

Most areas used by goose populations in the Arctic have experienced significant warming in recent years. For instance, on Bylot Island, one of our key study sites, the summer temperature (June, July and August) has increased by 2.8°C over a 35-year period (1976-2010; Gauthier et al. 2011). During the period 1990 to 2010, primary production in wetlands used by geese has almost doubled at this site (85% increase; Fig. 1), most likely a direct consequence of the warming temperature because the cumulative number of thawing degree-days during the summer is an important determinant of plant biomass at the end of the summer (Gauthier et al. 2011). Reproduction of geese is strongly affected by

weather conditions, especially in spring. When the spring is early and warm, the probability of laying eggs increases, laying is early and individuals lay larger clutches, thereby usually resulting in a high reproductive effort at the population level (Skinner et al. 1998, Reed et al. 2004, Madsen et al. 2007, Dickey et al. 2008). Predictive models based on habitat utilization during feeding (Speed et al. 2009) and nesting (Wisz et al. 2008) have been linked with climate change scenarios in some goose populations. Jensen et al. (2008) recently attempted to predict the future distribution of pink-footed geese in Svalbard taking into account that warm temperature should allow a longer summer season, thereby increasing the probability that geese will be able to complete their breeding cycle, and increase food availability. According to their model, a 2°C increase in summer temperature should lead to an expansion in goose distribution and ultimately an enhanced population growth.

Some of our recent findings, however, indicate that other factors may mitigate these potentially positive effects of climate warming on goose populations. As climate warms, various trophic levels (such as plants and herbivores or herbivores and predators) may respond differently, which may lead to a mismatch in the timing of events between trophic levels. We documented two contrasting examples of that in snow geese. We found evidence that in years when the spring is earliest and warmest, the growth of goslings is reduced because they hatch too late in the summer to benefit from the period of highest nutritive quality in plants (i.e. a mismatch; see Box 2). This will have a negative impact on the recruitment of young in the population in those years because survival of young during the fall migration is dependent on their mass at the end of the summer. Thus, as the climate warms, we can expect an increasing mismatch, which could lead to a reduction of recruitment in goose populations. The southward expansion of the breeding range of barnacle geese to its wintering range also led to a clear mismatch between reproductive timing and food supply (Van der Jeugd et al. 2009) and in temperate areas geese seem more vulnerable to parasites and infections (M.J.J.E. Loonen, unpubl. data). Juvenile growth is also much slower in temperate areas than in the

Arctic. Increasing summer temperature in Greenland have resulted in a similar trophic mismatch between caribou (*Rangifer tarandus*) and their food plants, which has been linked to recent population decline (Post and Forchhammer 2008, Post et al. 2008). This suggests that plant-herbivore mismatch may be a general phenomenon impacting many arctic wildlife herbivores.

Along west Hudson Bay, a climate-driven increased overlap between nesting geese and polar bears coming ashore after ice breakup provides a different example of trophic mismatch (see Box 3). Increased overlap allows bears to forage on energy-rich goose eggs, but sometimes result in widespread failure of goose nests. In this case, the increase match between bears and geese is beneficial to the predator but highly detrimental to the prey as it can ultimately lead to population decline (see Box 3). On Svalbard, increased presence of polar bears at barnacle goose colonies in recent years has also resulted in an augmentation of depredation of goose nests, which contributed to a decline in goose numbers in some coastal areas (Drent and Prop 2008).

Lecomte et al. (2009) recently showed that water availability and rainfall could affect the interaction between geese and another important predator, the arctic fox. They found that egg predation was reduced in years of high rainfall because fox predation occurs mostly when incubating females leave their nest to drink or feed and the probability of a successful attack increases with distance of the female from her nest. High rainfall increases water availability near the nest, which reduces the distance traveled by females to drink and increase her ability to defend her nest from a predator attack. Because climate change should affect precipitation regimes in the Arctic (ACIA 2005, IPCC 2007), this may impact nesting success of geese by changing water availability for incubating females. However, the direction of the effect is difficult to predict because, although the total precipitation should increase, it may be concentrated in fewer, more intense rainfall events.

Freshwater wetlands are one of the habitats most intensively used by geese in the High Arctic. Many wetlands typically occur in poorly drained areas where water movement is impeded by small scale topography often

ArcticWOLVES final synthesis report

due to underlying permafrost (Gauthier et al. 1996). A prominent example of that are the rich fens that develop in low-center polygons, a form of patterned ground created by the growth of ice-wedges in the permafrost (Fortier and Allard 2004). The stability of these wetlands depends on the integrity of the frozen ground and they are vulnerable to the rapid melting of ice-wedges (Fortier et al. 2007). Degradation of ice-wedge polygon networks strongly impacts local hydrology by inducing rapid drainage of affected polygons and their subsequent erosion. We found that gullies created by thermal erosion are affecting a significant number of wetland areas (up to 21 ha or 3-5% of the wetland in a prime brood-rearing area on Bylot Island; Godin and Fortier 2010). The development of thermo-erosion gullies modifies the local hydrographic network by draining low-center polygons. This can lead to a rapid shift in plant communities towards more mesic vegetation and a decrease, over a few years, of more than 60% in the cover of grasses and sedges, the preferred foraging plants of geese (N. Perreault and E. Lévesque, unpubl. data). Climate warming will likely enhance and accelerate these processes,

which could have far-reaching consequences for the habitat of geese and possibly other wildlife species of the tundra.

Conclusion

Geese are important herbivores of tundra wetlands. Most goose populations (though not all of them) are healthy, in part due to anthropogenic changes in their wintering habitats. High goose numbers can affect the tundra food web in several ways. High goose numbers generally result in a negative impact on plants such as severe loss in vegetation at dense colonies but may be beneficial for predators feeding on geese or their eggs and allow the maintenance of their populations at critical times (see TUNDRA FOOD WEBS chapter). Predicting how goose abundance will change as a result of climate warming remains challenging because we documented both positive impacts of warming (e.g. increased length of the breeding season and total food availability) and negative ones (e.g. increased mismatch between timing of goose breeding and plant phenology, increased overlap between nesting geese and predatory polar bears coming ashore or loss of wetland habitat



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Low-center polygons on Bylot Island, NU, Canada.

Box 1. *Overgrazing in dense goose colonies.*

In sub-Arctic and Arctic migration areas and breeding colonies, foraging by high numbers of snow and Ross's geese has led to significant loss of vegetation, adverse changes in soil properties and the establishment of alternative stable states (Jefferies et al. 2003). In spring, geese forage in salt marshes and supratidal marshes inundated by melt water using a method termed grubbing, whereby they uproot whole plants and destroy swards of turf forming grasses and sedges. At this time, most plant nutrients are still stored in below ground parts. Repeated grubbing over several years leaves the salt marsh denuded with depauperate seedbanks. They are open to secondary changes including transfer of nutrients to algal blooms, hypersalinity, decreased infiltration, erosion of organic soils, increased soil compaction and death of willows. These changes create an alternate state of exposed sediments that is resistant to re-colonization by plants. Geese also feed in inundated freshwater marshes and fens in spring using a method termed shoot-pulling, whereby they uproot the perennial shoots of taller sedges

and consume the basal tissues which are rich in carbohydrates. Repeated shoot-pulling eventually overcomes the plants' capacity to compensate, and areas are overtaken by mosses. Subsequently, the exposed mosses are exposed to increased evaporation and solar drying and except in the wetter environments, eventually die after which large areas are eroded by wind and water, leaving areas of exposed peat soils, a similar phenomenon as in salt marshes. In breeding colonies where tundra vegetation on permafrost or well drained sediments predominates, geese nesting in dense aggregations are resident for five weeks during egg-laying and incubation. Because they are site-faithful, repeated use over many years leaves a virtual desert, as they remove virtually all above ground stems of grasses, sedges and most forbs, leaving only some woody vegetation and mosses. In the worst cases, even the mosses are pulled up to make nest mounds. A large proportion of the west coast of Hudson Bay has been adversely affected by overgrazing by snow geese (Fig. B1.1).

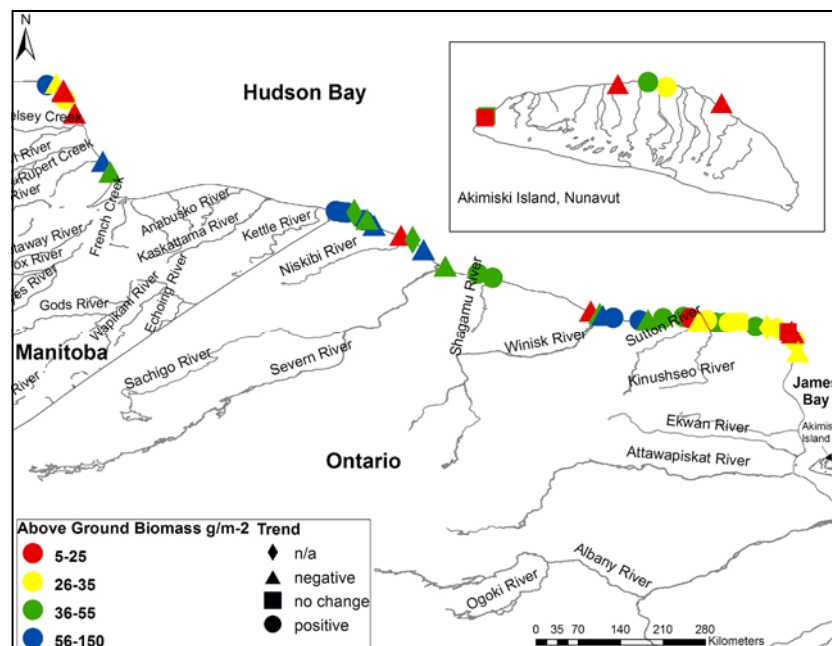


Figure B1.1. Effect of snow goose grazing on the salt marshes of the west coast of Hudson Bay, Canada. Colours refer to the grams per square metre of aboveground biomass in July 2009 as an index to the grazing level and state of habitat degradation (red=overgrazed and heavily damaged, yellow=overgrazed and moderately damaged, green=grazed but not damaged, blue=little or no grazing). Symbols refer to change in standing crop since 1995 (triangle=negative, square=no change, circle=positive, diamond=no 1995 data). (Hudson Bay Project, unpubl. data).

Box 2. A trophic mismatch between goose and plant phenology.

In many herbivores such as geese, the growth of young is dependent upon a good synchrony between hatching and the seasonal change in plant nutritive quality, especially protein, an essential nutrient for growth (Lepage et al. 1998). If plants respond more quickly than geese to global warming, this may lead to a mismatch between the availability of high quality food and the hatching date of goslings. We tested the mismatch hypothesis by increasing surface temperature using plexiglass open-top chambers that act as small greenhouses. Warming significantly increased graminoid plant biomass by 19% in wetlands and 17% in mesic prairies. There was no difference in nitrogen concentration early in the growing season, but plants in warmed plots had 7% to 14% less nitrogen (an index of protein) than in control plots in July, which suggests that warming speeds up the seasonal decline in nutritive quality. We also examined how the synchrony between hatching date of young and peak in nutritive quality of plants affects the growth of goslings. We found that gosling size and mass near fledging was negatively related to the mismatch between their hatching date and the date of peak nitrogen content in plants (Fig. B2.1). These results suggest that an accelerated decline in plant nutritive quality due to increased temperatures could have significant negative impacts on the growth of young.

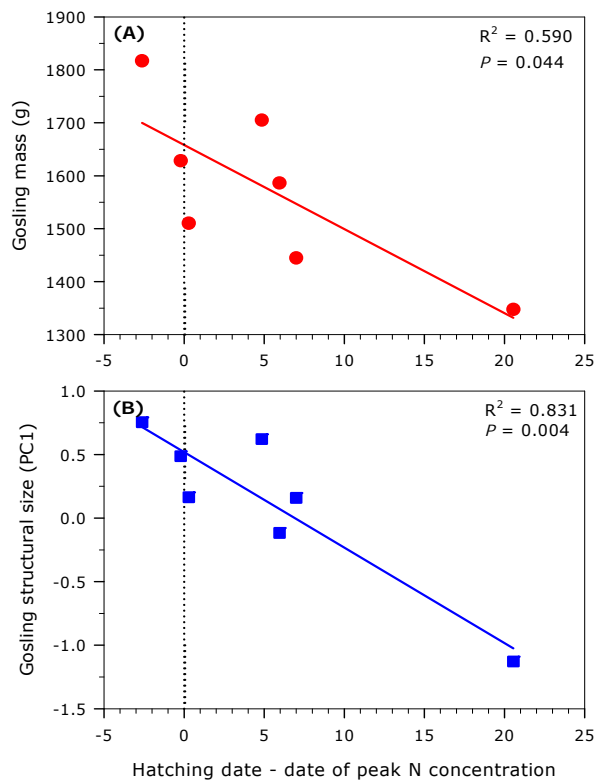


Figure B2.1. Relationship between the difference in hatching date of goose nests and date of peak nitrogen concentration of plants, and (A) body mass and (B) an index of structural size of goslings shortly before fledging on Bylot Island, NU, Canada. The dashed line indicates a perfect synchrony between hatching date of goslings and the date of peak nitrogen concentration of plants (M. Doiron et al. unpubl. data).



Open top chambers.



Greater snow goose family.

Box 3. Trophic matches between geese and predatory polar bears.

Polar bear (*Ursus maritimus*), which primarily feed on seals on the sea ice, face a strong energy deficit when they are forced to come ashore during the summer following ice break-up. In Hudson Bay, where climate warming has been especially strong over the past decades, the date of ice break up has advanced, forcing bears to come ashore earlier than in the past. In response to this warming trend, snow geese breeding in the colonies along the west coast of Hudson Bay have also been nesting earlier. However, the advance of the ice breakup date has been more rapid than the advance laying date of the geese (Fig. B3.1). Consequently, whereas in the past bears came ashore after most

goose nests had hatched, they now increasingly overlap with the period that geese are incubating their eggs, thereby providing them with energy-rich, easily obtained goose eggs. In years of high overlap, the predation rate on goose nests in areas such as Cape Churchill can be very high and can potentially lead to an almost complete failure of goose nests. Even though stochasticity associated with the asymmetrical advances in polar bear onshore arrival and the snow goose incubation period will lead to alternating years of high and low matches between bears and geese, in the long run this will have negative effects on the goose population, which is expected to decline in areas exposed to polar bear predation.

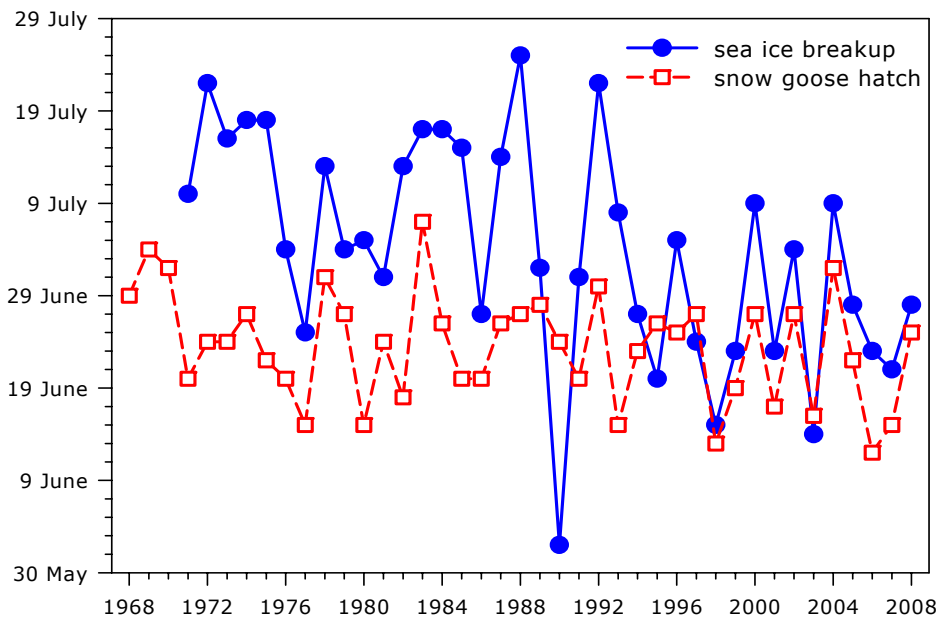


Figure B3.1. Time series for the mean dates of lesser snow goose hatch in the Cape Churchill region, and dates of sea ice break-up in the relevant portions of the West Hudson Bay, Canada (modified from Rockwell et al. 2011).



© Kenneth F. Abraham

Nesting female lesser snow goose.



© Robert F. Rockwell

Female polar bear with cub.



- 1 - male long-legged fly © Robert Chabot
- 2 - house fly © Robert Chabot
- 3 - winter crane fly © Robert Chabot
- 4 - non-biting midge © Robert Chabot
- 5 - fungus gnat © Robert Chabot
- 6 - mosquito © Robert Chabot
- 7 - wolf spider © Laura McKinnon

CHAPTER 5. ARTHROPODS

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Co-authors: Kenneth F. Abraham, Joël Bêty, Élise Bolduc, Christopher Buddle, Stacy Gan, Grant H. Gilchrist, Josée Lefebvre, Maria Leung, R.I. Guy Morrison and Donald G. Reid

Abstract

Arctic arthropods play key ecological roles in the functioning of the arctic tundra and changes in their distribution and abundance have the potential for far reaching ecological consequences across the arctic ecosystem. For example, because arthropods are the main prey of many shorebirds and songbirds, climate induced changes in their seasonal abundance could have negative effects on a considerable proportion of arctic-nesting birds. Our project sets out to provide a more comprehensive understanding of arctic arthropod communities and their environmental determinants with an emphasis on understanding seasonal variation in arthropod availability in relation to reproduction of insectivorous birds. We investigated spatial and inter-annual variability in their phenology and availability by systematically collecting arthropods with the same modified pitfall traps at 6 sites in the Canadian Arctic. We also constructed environmental based models in order to explain seasonal changes in arthropod availability. Our data indicated that most sites shared the same dominant arthropod groups (spiders, house flies, non-biting midges and fungus gnats), but diversity was higher at lower latitudes. Six species of butterflies, previously unrecorded, were caught on Herschel Island, making a total of 21 butterfly species now known to the island. Maximum arthropod availability was also up to 8 times greater at the lower latitude sites compared to high latitude sites. At most sites, abundance of arthropods peaked in late June - early July and the duration of this peak was longer at lower latitudes. Based on Bylot Island data, synchrony between shorebird hatch dates and peaks in arthropod availability was relatively low between 2005 and 2008. Environmental based models of arthropod availability indicated that daily mean temperature, cumulative temperatures above 0°C, mean daily wind speed, total daily precipitation, mean daily relative humidity and mean daily incidental radiation were the best predictors of their availability. The latitudinal trends in arthropod diversity, abundance and phenology revealed by our data may provide some insight into the expected short-term impacts of climate warming at least at higher arctic sites. As temperatures increase across the Arctic, our data indicate that diversity and overall biomass of arthropods may increase, especially in the High Arctic. The short lived peaks in abundance of arthropods currently characteristic of High Arctic sites may shift or broaden to resemble the longer period of abundance characteristic of lower arctic sites. However, given the great diversity of arctic arthropods, and their range of complex adaptations to the extreme arctic environment, it will be difficult to predict exactly how these communities will respond to changes in climate in the long term. Understanding the long-term impacts of climate change on Arctic arthropods will likely require more data on their basic life history at lower taxonomic levels such as genus and, if possible, species.

Arthropods in the Arctic

Arctic terrestrial arthropods (insects and spiders) are no doubt the most diverse group in the arctic ecosystem. Despite exhibiting the same decrease in species diversity with latitude as other arctic organisms (Bowden and Buddle 2010), over 2000 species of arthropods have been identified in the North American Arctic alone (Danks 1992) and many more remain undescribed. Among the smallest year-round residents of the Arctic, arthropods have, like their counterparts in the south, developed interesting adaptations to overwintering in the polar night where temperatures can drop to -60°C . While some species let themselves essentially freeze for the winter (Block et al. 1990), others can 'supercool' and remain unfrozen even in extremely low temperatures (Ring 1982). Despite their amazing adaptations to the cold arctic environment (Somme 1999, Danks 2004), arthropods are expected to be among the first organisms to respond to future changes in climate because they depend on heat from the environment to warm up their body (i.e. they are ectothermic). Consequently, many species depend on climatic parameters for spring emergence and subsequent reproductive activity (Holmes 1966, Hodkinson et al. 1996, Schekkerman et al. 2004). Because the distribution of many arthropod species is driven by temperature, this makes them model taxa to use as ecological indicators, especially in the north (Danks 1992).

Arctic arthropods play key ecological roles in the functioning of the arctic tundra as they can be decomposers (O'lear and Seastedt 1994, Hodkinson and Wookey 1999), pollinators (Kevan 1972, 1973), predators (Hodkinson et al. 1998) or prey (Tulp and Schekkerman 2008). Changes in their distribution and abundance have the potential for far reaching ecological consequences across the arctic ecosystem. For example, one of the keystone species of the arctic tundra is the lemming, which relies on abundant plant food resources for reproduction. Some of these plants, especially those in the High Arctic, rely on insect pollination for population persistence (flies, midges and bees; Kevan 1972, 1973). Arthropods are also the main prey for many insectivorous birds, which comprise a consid-

erable proportion of the avian biodiversity in the Arctic. Changes in seasonal abundance of arthropods, which is expected to occur with changes in climate, could have detrimental effects on insectivorous birds such as passerines or shorebirds (Meltofte et al. 2007, Pearce-Higgins et al. 2009; see SHOREBIRDS chapter). On the other hand, as temperatures increase in the Arctic, the overall abundance of insects as well as their biodiversity will likely increase as new species expand their range northward.

Spatial and temporal variability in arthropod phenology and availability

The main goal of the ArcticWOLVES arthropod studies was to provide a more comprehensive understanding of arctic arthropod communities and their environmental determinants, with an emphasis on understanding seasonal variation in arthropod availability in relation to reproduction of insectivorous birds. To meet this goal we investigated spatial and inter-annual variability in arthropod phenology and availability by systematically collecting arthropods across 6 sites in the Canadian Arctic (Akimiski Island, Southampton Island, Herschel Island, Bylot Island, Eureka and Alert). Unfortunately, no similar sampling could be conducted in Eurasia during our project. We also constructed environmental based models in order to explain seasonal changes in arthropod availability.

Given that our sampling sites were spread across such great distances in the Arctic, it is not surprising that there was considerable variation in arthropod family diversity among sites. Lower latitude sites such as Akimiski, Southampton and Herschel Islands boasted a high diversity of families at 63, 40 and 89 families respectively. Higher latitude sites such as Bylot Island, Eureka and Alert exhibited lower diversity with only 35, 29 and 26 families respectively. Across all sites, a total of 117 families were identified during 2007 and 2008. Dominant families present across all sites included Aranae (spiders: 4 to 13% of the total sampled across all sites; Fig. 1), Chironomidae (non-biting midges: 18 to 61%), Muscidae (house flies: 1 to 17%) and Mycetophilidae (fungus gnats: 1 to 24%). Dytiscidae (predaceous diving beetles) were found in high proportions at more southern sites such

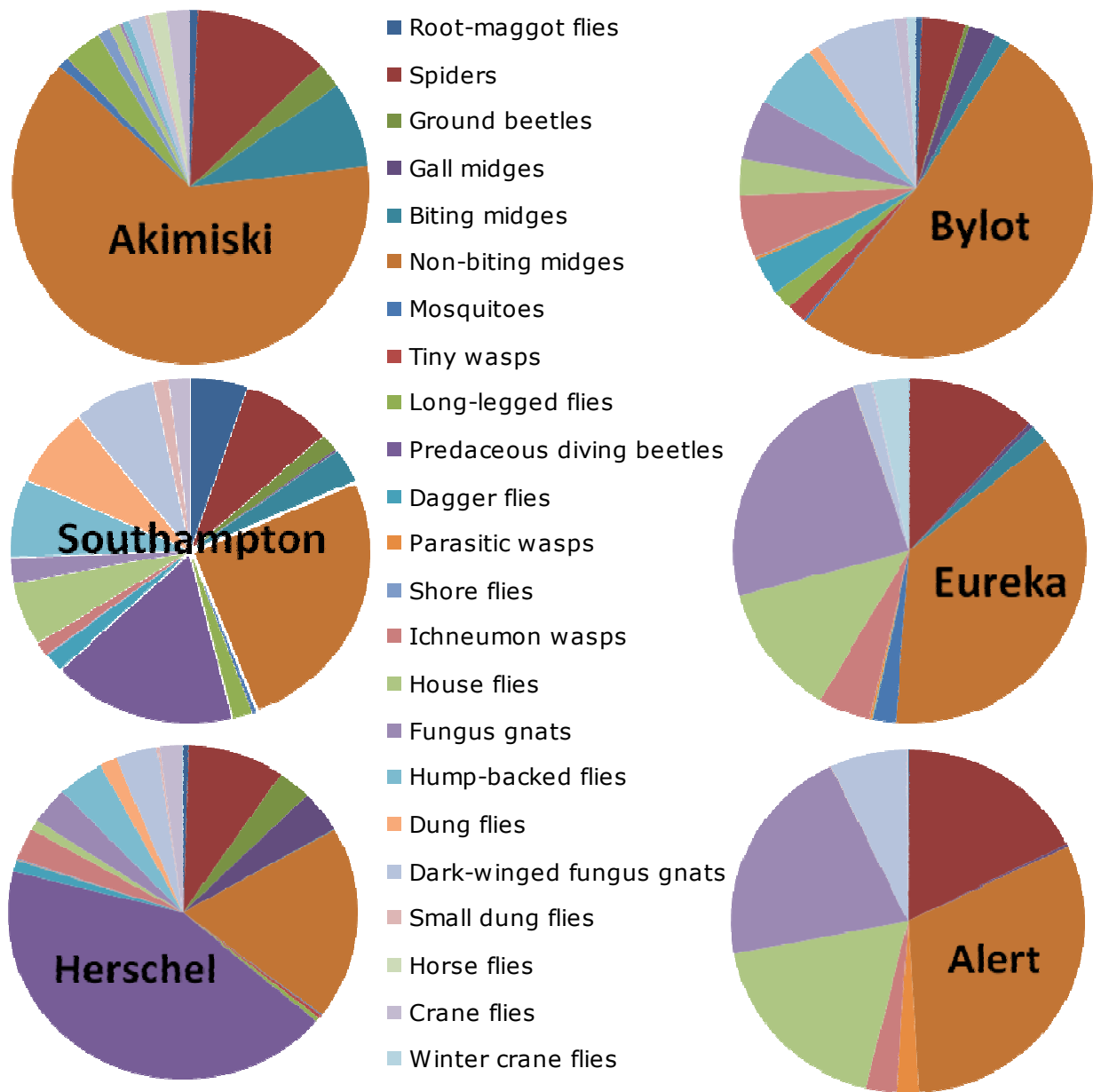


Figure 1. Proportion of arthropod families sampled at 6 sites in the Canadian Arctic during 2007 and 2008 combined. Due to the high diversity at some sites, only families representing greater than 1% of totals sampled (per trap/day) are presented.

as Southamptton and Herschel Islands (17 and 40% respectively) but were absent at all other sites (Fig.1).

There was considerable inter-annual variation in seasonal trends of arthropod availability in terms of timing, duration, and magnitude of peaks in total biomass both within and between sites (see Box 1). For the three sites where we sampled throughout the entire summer season, arthropod availability

was the highest between June 29 and July 9 (Fig. B1.1). For example, on Bylot Island peaks were short-lived each year (2 to 7 days) and usually fell within the same 14 day period (June 28 to July 14). The duration of the peak in arthropod availability appears to be longer at lower latitudes (see Fig. B1.1 in Box 1), which might allow breeding birds greater flexibility in breeding phenology with respect to the pulse of prey for fledglings.

Maximum arthropod availability was also greater at the lower latitude sites. At Akimiski (53°N), Southampton (64°N) and Herschel Islands (69°N) maximum arthropod availability throughout the season ranged from 187 to 902 mg/trap/day, which was up to 10 times greater than at the higher latitude sites, Bylot Island (73°N), Eureka (80°N) and Alert (82° N) with 85 to 119 mg/trap/day (see Box 1). Maximum arthropod availability at Herschel Island, which was located almost 55° of longitude further west than all the other sampling sites, was more than twice as high than at the sites located at the same or lower latitude in the eastern Arctic. However, the lack of other sampling sites along an east-west gradient prevents further examination of a longitudinal trend in arthropod availability in North America. When we excluded Herschel Island data, we found an almost linear decreasing latitudinal trend in maximum arthropod availability as we move from south to north in the eastern Canadian Arctic (Fig. 2).

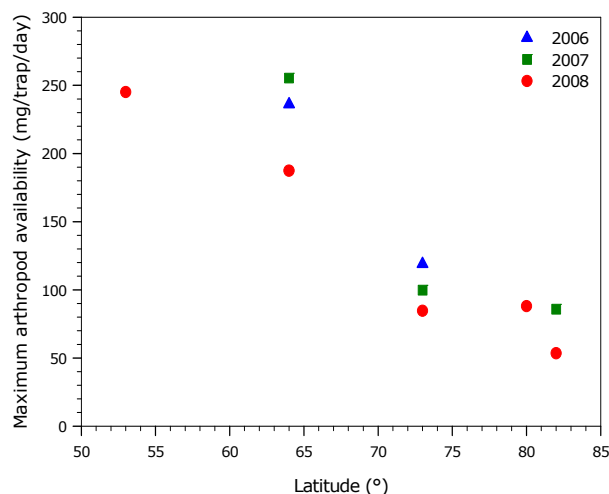


Figure 2. Latitudinal variation in maximum arthropod availability (mg/trap/day). Each point corresponds to the maximum reached at a given site and year (2006-2008). Sampling was interrupted during the summer of 2008 at Eureka (80°N) and Akimiski Island (53°N) thus the actual maximum may have been underestimated. Data from Herschel Island were excluded in order to obtain a latitudinal gradient within similar longitudes.

Based on arthropod samples collected over a period of 4 years on Bylot Island, we found that the seasonal availability of arthropods was determined primarily by the follow-

ing environmental parameters: daily mean temperature, cumulative temperatures above 0°C, mean daily wind speed, total daily precipitation, mean daily relative humidity, mean daily incidental radiation and the interaction between daily temperature and cumulative temperatures above 0°C. A model including all these variables was able to predict when the peak in arthropod availability would occur in a given season with considerable accuracy (up to 88% of the variability in the dataset was explained by these variables; Fig. B2.1 in Box 2). These results are similar to those found at another arctic site in the eastern hemisphere where temperature, wind speed and cumulative temperature were also important determining factors of seasonal arthropod abundance (Tulp and Schekkerman 2008). Such a model will now allow us to simulate past trends and, more importantly, to forecast future changes in arthropod availability in relation to changes in climate.

On Bylot Island, we found that synchrony between shorebird hatch dates and peak arthropod abundance was relatively low. Over a 4-year period, synchrony was relatively good in two years but poor in two other years (see Box 2). Synchrony between hatch and peaks in arthropod abundance are important for chick growth. We found that chicks hatching in synchrony with peaks in Tipulidae (crane flies) biomass had higher growth rates than chicks hatching outside these peak periods (see SHOREBIRDS chapter). Many arctic-nesting birds rely on insects as their primary prey (e.g. songbirds, shorebirds), thus it will be important to investigate whether a mismatch between hatch and peaks in insect abundance could be important in other arctic-nesting birds.

On Herschel Island and Komakuk, spring temperatures were also relatively warm in 2008 and snow persistence was relatively short, which was likely the reason behind the accelerated emergence of butterfly species in 2008. The same weather pattern is associated with the higher abundance of butterflies recorded in late June - early July of 2008, compared to 2007 and 2009. Butterflies were most commonly found in habitats rich with flowering plants. We caught six species of butterflies not previously recorded for Herschel Island, making a total of 21 species known to

ArcticWOLVES final synthesis report

the island. One of these, *Nymphalis vaualbum*, was considerably further north than previously documented (Layberry et al. 1998).



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Compton's tortoiseshell (*Nymphalis vaualbum*) caught on Herschel Island, Yukon, Canada.

Arthropods and climate change

Due to their complex adaptations to the extreme arctic environment, it is suggested that climate change may have several effects on arthropods (Danks 2004). In zones of permafrost, ground-dwelling arthropods are limited to a thin layer of unfrozen soil, the active layer (Chernov 1972). A reduction in permafrost due to increasing temperatures could increase the depth of soil available for arthropods, potentially providing a buffer against extreme weather events. However, Danks (2004) has suggested that warmer summer temperatures could increase cloud cover and thus decrease solar radiation, which would then lead to a reduction in the activity and reproduction of some insect populations. Changes in precipitation regimes, such as decreased precipitation or increased evaporation, may also have significant effects because many arthropods in the north with aquatic life stages rely upon temporary ponds which may decline in abundance or availability. Alternatively, in the event of increasing precipitation, large expanses of tundra could become saturated thus limiting access to oxygenated micro-sites.

The latitudinal trends in arthropod diversity, abundance and phenology revealed from our ArcticWOLVES data may provide some insight into the expected short-term impacts of climate warming at least at higher arctic sites. As temperatures increase in the High

Arctic, we may expect to see increases in both arthropod diversity and overall arthropod biomass. The short lived peaks in abundance of arthropods currently characteristic of High Arctic sites such as Bylot Island may shift or broaden to resemble the longer period of abundance characteristic of lower arctic sites such as Herschel Island. However, as previously mentioned, it will be difficult to predict exactly how arthropod communities will respond to changes in climate, not only because of the great diversity of species in question, but also due to the number of climatic variables at play (i.e. changes in precipitation, cloud cover, temperature, solar radiation, etc.).

The collaborative Northern Biodiversity Project

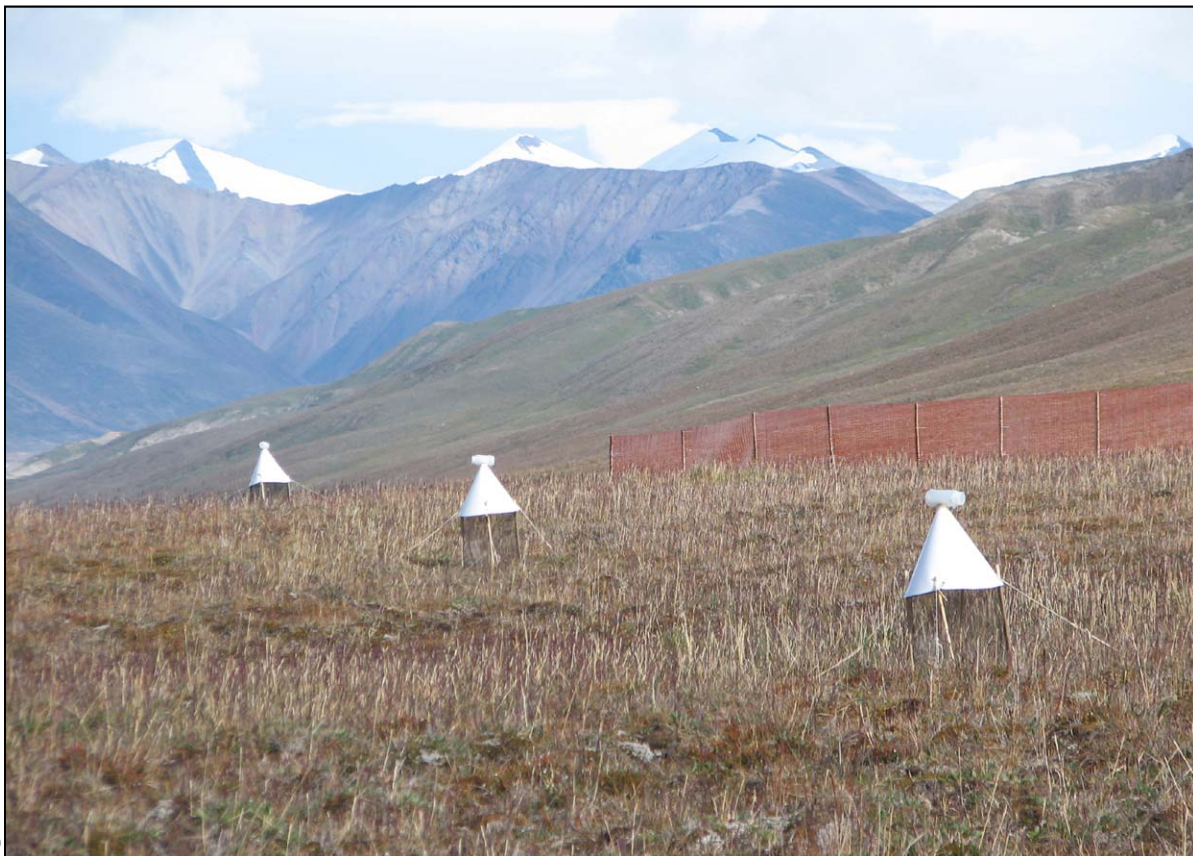
The Northern Biodiversity Project (www.northernbiodiversity.com) was initiated in 2010. This project's objective is to understand how northern biodiversity has and is adapting to a changing environment. Arthropods are being sampled across three major ecoclimatic zones in northern Canada, and data will be compared with baseline inventories from Canada's 1947-1962 Northern Insect Survey (NIS). We expect that some northern species will have declined drastically in abundance or disappeared, while more southern species may have extended their ranges northward. Both of these types of changes should result in new ecological relationships and possible ecosystem changes. Assessment of such ecological changes in the north is only possible by renewed monitoring and comparison to the baseline conditions as understood from the original NIS initiative. The Northern Biodiversity Program has finished its first year of sampling. Preliminary data suggest some "southern" species are firmly establishing populations in the North; for example, nests of the Arctic Yellowjacket (*Dolichovespula norvegica*), a largely northern boreal wasp species, were discovered on the tundra of Baffin Island, well away from the town of Iqaluit. In other words, although the species has been recorded previously in the town-site, its presence beyond the borders indicates the species is well adapted to completing its full life cycle on the open tundra. The project is also reporting high diversity and abundance of certain

biting fly species relative to past collections. These preliminary findings show that arthropods are suitable for monitoring biodiversity change in Canada's Arctic. The Northern Biodiversity Program will paint an important portrait of northern arthropod biodiversity and future work on food-web ecology in northern systems will benefit from this kind of biodiversity "benchmark".

Conclusion and future research

As key ecological players in the functioning of the arctic tundra, changes in the phenology and abundance of arthropods have the potential to affect several trophic levels within the tundra food web. Our research has highlighted the great spatial and inter-annual variation in arthropod abundance throughout the Canadian Arctic, along with the importance of arthropods as prey for one of the most diverse groups of arctic-nesting birds, the shorebirds. With samples collected over multiple years at up to 6 sites across the Canadian Arctic, we have initiated a unique and

extensive standardized inventory of the abundance of arctic arthropods. Though impressive, the data reported here (timing and magnitude of abundance and biomass of all species combined) represent only the tip of the iceberg. The basic life history of the vast majority of arctic arthropods remains understudied. This is a significant road block because understanding the effects of climate change on arctic food webs requires baseline data on the biology of keystone species. For example, the actual environmental controls on phenology of key species such as Tipulidae (crane flies), which are an important prey species for many shorebirds, are still not well understood. Future research should continue to refine our understanding of seasonal variation in arthropod availability and attempt to study variation at lower taxonomic levels such as genus and, if possible, species. However, with over 2000 species of arthropods in arctic North America (Danks 1992), this could prove to be a very interesting, though rather challenging task.



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Transect of arthropod traps on Bylot Island, NU, Canada.

Box 1. Arthropod phenology and availability in the Arctic.

To observe seasonal changes in the availability of arthropods, pitfall traps constructed in conjunction with modified Malaise traps were used to capture surface active and low-flying arthropods. Traps were composed of a 38 cm x 5 cm x 7 cm plastic pitfall trap above which extended a 40 cm x 40 cm vertical mesh screen topped with a white plastic cone funnelling into a bottle trap to capture flying insects. At most sites, we set two transects of 5 traps each, with 20 metres between traps, in the two dominant shorebird nesting habitats, for a total of 10 traps. Traps were sampled every 2 days throughout the summer. To account for variable sampling effort, total arthropod biomass was divided by the number of traps sampled and is presented as arthropod biomass (mg/trap/day). Results show considerable variability in insect abundance

among sites but also among years at the same site.



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Trap used to capture arthropods.

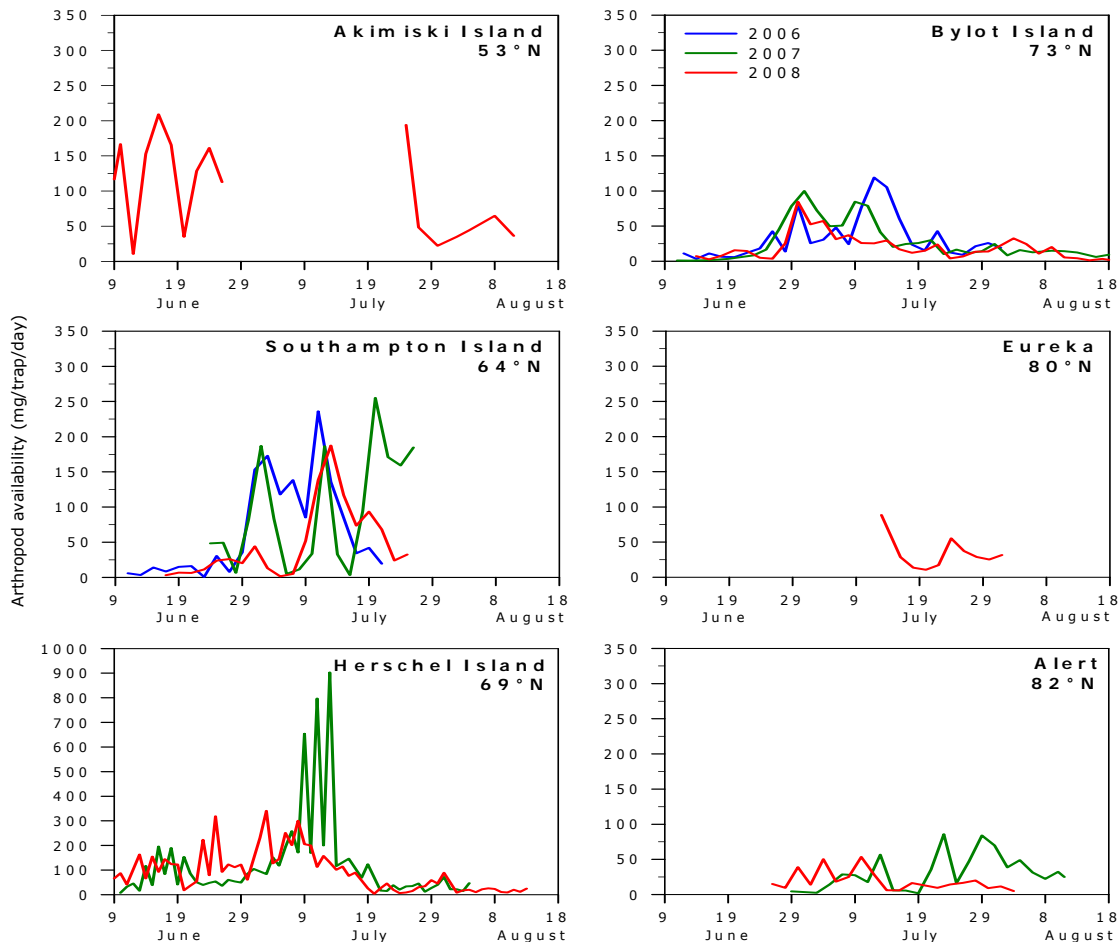


Figure B1.1. Seasonal variation in arthropod availability for 6 sites in the Canadian Arctic.

Box 2. Synchrony between arthropod seasonal abundance and shorebirds reproduction.

Between 2005 and 2008 on Bylot Island, we simultaneously monitored the phenology of arthropod abundance and shorebird nesting. Hatching dates of shorebird species occurred prior to the peak in arthropod abundance in 2005 and 2006, and after the peak in 2007 and 2008 (Fig. B2.1). In 2007, later arrival times for birds (likely due to bad weather conditions during migration) and an earlier emergence of arthropods led to the asynchrony between hatch and peaks in arthropod abundance (Fig. B2.1). In 2008, birds did not arrive late, however, arthropods emerged almost two weeks earlier than usual due to an abnormally warm spring on Bylot Island. This illustrates the large inter-annual variation in synchrony between hatch and peaks in arthropod abundance.



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White-rumped sandpiper chicks.

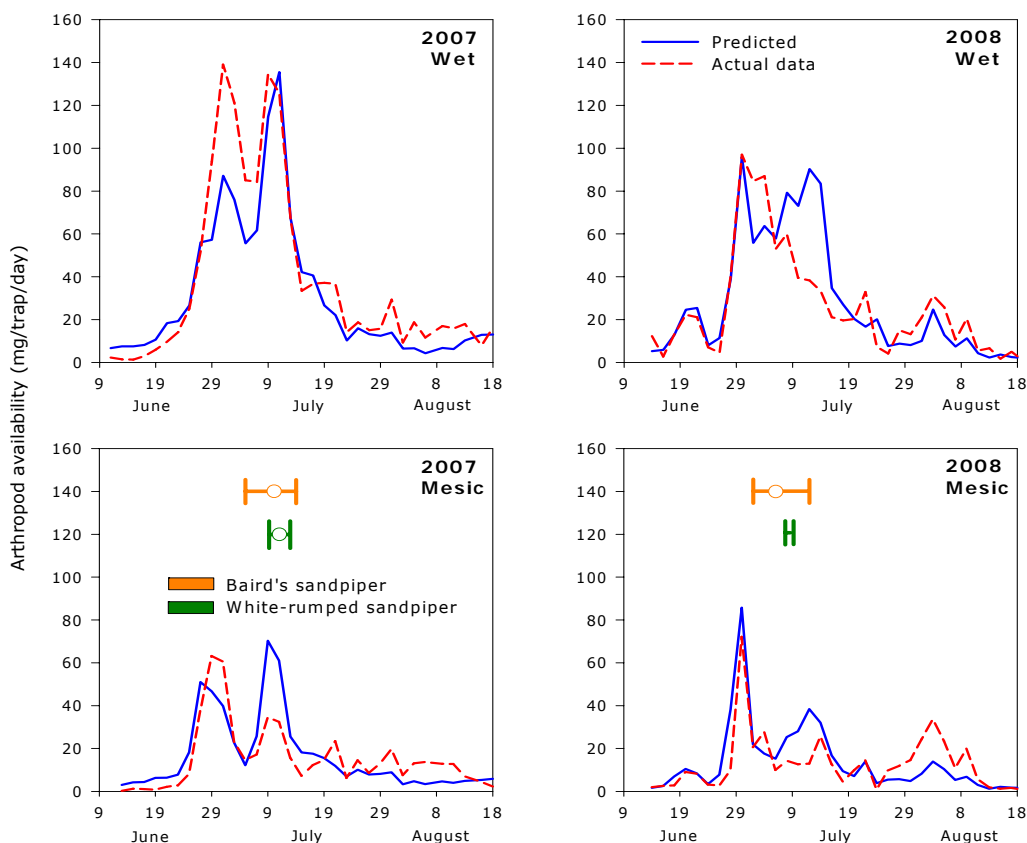


Figure B2.1. Seasonal abundance of arthropod availability predicted by a model based on environmental variables (solid blue line) compared to the seasonal abundance of arthropod measured in the field throughout the summer (dashed red line). The model is based on 4 years of data (2005-2008) for Bylot Island. Data is presented for wet and mesic habitats for 2007 and 2008. Hatching periods of Baird's (orange) and white-rumped sandpipers (green) are also shown. The open circle indicated the average hatch date of each species.



1 - male pectoral sandpiper © Mikhail Soloviev
 2 - curlew sandpiper © Mikhail Soloviev
 3 - pacific golden plover © Mikhail Soloviev
 4 - red knot © Jean-Rémi Julien
 5 - semipalmated plover © Nicolas Lecomte
 6 - grey plover © Mikhail Soloviev

7 - bar-tailed godwit © Peter Romanow
 8 - Wilson's snipe © Jean Iron
 9 - dunlin (breeding adult) © Jean Iron
 10 - terek sandpipers © Peter Romanow
 11 - ruddy turnstone (breeding adult) © Jean Iron
 12 - greater yellow leg © Kenneth F. Abraham

CHAPTER 6. SHOREBIRDS

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Abstract

With over 50 species nesting throughout the circumpolar arctic region each summer, shorebirds form an important component of arctic biodiversity. Unfortunately, populations of many of these species are currently in decline and the reasons for these declines are not yet well documented. As champion migrants, flying up to 30,000 km per year between their wintering grounds in the southern continents to their breeding grounds in the Arctic, shorebird populations may be limited by numerous factors occurring across the entire migratory flyway. Habitat degradation and loss at migratory stop-over sites and on the wintering grounds is suspected to be one of the key factors affecting survival of shorebirds, whereas on the breeding grounds, reproduction may be limited by predation, resource availability and severe weather events. During this project, we collected data on the abundance, distribution and reproductive ecology of shorebirds at several sites throughout the Canadian and Russian Arctic. Our goal was to better understand the factors limiting arctic shorebird populations, as well as provide insight into the potential effects of climate change on their populations. In Canada, shorebird species diversity varied across sites, with the greatest diversity of breeding shorebirds at the most southern sites and the lowest at the most northern sites. At one southern site, Herschel Island, new records of breeding birds included least sandpiper and buff-breasted sandpiper. Where measured, abundance of nests was generally low, and decreases in abundance since earlier studies were detected for ruddy turnstone, Baird's sandpiper and red-necked phalarope at the Herschel Island site. In Russia, changes in abundance and distribution of shorebirds were also documented. Advancements in lay dates were found for several species at the Herschel Island site (semipalmated sandpiper, Baird's sandpiper and American golden plover) but for only one species at the Bylot Island site (white-rumped sandpiper), likely attributable to rising temperatures over the last few decades. Synchrony between hatch dates and peaks in food resources at one High Arctic site, Bylot Island, was relatively low and resulted in reduced growth rates for Baird's sandpiper chicks. On Bylot Island, arctic fox were identified as the main predator of shorebird eggs and nest predation varied with the abundance of alternative prey such as goose eggs and lemmings. We documented large variation in nest predation risk across Arctic Canada as predation risk for shorebird eggs was highest at low latitude sites and decreased considerably with latitude. Our results suggest that the costs of migrating farther north are compensated for by decreases in predation risk for shorebirds breeding at higher latitudes. Though habitat loss across the migratory pathway will continue to be a conservation concern for shorebird populations, factors threatening reproduction may become more important in the context of expected changes to the arctic climate. Shorebird predator-prey relationships could be altered via changes in predator and alternative prey communities and/or changes in the timing of resource availability.

Arctic-nesting shorebird populations

Shorebirds form a very important component of arctic biodiversity, with approximately 50 species nesting throughout the circumpolar arctic region each summer (Meltofte et al. 2007). In the western hemisphere, shorebirds breed commonly in all arctic tundra habitats from the subarctic northern edge of the boreal forest to the northernmost tip of Ellesmere Island in the High Arctic. Canada's arctic tundra provides essential breeding grounds for 42 species of shorebirds whose annual migrations along various flyways take them to wintering destinations as far east as the Wadden Sea in northern Europe, or even as far south as Tierra del Fuego, Argentina (Fig. 1). Shorebirds breeding in the eastern hemisphere exhibit equally impressive migrations from their wintering grounds in southern Af-

rica and Australia to their breeding grounds in the Siberian Arctic (Fig. 1). Although shorebirds are abundant in the Arctic, their nests are dispersed, well camouflaged, and can be difficult to find, so that considerable effort is required to systematically estimate abundance of breeding birds. As a result, few studies have been conducted over a long enough period to provide estimates of breeding populations of shorebirds in the Arctic (Gratto-Trevor et al. 1998, Pattie 1990).

Much of the current trend information for arctic-nesting shorebirds in the western hemisphere is based on analyses of birds counted during migration or on the wintering grounds (Howe et al. 1989, Morrison et al. 1994, 2001, 2006). The few studies that have provided local indices of population trends on the breeding grounds have generally indicated

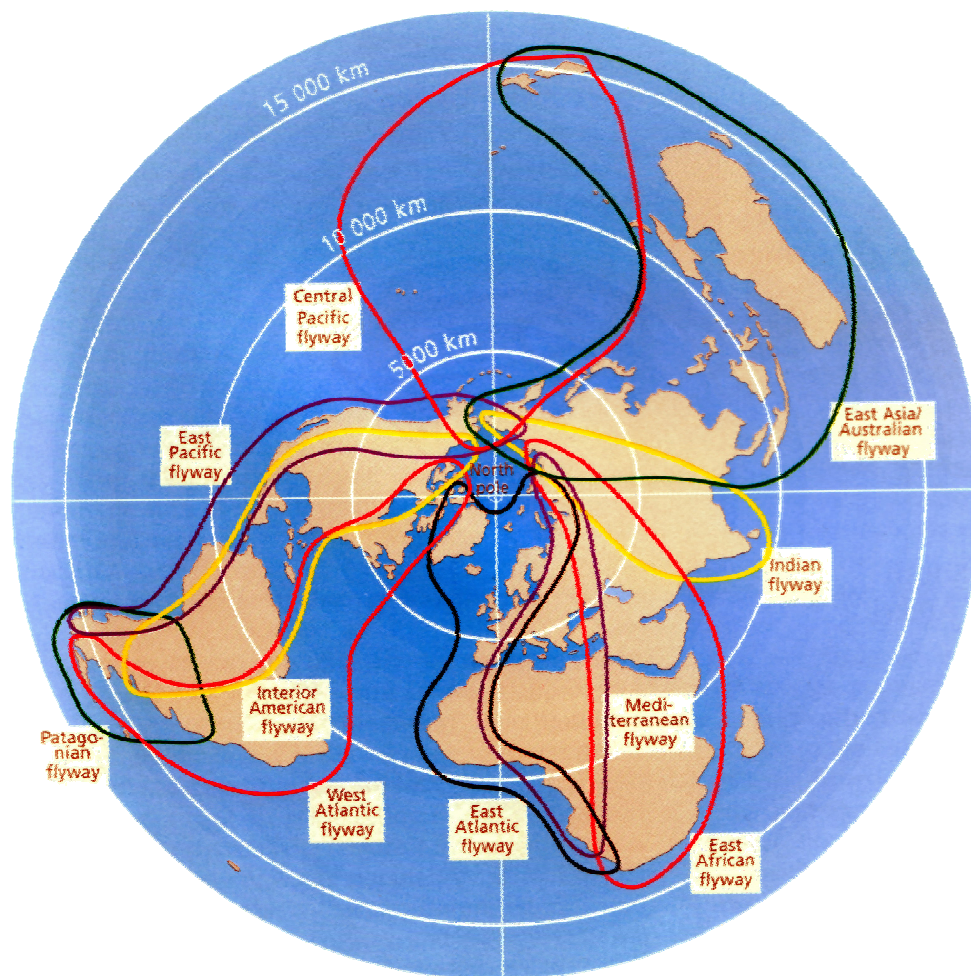


Figure 1. Shorebird flyways of the world (from van de Kam et al. 2004).

ArcticWOLVES final synthesis report

declines in the breeding populations of several species, especially between the 1970s and the 1990s (Pattie 1990, Hitchcock and Gratto-Trevor 1997, Gratto-Trevor et al. 1998, 2001). The one exception to these studies is that of Latour et al. (2005) where shorebird densities did not decline between the 1970s and 1990s at Cresswell Bay, Nunavut. Though a recent assessment of breeding populations from Arctic PRISM (Program for Regional and International Shorebird Monitoring) suggests that previous estimates of population size may have been low (Bart and Smith 2011), there is still a general consensus regarding population declines for many species.

In general, trends available for arctic breeding populations have been consistent with those found for migrating populations, though the latter have been slightly more alarming. Analyses of the ISS (International Shorebird Survey) and MSS (Maritime Shorebird Survey) data from 1974 to 1998 indicated declines in 22 of 30 (73%) Atlantic populations (9 significant), and in 11 of 29 (38%) Mid-West Interior populations in North America (Bart et al. 2007). One notable population decline is that of the wintering population of the North American red knot, which has declined from ~67,000 to ~30,000 birds in just over two decades (Morrison et al. 2004). Alternative hypotheses have been proposed for these documented changes, i.e. that the declines are associated with shifting distributions of birds or changes in rates of detection of birds, instead of actual population declines (Bart et al. 2007), but there is little hard evidence to date to support these hypotheses. Changes in behaviour caused by avian predators, however, have been reported (Lank et al. 2003, Ydenberg et al. 2004). Shifting distributions have only been documented for a few North American species such as American golden plovers (northward range extension to Devon Island; Pattie 1990) and stilt sandpiper (*Calidris himantopus*; westward shift in distribution; Klima and Jehl Jr 1998) and at least one Eurasian species, the ruff (*Philomachus pugnax*; eastward shift of breeding population; Rakhimberdiev et al. 2010).

Population limitation/regulation

As with many migratory birds, factors limiting shorebird populations can occur

across the entire migratory flyway including the summer breeding grounds, migratory stopover sites and wintering areas. Habitat degradation and loss at migratory stopover sites and on the wintering grounds is suspected to be one of the key factors limiting shorebird populations (Donaldson et al. 2001, Baker et al. 2004). Shorebirds rely heavily on both inland and coastal wetland areas as refuelling sites during migration. It has been estimated that almost half of the marshes present on the Atlantic and Gulf coasts of the USA have disappeared since 1900 (Dahl 1990, GLCF 2005). Remaining sites used by shorebirds may be threatened by habitat degradation leading to reduced food resources (Baker et al. 2004), high levels of contaminants (Braune and Noble 2009) and/or toxic levels of trace elements (Ohlendorf et al. 1986).

On the breeding grounds, reproduction is limited primarily by predation, resource availability and severe weather events. Predation is an important factor affecting several stages of the life cycle of shorebirds. For example, population increases of peregrine falcons (Rowell et al. 2003) have resulted in reduced feeding rates of shorebirds at stopover sites during migration and increased mortality (Ydenberg et al. 2002). Though predation of adults by avian predators can occur year round (Lank et al. 2003), nest predation may be an even greater limiting factor in population growth of shorebirds. In years of high predator abundance in the Arctic, nest success can be reduced to near 0%, limiting recruitment of young and resulting in cycles in annual population size (Summers et al. 1998, Blomqvist et al. 2002, Meltofte et al. 2007).

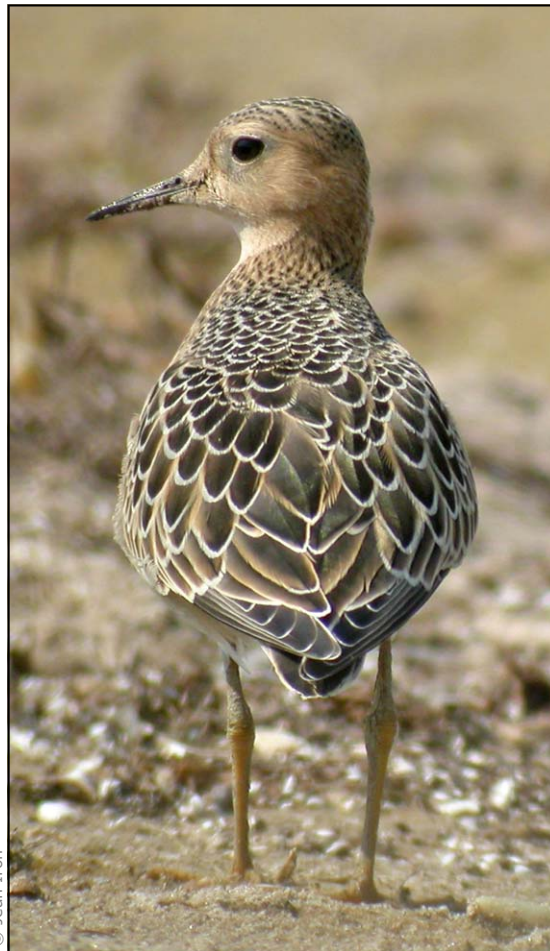


© François Rousseau
Stilt sandpiper on its nest.

Food resources appear to be most limiting during migration where individuals have a short period of time to gain body reserves for long, sometimes non-stop, flights to the breeding grounds (Baker et al. 2004, Morrison 2006, Atkinson et al. 2007). Resources can also limit growth and survival of young on the breeding grounds (Pearce-Higgins and Yalden 2004, Tjorve et al. 2007). Extreme weather events during migration and especially on arrival on arctic breeding grounds can also severely reduce adult body condition and survival (Morrison et al. 2007) and even result in years of complete breeding failure (Ganter and Boyd 2000) or direct mortality from starvation (Morrison 1975). While extreme weather can affect demography, more typical variability in weather was not found to have a dominant influence on reproductive success at a low arctic site (Smith 2009, Smith and Wilson 2010).

Shorebird distribution and abundance during IPY years

The ArcticWOLVES project generated important new data on the abundance, distribution and reproductive ecology of arctic-nesting shorebirds, which will aid us in understanding the potential effects of climate change on arctic shorebird populations. In North America we collected data on shorebird abundance along with nesting phenology at Bylot Island, Herschel Island, Akimiski Island and Alert. On Akimiski Island, data were also collected on timing of shorebird migration. Shorebird species diversity varied across sites, with Akimiski Island boasting the greatest diversity of breeding shorebirds at 11 species, and Alert the lowest at 4 breeding species (Table 1). New records of breeding birds included least sandpiper and buff-breasted sandpiper at Herschel Island. Where recorded, nesting densities were generally low, ranging from 0.4 to 1.0 nests/ha on Herschel Island and 0.01 to 0.07 nests/ha on Bylot Island. Marked changes in abundance since earlier studies were noted on Herschel Island, where shorebirds such as ruddy turnstone and red-necked phalaropes (*Phalaropus lobatus*), common in the mid-1980s (Talarico and Mossop 1986), were no longer nesting in many of the same areas during IPY years. As these species nest on beaches or close to tidally flooded wet-



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Juvenile buff-breasted sandpiper.

lands, it is possible that populations have declined because of rising sea levels and more frequent summer flooding of these habitats. For instance, a summer storm surge in 2008 destroyed numerous beach-nesting common eider (*Somateria mollissima*) nests and a semipalmated plover nest. Baird's sandpiper, one of the most abundant shorebirds on Herschel Island, also appears to have declined, likely associated with the documented increase in plant cover and proliferation of prostrate woody shrubs noted since the 1980s (Kennedy et al. 2001). Results during migration monitoring at Akimiski Island revealed that this is an important migration stopover site of regional if not hemispheric importance.

At an eastern hemisphere IPY site on the Yamal Peninsula in Russia, changes in abundance and distribution of shorebirds have also been documented. Whimbrel and bar-tailed godwit (*Limosa lapponica*), which were quite

ArcticWOLVES final synthesis report

rare on the forest-tundra zone in the 1970s, have dramatically increased in number and are now rather common (Ryzhanovsky and Paskhalniy 2007). Other, typically boreal breeding shorebirds, such as the terek sandpiper (*Xenus cinereus*) and greenshank (*Tringa nebularia*), have recently been detected on the tundra at the Erkuta field station on south-western Yamal (2005; V. Sokolov, unpubl. data). At the same time, species with southern ranges covering the Erkuta area, such as pacific golden plover (*Pluvialis fulva*) and curlew sandpiper (*Calidris ferruginea*), are no longer being detected as breeders and observations of other formerly abundant species such as the grey plover (*Pluvialis squatarola*), dunlin (*Calidris alpina*) and little stint (*Calidris*

minuta), have become rare in south-western Yamal (Sokolov 2006) compared to previous observations (Ryabitsev 1993).

Food resources and synchrony with hatch

At some sites, we collected data on nesting phenology in relation to the seasonal abundance of food resources in order to evaluate synchrony between shorebird hatch dates and peaks in food resources. On Bylot Island, although temperatures during the laying period were 1.2 to 2.6°C higher in 2005 to 2008 compared to data available from 1954 (Drury 1961), advances in lay dates could only be documented in one of three shorebird species studied, the white-rumped sandpiper. Shorebirds main prey (arthropods) are char-

Table 1. Shorebird species composition across sites of the ArcticWOLVES project in North America. 1 indicates species recorded as breeders and 0 indicates the absence of species.

Shorebird species	Akimiski	Herschel	Bylot	Alert
Black-bellied plover, <i>Pluvialis squatarola</i>	0	0	1	0
American golden plover, <i>P. dominica</i>	0	1	1	0
Semipalmated plover, <i>Charadrius semipalmatus</i>	1	1	0	0
Killdeer, <i>C. vociferous</i>	1	0	0	0
Hudsonian godwit, <i>Limosa haemastica</i>	1	0	0	0
Marbled godwit, <i>L. fedoa</i>	1	0	0	0
Short-billed dowitcher	1	0	0	0
Whimbrel, <i>Numenius phaopus</i>	1	0	0	0
Lesser yellowlegs, <i>Tringa flavipes</i>	1	0	0	0
Greater yellowlegs, <i>T. melanoleuca</i>	1	0	0	0
Spotted sandpiper, <i>Actitis macularia</i>	1	0	0	0
Ruddy turnstone, <i>Arenaria interpres</i>	0	0	0	1
Red phalarope, <i>Phalaropus fulicarius</i>	0	0	1	0
Red knot, <i>Calidris canutus</i>	0	0	0	1
Sanderling, <i>C. alba</i>	0	0	0	1
Semipalmated sandpiper, <i>C. semipalmatus</i>	0	1	0	0
Least sandpiper, <i>C. minuta</i>	1	1	0	0
White-rumped sandpiper, <i>C. fuscicollis</i>	0	0	1	0
Baird's sandpiper, <i>C. bairdii</i>	0	1	1	1
Pectoral sandpiper, <i>C. melanotos</i>	0	0	1	0
Buff-breasted sandpiper, <i>Tryngites subruficollis</i>	0	1	0	0
Common snipe, <i>Gallinago gallinago</i>	0	1	0	0
Wilson's snipe, <i>Gallinago delicata</i>	1	0	0	0
Total	11	7	6	4

acterized by sharp, short-lived peaks of abundance. Synchrony between hatch dates and peaks in food resources varied considerably between 2005 and 2008 on Bylot Island and only 1 out of 4 years (2006) exhibited relatively high synchrony (see ARTHROPODS chapter). Growth of shorebird chicks was negatively affected when there was a mismatch between hatch and peaks in food resources (Box 1). Higher growth rates in the presence of higher Tipulidae (crane flies) biomass were consistent with previous studies (Pearce-Higgins and Yalden 2004, Pearce-Higgins et al. 2005) confirming that synchrony with peak food resources is an important factor affecting chick growth in arctic-nesting shorebirds and requires further investigation.

On Herschel Island, both shorebird and passerine lay dates varied substantially between years (5 to 10 days) and were well correlated with timing of snow melt. Advances in lay dates (6 to 12 days) since 1986 (Talarico and Mossop 1986) were detected for three species, semipalmated sandpiper, Baird's sandpiper and American golden plover. Despite this advance, median hatch dates for semipalmated sandpiper and American golden plover were still in advance of the peak in arthropod abundance. The summer flush of arthropods at this low arctic site is spread out over a period of at least thirty days, and accumulated arthropod biomass throughout the season is much higher than at High Arctic sites, so any potential mismatch of nesting and arthropod phenologies might be less severe at Herschel Island. Mean June temperatures at Alert have also risen steadily since the 1970s, though no changes have been apparent in the arrival dates of shorebirds in this area.

Effect of predation at various spatial scales

Intensive studies on Bylot Island allowed us to document temporal and spatial variation in nest survival in relation to changes in predation risk and alternative prey abundance (lemmings and geese) for predators. Camera monitoring of shorebird nests over a period of 4 years revealed the arctic fox as the primary predator of shorebird eggs (McKinnon and Bêty 2009). Predation of nests by arctic fox on Bylot Island appears to be influenced by

the abundance of their preferred and alternate prey, lemmings and geese, respectively. By monitoring artificial nests at two sites on Bylot Island, we found that predation risk was lower in years of high lemming abundance. Similarly, inter-annual variation in daily nest survival of real nests was best explained by lemming abundance, with survival lowest in years of low lemming abundance. In years of low lemming abundance, we also demonstrated that predation risk on artificial nests was elevated in areas of high goose nest density within a snow goose colony. Camera monitoring of predator activity confirmed that arctic fox activity increased as goose nest density increased. These data provide evidence for a hierarchical alternative prey hypothesis which suggests that when preferred prey (lemmings) decrease in abundance, the main alternative prey in the system (goose eggs) become the second order preferred prey and the incidental prey (shorebird eggs) become the second order alternative prey.



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Arctic fox caught by one of our automatic cameras while predating a shorebird nest on Bylot Island, NU, Canada.

At Alert, where geese are not present, the most important factors influencing shorebird breeding success appeared to be predation (principally by arctic foxes and long-tailed jaegers), which varied with lemming abundance, and early spring weather conditions. On Herschel Island, an increase in populations of peregrine falcons (*Falco peregrinus*), one of the focal predators of adult shorebirds, was also documented during the ArcticWOLVES project. In the mid 1980s, peregrines were absent from the island (Talarico and Mossop

ArcticWOLVES final synthesis report

1986) but in 2007-2009 several pairs were located and recent prey remains analysis confirmed that they were feeding on shorebirds.

The role of predation on the reproductive ecology of shorebirds was also investigated on a large spatial scale by monitoring predation risk at 7 ArcticWOLVES sites in North America. By systematically measuring predation risk along a 3350 km north-south gradient across Arctic Canada, we provided the first quantitative evidence that the risk of nest predation decreases with increasing latitude, indicating that birds migrating farther north may acquire reproductive benefits in the form of reduced predation risk (Box 1; McKinnon et al. 2010). Never before has predation risk been measured experimentally across such a large geographic range. In addition to providing valuable and interesting insight into the ecology and evolution of migration in birds, publication of these results has provided quantitative evidence to renew the debate regarding the relative importance of predation versus competition in several fields of ecology. The magnitude of this scientific contribution can be measured not only in the high impact factor of the journal in which it was published, but also in the extensive scientific and international news media coverage which has followed.

Climate change and conservation issues

Shorebirds are income breeders (Klaassen 2001, Morrison and Hobson 2004), which means that they depend upon resources acquired on the breeding grounds for production of eggs. They are therefore particularly vulnerable to changes in early season weather and food availability (i.e. arthropods), and later in the summer to timing of food resources, which often reach peak in availability during the hatch and growth of young as shown above. Seasonal abundance of arthropods is driven by environmental conditions (Holmes 1966, Hodkinson et al. 1996, Schekerman et al. 2004), thus changes in climate could easily alter synchrony between hatch and peaks in food resources (mismatch), resulting in reduced growth and survival of chicks and juveniles (Pearce-Higgins and Yalden 2004). Consequences of a mismatch between hatch and peaks in food resources, owing to changes in climate, have already been documented for southern breeding shorebird

populations (Pearce-Higgins et al. 2009), although there are fewer studies of High Arctic populations despite documented changes in breeding phenology associated with changes in climate (Hoye et al. 2007). In contrast to Herschel Island, our results from Bylot Island suggest that most shorebird species do not appear to be advancing their breeding phenology in response to summer temperatures increase, even though peaks in arthropod availability occur earlier in summers with warmer temperatures (see ARTHROPODS chapter). This differential response to increasing summer temperatures indicates a high likelihood for a mismatch between hatch and peaks in resources in the near future. That we found lower growth rates for chicks hatching outside peak periods of Tipulidae biomass on Bylot Island provides additional evidence for the negative consequences of this potential mismatch for shorebird populations.

Because predation on the breeding grounds is an important limiting factor for shorebirds, there are also concerns that climate induced northward expansion of predators may increase predation risk on shorebirds in the High Arctic (Meltofte et al. 2007). The strong latitudinal trend in predation risk revealed across our ArcticWOLVES sites indicates that shorebird populations could be dependent upon High-Arctic sites as a safe haven from high predation risk at southern sites. Any climate-induced changes in arctic predator communities, be the changes in composition or density, could be catastrophic in the arctic ecosystem where many bird species have likely co-evolved migratory and breeding strategies in the presence of a predictable range of nest predation risk. On Bylot Island, our data indicate that shorebirds also benefit from reduced predation risk when lemming populations increase, and that this indirect relationship can also be influenced by the abundance of other alternative prey such as snow goose eggs. These data suggest that changes in frequency and/or amplitude of lemming cycles and the abundance of alternative prey species, which may occur with changes in climate, could also affect the balance between shorebirds and their predators (Gilg et al. 2009, Gilg and Yoccoz 2010). A changing climate may also influence thermo-static costs for shorebirds, which have been

shown to influence the distribution and morphology of shorebirds on the Arctic breeding grounds (Cartar and Morrison 2005). Yet, another potential effect of climate change which may be important during the entire migratory cycle is the loss of coastal foraging habitat due to rising sea levels (Galbraith et al. 2002, Austin and Rehfish 2003). Other non-climate related conservation concerns for shorebirds include illegal harvesting of some species (Ottema and Spaans 2008, Zöchler et al. 2010).

Conclusion and research needs

Though habitat loss and illegal harvest of shorebirds across the migratory pathway will continue to be a conservation concern for shorebird populations, factors threatening reproduction and recruitment of new individuals into the breeding population may become more important in the context of expected changes to the Arctic climate. Our Arctic-WOLVES project has documented some mechanisms through which the reproductive ecology of arctic-nesting shorebirds can be affected by trophic interactions. In the face of a changing climate, shorebird predator-prey

relationships may be altered via changes in predator and alternative prey communities and/or changes in the timing of resource availability. As arctic-nesting goose populations continue to increase (Gauthier et al. 2005), and lemming cycles are predicted to dampen as arctic temperatures increase (Hörnfeldt et al. 2005), future research should focus on investigating whether predator mediated apparent competition can lead to the exclusion of shorebirds from areas of low lemming abundance and high goose nesting density. Also, as anticipated changes in climate risk to alter the synchrony between hatch and peak food resources in arctic-nesting shorebirds, future ecological studies on shorebirds should continue to investigate potential fitness effects of this mismatch on shorebird reproduction, especially chick growth, survival and recruitment. Effort should also be directed towards a better understanding of both intrinsic (hormonal, genetic etc.) and extrinsic (temperature, snow melt, etc.) cues for timing of breeding in arctic-nesting shorebirds, how these cues relate to peaks in food abundance and how this latter relationship may be altered in the face of a changing Arctic climate.



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Adult spotted sandpiper.

Box 1. Effects of arthropod availability on growth of shorebird chicks.

During the summers of 2006 to 2008 on Bylot Island, Baird's sandpiper nests were visited at hatch so that chicks could be banded at age 0 in the nest and weighed. Marked birds were recaptured periodically during the growth period and reweighed. We analysed the growth of chicks in relation to the abundance of Tipulidae (crane flies; an important prey item for shorebirds) during the hatching period. Chicks that hatched in synchrony with the period of highest biomass for Tipulidae had greater mass (29.4 ± 2.0 g) after day 8 and a faster growth rate (Fig. B1.1) than chicks hatching outside the period of highest biomass (24.5 ± 0.7 g). Reduced juvenile growth rates in birds are a concern because they can lead to reduced survival between hatch and fledgling due to increased exposure to predation during the pre-fledgling period as well as reduced post-fledgling survival or fertility (Starck and Ricklefs 1998).



© Laura McKinnon

Baird's sandpiper chicks in hatching nest.



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Crane flies (Tipulidae).

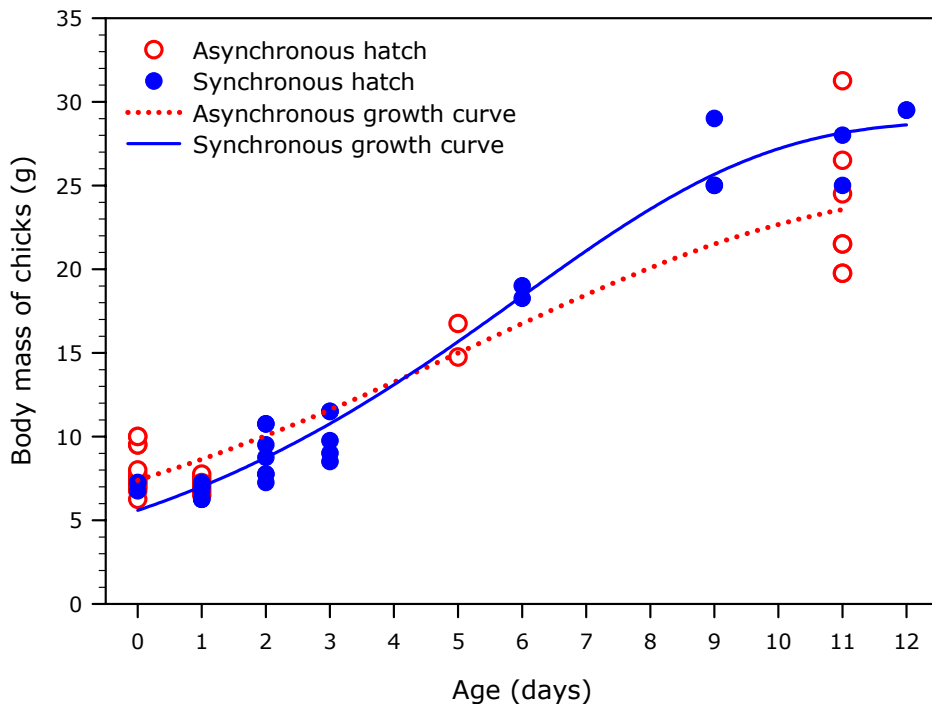


Figure B1.1. Plot of the growth curves for two groups of Baird's Sandpiper chicks ($n=41$), those with hatch dates falling within the defined peak period for Tipulidae (solid line; ideal period) and chicks with hatch dates outside the defined peak period for Tipulidae (dashed line). Raw data points are provided for chicks hatching within the ideal period (solid circle) and chicks hatching outside the ideal period (open circle; from McKinnon et al. in prep.).

Box 2. Latitudinal variation in predation risk.

As predation risk is a dominant force in the evolution of avian life history, we predicted that the risk of nest predation could play a key role in balancing the costs of long-distance migration. To test this, we systematically measured predation risk by monitoring the survival of 1555 artificial nests for a minimum of 2 summers at 7 shorebird breeding sites over a latitudinal gradient of 29° (~ 3350 km) in the Canadian Arctic. By monitoring artificial nests, we controlled for the heterogeneity in survival associated with real nests to yield a controlled effect of predation risk. We found that predation risk reduced by as much as 65% over the latitudinal gradient studied (Fig. B2.1). These results provide evidence that the costs of migrating farther north could be compensated for by decreases in predation risk when shorebirds breed at higher latitudes.

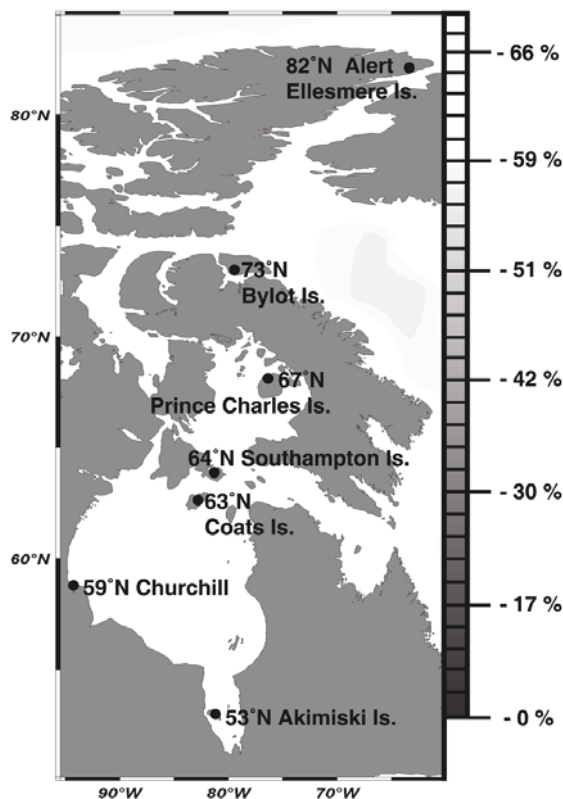


Figure B2.1. Average latitudinal decrease in predation risk and map of the shorebird breeding sites where artificial nests were monitored. The decrease in predation risk (3.6 % per degree relative to the southernmost site, Akimiski Island) is indicated at 5 degree intervals on the latitudinal scale to the right (from McKinnon et al. 2010).



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American golden plover nest.

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Hudsonian godwit nest.

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Whimbrel nest.



- 1 - peregrine falcon © Ivan Pokrovsky
- 2 - young rough-legged hawk © Ivan Pokrovsky
- 3 - glaucous gull © Olivier Gilg
- 4 - parasitic jaeger © Nicolas Lecomte
- 5 - short-eared owl © Dominic Doyle
- 6 - gyrfalcon © Peter Romanow
- 7 - long-tailed jaeger couple © Olivier Gilg
- 8 - nesting snowy owl female © Olivier Gilg
- 9 - white-tailed eagle © Nicolas Lecomte

CHAPTER 7. BIRDS OF PREY

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Abstract

Arctic predatory birds are a diverse group that includes raptors (falcons, hawks, eagles and owls) and tundra seabirds (jaegers and gulls). Many species show irruptive behaviour, which makes it difficult to assess population trends and possible range expansion or contraction. A few species such as the peregrine falcon in North America and Russia, the short-eared owl in Nunavut, the great skua in Greenland and the parasitic jaeger in Greenland and the Russian Far East have nonetheless shown recent range expansion and/or population increase. In contrast, there is evidence that populations of the gyrfalcon in the Yukon North Slope and some parts of Russia, the snowy owl in Europe and the Russian Far East and the pomarine jaeger in the Russian Far East may have recently declined. Population cycles of lemmings and voles have a strong impact on the local abundance and reproduction of most avian predators. However, this varies according to the degree of specialisation of predatory birds on small mammals and among sites. Snowy owls showed the strongest response to fluctuations in small mammal abundance. Rough-legged hawks and long-tailed jaegers also showed a strong response at some sites but not at others such as in northern Yukon and in some parts of Siberia. Intensive studies on Bylot Island showed that avian predators consume a very high proportion of the annual lemming production and could regulate the abundance of collared lemmings during the snow-free period. Satellite-tracking of snowy owls in North America allowed us to measure the scale of their annual movements. Female owls moved over long distances between consecutive breeding seasons (from 18 to 2224 km) and always settled and bred in areas where lemmings were abundant. Most owls attempted to breed every year in far apart areas, which confirms that when small mammals crash in an area, owls will not forego breeding but will rather move over long distances to find suitable breeding conditions (i.e. high small mammal populations). During winter, most female owls remained in the Arctic (north of 55° of latitude) but, surprisingly, they extensively used the sea ice for up to 101 days in the Eastern Canadian Arctic. Birds of prey are top predators and could act as indicator species for the tundra ecosystem. Climate induced changes such as increase in shrub abundance, shift in the distribution of small mammal species or collapse of lemming population cycles in some areas could negatively impact the populations of several birds of prey. An additional source of concern in some areas is illegal killing or trapping for trade. The new links revealed by our study between the terrestrial and marine ecosystems also suggest that some populations of predators such as the snowy owl may be supported by the marine ecosystem in winter. Therefore, a broader, cross-ecosystem perspective may be required when assessing the status or threats faced by these predators. Monitoring of avian predators should not only provide information on the status of their populations but also on the health of the whole Arctic ecosystem.

Predatory birds of the tundra fall into two broad taxonomic groups. They are the raptors, which include primarily the gyrfalcon (*Falco rusticolus*), peregrine falcon (*Falco peregrinus*), rough-legged hawk (*Buteo lagopus*), snowy owl (*Bubo scandiacus*), golden eagle (*Aquila chrysaetos*) and the seabirds, which include the pomarine jaeger (*Stercorarius pomarinus*), parasitic jaeger (*Stercorarius parasiticus*), long-tailed jaeger (*Stercorarius longicaudus*) as well as several species of gulls such as the glaucous gull (*Larus hyperboreus*). In Eurasia, the white-tailed sea eagle (*Haliaeetus albicilla*) and the great skua (*Stercorarius skua*) are also important. All predatory birds (except perhaps parts of the more southerly populations of the gyrfalcon) are migratory though the amplitude of their migrations is variable among species and sometimes among individuals. For instance, most snowy owls remain in arctic or sub-arctic areas in winter, and thus have relatively short migration, whereas rough-legged hawks migrate to temperate areas and peregrine falcons range from temperate to tropical areas in winter. Gulls generally migrate to temperate coastal areas but all jaegers migrate to pelagic areas in the tropics during winter.

Species ranges

Many birds of prey show irruptive behaviour in response to fluctuations in the abundance of their prey, which leads to large annual variations in the size of local populations. Such behaviour complicates the evaluation of their population status and trend or the detection of range expansion or contraction. In North America, the peregrine falcon has recently expanded its range in several areas (e.g. Mossop 1988, White 1994) though this may be largely a recolonization of its former range (Carrière et al. 2003). On Herschel Island in north Yukon, the ArcticWOLVES project documented successful nesting by several pairs of peregrines in 2007-2009, whereas Talarico and Mossop (1986) reported no nesting in the mid-1980s. This represents a population recovery following population decline in the mid 20th century because nesting had been documented on the Yukon North Slope in the 1930s. Similar northern expansion has been reported in eastern Greenland where peregrines have recently been reported breed-

ing north of 70°N (O. Gilg, pers. obs.). The gyrfalcon apparently expanded its range in parts of the Northwest Territories of Canada in the late nineteenth hundreds (Norment et al. 1999). We also documented a possible range expansion of the short-eared owl (*Asio flammeus*), a species more typical of temperate areas, in the eastern Canadian Arctic. A pair showing signs of territorial behaviour was observed for two years on Bylot Island, 1000 km north of the previously documented northern limit of their range in eastern North America (Therrien 2010).

In Eurasia, the snowy owl moved northward in Yamal, with possibly a contraction of its range in the south. For instance Osmolovskaya (1948) found several nests as far to the south as 67.5° but in recent decades all those reported were north of 69.5°. Several reports also suggest that other raptors species may be expanding their range northward. In Yamal, a nest of the endangered pale harrier (*Circus macrourus*) was found in shrubby tundra (67.3°) in 1998 (Morozov 1998), at least 1000 km north of the previously known breeding limit. Birds showing signs of territorial behavior were also found farther north (Erkuta river, 68.2° N, Sokolov et al. 2002; Yuribey river, 68.9° N, Golovatin et al. 2004). Along the Erkuta river, an unsuccessful nesting attempt by a sea eagle was recorded in 2009 (Sokolov et al. in prep.), which is at least 100 km north of its known breeding range. These changes in the Yamal region may be in part due to a local shift in small rodents community as the Siberian lemming (*Lemmus sibiricus*) has been replaced by voles (*Microtus* spp) in some areas (Sokolov et al. 2010). An expedition to the Lena Delta in 2010 confirmed for the first time 4 active nests of gyrfalcon in an area where it was previously only reported as a rare breeder (Dixon et al. in prep.). On Wrangel Island, the short-eared owl has been reported as an irregular visitor (Portenko 1973, Krechmar et al. 1979, Dorogoi 1983) and 3 cases of nesting were recorded in 1970s - 1980s. In recent years, its status has remained the same as birds are occasionally observed on the island, though not every year, and 4 nesting attempts (3 successful) have been recorded during the period 1990 to 2010. The great skua has been expanding both eastward and westward from

ArcticWOLVES final synthesis report

northern Europe. In Siberia, it is now present up to Obskaya Bay (72°E; Ryabitsev and Pokrovskaya 1995). In Northeast Greenland, there has also been a recent increase in observations of great skuas, especially in the North East Water Polynia (ca. 80°N). These birds most probably originate from Svalbard where great skua populations are rapidly increasing. They do not breed yet in Greenland but this might soon change.

Population status

Population status and trend of most species of birds of prey is poorly known. In North America, tundra populations of the peregrine falcon have been increasing over the last few decades as they recovered from declines that occurred during the mid 20th century due to pesticides (Bromley 1992, Shank et al. 1993, Kirk and Hislop 1998, Rowell et al. 2003). In some areas (e.g. eastern North America, Yukon), successful reintroduction contributed to the increases (Sinclair et al. 2003). Populations of the rough-legged hawk and snowy owl have been generally thought to be relatively stable (Kirk and Hislop 1998) and, in accordance with that, the abundance of these two species on Herschel Island did not appear to have changed much from the mid-1980s (Talarico and Mossop 1986) to the current IPY period. The short-eared owl was also recorded breeding at low densities on Herschel Island in 2007-2008, and has bred there in the past (Sinclair et al. 2003), but due to the lack of

survey effort the population trend is unknown. On the Yukon north slope (British Mountains and coastal plain), historical data indicate a cyclic pattern of population change in nesting gyrfalcons, attributed to cyclic changes in the abundance of their primary prey, the willow ptarmigan (*Lagopus lagopus*). During the ArcticWOLVES project D. Mossop re-surveyed gyrfalcon nests in 2007 and 2008, and found remarkably low numbers of nesting birds and low productivity of nests (Fig. 1). This may be a low phase of another population cycle, or may represent an overall decline in the abundance of this species. In 2008, 5 of 24 nesting sites historically occupied by gyrfalcons were then occupied by golden eagles (*Aquila chrysaetos*).

In Eurasia, tundra populations of the peregrine falcon have also increased, in particular in the Yamal region over the past 10 years (Sokolov et al., in prep.), for the same reasons as in North America. Populations of the sea eagle and golden eagle show a slow positive trend in the forest-tundra zone of Yamal (Mechnikova 2009) whereas populations of the rough-legged hawk seem to be rather stable. Populations of the gyrfalcon have decreased in some parts of Eurasia (Mechnikova 2009), possibly due to illegal trapping. Snowy owl populations show a negative trend in some part of Eurasia. For instance, owls breeding in the tundra area of northernmost Norway and especially in the Fennoscandian mountain tundra further south have decreased

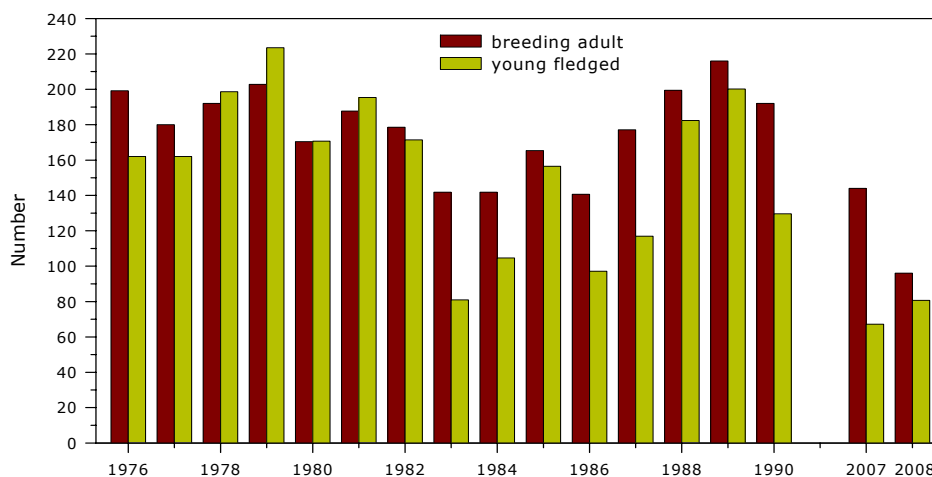


Figure 1. Long-term trend in gyrfalcon population (number of breeding adults) and productivity (number of young near fledging) on the Yukon North Slope, Canada (D. Mossop, unpubl. data).

considerably over the last decades (Jacobsen 2005). A slight decreasing trend in snowy owl abundance has also been observed on Wrangel Island in eastern Russia (see Box 1).

Little information is available on population trends of predatory seabirds of the tundra. Among the 3 jaeger species, long-tailed jaeger is the species that has the most widespread distribution and the highest density (Wiley and Lee 1998). Local variations in abundance of nesting jaegers are thought to be largely related to fluctuations of their main prey (lemmings) though less so in the parasitic jaeger, which has a more generalist diet than other jaegers (Wiley and Lee 1999). Nesting density of long-tailed jaegers on Herschel Island during the IPY years was similar to the mid-1980s (Talarico and Mossop 1986). On Wrangel Island, the long-tailed jaeger population also appears stable. However, the two other jaeger species present at the latter site show opposite trends. The pomarine jaeger has been decreasing as densities during peak lemming years declined from 2.7 nests/km² in the early 1980s to 0.67 nests/km² in recent years. In contrast, the parasitic jaeger has apparently increased as up to 20 nests per year have been recorded in recent years compared to 1-3 in the 1980s and 1990s (I. Menyushina, unpubl. data). This



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Parasitic jaeger.

may be an indication of a northward expansion of the species range in this part of the Arctic. Parasitic jaegers may also be increasing and expanding their range northward in eastern Greenland. On Hochstetter Forland (75°N), for example, where it was only a rare summer visitor until the late 1970s, it is now regularly breeding (O. Gilg, pers. obs.). For the glaucous gull, populations at the southern limit of its range such as those nesting on the Belcher Islands in Hudson Bay have experienced a decline, possibly due to change in sea-ice condition and the strong decline of eider populations, a major source of food for gulls there (Gilchrist and Robertson 1999). Further north, the only other information available comes from Bylot Island, where breeding densities of glaucous gulls have remained stable over the last 6 years. On Herschel Island, glaucous gulls appeared to be as abundant during IPY years as they were in the mid-1980s.

Predator-prey interactions

The investigation of trophic relations in a food web requires a good understanding of the diet of predators and of the role of change in prey availability in their reproduction and movements. Therefore, considerable effort was spent by the ArcticWOLVES project to document temporal and spatial variation in the diet of birds of prey (see Box 2). During the summer, the snowy owl and rough-legged hawk are small mammal specialists in North America as lemmings and voles make up >90% of their diet (Therrien et al., in prep.). However, some spatial variation in this pattern was found as rough-legged hawks in some parts of Russia appear to have a much broader diet, possibly due to a more diversified prey base at this low tundra site (see Box 2). Lemmings are also a major component of the diet of the long-tailed jaeger in North America (up to 70% in a year of peak lemming abundance) but this proportion decreases considerably during years of low lemming abundance. However, long-tailed jaegers can be somewhat opportunistic as we found that in presence of a rich and stable anthropogenic food source, they can modify considerably their diet (see TUNDRA FOOD WEB chapter). Tundra-nesting gulls are the most generalist as their diet includes a large proportion of

ArcticWOLVES final synthesis report

birds (especially geese when they are present) though they also consume small mammals.

Population cycles of lemmings and voles have a strong impact on the local abundance and reproduction of most avian predators. However, this varies according to the degree of specialisation of predatory birds on small mammals, and also among sites. On Bylot and Herschel Islands and in northeast Greenland, snowy owls show the strongest numerical response to fluctuations in small mammal abundance as they usually nest in a given area only in years of peak lemming abundance and move elsewhere between those peaks (Gilg et al. 2003, Gauthier et al. 2004). In contrast, on Wrangel Island snowy owls apparently nest in most years (see Box 1), possibly because lemming densities are higher there (see SMALL MAMMALS chapter). Rough-legged hawks showed a similar though less extreme numerical response to lemming abundance as some individuals also nested in low lemming years. However, a tight link between the abundance of nesting hawks and small mammals was not observed in all regions. On Herschel Island, hawk density fluctuated little and independently of small rodent abundance, as well as in Nenetsky, possibly because of the broader diet of hawks at the latter site (see Box 2). Despite their slightly more generalist diet, the reproduction of long-tailed jaegers on Bylot and Herschel Islands is also strongly affected by fluctuations in small mammal abundance as very few individuals nest in years of low abundance and those that do so usually fail to fledge young. As found for snowy owls, long-tailed jaeger populations on Wrangel Island appear to fluctuate less in response to changes in lemming abundance. Finally, the number of nesting gulls is generally more stable from year to year than that of other predatory birds and they are only weakly affected by small mammal abundance, although their nests tend to be less successful in low lemming years.

There is increasing evidence in the literature that avian predators can have a strong impact on the abundance of small mammals (e.g. see Gilg et al. 2003, 2006 for Greenland). On Bylot Island, results of the ArcticWOLVES project show that avian predators consume a very high proportion of the annual lemming production (J.-F. Therrien et

al. unpubl. data). In collared lemmings, the species preferred by predators, daily consumption by avian predators even exceeds the maximum daily potential growth rate over a wide range of abundance, thereby suggesting that predators could regulate this species during the snow-free period. The presence of brown lemmings, an alternative prey in this system, may enhance the impact of predators on collared lemmings. Finally, results obtained from modeling the flux of biomass in the tundra food web also suggest that the combined impact of avian and mammalian predators on small mammal is very strong (see TUNDRA FOOD WEBS chapter) and that they likely play a role in the regulation of cyclic populations.

Movements of birds of prey

The satellite-tracking of breeding snowy owls allowed us to measure the scale of their movements. We marked 12 adult females on Bylot Island in 2007 and 4 on Herschel Island in 2008 and tracked their movements for periods ranging from 1 to 3 years (Fig. 2). Female owls moved over long distances between breeding seasons, as birds marked on Bylot Island moved on average 725 km (range: 18 to 2224 km) between breeding sites in consecutive years and those marked on Herschel 525 km (range 270-780 km) (Therrien et al. in prep.). To our knowledge, these are the longest average breeding dispersal distances reported for any bird species. We should point out that Herschel Island has proven to be a rather anomalous arctic habitat for snowy owls in that substantial numbers of non-breeders settled there for prolonged periods in spring and summer of many years, and nesting is sporadic, with low reproductive success, and coincident with the relatively low amplitude lemming population peaks at this site (see also Talarico and Mossop 1986). We were able to confirm that most owls attempted to breed every year in far apart areas over a 4-year period (2007-2010; Therrien et al. submitted). Birds breeding on Bylot Island in 2007 nested in subsequent years in areas ranging from northern Quebec to the south, Prince Patrick Island to the west and the northern tip of Greenland to the north. Owls always settled in areas where lemmings were known to be abundant that year, which shows their ability to track fluctuations in small

mammal abundance over large areas. This also confirms that when small mammals crash in an area, females will not forego breeding but will rather move to other areas to find suitable breeding conditions, even if this entails movements exceeding 1000 km.

Satellite-tracking further revealed that most adult females wintered at high latitudes in North America (i.e. north of 55° of latitude). In the East, most birds spent the winter in the south Baffin/northern Quebec region though one bird wintered on Ellesmere Island, one in Newfoundland and one in the Great Plains (Fig. 2). In the west, owls wintered in central Alaska and Yukon south of the Brook Range, in the Ogilvie Mountains, and in Denali National Park. Their relatively restricted core winter ranges were often in areas with high abundance and habitat quality for snowshoe hares (*Lepus americanus*) and ptarmigans (*Lagopus* spp.). However, the most striking and surprising result was the extensive use of sea ice by owls wintering in the Eastern Canadian Arctic (see Box 3). This pattern, however, appears region-specific because snowy owls

marked in the West made little use of the sea ice. Four satellite-tracked owls marked during winter in northern Norway made little use of the sea ice in winter (Solheim et al. 2008, Jacobsen et al. 2009). During the summer, these birds moved east over the European part of the Russian Arctic up to western Taymyr (82°E).

Information on scale of movements of other species is limited as we were not able to track them with satellite transmitters, except for a few peregrine falcons marked in Yamal. These birds spread over a huge area in winter from southern Portugal in the west to the Persian Gulf in the east and central Africa in the south to southern Russia in the north (Sokolov et al. in prep.). Observations of long-tailed jaegers marked with colour bands suggest that these birds are faithful to their breeding territory and return to nest on average 90 m from where they bred in previous years. In contrast to snowy owls, jaegers apparently remain at their usual breeding site when lemmings crash and simply forego breeding.

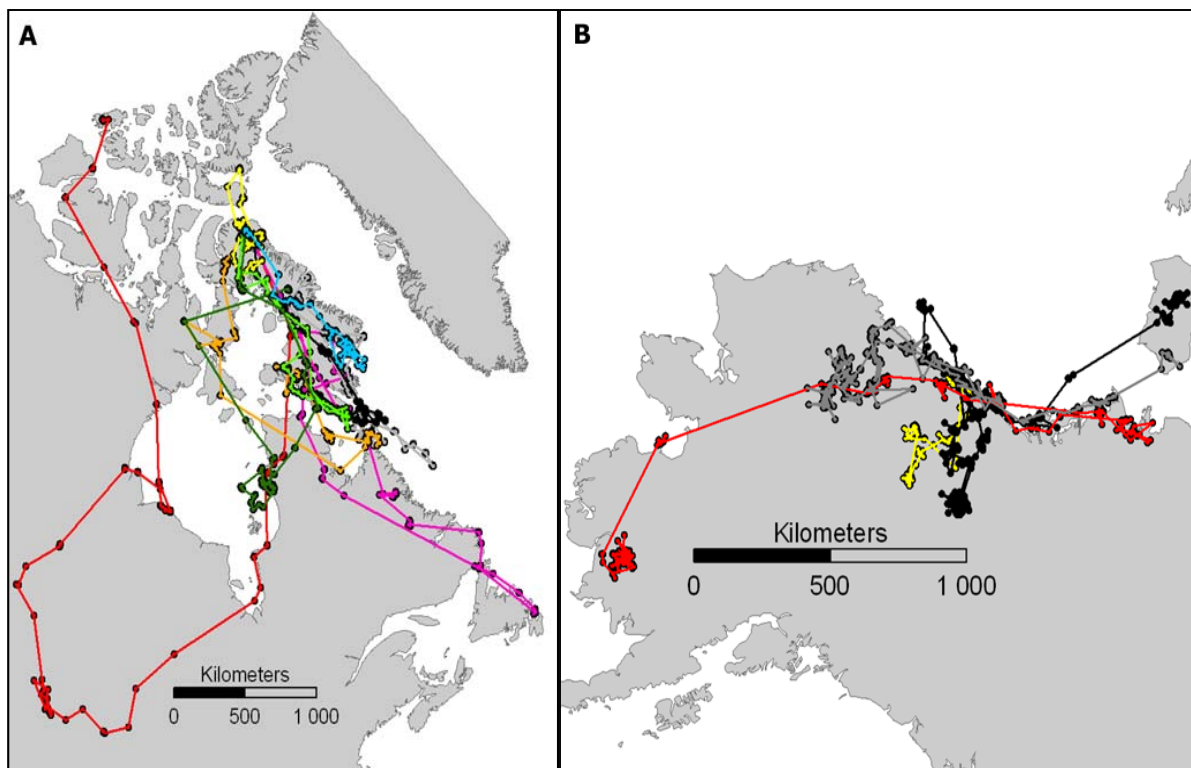


Figure 2. Year-round tracks of 10 adult female snowy owls marked on Bylot Island, NU, Canada (**A**) in summer 2007 and of 4 marked on Herschel Island (**B**) in summer 2008.

ArcticWOLVES final synthesis report

Anticipated threats, effects of climate change and conservation issues

In many areas of the circumpolar world such as northern Fennoscandia or northeast Greenland, a recent collapse of lemming population cycles has been reported (Ims et al. 2008, Kausrud et al. 2008, Gilg et al. 2009; see SMALL MAMMALS chapter for possible causes), though we have found no clear evidence yet for that in the Canadian Arctic archipelago. This may represent a significant threat for the populations of most species of predatory birds as their breeding success is so closely tied to the abundance of small mammals. The decline of snowy owls reported in Fennoscandia is mainly due to the absence of lemming peaks in these areas (Jakobsen 2005) though during the lemming peak of 2007 several pairs were breeding successfully in Finnmark. In central East Greenland (Traill Island), no snowy owls and very few long-tailed jaegers have successfully nested since

the collapse of the lemming cycles in the early 2000s (B. Sittler and O. Gilg, pers. obs.). Species that exhibit high breeding philopatry like the long-tailed jaeger are expected to disappear from this area within 10-20 years (i.e. the remaining life expectancy of breeding adults) if there is no recruitment or immigration. Snowy owls may be able to cope with such changes because they can track lemming outbreaks over vast areas, as shown above. However, if the spatial scale of the collapse in lemming cycles increases, they may also face population decline.

Another threat facing some species of raptors may be the collapse of nesting structures during the nesting season. Rough-legged hawks, peregrine falcons and snowy owls often build their nests on mud or sandy cliffs. In all three field seasons on Herschel Island, we observed that up to half of the nests failed when the soil cliffs collapsed due to the melting of permafrost under these



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Partly collapsed nest of rough-legged hawk on Herschel Island, Yukon, Canada.

slopes. All cliffs on Herschel are mud and clay, with high permafrost ice content, exposed by sea or stream erosion. However, such nest loss was not reported in the 1980s (Talarico and Mossop 1986). We hypothesize that two forces are speeding up the collapse of these cliffs: (i) increased rates of coastal erosion because of the documented longer ice-free season, rising sea level, and more intense storm activity that increase the eroding action of waves (Comiso et al. 2008); (ii) greater heat absorption and consequent melting in ice-rich soils directly exposed to sun because of reduced coastal fog which often forms above early summer pan ice. These two forces may interact since melted permafrost is much more susceptible to erosion by waves. Similar observations have been made in the Yamal region of Russia, suggesting that this may be a widespread phenomenon. These forces are directly related to climate warming and likely to become more and more problematic.

The large inter-individual variability in migratory patterns and the high breeding dispersal depicted by snowy owls suggest that this species does not exhibit distinct sub-populations across its circumpolar range. This statement is also supported by Marthinsen et al. (2009), who reported no phylogeographic genetic structure in Siberian, North American and Scandinavian snowy owls. This suggests that management of this species should be global rather than regional or local.

Conclusion

Birds of prey are top predators and could act as indicator species for the tundra ecosystem. For instance, climate induced changes to the tundra ecosystem such as increase in shrub abundance, shift in the distribution of small mammal species or collapse of lemming population cycles in some areas could negatively impact the populations of several birds of prey. Results of our project also support an increasing body of evidence suggesting that avian predators may regulate their prey populations, at least in some areas, and thus are key players in the functioning of the tundra food web. Our project allowed us to uncover new links between the terrestrial and marine ecosystems and suggest that some predator populations, such as the snowy owl in eastern North America, are subsidized by the arctic marine ecosystem in winter. Therefore, a broader perspective may be required when assessing the status or threats faced by some of these predators. At the moment, the populations of several raptors such as the gyrfalcon and the snowy owl are a source of concern in some areas. In contrast, populations of several tundra seabirds such as the parasitic jaeger and the great skua may be doing better. An additional source of concern for some raptors, especially in Russia, is illegal killing or trapping for trade. Therefore, special conservation measures may be required in some areas. Monitoring of avian predators should not only provide information on the status of their population but also on the health of the whole Arctic ecosystem.



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Peregrine falcon.

Box 1. Long-term study of snowy owls on Wrangel Island, eastern Russia.

Snowy owl populations have been monitored continuously on Wrangel Island since 1990 (Menyushina 1997, 2007b). This long-term study provides good background information for examining the reaction of local populations to recent climatic changes. Although snowy owl numbers on the island fluctuate in synchrony with fluctuating lemming populations, they nonetheless breed in most years except in years of very low lemming abundance (Fig. B1.1). There were some indications of a decline in the snowy owl population on the island. During the 1990-2000 period, the average number of nesting owls recorded annually was 71 (maximum: 121) for 9 years of presence but this number decreased to 60 (maximum: 107), for the period 2001-2010. Frequency of snowy owl occurrence recorded during route surveys also declined (0.58 owl/km during 1990-2000 vs. 0.48 owls/km during 2001-2010). Males always prevail among adults present on the island during the breeding season and the annual

number of breeding pairs is determined by the number of arriving females. The higher proportion of males may be an indication that female mortality during winter is higher than that of males. Although their clutch size does not fluctuate with lemming abundance, the number of chicks that fledge is dependent on lemming numbers (I. Menyushina, in prep.). High amount of cold rain during the breeding season also has a negative impact on survival of young in the nest. However, prolonged warm fall, as recently recorded on the island, may be a positive factor for the survival of young owls. In recent years, birds that started nesting as late as 22 June were successful in raising their brood due to the delayed onset of fall. Changing climate may also influence snowy owls through change in prey availability during winter. For instance, low numbers of ptarmigans in the Chukotka region of Russia where owls from Wrangel are thought to winter, possibly caused by climate change, may negatively influence their winter survival.

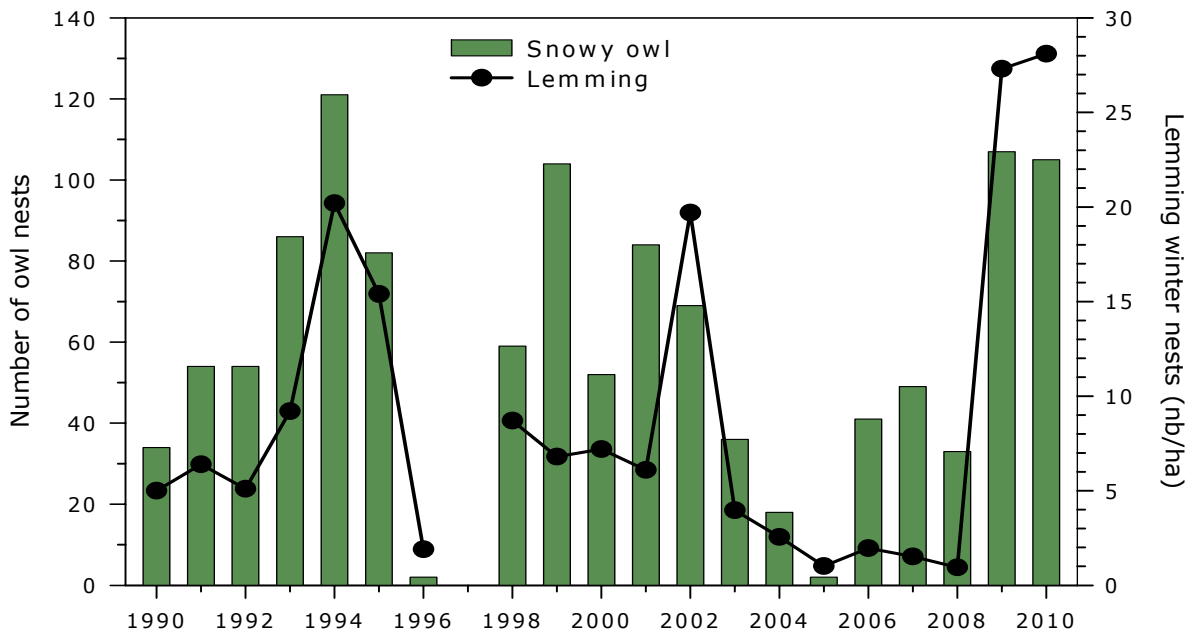


Figure B1.1. Dynamics of snowy owl nests ($n=1192$) on Wrangel Island during seasons of different abundance of lemmings from 1990-2010 (Menyushina 1997, 2007b; I. Menyushina and N. Ovsyanikov, unpubl. data).

Box 2. Analysis of the rough-legged hawk diet.

During our project, we investigated diets at many sites in North America and Eurasia using a variety of techniques: regurgitation pellets, prey remains, cameras at nests, and stable isotopes. As an example of application of these techniques, we show results obtained for the rough-legged hawk breeding in the low-shrub tundra zone of the Nenetsky Nature Reserve (68°20'N 53°18'E) in Russia.

Rough-legged hawk is believed to be a small rodent specialist during the breeding season but this inference has been mostly based on the analysis of pellets. Our results show that pellet analysis bias the diet towards small rodents. In fact, larger herbivores, such as hares and willow ptarmigan, made up a more important part of their diets according to stable-isotope analysis and prey remains analyses (Fig. B2.1). Thus, monitoring of rough-legged hawk based on diets ought to include other methods than pellet analysis. Their broad diet may indicate that it is more indicative of the composition of the community of small to medium-sized herbivores than was previously thought. Thus, rough-legged hawk diet, when assessed by a suitable combination of methods, may be a valuable indicator of the state of the tundra food web.



Young rough-legged hawk at nest with an automatic camera in the background.



Prey remains (A) and regurgitation pellet (B) found at a nest of rough-legged hawk.

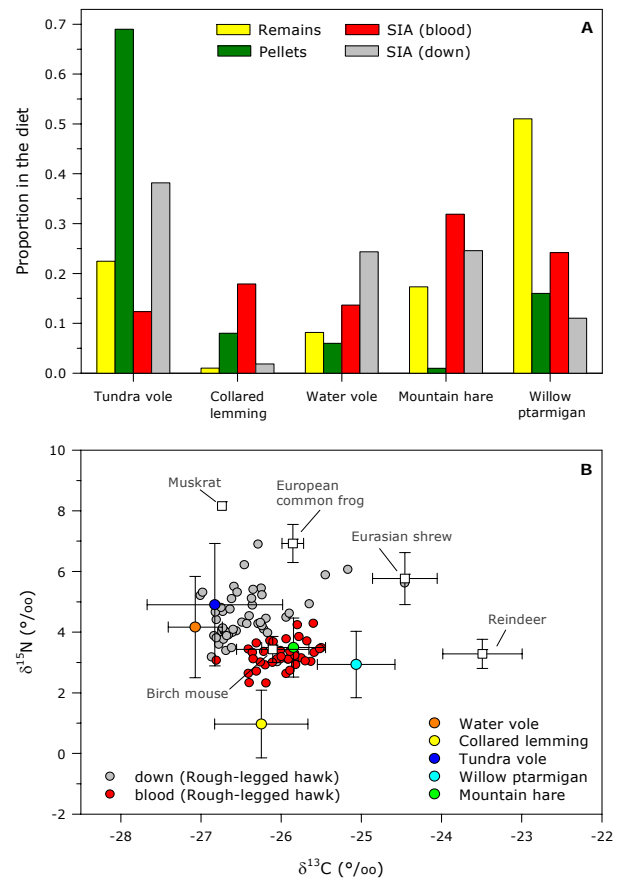


Figure B2.1. (A) Diet composition of the rough-legged hawk inferred by various methods (SIA = stable isotope analysis) and (B) stable isotope signatures of down and blood of chicks in comparison to the mean signatures of various prey species in the Nenetsky Nature Reserve, Russia, 2007-2009 (I. Pokrovsky, unpubl. data).



I. Pokrovsky processing a blood sample from a young rough-legged hawk.

Box 3. Use of sea ice by snowy owls in Eastern North America.

Terrestrial predators such as the snowy owl need to find sufficient prey throughout the year to sustain their basic metabolic needs and withstand the extreme Arctic conditions. This is especially critical during the long Arctic winter because the availability of the primary prey species of the tundra such as small mammals and migratory birds becomes very low due to protection offered by the snow cover or the departure of migratory species. Satellite tracking of snowy owls marked on Bylot Island revealed that most individuals breeding there overwinter at high latitudes in the Arctic and spend several weeks (up to 101 days) on the sea ice between December and April (Fig. B3.1). Females concentrated their activity in the Hudson and Davis straits and in Hudson Bay at a median distance of 40 km from the coast but sometimes as far as 210 km. Analysis of high-resolution satellite images of sea ice indicated that owls were primarily gathering around open water patches, which are commonly used by wintering seabirds (especially eiders), their potential prey in these areas. Such extensive use of sea ice by a tundra predator considered a small mammal specialist was unexpected, and suggests that

marine resources subsidize the populations of this predator in winter. As sea ice regimes in winter are expected to change over the next decades due to climate warming, this may affect the wintering strategy of this top predator and ultimately the functioning of the tundra ecosystem. Furthermore, satellite tracking of owls over a 3-year period allowed us to determine for the first time the annual survival rate of adult females, which was estimated between 85% and 92% (Therrien et al. submitted).



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Adult female snowy owl fitted with a satellite transmitter on Bylot Island, NU, Canada.

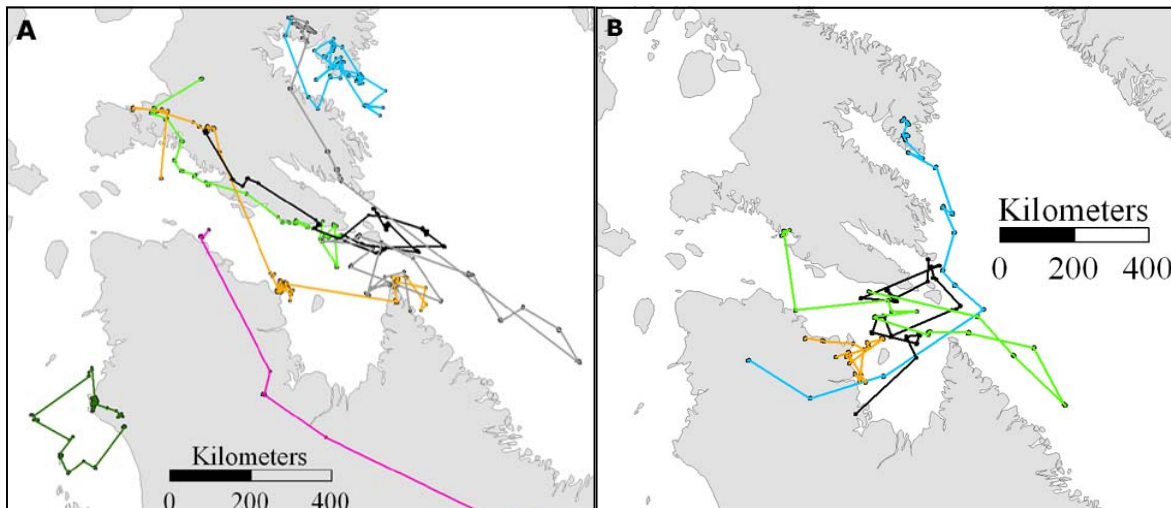


Figure B3.1. Satellite tracked movements of 9 adult female snowy owls overwintering in the Eastern Canadian Arctic during two consecutive winters. Individuals were tracked from 11 December 2007 to 28 April 2008 (A), and from 4 December 2008 to 27 March 2009 (B). Owls used extensively the sea ice in both years; 2007-2008: median = 41 days, range = 8 to 71 days; 2008-09: median = 59 days, range = 30 to 101 days (at that time of the year, the area used by owls is almost entirely covered by sea ice; modified from Therrien et al. 2011).



- 1 - arctic fox pups © Nicolas Lecomte
- 2 - adult arctic fox in its winter coat © Dominique Berteaux
- 3 - adult arctic fox in its summer coat © Eva Fuglei
- 4 - adult red fox at its den, Bylot Island, NU, Canada © Arnaud Tarroux
- 5 - red fox pups playing at their den, Herschel Island, Yukon, Canada © Daniel Gallant
- 6 - red fox den on the bank of Erkutayaha River, Yamal Peninsula, Russia © Ivan Pokrovsky

CHAPTER 8. ARCTIC AND RED FOXES

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Abstract

The arctic and red foxes are two different species that occur in the Arctic. The arctic fox inhabits virtually all arctic habitats whereas the red fox distribution is wider, covering the entire northern hemisphere. The status of arctic fox populations is believed to be good in most areas, although the species is critically endangered in Fennoscandia and in a few islands of the Northern Pacific. Red foxes have expanded their distribution during the 20th century, including in the Arctic. During this project, both species were heavily studied in Canada, Fennoscandia, and Russia. We confirmed that most arctic fox populations fluctuate widely in numbers between years in response to varying small mammal numbers. Long-time series established on Bylot Island (Canada) since 1996 and on Wrangel Island (Russia) since 1980 suggest that these population fluctuations follow cycles of varying length among locations. We also confirmed the importance of sea ice to arctic foxes, and documented through satellite telemetry their extraordinary winter movements between arctic islands. These movements are important for foraging purposes, but also for genetic mixing between populations. Arctic terrestrial predators live from a scarce prey base in the tundra, because the short growing season only allows for a small vegetation production, which in turn only allows for a small herbivore production. Competition between predators is thus an important aspect of their ecology. Arctic and red foxes compete where their distributions overlap. The red fox is dominant over the arctic fox and can exclude it from overlapping areas, such as in Scandinavia. However, in Northern Yukon, the two species seem to co-exist. These differences remain to be clearly explained. The warming climate is a source of threat to the arctic fox, because it tends to increase the area of overlap between these two competing species. Because the arctic fox plays an important role in the tundra, populations of this species are sometimes used as indicators of health of the tundra. For example, Sirmilik National Park of Canada uses data on the length and amplitude of arctic fox fluctuations, as well as on the proportion of dens used by arctic and red foxes, as local indicators of ecosystem integrity. Conservation and management actions are very intensive in Fennoscandia, where culling of red foxes and a combination of food supplementation, captive breeding, and local introductions of arctic fox are underway. We have identified important needs for future research. Among them are the importance of rabies to arctic fox, a better understanding of the competition between arctic and red fox, the importance of changing sea ice conditions to the ecology of arctic fox, and the need for long-term monitoring of key populations in relation to global environmental changes. Finally, since many of the changes affecting arctic and red foxes have a global perspective, it is important that the research and action programs are coordinated over a global scale. The International Polar Year has allowed us to make a first step in that direction.

The wide distribution of arctic and red foxes (*Vulpes lagopus* and *Vulpes vulpes*) in the circumpolar North, their major role in the trophic dynamics of the tundra, and the strong sensitivity of their relationship to climate change stimulated several ArcticWOLVES teams to study these two species in North America, Europe, and Russia. After briefly reviewing the status of these species, we present here some selected results that demonstrate very well the research benefits of international collaborations fostered by the International Polar Year and their implications in terms of conservation of these species.

Species ranges and recent changes

The arctic fox has a circumpolar distribution, occupying all types of arctic tundra habitats and ranging from northern Greenland at 88°N to the southern tip of Hudson Bay, Canada, 53°N (Angerbjörn et al. 2008). It also lives in the alpine tundra of Fennoscandia and on several islands of the Bering Sea (Angerbjörn et al. 2008). The arctic fox was introduced by the fur industry to some islands in the Aleutian chain at the end of the 19th century (Bailey 1992). The southern edge of the species' distribution may have moved north in most of the circumpolar North during the 20th century, resulting in a smaller total range (Chirkova 1967, Hersteinsson and Macdonald 1992). About ten subspecies of arctic foxes exist, each inhabiting a particular region of the species range (Geptner and Naumov 1967).

In contrast, the red fox is distributed across the entire northern hemisphere, from the Arctic Circle to North Africa, Central America, and the Asiatic steppes (Macdonald and Reynolds 2004). European subspecies were introduced into eastern United States and Canada in the 17th century, and subsequently mixed with local subspecies (Kamler and Ballard 2002). They have expanded their distribution during the 20th century, especially northward, both in North America and Eurasia (Marsh 1938, Macpherson 1964, Chirkova 1967, Hersteinsson and MacDonald 1992, Macdonald and Reynolds 2004). Red foxes are adaptable omnivores and can be closely associated with man, even thriving in agricultural and urban areas (Macdonald and Reynolds 2004). They have even been reported on the

northernmost island of Ellesmere (Macpherson 1964).

Recent population trends

The world population of arctic foxes is in the order of several hundred thousand animals. Most populations fluctuate widely in numbers between years in response to varying lemming numbers (Angerbjörn et al. 2008). Although only a few populations have been studied directly, population status is believed to be good in most areas (Angerbjörn et al. 2008). The species is common in the tundra areas of Russia, Canada, coastal Alaska, Greenland, Iceland and Svalbard. Exceptions are Fennoscandia, Mednyi Island (Russia) and Pribilof Islands (USA), where populations are at critically low levels. The world population of red foxes probably counts in the millions and the status of the species is very good.

Primary factors known or suspected to limit these species

Hunting and trapping for fur has long been a major mortality factor for the arctic fox. However, with the decline of the fur industry, the threat of over-exploitation is lowered for most arctic fox populations (Angerbjörn et al. 2008). In Yukon, for example, the total value of all fur production decreased from \$1.3 million in 1988 to less than \$300,000 in 1994. Because of their large reproductive capacity, arctic foxes can maintain population levels under high hunting pressure. In some areas, 50% of the total population was harvested sustainably (Nasimovič and Isakov 1985). Genetic pollution (gene swamping) by farm-bred arctic foxes may threaten native populations in some places of Fennoscandia (Norén et al. 2009). There can also be indirect threats such as diseases and high levels of organochlorine contaminants, or direct persecution (for example on St. Paul Island, Alaska; Angerbjörn et al. 2008). Due to their long-range migrations, arctic foxes are important carriers of diseases and parasites affecting humans. The arctic fox is a reservoir species and main vector of rabies in the Arctic, where the disease is widespread. It is also host to the cestode *Echinococcus multilocularis*, which in humans causes the often fatal disease alveolar echinococcosis.

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In contrast to arctic foxes, red foxes' versatility and generalist diet are likely to ensure their persistence despite changes in landscape and prey base. Culling can reduce numbers in large regions but this has never threatened species persistence on any geographical scale (Macdonald and Reynolds 2004).

Dependence of arctic foxes on lemmings

The trophic dynamic on most tundra ecosystems is dominated by large fluctuations in lemming abundance (see SMALL MAMMALS chapter). Foxes and other predators quickly track these fluctuations, so that their abundance and reproductive activity increase dramatically in peak lemming years (Ims and Fuglei 2005). Long-term research on arctic foxes has been carried out since the 1980s on Wrangel Island, Russia (Ovsyanikov, 1993) and Scandinavia (Angerbjörn et al. 1995), and since 1996 on Bylot Island, Canada. These studies provide unique opportunities to detect recent changes of processes in arctic fox populations in response to environmental changes.

The tight relation between lemmings and foxes is clear on our two long-term study sites (Fig. 1 and 2). While fluctuations of arctic fox populations on the islands strictly followed fluctuations of lemming numbers, for the last decade, density and litter size of arctic foxes have decreased on Wrangel Island. This decrease is thought to be caused by cumulative negative effects of global environmental changes. Immediate mechanism of population decline may be reduced survival of foxes during winter and reduced return of young foxes to their breeding areas on the island. A similar population decrease was not detected on Bylot Island.

Importance of sea ice to arctic foxes

From May 2007 to August 2010 we fitted more than 60 arctic foxes with satellite tracking collars on Bylot Island to record their movements over complete annual cycles. We found that summer food abundance influenced both summer home range size and the extent of movements outside the home range in winter. Foxes had larger home ranges and traveled further away on the sea-ice in winter during years of low food abundance or if territories were located in low-food areas (Tarroux

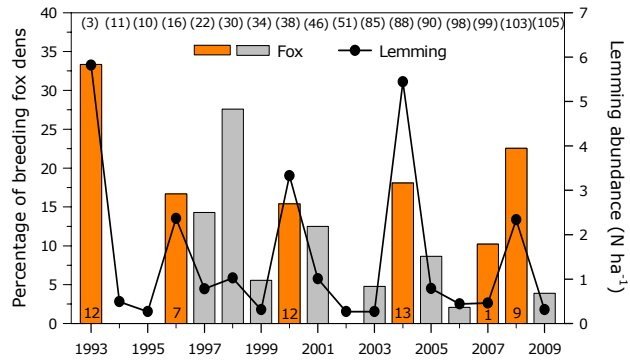


Figure 1. Temporal trends in lemming abundance (combined brown and collared lemmings) and arctic fox reproductive activity (known dens with pups) on Bylot Island, Nunavut, Canada from 1993 to 2009. Numbers in parentheses are the total number of fox dens known annually. Orange bars are years with owl nesting activity in our core study area (numbers within bars indicate number of owl nests found).

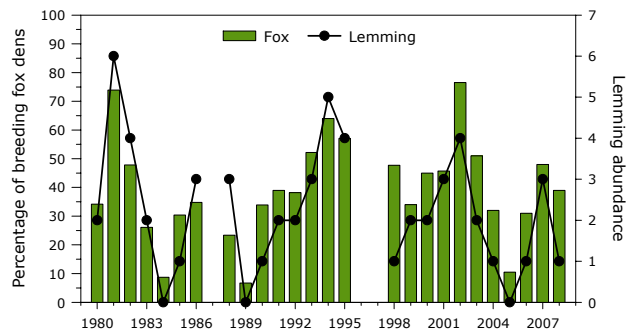
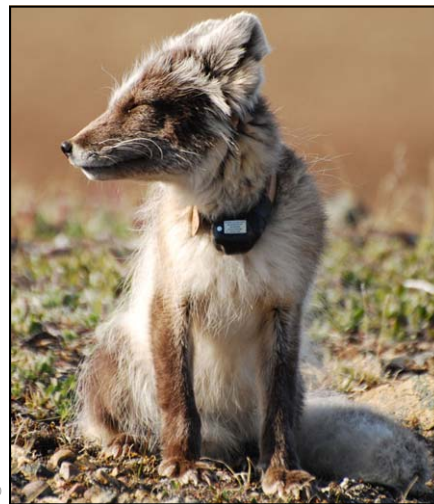


Figure 2. Temporal trends in lemming abundance and arctic fox reproductive activity (known dens with pups) on Wrangel Island, Russia, from 1980 to 2008. Lemming estimates is given for the same areas where fox were surveyed.



© Arnaud Tarroux

Adult arctic fox fitted with an Argos satellite collar on Bylot Island, Canada.

2011). All individuals used sea ice in winter, although at various degrees. Some individuals performed spectacular movements (Fig. 3), demonstrating the large movement capacity of the species. For example, one female and one male traveled extensively from February to July 2009, covering minimum distances of 4,599 km and 2,193 km, respectively (Tarroux et al. 2010). We recorded high and sustained travel rates on both land and sea ice that reached about 90 km/day for these two individuals. These results have implications for our understanding of navigational abilities, foraging ecology, trophic interactions with lemming populations, and genetic population structure of arctic foxes (Tarroux et al. 2010, Norén et al. 2011a, 2011b).

The population-level effects of individual movements are of particular interest. There is indeed remarkably low genetic differentiation between the world arctic fox populations (Dalén et al. 2005), which is a likely function of the species capacity of long distance movement across the sea ice. Between populations

connected by sea ice, geographic distance seems to be the only factor determining the degree of genetic differentiation. A recent study (Norén et al. 2011a, 2011b) showed that Iceland and Scandinavia were the most distinct populations, which is likely explained by these populations being surrounded by year-round open waters, preventing immigration. The distinctiveness of Scandinavia is likely further enhanced by a severe population bottleneck caused by heavy hunting at the end of the 19th and beginning of the 20th century (Nyström et al. 2006).

Role of other large predators in the dynamics of arctic foxes

Arctic terrestrial predators generally live from a scarce prey base in the tundra because the short growing season only allows for a small vegetation (or primary) productivity, which in turn only allows for only a small herbivore (or secondary) productivity. Among arctic terrestrial predators, mammals have a disadvantage over birds since they cannot fly

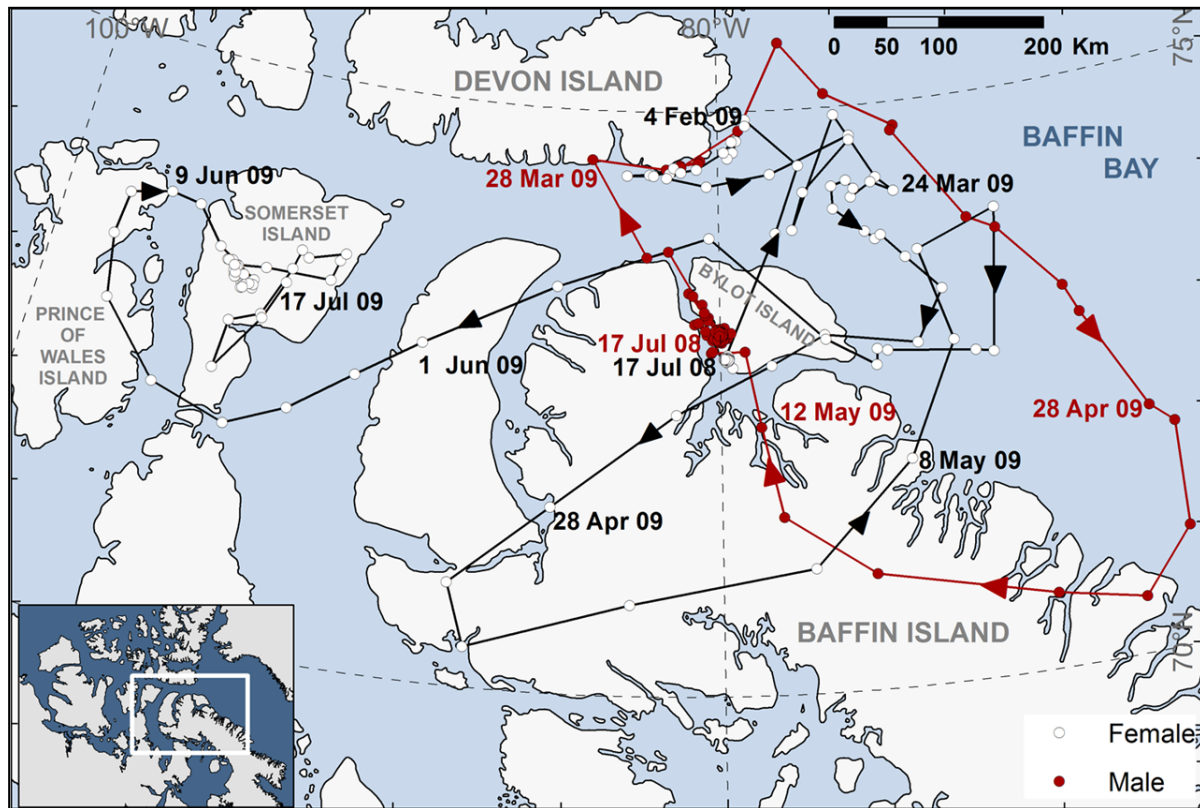


Figure 3. Locations and estimated straight-line movements of a female (black line) and a male (red line) adult arctic foxes tracked using satellite telemetry in the Eastern Canadian Arctic from 17 July 2008 to 17 July 2009 (modified from Tarroux et al. 2010).

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to the south in winter. Competitive relations among them are thus a critical component of their ecology. Possible consequences of competition are a reduction in survivorship, growth and reproduction of at least one of the competitors. The close interactions between red and arctic foxes in the Arctic tundra (Skrobov 1960) are a typical example of competition between two species which share similar resources.

Competition by interference (this is when individuals are aggressive between each other) is preeminent between the two fox species, with arctic foxes being excluded from the richest areas by dominant red foxes (Elmhagen et al. 2002, Tannerfeldt et al. 2002, Killengreen et al. 2007). Such interference can take the form of expulsion, with red foxes ousting breeding arctic foxes from their dens, as we observed during the ArcticWOLVES project (Rodnikova et al. 2011). Killing of arctic fox adults or pups by red foxes has also been reported (Pamperin et al. 2006). In Sweden, the arctic fox recently retreated to the highest parts of the alpine tundra, likely due to an increased competition for suitable dens and habitats at the lowest and richest parts of the mountains ranges, just above treeline (Elmhagen et al. 2002, Tannerfeldt et al. 2002). Similarly, in the low Arctic tundra of Norway, on Varanger peninsula, red foxes now have excluded arctic foxes from the richest and most productive areas, located close to the coast (Killengreen et al. 2007). On Bylot Island (Canada), red foxes have been ob-



© Daniel Gallant

Adult female red fox at her den on Herschel Island, Yukon, Canada.

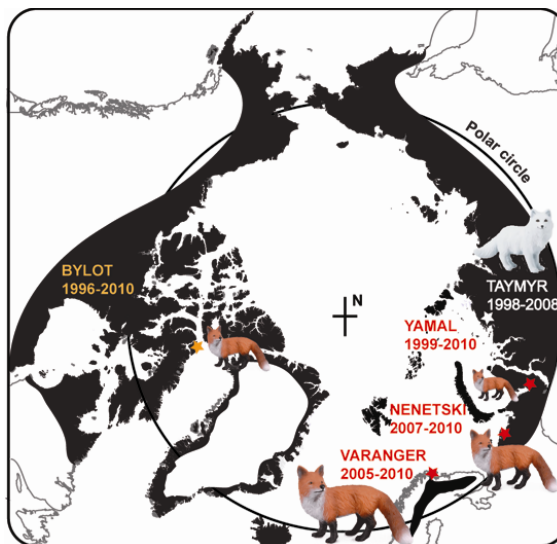


Figure 4. Five sites used during ArcticWOLVES to monitor the diet overlap between red and arctic foxes. The area in black shows the arctic fox distribution, while the sizes of red fox drawings roughly represent the relative abundance of the species at the five study sites. Note that no red fox was present at the Taymyr study site, which was thus chosen as control. The years indicated under each site name indicate the period during which foxes were monitored.

served breeding since 1996, but their population has remained low and stable since then. They usually occupy some of the biggest and well located dens in the study area, with no or limited breeding of arctic foxes around. This exclusion around red fox dens was also observed in Fennoscandia (Tannerfeldt et al. 2002). Surprisingly, on Hershel Island and adjacent coastal areas of the north Yukon, red and arctic foxes are both present and relative densities of the two species seem to have remained unchanged for the last four decades (D. Gallant et al. unpubl. data).

We know little about the other form of competition, which is called competition by exploitation. This is when individuals deplete resources used by the other species, but without overt aggressions between competitors. When a shared resource is in short supply (as it is happening during low phases of lemming cycles or far from large bird colonies), individual arctic foxes are affected by the amount of resource (e.g. hares) remaining after it has been exploited (or depleted) by other species such as the red fox. From most of our study sites hosting sympatric red and arctic foxes, we collected tissues (mostly fur), which can

reflect their diet via chemical analyses. At the circumpolar scale (Fig. 4), we showed that there is a large diet overlap between the two fox species, even at low red fox abundance. In addition, when red foxes are at high densities, arctic foxes are confined to a very narrow range of prey, some of them being in fact rare in several tundra sites (such as hares in Varranger). Overall, we showed that even without habitat exclusion by red foxes, arctic foxes were limited in terms of prey choice and quantity. We therefore found that both interference and exploitation competition led red foxes to exclude arctic foxes. This is important to understand how red foxes expand into the native land of arctic foxes.

Increased pressure from other large predators may also be detrimental to arctic fox. For example, on Wrangel Island, wolves and wolverines were observed to kill arctic foxes, and wolves were observed to use arctic fox dens in the last 5-6 years. In 2007-2008, about one third of arctic fox mortality (foxes found dead) was due to killing by wolves on Wrangel Island, and 12.5% of foxes were killed by wolverines. Red fox is a rare visitor on Wrangel Island since 1982 (Ovsyanikov and Menyushina 1987), with no sustained presence and no breeding attempts ever recorded. The pressure on arctic fox from other large predators increases from north to south, as the number of predators increases with primary and secondary productivities (see Box 1). Due to the absence of larger predators, Svalbard and Iceland are therefore important populations from a long-term conservation perspective.

Climatic effects on arctic fox

In 2009, the arctic fox was classified as a climate change flagship species (IUCN 2009). Like many other species adapted to polar life, the arctic fox will come under pressure as the globe is warming up. This species highly depends on open tundra habitats. If climate change induces shrinking of the tundra biome due to a northward expansion of forests (Callaghan et al. 2004a), the arctic fox is at risk.

In inland tundra, arctic foxes rely on peak abundance of lemmings to sustain viable populations (Braestrup 1941, Angerbjörn et al. 2004). In the short term, warmer and

more unstable winters with repeated freeze-thaw events will result in lemming peak years becoming rarer or cycles fading out all together (Ims et al. 2008, Kausrud et al. 2008, see SMALL MAMMALS chapter) and probably reduced opportunities for successful breeding. The lack of regular lemming peak years appear to be one of the problems of a declining arctic fox population in Fennoscandia, on the southern edge of the tundra (Tannerfeldt et al. 2002, Ims et al. 2008, Henden et al. 2008).



© Alfred Ørjebu

Arctic fox in its winter coat.

Freeze-thaw events associated with global warming result in the formation of ice crusts making food plants less accessible. Such processes will limit the forage availability not only for small herbivores but for large herbivores as well and may lead to increased winter mortality. In the short-term, this should benefit some arctic fox populations due to an increased availability of carcasses. Dramatic population crashes in reindeer and muskox following ice-crusting and "locked" pastures have been reported in the Arctic (Forchhammer and Boertmann 1993, Aanes et al. 2000) and resulted in increased breeding success of the arctic fox (Fuglei et al. 2003). In the longer term, a warmer climate will increase plant productivity and more herbivore prey for competitive dominant predators may move in from the south. The expansion of shrubs such as willows and dwarf birch are reported in the Alaskan tundra (Sturm et al. 2005, Chapin et al. 2005). Increased populations of typically shrub-browsing herbivores such as hare, grouse, vole and moose is likely

ArcticWOLVES final synthesis report

to increase the overall biomass, diversity and stability of herbivore prey for carnivores. This could have benefited the arctic fox if it had not been for the invasion of more southerly-distributed species acting as competitors and predators of the arctic fox.

Loss of sea ice (Serreze et al. 2007, Stroeve et al. 2007, Screen and Simmonds 2010) can have many effects on arctic fox. Two potential positive effects are that with increased storm activity at sea, more organic material is cast to the beaches, providing additional food resources for arctic foxes, which may be particularly important for young during dispersal. Another potential positive effect is that loss of connexion between islands may prevent red foxes from invading some arctic fox habitats. In the long term, some arctic islands may then become the last refuges for several, isolated populations of arctic foxes in a warmer globe. Unfortunately however, negative effects are probably much more important than positive ones. The sea ice is indeed a very important foraging habitat used by arctic foxes during winter. For example, on many

islands located in the Arctic Ocean, arctic foxes rely on rich and temporally stable marine food resources (Tarroux 2011). Ice-free sea prevents arctic foxes from dispersing off the islands in seasons of lemming scarcity, thus inducing increased mortality. Weakening of the arctic sea ice also makes travelling on sea ice more risky for foxes and fewer foxes may have a chance of returning to land for the breeding season even if they could manage to survive the winter on sea ice. In addition, the sea ice constitutes an important connection between arctic islands and continents (Tarroux et al. 2010), allowing the currently strong flow of genes between circumpolar arctic fox populations (Dalén et al. 2005, Carmichael et al. 2007, Geffen et al. 2007, Norén et al. 2011a, 2011b).

Another effect of climate warming on arctic fox is habitat loss due to permafrost melting. This can cause collapse of long existing optimal dens, which are a limited resource in the Arctic, as well as erosion and loss of hunting habitats, as was observed on Wrangel Island (E. Menyushina and N. Ovsyanikov, pers.



© Nikita Ovsyanikov

Erosion of tundra due to permafrost melting on Wrangel Island, Russia resulted in destruction of arctic fox denning and hunting habitats.

obs.).

Anticipated threats in the future and implications for conservation

There are no important threats documented for the red fox. Threats to the arctic fox (indirect effects of climate change such as disappearance of sea ice or weakening of lemming cycles, competition with other predators such as red fox, direct persecution, genetic pollution, rabies) vary locally and drive the agenda of arctic fox research in some parts of the world. For this reason, they have for the most part been described in earlier sections of this chapter.

It is interesting to note that because of the keystone role of arctic fox in the tundra ecosystem (see TUNDRA FOOD WEBS chapter), populations of this species are sometimes used as indicators of ecosystem functioning and health. For example, Sirmilik National Park of Canada uses the length and amplitude of arctic fox fluctuations, as well as the proportion of dens used by arctic and red foxes, as local indicators of ecosystem integrity. Conservation and management actions are very intensive in Fennoscandia, where culling of red foxes and a combination of food supplementation, captive breeding, and local introductions of arctic fox are underway (see Box 2). However, the global scale and complex causality of the main threat to the species (climate change) raise many questions on how to manage and conserve a polar species in a warming world.

Conclusion and research needs

In a conservation context, Angerbjörn et al. (2008) identified three main knowledge

gaps for the arctic fox: (1) little is known about the epidemiology of arctic rabies and the impact of diseases introduced by humans on fox populations; (2) given the current northward expansion of red foxes, studies are needed to determine the effects of competition between red and arctic foxes on various population parameters of arctic fox; (3) the non-recovery of the Fennoscandian population requires specific attention, especially in terms of disease and genetics. The ArcticWOLVES project has identified the following additional knowledge gaps: (4) research is needed to better understand the importance of changing sea ice conditions on the foraging ecology, dispersal behaviour and genetic structure of arctic fox populations; (5) there is a need for satellite tracking of arctic foxes to better understand large-scale movements; (6) long-term, circumpolar monitoring of trends and processes in key arctic fox populations in relation to global environmental changes are needed to understand changes in arctic food webs, including the expansion of red foxes into the Arctic; (7) studies are needed to decipher the role of different resource subsidies into maintaining viable populations of both fox species; (8) behavioral studies on arctic fox interactions with other predators in changing tundra ecosystems are needed; (9) research is needed to document levels of genetic variability in local arctic fox populations and population fragmentation under global environmental changes; (10) finally, since many of the changes affecting arctic and red foxes have a global perspective, it is important that the research and action programs are coordinated over a global scale.



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Arctic fox.

Box 1. Change in the guild structure of arctic scavengers across a latitudinal gradient.

During three winters, ArcticWOLVES researchers used photo cameras with reindeer (caribou) baits to analyze the guild structure of arctic scavengers. We chose four field sites distributed in three tundra zones. One site was located in the High-Arctic (Svalbard, Norway), two sites were in shrubby tundra (Nenetski and Yamal, Russia), and one was in the arctic-alpine transition (Varanger, Norway) (see map of ArcticWOLVES study sites in INTRODUCTION). This allowed us to get information from a large range of climates and food web structures.

We found a gradient in species richness of carnivores following the High-Arctic/sub-Arctic

gradient (Fig. B1.1). While we recorded only two scavenger species in Svalbard, sub-Arctic Varanger harbored ten species, most of which have their core distribution further south. Species richness in Nenetsky and Yamal was intermediate with four and five species respectively. Arctic fox was numerically dominant in all sites except Varanger. At this southernmost site, the red fox was the most common mammal, whereas raven was overwhelmingly dominant if we consider the whole carnivore guild. This disproportionate use of reindeer by boreal species bears consequences for the functioning of the native, arctic food web (Killengreen et al. 2011).



Figure B1.1. Gradient in species richness of carnivores following a latitudinal gradient from the High-Arctic (top) to the sub-Arctic (bottom). Pictures were taken at four ArcticWOLVES study sites. First (top) row: Svalbard (arctic fox, glaucous gull), second row: Nenetsky (arctic fox, red fox, wolverine, raven), third row: Yamal (arctic fox, crow, wolverine, raven, red fox), fourth (bottom) row: Varanger (raven, red fox, white-tailed eagle, crow, golden eagle, wolverine, arctic fox).

Box 2. Arctic fox conservation in Fennoscandia.

In Fennoscandia, the arctic fox population declined early in the 20th century and was close to extinction. Though the species was protected more than 80 years ago, the population has not yet recovered and was again close to extinction in the late nineties. There are three main reasons for this: (1) changes in rodent dynamics that have reduced access to this important prey (Henden et al. 2008), (2) increased competition with red foxes (Hersteinsson et al. 1989) and (3) the negative effects of being a small and very fragmented population (Herfindal et al. 2010). The red fox has a negative impact on the geographical distribution (Elmhagen et al. 2002, Dalén et al. 2004) because it takes over den sites in the most productive environments (Frafjord 2003, Killengreen et al. 2007), resulting in fewer arctic fox litters (Tannerfeldt et al. 2002).

The arctic fox population has started to increase in some areas due to intensive actions between 2001 and 2008 (Fig. B2.1A).

This increase is related to a combination of positive changes in the lemming density, red fox culling, and supplementary feeding during winter (each component contributing to about a third of the increase). In areas with intensive red fox culling, the number of arctic fox litters has more than doubled during the project period (Fig. B2.1B). In comparable areas with lower intensity of actions, the number of litters was stable or decreased (Fig. B2.1B). A reintroduction program where arctic fox cubs born in captivity were released into the wild has also restored two extinct populations (A. Landa et al. unpubl. data). Even though local populations responded well to the actions, the Fennoscandian population is still too small for long-term survival, and actions should be implemented in several other sub-populations. Red fox hunting is of major importance to stop the decline of the arctic fox population and to facilitate its recovery (A. Angerbjörn et al. unpubl. data). The results demonstrate the importance of red fox intraguild competition.

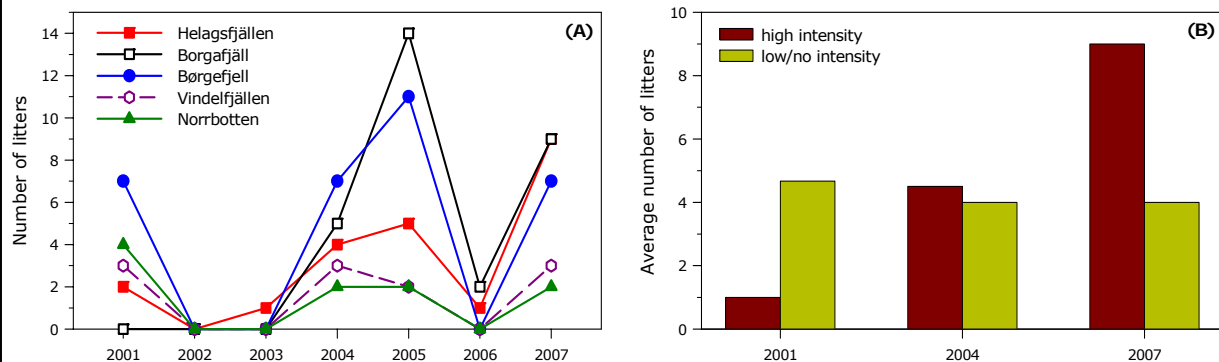


Figure B2.1. (A) Numbers of arctic fox litters in various regions of Sweden and Norway from 2001 to 2007 and (B) Average number of arctic fox litters in years with increasing numbers of rodents and differences between areas with high and low or no management actions (A. Angerbjörn et al. unpubl. data).



© Nicolas Lecomte



1 - snowy owl hunting a small mammal © Nicolas Lecomte
2 - arctic fox with a duck head and part of a gosling in its mouth © Maarten J.J.E. Loonen
3 - weasel with a small mammal in its mouth © Niels Martin Schmidt
4 - reindeers grazing on Varanger peninsula, Norway © Leif-Einar Støvern

CHAPTER 9. TUNDRA FOOD WEBS

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Abstract

Food web describes the network of trophic interactions among species: who eats whom within an ecosystem. Because of their harsh climate, tundra ecosystems support a low biodiversity and their structure thus appears to be relatively simple. However, we illustrate in this chapter several features that may complicate the view that the tundra is a simple food chain. One of the main goals of our project was to understand what processes controlled tundra food webs, whether plant production (bottom forces) or predators (top forces) were the main driving factors. A consequence of large variations in body size among herbivores is that predators cannot consume all species of herbivores equally. Indeed, because large herbivores like caribou or muskoxen can virtually escape from predation, they tend to be more limited by resource or climate whereas predation would tend to act as a major force driving the population dynamic of small herbivores. For instance, lemming (a key herbivore species) populations appear primarily regulated by predators at several sites such as on Bylot Island, Nunavut. Therefore, where large mammalian herbivores are absent, the food web appears more likely to be dominated by predator-prey interactions. The relative importance of plant-herbivore or predator-prey interactions in the dynamic of tundra ecosystems nonetheless varies spatially and is dependent upon the local species assemblage. Primary production, which varies with latitude and altitude, contributes to this spatial heterogeneity as food webs are simpler in the North or in high elevation areas compared to more southern or lower elevation areas. A key conclusion is also that the functioning of an ecosystem cannot be understood in isolation as subsidies from adjacent ecosystems can shape the structure and dynamic of food webs. Marine resources such as beached marine animals are important food resource that may sustain large predator populations. Humans can also have indirect and direct impacts on the food web dynamic. A first example of indirect effects is how the populations of tundra predators are influenced by large populations of migratory birds such as geese, which are driven by food resource acquired in southern agricultural landscapes during winter. Another example is provided by semi-domesticated reindeers (or caribous) in Fenoscandia, an important resource for local human populations. Their high densities can limit shrub expansion on the summer pastures and support predators through increasing availability of carcasses due to winter mortality. Finally, humans can also have direct impacts. For example, the presence of an anthropogenic food source (human waste) at the most northerly, permanently inhabited settlement on the planet (Alert, Nunavut) influenced the breeding activity of the long-tailed jaeger, an avian predator, by dampening the influence of cyclic fluctuations in lemming abundance. An important feature emerging from our project is the large amount of variation among sites. Ecosystem processes will respond differently to environmental changes depending on which component (plants, herbivores, predators) is primarily affected. Therefore, the impact of climate warming on food web dynamic may differ among study sites and depends on the main forces that structure the local ecosystem.

The tundra ecosystem

The arctic tundra biome (hereafter tundra) is characterized by short, treeless vegetation and is thus located north of the tree line, from ~55° of latitude in the south to 80° to the north. The word *tundra* primarily refers to areas with permanently frozen ground (permafrost), either continuous or discontinuous. Tundra vegetation is generally dominated by dwarf shrubs, sedges, grasses, mosses and lichens. Because of their harsh climate (low temperatures and precipitations, strong winds), tundra ecosystems support a low biodiversity and are thus relatively simple in their structure and processes (Elton 1927, Oksanen and Oksanen 2000, Krebs et al. 2003, Gauthier et al. 2004, but see Hodkinson and Coulson 2004). Therefore, it is often argued that studying the whole terrestrial plant and animal community and their interactions (i.e. the food web) should be less challenging there than in other terrestrial biomes. However, as we explain below, such a simplistic view of the Arctic food web may actually be hampering our efforts to understand it.

A food web describes the network of trophic interactions between species: who eats whom within an ecosystem (Loreau 2010). Figure 1 provides an example of the food web

for one of our study sites, Bylot Island. Food chains describe how biomass and energy is passed on through trophic levels in the ecosystem, from plants at the bottom of the chain to herbivores and predators at the top. Major tundra herbivores include caribou (*Rangifer tarandus*, named reindeer in Eurasia), muskoxen (*Ovibos moschatus*), arctic geese, arctic hares (*Lepus arcticus*) and small mammals (primarily lemmings). Weasels (*Mustela erminea* or ermines), jaegers (*Stercorarius* sp.), rough-legged hawks (*Buteo lagopus*), snowy owls (*Bubo scandiacus*) and arctic foxes (*Vulpes lagopus*) constitute the most common predators. Lemmings are of special interest because in many areas their populations undergo cyclic fluctuations of large amplitude over a period of 3 to 6 years (Gilg et al. 2003, Ims and Fuglei 2005, Gruyer et al. 2008, Schmidt et al. 2008) that strongly affect the abundance of many predators or at least their breeding outputs. For example, snowy owls typically breed only during years of peak lemming abundance (see BIRDS OF PREY chapter) and the number of active arctic fox dens is often directly related to lemming abundance (see ARCTIC AND RED FOXES chapter).

A key question of our project was to un-

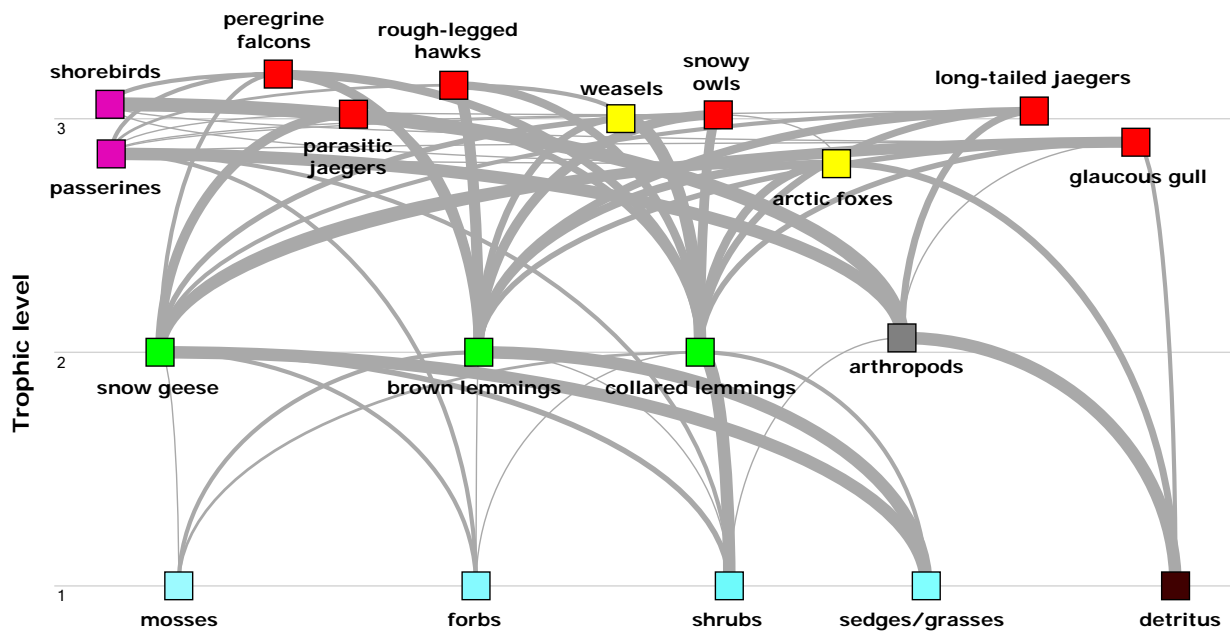


Figure 1. Summary of the food web of Bylot Island (Nunavut, Canada) during a typical lemming peak year. Line width is scaled based on the relative importance of each species in the diet. Purple = insectivorous birds, red = avian predators, yellow = mammalian predators, green = herbivores, grey = arthropods, blue = primary producers and brown = detritus (including marine subsidies) (from Legagneux et al. submitted).

ArcticWOLVES final synthesis report

derstand what processes controlled food webs, that is whether plant production (bottom forces) or predators (top forces) were the main driving factors. The diversity in herbivore and predator communities encountered across our multiple study sites suggests that variation in body size among herbivores may be an important determinant of these processes. The simple food chain view of predator-prey interactions ignores the fact that all predators are not equivalent and they cannot consume all species of herbivores equally. Indeed, because large herbivores like caribou or muskoxen can virtually escape from predation, they will tend to be more limited by resource or climate (Tveraa et al. 2007) whereas predation would tend to act as a major force driving the population dynamic of small herbivores (Gilg et al. 2003, Schmidt et al. 2008). On Bylot Island, where large mammalian herbivores are absent, the food web appears dominated by predator-prey interactions



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Muskox.



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Herd of caribou.

tions (see Box 1).

Body size could also drive the impact of herbivores on plant production. For instance, lemmings generally have a limited impact on vegetation except at some sites such as northern Fennoscandia or Alaska where they can occasionally reach very high densities (Moen et al. 1993, Turchin et al. 2000, Oksanen et al. 2008). In contrast, the highly gregarious caribou consume high amount of lichens during winter that can be easily overgrazed, exceeding the carrying capacity of their habitat (Manseau et al. 1996, Arseneault et al. 1997). Accordingly, we found that on Herschel Island, where caribou are present, plant-herbivore interactions play a dominant role in the food web (Legagneux et al. in prep.). Snow geese, which are an intermediate body size herbivore, are interesting because they exert a strong pressure on plants at some sites (e.g. West Hudson Bay) but much less at others (e.g. Bylot Island; see GEESE chapter). Although their smaller body size expose them more to predation than large mammalian herbivores, their highly colonial tendency can buffer predation while increasing their local impact on plants. On the other hand, muskoxen, a more solitary animal compared to caribou, does not seem directly limited by plant production (Kristensen 2009), but rather by the unavailability of forage dur-

ing winter, in part related to climatic conditions. Therefore, it appears that the relative importance of plant-herbivore or predator-prey interactions in the dynamic of tundra ecosystems varies spatially and is dependent upon the local species assemblage. Primary productivity is also affected by latitude and altitude and contributes to spatial heterogeneity as food webs are simpler in the North or in high elevation areas compared to southern or lower elevation areas.

Effects of global warming on producers and consumers

Ecosystem processes respond differently to environmental changes such as those in climate, species composition or abundance, depending on which component (plants, herbivores or predators) is primarily affected. One of the most conspicuous effects of climate warming is the “greening up” of the Arctic, especially in the low Arctic (Sturm et al. 2001, Tape et al. 2006). The increase in plant production induced by global warming may result in higher herbivore abundance and ultimately more predators in the system. However, despite the clear trend for an increase in plant production reported at many arctic sites (e.g. Hudson and Henry 2009; see GEESE chapter), this has not yet translated into increases in herbivore populations at those sites. Although this lack of response may simply be because herbivore populations are lagging behind, it is also possible that other factors are preventing herbivore populations of responding to this increase in plant biomass. Hence, even in the simple tundra ecosystem, such mechanistic links may not be that simple (see a detailed example in Box 1). If herbivores do not respond to increase in plant biomass, this could lead to the expansion of shrubs and in turn to a decline in vascular plant diversity due to shading effect at ground level (Tape et al. 2006, Walker et al. 2006).

In addition to increases in temperature and primary production, changes in precipitation regimes are likely to be part of global changes. This includes snow, a key feature of the tundra ecosystem during most of the year, which could be drastically modified in terms of quantity and quality (see SMALL MAMMALS chapter). Snow cover provides lemmings with insulation and partial refuge against predators

like foxes. Reduction in snow quality in recent years is thought to be largely responsible for the collapse of lemming cycles (or at least to major changes in their dynamics) in several parts of the Arctic (Ims et al. 2008, Kausrud et al. 2008, Gilg et al. 2009), with potentially strong cascading effects on other groups of the food web, particularly predators (Ims and Fuglei 2005, Gilg et al. 2009, Post et al. 2009). However, collapse of the lemming cycle appears limited to some sites and no evidence for it was found at several study sites of the ArcticWOLVES project, most notably those located in the High Arctic region (see SMALL MAMMALS chapter). Nonetheless, finding conclusive evidence for population decline requires long term data, especially for cyclic species, and many of the sites that we studied were monitored only during a short time period (i.e. during one or two cycles).

Marine subsidies

It is being increasingly recognized that the functioning of an ecosystem cannot be understood in isolation (Polis et al. 1997, Jefferies 2000, Polis et al. 2004). Frequently, a species belonging to a given ecosystem can be subsidized by allochthonous (synonym of alien, i.e. coming from other, neighbouring ecosystems) resources, which can have considerable effects on the dynamic of both its own population and of its local prey or predators (Polis et al. 1997, Polis et al. 2004, Gauthier et al. 2011). Subsidies can thus shape the structure and dynamic of food webs, especially when two ecosystems differing in productivity are connected (Polis and Hurd 1996). The impact of top predators on lower levels of the food chain can be strongly affected by the flow of energy from adjacent ecosystems (Leroux and Loreau 2008). Subsidies are particularly common between marine and terrestrial ecosystems (Polis et al. 1997, Anderson and Polis 1998). In fact, all ArcticWOLVES and Arctic Predators study sites are located within 25 km from the sea (Fig. 2), and thus can potentially benefit from allochthonous subsidies from the marine environment. Such biased distribution has historical and logistical causes and may have consequences on our understanding of the tundra ecosystem. However, this also reflects a reality because most of the arctic tundra is spa-

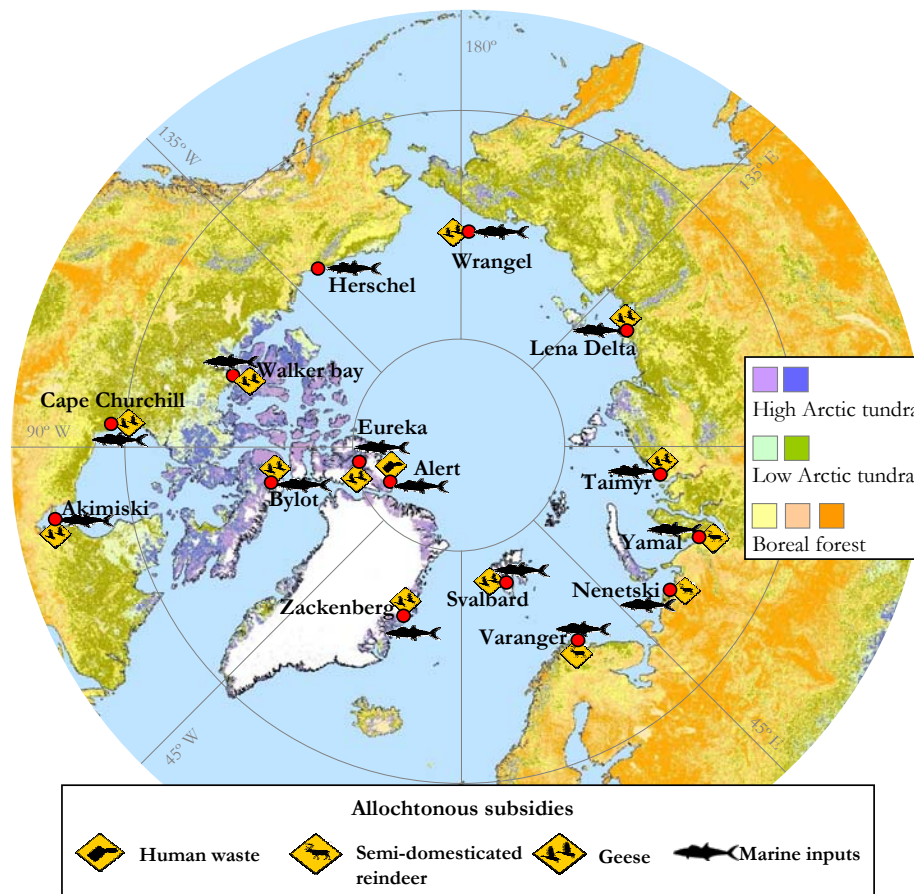


Figure 2. ArcticWOLVES and Arctic Predators study sites (red dots). Yellow panels represent allochthonous subsidies that could affect the food web at each site (see text). Background map is issued from a summary index of vegetation type and primary production (maximum NDVI, Walker et al. 2005).

tially close to the marine environment as Walker et al. (2005) calculated that approximately 80% of non-alpine tundra is located within 100 km of a coastline, making it essentially a coastal biome (Walker et al. 2005).

Marine nutrients enter terrestrial habitat in the forms of beached marine animals, dead organisms and detritus. In addition, several species such as seabirds acquire their energy at sea and rest or breed inland or in coastal areas, thereby providing a local abundance of marine-derived resources that can be exploited by terrestrial predators. Such subsidies can be especially significant in low-productivity ecosystems such as the arctic tundra (Gauthier et al. 2011). The Varanger peninsula (Fig. 2) represents a typical example of coastal arctic tundra, with the added peculiarity of an absence of sea ice year-round. The ocean surrounding the peninsula

harbours large stocks of pelagic fishes that sustain abundant seabird populations, likely to enter into the diet of terrestrial predators like foxes (see Box 2). Coastal areas thus represent a rich, productive and almost unlimited food source for many predators. It is possible that these subsidized areas facilitated the northward progression of red foxes (*Vulpes vulpes*) and its expansion toward the inland arctic tundra, which increased competition with the arctic foxes (*Vulpes lagopus*) and led to its exclusion in some areas (Killengreen et al. 2007, Killengreen et al. 2011).

Humans as components of the tundra ecosystem

Apart from the rich marine inputs, terrestrial ecosystems are also recipient of other subsidies, for instance from freshwater ecosystems (most of the insect communities de-

pend on freshwater lakes, ponds or wetlands at some point in their life cycle). However, human activities can also be a major source of subsidies for terrestrial ecosystems (Gompper and Vanak 2008, Weiser and Powell 2010), especially in locations where the human footprint is large (see Box 3). We present three cases showing that anthropogenic subsidies can significantly affect the tundra food web, either directly or indirectly.

Migratory connectivity: how southern human influence is transported by birds to the Arctic — Because migratory animals move across large distance encompassing whole continents or even more, they can bring up north human influences affecting southern ecosystems. Arctic geese accumulate endogenous energy reserves necessary to breed on staging areas prior to reaching their arctic breeding grounds (Drent et al. 2003). Most of their reserves are now acquired in agricultural landscapes, a human-created ecosystem. The food subsidy provided by modern agriculture is thus a form of allochthonous subsidy brought by the geese to the arctic tundra (Jefferies et al. 2004). This artificial food source fuelled population increases in many goose species resulting in very large breeding populations in the Arctic, which led to habitat degradation due to overgrazing at some sites (see GEESE chapter). For predators such as arctic foxes, high goose numbers represents a stable, predictable alternative prey source that may help them maintaining their populations during bottlenecks (such as low years of lemming abundance: Bêty et al. 2002, Gauthier et al. 2004, 2011) and increase their impact on other prey species of the food web (see SHOREBIRDS chapter).

Semi-domestic reindeers — Reindeer is an important resource (both culturally and economically) for many indigenous peoples in the Eurasian Arctic and their dynamic has increasingly reflected social changes that occurred in recent years. Reindeer abundance has for example increased in northern Fennoscandia or on Yamal peninsula whereas it has collapsed in some parts of Arctic Russia. Densities of semi-domesticated reindeer are now so high in Fennoscandia (10 to 50 times higher than for most wild populations) that they could prevent shrub expansion on the summer pastures (Ims et al. 2007). They can

also subsidize predators through increasing winter mortality of animals left overwinter on the summer pastures (see Box 2).

Tundra exploitation and provision — The two previous cases are examples of indirect impacts of human activities on the tundra food web. However, humans may also have direct impacts through exploitation (e.g. sport or commercial hunting) or the provision of supplementary food sources (e.g. human waste).

Overhunting or harvest can negatively impact wildlife populations and create a sink if hunting pressure is too high, thereby disrupting food webs. Several terrestrial Arctic species such as the wolverine (*Gulo gulo*, COSEWIC 2003) or the barren-ground brown bear (*Ursus arctos*, McLoughlin et al. 2003) are especially sensitive to sustained harvest and slight increase in quotas can quickly reduce their populations. In the past century, some snow goose populations have almost been hunted down in the south until a ban and effective protection allowed them to show a formidable come-back, with the unexpected outcome of the present-day overabundant populations (Gauthier et al. 2005).

The gradual decline in plant productivity as we go north (Fig. 2) is the main reason for the reduction in biodiversity and the impoverishment of food webs with latitude. The potential impact of human food subsidies on food webs is therefore expected to increase with latitude. Previous studies have shown that direct food inputs from human activity (e.g. industrial fisheries, refuse dumps or urban waste) can increase populations of opportunist seabird species (Pons and Migot 1995, Garthe et al. 1996). The presence of an anthropogenic food source (human waste) at the most northerly site of the ArcticWOLVES project, Alert, allowed us to show how such a food subsidy can impact a tundra predator (see Box 3).

Conclusion and perspectives

A key feature emerging from our ArcticWOLVES project is the large amount of variation among sites. In our effort to look for general patterns, we developed models of biomass fluxes to help us determine the major forces that drive tundra food webs (see Box 1). Although this research is still in progress, our first results highlight the importance of

ArcticWOLVES final synthesis report

body size. The primary factors regulating herbivore populations may vary according to their body size (Caughley and Krebs 1983). Because large herbivores can partially escape predation, they are more likely to be regulated by resources (or climatic conditions) whereas smaller ones (especially small mammals) suffer a lot more from predation, which is more likely to limit or regulate their populations. This pattern is in accordance with what was found in other terrestrial ecosystem (e.g. African savannas) where regulation processes (either from plants or predators) greatly depend on herbivore body size (Sinclair et al. 2003, Hopcraft et al. 2010). We also showed that the tundra ecosystem could heavily depend on other systems (mainly the marine ecosystem, but also freshwater ones). Assuming that ecosystems are closed can lead to erroneous conclusions, especially when productivity is low such as in the Arctic (Loreau and Holt 2004). Future tundra ecosystems

models should incorporate allochthonous inputs (meta-ecosystems, Loreau et al. 2003, Gauthier et al. 2011) to fully understand tundra food webs.

Processes occurring during winter likely have a strong influence on the functioning of tundra food webs, but fieldwork took place only during the summer months at most of our study sites. Hence, we are missing precious data during a critical period of the year. For instance, weasels are the main lemming predator and are present year round, but we know very little on the interaction between these two groups during winter. Spatial and temporal variation in snow quality, including conditions in the subnivean space, would be another avenue to be investigated in the coming years. Future research will have to overcome the logistic difficulties associated with winter work as this could shed some light on the variability observed across the Arctic.



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Varanger, Norway.

Box 1. Modelling of the Bylot Island food web.

We used a modelling tool (called ECO-PATH; Christensen and Pauly 1992; www.ecopath.org) to develop food web models based on the flux of biomass among various trophic levels at several of our study sites. Our aim was to answer four key questions: (i) What fraction of plant production is consumed by herbivores? (ii) What fraction of herbivore production is consumed by predators? (iii) Which species are keystones (i.e. a species that has an effect on other taxa much larger than expected given its biomass)? (iv) Do these patterns have changed over time, most notably in response to climate change? We show here the results of our model at one of our study sites, Bylot Island, NU. The key terrestrial wildlife and plant production have been monitored at this site from 1993 to 2009 (Gauthier et al. 2004). The main feature of Bylot Island is the absence of large mammalian herbivores (muskoxen and caribous) and the presence of a relatively large snow goose colony (see Fig. 1 for a schematic representation of the food web). Results from the model show that less than 10 % of the annual plant production at the landscape level is consumed by herbivores (lemmings, geese), but 20 to 100% of the annual herbivore production is consumed by predators. Lemmings in particular are heavily depredated. Our results highlight that the two sympatric lemming species occurring on Bylot Island do not show similar patterns. Collared lemmings are heavily predated regardless of the lemming phase and

also show limited fluctuations (7.2 fold between crash and peak years) compared with brown lemmings, which show higher amplitude fluctuations (44.3 fold between crash and peak years). Predation alone is likely to limit collared lemming abundance while additional mechanisms (such as delayed predation by weasels or maternal effects) may be required to account for the decline phase of brown lemmings. The proportion of plant production consumed by herbivores showed a decreasing trend over time whereas the proportion of herbivores consumed by predators remained high and fairly constant. The decreasing trend in herbivore consumption is largely explained by the climate-driven increase in plant production observed on Bylot Island (see GEESE chapter), which apparently has not affected yet the higher levels of the food web. Thus, plant production is apparently not regulating ecosystem processes on Bylot Island. In contrast, some predators act as keystone species. During years of peak lemming abundance, the snowy owl is a keystone species because it negatively impacts other predators (such as the arctic fox through intra-guild predation or competition, Fig. B1.1) and it reduces predation rate on alternative prey species, such as snow geese, through indirect interactions (Bêty et al. 2001). These results show that predation is likely to play a dominant role in the functioning and structuring of the tundra food web on Bylot Island.

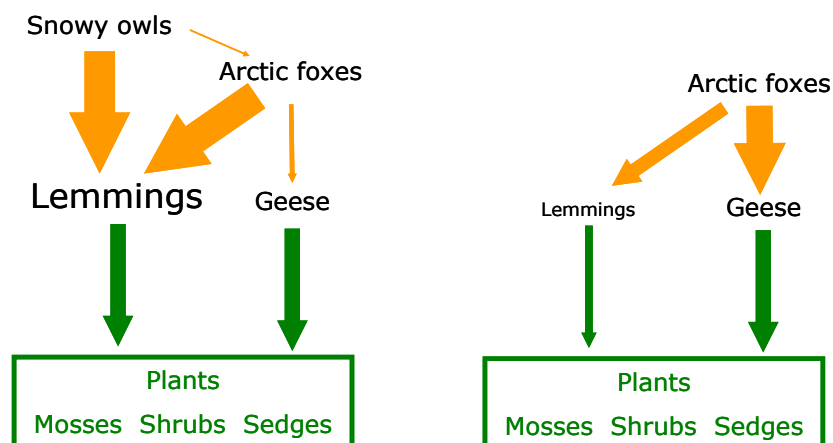


Figure B1.1. Simplified food web of Bylot Island in relation to lemming abundance: peak years (left diagram) vs. crash years (right diagram). Thickness of the arrows is proportional to the strength of the interactions.

Box 2. Semi-domesticated reindeer in Norway: an example of human-induced subsidy for the tundra ecosystem.

Despite a relatively simple structure, processes driving tundra food webs can be affected by temporal fluctuations occurring at several spatio-temporal scales (Ims and Fuglei 2005). Among those, the seasonal migrations of several species can be a major source of temporal fluctuations. For instance, in many areas reindeer uses the tundra as summer pasture and migrates south in the boreal forest during the winter (Callaghan et al. 2004b). The semi-domestication of these large herbivores, mostly in the Eurasian Arctic, has modified these seasonal movements, caused shifts in their range and resulted in increase in numbers, sometimes by several orders of magnitude (Moen and Danell 2003, Forbes et al. 2009). For instance, over the past 30 years, the herds on the Varanger peninsula, Northern Norway, have increased by 300%, reaching ca 3.6 reindeers/km², a high density for such a low productivity area. Furthermore, some reindeer now inhabit summer pastures all year round. Consequently, reindeer provide an abundant and predictable food source for several tundra predators, which turn to scavenging on carcasses from animals dying during winter months. This food subsidy is especially beneficial for predators during harsh winters. In several locations, this human-driven resource likely has a strong impact on predator guild structure as well as on the energy flux in the food web due to the thou-

sands of kilograms of meat readily available for consumption. This can be viewed as a mechanism driven by bottom-up processes (food to the predators provided by the carcasses; Fig. B2.1), potentially shifting the regime of predator-prey interactions for predators like the arctic fox and their other prey species (Killengreen et al. 2011).

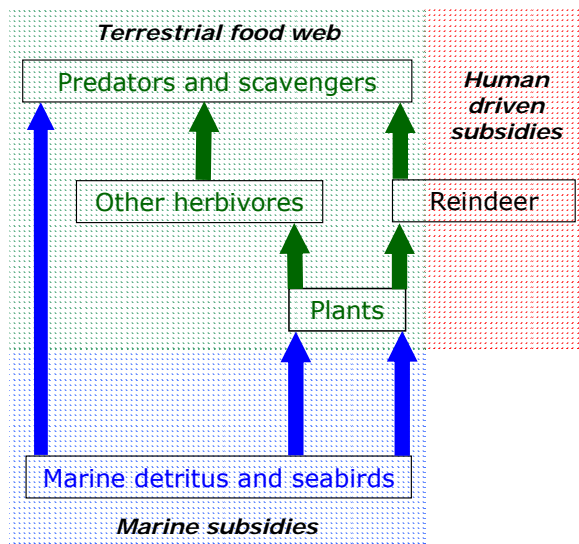


Figure B2.1. Simplified terrestrial food web in Varanger, Northern Norway, subsidized by marine and human-induced (reindeer) inputs. Consumers are then subsidized to higher abundances and to greater diversity than would be possible from in situ resources alone.



Semi-domesticated reindeers.

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Box 3. Impact of anthropogenic food sources on an arctic predator.

The Canadian military base of Alert, Ellesmere Island, Canada (83° N, 62° W; Fig. 2), is the most northerly, permanently inhabited settlement on the planet. The sewage of the base (which includes semi-liquid food refuse) represents a potentially rich and stable source of nutrients for predatory species living in this very low productivity environment. We used stable isotopes to determine to what extent this anthropogenic food source was used by long-tailed jaegers, the most abundant predator at this site, and if it could affect food web interactions. Because lemmings are an important prey item for jaegers (see BIRDS OF PREY chapter), we contrasted the diet and reproductive activity of jaegers in years of high and low lemming abundance. Jaegers switch from a diet dominated by marine prey in winter to one dominated by terrestrial prey in the summer. A large proportion of the summer diet of jaegers at Alert comes from the sewage but this anthropogenic source was much more important in years of low lemming abundance than in years of high lemming abundance (Fig. B3.1). This food subsidy apparently dampens the effect of lemming abundance on jaeger reproduction, because nest density was 2.5 times less between years of low and high lemming abundance compared to 65 times less on Bylot Island, a control site without any anthropogenic food source. These results suggest that anthropogenic food subsidy can affect the interaction between predators and their primary prey, here lemmings, and thus the stability of the food web.



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Long-tailed jaegers and shorebirds feeding at the military base sewage at Alert.



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Long-tailed jaeger.

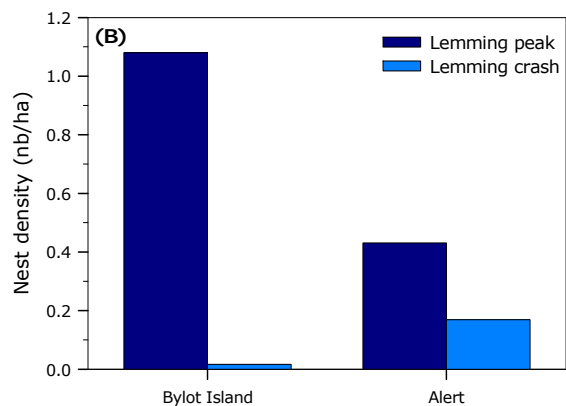
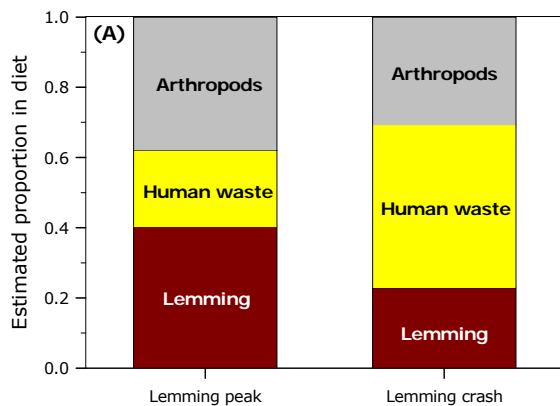


Figure B3.1. (A) Summer diet of the long-tailed jaeger during lemming peak or crash at Alert, Nunavut and (B) the nest density at Alert and Bylot Island according to lemming phase (Julien 2011).



1 - Mittimatalik (Pond Inlet), Nunavut, Canada © Dominique Berteaux
2 - Moose Factory, Manitoba, Canada © Jennifer Robus
3 - Peawanuck, Manitoba, Canada © Kaitlin Wilson

CHAPTER 10. INTEGRATING SCIENTIFIC AND TRADITIONAL ECOLOGICAL KNOWLEDGE

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Abstract

The Arctic is home to numerous indigenous communities who still maintain close cultural, economic, and spiritual ties to local ecosystems. Over the past 25 years, the idea of combining traditional ecological knowledge and scientific knowledge to better understand arctic ecology and to manage natural resources has gained a growing recognition. Several sub-projects have combined scientific and traditional ecological knowledge in our International Polar Year project. These studies have attempted to better understand the ecology of the arctic fox in the North Baffin region and to study the impacts of climate change on geese in the Hudson Bay Lowland. We have also started to investigate the contribution to environmental knowledge of the Arctic Borderlands Ecological Knowledge Coop, a Yukon community-based monitoring program. We interviewed local experts from Pond Inlet (Nunavut) about cultural use and importance of Arctic foxes, changes in abundance and distribution, winter feeding habits, moult, and arrival of red fox in the area. The integration of TEK and scientific knowledge expanded the spatial and temporal scales of documented scientific knowledge about arctic foxes. For instance, TEK pertaining to the winter ecology of arctic foxes provided insight into the existence of two distinct strategies, one marine and one terrestrial, which expanded current scientific knowledge at both the spatial (from tens to hundreds of kilometres) and temporal scales (from summer to annual). Our research in the Hudson Bay Lowland examined how climate change and its impacts on natural habitat may be affecting the spatial distribution of snow goose and Canada goose populations, and how this impacts access and harvest by Cree communities. We conducted interviews with local experts in Moose Factory and Peawanuck (Ontario). Hunter reported significant changes in goose distribution during both spring and fall migration, likely due to changes in climate and local habitats used by geese. In this case, TEK and scientific observations largely corroborated each other. Our project examining the Arctic Borderlands Ecological Knowledge Coop is analysing the 12 years of indigenous hunters' observations collected by the Coop program to better understand variations in the body condition of the Porcupine Caribou Herd and availability to communities. The Porcupine Caribou is a particularly important resource for Native people living in the Northern Yukon area and is one of the only long-term monitoring programs in the Arctic based on the knowledge of aboriginal people. Results will contribute insights into the benefits and drawbacks of community-based monitoring programs in terms of scientific and indigenous knowledge integration. We conclude from our studies that a strategic cycling between the collection of TEK and the acquisition of scientific knowledge should be organized to enhance our overall knowledge about the ecology of a given wildlife population. Bridging scientific and traditional knowledge not only has value to better understand species and ecosystems. It also gets people with similar interests (wildlife and the land) but different cultures to better know each other, in a context that needs the collaboration of all to better understand the origin and implications of extremely quick environmental changes currently affecting the circumpolar North.

Scientific and traditional knowledge

The Arctic is home to numerous indigenous communities who still maintain close cultural, economic, and spiritual ties to local ecosystems. These interrelated systems of human and nature are now experiencing social and environmental changes, occurring at rates which may challenge their capacity to adapt. To foster the sustainability of these northern social-ecological systems, it is critical to better detect and predict changes affecting them. This task is complex and requires information from various sources, including scientific information and the knowledge and perspectives of local indigenous people.

Over the past 25 years, the idea of combining traditional ecological knowledge (TEK, see Box 1 for definitions) and scientific knowledge to better understand arctic ecology and to manage natural resources has gained a growing recognition (references in Gagnon and Berteaux 2006). In Canada for example, the increased appreciation of TEK, coupled with native political and cultural claims, has led to legislation and policies requiring that TEK be considered alongside science in certain resource management decisions (Usher 2000). A cornerstone of the Nunavut Land Claims Agreement was the creation of a council that would ensure Inuit involvement in decisions regarding the preservation and development of land covered in the agreement (Gouvernement du Canada 1993). Furthermore, following the creation of the territory in 1999, Inuit traditional knowledge (see Box 1) has emerged as a guiding principle of the Government of Nunavut (Wenzel 2004).

This chapter summarizes three Arctic-WOLVES projects integrating TEK and scientific knowledge. These projects reached different stages of development during the International Polar Year (IPY). The first project, which ended at the beginning of IPY, investigated the complementarities between TEK and scientific knowledge to better understand the ecology of arctic fox and snow geese in the North Baffin region. The second project, which nearly entirely unfolded during IPY, linked science and TEK in understanding impacts of climate change on geese in the Hudson Bay Lowland. The third project started during IPY and is still at an early stage of development. It investigates the contribution of an international (Alaska-Yukon-Northwest Territories)

community-based monitoring program (the Arctic Borderlands Ecological Knowledge Coop) to the adaptive capacity of an arctic social-ecological system.

Project 1: Ecology of arctic fox in the North Baffin region

It is now a legislative requirement that Inuit knowledge be included in the management of Canada's National Parks in Nunavut (Nunavut Field Unit of Parks Canada 2004). In this project, we combined the interests of Mittimatalik (Pond Inlet) residents, Sirmilik National Park (Fig. 1), and academic scientists to investigate Inuit TEK pertaining to arctic foxes (*Vulpes lagopus*). This project was a crucial step in integrating Inuit TEK into the management of Sirmilik National Park because it put in place an approach to TEK collection and gathered abundant information on a species central to the local ecosystem.



Figure 1. Study area of Project 1. (A) Location of the Nunavut territory (darker beige), in which the red circle indicates the general study area location. (B) Close-up of the study area showing north Baffin Island and Bylot Island, Nunavut, Canada. The community of Mittimatalik is the closest and largest settlement located near the Sirmilik National Park (from Gagnon and Berteaux 2009).

Inuit from the Mittimatalik area formerly trapped arctic foxes extensively. From the 1920s, when the Hudson's Bay Company established a trading post in Mittimatalik, to the mid 1970s, fox fur represented the most important asset traded by Inuit to secure cash and other valuable goods (Sawtell 2005). Only a few hunters still trap foxes around Mitti-

ArcticWOLVES final synthesis report

matalik, and trapping is no longer a major economic activity in the area. Nonetheless, foxes are highly visible and are frequently observed by local hunters traveling on the land (Panipakoocho 2005). This made the species an ideal one to be the focus of a TEK project (see Box 2).

Ecological systems operate on a multitude of spatial and temporal scales (Wiens 1989, Levin 1992, 2000), and understanding how processes differ and interact among these scales is one of the great difficulties of ecological research (Wilbanks 2006). We tried to integrate TEK and scientific knowledge by emphasizing their complementarities across spatial and temporal scales. An observer can usually specialize in only a subset of existing scales because of the nature of economic motivations, time and logistical constraints, or personal and cultural interests. In particular, scientists and local community members usually have very different motives and access to different observational equipment for studying the natural world.

We interviewed 21 local experts who were selected from recommendations by Elders, members of the Mittimatalik Hunters and Trappers Organization, people from the Hamlet Office, and community members working for Parks Canada and the Nunavut Wildlife Management Board. Interviews conducted on the land were particularly effective in stimulating conversation. Gagnon and Berteaux (2009) give a detailed description of our methods.

We concentrate here on one of the key results of this study dealing with winter feeding ecology and distribution of the arctic fox. According to 16 local experts who mentioned at least one item eaten by arctic foxes, their winter diet is made up of various sources. Among these experts, 11/16 mentioned lemmings (*Dicrostonyx groenlandicus* and *Lemmus trimucronatus*), 12/16 mentioned carcasses of sea mammals, 2/16 referred to caribou (*Rangifer tarandus*), and 1/16 cited arctic hare (*Lepus arcticus*). One expert said that arctic foxes eat birds, although the species were not identified, and another referred to food caches. Three of the 16 experts called foxes scavengers who feed on anything they can find. Of the dozen informants who indicated that arctic foxes fed on the carcasses of

sea mammals, 7/12 specified that the animal remains originated from beached animals, 5/12 said that they were leftovers from polar bear kills, and 3/12 referred to carcasses left behind by hunters.

When discussing the winter diet of arctic foxes, 11 of 21 informants reported the existence of two overwintering strategies, one involving mainly the use of tundra and the other the use of sea ice (Fig. 2). They also mentioned physical characteristics that distinguished the two types of foxes. Of the respondents commenting on the "land" fox, 8/11 said that it had thicker fur, 4/11 reported that its fur was whiter, and 1/11 described it was longer. Two of them said that the land fox was larger, and one each said that it had less oily fat, had a thinner skin, was better to eat, and turned white earlier in the winter. Seven out of 11 informants provided potential reasons for the physical variations between the "land" and "sea" fox. Six out of seven mentioned differences in food sources as the main reason, and one stated that temperature differences between the floe edge and the land could explain variations in fur thickness. A large proportion of informants (17 of 21) also reported on a migration occurring in March–April, during which foxes move toward the sea ice to feed on newborn ringed seal pups.

We found many points of complementarity between the TEK we collected and current scientific knowledge. The integration of TEK and scientific knowledge expanded the spatial

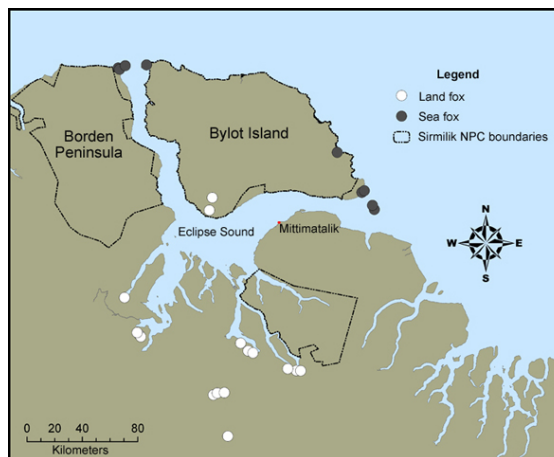


Figure 2. General spatial distribution of "land" and "sea" arctic fox, according to the TEK reported by local experts from Mittimatalik, Nunavut, Canada (NPC = National Park of Canada).

and temporal scales of documented knowledge about arctic foxes. For instance, TEK pertaining to the winter feeding ecology of arctic foxes expanded current scientific knowledge at both the spatial (from tens to hundreds of kilometres) and temporal scales (from summer to annual). Indeed, the winter diet of arctic foxes has rarely been quantified (Roth 2002), and never in the Mittimatalik area. Based on studies conducted elsewhere, the arctic fox is considered an opportunistic omnivore (Angerbjörn et al. 1994, Roth 2002), and its winter diet can consist of various items depending on the habitat occupied. Studies have suggested that two foraging strategies, one terrestrial and one marine, may be adopted by different segments of arctic fox populations, although this has not been shown to occur in the winter (Roth 2002). Scientists have also documented that arctic foxes may prey on ringed seal pups by entering their subnivean birth lairs in the spring (Smith 1976, Hammill and Smith 1991). However, because arctic foxes are opportunistic omnivores that occupy various habitats, it is difficult to generalize findings across populations (Angerbjörn et al. 1994, Roth 2002, Eide et al. 2005).

TEK added to our knowledge regarding the ecology of the fox population near Pond Inlet by providing: (i) evidence that local animals use a variety of habitats during winter, from land to sea ice; (ii) an overview of the food items consumed during winter; (iii) insight into the importance of seal pup consumption in early spring, and (iv) insight into the existence of two distinct winter foraging strategies. TEK also provided information regarding differences in fur characteristics between foxes adopting these two strategies; to our knowledge, this has not been documented scientifically. The existence of two strategies had only been documented by scientists outside of this study region based on fox summer diets in areas where they had access to large bird colonies (Fay and Stephenson 1989, Eide et al. 2005), or at a pan-arctic scale across fox populations living in very different habitats (Angerbjörn et al. 1994). Roth (2002, 2003) suggested that distinct segments of fox populations might use different winter foraging options, one terrestrial and one marine, in western Hudson Bay, Canada. However, his analy-

sis found no evidence of the two strategies in this population.

To gain the most benefits from complementarities, a strategic cycling between the collection of TEK and the acquisition of scientific knowledge could be organized to enhance our overall knowledge about the ecology of a given wildlife population. For example, TEK collected during this study expanded our knowledge about the ecology of the regional fox population by providing evidence that local animals use both the tundra and sea ice in winter. This was not documented by scientists working locally. However, since this study was performed, some Bylot Island foxes have been fitted with satellite transmitters (see ARCTIC AND RED FOXES chapter). The scientific knowledge provided by satellite data was congruent with TEK. The satellite data also showed how individual foxes use terrestrial and marine habitats throughout the winter, knowledge that is largely inaccessible to local experts, who cannot easily differentiate between individual foxes seen at different locations. In contrast, satellite data cannot provide behavioural or dietary information. Local experts could help interpret satellite data using TEK, leading to further novel research projects that may, in turn, again benefit from collecting additional TEK. If designed strategically, this cycle of enquiry can help overall knowledge grow more quickly than can the input of either local hunters or scientists alone. Furthermore, the involvement of local experts in all stages of the cycle can increase the likelihood that research will address topics that are locally relevant and that results will be transferred to local communities. This partnership may also strengthen mutual understanding between scientists and local inhabitants.

Project 2: Impacts of climate change on geese in the Hudson Bay Lowland

This project drew on both traditional ecological knowledge and scientific knowledge to better understand the impact of a changing climate on goose abundance, distribution and habitat in the Hudson Bay Lowland, and how these changes affect local coastal communities in terms of their access and harvest of geese. The communities involved included the Weenusk First Nation in Peawanuck, located

ArcticWOLVES final synthesis report

on the southern coast of Hudson Bay, and the Moose Cree First Nation in Moose Factory, located at the tip of James Bay.

The First Nations (Cree) of the Hudson Bay Lowland rely heavily on waterfowl for subsistence, as much in overall weight as moose (*Alces alces*) or caribou (Thompson and Hutchison 1987, Berkes et al. 1992). The proportion of community members who participate in the spring goose hunt has also remained high, as land and hunting tradition remains an important part of Cree culture (Berkes et al. 1992).

The wetlands of the Lowland are both breeding and staging grounds for several goose species of the Mississippi Flyway of North America, where individuals acquire critical reproductive fat reserves before reaching their arctic breeding grounds (Thomas and Prevet 1982). Canada geese (*Branta canadensis*) of the Mississippi Valley Population (MVP) and Southern James Bay Population (SJB), as well as lesser snow geese (*Chen caerulescens*) of the mid-continent population, migrate through the region, and nest within hunting range of the coastal communities. Habitat changes have occurred on the wintering grounds in the United States and along migration corridors, as well as on the breeding grounds (Kerbes et al. 1990, Abraham and Jefferies 1997). The climate of the Hudson Bay region is also experiencing change at an accelerated rate (ACIA 2005). Localized impacts, however, are less well known. Also less known are the impacts on the communities in terms of their access and harvest of geese.

We conducted interviews in Moose Factory and Peawanuck. Participants were chosen based on their experience on the land (Creswell 2009). Verification of the information collected in the interviews is critical, and several trips to the communities were made for this purpose. The themes from the local observations were compared to primarily quantitative data sources if they were at the same temporal, geographical and phenomenological scale (Duerden and Kuhn 1998). Instances where datasets were at the same scale were first identified, and then it was determined if the information was corroborating (the same), complementary (potentially the same but one of the scales was different), or contradictory. The final phase was to confirm

where the datasets agreed, or assess and speculate as to why they might disagree.

In Moose Factory, local observations and aerial surveys agree that there has been a decrease in the number of snow geese seen in the area since the 1980s. Local observations for Canada geese also indicate that there has been a decrease since the 1980s. Aerial surveys indicate that SJB Canada geese decreased since the 1970s but have remained stable since the early 1990s. There were also local observations of a shift in the pattern of the spring migration for Canada geese, where the geese are being observed as flying inland as opposed to along the coast as they have in the past. Additionally, hunters have observed geese now following the power line along the west coast of James Bay. This observation could not be corroborated by scientific evidence, although a possible explanation could be that the open areas by the power lines melt faster and therefore attract the geese to feed earlier than on the coast. Hunters also reported spring temperatures being warmer, with the Moose River breaking up significantly sooner. These observations are corroborated by local weather station data and records of the river break up. Local observations on changes to the composition of the grasses on the coast are also corroborated by preliminary localized studies on the coastal vegetation.

In Peawanuck, hunters reported an increase in the number of both snow geese and Canada geese in the area since the 1970s, which is corroborated by aerial surveys. Hunters have also reported a shift in the fall migration, with snow geese leaving Hudson Bay in August and early September, as opposed to mid-October. Hunters have attributed this shift to changes occurring to the vegetation on the summer feeding grounds of the geese. There have been no local vegetation studies with which to compare this observation, although this observation is complementary as regionally the coastal vegetation has been documented as changing (see GEESE chapter). Similar observations were given by hunters on the increase in spring temperatures, and are corroborated by local weather station data.

This study found many areas of convergence between TEK and science. The few areas of divergence were mostly based on a lack

of information at the same scale. This study is significant in terms of providing insight into trends of goose population abundance, distribution and habitat change. It has also shown that there is spatially and temporally limited scientific data on changes occurring on the Hudson Bay coast, and has identified a need for future work. The vegetation and temperature are changing, as was made clear in the interviews, and it is important to understand how this will impact the feeding and nesting behaviours of the geese. While they have not yet impacted the success of the spring goose hunt, it is likely that these changes have also not yet met the critical threshold of a mismatch. This study is a good example of how drawing on multiple knowledge systems has improved our understanding of goose-community-environment interactions. Such linkages are important, as they will improve the collective understanding of both communities and research partners in changing environmental conditions in these coastal regions.

Project 3: The Arctic Borderlands Ecological Knowledge Coop case study

This project examines how a community-based monitoring program involving scientists and indigenous communities contributes to knowledge acquisition and transmission about a northern social-ecological system, and how it contributes to build trust and a sense of community among its participants. More specifically, we are analysing the 12 years of indigenous hunters observations collected by the Arctic Borderlands Ecological Knowledge Coop (ABEKC) program, which was originally designed to better understand variations in body condition of the Porcupine Caribou Herd and its availability to communities.

The ABEKC was created in 1994 when representatives from First Nations, Inuvialuit, government agencies, scientists and co-management groups started an ecological monitoring program within the range of the Porcupine Caribou Herd, which includes parts of Alaska, the Yukon and Northwest Territories. The Porcupine Caribou is a particularly important resource for Native people living in this area, but the herd is declining in size since 1989. Causes of the decline remain uncertain. Three main issues were identified in 1994 as being central to the program: climate

change, contaminants, and regional development. It was also decided that an important aspect of the ABEKC would be to bring scientific and local knowledge together. Formally, the goals of the ABEKC are to (i) monitor and assess ecosystem changes in the range of the Porcupine Caribou Herd and adjacent coastal and marine areas, (ii) encourage use of both science-based studies and studies based on local and traditional knowledge in ecological monitoring and ecosystem management, (iii) improve communications and understanding among governments, aboriginal and non-aboriginal communities and scientists with regard to ecosystem knowledge and management, and (iv) foster capacity-building and training opportunities in northern communities in the context of the above-listed goals (Kofinas et al. 2002, Arctic Borderlands Ecological Knowledge Society 2008).

The ecological monitoring program of the ABEKC includes two aspects. First, it developed a database of 65 scientific indicators (collected by different sources), updated annually, that cover a wide range of topics including weather information, plant growth, bird abundance, etc. Second, the ABEKC, via community researchers, runs a community-based monitoring program during which an average of 17 local experts per community are interviewed each year in 4 to 8 communities on topics including weather, caribous, fishes, berries, etc. During each interview, maps are produced that identify important areas mentioned by the interviewee. At the beginning of the ABEKC, communities who participated to this monitoring program included Aklavik, Old Crow, Fort McPherson and Arctic Village. Since 2003, the ABEKC expanded to include Inuvik, Kaktovik, Tuktoyaktuk and Tsiigehtchic. As of 2008, 1190 interviews were conducted by the program. There is now a strong desire to analyse and synthesise the information collected to make it more readily available to management agencies and the public, and our project is contributing to this endeavour. In 2005, the ABEKC contracted an independent firm to perform a survey on how ABEKC data could be made relevant to decision-makers. Eighteen individuals involved in environmental management in the Borderlands region answered the questionnaire, which revealed that ABEKC data played a limited role in decision-making.

ArcticWOLVES final synthesis report

Recommendations were then made to increase data accessibility and use.

The ABEKC is an excellent case study for ArcticWOLVES because it is, to our knowledge, one of the only (perhaps the only) long-term ecological monitoring program based on the knowledge of aboriginal people implemented in the Arctic, and much has to be learned about this initiative. Results from this research currently underway will also contribute insights into the benefits and drawbacks of community-based monitoring programs in terms of scientific and indigenous knowledge integration, and in terms of increased adaptive capacity in face of change.

Conclusion

During the ArcticWOLVES project, we learned many lessons from our attempts to bridge scientific and traditional ecological knowledge. The following are two interesting lessons. First, the boundary between the two knowledges was not always as clear as anti-

pated. For example, scientists often use their intuitions and field experience to better understand their study systems, while indigenous hunters sometimes use scientific methods (such as comparing the success of various trapping methods through repeated trials) for the same reason. It is thus not always easy to assign a given piece of knowledge as being of scientific or non-scientific origin, especially when it comes to knowledge of local value. Second, the value of bridging scientific and traditional knowledge is not only limited to gaining a better understanding of wildlife species and the ecosystem. It also has great value in getting people with similar interests (wildlife and the land) but different cultures to interact and better know each other. In a context that needs the collaboration of all to fully understand the causes and implications of the extremely quick environmental changes currently affecting the circumpolar North, meaningful interactions between scientists and indigenous people are extremely valuable.



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Box 1. TEK, LEK, ITK, IK, IQ: what is this?

Traditional ecological knowledge (TEK), local ecological knowledge (LEK), Inuit traditional knowledge (ITK), Inuit or indigenous knowledge (IK) and Inuit Qaujimagatuqangit (IQ) are some of the common terms referring to the non-scientific knowledge that Northern people have about wildlife and ecosystems, and that is increasingly of interest to scientists. What are the definitions of those terms and which one should be used? Answering this question is difficult and context-specific. This box gives some definitions generally found in the literature, and explains our choice of terms in the chapter.

- Traditional ecological knowledge (TEK): often defined as “a cumulative body of knowledge, practice, and belief, evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment”. In this definition, the word ‘traditional’ emphasizes ancient roots and generational continuity in knowledge content. TEK thus encompasses factual knowledge about ecological components and

processes, practices of environmental use, and cultural values, ethics, and philosophies defining human relationships within the natural world (Berkes 2008).

- Local ecological knowledge (LEK): like TEK but refers more specifically to a place-based knowledge acquired more recently over the lifetime of individuals.
- Inuit traditional knowledge (ITK) or Inuit knowledge (IK): like TEK but refers to the knowledge of the Inuit people.
- Indigenous knowledge (IK): like Inuit knowledge but refers to all indigenous people.
- Inuit Qaujimagatuqangit (IQ): often considered similar as ITK.

In this chapter, we often use TEK to refer to all the non-scientific ecological knowledge that was shared with us by Northern people during ArcticWOLVES. Other terms may have been more appropriate on some occasions (B. Archie, pers. comm.). Our choice was mostly motivated by the desire to keep things simple and did not entail any strong opinion about the relative merits of the terms.



Catherine-Alexandra Gagnon interviews hunter M. Qaunaq during an elder-youth camp on Bylot Island, NU, Canada.

Box 2. How easy is it to gather TEK about a given species?

Gagnon and Berteaux (2009) proposed a conceptual graph (Fig. B2.1) showing how the level of the local community's interest and contact with a given species influences the ease with which it is possible to gather TEK about this species in an unbiased way. When a community has little interest in or contact with a given species (for example, a cryptic insect), TEK is low and therefore cannot be gathered productively (left side of the curve). On the other hand, when the community has a very high interest in a species (for example, polar bears, *Ursus maritimus*), issues surrounding the species can also be strongly politically charged, and TEK becomes difficult to acquire without bias (right side of the curve). The arctic fox and geese studied in Projects 1 and 2 provided an ideal context to collect TEK (gray area, center of the graph), because these species are visible and harvested but do not elicit very strong reactions.



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Elisapee Ootoova and Lucy Quasa participating to an interview held at an old goose hunting location, Bylot Island, NU, Canada.

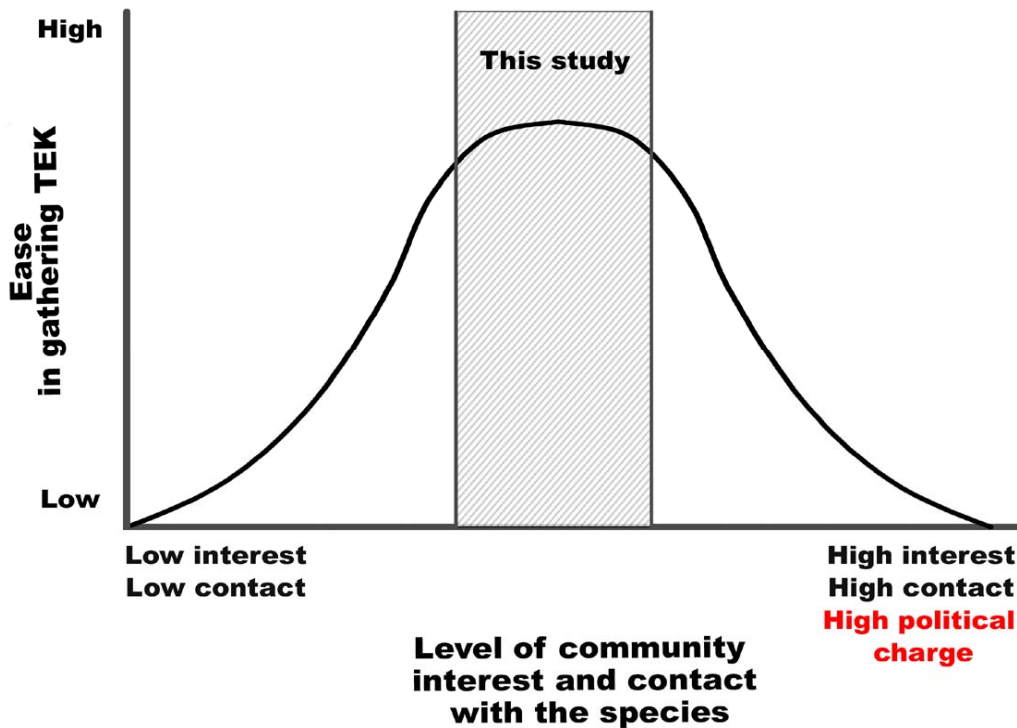


Figure B2.1. Conceptual graph showing how the level of a community's interest in and contact with a species influences the ease with which it is possible to gather TEK about this species (from Gagnon and Berteaux 2009).

CHAPTER 11. GENERAL CONCLUSION

Gilles Gauthier and Dominique Berteaux

The International Polar Year program provided an unprecedented opportunity for collaborative and comparative research. The project ArcticWOLVES was highly successful in fostering collaborative research among more than 150 researchers and students coming from a large array of institutions spread over 9 countries. All these people worked on a common theme across the circumpolar Arctic, effectively linking through research more than 16 primary field sites that constituted privileged observatories of wildlife in vulnerable ecosystems (see Fig. 1 in INTRODUCTION chapter). Our project created strong partnerships with several northern organizations and communities, especially in Canada. Despite the immense difficulties and challenges associated with such a large-scale endeavour, we are proud of the results achieved by our project, which shows the added value of large international programs. The results summarized in this report provide a glimpse of the most significant achievements of our project. The international dimension of ArcticWOLVES is clearly shown by the diverse nationalities of the chapter authors for this report, with 8 countries involved. Although most of what is presented in our synthesis report has been published in the scientific literature (our team has already published 51 papers in scientific journals), a continuous flow of publications is expected over the next few years. A full list of the publications issued from ArcticWOLVES can be found on our web site (www.cen.ulaval.ca/arcticwolves/), which will continue to be updated in the future.

A new pattern emerging from our study is that, when large mammalian herbivores are absent, the food web appears more likely to be dominated by predator-prey than by plant-herbivore interactions. However, we encountered large variations among sites in this pattern depending of local features. Among the small to mid-size wildlife of the tundra food web, small mammals are the most important herbivores. Populations of tundra small mammals generally exhibit strong amplitude cycles of abundance but these patterns show consid-

erable variability among sites, with recent changes occurring at some sites. The variability among sites largely comes from differences in the length of the period of low abundance between irruptions and from the range of abundance between the lowest and highest years. In Canada, the combined predation rate of several species appears an important regulating factor of both cyclic and non-cyclic small mammal populations at several sites. However, certain snow conditions such as a deep and low-density snow pack also appear to be necessary for strong winter population growth leading to peak populations during the summer. Competitive interactions among co-habiting species of small mammals also influence the patterns of change in population abundance.

Geese are another important herbivore at many arctic sites but, in contrast to lemmings, their abundance varies enormously through space, from near absence at some sites to very high abundance at sites with nesting colonies. Geese only come to the Arctic to breed during the summer and the populations of several species have increased considerably in recent decades due to events occurring on their wintering ground. At very high goose density, predator limitation weakens considerably and the system becomes dominated by goose-plant interactions, with potentially strong negative impact on tundra vegetation. This provides a prime example of how changes due to human activities occurring thousands of kilometres away from the Arctic may impact the tundra due to migratory connectivity in bird populations. However, as the climate warms, we uncover new mechanisms that will likely affect the synchrony of events between goose reproduction and either their food plants or their predators, which could eventually lead to a reduction of recruitment into goose populations.

Arctic arthropods play essential ecological roles in the functioning of the tundra, for instance as the main prey of many shorebirds and songbirds. Therefore, changes in their distribution and abundance have the potential

ArcticWOLVES final synthesis report

for far reaching ecological consequences across the arctic ecosystem. As temperatures increase across the Arctic, our data indicate that diversity and overall biomass of arthropods should increase and their short-lived peaks in abundance currently characteristic of High-Arctic sites may shift or broaden to resemble the longer period of abundance characteristic of lower arctic sites. These changes in resource availability may have a negative impact on the reproduction of insectivorous birds. However, arctic shorebird populations may be even more affected by change in predator abundance. We found a large variation in nest predation risk across the Canadian Arctic as predation risk for shorebird eggs decreased considerably with latitude. Our results suggest that the costs of migrating farther north are compensated for by decreases in predation risk for individuals breeding at higher latitudes. Shorebird predator-prey relationships could be altered via changes in the abundance of predators or of alternative prey for predators, especially at High-Arctic sites.

Another key conclusion of our project is that the functioning of an ecosystem cannot be understood in isolation as subsidies from adjacent ecosystems can shape the structure and dynamic of food webs. This is most evident for top predators of the tundra such as the arctic fox (*Vulpes lagopus*) and several avian predators. The extensive use of the sea ice by arctic foxes and snowy owls (*Bubo scandiacus*) that we documented show that the marine habitat may provide essential foraging ground for the maintenance of several of these predator populations during the winter. Therefore, a broader, cross-ecosystem perspective may be required when assessing the status or threats faced by these predators. Competition between predators is also an important aspect of their ecology. A prominent example is provided by arctic and red foxes (*Vulpes vulpes*) as the two species compete where their distributions overlap, with the red fox being dominant over the arctic fox. Because red foxes will likely expand their distribution northward and their abundance with a warming climate, this will tend to increase the area of overlap between these two competing species, which will be a threat for the arctic fox.

Several projects within ArcticWOLVES col-

lected traditional ecological knowledge, especially in Canada. This allowed us to corroborate, complement or find contrasts with the scientific results that were already present in the literature or were generated by our project. This also allowed us to develop some of the methodology that is now needed to integrate into a coherent framework the scientific and non scientific knowledge that is available about Arctic ecosystems.

Although an improved understanding of the fundamental processes regulating the tundra food web and several key wildlife species and of their vulnerabilities to a changing environment represent our most significant achievements, our project has provided a number of other significant legacies. Among those, our project is leaving a comprehensive database of most of the information collected at the Canadian sites during the International Polar Year program and, in some cases, during previous years as well. This database, which is available on line (www.cen.ulaval.ca/arcticwolves/arcticwolveswebbd.htm), includes data on the abundance, distribution, reproduction and ecology of a large number of arctic wildlife species that will be useful for future studies. These data were collected using standardised sampling protocols (www.cen.ulaval.ca/arcticwolves/) across sites, which constitute another significant legacy of our project because they provide a set of tested methodologies for monitoring the status or trends of several arctic species in the future.

The cross-institutional engagement within Canada and abroad gave strong research output resulting from research replicated across different and diverse sites, as well as opportunities for group meetings to discuss the science. The international engagement of the IPY program allowed the development of durable international collaborations, especially among Canadian, Norwegian, Russian and Danish colleagues. Several of these collaborations will extend well beyond the International Polar Year and will increase our scientific capacity in the north. This certainly represents another enduring legacy of the program.

The International Polar Year was also a unique opportunity to enhance arctic research infrastructure, and some of our field sites benefitted from that, especially in Canada.

Conclusion

Improved and upgraded research facilities along with new scientific equipment will allow a continuation of several of the objectives of our project beyond the International Polar Year. This is very important because we believe that our synthesis report clearly shows the added value of long-term studies, such as those that have been carried out at several field sites of the ArcticWOLVES project. Long-term studies are essential to assess and detect the effects of a changing climate on the

tundra food web and ultimately on the ecosystem services to human beings.

In closing, we believe that our project easily met, and in most cases exceeded, the objectives initially set out by the International Polar Year program. We feel privileged to have been part of this ambitious international program and we trust that the output from the ArcticWOLVES project met the highest standards and will provide a lasting legacy to Arctic science.



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ArcticWOLVES final synthesis report

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REFERENCES

- Aanes, R., B.-E. Saether, and N. A. Oritsland. 2000. Fluctuations of an introduced population of Svalbard reindeer: the effect of density dependence and climatic variation. *Ecography* 23:437-443.
- Abraham, K. F., and R. L. Jefferies. 1997. High goose populations: causes, impacts and implications. Pages 7-61 in B. D. J. Batt, editor. Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C., USA and Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Abraham, K. F., R. L. Jefferies, and R. T. Alisauskas. 2005. The dynamics of landscape change and snow geese in mid-continent North America. *Global Change Biology* 11:841-855.
- ACIA. 2005. Arctic Climate Impact Assessment - Scientific Report. Cambridge University Press, Cambridge, UK.
- Ale, S. B., D. W. Morris, A. Dupuch, and D. E. Moore. 2011. Habitat selection and the scale of ghostly coexistence among Arctic rodents. *Oikos* 120:1191-1200. [DOI: 10.1111/j.1600-0706.2010.18933.x]
- Alisauskas, R. T., and R. F. Rockwell. 2001. Population dynamics of Ross's geese. Pages 55-67 in T. J. Moser, editor. The Status of Ross's geese. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C., USA and Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Alisauskas, R. T., R. F. Rockwell, K. W. Dufour, E. G. Cooch, G. Zimmerman, K. L. Drake, J. O. Leafloor, T. J. Moser, and E.T. Reed. 2011. Harvest, survival, and abundance of midcontinent lesser snow geese relative to population reduction efforts. *Wildlife Monograph, in press*.
- Anderson, W. B., and G. A. Polis. 1998. Marine subsidies of island communities in the Gulf of California : evidence from stable carbon and nitrogen isotopes. *Oikos* 81:75-80.
- Angerbjörn, A., P. Hersteinsson, and M. Tannerfeldt. 2004. Arctic foxes. Consequences of resource predictability in the arctic fox – two life history strategies. Pages 163-172 in D. W. Macdonald, and C. Sillero-Zubiri, editors. *Biology and conservation of wild canids*. Oxford University Press, Oxford, UK.
- Angerbjörn, A., P. Hersteinsson, and M. Tannerfeldt. 2008. *Alopex lagopus*. In IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4. [www.iucnredlist.org]
- Angerbjörn, A., P. Hersteinsson, K. Liden, and E. Nelson. 1994. Dietary variation in arctic foxes (*Alopex lagopus*) - an analysis of stable carbon isotopes. *Oecologia* 99:226-232.
- Angerbjörn, A., M. Tannerfeldt, A. Bjärvall, M. Ericson, J. From, and E. Norén. 1995. Dynamics of the arctic fox population in Sweden. *Annales Zoologici Fennici* 32: 55-68.
- Arctic Borderlands Ecological Knowledge Society. 2008. About the Co-op. [http://www.taiga.net/coop/about.html]
- Arseneault, D., V. Normand, C. Boismenu, Y. Leblanc, and J. Deshayé. 1997. Estimating lichen biomass and caribou grazing on the wintering grounds of Northern Quebec: an application of fire history and Landsat data. *Journal of Applied Ecology* 34:65-78.
- Atkinson, P. W., A. J. Baker, K. A. Bennett, N. A. Clark, J. A. Clark, K. B. Cole, A. Dekinga, A. Dey, S. Gillings, P. M. Gonzalez, K. Kalasz, C. D. T. Minton, J. Newton, L. J. Niles, T. Piersma, R. A. Robinson, and H. P. Sitters. 2007. Rates of mass gain and energy deposition in red knot on their final spring staging site is both time- and condition-dependent. *Journal of Applied Ecology* 44: 885-895.
- Austin, G. E., and M. M. Rehfish. 2003. The likely impact of sea level rise on waders (Charadrii) wintering on estuaries. *Journal for Nature Conservation* 11(1): 43-58.
- Bailey, E. P. 1992. Red foxes, *Vulpes vulpes*, as biological control agents for introduced arctic foxes, *Alopex lagopus*, on Alaskan islands. *Canadian field-naturalist* 106:200-205.
- Baker, A. J., P. M. Gonzalez, T. Piersma, L. J. Niles, I. D. S. do Nascimento, P. W. Atkinson, N. A. Clark, C. D. T. Minton, M. K. Peck, and G. Aarts. 2004. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings of the Royal*

ArcticWOLVES final synthesis report

- Society of London Series B-Biological Sciences 271(1541): 875-882.
- Bart, J., S. Brown, B. Harrington, and R. Morrison. 2007. Survey trends of North American shorebirds: population declines or shifting distributions? *Journal of Avian Biology* 38 (1): 73-82.
- Bart, J., and P. A. Smith. 2011. Summary and conclusions. Chapter 14 *in* J. Bart, and V. Johnston, editors. *Shorebirds in the North American Arctic: results of ten years of an arctic shorebird monitoring program*. *Studies in Avian Biology, in press*.
- Bartelt, P., and M. Lehning. 2002. A physical SNOWPACK model for the Swiss avalanche warning. Part I: numerical model. *Cold Regions Science and Technology* 35:123-145.
- Bauer, S., M. VanDinther, K. A. Hogda, M. Klaassen, and J. Madsen. 2008. The consequences of climate-driven stop-over sites changes on migration schedules and fitness of Arctic geese. *Journal of Animal Ecology* 77:654-660.
- Bazely, D. R., and R. L. Jefferies. 1996. Trophic interactions in arctic ecosystems and the occurrence of a terrestrial trophic cascade. Pages 183-205 *in* S. J. Woodin and M. Marquiss, editors. *Ecology of Arctic environments*. Special Publication No 13 of the British Ecological Society, Blackwell Science, Oxford, UK.
- Berg, T. B., N. M. Schmidt, T. T. Hoye, P. J. Aastrup, D. K. Hendrichsen, M. C. Forchhammer, and D. R. Klein. 2008. High-Arctic plant-herbivore interactions under climate influence. Pages 275-298 *in* H. Møltøfte, T. R. Christensen, B. Elberling, M. C. Forchhammer, and M. Rasch, editors. *High-Arctic Ecosystem Dynamics in a Changing Climate*. Academic Press, London, UK.
- Berkes, F. 2008. *Sacred ecology: traditional ecological knowledge and resource management*. Taylor & Francis, Philadelphia, Pennsylvania, USA.
- Berkes, F., P. George, J. Turner, A. Hughes, B. Cummins, and A. Haugh. 1992. *Wildlife harvests in the Mushkegowuk region*. Research Program for Technology and Assessment in Subarctic Ontario. TASO Report, Second Series No 6., McMaster University, Hamilton, Ontario, Canada.
- Berteaux, D., M. M. Humphries, C. J. Krebs, M. Lima, A. G. McAdam, N. Pettorelli, D. Réale, T. Saitoh, E. Tkadlec, R. B. Weladji, and N. C. Stenseth. 2006. Constraints to projecting the effects of climate change on mammals. *Climate Research* 32:151-158.
- Bêty, J., G. Gauthier, J.-F. Giroux, and E. Korpimäki. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. *Oikos* 93:388-400.
- Bêty, J., G. Gauthier, E. Korpimäki, and J.-F. Giroux. 2002. Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. *Journal of Animal Ecology* 71:88-98.
- Block, W., J. Baust, F. Franks, I. Johnston, and J. Bale. 1990. Cold tolerance of insects and other arthropods [and discussion]. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 326:613-633.
- Blomqvist, S., N. Holmgren, S. Akesson, A. Hedenstrom, and J. Pettersson. 2002. Indirect effects of lemming cycles on sandpiper dynamics: 50 years of counts from southern Sweden. *Oecologia* 133:146-158.
- Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulseley, and M. Forister. 2003. The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist* 161:1-29.
- Boonstra, R., J. M. Barker, J. Castillo, and Q. E. Fletcher. 2007. The role of the stress axis in life history adaptations in rodents. Pages 139-149 *in* J. O. Wolff, and P. W. Sherman, editors. *Rodent societies: ecological and evolutionary perspective*. University of Chicago Press, Chicago, Illinois, USA.
- Bowden, J. J., and C. M. Buddle. 2010. Spider assemblages across elevational and latitudinal gradients in the Yukon Territory, Canada. *Arctic* 63:261-272.
- Braestrup, F. W. 1941. A study of the arctic fox in Greenland. Immigrations, fluctuations in numbers based mainly on trading statistics. *Meddelelser om Grønland* 131:1-101.
- Braune, B. M., and D. G. Noble. 2009. Environmental contaminants in Canadian shorebirds. *Environmental Monitoring and Assessment* 148:185-204.
- Bromley, M. 1992. Updated Status Report on the Tundra Peregrine Falcon *Falco peregrinus tundrius* in Canada. Committee on the Status of Endangered Wildlife in Canada,

- Ottawa, Ontario, Canada.
- Brommer, J. E., H. Pietiainen, K. Ahola, P. Karrell, T. Karstinen, and H. Kolonen. 2010. The return of the vole cycle in southern Finland refutes the generality of the loss of cycles through 'climatic forcing'. *Global Change Biology* 16:577-586.
- Callaghan, T. V., L. O. Björn, Y. Chernov, T. Chapin, T. R. Christensen, B. Huntley, R. A. Ims, M. Johansson, D. Jolly, S. Jonasson, N. Matveyeva, N. Panikov, W. Oechel, G. Shaver, J. Elster, H. Henttonen, K. Laine, K. Taulavuori, E. Taulavuori, and C. Zockler. 2004b. Biodiversity, distributions and adaptations of arctic species in the context of environmental change. *Ambio* 33:404-417.
- Callaghan, T. V., L. O. Björn, Y. Chernov, T. Chapin, T. R. Christensen, B. Huntley, R. A. Ims, M. Johansson, D. Jolly, S. Jonasson, N. Matveyeva, N. Panikov, W. Oechel, G. Shaver, S. Schaphoff, and S. Sitch. 2004a. Effects of changes in climate on landscape and regional processes, and feedbacks to the climate system. *Ambio* 33:459-468.
- Calvert, A. M., G. Gauthier, E. T. Reed, L. Bélanger, J.-F. Giroux, J.-F. Gobeil, M. Huang, J. Lefebvre, and A. Reed. 2007. Present status of the population and evaluation of the effects of the special conservation measures. Pages 5-64 in E. T. Reed and A. M. Calvert, editors. An evaluation of the special conservation measures for Greater snow geese: report of the Greater Snow Goose Working Group. Arctic Goose Joint Venture Special Publication. Canadian Wildlife Service, Quebec, Quebec, Canada.
- Carmichael, L. E., D. Berteaux, M. Dumond, E. Fuglei, D. Johnson, J. Krizan, J. A. Nagy, A. Veitch, and C. Strobeck. 2007. Historical and ecological determinants of genetic structure in arctic canids. *Molecular Ecology* 16: 3466-3483.
- Carrière, S, D. Abernethy, M. Bradley, R. G. Bromley, S. B. Matthews, J. Obst, and M. Settingington. 2003. Raptor population trends in the Northwest Territories and Nunavut: a peregrine falcon case study. *Bird Trends Canada* 9:57-62.
- Cartar, R. V., and R. I. G. Morrison. 2005. Metabolic correlates of leg length in breeding arctic shorebirds: the cost of getting high. *Journal of Biogeography* 32: 377-382.
- Casey, T. M. 1981. Nest insulation: energy savings to brown lemmings using a winter nest. *Oecologia* 50:199-204.
- Caughley, G. and C. J. Krebs. 1983. Are big mammals simply little mammals writ large. *Oecologia* 59:7-17.
- CAVM Team. 2003. Circumpolar Arctic Vegetation Map. Scale 1 :7,500,000. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, Anchorage, Alaska, USA.
- Chapin, F. S., M. Sturm, M. C. Serreze, J. P. McFadden, J. R. Key, A. H. Lloyd, A. D. McGuire, T. S. Rupp, A. H. Lynch, J. P. Schimel, J. Beringer, W. L. Chapman, H. E. Epstein, E. S. Euskirchen, L. D. Hinzman, G. Jia, C. L. Ping, K. D. Tape, C. D. C. Thompson, D. A. Walker, and J. M. Welker. 2005. Role of land-surface changes in Arctic summer warming. *Science* 310:657-660.
- Chernov, Y. I. 1972. Animal population structure in the subzone of typical tundras of the Western Taimyr. Pages 63-79 in F. E. Wielgolaski and T. Rosswall, editors. Biological productivity of tundra. IBP Tundra Biome Steering Committee, Oslo, Norway and Stockholm, Sweden.
- Chernyavskii, F. B. and A. V. Tkachev. 1982. Population cycles of lemmings in the arctic. Nauka Press, Moscow, Russia. [in Russian]
- Chirkova, A. F. 1967. Arctic fox (biology, practical significance). Pages 208-265 in V. G. Geptner, N. P. Naumov, P. B. Jurgenson, A. A. Sludsky, A. F. Chirkova, and A. G. Bannikov, editors. Mammals of USSR, volume 2, part 1. Vyshaya shkola, Moscow. [in Russian]
- Christensen, V., and D. Pauly. 1992. Ecopath-II - a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61:169-185.
- Comiso, J. C., C. L. Parkinson, R. Gersten, and L. Stock. 2008. Accelerated decline in the Arctic sea ice cover. *Geophysical Research Letters* 35:L01703.
- COSEWIC. 2003. COSEWIC assessment and update status report on the wolverine *Gulo gulo* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada.
- Creswell, J. W. 2009. Research design: qualitative, quantitative, and mixed methods approaches, third edition. Sage Publications,

ArcticWOLVES final synthesis report

- Thousand Oaks, California, USA.
- Dahl, T. 1990. Wetlands losses in the United States, 1780's to 1980's. U.S. Fish and Wildlife Service, Washington, D.C, USA.
- Dalén, L., E. Fuglei, P. Hersteinsson, C. Kapel, J. Roth, G. Samelius, M. Tannerfeldt, and A. Angerbjörn. 2005. Population history and genetic structure of a circumpolar species: the arctic fox. *Biological Journal of the Linnean Society* 84:79-89.
- Danks, H. V. 1992. Arctic insects as indicators of environmental change. *Arctic* 45:159-166.
- Danks, H. V. 2004. Seasonal adaptations in arctic insects. *Integrative and Comparative Biology* 44:85-94.
- Dickey M.-H., G. Gauthier, and M.-C. Cadieux. 2008. Climatic effects on the breeding phenology and reproductive success of an arctic-nesting goose species. *Global Change Biology* 14:1973-1985.
- Didiuk, A. B., and R. S. Ferguson. 2005. Land cover mapping of Queen Maud Gulf Migratory Bird Sanctuary, Nunavut. Occasional Paper Number 111, Canadian Wildlife Service, Edmonton, Alberta, Canada.
- Donaldson, G. M., C. Hyslop, R. I. G. Morrison, H. L. Dickson, and I. Davidson. 2001. Canadian Shorebird Conservation Plan. Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Dorogoi I. V. 1983. Predators as factor of lemmings number dynamics in tundra zone of the North-East of Siberia. Ph.D. thesis, Univeraity of Vladivostok, Vladivostok, Russia. [in Russian]
- Drent, R. H., C. Both, M. Green, J. Madsen, and T. Piersma. 2003. Pay-offs and penalties of competing migratory schedules. *Oikos* 103:274-292.
- Drent, R. H., and J. Prop. 2008. Barnacle goose *Branta leucopsis* survey on Norden-skiöldkysten, west Spitsbergen 1975–2007: breeding in relation to carrying capacity and predator impact. *Circumpolar Studies* 4:59-83.
- Drury, W. H. 1961. The breeding biology of shorebirds on Bylot Island, Northwest Territories, Canada. *Auk* 78:176-219.
- Duchesne, D., G. Gauthier and D. Berteaux. 2011a. Evaluation of a method to determine the breeding activity of lemmings in their winter nests. *Journal of Mammalogy* 92: 511-516. [doi: 10.1644/10-MAMM-A-279.1]
- Duchesne, D. Gauthier, and D. Berteaux. 2011b. Habitat selection, reproduction and predation of wintering lemmings in the Arctic. *Oecologia*, *in press*. [doi:10.1007/s00442-011-2045-6]
- Duerden, F., and R. G. Kuhn. 1998. Scale, context, and application of traditional knowledge of the Canadian north. *Polar Record* 34:31-38.
- Durant, J. M., D. O. Hjermann, G. Ottersen, and N. C. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33:271-283.
- Ebbinge, B. S. and Y. L. Mazurov. 2005. Pristine wilderness of the Taimyr peninsula: 2004 report. Heritage Institute, Moscow.
- Edwards, K. A. 2010. Soil microbial and nutrient dynamics during late winter and early spring in low Arctic sedge meadows. PhD thesis, University of Toronto, Toronto, Ontario, Canada.
- Edwards, K. A., and R. L. Jefferies. 2010. Early-spring nitrogen uptake by *Carex aquatilis* in low-Arctic wet sedge meadows. *Journal of Ecology* 98:737-744.
- Edwards, K. A., J. McCulloch, G. P. Kershaw, and R. L. Jefferies. 2006. Soil microbial and nutrient dynamics in a wet Arctic sedge meadow in late winter and early spring. *Soil Biology and Biochemistry* 38:2843-2851.
- Eichhorn, G., R. H. Drent, J. Stahl, A. Leito, and T. Alerstam. 2009. Skipping the Baltic: the emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese. *Journal of Animal Ecology* 78:63-72.
- Eide, N. E., P. M. Eid, P. Prestrud, and J. E. Swenson. 2005. Dietary responses of arctic foxes *Alopex lagopus* to changing prey availability across an Arctic landscape. *Wildlife Biology* 11:109-121.
- Elmhagen, B., M. Tannerfeldt, and A. Angerbjörn. 2002. Food-niche overlap between arctic and red foxes. *Canadian Journal of Zoology* 80:1274-1285.
- Elton, C. S. 1927. *Animal ecology*. Sidgwick & Jackson, London, UK.
- Erlinge, S., K. Danell, P. Frodin, D. Hasselquist, P. Nilsson, E.-B. Olofsson, and M. Svensson. 1999. Asynchronous population dynamics of Siberian lemmings across the Palearctic tundra. *Oecologia* 119:493-500.

- Fay, F. H., and R. O. Stephenson. 1989. Annual, seasonal, and habitat-related variation in feeding-habits of the arctic fox (*Alopex lagopus*) on St-Lawrence-Island, Bering Sea. *Canadian Journal of Zoology* 67:1986-1994.
- Fedorov, V. B., K. Fredga, and G. H. Jarrell. 1999. Mitochondrial DNA variation and the evolutionary history of chromosome races of collared lemmings (*Dicrostonyx*) in the Eurasian arctic. *Journal of Evolutionary Biology* 12:134-145.
- Forbes, B. C., F. Stammler, T. Kumpula, N. Meschtyb, A. Pajunen, and E. Kaarlejärvi. 2009. High resilience in the Yamal-Nenets social-ecological system, West Siberian Arctic, Russia. *Proceedings of the National Academy of Sciences of the United States of America* 106:22041-22048.
- Forchhammer, M., and D. Boertmann. 1993. The muskoxen *Ovibos moschatus* in north and northeast Greenland: population trends and influence of abiotic parameters on population dynamics. *Ecography* 16:299-308.
- Fortier, D., and M. Allard. 2004. Lare Holocene syngenetic ice-wedge polygons development, Bylort Island, Canadian Arctic Archipelago. *Canadian Journal of Earth Science* 41:997-1012.
- Fortier, D., M. Allard, and Y. Shur. 2007. Observation of rapid drainage system development by thermal erosion of ice wedges on Bylot Island, Canadian Arctic Archipelago. *Permafrost and Periglacial Processes* 18:229-243.
- Fox, A. D., B. S. Ebbinge, C. Mitchell, T. Heinicke, T. Aarvak, K. Colhoun, P. Clausen, S. Dereliev, S. Faragó, K. Koffijberg, H. Kruckenberg, M. J. J. E. Loonen, J. Madsen, J. Mooij, P. Musil, L. Nilsson, S. Pihl, and H. van der Jeugd. 2010. Current estimates of goose population sizes in western Europe, a gap analysis and a assessment of trends. *Ornis Svecica* 20:115-127.
- Fox, A. D., J. Madsen, H. Boyd, E. Kuijken, D. W. Norriss, I. M. Tombre, and D. A. Stroud. 2005. Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. *Global Change Biology* 11:881-893.
- Frafjord, K. 2003. Ecology and use of arctic fox *Alopex lagopus dens* in Norway: tradition overtaken by interspecific competition? *Biological Conservation* 111:445-453.
- Fuglei, E., N. A. Øritsland, and P. Prestrud. 2003. Local variation in arctic fox abundance on Svalbard, Norway. *Polar Biology* 26:93-98.
- Gadallah, F. L., and R. L. Jefferies. 1995. Comparison of the nutrient contents of the principle forage plants utilized by lesser snow geese on the summer breeding grounds. *Journal of Applied Ecology* 32:263-275.
- Gagnon, C.-A., and D. Berteaux. 2006. Integrating traditional and scientific knowledge: management of Canada's National Parks. Pages 209-221 *in* R. Riewe and J. Oakes, editors. *Climate change: linking traditional and scientific knowledge*. Aboriginal Issues Press, University of Manitoba, Winnipeg, Manitoba, Canada.
- Gagnon, C.-A., and D. Berteaux. 2009. Integrating traditional ecological knowledge and ecological science: a question of scale. *Ecology and Society* 14:19. [<http://www.ecologyandsociety.org/>]
- Galbraith, H., R. Jones, R. Park, J. Clough, S. Herrod-Julius, B. Harrington, and G. Page. 2002. Global Climate change and sea level rise: potential losses of intertidal habitat for shorebirds. *Waterbirds* 25:173-183.
- Ganter, B., and H. Boyd. 2000. A tropical volcano, high predation pressure, and the breeding biology of Arctic waterbirds: a circumpolar review of breeding failure in the summer of 1992. *Arctic* 53:289-305.
- Garthe, S., C. J. Camphusyen, and R. W. Furness. 1996. Amounts discarded by commercial fisheries and their significance as food for seabirds in the North Sea. *Marine Ecology-Progress Series* 136:1-11.
- Gauthier, G., D. Berteaux, C. J. Krebs, and D. Reid. 2009. Arctic lemmings are not simply food limited – a comment. *Evolutionary Ecology Research* 11:483-484.
- Gauthier, G., D. Berteaux, J. Bêty, A. Tarroux, J.-F. Therrien, L. McKinnon, P. Legagneux, and M.-C. Cadieux. 2011. The arctic tundra food web in a changing climate and the role of exchanges between ecosystems. *Ecoscience* 18: *in press*.
- Gauthier, G., J. Bêty, J.-F. Giroux, and L. Rochefort. 2004. Trophic interactions in a high arctic snow goose colony. *Integrative and Comparative Biology* 44:119-129.

ArcticWOLVES final synthesis report

- Gauthier, G., J.-F. Giroux, A. Reed, A. Béchet, and L. Bélanger. 2005. Interactions between land use, habitat use and population increase in greater snow geese: what are the consequences for natural wetlands? *Global Change Biology* 11:856-868.
- Gauthier, G., J.-F. Giroux, and L. Rochefort. 2006. The impact of goose grazing on arctic and temperate wetlands. *Acta Zoologica Sinica* 52(supplement):108-111.
- Gauthier, G., L. Rochefort, and A. Reed. 1996. The exploitation of wetland ecosystems by herbivores on Bylot Island. *Geoscience Canada* 23:253-259.
- Gauthier, G., R. J. Hughes, A. Reed, J. Beaulieu, and L. Rochefort. 1995. Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). *Journal of Ecology* 83:653-664.
- Geffen, E., S. Waidyratne, L. Dalen, A. Angerbjörn, C. Vila, P. Hersteinsson, E. Fuglei, P. A. White, M. Goltsman, C. M. O. Kapell, and R. K. Wayne. 2007. Sea ice occurrence predicts genetic isolation in the arctic fox. *Molecular Ecology* 16:4241-4255.
- Geptner, V. G., and N. P. Naumov. 1967. Arctic fox (systematic, geographical distribution). Pages 194-208 *in* V. G. Geptner, N. P. Naumov, P. B. Jurgenson, A. A. Sludsky, A. F. Chirkova, and A. G. Bannikov, editors. *Mammals of USSR, volume 2, part 1. Vyshaya shkola, Moscow.* [in Russian]
- Gilchrist, H. G., and G. J. Robertson. 1999. Population trends of gulls and Arctic terns nesting in the Belcher Islands, Nunavut. *Arctic* 52: 325-331.
- Gilg, O. 2002. The summer decline of the colored lemming in high arctic Greenland. *Oikos* 99:499-510.
- Gilg, O., I. Hanski, and B. Sittler. 2003. Cyclic dynamics in a simple vertebrate predator-prey community. *Science* 302:866-868.
- Gilg, O., B. Sittler, and I. Hanski. 2009. Climate change and cyclic predator-prey population dynamics in the high Arctic. *Global Change Biology* 15:2634-2652.
- Gilg, O., B. Sittler, B. Sabard, A. Hurstel, R. Sané, P. Delattre, and I. Hanski. 2006. Functional and numerical responses of four lemming predators in high arctic Greenland. *Oikos* 113:196-213.
- Gilg, O., and N. G. Yoccoz. 2010. Explaining bird migration. *Science* 327:276.
- GLCF. 2005. Coastal Marsh Project. University of Maryland, College Park, Maryland, USA. [<http://glcf.umd.edu/data/coastal/research.shtml>]
- Godin, E., and D. Fortier. 2010. Geomorphology of thermo-erosion gullies – case study from Bylot Island, Nunavut, Canada. Pages 1540-1547 *in* Proceedings of the 6th Canadian Permafrost Conference and 63rd Canadian Geotechnical Conference, Calgary, Alberta.
- Golovatin M. G., S. P. Paskhalny, and V. A. Sokolov. 2004. Data on birds of Yuribey river (Yamal). Pages 80-95 *in* V. K. Ryabitsev, editor. *Materials on distribution of birds in the Ural Mountains, Ural region and Western Siberia.* Ekaterinburg, Russia. [in Russian]
- Gompper, M. E., and A. T. Vanak. 2008. Subsidized predators, landscapes of fear and disarticulated carnivore communities. *Animal Conservation* 11:13-14.
- Gouvernement du Canada. 1993. Accord entre les Inuit de la région du Nunavut et Sa Majesté la Reine en chef du Canada. Tungavik Federation of Nunavut et Ministère des Affaires indiennes et du Nord canadien, Ottawa, Ontario, Canada.
- Gratto-Trevor, C. L., V. H. Johnston, and S. T. Pepper. 1998. Changes in shorebird and eider abundance in the rasmussen lowland, NWT. *Wilson Bulletin* 110:316-325.
- Gratto-Trevor, C. L., V. H. Johnston, and S. T. Pepper. 2001. Evidence for declines in Arctic populations of shorebirds. *Bird Trends* 8:27-29.
- Gruyer, N., G. Gauthier, and D. Berteaux. 2008. Cyclic dynamics of sympatric lemming populations on Bylot Island, Nunavut, Canada. *Canadian Journal of Zoology* 86:910-917.
- Gruyer, N., G. Gauthier, and D. Berteaux. 2010. Demography of two lemming species on Bylot Island, Nunavut, Canada. *Polar Biology* 33:725-736.
- Hammill, M. O., and T. G. Smith. 1991. The role of predation in the ecology of the ringed seal in Barrow Strait, Northwest Territories, Canada. *Marine Mammal Science* 7:123-135.
- Helgen, K. M., F. R. Cole, L. E. Helgen and D. E. Wilson. 2009. Generic revision in the

- Holarctic ground squirrel genus *Spermophilus*. *Journal of Mammalogy* 90:270-305.
- Henden, J. A., B. J. Bardsen, N. G. Yoccoz, and R. A. Ims. 2008. Impacts of differential prey dynamics on the potential recovery of endangered arctic fox populations. *Journal of Applied Ecology* 45:1086-1093.
- Herfindal, I., J. D. C. Linnell, B. Elmhagen, N. E. Eide, R. Andersen, K. Frafjord, H. Henttonen, A. Kaikusalo, M. Mela, M. L. D. Tannerfeldt, O. A. L. Strand, and A. Angerbjörn. 2010. Population persistence in a landscape context: the case of endangered arctic fox populations in Fennoscandia. *Ecography* 33:932-941.
- Hersteinsson, P., A. Angerbjörn, K. Frafjord, and A. Kaikusalo. 1989. The arctic fox in nordic countries, a review. *Biological Conservation* 49:67-81.
- Hersteinsson, P., and D. W. Macdonald. 1992. Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos* 64:505-515.
- Hitchcock, C., and C. L. Gratto-Trevor. 1997. Diagnosing a shorebird local population decline with a stage-structured population model. *Ecology* 78:522-534.
- Hodkinson, I. D., and S. J. Coulson. 2004. Are high Arctic terrestrial food chains really that simple? The Bear Island food web revisited. *Oikos* 106:427-431.
- Hodkinson, I. D., S. J. Coulson, N. R. Webb, W. Block, A. T. Strathdee, J. S. Bale, and M. R. Worland. 1996. Temperature and the biomass of flying midges (Diptera: Chironomidae) in the high Arctic. *Oikos* 75:241-248.
- Hodkinson, I., N. Webb, J. Bale, W. Block, S. Coulson, and A. Strathdee. 1998. Global change and arctic ecosystems: conclusions and predictions from experiments with terrestrial invertebrates on spitsbergen. *Arctic and Alpine Research* 30:306-313.
- Hodkinson, I., and P. Wookey. 1999. Functional ecology of soil organisms in tundra ecosystems: towards the future. *Applied Soil Ecology* 11:111-126.
- Holmes, R. T. 1966. Feeding ecology of the red-backed sandpiper (*Calidris alpina*) in arctic alaska. *Ecology* 47:32-45.
- Holt, R. D. 1977. Predation, apparent competition, and structure of prey communities. *Theoretical Population Biology* 12:197-229.
- Hopcraft, J. G. C., H. Olff, and A. R. E. Sinclair. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology and Evolution* 25:119-128.
- Hörnfeldt, B., T. Hipkiss, and U. Eklund. 2005. Fading out of vole and predator cycles? *Proceedings of the Royal Society B-Biological Sciences* 272:2045-2049.
- Howe, M., P. Geissler, and B. Harrington. 1989. Population trends of North American shorebirds based on the International Shorebird Survey. *Biological Conservation* 49:185-199.
- Hoye, T. T., E. Post, H. Mølltofte, N. M. Schmidt, and M. C. Forchhammer. 2007. Rapid advancement of spring in the High Arctic. *Current Biology* 17:R449-R451.
- Hudson, J. M. G., and G. H. R. Henry. 2009. Increased in plant biomass in a High Arctic heath community from 1981 to 2008. *Ecology* 90:2657-2663.
- Ims, R. A., and E. Fuglei. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience* 55:311-322.
- Ims, R. A., J.-A. Henden, and S. T. Killengreen. 2008. Collapsing population cycles. *Trends in Ecology and Evolution* 23:79-86.
- Ims, R. A., and H. Steen. 1990. Regional synchrony of cyclic microtine populations: a theoretical evaluation of the role of nomadic predators. *Oikos* 57:381-387.
- Ims, R. A., N. G. Yoccoz, K. A. Brathen, P. Fauchald, T. Tveraa, and V. Hausner. 2007. Can reindeer overabundance cause a trophic cascade? *Ecosystems* 10:607-622.
- Ims, R. A., N. G. Yoccoz, and S. T. Killengreen. 2011. Determinants of lemming outbreaks. *Proceedings of the National Academy of Sciences* 108:1970-1974. [<http://www.pnas.org/cgi/doi/10.1073/pnas.1012714108>]
- IUCN. 2009. Species and climate change: more than just the polar bear. The IUCN Red List of Threatened Species, Gland, Switzerland. [<http://www.iucn.org/what/tpas/biodiversity/resources/publications/>]
- IPCC. 2007. Climate change 2007: The physical science basis. Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK.

ArcticWOLVES final synthesis report

- Jacobsen, K. O. 2005. Snøugle (*Bubo scandiacus*) I Norge. Hekkeforekomster I perioden 1968-2005. NINA report No 84.
- Jacobsen, K. O., R. Solheim, I. J. Oien, and T. Aarvak. 2009. Snøugle vandringer fortsetter. *Var fuglefauna* 32:172-176.
- Jarrell, G. H., and K. Fredga. 1993. How many kinds of lemmings? A taxonomic overview. Pages 45-57 in N. C. Stenseth and R. A. Ims, editors. *The biology of lemmings*. Academic Press, London, England.
- Jefferies, R. L. 2000. Allochthonous inputs: integrating population changes and food-web dynamics. *Trends in Ecology and Evolution* 15:19-22.
- Jefferies, R. L., A. P. Jano, and K. F. Abraham. 2006. A biotic agent promotes large-scale catastrophic change in coastal marshes of Hudson Bay. *Journal of Ecology* 94:234-242.
- Jefferies, R. L., R. F. Rockwell, and K. F. Abraham. 2003. The embarrassment of riches: agricultural food subsidies, high goose numbers and loss of Arctic wetlands – a continuing saga. *Environmental Reviews* 11:193-232.
- Jefferies, R. L., R. F. Rockwell, and K. F. Abraham. 2004. Agricultural food subsidies, migratory connectivity and large-scale disturbance in arctic coastal systems: A case study. *Integrative and Comparative Biology* 44:130-139.
- Jefferies, R. L., A. N. Walker, K. A. Edwards, and J. Dainty. 2010. Is the rise and decline of soil microbial biomass in late winter coupled to seasonal changes in the physical state of cold northern soils? *Soil Biology and Biochemistry* 42:129-135.
- Jensen, R. A., J. Madsen, M. O'Connell, M. S. Wisz, H. Tømmervik, and F. Mehlum. 2008. Prediction of the distribution of Arctic-nesting pink-footed geese under a warmer climate scenario. *Global Change Biology* 14:1-10.
- Julien, J.-R. 2011. Écologie alimentaire et dynamique de population du labbe à longue queue (*Stercorarius longicaudus*) à Alert, Île Ellesmere, Nunavut. MSc thesis, Université Laval, Quebec City, Quebec, Canada.
- Kamler, J. F., and W. B. Ballard. 2002. A review of native and nonnative red foxes in North America. *Wildlife Society Bulletin* 30: 370-379.
- Kausrud, K. L., A. Myrsetrud, H. Steen, J. O. Vik, E. Ostbye, B. Cazelles, E. Framstad, A. M. Eikeset, I. Myrsetrud, T. Solhey, and N. C. Stenseth. 2008. Linking climate change to lemming cycles. *Nature* 456:93-98.
- Kelley, J. R., D. C. Duncan, and D. R. Yparra-guirre. 2001. Distribution and abundance. Pages 11-17 in T. Moser, editor. *The status of Ross's geese*. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington D.C., USA and Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Kennedy, C., C. Smith, and D. Cooley. 2001. Observations of change in the cover of polar grass, *Arctagrostis latifolia*, and arctic lupine, *Lupinus arcticus*, in upland tundra on Herschel Island, Yukon Territory. *Canadian Field-Naturalist* 115:323-328.
- Kerbes, R. H., P. M. Kotanen, and R. L. Jefferies. 1990. Destruction of wetland habitats by lesser snow geese: a keystone species on the west coast of Hudson Bay. *Journal of Applied Ecology* 27:242-258.
- Kerbes, R. H., K. M. Meeres, R. T. Alisauskas, F. D. Caswell, K. F. Abraham, and R. K. Ross. 2006. Inventory of nesting mid-continent lesser snow and Ross's geese in eastern and central Arctic Canada, 1997-98. Canadian Wildlife Service Technical Report series, Winnipeg, Manitoba, Canada.
- Kevan, P. 1972. Insect pollination of high arctic flowers. *The Journal of Ecology* 60:831-847.
- Kevan, P. 1973. Flowers, insects, and pollination ecology in the Canadian high Arctic. *Polar Record* 16:667-674.
- Killengreen S. T., R. A. Ims, N. G. Yoccoz, K. A. Brathen, J. A. Henden, and T. Schott. 2007. Structural characteristics of a low Arctic tundra ecosystem and the retreat of the arctic fox. *Biological Conservation* 135:459-472.
- Killengreen, S. T., N. Lecomte, D. Ehrlich, T. Schott, N. G. Yoccoz, and R. A. Ims. 2011. The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the Arctic tundra. *Journal of Animal Ecology*, *in press*. [doi: 10.1111/j.1365-2656.2011.01840.x]
- Kirk, D. A., and C. Hyslop. 1998. Population status and recent trends in Canadian raptors: A review. *Biological Conservation* 83:91-118.

- Klaassen, M. 2001. Ornithology - Arctic waders are not capital breeders. *Nature* 413:794-794.
- Klima, J., and J. Jehl Jr. 1998. Stilt sandpiper (*Calidris himantopus*). In A. Poole and F. Gill, editors. *The Birds of North America*, no. 341. Philadelphia, Pennsylvania, USA.
- Kofinas, G., with the Communities of Aklavik, Arctic Village, Old Crow and, Fort McPherson. 2002. Community contributions to ecological monitoring: knowledge co-production in the U.S.-Canada Arctic Borderlands. Pages 55-91 in I. Krupnik and D. Jolly, editors. *The earth is faster now: indigenous observations of arctic environmental change*. Arctic Research Consortium of the United States. Fairbanks, Alaska, USA.
- Kokorev, Y. I., and V. A. Kukson. 2002. Population dynamics of lemmings, *Lemmus sibiricus* and *Dicrostonyx torquatus*, and arctic fox, *Alopex lagopus*, on the Taimyr Peninsula, Siberia, 1960-2001. *Ornis Suecica* 12:139-143.
- Kotanen, P. M., and R.L. Jefferies. 1997. Long-term destruction of wetland vegetation by lesser snow geese. *Écoscience* 4:179-182.
- Krebs, C. J. 2011. Of lemmings and snow shoe hares: the ecology of northern Canada. *Proceedings of the Royal Society London B* 278:481-489.
- Krebs, C. J., R. Boonstra, and A. J. Kenney. 1995. Population dynamics of the collared lemming and the tundra vole at Pearce Point, Northwest Territories, Canada. *Oecologia* 103:481-489.
- Krebs, C. J., K. Danell, A. Angerbjorn, J. Agrell, D. Berteaux, K. A. Brathen, O. Danell, S. Erlinge, V. Fedorov, K. Fredga, J. Hjalten, G. Hogstedt, I. S. Jonsdottir, A. J. Kenney, N. Kjellen, T. Nordin, H. Roininen, M. Svensson, M. Tannerfeldt, and C. Wiklund. 2003. Terrestrial trophic dynamics in the Canadian Arctic. *Canadian Journal of Zoology* 81:827-843.
- Krebs, C. J., A. J. Kenney, S. Gilbert, K. Danell, A. Angerbjorn, S. Erlinge, R. G. Bromley, C. Shank and S. Carrière. 2002. Synchrony in lemming and vole populations in the Canadian arctic. *Canadian Journal of Zoology* 80:1323-1333.
- Krebs, C. J., D. G. Reid, A. J. Kenney and B. S. Gilbert. 2011. Fluctuations in lemming populations in north Yukon, Canada, 2007-2010. *Canadian Journal of Zoology* 89:297-306.
- Krechmar, A. V., A. I. Artyukhov, I. V. Dorogoi, and E. V. Siroechkovskiy. 1979. Additional data on avianfauna of Wrangel Island. Pages 126-134 in A. V. Krechmar and F. B. Chernyavski, editors. *Birds of the North-East of Asia, Vladivostok*. [in Russian]
- Kristensen, D. K. 2009. Impact of muskoxen on the vegetation in the Zackenberg Valley, Northeast Greenland. MSc thesis, Institute of Biology, University of Southern Denmark, Odense, Denmark.
- Kuijper, D. P. J., R. Ubels, and M. J. J. E. Loonen. 2009. Density-dependent switches in diet: a likely mechanism for negative feedbacks on goose population increase? *Polar Biology* 32: 1789-1803.
- Lank, D. B., R. W. Butler, J. Ireland, and R. C. Ydenberg. 2003. Effects of predation danger on migration strategies of sandpipers. *Oikos* 103:303-319.
- Latour, P. B., C. S. Machtans, and G. W. Beyersbergen. 2005. Shorebird and passerine abundance and habitat use at a High Arctic breeding site: Creswell Bay, Nunavut. *Arctic* 58:55-65.
- Layberry, R. A., P. W. Hall, and J. D. Lafontaine. 1998. *The butterflies of Canada*. University of Toronto Press, Toronto, Ontario, Canada.
- Lecomte, N., G. Gauthier, and J.-F. Giroux. 2009. A link between water availability and nesting success mediated by predator-prey interactions in the Arctic. *Ecology* 90:465-475.
- Legagneux, P., G. Gauthier, D. Berteaux, J. Bêty, M.-C. Cadieux, F. Bilodeau, E. Bolduc, L. McKinnon, A. Tarroux, J.-F. Therrien, L. Morissette, and C.J. Krebs. Disentangling trophic relationships in a high arctic tundra ecosystem through food web modeling. *Ecology*, *submitted*.
- Lehning, M., P. Bartelt, B. Brown, and C. Fierz. 2002b. A physical SNOWPACK model for the Swiss avalanche warning. Part III: meteorological forcing, thin layer formation and evaluation. *Cold Regions Science and Technology* 35:169-184.
- Lehning, M., P. Bartelt, B. Brown, C. Fierz, and P. Satyawali. 2002a. A physical SNOWPACK model for the Swiss avalanche warning. Part II: snow microstructure. *Cold Regions*

ArcticWOLVES final synthesis report

- Science and Technology 35:147-167.
- Lepage D., G. Gauthier, and A. Reed. 1998. Seasonal variation in growth of greater snow goose goslings: the role of food supply. *Oecologia* 114:226-235.
- Leroux, S. J., and M. Loreau. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecology Letters* 11:1147-1156.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943-1967.
- Levin, S. A. 2000. Multiple scales and the maintenance of biodiversity. *Ecosystems* 3:498-506.
- Loreau, M. 2010. From populations to ecosystems: theoretical foundations for a new ecological synthesis. Princeton University Press, Princeton, New Jersey, USA.
- Loreau, M., and R. D. Holt. 2004. Spatial flows and the regulation of ecosystems. *American Naturalist* 163:606-615.
- Loreau, M., N. Mouquet, and R. D. Holt. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters* 6:673-679.
- Macdonald, D. W., and J. C. Reynolds. 2004. Chapter 5.3 : Red fox *Vulpes vulpes* Linnaeus, 1758. Page 129-136 in C. Sillero-Zubiri, M. Hoffmann, and D. W. Macdonald, editors. *Canids: foxes, wolves, jackals and dogs. Status Survey and Conservation Action Plan*. IUCN/SSC Canid Specialist Group. Gland, Switzerland and Cambridge, UK. [<http://www.canids.org/cap/index.htm>]
- Macpherson, A. H. 1964. A northward range extension of the red fox in the eastern Canadian Arctic. *Journal of Mammalogy* 45:138-140.
- Madsen, J., G. Cracknell, and A. D. Fox. 1999. Goose populations of the Western palearctic. A review of status and distribution. Wetlands International Publication No. 48, Wetlands International, Wageningen, The Netherlands and National Environmental Research Institute, Rönne, Denmark.
- Madsen, J., M. Tamstorf, M. Klaassen, N. Eide, C. Glahder, F. Riget, H. Nyegaard, and F. Cottaar. 2007. Effects of snow cover on the timing and success of reproduction in high-Arctic pink-footed geese *Anser brachyrhynchus*. *Polar Biology* 30:1363-1372.
- Manseau, M., J. Huot, and M. Crête, 1996. Effects of summer grazing by caribou on composition and productivity of vegetation: Community and landscape level. *Journal of Ecology* 84:503-513.
- Marsh, D. B. 1938. The influx of the red fox and its colour phases into the Barren Lands. *Canadian Field Naturalist* 52:60-61.
- Marthinsen, G., L. Wennerberg, R. Solheim, and J. T. Lifjeld. 2009. No phylogeographic structure in the circumpolar snowy owl (*Bubo scandiacus*). *Conservation Genetics* 10:923-933.
- McKinnon, L., and J. Bêty. 2009. Effect of camera monitoring on survival rates of High-Arctic shorebird nests. *Journal of Field Ornithology* 80:280-288.
- McKinnon, L., P. A. Smith, E. Nol, J.-L. Martin, K. F. Abraham, H. G. Gilchrist, R. I. G. Morrison, and J. Bêty. 2010. Lower predation risk for migratory birds at high latitudes. *Science* 327:326-327.
- McLoughlin, P. D., M. K. Taylor, H. D. Cluff, R. J. Gau, R. Mulders, R. L. Case, and F. Messier. 2003. Population viability of barren-ground grizzly bears in Nunavut and the Northwest Territories. *Arctic* 56:185-190.
- Mechnikova, S. A. 2009. Birds of prey of Southern Yamal: peculiarities of their breeding and density. PhD thesis, Moscow University, Moscow, Russia. [in Russian]
- Meltofte, H., T. Piersma, H. Boyd, B. McCaffery, B. Ganter, V. V. Golovnyuk, K. Graham, C. L. Gratto-Trevor, R. I. G. Morrison, E. Nol, H. Rösner, D. Schamel, H. Schekkerman, M. Y. Soloviev, P. S. Tomkovich, D. M. Tracy, I. Tulp, and L. Wennerber. 2007. Effects of climate variation on the breeding ecology of Arctic shorebirds. *Bioscience* 59:1-48.
- Menyushina, I. E. 1997. Snowy owl (*Nyctea scandiaca*) reproduction in relation to lemming population cycles on Wrangel Island. Pages 572-582 in J. R. Duncan, D. H. Johnson, and T. H. Nicholls, editors. *Biology and Conservation of Owls in the northern hemisphere*. Second International Owl Symposium, USDA Forest Service General Technical Report NC-190.
- Menyushina, I. E. 2007a. Wrangel Island and its predators. Unpublished report of the IPY Arctic Predators project. [<http://www.arctic-predators.uit.no/NewsSUMMER07.html>]
- Menyushina, I. E. 2007b. Changes of reproductive parameters of the snowy owl popula-

- tion (*Nyctea scandiaca*, L.) on Wrangel Island during two lemming cycles. Pages 32-58 in A. R. Gruzdev, editor. Nature of Wrangel Island: contemporary research. St-Petersburg, Russia. [in Russian]
- Moen, J., and O. Danell. 2003. Reindeer in the Swedish mountains: An assessment of grazing impacts. *Ambio* 32:397-402.
- Moen, J., P. A. Lundberg, and L. Oksanen. 1993. Lemming grazing on snowbed vegetation during a population peak, Northern Norway. *Arctic and Alpine Research* 25:130-135.
- Morozov, V. V. 1998. Pale harrier *Circus macrourus* on the south of Yamal. *Russian Journal of Ornithology*, express issue 47: 3-5.
- Morris, D. W. 1988. Habitat-dependent population regulation and community structure. *Evolutionary Ecology* 2:253-269.
- Morris, D. W. 2003. Shadows of predation: habitat-selecting consumers eclipse competition between co-existing prey. *Evolutionary Ecology* 17:393-422.
- Morris, D. W., D. L. Davidson and C. J. Krebs. 2000. Measuring the ghost of competition: insights from density-dependent habitat selection on the co-existence and dynamics of lemmings. *Evolutionary Ecology Research* 2:41-67.
- Morris, D. W., and J. T. MacEachern. 2010. Sexual-conflict over habitat selection: the game and a test with small mammals. *Evolutionary Ecology Research* 12:507-522.
- Morris, D. W., D. E. Moore, S. B. Ale, and A. Dupuch. 2011. Forecasting ecological and evolutionary strategies to global change: an example from habitat selection by lemmings. *Global Change Biology* 17:1266-1276.
- Morrison, R. I. G. 1975. Migration and morphometrics of European knot and turnstone on Ellesmere Island, Canada. *Bird-Banding* 46:290-301.
- Morrison, R. I. G. 2006. Body transformations, condition, and survival in Red Knots *Calidris canutus* travelling to breed at Alert, Ellesmere Island, Canada. *Ardea* 94:607-618.
- Morrison, R. I. G., N. C. Davidson, and J. R. Wilson. 2007. Survival of the fattest: body stores on migration and survival in red knots *Calidris canutus islandica*. *Journal of Avian Biology* 38:479-487.
- Morrison, R. I. G., C. Downes, and B. Collins. 1994. Population trends of shorebirds on fall migration in eastern Canada 1974-1991. *Wilson Bulletin* 106:431-447.
- Morrison, R. I. G., R. E. J. Gill, B. A. Harrington, S. K. Skagen, G. W. Page, C. L. Gratto-Trevor, and S. M. Haig. 2001. Estimates of shorebird populations in North America. Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Morrison, R. I. G., and K. A. Hobson. 2004. Use of body stores in shorebirds after arrival on High-Arctic breeding grounds. *Auk* 121:333-344.
- Morrison, R. I. G., B. J. Mccaffery, R. E. Gill, and S. K. Skagen. 2006. Population estimates of North American shorebirds, 2006. *Wader Study Group Bulletin* 111:67.
- Morrison, R. I. G., R. K. Ross, and L. J. Niles. 2004. Declines in wintering populations of red knots in southern South America. *Condor* 106:60-70.
- Mossop, D. 1988. Current Status of Peregrine Falcons in Yukon, Canada. Pages 65-68 in T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White, editors. Peregrine falcon populations: their management and recovery. The Peregrine Fund, Inc. Boise, Idaho, USA.
- Nasimovič, A. A., and J. A. Isakov. 1985. Arctic fox, red fox and raccoon dog: distribution of populations, ecology and preservation. Nauka Press, Moscow, Russia. [in Russian]
- Norén, K., L. Carmichael, L. Dalén, P. Hersteinsson, G. Samelius, E. Fuglei, C. M. O. Kapel, I. Menyushina, C. Strobeck, A. Angerbjörn. 2011a. Arctic fox (*Vulpes lagopus*) population structure: circumpolar patterns and processes. *Oikos* 120:873-885. [doi: 10.1111/j.1600-0706.2010.18766.x]
- Norén, K., L. Carmichael, E. Fuglei, N. Eide, P. Hersteinsson, and A. Angerbjörn. 2011b. Pulses of movement across the sea ice: population connectivity and temporal genetic structure in the arctic fox. *Oecologia* 166:973-984. [doi:10.1007/s00442-011-1939-7]
- Norén, K., K. Kvaløy, V. Nyström, A. Landa, L. Dalén, N. E. Eide, E. Østbye, H. Henttonen, and A. Angerbjörn. 2009. Farmed arctic foxes on the Fennoscandian mountain tundra: implications for conservation. *Animal Conservation* 12:434-444.

ArcticWOLVES final synthesis report

- Norment, C. J., A. Hall, and P. Hendricks. 1999. Important bird and mammal records in the Thelon River valley, Northwest Territories: Range expansions and possible causes. *Canadian Field-Naturalist* 113:375-385.
- North American Waterfowl Management Plan Committee. 2004. North American Waterfowl Management Plan 2004. Implementation framework: strengthening the biological foundation. Canadian Wildlife Service, U.S. Fish and Wildlife Service, Secretaria de Medio Ambiente y Recursos Naturales.
- Nowak, R.M. 1991. Walker's mammals of the world. The Johns Hopkins University Press, Baltimore, Maryland, USA.
- Nunavut Field Unit of Parks Canada. 2004. Business case, priority ecological integrity themes fund: using Inuit knowledge in management, research and monitoring of Nunavut national parks. Parks Canada Agency, Iqaluit, Nunavut, Canada.
- Nyström, V., A. Angerbjörn, and L. Dalén. 2006. Genetic consequences of a demographic bottleneck in the Scandinavian arctic fox. *Oikos* 114:84-94.
- Ohlendorf, H. M., D. J. Hoffman, M. K. Saiki, and T. W. Aldrich. 1986. Embryonic mortality and abnormalities of aquatic birds: apparent impacts of selenium from irrigation drainwater. *Science of the Total Environment* 52:49-63.
- Oksanen, L., and T. Oksanen. 2000. The logic and realism of the hypothesis of exploitation ecosystems. *American Naturalist* 155:703-723.
- Oksanen, T., L. Oksanen, J. Dahlgren, and J. Olofsson. 2008. Arctic lemmings, *Lemmus* spp. and *Dicrostonyx* spp.: integrating ecological and evolutionary perspectives. *Evolutionary Ecology Research* 10:415-434.
- O'lear, H., and T. Seastedt. 1994. Landscape patterns of litter decomposition in alpine tundra. *Oecologia* 99:95-101.
- Osmolovskaya, V. I. 1948. Ecology of birds of prey of the Yamal Peninsula. Materials of Institute of Geography, Academy of Science of the USSR, 41:5-77. [in Russian]
- Ottema, O., and A. Spaans. 2008. Challenges and advances in shorebird conservation in the Guianas, with a focus on Suriname. *Ornitología Neotropical* 19:339-346.
- Ovsyanikov, N. G. 1993. Behaviour and social organization of the Arctic fox. CNIL Publishers, Moscow, Russia. [in Russian]
- Ovsyanikov, N. G., and I. E. Menyushina. 1987. Observations on red fox in the arctic fox settlement on Wrangel Island. *Bulletin MOIP, Section Biology* 92:49-55. [in Russian]
- Pamperin, N. J., E. H. Follmann, and B. Petersen. 2006. Interspecific killing of an arctic fox by a red fox at Prudhoe Bay, Alaska. *Arctic* 59:361-364.
- Panipakoocho, E. H. 2005. Inuit knowledge about geese, foxes and changes in the environment (Mini-DV Recording No. IKP-SNP-CG-012). Inuit Knowledge Project of Parks Canada, Mittimatalik, Nunavut, Canada.
- Pattie, D. 1990. A 16-year record of summer birds on Truelove Lowland, Devon Island, Northwest Territories, Canada. *Arctic* 43:275-283.
- Pearce-Higgins, J. W., and D. W. Yalden. 2004. Habitat selection, diet, arthropod availability and growth of a moorland wader: the ecology of golden plover *Pluvialis apricaria* chicks. *Ibis* 146:335-346.
- Pearce-Higgins, J. W., D. W. Yalden, T. W. Dougall, and C. M. Beale. 2009. Does climate change explain the decline of a trans-Saharan Afro-Palaeartic migrant? *Oecologia* 159:649-659.
- Pearce-Higgins, J. W., D. W. Yalden, and M. J. Whittingham. 2005. Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae). *Oecologia* 143:470-476.
- Pedersen, A. 1942. Säugetiere und Vögel. Dansk Nordostgrønlands Expedition. 1938-39. *Meddelelser om Grønland* 128:1-119.
- Piersma, T., and A. Lindstrom. 2004. Migrating shorebirds as integrative sentinels of global environmental change. *Ibis* 146 (S1):61-69.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289-316.
- Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist* 147:396-423.
- Pons, J. M., and P. Migot. 1995. Life-history

- strategy of the herring gull: changes in survival and fecundity in a population subjected to various feeding conditions. *Journal of Animal Ecology* 64:592-599.
- Polis, G. A., M. E. Power, and G. R. Huxel. 2004. *Food webs at the landscape level*. The University of Chicago Press, Chicago, Illinois, USA.
- Popov, I. Y. 2009. Some characteristics of lemmings inhabitation in western Taimyr: problems of animals study and protection in the North. Pages 194-196 in A. Taskaev, editor. *Proceedings of All-Russian Scientific Conference*, Komi Science Centre, Institute of Biology and Ministry of Komi Republic on Natural Resources and Environmental Protection, Syktyvkar, Russia. [in Russian]
- Portenko, L. A. 1973. *Birds of Chukotka Peninsula and Wrangel Island*. Moscow & Leningrad Science, volume 2. [in Russian]
- Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B - Biological Sciences* 363:2369-2375.
- Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, T. T. Høye, R. A. Ims, E. Jeppesen, D. R. Klein, J. Madsen, A. D. McGuire, S. Rysgaard, D. E. Schindler, I. Stirling, M. P. Tamstorf, N. J. C. Tyler, R. van der Wal, J. Welker, P. A. Wookey, N. M. Schmidt, and P. Aastrup. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325:1355-1358.
- Pozdnyakov, V. I. 2004. Cyclicity of lemming populations in the Lena River delta, Siberia: synthesis of available information. *Arctic Birds* 6:35-38.
- Rakhimberdiev, E., Y. Verkuil, A. Saveliev, R. Väisänen, J. Karagicheva, M. Soloviev, P. Tomkovich, and T. Piersma. 2010. A global population redistribution in a migrant shorebird detected with continent wide qualitative breeding survey data. *Diversity and Distributions* 17:141-151.
- Reed, A., J.-F. Giroux, and G. Gauthier. 1998. Population size, productivity, harvest and distribution. Pages 5-31 in B. D. J. Batt, editor. *The greater snow goose: report of the Arctic Goose Habitat Working Group*, Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C., USA and Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Reed, A., R. J. Hughes, and H. Boyd. 2002. Patterns of distribution and abundance of greater snow geese on Bylot Island, Nunavut, Canada 1983-1998. *Wildfowl* 53:53-65.
- Reed, E. T., G. Gauthier, and J.-F. Giroux. 2004. Effects of spring conditions on breeding propensity of greater snow goose females. *Animal Biodiversity and Conservation* 27:35-46.
- Reid, D., F. Bilodeau, C. J. Krebs, G. Gauthier, A. J. Kenney, B. S. Gilbert, M. C. Y. Leung, D. Duchesne, and E. Hofer. 2011. Lemming winter habitat choice: a snow-fencing experiment. *Oecologia*, *in press*.
- Reid, D. G., and C. J. Krebs. 1996. Limitations to collared lemming population growth in winter. *Canadian Journal of Zoology* 74:1284-1291.
- Ring, R. 1982. Freezing-tolerant insects with low supercooling points. *Comparative Biochemistry and Physiology Part A: Physiology* 73:605-612.
- Rockwell, R. F., L. J. Gormezano, and D. N. Koons. 2011. Trophic matches and mismatches: can polar bears reduce the abundance of nesting snow geese in western Hudson Bay. *Oikos* 120(5):696-709. [doi: 10.1111/j.1600-0706.2010.18837.x]
- Rodnikova, A., R. A. Ims, A. Sokolov, G. Skogstad, V. Sokolov, V. Shtro, and E. Fuglei. 2011. Red fox takeover of arctic fox breeding den: an observation from Yamal Peninsula, Russia. *Polar Biology*, *in press*. [doi: 10.1007/s00300-011-0987-0]
- Roth, J. D. 2002. Temporal variability in arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice. *Oecologia* 133:70-77.
- Roth, J. D. 2003. Variability in marine resources affects arctic fox population dynamics. *Journal of Animal Ecology* 72:668-676.
- Rowell, P., G. L. Holroyd, and U. Banasch. 2003. Summary of the 2000 Canadian Peregrine Falcon Survey. *Bird Trends Canada* 9:52-56.
- Ryabitshev, V. K. 1993. Territorial relations and the dynamics of bird communities in the Subarctic. Nauka Press, Ekaterinburg, Russia. [in Russian]

ArcticWOLVES final synthesis report

- Ryabitsev, V. K., and I. V. Pokrovskaya. 1995. Great Skua detection in the south of Ob-skaya Bay. Page 69 *in* V. K. Ryabitsev, editor, Materials on distribution of birds in the Ural Mountains, Ural region and Western Siberia. Ekaterinburg, Russia. [in Russian]
- Ryzhanovsky, V. N., and S. P. Paskhalniy. 2007. Population dynamics of birds of the Lower Ob region in connection with global warming. Part 2: Subarctic ecosystems: structure, dynamics and protection problems. Scientific Bulletin of YNAO 6(50):58-74. [in Russian]
- Sawtell, S. 2005. Pond Inlet. Page 1682 *in* M. Nuttall, editor. Encyclopedia of the Arctic, second edition. Routledge, New York, New York, USA.
- Schekkerman, H., I. Tulp, K. M. Calf, and J. J. de Leeuw. 2004. Studies on breeding shorebirds at Medusa Bay, Taimyr, in summer 2002. Wageningen, Alterra, Alterra-rapport 922.
- Schmidt, N. M., T. B. Berg, M. C. Forchhammer, D. K. Hendrichsen, L. A. Kyhn, H. Meltøfte, and T. T. Høye. 2008. Vertebrate predator-prey interactions in a seasonal environment. Pages 345-370 *in* H. Meltøfte, T. R. Christensen, B. Elberling, M. C. Forchhammer, and M. Rasch, editors. High-Arctic Ecosystem Dynamics in a Changing Climate. Academic Press, London, UK.
- Screen, J. A., and I. Simmonds. 2010. The central role of diminishing sea ice in recent arctic temperature amplification. Nature 464:1334-1337.
- Serreze, M., M. M. Holland, and J. Stroeve. 2007. Perspectives on the Arctic's shrinking sea-ice cover. Science 315:1533-1536.
- Shank, C. C., R. G. Bromley, and K. G. Poole. 1993. Increase in breeding population of tundra peregrine falcons in the Central Canadian Arctic. Wilson Bulletin 105:188-190.
- Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator-prey system. Nature 425:288-290.
- Sinclair, P. H., W. A. Nixon, C. D. Eckert, and N. L. Hughes. 2003. Birds of the Yukon Territory. UBC Press, Vancouver, British Columbia, Canada.
- Sittler, B. 1995. Responses of stoat (*Mustela erminea*) to a fluctuating lemming (*Dicrostonyx groenlandicus*) population in Northeast Greenland: preliminary results from a long-term study. Annales Zoologici Fennici 32:79-92.
- Sjögersten, S., R. van der Wal, M. J. J. E. Loonen, and S. J. Woodin. 2011. Recovery of ecosystem carbon fluxes and storage from herbivory. Biogeochemistry, *in press*. [doi: 10.1007/s10533-010-9516-4]
- Sjögersten, S., R. van der Wal, and S. J. Woodin. 2008. Habitat type determines herbivory controls over CO₂ fluxes in a warmer Arctic. Ecology 89:2103-2116.
- Skinner, W. R., R. L. Jefferies, T. J. Carleton, R. F. Rockwell, and K. F. Abraham. 1998. Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. Global Change Biology 4:3-16.
- Skrobov, V. D. 1960. On the interrelations of the arctic fox and red fox in the tundra of the Nenets national region. Zoologicheskii Zhurnal 39:469-471. [in Russian, English summary]
- Slough, B. G. 1987. Arctic fox den survey, Herschel Island, 1986. Pages 20-26 *in* B. G. Slough and R. M. Ward, editors. Furbearer Management Program 1987. Unpublished Report of the Yukon Department of Renewable Resources, Whitehorse, Yukon, Canada.
- Smith, P. A. 2009. Variation in shorebird nest survival: proximate pressures and ultimate constraints. PhD thesis, Carleton University, Ottawa, Ontario, Canada.
- Smith, P. A., and S. Wilson. 2010. Intraseasonal patterns in shorebird nest survival are related to nest age and defence behaviour. Oecologia 163:613-624. [doi:10.1007/s00442-010-1644-y]
- Smith, T. G. 1976. Predation of ringed seal pups (*Phoca hispida*) by the arctic fox (*Alopex lagopus*). Canadian Journal of Zoology 54:1610-1616.
- Sokolov, A. A. 2002. Functional relationship of the rough-legged buzzard (*Buteo lagopus*) and small rodents in the shrub tundra of Yamal. PhD thesis. University of Ekaterinburg, Ekaterinburg, Russia.
- Sokolov, A. A., N. A. Sokolova, V. G. Shtro, and V. A. Sokolov. 2010. Siberian lemmings leave southern Yamal tundra: indication of global change? International Polar Year Oslo Scientific Conference, Oslo, Norway.

- [poster]
- Sokolov, V. A. 2006. Comparative analysis of the nesting bird fauna in south-western Yamal. Proceedings of Chelyabinsk Scientific Centre UD RAS 3:109-113.
- Sokolov, V. A., S. V. Kornev, A. A. Sokolov, and A. E. Ogarkov. 2002. New data on rare and endangered birds on southwest of Yamal. Pages 237-239 in V. K. Ryabitsev, editor. Data on distribution of birds on Ural and Northwest Siberia. Akademkniga, Ekaterinburg, Russia.
- Solheim, R., K. O. Jacobsen, and I. J. Oien. 2008. Snøuglenes vandringer: Ett ar, tre ugler og ny kunnskap. Var fuglerfauna 31:102-109. [in Russian]
- Somme, L. 1999. The physiology of cold hardiness in terrestrial arthropods. European Journal of Entomology 96:1-10.
- Speed, J. D. M., S. J. Woodin, H. Tømmervik, M. P. Tamstorf, and R. van der Wal. 2009. Predicting habitat utilization and extent of ecosystem disturbance by an increasing herbivore population. Ecosystems 12:349-359.
- Starck, J. M., and R. E. Ricklefs. 1998. Avian growth and development: evolution within the altricial-precocial spectrum. Oxford University Press, New York, New York, USA.
- Stenseth, N. C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. Oikos 87:427-461.
- Stenseth, N. C., O. N. Bjornstad, and W. Falck. 1996. Is spacing behaviour coupled with predation causing the microtine density cycle? A synthesis of current process-oriented and pattern-oriented studies. Proceedings of the Royal Society. Biological Sciences 263:1423-1435.
- Stenseth, N. C., and R. A. Ims. 1993. Population dynamics of lemmings: temporal and spatial variation – an introduction. Pages 61-96 in N. C. Stenseth and R. A. Ims, editors. The biology of lemmings. Academic Press, London, England.
- Stroeve, J., M. M. Holland, W. Meier, T. Scambos, and M. Serreze. 2007. Arctic sea ice decline: faster than forecast. Geophysical Research Letters 34:L09501. [doi: 10.1029/2007GL029703]
- Sturm, M., C. Racine, and K. Tape. 2001. Climate change - Increasing shrub abundance in the Arctic. Nature 411:546-547.
- Sturm, M., J. Schimel, G. Michaelson, J. M. Welker, S. F. Oberbauer, G. E. Liston, J. Fahnestock, and V. E. Romanovsky. 2005. Winter biological processes could help convert arctic tundra to shrubland. Bioscience 55:17-26.
- Summers, R. W., L. G. Underhill, and E. E. Syroechkovski. 1998. The breeding productivity of dark-bellied brent geese and curlew sandpipers in relation to changes in the numbers of arctic foxes and lemmings on the Taimyr Peninsula, Siberia. Ecography 21:573-580.
- Talarico, D., and D. Mossop. 1986. A three-year summary of avifauna research on Herschel Island: an interim report for use in Park management and interpretive programs. Unpublished Report of the Yukon Department of Renewable Resources, Whitehorse, YT, Canada.
- Tannerfeldt, M., B. Elmhagen, and A. Angerbjörn. 2002. Exclusion by interference competition? The relationship between red and arctic foxes. Oecologia 132:213-220.
- Tape, K., M. Sturm, and C. Racine. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biology 12:686-702.
- Tarroux, A. 2011. Patrons d'utilisation de l'espace et des ressources chez un carnivore terrestre de l'Arctique: le renard polaire. PhD thesis, Université du Québec à Rimouski, Rimouski, Quebec, Canada.
- Tarroux, A., D. Berteaux, and J. Bêty. 2010. Northern nomads: ability for extensive movements in adult arctic foxes. Polar Biology 33:1021-1026.
- Therrien, J.-F. 2010. Territorial behavior of Short-eared Owls, *Asio flammeus*, at more than 1000 km north of their current breeding range in north-eastern Canada: evidence of range expansion? Canadian Field-Naturalist 124:58-60.
- Therrien, J.-F., G. Gauthier, and J. Bêty. 2011. An avian terrestrial predator of the Arctic relies on the marine ecosystem during winter. Journal of Avian Biology, *in press*. [doi:10.1111/j.1600-048X.2011.05330.x]
- Therrien, J.-F., G. Gauthier, and J. Bêty. Survival and reproduction of adult snowy owls tracked by satellite. Journal of Wildlife Management, *submitted*.

ArcticWOLVES final synthesis report

- Thomas, V. G., and J. P. Pevett. 1982. The roles of the James Bay Lowland in the annual cycle of geese. *Le Naturaliste Canadien* 109:913-925.
- Thompson, J. E., and W. A. Hutchison. 1987. Resource use by native and non-native hunters of the Ontario Hudson Bay Lowland. Ontario Ministry of Natural Resources Report, Moosonee, Ontario, Canada.
- Tjorve, K. M. C., H. Schekkerman, I. Tulp, L. G. Underhill, J. J. De Leeuw, and G. H. Visser. 2007. Growth and energetics of a small shorebird species in a cold environment: the little stint *Calidris minuta* on the Taimyr Peninsula, Siberia. *Journal of Avian Biology* 38:552-563.
- Tombre, I. M., K. A. Høgda, J. Mdsen, L. R. Griffin, E. Kuijken, P. Shimmings, E. Rees, and C. Verscheure. 2008. The onset of spring and timing of migration in two arctic nesting goose populations: the pink-footed goose *Anser bachyrhynchus* and the barnacle goose *Branta leucopsis*. *Journal of Avian Biology* 39:691-703.
- Tulp, I., and H. Schekkerman. 2008. Has prey availability for arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. *Arctic* 61:48-60.
- Turchin, P., L. Oksanen, P. Ekerholm, T. Oksanen, and H. Henttonen. 2000. Are lemmings prey or predators? *Nature* 405:562-565.
- Tveraa, T., P. Fauchald, N. G. Yoccoz, R. A. Ims, R. Aanes, and K. A. Hogda. 2007. What regulate and limit reindeer populations in Norway? *Oikos* 116:706-715.
- Usher, P. J. 2000. Traditional ecological knowledge in environmental assessment and management. *Arctic* 53:183-193.
- Valéry, L., M.-C. Cadieux, and G. Gauthier. 2010. Spatial heterogeneity of primary production as both cause and consequence of foraging patterns of an expanding Greater Snow Goose colony. *Ecoscience* 17:9-19.
- van de Kam, J., B. Ens, T. Piersma, and L. Zwarts. 2004. Shorebirds: an illustrated behavioural ecology. KNNV Publishers, Utrecht, The Netherlands.
- Van der Jeugd, H. P., G. Eichhorn, K. E. Litvin, J. Stahl, K. Larsson, A. J. van der Graaf, and R.H. Drent. 2009. Keeping up with early springs: rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. *Global Change Biology* 15:1057-1071.
- Van der Wal, R., S. Sjögersten, S. J. Woodin, E. J. Cooper, I. S. Jónsdóttir, D. Kuijper, A. D. Fox, and A. D. Huiskes. 2007. Spring feeding by pink-footed geese reduces carbon stocks and sink strength in tundra ecosystems. *Global Change Biology* 13:539-545.
- Van Eerden, M. R., R. H. Drent, J. Stahl, and J. P. Bakker. 2005. Connecting seas: western Palearctic continental flyway for water birds in the perspective of changing land use and climate. *Global Change Biology* 11:849-908.
- Walker, D. A., M. K. Reynolds, F. J. A. Daniels, E. Einarsson, A. Elvebakk, W. A. Gould, A. E. Katenin, S. S. Kholod, C. J. Markon, E. S. Melnikov, N. G. Moskalenko, S. S. Talbot, B. A. Yurtsev, and C. Team. 2005. The Circumpolar Arctic vegetation map. *Journal of Vegetation Science* 16:267-282.
- Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V. Callaghan, A. B. Carroll, H. E. Epstein, I. S. Jonsdottir, J. A. Klein, B. Magnusson, U. Molau, S. F. Oberbauer, S. P. Rewa, C. H. Robinson, G. R. Shaver, K. N. Suding, C. C. Thompson, A. Tolvanen, O. Totland, P. L. Turner, C. E. Tweedie, P. J. Webber, and P. A. Wookey. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America* 103:1342-1346.
- Ward, D. H., A. Reed, J. S. Sedinger, J. M. Black, D. V. Derksen, and P. M. Castelli. 2005. North American Brant: effects of changes in habitat and climate on population dynamics. *Global Change Biology* 11:869-880.
- Weiser, E. L., and A. N. Powell. 2010. Does garbage in the diet improve reproductive output of glaucous gulls? *Condor* 112:530-538.
- Wenzel, G. 2004. From TEK to IQ: Inuit Qaujimaqatungit and Inuit Cultural Ecology. *Arctic Anthropology* 41:238-250.
- White, C. M. 1994. Population trends and current status of selected western raptors. *Studies in Avian Biology* 15:161-172.
- Wiens, J. A. 1989. Spatial Scaling in Ecology.

References

- Functional Ecology 3:385-397.
- Wilbanks, T. J. 2006. How scale matters: some concepts and findings. Pages 21-35 in W. V. Reid, F. Berkes, T. J. Wilbanks, and D. Capistrano, editors. Bridging scales and knowledge systems: concepts and applications in ecosystem assessment. Island Press, Washington, D.C., USA.
- Wiley, R. H., and D. S. Lee. 1998. Long-tailed Jaeger (*Stercorarius longicaudus*). In A. Poole and F. Gill, editors. The Birds of North America, no. 365. Philadelphia, Pennsylvania, USA.
- Wiley, R. H., and D. S. Lee. 1999. Parasitic Jaeger (*Stercorarius parasiticus*) In A. Poole and F. Gill, editors. The Birds of North America, no. 445. Philadelphia, Pennsylvania, USA.
- Wilson, D. J., C. J. Krebs, and A. R. E. Sinclair. 1999. Limitation of collared lemming populations during a population cycle. *Oikos* 87:382-398.
- Wisz, M. S., M. P. Tamstorf, J. Madsen, and M. Jespersen. 2008. Where might the western Svalbard tundra be vulnerable to pink-footed goose (*Anser brachyrhynchus*) population expansions? Clues from species distribution models. *Diversity and Distribution* 14: 26-37.
- Ydenberg, R. C., R. W. Butler, D. B. Lank, C. G. Guglielmo, M. Lemon, and N. Wolf. 2002. Trade-offs, condition dependence and stop-over site selection by migrating sandpipers. *Journal of Avian Biology* 33:47-55.
- Ydenberg, R. C., R. W. Butler, D. B. Lank, B. D. Smith, and J. Ireland. 2004. Western sandpipers have altered migration tactics as peregrine falcon populations have recovered. *Proceedings of the Royal Society of London Series B-Biological Sciences* 271:1263-1269.
- Zöchler, C., T. H. Hla, N. Clark, E. Syroechkovskiy, and N. Yakushev. 2010. Hunting in Myanmar is probably the main cause of the decline of the spoon-billed sandpiper *Calidris pygmeus*. *Wader Study Group Bulletin* 117:1-8.

