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Long-term study of the tundra food web at a hotspot of Arctic biodiversity, the Bylot Island Field Station

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Abstract

We present the history of research activities at the Bylot Island Field Station of the Centre d'études nordiques, a hotspot of biodiversity in the Canadian Arctic. Intensive wildlife studies started at the station in the late 1980s, initially focussing on greater snow goose ecology and its impacts on the tundra vegetation. Since then, studies have expanded to encompass the whole vertebrate food web and have become one of the most comprehensive ecological monitoring programs in the Canadian Arctic. The main vertebrate species monitored include snow geese, lemmings, shorebirds, avian predators, buntings, and Arctic foxes. Over time, we recorded 66 bird and 10 mammal species, including 51 confirmed breeders. Contributions of the program to the field of ecology are numerous, but our demonstration of the dominant role played by predator–prey interactions in the Arctic food web is especially significant for the understanding of direct and indirect trophic interactions. Our studies provided essential information for management decisions taken to control the overabundant greater snow goose population and supported international efforts to assess the state of Arctic biodiversity. Future directions will reflect the need to deepen our understanding of trophic interactions and the effects of climate change using innovative advanced technologies.

Key words: snow goose, lemmings, shorebirds, birds of prey, Arctic fox, trophic interactions

Résumé

Nous présentons l'historique des activités de recherche à la station de terrain de l'île Bylot du Centre d'études nordiques, un haut lieu de la biodiversité dans l'Arctique canadien. Des études fauniques intensives ont débuté à la station à la fin des années 1980 et se sont initialement concentrées sur l'écologie de la grande oie des neiges et ses impacts sur la végétation de la toundra. Depuis ce temps, ces études se sont étendues à l'ensemble du réseau trophique des vertébrés et sont devenues l'un des programmes de suivi écologique les plus complets de l'Arctique canadien. Les principales espèces de vertébrés suivies sont les oies des neiges, les lemmings, les oiseaux de rivage, les prédateurs aviaires, les plectrophanes et les renards arctiques. Au fil des années, nous avons recensé 66 espèces d'oiseaux et 10 espèces de mammifères, dont 51 comme reproducteurs confirmés. Les contributions du programme au domaine de l'écologie sont nombreuses mais notre démonstration du rôle dominant joué par les interactions prédateurs-proies dans l'Arctique est particulièrement significative pour la compréhension des interactions trophiques directes et indirectes. Nos études ont contribué des informations essentielles pour les décisions de gestion prises pour contrôler la surabondance de la population de grandes oies des neiges et ont soutenu les efforts internationaux pour évaluer l'état de la biodiversité Arctique. Les orientations futures refléteront la nécessité d'approfondir notre compréhension des interactions trophiques et des effets des changements climatiques en utilisant des avancées technologiques innovants.

Mots-clés : oie des neiges, lemmings, limicoles, oiseaux de proies, renard arctique, interactions trophiques

Introduction

The Arctic tundra is one of the largest biomes in Canada covering ca 1.4 M km^2 across three territories and the northern portions of Quebec, Manitoba, and Labrador (Walker et al. 2005; Willig et al. 2006). However, it is one of the least studied biomes because conducting Arctic field work poses enormous difficulties due to remoteness, harshness of the climate, and high costs (Mallory et al. 2018). Studying wildlife poses additional challenges due to animal movements, both locally and over long distance (e.g., migration), which forces researchers to adapt the timing and spatial scale of their activities accordingly. The paucity of long-term research programs focusing on Arctic vertebrates is unfortunate considering the numerous threats, such as industrial development and climate warming, facing the unique Arctic biodiversity (Meltofte 2013).

Even though much of the Canadian Arctic tundra is still a pristine environment, it is increasingly exposed to anthropogenic pressures. For instance, increasing exploitation of natural resources (e.g., mining or oil and gas extraction) in the North poses multiple risks to wildlife due to disturbance, habitat alteration, or pollution (Tolvanen et al. 2019). However, climate warming is probably the most serious threat faced by the cold-adapted Arctic vertebrates (Aronsson et al. 2021) as this region is currently experiencing the strongest warming trend on Earth, about four times faster than the global average (Rantanen et al. 2022). Climate-induced perturbations to Arctic ecosystems have already been documented and include shifts in phenology, increased mortality during extreme weather events, and appearance of invasive species (Gilg et al. 2012; Post et al. 2019). Early detection of changes to the Arctic biodiversity can only be achieved if we have robust baseline data of key biological parameters and ongoing, long-term ecological monitoring (Willis et al. 2007). Considering the low vertebrate species richness of tundra ecosystems (Willig et al. 2003; Jenkins et al. 2013), monitoring programs focusing on regions with a relatively high biodiversity should be the most effective to detect changes.

Bylot Island harbours a high vertebrate diversity for its latitude and can be considered a biological hotspot for the Canadian Arctic (Zoltai et al. 1983; see also below). The island was designated a Migratory Bird Sanctuary by the Canadian Wildlife Service in 1965 with the express purpose of protecting the nesting grounds of thick-billed murres (*Uria lomvia*), black-legged kittiwakes (*Rissa tridactyla*), and greater snow geese (scientific names of other vertebrate species appear in Tables), and it became part of Sirmilik National Park when created in 1999. Moreover, waters surrounding the island were designated as the Tallurutiup Imanga National Marine Conservation Area in 2019, the first marine protected area in the Canadian Arctic. The south plain of Bylot Island is also in the process of being designated a Key Biodiversity Area by Birds Canada (https://arcg.is/0q0m4i0). A team from Université Laval and the Canadian Wildlife Service selected this site to set up a small research camp focusing primarily on wildlife in the late 1980s. Over the years, this has become one of the longest running and most comprehensive ecological monitoring program in the Canadian Arctic (Gauthier et al. 2013). In this paper, we review the history of the Bylot Island Field Station, present an overview of its vertebrate monitoring program, describe some of its key findings, show its contributions to government policies, and highlight some future research directions.

Study area

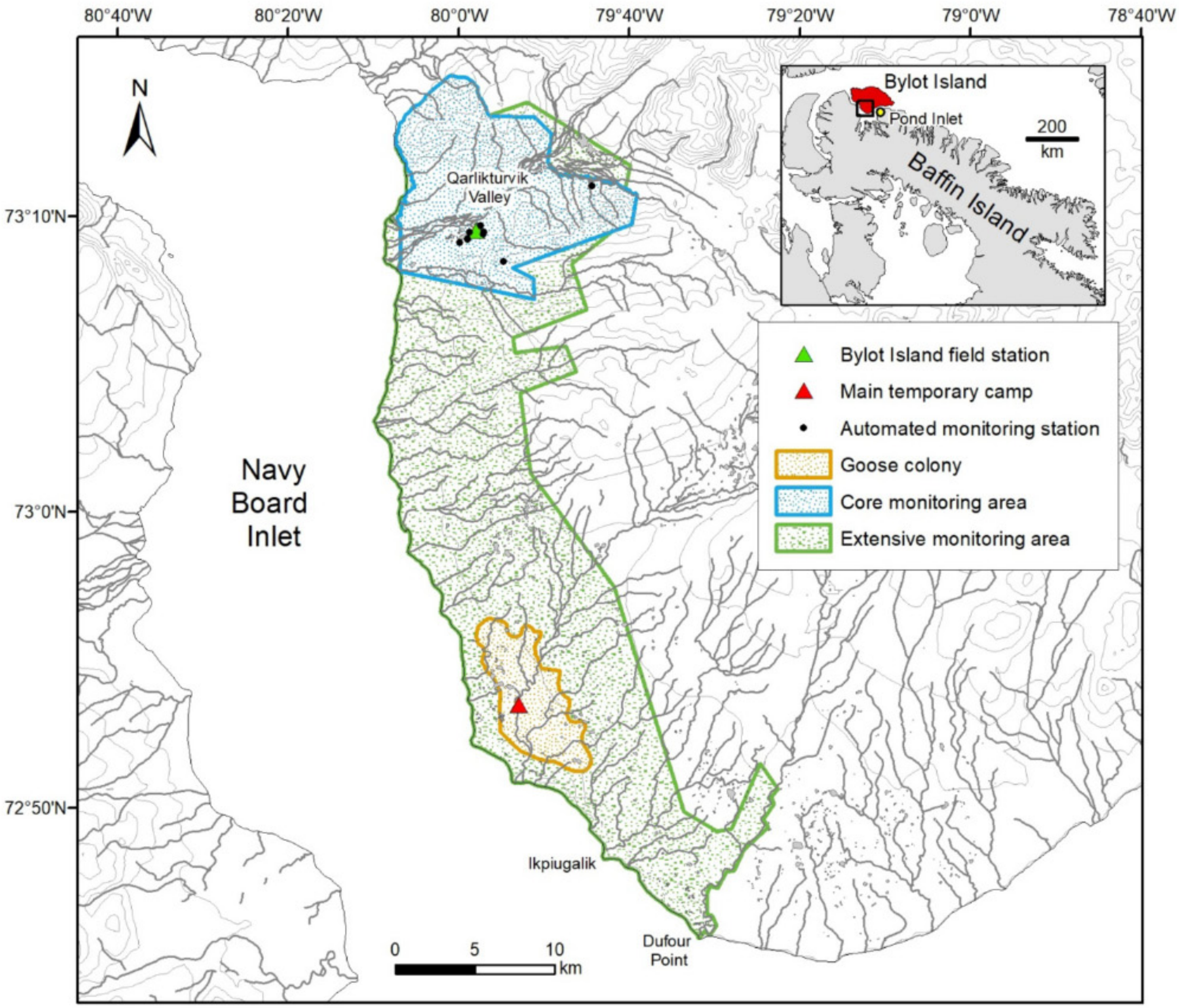
Bylot Island is located at the northern tip of Baffin Island and at the entrance of the Northwest Passage (Fig. 1). It is bordered to the north by Lancaster Sound, to the east by Baffin Bay, to the south by Pond Inlet and Eclipse Sounds, and to the west by Navy Board Inlet. Most of the 11 100 km^2 island is covered by mountains up to 1900 m and a large ice cap, with several glaciers flowing to lowlands or directly to the sea (Dowdeswell et al. 2007). Cliffs are common to the north and east, and are home to several large seabird colonies (Gaston et al. 2017). The southern portion of the island is characterized by a 1600 km^2 rolling plain, mostly from 0 to 300 m ASL, located between the mountains and the sea. This south plain has a relatively mild climate for the latitude due to its southern exposure and the presence of high mountains that partially block cold northerly winds. Its geology is also different from the surrounding mountains on Bylot and Baffin Islands as it is dominated by tertiary sedimentary rocks, mostly sandstone and shale (Jackson and Davidson 1975; Klassen 1993). These conditions have promoted the development of an unusually lush tundra vegetation for the latitude. Over the period 1994 to 2006, average annual temperature was −14.5 °C, average temperature during the summer months (June to August) was 4.5 °C, and average number of thawing degree-days was 438 (Cadieux et al. 2008; CEN 2022). The study site is located in the bioclimatic zone C of Walker et al. (2005)

Three broad habitats, largely determined by soil moisture, can be found in the south plain of Bylot Island. Wetlands occur in low-lying areas along streams, around shallow ponds, and, most commonly, in low-centre tundra polygons created by the growth of ice wedges in the permafrost. These sites are typically moss-covered fens dominated by grasses and sedges such as *Dupontia fisheri*, *Carex aquatilis*, and *Eriophorum scheuchzeri*. Mesic tundra covers most of the landscape on plateaus and gentle slopes. Common plants of this habitat include prostrate shrubs (*Salix* spp., *Vaccinium uliginosum*, and *Cassiope tetragona*), forbs (*Luzula* spp., *Oxytropis maydelliana*, *Astragalus alpinus*, *Oxyria digina*, and *Polygonum viviparum*), grasses (*Arctagrostis latifolia* and *Poa arctica*), and some mosses (e.g., *Aulacomnium* spp.). Finally, exposed areas with dry, gravel soil such as ridges or high-elevation sites have a very sparse vegetative cover consisting of only a few plant species, such as *Dryas integrifolia* or *Saxifraga oppositifolia* (Gauthier et al. 1996; Duclos 2002). The site is also at the northern limit of distribution of the only erect shrub species in the region, *Salix richardsonii* (Lamarque et al. 2023).

History of research in the area

Modern Inuit and their ancestors have accumulated knowledge in the North Baffin region for approximately 4000 years (Mary-Rousselière 1985). Up to these days, Inuit have travelled extensively over the tundra, water, and ice of the region, including on Bylot Island where generations of Inuit have established camps during spring in the Ikpiugalik area (close to our main temporary camp; Fig. 1) to hunt geese and collect eggs. Inuit also frequented and established camps at other locations on Bylot Island, including the Qarlikturvik Valley, to hunt for caribou, trap foxes and pick berries (Ootoova 2005). It is through activities such as travelling, fishing, hunting, trapping, and sewing that Inuit de-

Fig. 1. Location of the Bylot Island Field Station, Nunavut, Canada, and of the areas where the monitoring program takes place on the island. The goose colony is also a core monitoring area. Source of the base map: Natural Resources Canada (https://atlas.gc.ca/toporama/en/index.html). Datum: NAD83.



velop a meticulous and complex first-hand knowledge of their environment (Gearheard et al. 2010; Pfeifer 2023), and these traditional activities continue nowadays on Bylot Island. As first researchers of the region, they have developed their own *Inuit knowledge science* (Pfeifer 2023) of North Baffin. Their continuous and ongoing observations and relation with the land, combined with millennia-old practical traditions, has formed one of the pillars of *Inuit Qaujimajatuqangit* (IQ; also termed Indigenous knowledge of the Inuit), a unified system of knowledge, beliefs, and values (Tagalik 2010; see also Wenzel 2004). Some of our work attempted to bridge science-based and Inuit ecological knowledge (see below).

The first naturalists to visit Bylot Island during the modern era and to collect specimens were J. Dewey Soper from the Victoria Memorial Museum in 1923 and the botanist Oscar Malte from the National Herbarium of Canada in 1927 (Martin 1995; Smith 2014). The first scientific expedition to document the richness of the plant and animal species of the island took place in summer 1954 and included, among others, Josselyn Van Tyne from the Museum of Zoology at the University of Michigan and William Drury from the Biology Department of Harvard University (Scherman 1956). Louis Lemieux, who was at that time a PhD student at Université Laval, spent the whole summer of 1957 on Bylot Island to study the snow goose and its habitat (Lemieux 1959). He used banding drives to mark a few hundred flightless snow geese during their moult and some of these birds were later observed or shot by hunters at Cap Tourmente along the St. Lawrence estuary. This was the first confirmation of the breeding location of greater snow geese migrating through southern Québec. Leslie Tuck from the Canadian Wildlife Service also conducted the first census of the seabird colonies of Bylot Island in 1957 (Lepage et al. 1998).

From 1970 to 1974, several campaigns were organized by J. Douglas Heyland from the Quebec Department of Tourism, Fish, and Game to map nesting sites and band greater snow geese in the North Baffin region, including on Bylot Island (Heyland et al. 1974). These banding data were later analysed by Menu et al. (2002) and provided the first robust estimates of survival for this population. Austin Reed from the Canadian Wildlife Service initiated a systematic survey of the greater snow goose colony on Bylot Island in 1983 and repeated it every 5 years until 2008 (Reed and Chagnon 1987; Reed et al. 1992; Reed et al. 2002). Seabird colonies on Bylot Island have also been partially surveyed by David Nettleship during the 1970s (Lepage et al. 1998) and more recently (2013) by Anthony Gaston, both from the Canadian Wildlife Service (Gaston et al. 2017).

History of the Bylot Island Field Station

In summer 1988, a reconnaissance trip was conducted by Gilles Gauthier and Yves Bédard from Université Laval with the assistance of the local guide Lamechi Kadloo to find a suitable site to study greater snow geese on Bylot Island. The following year, a field camp made of tents was established in a large glacial valley locally known as the Qarlikturvik Valley (Fig. 1) with the support of the Polar Continental Shelf Program (PCSP), Natural Resources Canada. The initial research objectives were to study the feeding ecology and nutrient allocation of breeding snow geese, as well as the impact of goose grazing on Arctic vegetation. At that time, exploding snow goose populations and their destruction of wetland vegetation at several Arctic sites were already emerging as major conservation issues (Kerbes et al. 1990). During the 1990s, studies of nesting and feeding ecology of greater snow geese and goose banding were the main research activities conducted jointly by Gilles Gauthier and Austin Reed. This initial work was primarily funded by the Canadian Wildlife Service, Université Laval, and the Natural Sciences and Engineering Research Council of Canada.

In 1991, a first semi-permanent structure, a parcoll loaned by PCSP, was established, which allowed storage of material at the camp site over winter (Fig. 2A). Because the Qarlikturvik Valley is primarily a brood-rearing area for greater snow geese, the need for a satellite field camp in the main nesting colony, located 30 km further south, rapidly became obvious to efficiently monitor goose nesting activity. In 1994, a temporary camp was set in the heart of the snow goose colony for the duration of the nesting season (Fig. 1). The camp, located in a narrow and steep valley to minimize disturbance to nesting birds on the surrounding plateau, became a second hub for research activities on the island. Goose–plant interaction studies were also an important topic right from the start and Line Rochefort, a plant ecologist from Université Laval, was involved in those initial studies (Gauthier et al. 1995). In the mid 1990s, goose exclosures were set up to monitor the long-term effect of goose grazing on the wetland vegetation (Gauthier et al. 2004; Valery et al. 2010).

The great potential of the south plain of Bylot Island for wildlife and other environmental studies rapidly became evident. For instance, as the importance of predation on goose nesting success became apparent, new studies on predators such as the Arctic fox and birds of prey (snowy owls and others), and on their primary prey, lemmings, were initiated (see below). This attracted other researchers during the late 1990s and 2000s, which further expanded the scope, intensity, and spatial scale of research activities. Esther Lévesque from Université du Québec à Trois-Rivières started studies on plants in 1998, followed by Dominique Berteaux who initiated intensive studies on Arctic foxes in 2003 and Joël Bêty who did the same on shorebirds in 2005, both from Université du Québec à Rimouski. The Canadian Wildlife Service continued to be involved in the project and Josée Lefebvre replaced Austin Reed in 2009 when he retired. As the research team grew, the old parcoll was replaced in 2003 by two Weatherhaven shelters to provide larger and more comfortable working space for researchers (Fig. 2B). It is at that time that the field station was integrated to the Qaujisarvik network of field research stations of the Centre d'études nordiques (CEN; Bhiry et al. 2021). Further improvements came in 2009 when the Weatherhaven shelters were replaced by two permanent buildings (see below), thanks to special funding from the Canadian Foundation for Innovation and the Arctic Research Infrastructure Fund, an initiative of the Canadian Government during the International Polar Year 2007–2009.

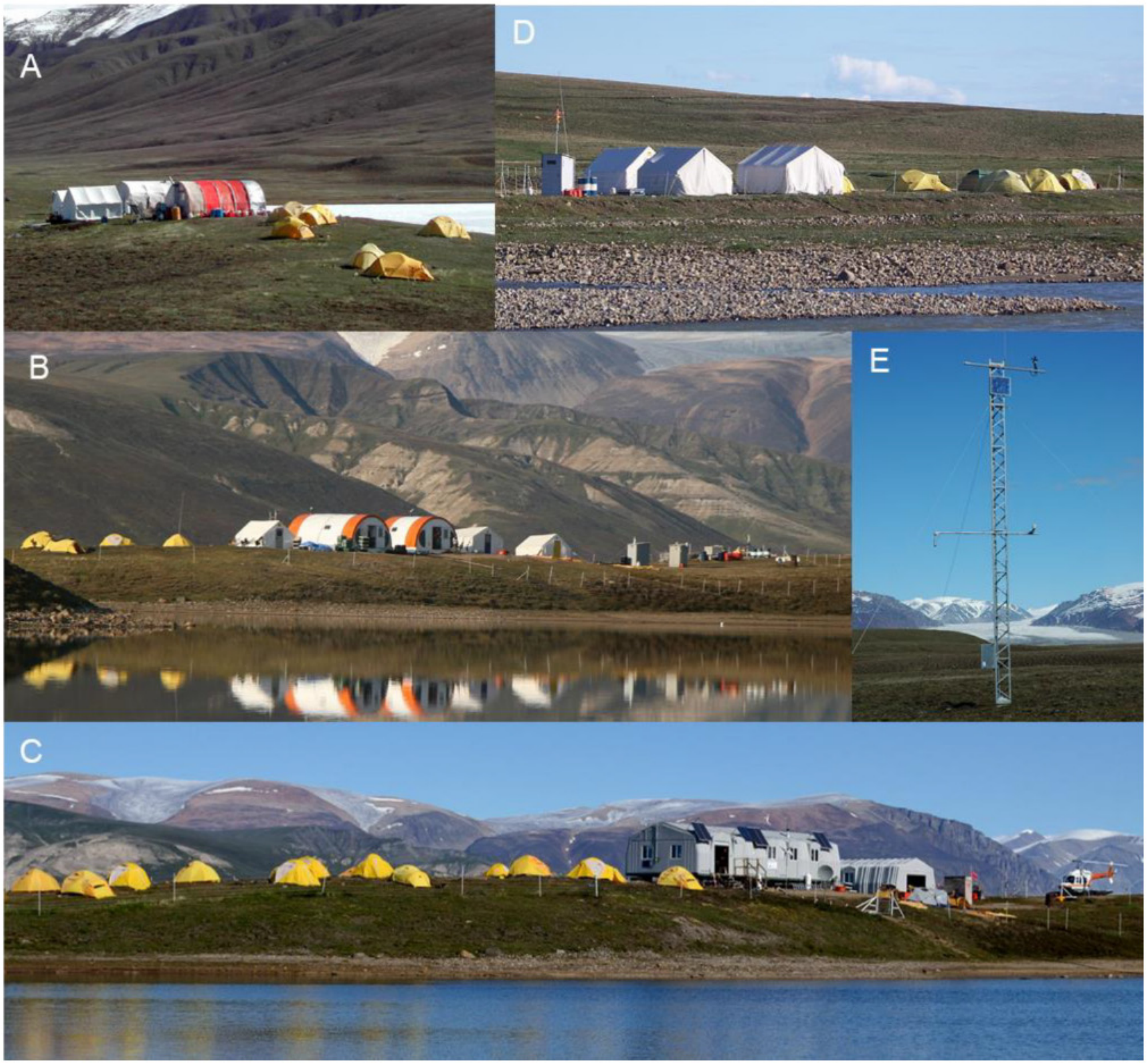
The sustained support from PCSP was essential to maintain research activities at the Bylot Island Field Station for more than three decades. The presence of a PCSP helicopter based in nearby Pond Inlet from mid-June to the end of August starting around 2000 was a key element of the success of the station. Helicopter and Twin Otter support (120 to 160 h and 25 to 35 h, respectively, were provided annually by PCSP to researchers since 2000), facilities available at the station and the rich diversity of landscape on the island prompted many researchers to initiate studies in other disciplines at the site over the past 20 years. This includes permafrost specialists Michel Allard (Université Laval) and Daniel Fortier (Université de Montréal), limnologist Isabelle Laurion (Institut National de la Recherche Scientifique), snow specialist Florent Dominé (Université Laval), and hydrologist Christophe Kinnard (Université du Québec à Trois-Rivières) to name a few.

Research at the Bylot Island Field Station now enters a fourth decade and is still vigorous. Thanks to the production of >75 graduate student theses, >250 papers published in peer-reviewed journals, and numerous reports, the quality of the research and monitoring activities conducted at the site is well recognized at the national and international levels and has inspired similar programs elsewhere (e.g., COAT program in Norway, Ims et al. 2013; https://www.coat.no/en/).

Field station description

The Bylot Island Field Station is located in the Qarlikturvik Valley (73° 08′N, 80° 00′W), 84 km from the community of Pond Inlet (Mittimatalik) (Fig. 1). It is positioned on a large esker overlooking a small lake, which is the source of human drinking water. The main building of the station (96 m^2) consists of an insulated, modular fiberglass unit that can accommodate 16 persons on a sustained basis and includes a laboratory, a kitchen/dining area, three bedrooms accommodating four people each, and a storage room (Fig. 2C). Equipment at the station comprises a large propane stove, a 12 V

Fig. 2. Photographs of the Bylot Island Field Station at different periods (A-2000, B-2005, C-2012), of the main temporary camp (D) and of the 10 m high weather station (E). Photo credits: A and B: Denis Sarrazin, C: Andréanne Beardsell, D: Guillaume Souchay, E: Gilles Gauthier.



refrigerator, a propane freezer, and a propane heated shower. Power for computers, internet (available at the station), and for recharging batteries of scientific equipment is provided by solar panels (1.2 kW) and a 3 kW generator is used to run larger apparatus such as a drying oven and a Smart Ash® garbage incinerator. Solid human waste is recovered in sealed containers and flown out by helicopter to the Pond Inlet sewage lagoon to avoid contamination of the park environment. During the summer, most people sleep in individual tents beside the main building. A modular fiberglass garage is also available to store field equipment. The buildings and tents are protected from polar bears by a permanent electric fence even though bears do not represent a major threat on the island with only a few long-distance sightings every year. Nonetheless, all station users must attend a safety training session before arrival and must carry a scaring pistol and pepper spray when they go in the field. We operate a radio repeater located on high ground on nearby Baffin Island, which allows VHF radio communication between the station, teams in the field, the helicopter pilot, and the Parks Canada office in Pond Inlet.

The station is in operation from early May to late August (about 95 days) and is usually at full capacity after late June. Access to the station is possible by snowmobile from Pond Inlet during winter and spring until mid-June. Otherwise, access is by helicopter only. In spring, fixed-wing aircraft (Twin Otter) can land on skis on the lake in front of the station to bring material and fuel for the season. At camp closure in late summer, fixed-winged aircraft can only land on a gravel terrace along the coast, 10 km from the station. Ma-

Table 1. Biodiversity monitoring at the Bylot Island Field Station.

Group	Main species	Year	Parameters monitored: Abundance	Phenology	Breeding activity	Brood or litter size	Breeding success	Data reference
Waterfowl	Greater snow goose	1989	1	1	1	1	1	Gauthier and Cadieux (2020*b*)
	Cackling goose	2014 (2019)	1	1	1	1	1	
Raptor	Snowy owl	1993	1	1	1	1	1	Gauthier et al. (2020)
	Rough-legged hawk	2004	1	1	1	1	1	Gauthier et al. (2020)
	Peregrine falcon	2004	1	1	1	1		
Shorebird	American golden plover	2005 (2010)	1	1	1	1	1	Bêty (2020*a*)
	Common ringed plover	2010	1	1	1	1	1	Bêty (2020*a*)
	Baird's sandpiper	2005	1	1	1	1	1	Bêty (2020*a*)
	White-rumped sandpiper	2005	1	1	1	1	1	Bêty (2020*a*)
Seabird	Glaucous gull	2004	1	1	1	1	1	Gauthier et al. (2020)
	Long-tailed jaeger	2004	1	1	1	1	1	Gauthier et al. (2020)
	Parasitic jaeger	2004	1	1	1	1	1	
Passerine	Common raven	2004	1	1	1	1		
	Lapland longspur	1995	1	1	1	1	1	Gauthier and Bêty (2020)
Mammal	Brown lemming	1993	1		1			Gauthier (2020)
	Collared lemming	1994	1		1			Gauthier (2020)
	Arctic fox	1993 (2003)	1	1	1	1	1	Berteaux (2020)
	Red fox	1993 (2003)	1	1	1	1	1	Berteaux (2020)
	Ermine	2008			1	1		
Incidental observations		1992 (2007)	1	1				Gauthier and Cadieux (2020*c*)
Arthropods		2007	1	1				Bêty (2020b)
Graminoid plants		1990	1					Gauthier and Cadieux (2020*a*)

Note: Year is when monitoring of each listed component started and values in parentheses are when major expansion of the monitoring occurred for that component.

terial and garbage then need to be slung from the station to the landing site by helicopter. Snowmobiles are used in May and early June, but after snow melt all research activities are carried out on foot because ATVs are not allowed due to strict vegetation protection rules in National Parks. During the summer, several temporary camps are in operation from a few days to ca 6 weeks to conduct various field activities across a ca 600 km^2 area (Fig. 1). The largest one is located in the snow goose colony during the bird nesting season and can accommodate eight people (Fig. 2D). In recent years, from 45 to 50 persons have used the station and its temporary camps annually (1600 to 1800 person-days).

The CEN, which operates the field station, also maintains 14 automated stations that were gradually set up between 1992 and 2016 to record various environmental parameters year-round all over the Qarlikturvik Valley (Fig. 1). This includes three full weather stations, the most complete one being a 10 m high tower (Fig. 2E) that records air and ground temperature, relative humidity, wind speed and direction, solar radiation, and snow depth. Other stations are more specialized and record a subset of parameters such as precipitation, ground and permafrost temperature (up to 11 m deep), snow temperature and thermal conductivity, and long- and short-wave radiations. These weather stations are part of the SILA (climate in Inuktitut) network of environmental monitoring stations operated by the CEN across Nunavik and eastern Nunavut. Data from these automated stations are available on the data portal Nordicana D (https://nordicana.cen.ulaval.ca/) of the CEN (CEN 2022).

Vertebrate biodiversity monitoring

The main focus of studies at the Bylot Island Field Station is wildlife ecology, although research on numerous other disciplines is also taking place, including plant ecology, limnology, geomorphology, hydrology, and snow physics. The number of wildlife species studied increased over time from a single one initially, the greater snow goose, to 19 species in recent years (Table 1, Fig. 3). Although monitoring was not an initial goal per se of our field studies, its value became apparent very quickly. Consequently, standardized protocols were designed for our focal species early during the program to ensure consistent and repeatable data collection by numerous graduate students and field assistants over the years. Main biological parameters monitored for our focal species include abundance, reproductive effort and success, and phenology (Table 1). The Qarlikturvik Valley and the goose colony are our core monitoring areas (Fig. 1). However, the spatial scale of monitoring activities was adapted to characteristics of the species of interest, being largest (ca 600 km^2 for our extensive monitoring area that extends to Dufour Point to the south,

Fig. 3. Photographs of the major wildlife species studied at the Bylot Island Field Station: Greater snow goose (A, view of the colony), Arctic fox (B), snowy owl (C), long-tailed jaeger (D), brown lemming (E), ermine (F), shorebirds (common ringed plover (G) and American golden plover (H)) and Lapland longspur (I). Photo credits: A: Dominique Berteaux, B: Louis-Pierre Ouellet, C, D and H: Andréanne Beardsell, E and G: Don Jean Léandri-Breton, F : Christian Marcotte, I : Dominique Fauteux.

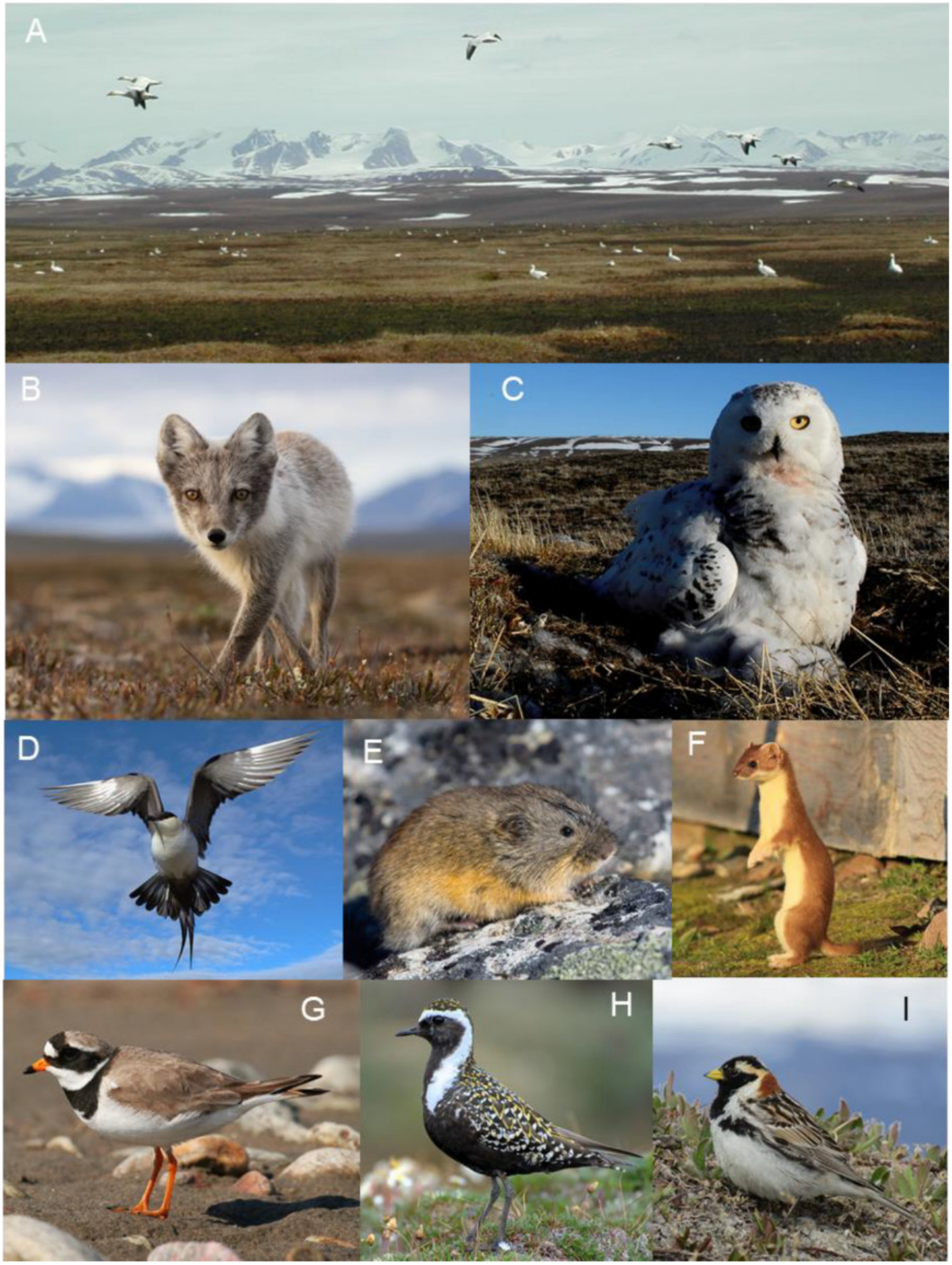


Fig. 1) for mesocarnivores like the Arctic fox (Berteaux et al. 2017*c*) and bird species like shorebirds and raptors (Lamarre et al. 2017; Duchesne et al. 2021), which all occur at relatively low densities.

The largest expansion in our monitoring activities occurred during the International Polar Year (IPY 2007–2009). At that time, our team led the international project Arctic Wildlife Observatories Linking Vulnerable EcoSystems (ArcticWOLVES), which focused on the study of the tundra food web at multiple sites across the circum-Arctic region (Gauthier and Berteaux 2011). Funding obtained from the IPY program and other sources helped us to organize our monitoring data into structured databases. Subsequently, funding from Polar Knowledge Canada allowed us to publish these databases on the Nordicana D data portal, thereby making them freely available (Table 1).

We recorded opportunistic sightings of all wildlife species since the beginning of the project. However, starting in 2007, these observations began to be recorded systematically along with sampling effort (Gauthier and Cadieux 2020*c*). Systematically collected incidental observations have been shown to be useful to track change in abundance or phenology of wildlife species, including in the Arctic (Hochachka et al. 2000; Fauteux et al. 2018*a*; Bolduc et al. 2023). A total of 66 species of birds (44 of which are breeding) and 10 species of mammals (7 of which are breeding) were observed during our field activities on the south plain of Bylot Island or the adjacent coastal area over a 34-year period (Table 2). Based on our incidental observation database, 19 species of birds can be considered abundant (frequency of occurrence >10%; one loon species, two goose species, two duck species, two birds of prey, one crane species, four shorebird species, three seabird species, and four passerine species), 12 are common, and 35 are rare or accidental (frequency of occurrence <1%). Similarly, two mammal species (the Arctic fox and brown lemming) are abundant, three are common, and five are rare or accidental (Table 2). We recorded 10 species of birds not previously reported on Bylot Island or the Pond Inlet region (Lepage et al. 1998).

Some key finding from long-term research and monitoring

Plant–herbivore interaction has long been considered a dominant trophic interaction in the tundra. Examples of that include the strong grazing impact of snow geese on subarctic wetlands (Kerbes et al. 1990; Jefferies et al. 2004) or of lemmings on the tundra vegetation in some areas (Johnson et al. 2011; Olofsson et al. 2014). However, early in the study of greater snow goose ecology, it became obvious that predation was a key factor driving its annual productivity along with spring weather (Gauthier et al. 2004; Morrissette et al. 2010). We uncovered a strong indirect interaction between lemming abundance and goose breeding success due to shared predators, in particular the Arctic fox. Lemmings are the main prey of foxes and their populations exhibit large cyclic population fluctuations, including on Bylot Island (Gruyer et al. 2008; Gauthier et al. 2013). When lemming populations crash, foxes show an immediate behavioural response and increase their predatory activity on bird nests and in particular goose eggs (Bêty et al. 2002; Lecomte et al. 2008; Beardsell et al. 2022), leading to a strong decrease in goose nesting success (Royer-Boutin 2015). Indirect interaction between geese and lemmings due to shared predators provides a good example of short-term apparent mutualism in a vertebrate community (Bêty et al. 2002).

Further studies revealed that predation also has major effects on other tundra birds. Predation level on bird nests is the outcome of a complex temporal and spatial interaction due to the combined effects of lemming population fluctuations (see above) and the presence of a snow goose colony, which affects the reproduction and spatial distribution of foxes (Giroux et al. 2012; Chevallier et al. 2020). Consequently, predation risk of shorebird nests increases when lemming abundance decreases as well as inside the goose colony (Lamarre et al. 2017). This affects the spatial distribution of shorebirds and even of some avian predators (jaegers and hawks), as their abundance decreases in the goose colony (Lamarre et al. 2017; Duchesne et al. 2021). Ultimately, this may affect the persistence of local shorebird populations (Beardsell et al. 2023). Interestingly, species using prey refuges (islets in wetlands, cliff edges, or gravel beds along rivers) are less or not affected by the presence of the goose colony (Duchesne et al. 2021).

Long-term monitoring of brown lemming demography and of their predators, combined with experimental manipulation and modelling, also showed that predation was the main driver of cyclic population fluctuations of brown lemmings on Bylot Island (Legagneux et al. 2012; Therrien et al. 2014; Fauteux et al. 2015, 2016; Fauteux and Gauthier 2022). Additional modelling work suggested that seasonality was an essential component of this dynamics and that it was not driven by a single predator but required a whole suite of predators, each with different life-history characteristics (Hutchison et al. 2020; Bergeron 2022). These results challenged the view that lemming cycles were primarily driven by a plant–herbivore interaction across the tundra biome (Oksanen et al. 2008; Gauthier et al. 2009). In summary, long-term studies of vertebrates on Bylot Island revealed that predation was a pervasive force in the tundra food web. Our work contributed to a paradigm shift where predator–prey interactions are now considered as important, if not more, than plant–herbivore interactions in shaping the tundra food web (Legagneux et al. 2014).

Other key findings emerging from our long-term research and monitoring are worth mentioning, although they cannot be detailed here. For example, long-term tracking of 170 Arctic foxes with satellite collars from 2007 to 2021 allowed us to investigate their long-distance dispersal (Gravel et al. 2023). This provided new knowledge critical to understand the circumpolar genetic structure of the species and how Arctic foxes can spread zoonoses at the continental scale. Similarly, tracking of snowy owls (Robillard et al. 2018), long-tailed jaegers (Seyer et al. 2021), and common ringed plovers (Le´andri-Breton et al. 2019) showed that the studied tundra food web is imbedded in a meta-ecosystem functioning at a much larger scale than Bylot Island (Moisan et al.

Table 2. List of vertebrate species observed on Bylot Island (south plain) since 1989.

Common name	Scientific name	Breeder[1]	Occurrence (%)	Abundance (*N*/100 h)
BIRDS				
Common loon	*Gavia immer*		<0.1	ac[2]
Pacific loon	*Gavia pacifica*	B	10.0	3.4
Red-throated loon	*Gavia stellata*	B	34.9	15.2
Yellow-billed loon	*Gavia adamsii*		0.4	0.1
Northern fulmar	*Fulmarus glacialis*		0.3	0.5
Brant goose	*Branta bernicla*	(B)	0.1	ac
Cackling goose	*Branta hutchinsii*	B	35.0	33.6
Canada goose	*Branta canadensis*		NA[3]	ac
Greater snow goose	*Anser caerulescens atlanticus*	B	72.5	3851.5
Ross's goose	*Anser rossii*	B	0.3	0.1
Greater white-fronted goose	*Anser albifrons*		0.1	ac
Tundra swan	*Cygnus columbianus*	B	0.9	0.2
Mallard duck	*Anas platyrhynchos*		<0.1	ac
Northern pintail	*Anas acuta*		<0.1	ac
Green-winged teal	***Anas crecca***		**0.1**	**ac**
American wigeon	*Mareca americana*		–[4]	ac
Common eider	*Somateria mollissima*		0.3	0.2
King eider	*Somateria spectabilis*	B	30.1	25.4
Long-tailed duck	*Clangula hyemalis*	B	56.3	45.8
Red-breasted merganser	*Mergus serrator*		<0.1	ac
Golden eagle	***Aquila chrysaetos***		**–**	**ac**
Rough-legged hawk	*Buteo lagopus*	B	11.9	4.2
Peregrine falcon	*Falco peregrinus*	B	6.2	1.2
Merlin	***Falco columbarius***		**0.1**	**ac**
Gyrfalcon	*Falco rusticolus*	B	1.1	0.2
Snowy owl	*Bubo scandiacus*	B	12.2	4.8
Short-eared owl	***Asio flammeus***	**B**	**0.3**	**0.1**
Rock ptarmigan	*Lagopus muta*	B	10.0	3.1
Sandhill crane	*Antigone canadensis*	B	55.9	31.0
American golden plover	*Pluvialus dominica*	B	45.8	39.2
Black-bellied plover	*Pluvialus squatarola*	B	6.1	3.1
Killdeer	*Charadrius vociferus*		–	ac
Common ringed plover	*Charadrius hiaticula*	B	11.1	6.5
Greater yellowlegs	***Tringa melanoleuca***		**0.1**	**ac**
Ruddy turnstone	*Arenaria interpres*	B	2.3	0.7
Red knot	*Calidris canutus*	B	4.9	3.1
Purple sandpiper	*Calidris maritima*	(B)	0.7	0.2
Sanderling	*Calidris alba*	B	0.3	0.2
Dunlin	*Calidris alpina*	B	0.1	ac
Pectoral sandpiper	*Calidris melanotos*	B	7.2	3.4
Baird's sandpiper	*Calidris bairdii*	B	43.8	32.6
White-rumped sandpiper	*Calidris fuscicollis*	B	23.8	15.1
Stilt sandpiper	***Calidris himantopus***		**<0.1**	**ac**
Buff-breasted sandpiper	***Calidris subruficollis***	**B**	**0.3**	**0.1**
Red phalarope	*Phalaropus fulicarius*	B	9.2	3.6
Red-necked phalarope	*Phalaropus lobatus*		0.5	0.2
Glaucous gull	*Larus hyperboreus*	B	79.4	72.3
Iceland gull (ssp Thayer)	*Larus glaucoides thayeri*	(B)	1.0	0.3
Sabine's gull	*Xerma sabini*	B	<0.1	ac
Black-headed gull	***Chroicocephalus ribundus***		**–**	**ac**
Black-legged kittiwake	*Rissa tridactyla*	(B)	0.1	1.5
Arctic tern	*Sterna paradisaea*	B	4.7	5.3

Table 2. (*concluded*).

Common name	Scientific name	Breeder[1]	Occurrence (%)	Abundance (N/100 h)
Black guillemot	*Cepphus grylle*	(B)	0.1	ac
Long-tailed jaeger	*Stercorarius longicaudus*	B	66.8	89.1
Parasitic jaeger	*Stercorarius parasiticus*	B	42.7	41.5
Pomarine jaeger	*Stercorarius pomarinus*		0.8	0.3
Common raven	*Corvus corax*	B	56.5	31.3
Horned lark	*Eremophila alpestris*	B	31.4	15.2
Barn swallow	*Hirundo rustica*		0.3	0.1
Tree swallow	***Tachycineta bicolor***		–	ac
Northern wheatear	*Oenanthe oenanthe*	B	0.4	0.2
American pipit	*Anthus rubescens*	B	6.3	3.2
Savannah sparrow	***Passerculus sandwichensis***		<0.1	ac
Lapland longspur	*Calcarius lapponicus*	B	87.0	262.8
Snow bunting	*Plectrophenax nivalis*	B	14.9	10.2
Hoary redpoll	*Acanthis hornemanni*	B	0.5	0.1
MAMMALS				
Brown lemming	*Lemmus trimucronatus*	B	14.2	5.2
Collared lemming	*Dicrostonyx groenlandicus*	B	4.6	1.5
Lemming sp.	-		4.8	2.6
Arctic hare	*Lepus arcticus*	B	3.2	0.9
Caribou	*Rangifer tarandus*		–	ac
Ermine	*Mustela richardsonii*	B	2.0	0.5
Arctic fox	*Vulpes lagopus*	B	34.5	9.0
Red fox	*Vulpes vulpes*	B	0.4	0.1
Wolf	*Canis lupus*		<0.1	ac
Polar bear	*Ursus maritimus*	(B)	0.5	0.1
Ringed seal	*Phoca hispida*		–	–

Note: Occurrence is the percentage of daily checklists ($N = 3584$ checklists) where the species was recorded and relative abundance is the number of individuals recorded per 100 h spent in the field ($N = 23\,708$ person-hours) during systematic collection of incidental observations, 2007–2022 (Gauthier and Cadieux 2020*c*). Species in bold were recorded for the first time on Bylot Island by our team. Scientific names of vertebrate species mentioned in the text appear here.
[1]B, recorded breeding on the south plain of Bylot Island; (B), recorded breeding elsewhere on Bylot Island or by other teams.
[2]ac, accidental (abundance <0.05 individual per hour; mostly ≤5 individuals observed in total, often only one)
[3]Cackling geese were formerly lumped with Canada geese. A few observations of Canada geese are confirmed, but some old observations were likely cackling geese; hence, no quantitative information available.
[4]–, Species observed before 2007 or outside our systematic collection of incidental observations.

2023). Our long-term research was also instrumental in deciphering the influence of snow and ice on wildlife ecology (Domine et al. 2018), with obvious benefits for our understanding of the effects of climate change effects. In particular, we described how water phase transitions generate some critical places and times that play a disproportionate role in the ecology of tundra wildlife (Berteaux et al. 2017*b*). Examples of such places and times include respectively the soil–snow interface where increased snow hardness prevents subnivean travel and feeding by small mammals, and the spring snow melt period when habitat reflectance changes, thus modifying camouflage opportunities to predators and prey.

Unexpected findings

Long-term research programs are prone to yield unexpected results from time to time and the Bylot Island one is no exception. Initial investigation of goose bioenergetics contradicted the idea that they were strict capital breeders, as previously documented in sub-Arctic snow geese (Ankney and MacInnes 1978). Proximal analyses of goose carcasses during laying suggested that a large proportion of egg nutrients came from food acquired in the Arctic and not from body reserves accumulated on southern staging areas (Choiniere and Gauthier 1995). Despite some initial critics, subsequent analyses using stable isotopes provided a robust confirmation that greater snow geese used a mixed income/capital strategy to lay their eggs (Gauthier et al. 2003). The innovative approach developed in this study paved the way for subsequent studies that used stable isotopes to examine the contribution of exogenous versus endogenous nutrients to egg formation in other avian species (Hobson 2006).

Tundra-nesting snowy owls were traditionally considered a small-mammal specialist with the bulk of the population migrating south in winter (Parmelee 1992). Satellite tracking of owls nesting on Bylot Island revealed a different pattern as most adult females and the single male marked spent the winter in the Arctic instead of moving south to temperate areas (Robillard et al. 2018). Even more surprising, most of them extensively used the Arctic sea ice in winter and settled preferentially near polynias (Therrien et al. 2011) where they apparently fed on seabirds (Robillard et al. 2017, 2021), as previously suggested by anecdotal reports (Robertson and Gilchrist 2003). Nonetheless, our studies were the first to show that it is the dominant wintering strategy of adult snowy owls breeding in the eastern Canadian Arctic.

Although natural history observations are an important part of ecology and evolution, they are often underappreciated because they do not fit the hypothetico-deductive method. Yet, we made many natural history observations that constituted a scientific "aha" or "wow" moment that broadened our thinking. For example, we reported the first observation of predation of Arctic fox pups by common ravens, thus showing how continuous monitoring of dens using automated cameras allows documentation of rare trophic links (Chevallier et al. 2016). Our long-term study of lemmings combined with a predator reduction experiment allowed us to capture a brown lemming over three consecutive summers (Fauteux et al. 2018*b*). This demonstrated that brown lemmings are physiologically capable of living up to 24 months in the High Arctic rather than only a few months as commonly assumed, and that a shift in the age-structure of lemming populations is possible in periods or at locations of high survival.

Community involvement in research and Inuit ecological knowledge

Involvement of the Bylot Island researchers in the community of Pond Inlet has been sustained for more than two decades. Every year, Inuit from the community are hired to work as field assistants at what is locally known as the Goose Camp. Students and researchers regularly organize numerous outreach activities including presentations at the local school, public conferences, or animation of a booth at the COOP with videos and material used to study wildlife. In June 2006, we organized a 1 week Elder-Youth–Scientist camp on Bylot Island. Discussions focused on Inuit knowledge about local wildlife and other activities such as seal hunting, storytelling, traditional cooking, and survival skill sharing also took place. Workshops to exchange on research activities with representatives of local groups such as the Hunters and Trappers Organization (HTO) or the Hamlet Office are periodically organized. One of the most extensive workshops was a consultation on ecological monitoring in the north Baffin region held in February 2018 and was attended by over 50 participants (Gérin-Lajoie et al. 2018). Multiple knowledge gaps and research needs were identified by local participants during the consultation. This led to the initiation in 2019 of a new long-term study on contaminants in bird eggs consumed by local Inuit, primarily snow goose and murre eggs, in collaboration with the Mittimatalik HTO. Our team also maintains a trilingual website (English, French, and Inuktitut) on research activities at the Bylot Island Field Station (https://bylot.cen.ulaval.ca/).

Being able to pair Indigenous and local knowledge with science-based knowledge is vital to the work of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) and the Convention on Biological Diversity (CBD) (Tengo et al. 2017). In Canada, establishing a dialogue between Indigenous and non-Indigenous perspectives is also necessary to advance reconciliatory efforts (Reid et al. 2021). Equitably embracing these multiple perspectives is not easy, however, and requires long-term partnerships between local communities and research teams. Using participatory approaches in Pond Inlet, we conducted an Inuit and science-based knowledge project about snow geese and Arctic foxes (Gagnon and Berteaux 2009). The project led to the documentation and archival of local stories and knowledge about the species, as well as to another Elder-Youth camp. It also contributed to expand the spatial and temporal scales of knowledge on the ecology of Arctic foxes, and to a lesser extent of snow geese. Through this project, we demonstrated the importance of spatial and temporal scales when attempting to interweave different types of knowledge and later applied our learned skills to other tundra systems (Gagnon et al. 2020). Other joint projects between scientists and the community or Inuit organizations are in development.

Direct contributions from research and monitoring to policy or legislation

Scientific information generated by the long-term study of greater snow geese on Bylot Island has been vital for the management of this population by the Canadian Wildlife Service and the US Fish and Wildlife Service over the past 35 years (Lefebvre et al. 2017). For instance, initial designation of the population as overabundant and modelling of the impact of various harvest scenarios on future population growth were based in part on results from our studies (Batt 1998). This led to the implementation in 1999 of a spring conservation harvest in southern Quebec to stop the growth of the population, a première in North America since the Migratory Bird Act of 1917 between Canada and the USA, as well as more liberal regulations during the fall and winter hunting seasons. Monitoring of the impacts of these unprecedented management actions, and subsequent ones such as the Conservation Order implemented in 2009 in the USA (another special hunting season), was again largely based on field studies conducted on Bylot Island (Calvert and Gauthier 2005; Reed and Calvert 2007; LeTourneux et al. 2022). These management actions, which were successful in stopping the growth of the population, and the monitoring of their impacts on the demography of greater snow geese are considered a success story in North America (Lefebvre et al. 2017).

The Bylot Island Field Station has been a member of several networks, such as the International Network for Terrestrial Research and Monitoring in the Arctic (INTERACT; https://eu-interact.org/) since 2010. The Circumpolar Initiative on Predator–Prey interactions in Arctic Terrestrial Ecosystems (Interaction Working Group), a follow up of the IPY project ArcticWOLVES, aimed at monitoring breeding shorebirds and measuring the cascading effect of indirect trophic interaction at the circumpolar scale, is co-led by our team. The vertebrate monitoring program of Bylot Island is also affiliated with the Circumpolar Biodiversity Monitoring Program of the Conser-

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vation of Arctic Flora and Fauna (CAFF, https://www.caff.is/; Christensen et al. 2013). Results from our studies have been used in major international syntheses such as in chapters on birds, mammals, and terrestrial ecosystems in the Arctic Biodiversity Assessment report of CAFF (Meltofte 2013). More recently, our team co-led circumpolar assessments of key tundra vertebrate groups including Arctic foxes (Berteaux et al. 2017a) and lemmings (Ehrich et al. 2020), which helped in identifying conservations needs. At a more local scale, our results are used by Parks Canada to monitor the ecological integrity of the Sirmilik National Park.

Future monitoring prospects

The long-term studies of the vertebrate fauna of Bylot Island provide a robust and unique dataset to detect, understand, and predict how climate change and other environmental stressors should affect Arctic biodiversity in the future. Despite the wealth of information generated by this program, some gaps remain, in particular during the long Arctic winter, a period where field studies are extremely difficult but when significant biological processes still occur (Berteaux et al. 2017*b*). Yet, increasing evidence that periodic changes in the strength of trophic interactions triggered by seasonality can be a major factor shaping the tundra food web (Hutchison et al. 2020) reinforces the importance of studying wildlife populations all year round, including during the data-deficient winter. In the past two decades, there has been a surge of technological developments in biologging equipment adapted to monitor animal movements and their behaviour at multiple scales under extremely cold temperatures. A greater integration of these advanced technologies in our field studies is a promising avenue to broaden the spatial and temporal scales of our monitoring and improve our understanding of the rapidly changing Arctic biota.

At the very fine spatial scale, the development of a new generation of automated cameras capable of filming lemmings and their mustelid predators under the snow (Kalhor et al. 2021; Mölle et al. 2022) should help us to monitor their abundance and behaviour during the winter. It could also measure more accurately the intensity of lemming winter reproduction, a key factor to explain their cyclic population fluctuations (Fauteux et al. 2015; Domine et al. 2018). These winter processes are likely to be affected by changing snow conditions due to climate warming (Berteaux et al. 2017*b*).

At larger spatial scales, high-throughput tracking technologies bring new approaches to the study of animal movement (Nathan et al. 2022), thus opening new avenues in behavioural and community ecology, as well as in the global ecology of the changing Arctic. Integrating large-scale migratory movements of animals at the ecological community level should help us to assess the vulnerability of those communities to changes occurring in distant locations connected through animal movements (Moisan et al. 2023). Although our most recent work makes use of big-data approaches (Clermont et al. 2021*a*, 2021*b*), we have not yet tracked simultaneously multiple interacting species at fine temporal and spatial scales. Applying these innovative approaches should allow us to estimate biological parameters that are currently hard to obtain under natural conditions (e.g., prey encounter rate, predator consumption rate), thereby improving mechanistic models of predator–prey interactions (Beardsell et al. 2022, 2023) and population dynamics (Hutchison et al. 2020; Bergeron 2022). Doing so will undoubtedly benefit our future work since biological interactions, which are the cement of food webs, and impacts of climate change are two central concepts structuring our monitoring and research efforts. That being said, future monitoring of the Bylot Island ecosystem will always depend on good boots, strong backpacks, and long hours spent in the tundra, since valid data interpretation will remain impossible without a solid experience of field conditions and patient observations of Arctic wildlife.

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Data availability

Monitoring data from the Bylot Island Field Station are available online on the Nordicana D data portal of the Centre d'études Nordiques, Université Laval (https://nordicana.cen.ulaval.ca). Full references of all database listed in Table 1 are presented in the References section.

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Competing interests

The authors declare there are no competing interests.

Ethical statement

All vertebrate research on Bylot Island has been approved by ethical committees of Université Laval, Université du Québec à Rimouski or the Canadian Museum of Nature in accordance to the Canadian Council on Animal Care (CCAC) guidelines.

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APPENDIX A

Table A1. List of all funding agencies.

Funding agency	Funding program
Natural Sciences and Engineering Research Council of Canada	Discovery Grant Northern Supplement Research Tools and Instruments Special program of the International Polar Year Discovery Frontiers (ADAPT) Canada Research Chairs Collaborative Research and Training Experience program (CREATE)
Fonds Québécois de Recherche Nature et Technologies	Équipes de recherche Relève professorale Regroupement Stratégique (Centre d'études nordiques)
Natural Resources Canada	Polar Continental Shelf Program
Network of Centers of Excellence Canada	ArcticNet
Canada First Research Excellence Fund	Sentinel North Program
Polar Knowledge Canada	Northern Scientific Training Program Science and Technology Program
Environment and Climate Change Canada	Contribution Agreement Arctic Goose Joint Venture Northern Ecosystem Initiative Access to the Pond Inlet Research Station
Canada Foundation for Innovation	John R. Evans Leaders Fund Innovation Fund
Parks Canada Agency	
International Polar Year program of the Government of Canada	Science and research projects Arctic Research Infrastructure Fund Logistics for Health and Safety
Crown–Indigenous Relations and Northern Affairs Canada	Northern Contaminant Program
Duck Unlimited Canada	
Kenneth M. Molson Foundation	Kenneth M. Molson Foundation's donation for wildlife research, conservation, and habitat
Garfield Weston Foundation	
First Air—Canadian North	
Nunavut Wildlife Management Board	
Université Laval	
Université du Québec à Rimouski	Support to research groups