

Svalbard reindeer

(*Rangifer tarandus platyrhynchus*)

A status report



Åshild Ønvik Pedersen, Ingrid M. G. Paulsen, Steve Albon, Gustav Busch Arntsen, Brage B. Hansen, Rolf Langvatn, Leif Egil Loe, Mathilde Le Moulllec, Øystein Overrein, Bart Peeters, Virve Ravolainen, Erik Ropstad, Audun Stien, Nicholas J. C. Tyler, Vebjørn Veiberg, Renè van der Wal, Roy Andersen, Larissa T. Beumer, Isabell Eischeid, Mads Forchhammer, R. Justin Irvine, Filippo Marolla, Gabriel Pigeon, Eigil Reimers, and Liv Monica Trondrud



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The Norwegian Polar Institute is Norway's central governmental institution for management-related research, mapping and environmental monitoring in the Arctic and the Antarctic. The Institute advises Norwegian authorities on matters concerning polar environmental management and is the official environmental management body for Norway's Antarctic territorial claims.

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Preface

The Svalbard Environmental Protection Fund granted the Norwegian Polar Institute (NPI) funds for the project «Svalbard reindeer 2017 – status, research needs and knowledge gaps» (project 16/70). The groundwork for this comprehensive report, which builds on scientific and grey literature, was made in a workshop hosted by NPI at the University Centre in Svalbard (UNIS), in November 2017. National and international experts on the Svalbard reindeer (*Rangifer tarandus platyrhynchus*) from NPI, Aarhus University, James Hutton Institute, Norwegian Institute for Nature Research (NINA), Norwegian University of Life Sciences (NMBU), Norwegian University of Science and Technology (NTNU), UiT – The Arctic University of Norway and University of Aberdeen joined forces with managers from the Governor of Svalbard, NPI and the Directorate for Nature Management and students to answer project goals.

The scientific committee for the workshop consisted of Åshild Ønvik Pedersen, Virve Ravolainen, Øystein Overrein (NPI), Audun Stien (NINA) and Mads Forchhammer (UNIS). The report consists of contributions from a selected group of authors, and Ingrid M. G. Paulsen and Åshild Ønvik Pedersen acted as editors. Steve Albon, Rolf Langvatn and Eigil Reimers contributed with their long-term experience in Svalbard reindeer research and gave advice on the final report content. René van der Wal assisted the final editing of the report. Along with this report we have built an EndNote library of available literature on Svalbard reindeer, which is available through the websites of NPI and the Svalbard Environmental Protection Fund.

We thank the Svalbard Environmental Protection Fund for financially supporting the project. Further, we thank Ivar Stokkeland (NPI) for his huge effort of scanning books and reports, Heli Routti (NPI) for quality checking text and Berit Jakobsen (UNIS) for access to the digital database developed by Rolf Langvatn in 2003.

Longyearbyen, September 2019



The Svalbard reindeer is the only resident large herbivore and a key-species of the Svalbard tundra ecosystem.
Photo: Tore Nordstad/NPI.

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Executive summary

The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) is the only large resident herbivore in the High Arctic Svalbard archipelago (74-81° North, 10-35° East). The earliest known presence of this endemic species dates to more than 5000 years before present, and recent genetic evidence indicates an eastern colonisation route. The Svalbard reindeer is key to the structure and functioning of the tundra food web due to its interactions with other species across the various trophic levels. Currently, the Svalbard reindeer populations have recovered from overexploitation, after protection in 1925, and is present in most vegetated parts of the archipelago. Unlike many other reindeer subspecies, the Svalbard reindeer has increased in density and expanded its spatial range. Today its total population size is estimated to be approximately 22,000 individuals.

Our knowledge of the biology of this subspecies of reindeer, comes mainly from research conducted over the last 50 years. A wide range of aspects has been investigated, revealing remarkable physiological adaptations of Svalbard reindeer to the High Arctic environment and counter-intuitive impacts of climate change on its population dynamics. Yet, many aspects of the species' biology, impact on the wider ecosystem and susceptibility to various environmental changes remain not well understood.

Anatomical, physiological and behavioural adaptations enable the Svalbard reindeer to live comfortably in its environment. The reindeer maintain core body temperatures close to 38°C even in winter, by reducing energy requirements and enhancing their ability to extract energy from the environment. They optimally utilise the short growing season, and fat content at the end of the growing season can be up to one-third of their body weight. Their small body size is likely an adaptation to scarce resources, and their thick fur offers excellent insulation against strong winds and sub-zero temperatures in winter. However, there are many knowledge gaps related to their adaptive capacity – both behavioural and physiological responses in individuals and populations – to the dramatic changes of the Svalbard tundra environment.

The range use of Svalbard reindeer is limited by physical barriers imposed by open seas, glaciers and mountains. In the vegetated lowlands during summer, they forage on vascular plants, most of which are of high nutritional quality throughout the growing season. In winter, reindeer switch to foraging on mosses and dead plants. Lichens, which constitute an important winter food of most other *Rangifer* populations, are almost entirely lacking from their diet. In the absence of predators and harassing insects, the Svalbard reindeer mainly selects habitats based on seasonal energy and nutrient requirements. Unlike many other *Rangifer*

sub-species, the Svalbard reindeer is non-migratory, lives either solitary or in small groups and displays high site fidelity to rather small home ranges. However, in harsh winters, the reindeer may move in search for forage, or use alternative feeding strategies such as high-elevational or shore feeding. Knowledge of many aspects related to habitat selection at different spatial and temporal scales, and the linkages to fitness components of individuals and populations, remains unknown.

Long-term time series of reindeer population abundance have formed the basis for understanding how populations of Svalbard reindeer are regulated. Annual population fluctuations are mainly driven by density dependent competition for food resources in winter and winter weather variability, with an addition effect of parasites. Current hunting practices have limited impacts on reindeer populations and are anticipated to be sustainable. Hunting of reindeer is strictly regulated and the annual offtake from the quota-based harvest ranges from 117 to 235 individuals. Similarly, no studies have found long-term negative impacts from diseases, human traffic or environmental contaminants on reindeer populations.

Fluctuations in population size appear linked to recent climate warming. Rain, falling on frozen ground or snow during increasingly frequent warm spells in winter causes ground ice, which prevents access to forage and can cause high mortality and reduced reproduction. Summer warming boosts plant productivity and allows female reindeer to build up greater fat reserves before the onset of winter. While we know about the positive effects of warmer summers on forage production and reindeer body mass in autumn, the negative effects of rain-on-snow on body mass in April and on subsequent population growth rate, there remain many questions that require answers. Some of these are the consequences of a longer snow-free season and the timing of rain-on-snow events on Svalbard reindeer reproduction and mortality.

The Norwegian government has set goals for maintaining and protecting Svalbard's relatively untouched nature. This includes the conservation and management of the Svalbard reindeer and its habitats, so that they are not affected in a negative way. To meet this goal, further knowledge on the cumulative human stressors – with climate change being the most prominent – that affect the distribution, population size and fluctuations, is required to maintain healthy populations in this rapidly changing High Arctic environment.

1 Introduction

1.1 Background and rationale

Since the discovery of the archipelago in 1596 and up to the Second World War, information on the endemic Svalbard reindeer (*Rangifer tarandus platyrhynchus*) originates from whalers, trappers and various expeditions with occasional anecdotal reports. The first written note on the Svalbard reindeer is from 1827 (Anon 1827). In 1829, Svalbard reindeer was classified as a subspecies for the first time (Vrolik 1829), while a more extensive description was published in the wake of a Swedish expedition to Spitsbergen in 1858 (Andersøn 1863, Malmgren 1865). Moreover, some information on harvest of the populations was derived from trading lists of reindeer skins, and various sources reported on their distribution and population numbers. Information and available literature sources up to the 1950s were summarised by Lønø (1959).

Scientific research on the Svalbard reindeer started in the 1970s with the *Man and the Biosphere Programme* (MAB). This programme took a broad approach to Svalbard reindeer ecology and focused on history and origins of the subspecies, population abundance estimation, nutritional ecology, energetics, genetics and parasitology. Many reports and scientific papers were published from the MAB programme, and this work was summarised by Øritsland (1986). In cooperation with MAB, several studies also addressed the physiological aspects of Svalbard reindeer adaptations to Arctic conditions. These findings were summarised by Blix (2016). In parallel to the MAB programme, population monitoring was first initiated in 1978 on Brøggerhalvøya, West Spitsbergen (Persen et al. 1983, Staaland et al. 1993) and in 1979 in Adventdalen and Reindalen, Central Spitsbergen (Tyler 1986a, Solberg et al. 2001). See figure 1 for locations of these study areas in Svalbard.

Results from the MAB programme generated new questions, which could only be approached by studying individuals, for example using visible markings, including ear tags and neck collars. The advent of new radio technology, which became functionally reliable and affordable in the late 1990s, enabled studies to focus on individually identifiable reindeer within the monitored populations (Langvatn et al. 1999). In particular, since the Millennium GPS collars have generated large individual-based datasets with high precision on activity and movement of female reindeer in Nordenskiöld Land (Loe et al. 2016) and in coastal locations of Forlandsundet and Kongsfjorden (Pedersen et al. 2018). During the last two decades, the main research focus has been on the cumulative effects of climate change on reindeer vital rates, demography and population dynamics.

Today, the scientific work accumulated gives a better understanding than ever before of how Svalbard reindeer have adapted to, and interact with, their High Arctic environment. This knowledge is crucial to understand how the species and ecosystem respond to the large environmental changes associated with climate change. The present report summarises the knowledge from scientific papers, reports, theses, books and anecdotes, mainly from the early 1970s up to the present. Based on this information, we outline knowledge gaps and research needs.

As part of the delivery to the Svalbard Environmental Protection Fund, we have extended and completed the bibliography on Svalbard reindeer initiated at the University Centre in Svalbard (UNIS) in 2003. This bibliography contains an up-to-date list of published reports, scientific papers and grey-literature and is available with the digital edition of this report.

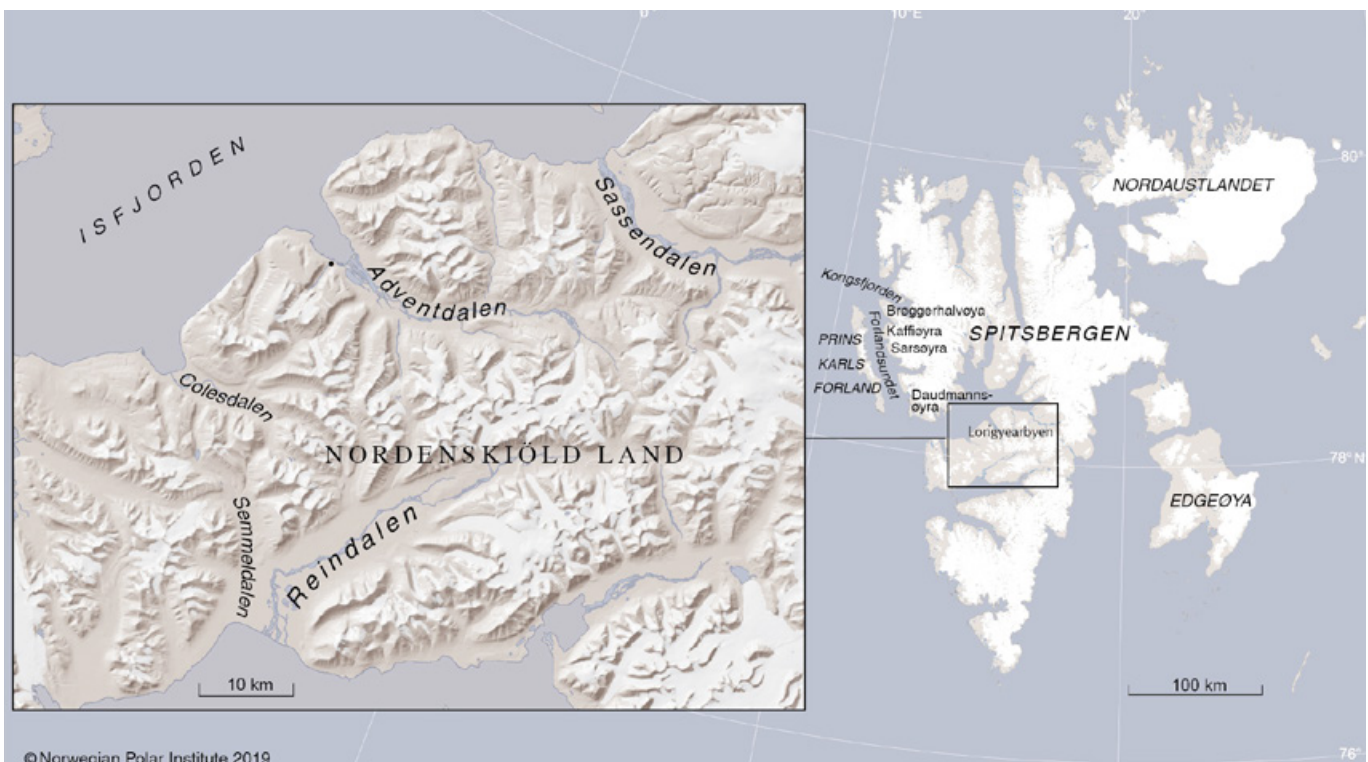


Figure 1. Map of place names related to studies on Svalbard reindeer in the High Arctic archipelago of Svalbard. Illustration: Oddveig Ø. Ørvoll/NPI.



The time series of Svalbard reindeer female capture–mark–recapture data from inland (1994 till present) and coastal regions (2014 till present) allow for studying individuals throughout their lifespan. Here scientists handle a captured female reindeer. Photo: Mads Forchhammer/UNIS.

1.2 History and evolution

When and how the Svalbard reindeer arrived in the archipelago has been debated due to the geographic isolation of the Svalbard archipelago and the vast distance from other reindeer populations (Lønø 1959, Staaland and Røed 1986). The earliest known evidence dates back to more than 5000 years before present (BP) based on carbon dating of reindeer droppings (Van der Knaap 1986). Reindeer may have colonised Svalbard naturally sometime after the peak of the last ice age 20,000–18,000 BP (Gravlund et al. 1998), but most probably this occurred later when the climate became milder (6700–5000 BP; Van der Knaap 1986). Røed (2005) reports three separate origins from the last glaciation of today's wild reindeer species. The most influential origin contributed to the gene pool of most extant subspecies, including the Arctic subspecies (*R.t platyrhynchus*, *R.t pearyi* and *R.t groenlandicus*). Due to these genetic similarities across reindeer subspecies in different geographic localities, this suggests existence of a large and continuous reindeer population ranging across extensive tundra areas in Eurasia and Beringia during the last glaciation.

Recent evidence (Kvie et al. 2016) indicates an eastern colonisation route. The High Arctic archipelago of Franz Josef Land, 400 km east of Svalbard, may have been used as a possible migration route, as bone remains on the archipelago date back to 6000 BP (Forman et al. 2000). The endemic Svalbard reindeer is the most isolated species of all 12 described subspecies of reindeer (Fig. 2; Gunn 2016). This has led to different morphological traits and low genetic diversity (Côté et al. 2002). The Svalbard reindeer, with a small body size, short legs and a rounded, small head resembles the appearance of other High Arctic subspecies, including the *R.t pearyi* from the Canadian Arctic islands (Box 1).



Figure 2. Distribution of reindeer and caribou (*Rangifer*) in the Arctic. Figure from CAFF Arctic Flora and Fauna (2001). Figure modified by Oddveig Ø. Ørvoll/NPI.

Svalbard reindeer body characteristics

Body appearance: Svalbard reindeer have short legs and a relatively small, stunted and round head. The males are larger in body size than the females (sexual dimorphism). Their cranial length and the nose bone and volume are considerably smaller compared to other subspecies of reindeer, which gives Svalbard reindeer their characteristic look. This is reflected in their Latin name *Rangifer tarandus platyrhynchus*, which means the flat-nosed reindeer.

Pelage: The fur of Svalbard reindeer is brown across the back and pale-yellow to white on the stomach. During winter, their fur is paler than during summer. The thick winter fur makes animals appear fat and their legs even shorter.

Antlers: Male reindeer develop antlers during the spring months (April to June). Prior to the rut (October) they lose the velvet on the antlers. Males shed their antlers from early winter (November to January). The growth of female antlers starts in June (after calving) and they shed their antlers prior to the next calving season.

Source: <https://www.npolar.no/arter/valbardrein/>

See also the EndNote library Svalbardrein.enl, which is available with the digital edition of the report.

This library has numerous references that detail the content of this textbox.



Svalbard female reindeer with calf.
Photo: Bjørn Frantzen/NIBIO.



Svalbard male reindeer.
Photo: Bart Peeters/NPI.

1.3 Distribution and abundance

Large parts of Svalbard are covered by glaciers (60 %), while the remaining land areas are vegetation covered (15 %) or barren, rocky (25 %) areas (Johansen et al. 2012). Vegetated areas suitable for reindeer grazing are mainly found on the larger peninsulas and relatively close to the coast. An extensive survey across the archipelago (2013–2016; Fig. 3) showed that the largest populations occur on Nordenskiöld Land and Edgeøya (Le Moulllec 2019a).

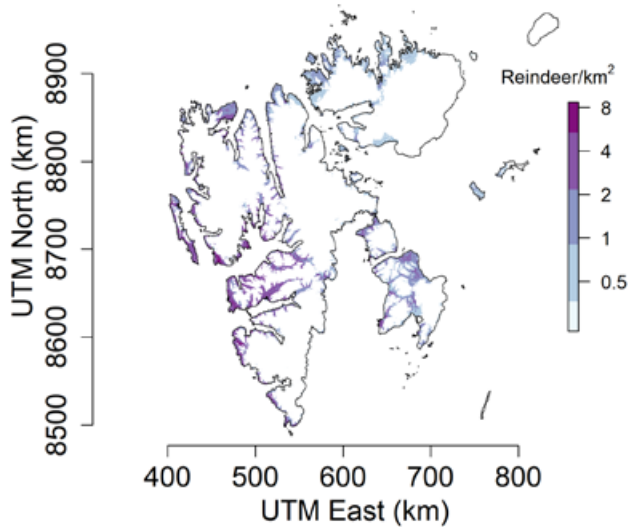


Figure 3. Svalbard reindeer current distribution and density map. Reindeer density prediction is obtained from spatial density models based on distance sampling transects conducted in 2013–2016 across the archipelago. Adapted from Le Moulllec (2019a).

At the time when humans began to explore and exploit the natural resources in Svalbard, reindeer were present across the vegetated areas of the archipelago – based on carbon-dated subfossils and literature reports (Le Moulllec 2019a) – but intensive, unregulated hunting quickly reduced the reindeer population to around 1000 individuals in the early 20th century (Wollebæk 1926). At the time of protection in 1925, only four spatially segregated populations remained (Lønø 1959). After protection, the population recovered and spread to most vegetated areas of Svalbard (except Bjørnøya and Kvitøya), mainly by natural recolonisation of former ranges (Le Moulllec 2019a). However, humans also contributed to the recolonisation by reintroducing 15 reindeer to Brøggerhalvøya (1978) (Holand et al. 1981, Staaland et al. 1993, Aanes et al. 2000) and 12 to Daudmannsøyra (1984–85) (Gjertz 1995). The reintroduced reindeer population on Brøggerhalvøya grew quickly and dispersed to other areas in Forlandsundet (Sarsøyra, Kaffiøyra and Prins Karls Forland) and Kongsfjorden (Aanes et al. 2000). The harvest of Svalbard reindeer was re-opened in 1983, first for research purposes and from 1989 onwards also for residents (Overrein 2003), by which time the population size was estimated to be approximately 11,000 reindeer (Øritsland 1986). At present, the Svalbard reindeer population is estimated to be around 22,000 [range (95 % CI): 21,000–23,000], with capacity to increase further, as incomplete recovery from past overharvest is still detected in some areas (Le Moulllec 2019a).



Svalbard reindeer is the northernmost subspecies of Rangifer. The species has adapted to the High Arctic environment in Svalbard over several thousands of years. Photo: Ronny Aanes/NPI.

2 Adaptations to the Arctic environment

The Arctic is often portrayed as a barren, inhospitable place where life itself is a struggle. Research, however, shows that even in the depth of winter most resident, non-hibernating mammals like Svalbard reindeer are warm and well-fed. Anatomical, physiological and behavioural adaptations enable polar species to live comfortably in an environment where, without special equipment, humans would quickly perish.

Life in the Arctic presents a variety of challenges, the most obvious being the low ambient temperature, scarcity of food and continuous darkness in winter. None of these are unique to the Arctic: Himalayan yaks (*Bos grunniens*) are exposed to severe cold in winter; Saharan addax (*Addax nasomaculatus*) face scarcity of food; moles (*Talpidae*) live in darkness. The distinguishing feature of Polar regions, however, is that these three features occur simultaneously.

Svalbard reindeer are homoeothermic endotherms: like most mammals they maintain a body core temperature (T^b) close to 38°C. Unlike most mammals, however, they live in an environment where the mean ambient temperature (T^a) in winter (October to April) is some 50°C below this. The problem the reindeer face is not merely that of defending their core temperature against such a large thermal gradient (i.e., $T^a - T^b$) but, owing to scarcity of food, of having to do so at low expenditure of energy. Their solution involves three strategies: (1) reducing energy requirements, (2) enhancing their ability to extract energy from the environment and (3) storing energy.

2.1 Reducing energy requirements in winter

Svalbard reindeer minimise their requirement for energy, and hence for food, in winter mainly in two ways: 1) They restrict heat loss to the environment and 2) they minimise energy retention.

2.1.1 Adaptation to cold

Svalbard reindeer invoke both physical and physiological adaptations to restrict heat loss and hence reduce their energy requirements in winter.

Physical adaptations

Svalbard reindeer are more compact in body size compared to mainland sub-species. They have notably short muzzles, from which their subspecific name '*platyrhynchus*' derives (πλατύς [platus]: flat and broad; ῥύγχος [rhúnkhos]: snout), short ears and conspicuously short legs (Vrolik 1829, Wollebæk 1926); Fig. 4). This conformation increases thermal efficiency in two ways. First, it minimises the overall surface area to volume ratio of the animals. Second, it reduces the relative length of thin appendages which, having small radiuses, are efficient radiators. The animals also have a very thick winter coat (Fig. 5). The long guard hairs extending from the skin to the surface of the coat are presumably hollow and contain a honeycomb of air-filled cavities separated by thin septa like those of Eurasian mountain reindeer (*R. t. tarandus*; Timisjärvi et al. 1984, Blix et al. 2015), although this has not been confirmed.

The winter coat of Svalbard reindeer affords the animals superb insulation (Nilssen et al. 1984b), which seems not to be affected even by very strong wind (Cuyler and Øritsland 2002).



Figure 4. Adult female Svalbard reindeer (top) and Eurasian mountain reindeer, both in winter coat. Svalbard reindeer have notably shorter muzzles, short ears and short legs compared to their mainland sub-species. Photos: Nicholas Tyler.

Physiological adaptations

Reindeer limit conductive heat loss by peripheral cooling thereby reducing the temperature gradient between poorly insulated extremities (e.g., face and feet) and the environment. The temperature of the feet of reindeer, for instance, may approach 0°C (Irving and Krog 1955). Peripheral cooling is achieved by reducing peripheral circulation and by vascular arrangements that facilitate counter-current heat exchange. Thus, warm arterial blood ascending to the periphery is cooled by venous blood returning from it. Vasomotor (circulatory) control allows variation in the distribution of blood flow and the extremities can be employed to conserve or alternatively to dissipate heat, depending on the heat load on the animal (Johnsen et al. 1985b, Blix 2016).

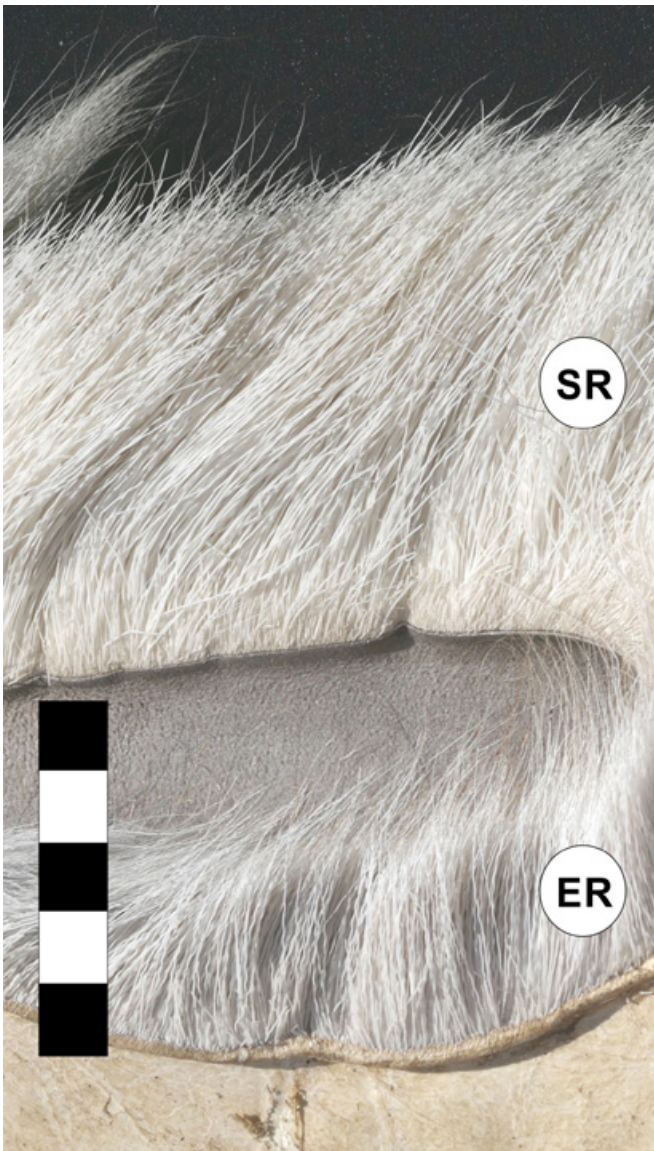


Figure 5. The winter coat of Svalbard reindeer (SR) is twice as deep as that of Eurasian mountain reindeer (ER). The photos show samples of fur close to the tail in adult reindeer: SR female; ER sex not known. Scale bar in 1 cm intervals. Photo: Nicholas Tyler.

Reindeer reduce evaporative heat and water loss from the respiratory tract by counter-current heat exchange in the nasal mucosa (the lining of the snout and nose). By this means the animals are able to recover at expiration (breathing out) around 65 % of the heat and 80 % of the water added to air at inspiration (breathing in; Blix and Johnsen 1983, Johnsen et al. 1985a, Blix 2016). This is an active process and the animals are capable of adjusting the efficiency of nasal heat exchange and hence of maintaining thermal balance despite great seasonal changes in body insulation (Blix and Johnsen 1983, Johnsen et al. 1985a, Johnsen et al. 1985b, Mercer et al. 1985).

Reindeer are exceedingly well adapted to the cold and, with the exception of newborn calves, it is almost inconceivable that they suffer hypothermia except under exceptionally severe circum-

stances. Newborn calves potentially suffer hypothermia when exposed to wet and windy weather. They are born with substantial amounts of brown fat — a thermogenic (heat producing) tissue — to protect themselves from the cold (Lentz and Hart 1960, Markussen et al. 1985, Soppela et al. 1986, Soppela et al. 1992).

Not surprisingly, the insulation which protects reindeer from the cold renders them susceptible to over-heating when they exercise vigorously. A winter insulated Svalbard reindeer running at $9 \text{ km} \cdot \text{h}^{-1}$ produces four times more heat than one at rest (Nilssen et al. 1984a). Reindeer are capable of panting (Aas-Hansen et al. 2000) and of peripheral vasodilatation (i.e., widening of blood vessels to increase the volume of flow to surface tissues; Johnsen et al. 1985b), but these may not be sufficient to enable the exercising animal to lose heat as fast as it is produced. Animals in this situation may employ nasal heat exchange to cool the brain while simultaneously allowing heat to accumulate in the rest of the body, resulting in increased core temperature (Johnsen et al. 1987, Johnsen and Folkow 1988, Blix et al. 2011).

None of the mechanisms in thermoregulation outlined here have been investigated in Svalbard reindeer; all, however, may reasonably be assumed to apply and are perhaps even enhanced in this sub-species.

2.1.2 Metabolic adaptation to seasonal environment

Svalbard reindeer are genetically programmed to capitalise on the abundance of food available in summer and to reduce their metabolic requirements in anticipation of the predictable scarcity of food in winter. Loss of weight and depletion of energy reserves in winter are conspicuous features of their programme of physiological responses to winter conditions.

Anabolic and catabolic phases

Svalbard reindeer annually transit between two contrasting phases of metabolic function: an anabolic (fat) phase in summer and a catabolic (lean) phase in winter. The anabolic (summer) phase is characterised by a vigorous physiological drive to grow. Hence, the animals display high appetite, a high level of foraging activity (Van Oort et al. 2007), high food intake (Larsen et al. 1985), high heart rate (Arnold et al. 2018) and rapid weight gain (Tyler 1987a; Fig. 6). Growth and fattening are enhanced by adaption of gastrointestinal microflora (see section 2.2.3) and by enhancement of the ability of adipocytes (fat cells) to take up metabolites from the blood and synthesise fat (lipids; Larsen et al. 1985). In the catabolic (winter) phase, by contrast, there is a spontaneous reduction in the physiological drive to grow. Hence, the animals display reduced appetite, reduced feeding activity, low food intake and loss of weight (Fig. 6).

The chief characteristic of the catabolic phase is anorexia which results in sustained negative energy balance, cessation of growth and loss of weight. This response is not in the least unusual and has been documented in many northern species of deer (e.g., French et al. 1960, Bandy et al. 1970, Loudon et al. 1989, Parker et al. 1993, Worden and Pekins 1995, Weber and Thompson 1998). The animals do not defend their fat autumn reserves even when they have the opportunity to do so and the resulting loss of weight and depletion of energy reserves in winter is therefore not evidence of undernutrition. Indeed, loss of weight is not even evidence of mobilisation of tissue reserves, but may largely reflect reduction

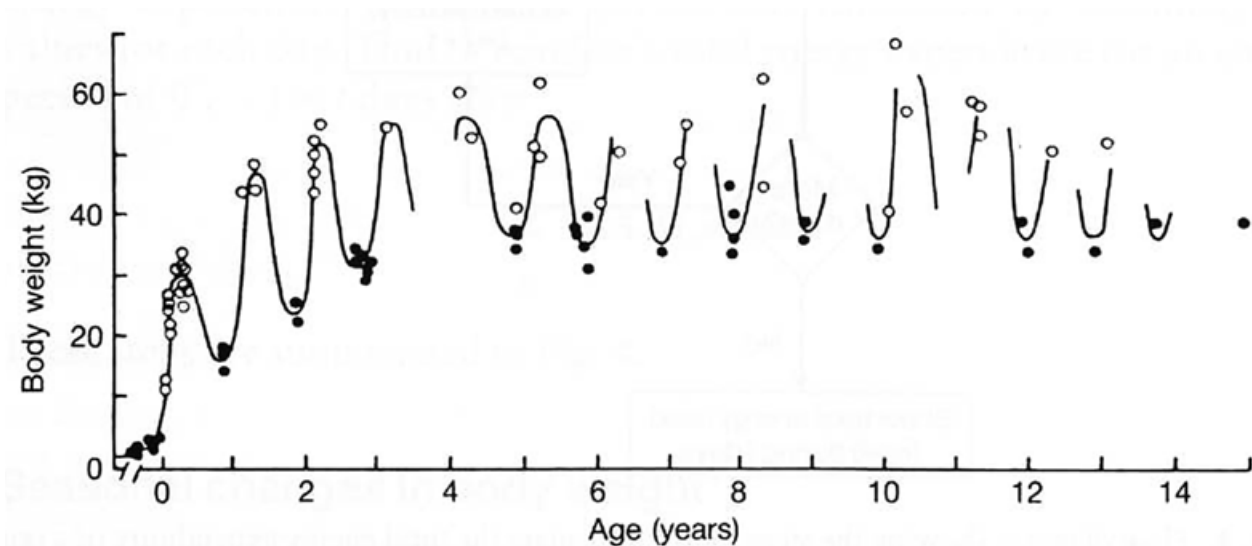


Figure 6. Growth curve for female Svalbard reindeer. Total body weight (kg) less the weight of the contents of the reticulo-rumen (all specimens) and the weight of the uterus and its contents (winter specimens). Each point represents one reindeer. Open circles indicate summer and autumn (July to October) specimens; solid circles indicate late winter (April to May) specimens. Figure from Tyler (1987a).

in the weight of the contents of the digestive tract concomitant with seasonal anorexia (Tyler et al. 1999). Environmental factors of course influence the energy balance and physical integrity of Svalbard reindeer to some extent, but their effects on the growth and performance of the animals are moderated by developmental and metabolic programmes resident in the genome. Contrasting seasonal phenotypes (fat in summer and lean in winter) in northern mammals like Svalbard reindeer reflect solutions to the potential challenges of the environment, not the failure of homeostasis (defence of state) in one season and its success in another.

Regulation of the annual cycle

The annual rhythms of morphology, physiology and behaviour in seasonal species – outlined above in reindeer – are driven by innate, self-sustaining timers. They proceed independently of environmental stimuli, albeit that they are synchronised to the environmental cycle by changes in day length (photoperiod) transduced via the melatonin signalling pathway (Lincoln et al. 2006, Hazlerigg et al. 2017). The mechanisms underlying these responses have been described in detail in a range of seasonal birds and mammals (e.g., West and Wood 2018), but not specifically in Svalbard reindeer.

2.2 Extracting energy from the environment

2.2.1 Finding and selecting food

For three and a half months each year, Svalbard reindeer live in continuous dim light (civil twilight or less). One problem under these circumstances must be simply finding food. Presumably the use of small, seasonal home ranges (Tyler and Øritsland 1989, see section 3.2.1) means that each reindeer is familiar with the local distribution of plants and therefore has a good idea of where

to go in search of its next meal. The difficulty of locating food is presumably further relieved by visual adaptation to low light levels which is a characteristic of this species.

The visual range of reindeer extends into the ultraviolet (UV; Hogg et al. 2011). This is thought to enhance their ability to discriminate plants in snow in low, but relatively UV-rich, light (Tyler et al. 2014). In addition, their visual sensitivity increases around 1000-fold in winter owing in part to structural changes in the reflective surface behind the central retina (tapetum lucidum (TL); Stokkan et al. 2013). Visual adaptation to low light levels has not been described in Svalbard reindeer, but the TL of these animals appears blue in winter and presumably scatters light internally like the winter adapted eyes of mainland reindeer (Fig. 7).

Svalbard reindeer are intermediate feeders and display several features consistent with their feeding selectively among small tundra plants, including a narrow muzzle and a protruding incisor arcade (Mathiesen et al. 2000a).

2.2.2 Quality of the diet

It is frequently stated that Svalbard reindeer enjoy a nutritionally rich diet in summer and a poor diet in winter. This has not, however, been rigorously quantified. Concentrations of cellulose, hemicellulose and protein in rumen contents vary little between summer and winter (Sørmo et al. 1999). Concentrations (mmol) and the rates of production ($\text{mmol} \cdot \text{h}^{-1}$) of short chain fatty acids in the rumen and distal fermentation chamber are generally lower in winter than in summer but the values are difficult to interpret because large seasonal differences in food intake (see above) influence ruminal retention and rate of absorption of metabolites (Sørmo et al. 1997, Mathiesen et al. 2005).



Figure 7. Adaptation to dim light: the blue reflection off the tapetum lucidum of the retina seen in this Svalbard reindeer calf in late November is associated with a 1000-fold increase in retinal sensitivity in winter compared to summer. The photo is included in the report only to show the blue reflection in the eye. Photo: Nicholas Tyler.

2.2.3 Processing food

Mastication

Consistent with their apparent ability to maintain, through selective feeding, a relatively high quality diet, Svalbard reindeer have a reduced need for chewing and consequently have relatively low crowned molariform teeth and small *M. masseter* (chewing) muscles (Mathiesen et al. 2000a). Wear of molariform teeth, resulting in a reduced mastication (evidenced by a decrease in the proportion of small plant particles in the rumen; Veiberg et al. 2007), is nevertheless a proximate cause of starvation and death (Tyler 1987b).

Functional anatomy of the gastrointestinal tract

The digestive system of Svalbard reindeer is large compared to that of mainland reindeer. Selection has favoured increased volume of the fermentation chambers and thereby a reduction in the rate of passage of digesta and an increase in its digestibility (Staal and White 1991, Sørmo et al. 1999, Mathiesen et al. 2000b). Relatively short intestines encourage rapid passage of digesta from the abomasum to the distal fermentation chamber where fermentation continues (Sørmo et al. 1999).

Gastrointestinal microbes

The digestion of plants and other food material in ruminants depends on a symbiotic association with microbes resident within the gut (chiefly in the rumen and in the caecum or distal fermentation chamber as it is now known). The composition of microflora communities in the gut of Svalbard reindeer is highly specialised for fibre digestion and nitrogen metabolism. It affords the animals a remarkable ability to exploit both the nutritional richness of forage available to them in summer and to extract nutrients from their winter forage.

Like all ruminants, Svalbard reindeer rely on cellulolytic microorganisms in the gut to ferment (digest) the plants they eat. Among

culturable bacteria, species known to utilise soluble carbohydrates dominate in summer and species that utilise fibrous polysaccharides dominate in winter. These organisms are present in very large numbers: to take a single instance, the density of culturable cellulolytic bacteria in Svalbard reindeer is 6–14 times higher than in mainland reindeer *R. t. tarandus* (Sundset et al. 2007). Viable numbers of culturable bacteria in the rumen decrease by about 80 %, from summer to winter but winter populations are still high compared to numbers found in domestic ruminants (Mathiesen et al. 1984, Orpin et al. 1985, Mathiesen et al. 1987, Orpin and Mathiesen 1990, Mathiesen et al. 2005).

Svalbard reindeer host high densities of ciliate protozoans in the rumen. In contrast to mainland reindeer (*R. t. tarandus*), Svalbard reindeer appear to host only entodiniomorphid ciliates but no holotrich ciliates (Westerling 1970, Orpin and Mathiesen 1988, Orpin and Mathiesen 1990). Densities of ciliates vary seasonally, decreasing from 105 cells · ml⁻¹ rumen fluid in summer to 104 cells · ml⁻¹ (i.e., 90 %) from summer to winter (Mathiesen et al. 2005).

Rumen fungi are also present in abundance. These include *Neocallimastix frontalis*, a species which utilises a range of polysaccharides including cellulose and the hyphae of which may penetrate plant vascular tissue that is not accessible to bacteria (Orpin et al. 1985). The density of zoospores in Svalbard reindeer in winter is several orders of magnitude greater than in mainland sub-species of reindeer both in summer and in winter (Mathiesen et al. 2005).

These data provide a good picture of the composition and seasonal dynamics of the gastrointestinal microflora, but may nevertheless underestimate its density and its diversity. Cultivation-based studies have limited ability to detect microorganisms and modern, molecular-based studies reveal a hitherto unknown diversity of

microorganisms, including a high proportion of novel strains in the Svalbard reindeer rumen. Cellulose-degrading loci and polysaccharide utilisation loci-like systems exist at exceptionally high frequencies (Sundset et al. 2007, Sundset et al. 2009, Pope et al. 2012). Remarkably, there appear to be no substantial seasonal differences in either the abundance of microbes or in the bacterial and protozoal population composition when numbers are quantified using real-time PCR and molecular techniques (Sundset et al. 2009).

The food value of herbage ('diet quality') is a function of the anatomical, physiological and microbial characteristics of the gut in which it is digested. We currently know remarkably little about the diet of Svalbard reindeer (i.e., what the animals actually select and eat), or its food value in different seasons. It is clear, however, that the consortia of microorganisms that break down plant material in the guts of these animals are both more diverse and have more sophisticated digestive weaponry than has hitherto been realised.

2.2.4 Foraging activity

In most large ruminants foraging is closely associated with the daily cycle of light intensity. The animals display a peak of foraging activity around dawn and another at dusk. This pattern, clearly apparent in mainland subspecies of reindeer (Fig. 8), is a consequence of the suppression of activity in darkness. The low levels of feeding at night result in falling ruminal production of metabolites and increased hunger towards dawn, and increased motivation to feed at dusk to ensure a flow of metabolites in the forthcoming night (Gregorini 2012).

Foraging activity in Svalbard reindeer, by contrast, is only marginally influenced by the daily cycle of light intensity. The animals are active around the clock around the year (Fig. 8). They obviously have no alternative but to be active and feed in darkness during the polar night, and suppression of activity by darkness is not an issue in summer when there is continuous daylight. Nor are they exposed to night active predators and so are under no selective pressure to reduce activity at night at those times of year when there is a daily cycle of light intensity (i.e., around the equinoxes; Tyler et al. 2016). Furthermore, being only weakly gregarious they are not they subject to any high degree of social synchronisation like gregarious mainland reindeer (Van Oort et al. 2007).

The environment of Svalbard reindeer is effectively non-rhythmic on a 24 hours basis. Consistent with this, the daily activity of the animals is subject to weak endogenous regulation (Van Oort et al. 2007, Arnold et al. 2018) but shows instead strong ultradian rhythmicity (i.e., rhythms with a period \ll 24 hours) based on the grazing cycle (Van Oort et al. 2007, Arnold et al. 2018). The grazing cycle consists of a bout of activity (principally foraging; Tyler (1987b) followed by a bout of inactivity (rest and rumination) both of which repeat in alternating sequence across the 24 hours day. The grazing cycle has a period of around five hours (range 3–9 h) in summer and seven hours (range 5–11 hours) in winter and the reindeer therefore display around five cycles \cdot day⁻¹ in summer and three cycles \cdot day⁻¹ in winter (Van Oort et al. 2007). The difference in frequency between summer and winter is due mainly to an increase in time allocated to rest and rumination in winter which leads, in turn, to a marked decrease in the overall level of activity of the animals at that time (Van Oort et al. 2007).

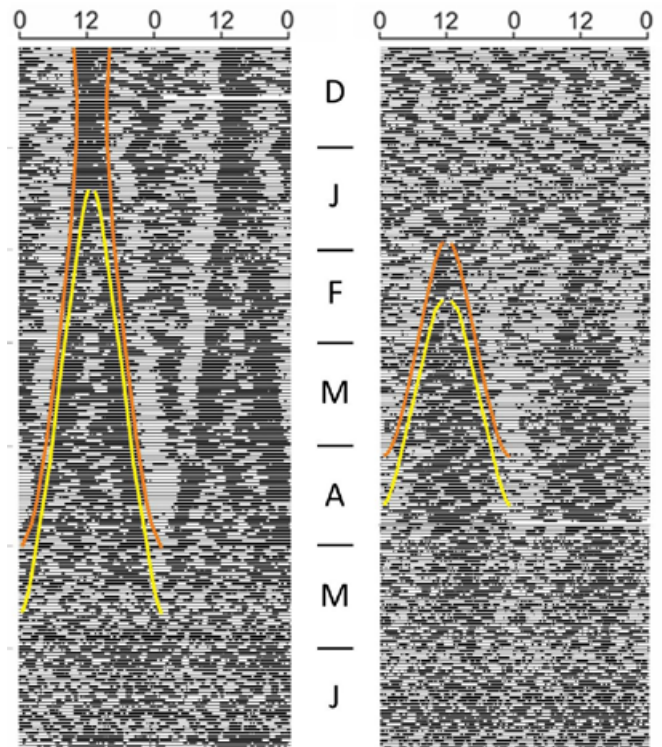


Figure 8. In contrast with Eurasian mountain reindeer in northern Norway, the daily pattern of activity in Svalbard reindeer is only weakly associated with the daily cycle of light intensity. Double-plotted actogram running from December to June for six free-ranging sub-adult female Eurasian mountain reindeer in northern Norway (left) and for six free-ranging sub-adult male Svalbard reindeer (right). Each line represents two consecutive days (days 1–2, days 2–3, etc.); the abscissa is time of day (hours). Bouts of activity (black horizontal bars) are interspersed with bouts of inactivity (open spaces). Coloured lines indicate the instant of civil twilight in the morning and evening (orange) and of sunrise and sunset (yellow). Figure adapted from Van Oort et al. (2005).

2.3 Storing energy

Svalbard reindeer, like other winter resident, non-hibernating High Arctic herbivores (e.g., Svalbard ptarmigan *Lagopus muta hyperborea*, Mortensen et al. 1983, muskoxen *Ovibos moschatus*, Adamczewski et al. 1997), accumulate substantial amounts of fat in summer and autumn that they mobilise in winter (Reimers et al. 1982).

2.3.1 Structure and size of energy stores

Fat (lipid) is stored in adipose ('fat') tissue at numerous sites within the body cavity, between skeletal muscles, in the long bones and in the subcutaneous space along the back, which is by far the largest depot (Tyler 1987a, Pond et al. 1993) Fig. 9).

At peak fatness (October) adult females carry approximately 11 kg of dissectible fat (range 6 – 15 kg) which constitutes approximately 20 % of their live body mass (Tyler 1987a). Calves carry less fat (around nine kg) but are smaller and so this constitutes a similar proportion of the live body mass (around 25 %). There are no corresponding data for males.



A mild autumn increases survival and subsequent reproduction. Photo: Åshild Ønvik Pedersen/NPI.

Figure 9. Svalbard reindeer accumulate substantial amounts of fat in summer which they subsequently mobilise in winter. Most fat is stored in the subcutaneous space along the back. The photograph shows the massive deposit of fat along the back of a calf aged approximately 10 weeks. Photo: Nicholas Tyler.



Adult females use around 80 % of the fat they accumulate in summer during winter and by the end of May most animals are quite lean (mean weight of dissectible fat = 2 kg; Tyler 1987a). There is, however, substantial individual variation and some individuals carry more fat at the end of winter than others do at the end of summer (Tyler 1987a).

Seasonal changes in fat stores in Svalbard reindeer seem to involve the sequential filling of adipocytes (fat cells) in summer and their emptying in winter (Larsen et al. 1985). Interestingly, however, peak fatness is more closely related to the number of adipocytes than with their volume. It therefore may be that adipocytes proliferate and disappear in synchrony with the annual cycle of storage and retrieval of energy (Pond et al. 1993). This has not been investigated in reindeer.

2.3.2 Function of energy stores

Adult female Svalbard reindeer carry sufficient energy reserves in October to cover, on average, around 25 % of the animals' energy

expenditure in winter, not including the cost of gestation (Tyler 1987a). Few animals, however, use their entire energy reserves in winter so the proportion of energy expenditure covered by these must be significantly lower than this. No corresponding calculations have been made for adult males or for calves.

Little is known about how the rate of mobilisation of energy reserves in Svalbard reindeer is regulated. Pregnant females appear to mobilise energy reserves at a slower rate than non-pregnant females towards the end of winter (i.e., in April and May which are the last two months of gestation). They seem, instead, to save their remaining reserves for early lactation (Tyler 1987a). This suggests there is interaction between the regulatory systems that govern reproduction and metabolism, respectively. It is conceivable that the neuronal centres in the hypothalamus which govern feeding are stimulated in pregnant animals in late winter. A response like this would be directly analogous to the way in which feeding is inhibited in male deer during the rut (e.g., Suttie et al. 1983). Neither situation has been investigated in reindeer.

3 Population ecology

3.1 Life history

3.1.1 Birth mass

Newborn Svalbard reindeer calves, caught in early June 1997 and 1998 (N = 19), had a mean weight of 3.5 kilos. There was no difference in body mass between male and female calves. Three new-born calves caught in 1996, after a winter with severe ground ice that made much of the foraging areas inaccessible, had a mean birth mass of just 2.7 kilos. The lower body mass is likely a result from the harsh winter conditions (Albon, unpublished data).

3.1.2 Growth patterns

Calves grow rapidly in their first summer. In this period, they gain as much as seven kilos per month so that by late October female calves enter the winter weighing 37.8 ± 1.15 kg with a hind leg length of 251.7 ± 1.8 mm (N = 32 shot in Nordenskiöld Land 1994–2007; Albon, unpublished data). Skeletal growth in females tends to be completed during their third year of life (age two, mean hind leg length = 282 mm), whereas body mass increases throughout their fourth year of life (Albon, unpublished data; see also Hansen et al. 2012, Pedersen et al. 2014). Hereafter there is little change until about age 14 (Pigeon et al. 2018). Mean adult female October mass is approximately 72 kg (Albon et al. 2017). The seasonal difference in body mass can vary up to 42 % and fat can make up over 15–30 % of the total body weight at the end of summer (Tyler 1986a, Albon et al. 2017).

In October when calves are about five months old, male calves are neither heavier, nor skeletally larger than female calves. However, from here on the growth strategy of the sexes differs. Data from April captures show that at 10 months of age hind leg length

of males is much longer than females (males: 258.5 ± 0.9 mm; females: 252.5 ± 0.8 mm, $P < 0.001$). Also, although both sexes lose mass over the winter, male calves are heavier than females in April (males: 25.6 ± 0.4 kg; females 23.7 ± 0.4 kg, $P < 0.001$) (Albon, unpublished data).

3.1.3 Age and size at maturity

From the first winter onwards, morphological differences between sexes increase with age, but are most marked after females start breeding – most conceiving for the first time as two-year olds. Females grow comparatively little after sexual maturity, whereas males continue to grow and by the age of four male body mass in October was found to be 40 % heavier than females (Albon, unpublished data).

3.1.4 Reproduction

Females may ovulate for the first time as yearlings (Albon et al. 2017). However, since yearlings are still growing, their ovulation rates are very variable between years (coefficient of variation = 115 %, compared to 14 % in adults) and typically low. Annual variation in ovulation rate is positively correlated to the mean body mass in all age classes (Fig. 10a). Differences in ovulation rates between age classes was due to differences in body mass, with no additional effect of age per se (Albon et al. 2017).

Over-winter loss of reproductive potential (i.e. difference between October ovulation rate and April pregnancy rate) can be as high as



A newborn reindeer calf with its mum in early June. The mean weight of newborn calves is 3.5 kilos. Photo: Sophie Cordon.



Reindeer calf in July. During their first summer reindeer calves gain as much as seven kilos per month. Photo: Sophie Cordon.

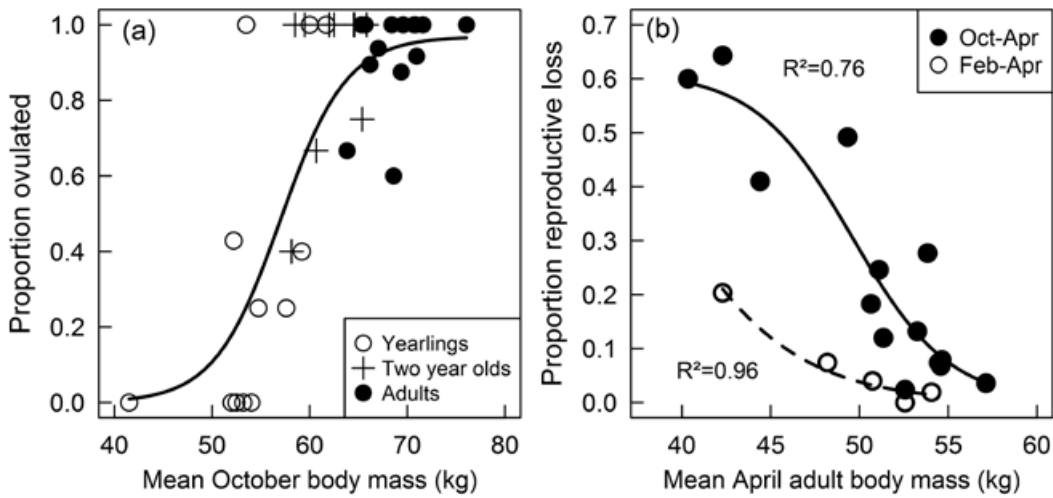


Figure 10. a) Annual proportion of Svalbard reindeer females that ovulated plotted against mean October body mass for three age classes, and b) over winter reproductive losses of females plotted against mean April adult body mass. Figure from Albon et al. (2017).

65 %, when ice-locked pastures inhibit feeding, and mothers starve (Fig. 10b). April body mass not only determines the proportion of females that remain pregnant in April (Fig. 11a), but also predicts whether that offspring will survive the last stages of gestation and the first few days of life (Fig. 11b), and ultimately the proportion of females with a calf at foot at the end of the summer (Fig. 11c). When body mass is particularly low, there may be less than 10 % of females with a calf in summer (Tyler et al. 2008, Veiberg et al. 2017b). Recently, Loe et al. (2019) found that reproductive females grew smaller antlers and weighed less than non-reproductive females to compensate for the cost of reproduction.

Svalbard reindeer give birth to a single calf. Although twinning has been recorded in other Rangifer, it is comparatively rare (Nowosad 1973) and most likely to occur in low density populations with high resource availability (Cuyler and Østergaard 2005). Age-specific variation in fecundity was consistent across years, but noticeably lower in females older than 12 years (Lee et al. 2015; Fig. 12a). To date there is no information on the sex ratio of offspring at birth or on differential neonatal survival.

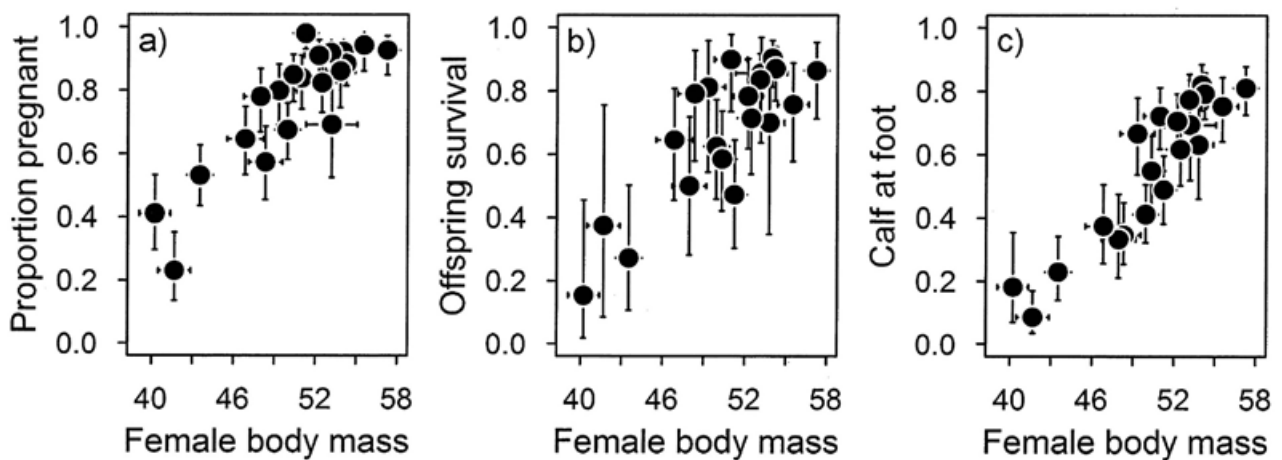


Figure 11. a) The proportion of adult Svalbard reindeer females pregnant in April, b) offspring surviving from April to August and c) females with a calf at foot (right panel) plotted against April adult female body mass each year. Figure from Veiberg et al. (2017b).

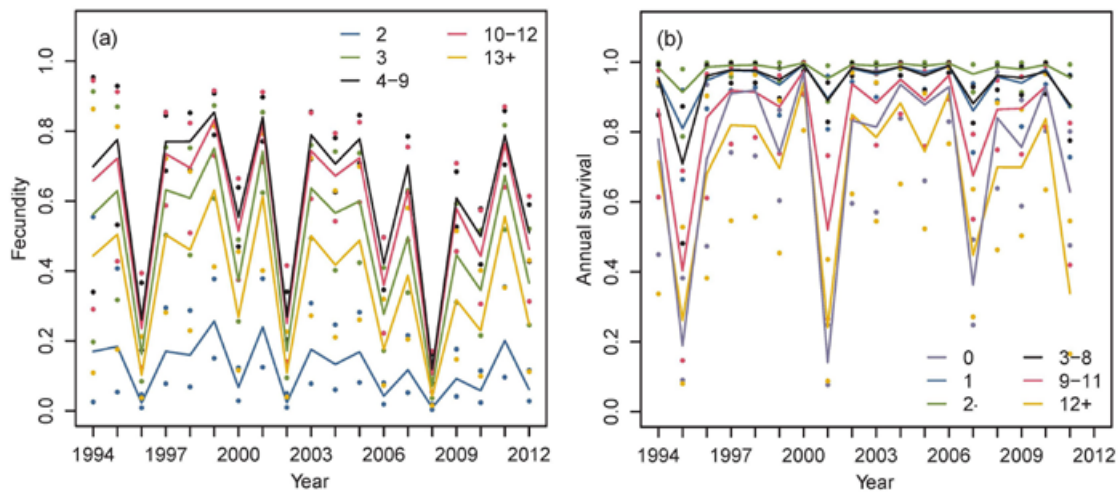


Figure 12. a) Age-specific survival of Svalbard reindeer females from each year to the next and b) estimated fecundity of different age classes plotted for each year between 1994 and 2012. Figure from Lee et al. (2015).

3.1.5 Survival

Age-specific variation in survival is strongly concordant across years, although very much lower in calves and females of 12 years and older (Lee et al. 2015; Fig. 12b). For example, calf and prime-aged females (3–8 year olds) survival was particularly strongly correlated (Fig. 13a). Moreover, annual variation in survival of 3–8 year old females was strongly related to their body mass in April meaning that heavy females had higher survival (Fig. 13b; Albon et al. 2017). Most animals die of starvation during the winter. Wear of molariform teeth, resulting in reduced grazing abilities is nevertheless a leading cause of starvation and death (Tyler 1987b). The tooth wear originates from grazing vegetation on rocky wind-blown ridges, especially during winter (Reimers 1983, Veiberg et al. 2007).

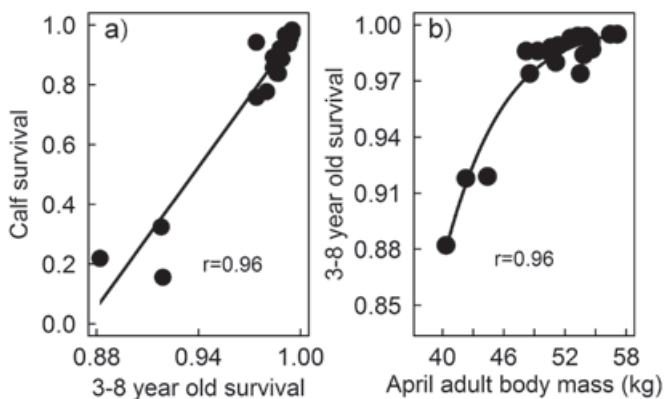


Figure 13. a) Estimated mean calf survival plotted against 3–8 year old survival, and b) annual mean survival values of 3–8 year old females plotted against mean April adult female body mass. Figure from Albon et al. (2017).

3.1.6 Lifespan

The oldest female Svalbard reindeer recorded to date died at 17 years of age (Reimers et al. 1982, Hansen et al. 2012). Interestingly, environmental conditions experienced early in life have consequences for both lifetime reproductive success (Douhard et al. 2016), as well as expected longevity in female Svalbard reindeer. Mean lifespan for calves caught at 10 months of age was 5.3 years for cohorts that experienced severe winter icing, either during gestation or in their first winter, and 7.3 years for those whose early development was in more benign winters (Albon, unpublished data).

Less is known about the life expectancy of males. The oldest male Svalbard reindeer carcass recorded was 16 years old (Hansen et al.



Dead male Svalbard reindeer. Starvation during the winter is a primary cause of death in Svalbard reindeer. Photo: Eva Fuglei/NPI.



Environmental conditions experienced early in life have consequences for both lifetime female reproductive success and longevity.
Photo: Bjørn Frantzen/NIBIO.

2012), but in general they have lower life expectancy than females, rarely going beyond 12 years of age (Reimers et al. 1982). On Edgeøya, mean life expectancy of male reindeer were found to be 5.1 years (maximum 11 years), one year less than female reindeer in the same area (mean 6.2 years, maximum 16 years) (Bie 1977). Males are influenced by environmental conditions to a similar extent as females. Most of the difference in survival between males and females is likely driven by sexual differences in reproductive strategy. During the rutting season, adult males expend a lot of the energy reserves gained over the summer. This makes older males more vulnerable to harsh winter conditions than either sub-adult males (except calves) or females, and ultimately contributes to climate-driven variation in adult sex ratios (Peeters 2017).

3.1.7 Seasonality and impacts on life history events

After eight months of winter in Svalbard, the short snow-free period (mid-June to September) and even shorter period of plant growth (mid-June to mid-August) make the contrast between seasons extreme. The life history events of the reindeer are closely timed with the seasonality of the High Arctic environment (Fig. 14). In most years, the timing of births tends to coincide with snow melt and the spring green-up, presumably to optimise lactation and the period of calf growth and recovery of body mass in older animals. Typically, births are strongly synchronised and take place in a ten-day-period in early June (Veiberg et al. 2017a). In Nordenskiöld Land, the females normally calve between 2 and 13 June with mean calving date 7 June (over the years 1979–2015) (Danielsen 2016, Veiberg et al. 2017a), while within coastal populations the calving happened between 3 and 26 June with mean calving date 13 June (Paulsen 2018). Mating occurs in mid/late October (Skogland 1989), when female body mass peaks (Albon et al. 2017).

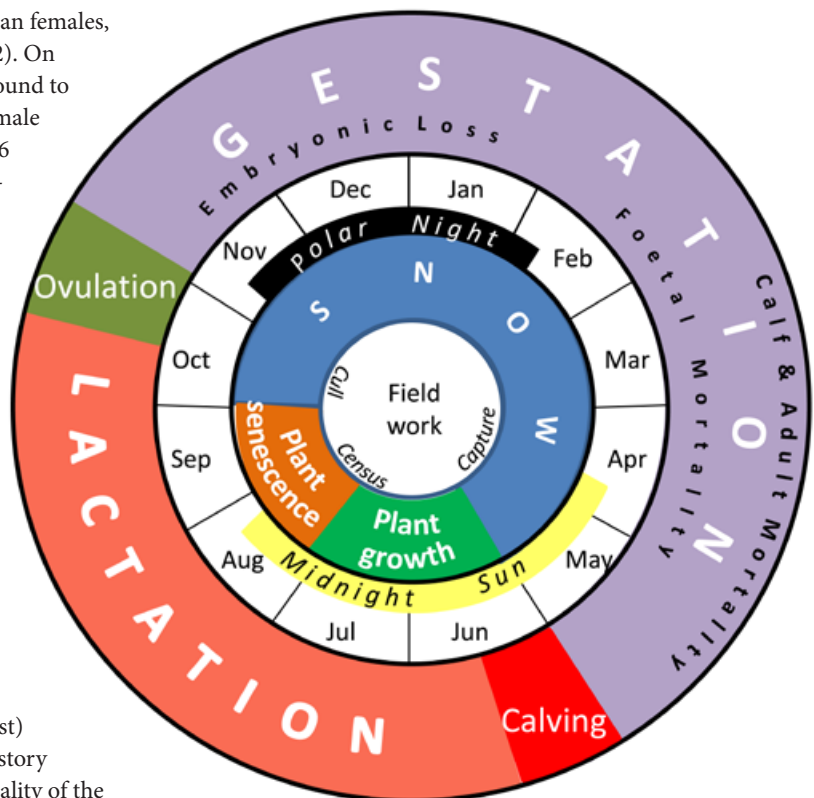


Figure 14. Svalbard reindeer female life history events across the seasons. Showing the major reproductive and survival stages (outer ring) in the annual cycle seasons (inner ring) in terms of winter (snow), summer (plant growth and senescence), the period of 24-hours darkness (Polar night) and 24 hours light (Midnight sun). The inner circle shows the timing of researchers' main field work activities. Figure from Albon et al. (2017).

3.1.8 Body mass variability and its demographic implications

Body mass of the reindeer relates to the environmental conditions and is commonly used to study demography, fitness, reproduction and other measures of individuals and populations. The mass of females across these years was highest after warm summers, which typically generate greatest plant productivity (Van der Wal and Stien 2014). Although ovulation rates in adult females are typically very high (mean 0.92 ± 0.03 SE), there was nonetheless a positive correlation with annual estimates of body mass (Albon et al. 2017).

Body mass in April varied even more between years, from as little as 40 kg to more than 55 kg (Albon et al. 2017), largely in response to rain-on-snow (ROS) events (Fig. 15a) causing ice-locked pastures with inaccessible forage (Hansen et al. 2014). In addition, there was also a positive effect of warming in October (Fig. 15b), presumably because this extended the snow-free period and facilitated a prolonged period of easy access to forage (Albon et al. 2017).

As illustrated earlier, late-winter body mass strongly influences the loss of reproductive potential, as well as survival of calves and older animals. Consequently, April body mass is a major determinant of the population growth rate, accounting for as much as 88 % of its annual variation (Fig. 16; Albon et al. 2017).

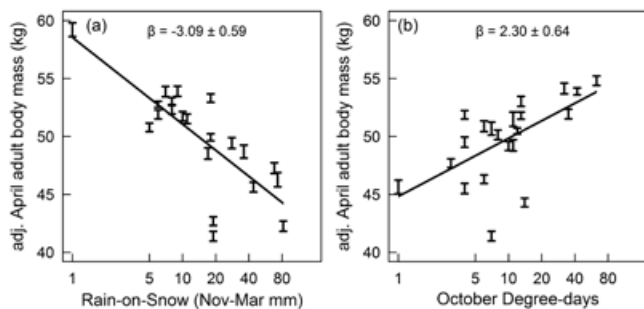


Figure 15. a) Adult Svalbard reindeer female April body mass plotted against annual measures of rain-on-snow (ROS) and b) October degree-days. In each plot the body mass values are adjusted for the effects of the other explanatory variable. Figure from Albon et al. (2017).

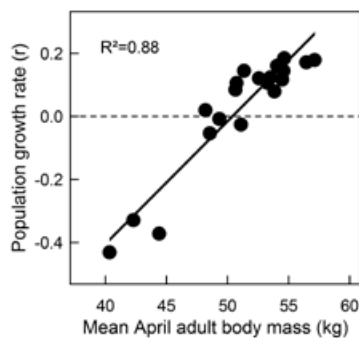


Figure 16. The intrinsic population growth rate, r , plotted against mean April Svalbard reindeer adult body mass. Figure from Albon et al. (2017).

3.2 Habitats, foraging resources and spatial ecology

3.2.1 Seasonal habitat selection and range use

The range use of Svalbard reindeer is limited by the physical barriers imposed by open sea, glaciers and mountains, which tend to confine reindeer to the vegetated lowlands and coastal margins. In the absence of predators and harassing insects (Staal and Røed 1986), the Svalbard reindeer mainly select which areas to use (habitat selection) based on seasonal energy and nutrient requirements. In summer, the Svalbard reindeer maximise the build-up of fat reserves. In winter, the strategy is to make the fat reservoir last as long as possible (see section 2.1.1 on physiological adaptations to the cold). The fat reservoir normally covers only about 25 % of the winter energy needs (Tyler 1986b). Therefore, survival and fecundity depend on winter body mass loss (Albon et al. 2017), which in turn is affected by snow and ground ice influencing the accessibility of forage in winter (Hansen et al. 2009a, Albon et al. 2017).

In summer, Svalbard reindeer mainly graze in various types of lowland moss tundra, wetlands, meadows and lower foothills where the vegetation consist of grasses, sedges, forbs, dwarf willow and mosses. Productive slopes under seabird colonies are utilised as well (Staal 1986). Snow melt during spring determines the accessibility of vegetation and the onset of plant growth, and with it comes a dramatic increase of forage quality (Beumer et al. 2017). The use of vegetation types changes from spring to autumn (Loe 1999). During and shortly after snowmelt, most reindeer in the Colesdalen-Semmeldalen-Reindalen area are grazing in the so-called Luzula heath, while moister graminoid swards are increasingly used as summers progress. Although little research has been done on detailed feeding behaviour and dietary choice in summer (Staal and Røed 1986, Bjørkvoll et al. 2009), the observed shift in habitat use likely reflects a combination of accessibility and selection for as high as possible plant biomass (Van der Wal et al. 2000, Van der Wal and Hessen 2009). The overall grazing pressure, also on preferred plant species, appears low in most vegetation patches (Wegener and Odasz-Albrigtsen 1998, Van der Wal et al. 2000), but has not been extensively studied in different habitat and resource situations. Dense graminoid swards may experience higher grazing pressure (Van der Wal and Brooker 2004). Generally, the better the resources available, the more selective the Svalbard reindeer is when it comes to habitats, diet and foraging behaviour (Hansen et al. 2009a, Hansen et al. 2009b). Yet, the short growing season, low temperatures and low light levels collectively limit the build-up of structural plant tissues, meaning that during summer Svalbard reindeer can forage on leaves of far higher quality than is the case at lower latitudes (Fig. 17; Van der Wal and Hessen 2009).

Areas with different foraging resource levels can inform about foraging behaviour, such as, at the time, heavily grazed and therefore low productive Brøggerhalvøya and the relatively more productive Sarsøyra (Hansen et al. 2009b). On Brøggerhalvøya, where the forage resource level at the time was low, most reindeer selected for productive habitat when choosing their home range and patches within it. Habitat selection on Sarsøyra was more affected by abiotic conditions, such as moisture. On Sarsøyra the reindeer used patches with even less biomass than the average reindeer at the poorer Brøggerhalvøya. As both the reindeer populations and the forage resources vary over time, the habitat

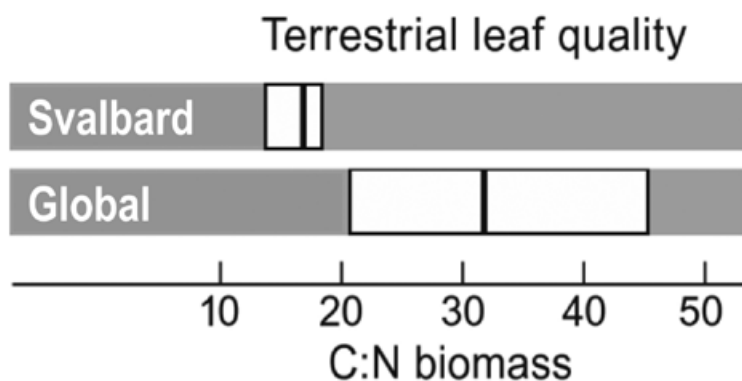


Figure 17. Quality of plant leaves during summer in Svalbard compared to those elsewhere in the world. Plant quality is expressed as Carbon to Nitrogen ratio, whereby a low value means high quality; portrayed are the median (black line) and 25 % confidence intervals (white boxes). This Svalbard dataset comprised 27 species of the more common species, including graminoids, non-woody forbs, deciduous and evergreen shrubs and horsetails. Figure modified from Van der Wal and Hessen (2009).

selection by the reindeer may change and is hence not expected to be geographically stable.

Home range size for adult female GPS-marked Svalbard reindeer was 24.4 km² (range: 7.1 km² to 60.9 km²) (mean home range size 1 July to 15 September) (Kinck 2014). In this summer period, there is no difference in home range size for females with and without calves (see also Henriksen et al. 2003). Individuals tend to use the same summer range each year (mean overlap=71 %; range: 20 % to 100 %). Female summer home range sizes are related to habitat productivity (Hansen et al. 2009b). The better the resources, the smaller the home ranges and the less the reindeer move.

In winter, snow depth and snow density, as well as ground ice formation following mild weather spells, determine the spatial distribution of Svalbard reindeer (Hansen et al. 2009a). Thus, reindeer are often confined to feeding on exposed wind-blown

ridges, where mountain aven (*Dryas octopetala*) is the most common plant species; otherwise, they have to dig craters in the snow to access the vegetation underneath. Cratering behaviour in Svalbard reindeer has been studied in two different populations. Reindeer along the northwest coast of central Spitsbergen select sites for cratering with no ground ice, low snow depth and high vegetation quality (e.g., more *Salix*, graminoids and lichens and less moss) than in nearby control sites (Fig. 18; Hansen et al. 2010a). In a winter with little icing, reindeer in Adventdalen on Nordenskiöld Land, likewise cratered in sites with shallow and little hard snow, and avoided cratering in the few sites where vegetation was completely covered by ground ice (Beumer et al. 2017). However, this selective behaviour against deep and hard snow became only evident once overall snow conditions became more challenging throughout winter. Under good conditions in early winter reindeer selected deep or hard snow. Food plants are increasingly abundant in slopes with deep snow cover, potentially justifying the slightly



In summer the Svalbard reindeer use the lowland habitats with abundant food resources. Photo: Bart Peeters/NPI.

higher energetic costs of digging deeper or through harder snow. Once conditions worsened, the reindeer shifted to avoiding deep or hard snowpack, probably at the cost of finding less food and lower quality food. As forage accessibility became increasingly restricted by snow conditions, diet quality (as measured by faecal C:N ratios) decreased (Beumer et al. 2017).

The avoidance of ice-covered vegetation and deep snow supports the hypothesis that reindeer utilise smell to locate food under the snowpack and hence to discriminate between suitable and unsuitable sites for cratering (Bergerud and Nolan 1970). Throughout winter, craters in snow deeper than approximately 30 cm have not been documented in Svalbard (Beumer et al. 2017), while 50–70 cm is suggested to be the maximum snow depth for cratering in North American caribou (Laperriere and Lent 1977). While severe rain-on-snow (ROS) events may lead to ground icing, rendering vegetation across large areas inaccessible, the effect of snow fall is expected to be more gradual. Snow depth depends strongly on wind direction during and after snowfall as well as on the local topography (ridge-snow bed gradients).

Winter home range size (1st of November to 31st of May) depends strongly on forage abundance (Hansen et al. 2009a) as well as forage accessibility, such as ground ice conditions (Kinck 2014). In dry, cold winters without ground ice, the average home range size of 25.6 km² (range: 10.7–69.5 km²) is comparable to the size of summer home ranges. However, home ranges were larger in warm, wet and icy winters compared to dry, cold winters with a mean of 33.7 km² (range: 8.9 km² to 98.5 km²) (Kinck 2014). When forage abundance increases in winter, the reindeer seem to select habitat based on quality as well as have smaller home range size (Hansen et al. 2009a). Thus, changes in forage abundance can strongly influence winter habitat-space use.

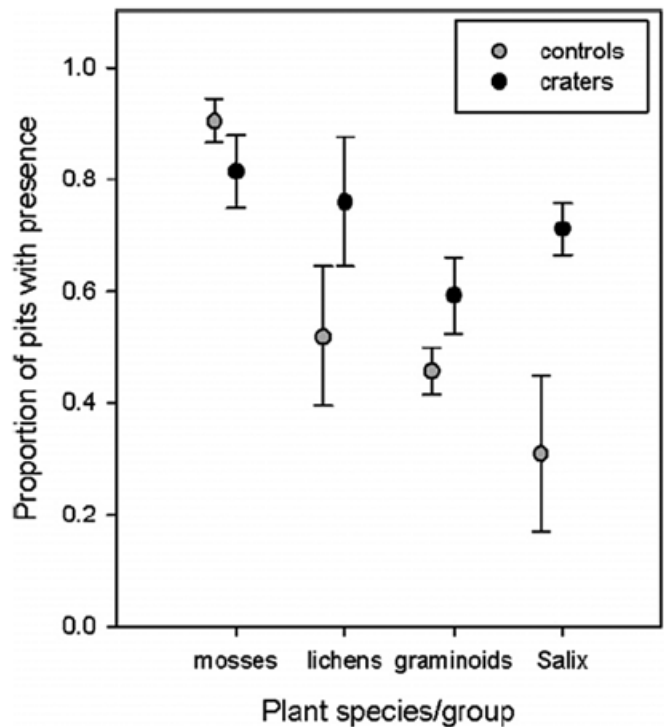


Figure 18. Mean (\pm SD) proportion of analysed cratering pits with presence of four major winter forage types for Svalbard reindeer. Pits are divided into feeding craters used by reindeer and nearby (1–4 meters distance) controls. Figure from Hansen et al. (2010a).



Snow is a major factor determining winter forage availability for the reindeer. Photo: Siri Birgitte Uldal/NPI.

3.2.2 Diet

Approximately 180 different vascular plant species are found in Svalbard, more than 380 species of bryophytes and over 740 lichens species (Øvstedal et al. 2009, Prestø et al. 2014, www.svalbardflora.no). The aboveground plant biomass varies greatly between habitat types, ranging from very low values of less than 10 g/m² to somewhat over 500 g/m² (Johansen and Tømmervik 2014, Van der Wal and Stien 2014). This means that there is large spatial variability in food resources.

Svalbard reindeer forage on vascular plants (including flowers and seeds) but also mosses (e.g., Staaland et al. 1993, Van der Wal et al. 2000, Bjørkvoll et al. 2009, Åhman and White 2019). While lichens constitute an important part of the winter diet of most Rangifer populations, it is almost entirely lacking in the diet of Svalbard reindeer. However, when accessible, Svalbard reindeer do consume lichens (Hansen et al. 2009a), such as the snow-bed Iceland lichen (*Cetraria delisei*) and other fruticose lichens (Joo et al. 2014). The impact of Svalbard reindeer on lichens is dependent on growth form, with fruticose lichens suffering from grazing, whereas foliose lichens might indirectly benefit from higher densities of reindeer

or, like crustose lichens, be controlled by other factors (Van der Wal et al. 2001a)

The diet of Svalbard reindeer varies according to seasonal availability of forage plants (Fig. 19; Bjørkvoll et al. 2009). In summer graminoids comprise the largest proportion of the diet of female reindeer, followed by forbs such as alpine bistort (*Bistorta vivipara*), mountain sorrel (*Oxyria digyna*) and the dwarf shrub polar willow (*Salix polaris*). In summer the reindeer even ingest goose dropping that are nutritious and can be very abundant locally (Van der Wal and Loonen 1998). In early winter, graminoids (grasses and sedges) are particularly important dietary components. In late winter their proportion in the diet has dropped and that of polar willow and mosses increased (Bjørkvoll et al. 2009). Mosses are of low dietary value (Van der Wal et al. 2000), but are in many parts of Svalbard available in amounts far greater than all vascular plants and lichens combined. Hence, part of the ingestion probably occurred whilst aiming to consume polar willows or other desired food items growing amongst layers of moss.

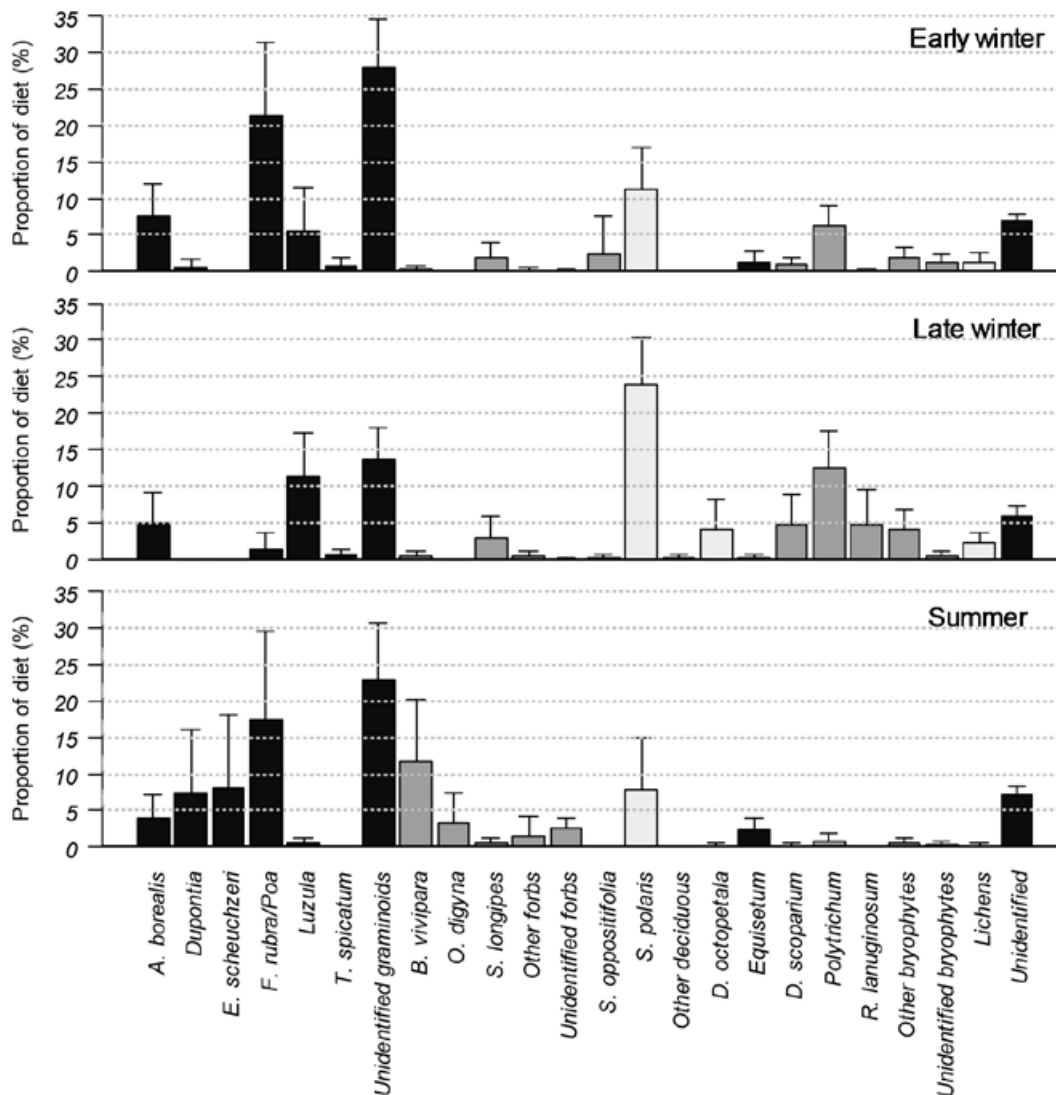


Figure 19. Percentages of species/ species groups \pm SD across individuals in the diet in the early winter (N = 26), the late winter (N = 24), and the summer (N = 22) based on rumen samples from female Svalbard reindeer culled during 1999–2002. The different growth forms are displayed using different shadings (from left); graminoids forbs and evergreen cushion plants, deciduous and evergreen shrubs, sphenophytes, bryophytes, lichens, and unidentified plant fragments. Figure from Bjørkvoll et al. (2009).

Principal components of the Svalbard reindeer summer diet – Mountain sorrel (*Oxyria digyna*), alpine bistort (*Bistorta vivipara*) and polar willow (*Salix polaris*).
Photo: Left, Åshild Ønvik Pedersen/NPI; middle, NN/ NPI, right, Gunn Sissel Jaklin/NPI, upper right, Tore Nordstad/ NPI.



A young reindeer feeding on seaweed and kelp at the shore.
Photo: Malin Daase/UiT.

3.2.3 Seasonal migration

Geographical barriers leave the reindeer with few opportunities for seasonal long distance migrations as seen in many other Rangifer populations (Tyler and Øritsland 1989). It is nevertheless possible that individual reindeer use the same winter and summer ranges year after year, and that these ranges do not overlap. This has been investigated in two studies, who report similar results. Hansen et al. (2010b) found that 35 % of marked reindeer in the Brøgger peninsula were migratory while the rest were stationary. This strategy indicated site fidelity to former calving ranges and was later supported by studies on GPS-collared reindeer in Nordenskiöld Land where females with calves returned to calving ranges in certain side-valleys to give birth, although fidelity to immediate calving locations was low (Paulsen 2018). Similarly, Meland (2014) found that one third of the marked reindeer in the Reindalen-Colesdalen population could be classified as seasonal migrants with summer and winter ranges about 10 km apart. In both studies, migration was a flexible strategy, which was adopted by individuals in only some years. The migratory strategy seems to be a result of food limitation in winter – individuals escape in years of poor winter pastures, but tend to return to the same summer pasture that they used in the previous summer (Meland 2014). The lack of sea ice currently reduces the possibilities for using it as a dispersal corridor (Pedersen et al. 2018).

3.2.4 Behavioural buffering of adverse winter conditions

Rain-on-snow (ROS) events have a major impact on the population dynamics of Svalbard reindeer (see section 3.5 Population dynamics). Such events also impact reindeer space use. Stien et al. (2010) found that satellite-marked female reindeer moved out of their home range when exposed to a ROS event and that the formation of ground ice triggered the movements. Using GPS marked females Loe et al. (2016) showed that 80 % of the studied reindeer moved towards less icy areas in years with substantial ground ice formation. By doing so, they frequented areas with higher survival prospects and higher expected fecundity during the next breeding season (Fig. 20). The study suggested that the females had knowledge of areas with anticipated higher forage accessibility during icy winters, making them able to buffer adverse conditions through movements. Box 2 visualise some of these long-distance movements.

Hansen et al. (2019b) showed that Svalbard reindeer populations along the west coast of Forlandsundet, which are increasingly isolated by the lack of sea ice, increased their consumption of marine food resources such as washed-ashore kelp and seaweed in response to ROS events and ice-locked pastures. This inclusion of resource subsidies in years with restricted forage access is another indication of behavioural plasticity in Svalbard reindeer.

In a long-term perspective, behavioural buffering may be important for population persistence in mobile species with long generation times and therefore limited ability for rapid evolutionary adaptation (Loe et al. 2016, Hansen et al. 2019b).

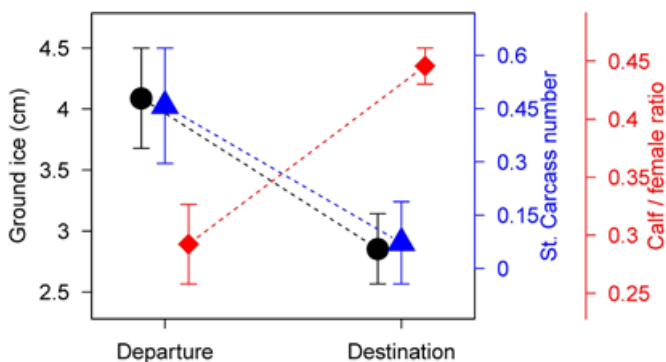


Figure 20. Ground ice thickness (black circles), mortality index (blue triangles), and calf/female ratio (red diamonds) at departure and destination locations for GPS-marked Svalbard reindeer females with range displacement in icy winters (2009/2010 and 2011/2012). Figure from Loe et al. (2016).

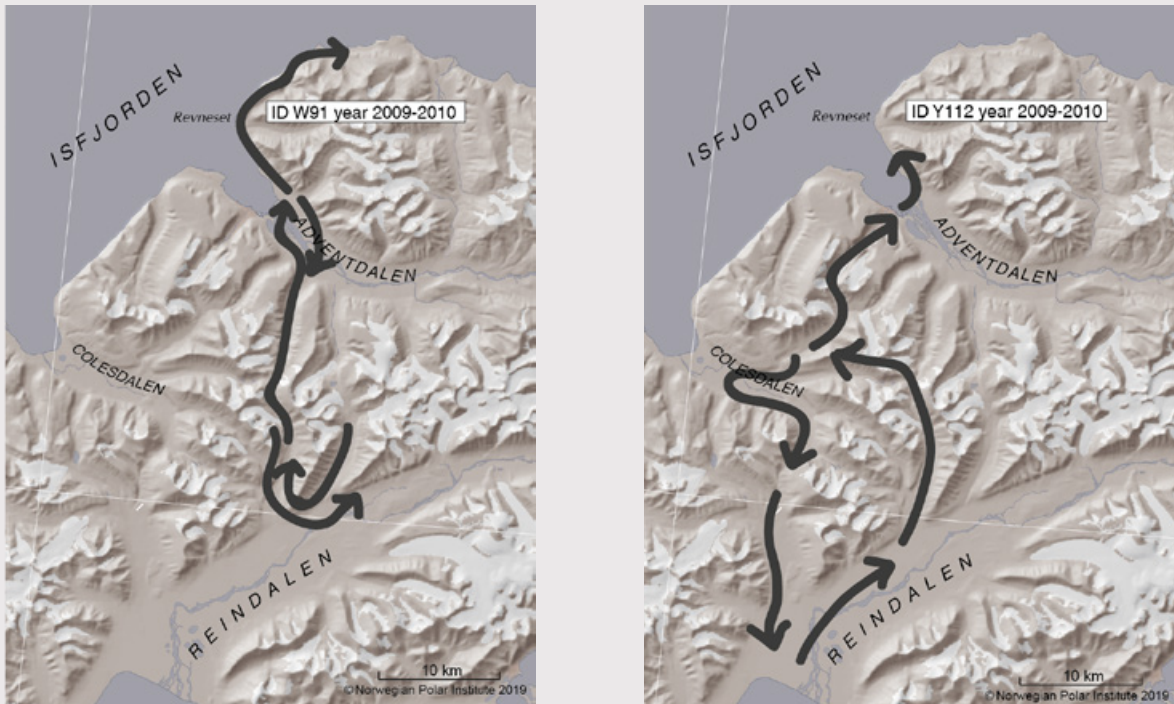


In winter, snow and basal ground ice determine forage conditions and spatial distribution of the Svalbard reindeer. Photo: Siri Birgitte Uldal/NPI.

Examples of long-distance movements of GPS-marked individuals

The GPS-studies generally support that Svalbard reindeer females are relatively stationary with small home ranges (often < 25 km²), however, here we present some notable exceptions. We have detected a few long movements (between 20–50 km), all occurring in February–April. None of the movements resulted in documented permanent dispersal. Three GPS-marked females from Reindalen moved to the Adventalen area in the winters 2009–2010 and 2011–2012 following rain-on-snow (ROS) events. They arrived in Diabas (left panel), Revneset (right panel) and Todalen (not shown on map), respectively. All returned to Reindalen to calve the following summer. Finally, and most spectacularly, a female reindeer marked in Sassendalen tried to cross the Tunabreen glacier, whereby she fell into a crevasse and died. The collar continued to send positions, which allowed retrieval from the glacier (Mathilde Le Moulec pers. comm.).

See Loe et al. (2016) and Albon et al. (2017) for a description of the study areas and methods used in the long-term capture–mark–recapture studies on Nordenskiöld Land.



Movements of female reindeer W91 (left) and Y112 (right) after rain-on-snow (ROS) events in winter 2009–2010.
Illustration: Oddveig Ø. Ørvoll/NPI.



The Svalbard reindeer occur in small groups or solitary as this male in summer. Photo: Bart Peeters/NPI.

3.3 Social organisation

3.3.1 The solitary reindeer

Unlike most other Rangifer, which aggregate in large herds, the Svalbard reindeer regularly occur alone, as mother–calf pairs or in small groups (< 10 individuals) (Alendal and Byrkjedal 1976, Alendal et al. 1979, Tyler 1991, Loe et al. 2006). The likely evolutionary reason for this is that when the first reindeer colonised Svalbard several thousands of years ago (Van der Knaap 1986), they escaped their natural predators. In the absence of this behavioural driver, a more solitary and independent social organisation proved more advantageous for individual optimisation of activity and energy budgets. Apart from the mother–calf pairs, the spatial co-occurrence of animals is thought to be driven by the spatial distribution and accessibility of food resources (Loe et al. 2006).

3.3.2 Seasonal variation in group size

Most groups of Svalbard reindeer are small with median values (May to October) ranging between two and four individuals (Tyler 1991, Loe et al. 2006). In spring (calving) and in early summer, fresh vegetation becomes gradually available as the snow thaws. Although this creates a patchy distribution of feeding locations with improved forage availability, reindeer normally occur in small groups. Later in summer, forage becomes widely distributed, allowing animals to spread out. During this period, the group size is at its lowest. As the vegetation withers in autumn (pre-rut), food availability again becomes spatially delimited. This coincides with the initiation of the mating season. During the rut, the main driver of group dynamics changes from being primarily food to being strongly influenced by the reindeer mating strategy. The formation of mating groups (harems) causes an increase in median group size (Heatta 2009). In harsh winters, animals may aggregate in larger groups on spatially delimited areas. Groups of up to 60 individuals have been observed during winter surveys (Pedersen, unpublished data).

3.3.3 The rut

During the rutting period in October, social interactions and organisation are radically changed. The most notable behavioural changes are seen among the adult males and are related to prolonged courtship displays towards females, self-marking and aggressive displays and contests with rival males (Thomson 1977). The frequency of male–female interactions in Svalbard reindeer has been found to peak around 12–13 October, and is assumed

to coincide with the peak in mating (Skogland 1989). The male mating strategy involves gathering and guarding of female harems that may vary considerably in size (Fig. 21) – typically 1–5 females, but occasionally as many as 19 (Heatta 2009). In a study of mating behaviour in Svalbard reindeer, harem size increased with the number of guarding males and with the size of the dominant male (Heatta 2009, Vestues 2009).

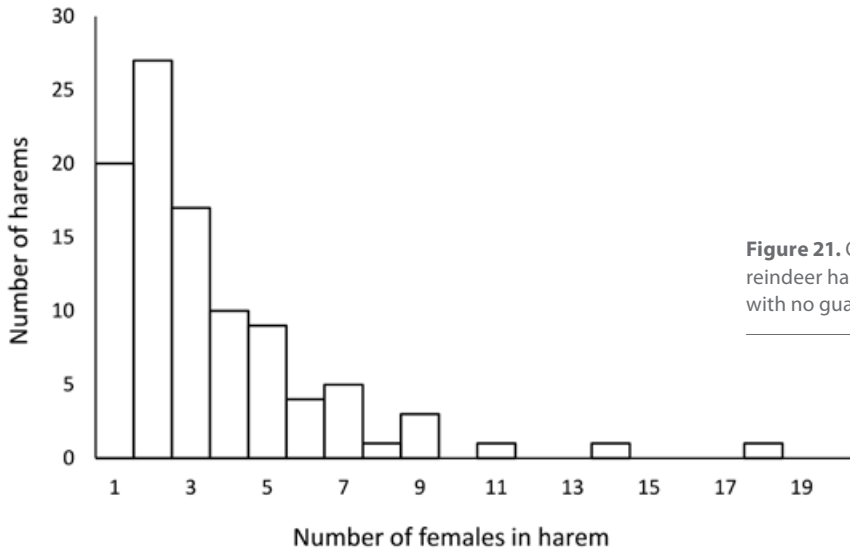


Figure 21. Observed frequency distribution of Svalbard reindeer harems (N = 147), excluding only female clusters with no guarding male (Heatta 2009, Vestues 2009).



Prior to the rut the velvet is shed on the antlers. Photo: Sophie Cordon.

3.3.4 Mother–calf interaction

Immediately after birth in early June, Skogland (1989) found that Svalbard reindeer calves took longer to stand for the first time (54.5 ± 7.8 min) than mainland reindeer (28.6 ± 4.6 min). In addition, Svalbard reindeer mother–calf pairs spent longer time at the actual birth sites (420 vs 270 min) compared to mainland reindeer. These factors probably reflect the reduced need for anti-predation behaviour in Svalbard reindeer. Apart from suckling, Skogland (1989) discovered that post-calving Svalbard reindeer mothers and calves interacted significantly less than gregarious alpine reindeer living in herds.

During the period of lactation, mother–calf pairs represent the most consistent social units in Svalbard reindeer. Timing of weaning in most reindeer and caribou populations is associated to the rutting period approximately 20 weeks after birth (White and Luick 1984). This is likely also the general rule of thumb for Svalbard reindeer. Still, mid-winter suckling has been observed (E. Reimers unpublished data) and lactation has been recorded in adult females shot in both December, February and March (R. Langvatn unpublished data). This strategy of delayed weaning is probably associated with a breeding pause (White and Luick 1984). After weaning, the social link between mother and offspring is naturally weakened, but females and calves are still often observed together during late winter.



During the period of lactation, mother–calf pairs represent the most consistent social units in Svalbard reindeer Photo: Sophie Cordon.

3.3.5 Sexual segregation

Mechanisms causing sexual segregation has been investigated in Svalbard reindeer. Loe et al. (2006) separated sexual segregation into three components: 1) spatial segregation, meaning that males and females use different areas; 2) habitat selection, meaning that they use different vegetation types; and 3) social segregation, meaning that they occur in different groups. Svalbard reindeer males and females are segregated according to all three criteria, but to a different extent (Fig. 22). Habitat segregation is relatively weak, indicating that males and females utilises the same vegetation type, at least coarsely (at a 1 km^2 scale). However, there may be spatial differences in plant biomass or species abundance within vegetation types. Therefore, the potential impact of nutritional needs on spatial segregation cannot be ruled out.

Social segregation between males and females is strongest in early summer, meaning that the sexes tend to stay in same-sex groups (Loe et al. 2006). Because spatial segregation is much weaker than social segregation, i.e., they tend to use the same places but at different times, differences in activity budgets are likely to be the most important mechanism for sexual segregation in Svalbard reindeer. There is a pronounced seasonality in segregation, which is clearest in early summer when many females have a calf at heel (Fig. 22). As expected, segregation decreases as the mating season approach, and no sexual segregation is found during the mating season (Loe et al. 2006).

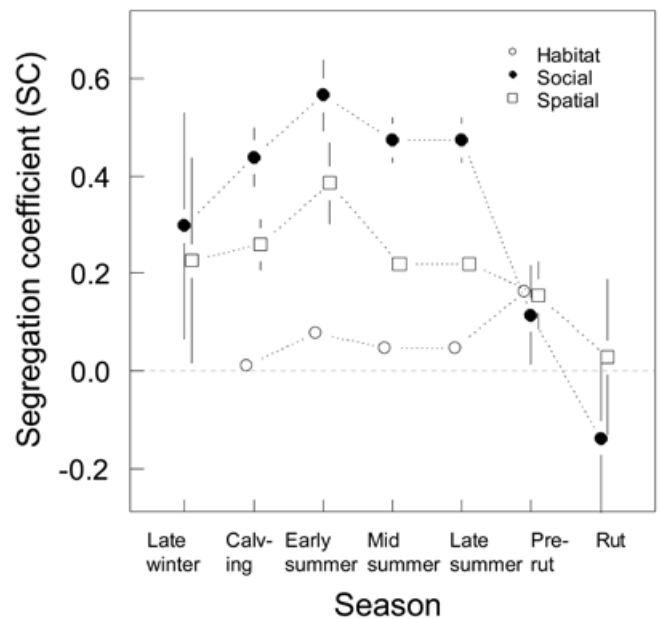


Figure 22. Seasonal variation in social, habitat and spatial (1 km^2 scale) segregation in Svalbard reindeer. Sexes are segregated if the coefficient is higher than zero and aggregated when lower than zero. If confidence intervals calving (2–19 June), early summer (20–30 June), mid-summer (1–31 July), late summer (1–31 August), pre-rut (1 September–15 October) and rut (16–19 October). Figure from Loe et al. (2006).

3.4 Population genetics

Populations living at the margins of the species' range are often genetically depauperated (low genetic diversity; Eckert et al. 2008). Svalbard reindeer have among the lowest genetic diversity observed in subspecies of caribou and reindeer (Côté et al. 2002, Røed 2005, Yannic et al. 2013, Kvie et al. 2016, Peeters 2019). This is probably related to their strong geographic isolation, which has led to severe genetic drift and loss of genetic variability since the time of colonisation. Recent extinction-colonisation dynamics due to overharvesting also contributed to the observed low genetic diversity and genetic differentiation (Peeters 2019). However, no clear signals of a recent bottleneck have been detected in populations in Nordenskiöld Land at the centre of their range (Côté et al. 2002).

The philopatric behaviour in Svalbard reindeer (i.e., remaining in one area) likely contributed to significant genetic differentiation even among subpopulations that are less than 50 km apart (Côté et al. 2002, Peeters 2019). Gene flow is limited by natural barriers such as glaciers, mountains and recent reductions in sea-ice cover, an important driver of genetic structure across the archipelago (Peeters 2019). Thus, six strongly differentiated genetic populations or "clusters" were identified across Svalbard (Fig. 23; Peeters et al. 2019). Genetic diversity was highest in Central Spitsbergen, Nordenskiöld Land, and decreased towards the outer distribution, where populations such as those in North and South Spitsbergen, East Svalbard (Barentsøya and Edgeøya), and Nordaustlandet showed significant signatures of inbreeding (Peeters et al. 2019). As the climate warms, the loss of sea-ice as an important dispersal corridor within and between island systems is expected to further increase the genetic isolation of populations (Jenkins et al. 2016, Peeters et al. 2019).

3.5 Population dynamics and monitoring

3.5.1 Population dynamics

There is consensus that the large short-term fluctuations seen in Svalbard reindeer abundances are mainly driven by annual variation in winter weather combined with density-dependent regulation (Reimers 1982b, Aanes et al. 2000, Solberg et al. 2001, Kohler and Aanes 2004, Tyler et al. 2008, Hansen et al. 2013, Albon et al. 2017, Hansen et al. 2019a). Particularly important is the incidence of rain-on-snow (ROS) events, which cause icing and thereby influence access to forage. However, how milder and rainier winter weather shapes snow-ice conditions is not straightforward (Tyler 2010, Peeters et al. 2019). Furthermore, the effects of ROS may operate in complex interactions with internal population-regulatory mechanisms such as density dependence (Hansen et al. 2019a, Hansen et al. 2019c).

Population density effects

Direct density dependence typically results in the sawtooth-shaped patterns of population dynamics often observed in Svalbard reindeer (Solberg et al. 2001, Aanes et al. 2003, Tyler et al. 2008, Hansen et al. 2011, Hansen et al. 2013). Regardless of the shape of density regulation, the negative effects of high reindeer density on population growth rates are likely due to increased competition for available food resources in winter, the critical season for both survival and fecundity rates (Reimers 1982a, Tyler 1987b, Albon et al. 2017). In addition, density dependence may operate through body mass gain in summer (Albon et al. 2017) and indirectly through delayed effects of reindeer density on the parasite (gastrointestinal nematode) burden (Albon et al. 2002).

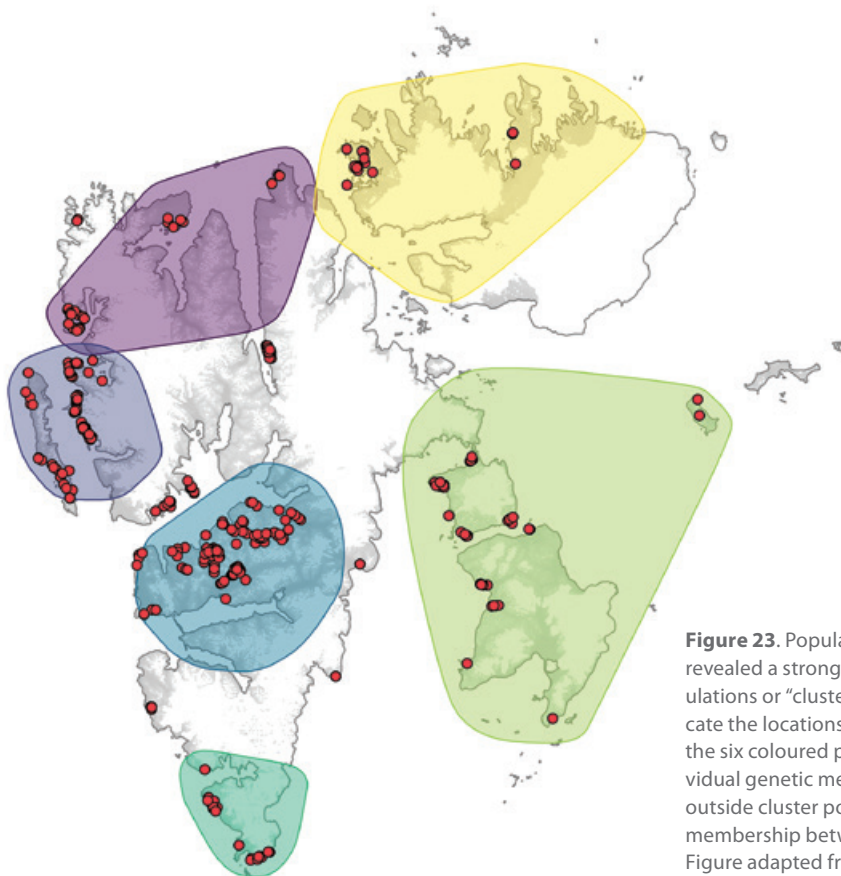


Figure 23. Population genetics analysis of Svalbard reindeer revealed a strong genetic structure of six genetically distinct populations or "clusters" across their distribution range. Red dots indicate the locations of individual genetic samples ($n = 411$), whereas the six coloured polygons represent spatial extrapolations of individual genetic memberships to their respective cluster. Individuals outside cluster polygons were generally characterised by a mixed membership between two or more clusters. Figure adapted from Peeters et al. (2019).

Weather and climate effects

The annual amount of winter precipitation has a negative impact on population growth rates in both Brøggerhalvøya (Aanes et al. 2000) and Nordenskiöld Land (Solberg et al. 2001). Although large snowfall amounts indeed do constrain population growth rates (Hansen et al. 2019c), Solberg and colleagues (2001) suggested that precipitation falling as rain was more influential than precipitation falling as snow. This was attributed to the observation that particularly rainy winters (ROS events) were often characterised by the formation of a thick ice layer on the tundra (i.e. basal ground ice; Kohler and Aanes 2004, Peeters et al. 2019), encapsulating forage plants and making them inaccessible for reindeer (Hansen et al. 2010a). Mark-recapture studies have demonstrated that the effects of ROS and icing on vital rates and population growth rates operate through increased over-winter body mass loss (Albon et al. 2017). Analysis of the dramatic population crash observed on Brøggerhalvøya during the winter 1993–94 suggested that this was due to high reindeer densities combined with record amounts of ROS in early winter, causing extensive ice formation (Kohler and Aanes 2004). Other studies – across different populations – have later confirmed the overall negative effect of ROS on vital rates (Stien et al. 2012, Loe et al. 2016, Albon et al. 2017) and population growth rates (Kohler and Aanes 2004, Hansen et al. 2011, Hansen et al. 2013, Hansen et al. 2019a, Hansen et al. 2019c). Accordingly, spatially auto-correlated fluctuations in ROS and basal ground ice explain part of the observed patterns of spatial synchrony in reindeer mortality and fecundity, and, in turn, population dynamics across the archipelago (Fig. 24 a-e; Hansen et al. 2019c).

Because the formation of ice depends on snow depth (Peeters et al. 2019), as well as timing and duration of rain, warm spells during winter may sometimes be associated with ablation (i.e., melting), resulting in no icing on the exposed ridges. This may in some cases have positive effects on forage accessibility for the reindeer (Tyler et al. 2008). Thus, given continued winter warming (Førland et al. 2011) the effects of rainier winters on snow-pack characteristics, feeding conditions and population growth will likely be nonlinear and far more complex than observed in the past. Nonetheless,

the recent (Peeters et al. 2019) and expected near-future (Hanssen-Bauer et al. 2019) increase in frequency of extreme icing may have unexpected consequences for the reindeer population dynamics (Hansen et al. 2019a). Because ROS effects interact with intrinsic population regulation acting through age-structure fluctuations and density dependence, the ROS effect is strongly negative when occurring at high population size, yet only negligible at low population size.

Moreover, some studies now indicate net positive, rather than net negative, effects of current climate change on local as well as overall abundance of Svalbard reindeer (Albon et al. 2017, Hansen et al. 2019a, Hansen et al. 2019c, Le Moullec 2019b). Warmer and longer summers lead to better growing conditions for the food plants (Aanes et al. 2002, Van der Wal and Stien 2014) and overall vegetation ‘greening’ (Vickers et al. 2016), as well as a shorter season with snow cover and restricted food accessibility for the reindeer (Hansen et al. 2019c). This improves the potential for fat accumulation in summer and, thereby, the body condition in the autumn (Albon et al. 2017). It is still not clear how this eventually impacts vital rates, but warmer October weather (i.e., possibly snow free conditions) indeed seems to have a positive effect on body mass the following April (Albon et al. 2017). Accordingly, a positive impact of longer or warmer summers on vital rates or population growth rates has been demonstrated in some populations (Hansen et al. 2013, Hansen et al. 2019a, Hansen et al. 2019c), but the potential effects related to vegetation ‘greening’ per se are more likely to occur as gradual increase in the carrying capacity of the tundra. Local heterogeneity in climate and climate trends, and the (density-dependent) ecological responses, seem to generate spatially contrasting net results of worsening winter-feeding conditions versus longer and warmer summers (Fig. Hansen et al. 2019b). However, despite the resultant local variation in population trends, the overall abundance of Svalbard reindeer (based on $N = 10$ monitored populations) has been slightly increasing since the late 1990s (Fig. 24 f-g; Hansen et al. 2019c), indicating a positive net effect of recent climate change at the meta-population level.



The population fluctuations of Svalbard reindeer are mainly driven by intraspecific competition for forage resources and weather variability. Photo: Sophie Cordon.

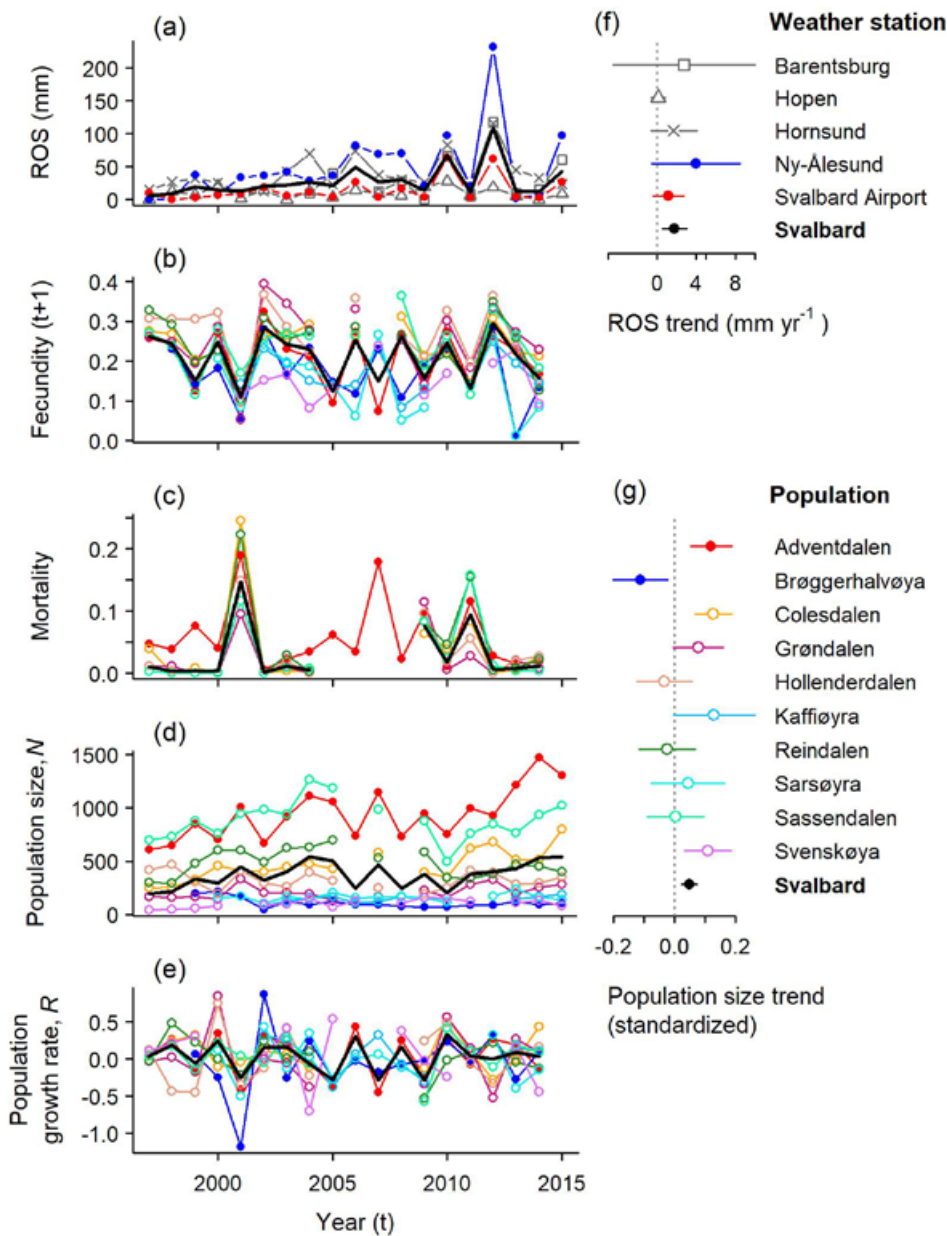


Figure 24. Annual fluctuations and temporal trends in rain-on-snow (ROS) and reindeer population parameters in Svalbard during the period used for population synchrony analyses (1997–2015). (a) Annual ROS (mm) recorded at five weather stations. (b–e) Annual reindeer fecundity, mortality, population sizes and growth rates based on summer ground and helicopter counts. (f–g) Linear trend estimates of ROS and reindeer population sizes over the study period. Whiskers indicate 95% confidence interval. In (a–e), solid black lines show ‘across Svalbard-scale’ estimates from linear mixed regression models.

3.5.2 Population monitoring

The Svalbard reindeer is monitored because it is a key species in the terrestrial food-web, is important for recreational local hunting and is vulnerable to climate change (Ims et al. 2014). Three long-term time series on reindeer abundance from Adventdalen (1979 – ; non-hunted), Reindalen (1979 – ; hunted) and Brøggerhalvøya (1978 – ; non-hunted), as well as number of reindeer harvested by the annual recreational quota based harvest, is the core of the reindeer monitoring in Environmental Monitoring of Svalbard and Jan Mayen (MOSJ; www.mosj.no, Box 3). These reindeer abundance time series have been the basis for understanding the role of density dependence and environmental drivers on reindeer population dynamics (e.g., Solberg et al. 2001, Aanes et al. 2003, Hansen et al. 2013, Albon et al. 2017, Hansen et al. 2019a).

The *Climate-Ecological Observatory for Arctic Tundra* (COAT) builds on and expands the ongoing monitoring of the reindeer, its grazing resources and interactions within the food web (Ims et al. 2013, Box 4). The reindeer monitoring addresses direct impact pathways on reindeer survival, for example, the effects of climate (winter versus summer warming) and management (sex and age composition of the hunting quotas), as well as indirect impacts acting through trophic interactions in the food web. The abundance time series and the long-term individual-based capture–mark–recapture data (described in Lee et al. 2015, Albon et al. 2017) from Nordenskiöld Land and the west coast of Spitsbergen (Pedersen et al. 2018) are important in this ecological monitoring context. These time-series have clearly demonstrated that maintaining ecological data collection over time is important to many aspects of our understanding of Arctic terrestrial ecosystems (e.g. Hansen et al. 2013, Albon et al. 2017, Hansen et al. 2019c).

Population abundance monitoring of Svalbard reindeer

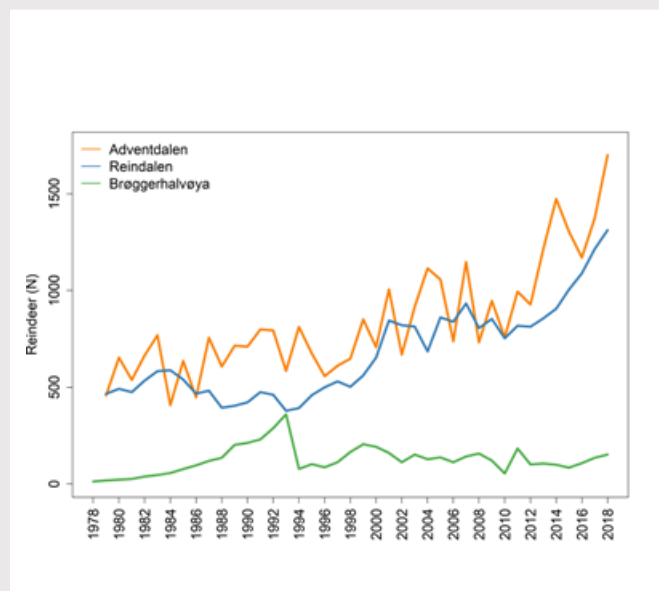
The Svalbard reindeer population abundance has more than tripled in the core monitoring areas on Nordenskiöld Land, Adventdalen and Reindalen, since the monitoring started in 1979. Both time series show that the population increased comparatively slowly from 1979 to the mid-1990s compared to the stronger increase during the last two decades. The re-introduced population in Brøggerhalvøya (1978) increased quickly, but crashed in the winter 1993–94. From one year to the next, the population experienced a reduction from 360 to 78 reindeer due to a combination of ice-locked pastures after a heavy rainfall (November 1993) and past over-grazing. Presently, the population size on Brøggerhalvøya has stabilised around a lower population level.

The contrasting developments between the continental and coastal reindeer populations during the last four decades arise from spatial differences in climate change and its effects on population dynamics. The coastal (Brøggerhalvøya) population experienced a larger increase in rain-on-snow (ROS) events and a stronger negative effect of the associated basal ground ice on population growth rates than the continental (Adventdalen) population. In contrast, the continental population experienced stronger summer warming and a positive effect on population growth rates. Thus, the contrasting effects of climate warming on two of the core monitoring populations – with increased ROS and harsher winter and with higher summer temperatures and improved carrying capacity – led to negative and positive population abundance trends (Hansen et al. 2019c).

COAT (www.coat.no) and MOSJ (www.mosj.no/no/) include population abundance data from all these locations in their long-term monitoring of Svalbard reindeer population abundance. These annual time series are proven precise and unbiased (Le Moullec et al. 2017) and have been the basis for several scientific articles that have studied population dynamics in relation to density dependent processes and climatic variability (Aanes et al. 2000, Solberg et al. 2001, Aanes et al. 2003, Hansen et al. 2011, Albon et al. 2017, Hansen et al. 2019c).



Svalbard reindeer counting locations on Brøggerhalvøya, Adventdalen og Reindalen. Illustration: Oddveig Ø. Ørvoll/NPI 2019.



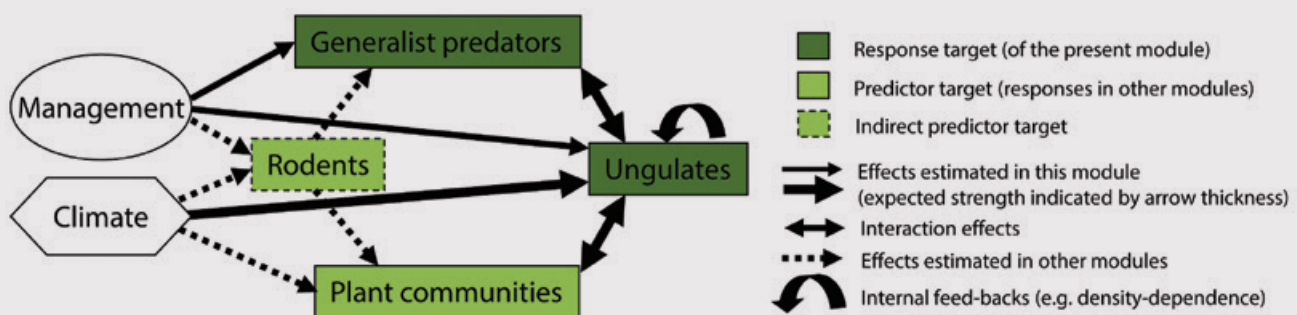
Population size of Svalbard reindeer in Adventdalen (1979–2018; total counts), Reindalen (1979–2018; transect counts) and Brøggerhalvøya (1978–2018; total counts). Note that for Reindalen the annual population size is shown as 3-year averages.



The population dynamics of the Svalbard reindeer are mainly driven by annual fluctuations in winter weather and feeding conditions, combined with density-dependent regulation, Photo: Odd Arne Olderbakk.

Box 4

COAT climate impact path model predictions for Svalbard reindeer



The conceptual model representing the Svalbard reindeer monitoring module described in the Science plan of the COAT Climate-Ecological Observatory for Arctic Tundra (Ims et al. 2013). The model specifies climate and management impact pathways on the prioritised monitoring target – the Svalbard reindeer. The main direct impact path is expected to act through warmer winters causing rain-on-snow and ground ice that limit forage accessibility and cause starvation in reindeer, and through warmer and longer summers causing green forage available for a longer period of the year and thereby improved survival and reproductive rates. Changed abundance of reindeer will impact plant communities through changed grazing pressure and may contribute to vegetation state changes. Availability of Svalbard reindeer carcasses will also influence the Arctic fox (*Vulpes lagopus*) populations. The path model also addresses the potentially modifying effects of geese on vegetation state changes.

4 Health and diseases

Reindeer are susceptible to a range of infectious agents, including parasites (Kutz et al. 2012, Josefsen et al. 2014), bacteria (Mørk et al. 2014) and viruses (Tryland et al. 2014). Some infectious diseases transmit between reindeer only, while others also use other animal host species (Tryland and Kutz 2018). The low number of mammalian species, including a lack of other ungulate species, and the isolated geographical position of Svalbard has placed Svalbard reindeer in a fortunate position when it comes to occurrence and spread of infectious diseases. According to current literature there are few diseases of concern in Svalbard reindeer (Pedersen et al. 2014).

4.1 Parasites

4.1.1 Intestinal parasites

Gastrointestinal nematodes are ubiquitous in nature and infect almost all wildlife species including the Svalbard reindeer. Although infection levels are usually sub-lethal, they can cause pathological changes in the gut that disrupt digestion, reduce appetite and impair nutrient uptake. Infections can, thus, have negative impacts on body condition, which is a key determinant of growth, fecundity and winter survival in many ungulates (Tryland and Kutz 2018). The parasite community of the Svalbard reindeer is simple, being dominated by two species of stongyle

nematodes in the abomasum with contrasting life-histories: *Ostertagia gruehneri* and *Marshallagia marshalli* (Halvorsen et al. 1999, Irvine et al. 2001; Fig. 25). Both species develop to their adult stage in the abomasum of the Svalbard reindeer, where they produce eggs that are released on to the tundra with the reindeer faeces. On the ground the eggs hatch, the larvae develop into an infective stage and move into the stems of plants and are then ingested by grazing reindeer where they develop in the abomasum into adults. Eggs and infective larvae are very resistant to freezing, and the larvae are also resistant to desiccation (Carlsson et al. 2013). While the general life history is similar for *O. gruehneri* and *M. marshalli*, experimental and observational studies have shown that the species differ profoundly in other aspects of their ecology. Adult *O. gruehneri* are present in the host throughout the year, but focus their reproductive efforts to the summer season when temperatures are suitable for egg hatching and larval development. Over the winter adult *O. gruehneri* stop producing eggs (Irvine et al. 2000, Irvine et al. 2001). In contrast, *M. marshalli* produce eggs throughout the winter, even though the eggs have to wait for the spring and summer for temperatures suitable for hatching. Low infection rates in the summer combined with a short life expectancy in the adult stage result in no adults to produce eggs in the reindeer in summer (Irvine et al. 2000, Irvine et al. 2001, Carlsson et al. 2012, Carlsson et al. 2013).

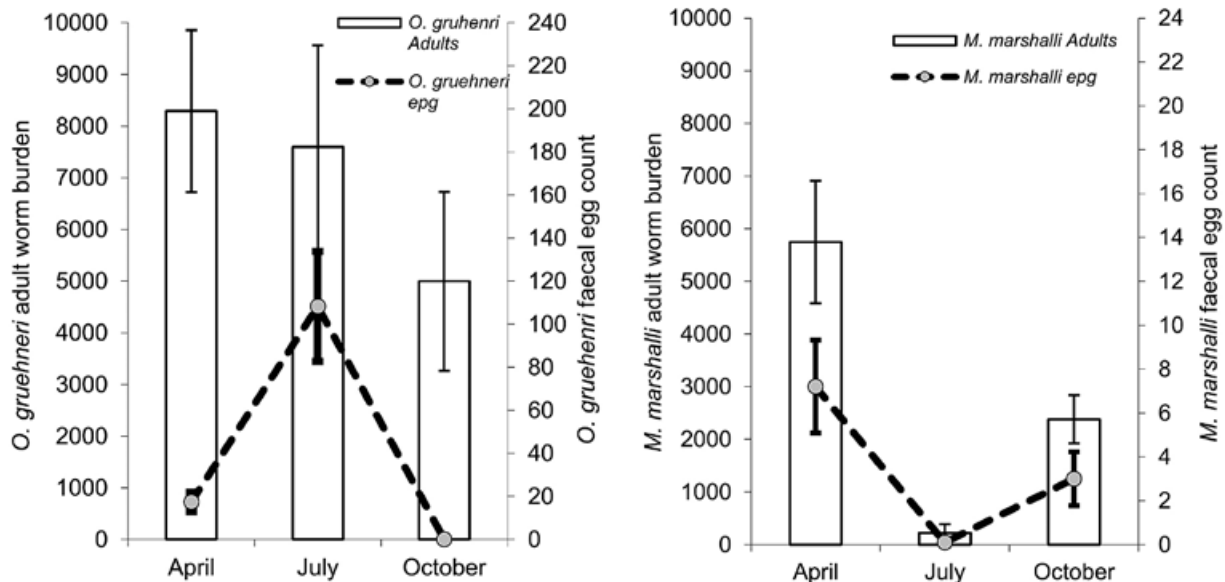


Figure 25. The burden of eggs (epg = faecal egg output) and worms for the two parasites, *Ostertagia gruehneri* (left) and *Marshallagia marshalli*, in 128 Svalbard reindeer sampled in April, July and October between 1995 and 1999. Figure from Irvine et al. (2001).

4.1.2 Other parasites

Two cestodes, *Moniezia benedini* and *Taenia krabbei*, have been reported in Svalbard reindeer with high prevalences (Bye 1985). It is not known if or how these parasites influence the health status of the animals. Reindeer serve as an intermediate host for *T. krabbei* which develops into its adult stage in the Arctic fox (*Vulpes lagopus*). There have been reports of very high infection intensities of the larval stage of *T. krabbei* in individuals of Svalbard reindeer shot by hunters (Stien 2009). The larval stage looks like small whitish eggs, typically about five mm long and two mm wide, and can make the meat unappealing for human consumption, but are not infectious for humans. *M. benedini* inhabits the small intestine and has only been found in calves (Bye 1985). This species' life cycle requires oribatid mites as an intermediate host.

4.2 Viral diseases

4.2.1 Rabies

Rabies is a fatal disease that can spread between animals and humans (termed zoonotic). Rabies is caused by viruses belonging to the genus *Lyssavirus* in the family of *Rhabdoviridae*. The first confirmed outbreak of rabies in Svalbard occurred in 1980 (Krogstrup et al. 1981, Ødegaard and Krogstrup 1981) after which there has been reports of sporadic outbreaks. The current understanding is that rabies outbreaks in Svalbard are the result of introductions via Arctic foxes migrating from other parts of the Arctic (Mørk et al. 2011). The low population density of Arctic foxes in Svalbard is considered the main reason for Svalbard is considered

the main reason for low prevalence. Other species, including reindeer and humans, can be infected by foxes carrying the disease. In Svalbard only a limited number of reindeer have been diagnosed with rabies, and even fewer have been observed alive. In recent outbreaks paralysis has been the dominant clinical symptom, but also aggression has been observed in reindeer (Mørk et al. 2011). The outbreaks of rabies in Svalbard have received much attention due to their relevance for humans. The last outbreak was in 2011 with eight infected reindeer (MacDonald et al. 2011, Mørk et al. 2011) and after that only one reindeer, in 2018, has been diagnosed with rabies (Sysselmannen 2018).

4.2.2 Other viruses

Reindeer may become infected with other viruses, such as the Bovine viral diarrhoea virus (BVDV), Bovine herpesvirus-1 (IBR/IPV), Orf virus (ecthyma), Cervid herpesvirus 2 (CvHV2) and Parainfluenza type 3 virus (PIV-3). These viruses are known to contribute to disease in reindeer elsewhere. However, none of these virus infections have been documented in Svalbard reindeer (Stuen et al. 1993, Klein and Tryland 2005, Tryland 2013).

4.3 Bacterial diseases

Although disease outbreaks of bacterial origin have been reported in reindeer, there is so far no indication that bacteria play an important role in disease occurrence in Svalbard reindeer.



Rabies can transfer from Arctic fox to Svalbard reindeer (*Rangifer tarandus platyrhynchus*). There is one documented outbreak (2011) where eight reindeer were diagnosed with rabies. Photo: Bjørn Frantzen/NIBIO.

5 Trophic interactions

5.1 Herbivore–plant interactions

The food web where Svalbard reindeer interact with plants and other herbivores is relatively simple. There is only one other resident vertebrate herbivore, the Svalbard rock ptarmigan, and in addition to the resident animals, a high number of geese that migrate to the archipelago for the summer. The perhaps most important plant functional groups that the herbivore utilise are mosses (a taxonomically and functionally very diverse group), forbs, grasses, sedges and rushes, deciduous dwarf shrubs as well as evergreen shrubs (Bjørkvoll et al. 2009, Ims et al. 2013). It is a noticeable feature of the vegetation in Svalbard that fruticose (upright, branching) lichens are very rare. This is likely due to trampling and also selective feeding on these lichens by Svalbard reindeer. In areas where reindeer densities are very low, fruticose lichens are present, but at high reindeer densities, the absence of lichens means that reindeer rely on mosses and vascular plants for food (Cooper and Wookey 2001, Van der Wal et al. 2001a, Van der Wal and Brooker 2004).

Direct measures of grazing pressure inflicted by Svalbard reindeer on vascular plants suggest a relatively low impact on the vegetation (Wegener and Odasz-Albrigtsen 1998, Van der Wal et al. 2000, Van der Wal and Brooker 2004). However, a limiting factor for vascular plant growth and primary production in the Arctic is low soil temperature and moisture. The moss layer has an insulating effect on the soil layer, keeping it cool in the summer, and there is compelling evidence for a negative impact of herbivores on the thickness of the moss layer (Van der Wal et al. 2001b, Van der Wal and Brooker 2004). In particular, grasses respond positively to a reduced moss layer and the associated increase in soil temperature (Fig. 26). Inspired by these results from Svalbard, Van der Wal (2006) suggested that reindeer grazing pressure is a main determinant of the state of Arctic tundra vegetation, postulating that: 1) At low reindeer densities the tundra may be dominated by fruticose lichens; 2) at intermediate reindeer densities lichens give way to mosses that limit grass growth; and 3) at even higher densities of reindeer the moss layer is reduced and grasses become dominant (Fig. 27).

Large changes in reindeer populations naturally bring about effects on vegetation, as predicted by the model and evidenced by real life examples. The reindeer population irruption after the reintroduction on Brøggerhalvøya generated strong effects on the vegetation, including a decline in the cover of mosses reduces by and percentage, vascular plants and lichens (Hansen et al 2007). After years of increasing reindeer numbers, the Brøggerhalvøya population declined strongly in 1993–1994. This relief in grazing pressure caused some changes in vegetation, recorded in 1998–1999. Previously dominant fruticose lichens changed species composition from *Cetraria* species the reindeer forage on, to *Stereocaulon* spp. that is less relevant as forage and somewhat more trampling tolerant. Mosses recovered completely and even exceeded pre-reindeer levels six years after the population peak. Recovery of vascular plants was more delayed and only partial due to a long-term suppression of common species that are important as reindeer forage. This may in part be due to the parallel increase in grazing pressure by barnacle geese (*Branta leucopsis*), which locally has resulted in almost complete suppression of vascular plants in moss tundra (Sjögersten et al. 2011). In those areas where barnacle goose impacts are greatest, so little forage is left for reindeer that males feed on goose faeces instead (Van der Wal and Loonen 1998). The predictions from the Van der Wal (2006) model partially held true in the Brøggerhalvøya case, as mosses and lichens did have reduced abundance after the increase in reindeer population, while the suggested graminoid state at very high reindeer densities was not realised. The suppression of major forage species, like grasses, and a sustained reduction in herbivore densities suggest that overgrazing occurred during the population irruption, possibly inducing a long-term decline in reindeer carrying capacity. This supports top-down control of vegetation by reindeer and, in this area, barnacle geese combined (Van der Wal and Hessen 2009).

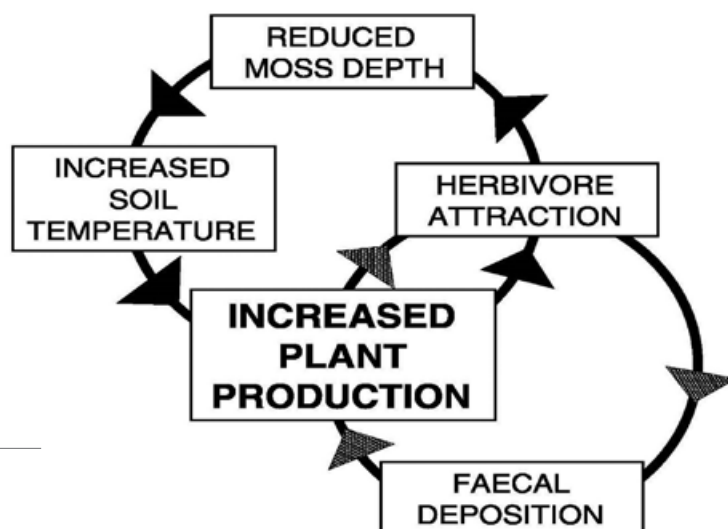


Figure 26. Conceptual model of the impact of Arctic herbivores on the abundance of vascular plants. Figure from Van der Wal and Brooker (2004).

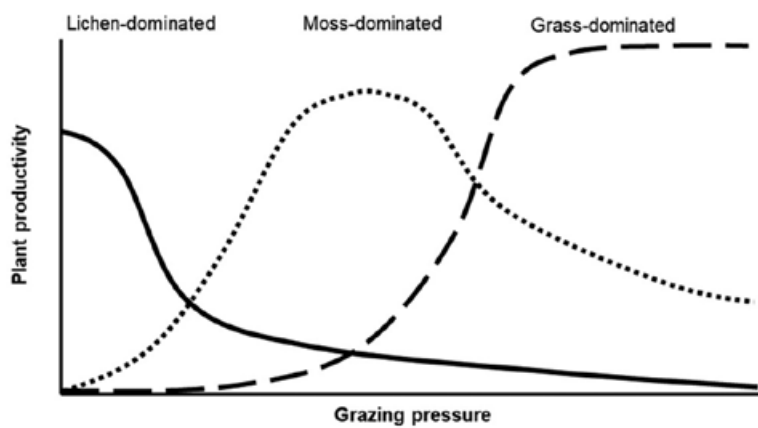


Figure 27. Schematic representation of the occurrence of tundra vegetation states in relation to grazing pressure exerted by reindeer. Herbivore-driven state transitions from lichen to moss to graminoid-dominated states are associated with an increase in plant productivity (on a standardised scale) and carrying capacity for reindeer populations. Figure from Van der Wal (2006).



Winter co-feeding of Svalbard reindeer and Svalbard rock ptarmigan. Photo: Nicholas Lecomte/NPI.

5.2 Parasite–host dynamics

The interaction of gastrointestinal nematodes in the Svalbard reindeer hosts has received considerable attention (Halvorsen and Bye 1999, Albon et al. 2002, Stien et al. 2002a, Stien et al. 2002b). The two numerically dominant parasitic nematode (*O. gruehneri* and *M. marshalli*) seem to differ in their impact on their host (see chapter 5: Health and diseases). Previous experimental work on this host–parasite system, demonstrated that *O. gruehneri* reduce reindeer fecundity at high infection intensities through its negative effect on host body condition (Stien et al. 2002b). Furthermore, the

study provided unique evidence for the delayed density-dependent parasite-mediated changes in fecundity to play a role in the regulation of the Svalbard reindeer population (Fig. 28; Albon et al. 2002). However, experimental manipulation of the abundance of the winter transmitted *M. marshalli* did not result in significant effects on host body mass or pregnancy rates (Carlsson et al. 2018). Suggesting that *M. marshalli* do not have an effect on the host population similar to the one observed for *O. gruehneri*.

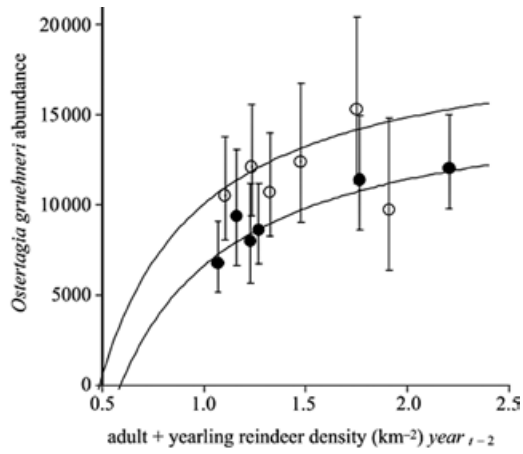


Figure 28. The estimated *Ostertagia gruehneri* abundance in October in relation to adult and yearling reindeer summer density two years earlier in two of the study locations, Colesdalen (filled circles) and Sassendalen (open circles). See Figure 2 in Albon et al. (2002) for estimates for regression lines. Error bars give 95 % confidence limits for the estimates. Figure from Albon et al. (2002).

5.3 Predator–prey interactions

Polar bears (*Ursus maritimus*) rarely kill reindeer in Svalbard (but see Derocher et al. (2000), however, remains of reindeer have been found in polar bear scats (Iversen et al. 2013). Arctic foxes may kill reindeer calves (Hansson et al. 1990, Prestrud 1992), but primarily scavenge carcasses (Jepsen et al. 2002, Eide et al. 2004). The abundance of reindeer carcasses varies between years, and in inland areas this impact the reproductive success of Arctic foxes (Fig. 29; Eide et al. 2004, Eide et al. 2012). Winters with many reindeer carcasses lead to high reproductive success, while in years with a low number of carcasses few Arctic fox dens were occupied. The main prey of Arctic foxes is sea birds and geese and the coupling of the population dynamics of the Svalbard reindeer and the Arctic fox (Fuglei et al. 2003, Hansen et al. 2013), suggests that the Svalbard reindeer indirectly may impact predation rates on bird species in Svalbard (Fuglei et al. 2003). Accordingly, Fuglei et al. (2003) found that temporal variation in the survival of goslings of Barnacle geese was associated with fluctuations in the local Arctic fox population size, which again was associated with fluctuations in the local Svalbard reindeer population size.

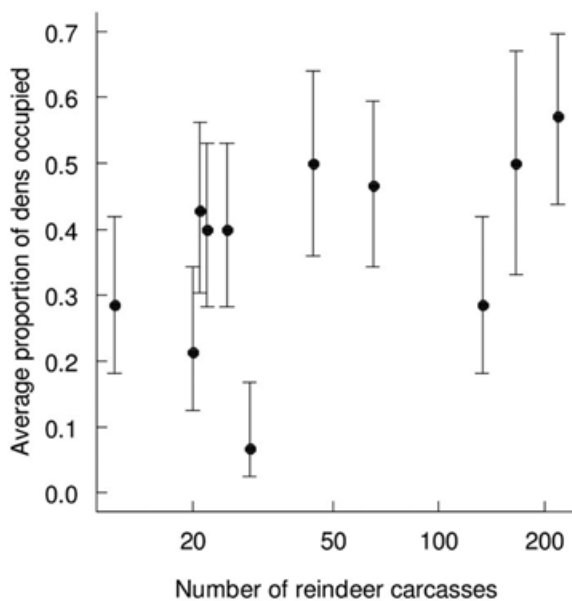


Figure 29. Average proportion of Arctic fox dens (± 1 SE) plotted against the number of reindeer carcasses found in Adventdalen the same year on a logarithmic scale. Figure from Eide et al. (2012).



Arctic foxes and polar bears scavenge on Svalbard reindeer carcasses. Photos: Sophie Cordon.

6 Human impacts

6.1 Harvesting management

The harvesting of Svalbard reindeer is regulated by the Svalbard Environmental Protection Act, the Regulations about harvest in Svalbard and the Regulations concerning local regulation of hunting of Svalbard rock ptarmigan and Svalbard reindeer in Svalbard (www.lovdatab.no; www.sysselmannen.no). The Act states that (section 24): “*The fauna shall be managed in such a manner that the natural productivity and diversity of species and their habitats are maintained, and Svalbard’s natural wilderness is protected for future generations. Controlled and limited harvesting may take place within this framework.*” The management plan (Punsvik 2009), reviewed in Benberg and Punsvik (2016,) details and give guidance to the current harvesting practises that aim to mimic the natural age and sex specific composition of the standing populations.

Currently, the Svalbard reindeer are hunted in six units (land area of 815 km² < 250 m altitude; Fig. 30) in Nordenskiöld Land through a quota for local residents to hunt between August 15 and September 20. Additionally, local trappers (1–3 per year) harvest up to 35 animals in their trapping areas. The spatial distribution of the quota and the number of animals in each hunting category

(calf, female/young, male and free animal) is under the control of the Governor of Svalbard, with quotas based on population counts from helicopter (Punsvik 2009). Based on movement data from GPS-marked females, Loe et al. (2017) found that Grøndalen/Hollendardalen and Colesdalen/Reindalen had common populations, and that quotas may be set jointly. Only Diabas and Sassen appeared as separate units with limited movements of reindeer across the unit borders.

Annually, between 300 and 350 licences are distributed to hunters and around 60 % of the quota is shot. The annual offtake between 1983 and 2018 ranged from 117 to 235 (www.mosj.no), which only comprises a small proportion of the number of reindeer counted before the hunting season (Stien et al. 2012, Pedersen et al. 2014). Stien et al. (2012) calculated that the annual offtake of animals older than one year varied between 6–14 % of the population in the hunting units before the hunting season. The hunters report mandatory information (e.g., sex, age, culling location, and jaw for age determination) shortly after the hunt to the Governor of Svalbard.



Figure 30. Location of the six hunting units for annual quota-based harvest of Svalbard reindeer on Nordenskiöld Land (large map) in the Svalbard archipelago on Central Spitsbergen (small map). Illustration: Oddveig Ø. Ørvoll/NPI.



Reindeer hunting in Hollendardalen 2013. Photo: Ruben Eidesen/UNIS.

6.2 Impacts of hunting on population dynamics

At present, there is limited information about potential impact of the harvest on Svalbard reindeer populations (Stien et al. 2012, Pedersen et al. 2014). Stien and his colleagues (2012) found that the current hunting management practices in Svalbard had minimal impact on Svalbard reindeer population dynamics. The most important age and sex category influencing population dynamics are adult females and the study concluded that it is possible to harvest more females (up to 13 %) than the current level (4–10 %). Also, the current hunting practices with as many males as females being hunted, stabilises the sex ratios close to the ratios that would be achieved without hunting. The report concludes that the number of annual hunting permits issued can be increased up to 400–450 animals on Nordenskiöld Land without having negative effects on the populations. However, Stien et al. (2012) point out to that effects from climate change on populations should be better integrated in the modelling of impacts on populations dynamics from harvest. Currently, an ongoing national effort through the project *Sustainable management of renewable resources in a changing environment – an integrated approach across ecosystems (SUSTAIN; 2015–2019)* aims to study impacts from the interaction between harvest and climate changes on Svalbard reindeer population structure and composition (see Peeters 2019).

6.3 Traffic disturbance

The behavioural responses of Svalbard reindeer to human activity has mainly focused on disturbances from snow scooter traffic or humans on foot on individual reindeer. The first study by Tyler (1991) experimentally approached 366 reindeer by snowmobile and measured reaction and flight distances. The group median for minimum reaction distances in Sassendalen and Adventdalen was measured to 640 m and median distance at initial flight was 80 m. The reactions were stronger in Sassendalen, an area with less traffic at that time, than in Adventdalen. Median flight response was estimated to give approx. 0.4 % increase in daily energy expenditure and 0.7 % loss of daily grazing time. Interestingly, reindeer in and around Longyearbyen displayed shorter reaction distances as they likely were habituated to scooter traffic. Recently, Tandberg (2016) found that GPS-marked female reindeer avoided areas closest to commonly used snowmobile trails, especially during the peak season of snow scooter driving. Although this resulted in avoidance of areas with potential winter forage, the author concluded that the reduction corresponded to only a moderate loss of winter pastures for the Svalbard reindeer.

Response distances and vigilance to humans on foot was investigated in three studies varying human activity and hunting restrictions (Colman et al. 2001, Reimers et al. 2011, Hansen and Aanes

2015). The studies found that Svalbard reindeer in areas with relatively high human activity in summer and no hunting (Adventdalen) had lower vigilance, shorter flight and running distances when approached by human on foot compared to reindeer in locations with relatively low human activity (e.g., Reinsdyrflya and Edgeøya). The difference in behavioural responses was likely due to habituation to humans (Colman et al. 2001). Differences in vigilance and fright behaviour based on sex and reproductive status was also measured showing that females with calves had highest vigilance and greater escape distances compared to males or barren females (Reimers et al. 2011). In addition, polar bears may play a role in the high vigilance behaviour of Svalbard reindeer on Edgeøya (Reimers and Eftestøl 2012).

6.4 Environmental pollution

In the Arctic, the main sources of most heavy metals and persistent organic pollutants (POPs) are from long-range transport of contaminants through air or water currents from anthropogenic activities in temperate regions and coastal erosion (Poikolainen 2004, Hung et al. 2010). Few studies have investigated the contaminant levels in the Svalbard reindeer despite the fact that heavy metals can enter the food web through snow (Poikolainen 2004).

Heavy metal accumulation (e.g., arsenic, cadmium, chromium, copper, mercury, nickel, lead, selenium and zinc) are low in Svalbard reindeer. For instance, the cadmium levels are comparable to

levels found in mainland reindeer in Norway (Norheim et al. 1990, Severinsen and Skaare 1997). The heavy metal concentration in reindeer tissue, obtained around the local settlement of Longyearbyen with local contaminant sources (e.g., coal mines), is however comparable to levels in reindeer found elsewhere in Svalbard (Røed 2018). Reindeer from coastal locations (Kapp Linnè) have the highest heavy metal accumulation, which could be attributed to higher exposure to long-range transport of contaminants (Røed 2018).

The levels of persistent organic pollutants (POPs) in Svalbard reindeer tissue have been investigated in only a few studies, which reported levels below the threshold of what is anticipated to have negative health effects (Severinsen and Skaare 1997, Carlsson 2012, Melien 2014). The analysed compounds include polychlorinated biphenyls (PCBs) and organochlorine pesticides, such as hexachlorobenzene (HCBs), hexachlorocyclohexane (HCH), chlordane's, and dichlorodiphenyltrichloroethane (DDT) (Severinsen 1997, Melien 2014), and perfluoroalkyl substances (Carlsson 2012), commonly observed in Arctic environments (Letcher et al. 2010). Interestingly, several contaminants e.g., long-chained perfluoroalkyl carboxylates (PFCAs), such as HCB and heavy metals (Hg) decreased in Arctic foxes during years when reindeer carcasses are plentiful (Andersen et al. 2015, Routti et al. 2017, Hallanger et al. 2019). This means access to prey species with low levels of contaminants reduced contaminant levels in Arctic foxes when switching from marine to terrestrial diet with lower POP concentrations (Andersen et al. 2015, Routti et al. 2017, Hallanger et al. 2019).



The reindeer may habituate to humans as observed around the few local settlements. Photo: Siri Birgitte Uldal/NPI.

7 Key knowledge gaps and research needs

The Norwegian government and the sectoral legislations, such as the Svalbard Environmental Protection Act, have set goals for maintaining and protecting the virtually untouched nature in Svalbard with intact ecosystems and species. This includes both conservation and management of endemic species, such as the Svalbard reindeer, so that populations are not affected in a negative way. To meet this goal, understanding factors affecting life history parameters, vital rates and population dynamics is of great significance for maintaining healthy populations in a rapidly changing environment.

The workshop leading up to this report aimed at summarising current knowledge status on Svalbard reindeer and identify important knowledge gaps. During the workshop, the participants identified many detailed key knowledge gaps to guide future directions of Svalbard reindeer research. The recommendations were further elaborated through the process of writing this report. The following section is structured following the topics of the report. Each topic is divided into overall knowledge gaps and specific research needs, and covers a range of areas from research interests to knowledge that can directly feed into the environmental management. The overall knowledge gaps that were identified each have specific questions that should be looked upon as examples of research needs rather than an exclusive list of unsolved specific questions.

Foraging resources, habitats and spatial ecology

General knowledge gaps within foraging ecology relate to habitat selection at different spatial and temporal scales, and the linkages to fitness components of individuals and populations.

Specific research needs include:

- Seasonal and year-to-year patterns of plant quantity and quality and the consequences of them for reindeer foraging ecology and individual fitness components.
- Diet and habitat selection during shoulder seasons.
- Phenotypic differences, i.e., differences in observable characteristics of individuals related to foraging behaviour or physiological adaptations, in the ability to improve fitness by habitat selection and movement in seasonal energy landscapes.
- Development of high-resolution digital spatial layers (i.e., vegetation, habitat suitability, biomass, vegetation productivity) using new technologies in remote sensing, at the spatial and temporal scales relevant to the existing high-resolution tracking data.
- Fitness consequences from changes in diet from regular forage to alternative sources like seaweed and kelp.

Life history and demography

General knowledge gaps within life-history and demographics of reindeer are understanding natural selection under climate change.

Specific research needs include:

- The cumulative effects from climate (e.g., increase in winter rain and ground ice and extended grazing seasons) on life history parameters and demography.
- Age and sex specific responses, and density dependence under different climatic scenarios.

- Development of integrated population models for the reindeer populations that have been subject to long-term monitoring, following the study of Lee et al. (2015) of the Reindalen-Semmeldalen-Colesdalen population.
- Better understanding of life history and dynamics in reindeer living in locations in Svalbard that currently lack monitoring.

Population dynamics

A general knowledge gap within population dynamics and regulation is causality in the observed processes and interactions in the populations.

Specific research needs include:

- Enhancing the mechanistic understanding of the relative role of the different seasons and how changes in seasonality (e.g., length of grazing season) affect population dynamics.
- How the magnitude and timing of winter weather affect winter forage availability and thus population dynamics.
- Reindeer parasites communities, both established communities and possible introduction of new parasites with the warming trend, and how these parasites affect individual fitness components and ultimately population regulation.
- Population responses to changes in environmental conditions across larger archipelago wide spatial and ecological gradients.

Population genetics

General knowledge gaps within population genetics relate to the possible unique adaptive traits that can have evolved due to the isolation of the Svalbard reindeer.

Specific research needs include:

- Linking spatial genetic structure to differences in morphology/fitness on an archipelago wide scale.



Understanding factors affecting life history, vital rates and population dynamics is important to maintain healthy Svalbard reindeer populations.
Photo: Nicholas Lecomte.

- Estimates of genetic diversity, inbreeding and differentiation because this can shed light on the levels of isolation of peripheral populations, particularly North Spitsbergen, Nordaustlandet and Edgeøya, which survived the long-term overharvesting period.
- Comparison of the genetic diversity in naturally recolonised populations and the reintroduced populations near Ny-Ålesund, which can improve our understanding of the rate of genetic drift in newly established populations and the importance of the genetic diversity in the source population.

Adaptive capacity and behavioural buffering

General knowledge gaps relate to how the Svalbard reindeer adapt to the rapid climatic and environmental changes that currently take place in Svalbard.

Specific research needs include:

- Adaptive capacity, both behavioural and physiological responses (e.g., aspects of thermoregulation, energy storage and retrieval), in individuals and within different populations, to the changes in the ecosystem from climate change.
- How resilient are the reindeer to the multitude of changes in their environment, and what are the long-term consequences for individual fitness components, vital rates and populations?

Trophic interactions

General knowledge gaps relate to the Svalbard reindeer and its interactions with the tundra ecosystem and its food web.

Specific research needs include:

- In habitats with different resource levels, how reindeer affect the tundra ecosystem, including impacts on vegetation, nutrient dynamics and intensification of disturbances to the tundra caused by other sources.
- Reindeer interactions with other resident and migratory herbivores, such as geese, related to food competition and spatial habitat overlap.
- The role of bird cliffs as a foraging resource for reindeer and a hot-spot for ecosystem interactions.
- Frequency and types of interactions between polar bears and reindeer, and whether the frequency of these interactions will change in the future.

Climate systems and processes

General knowledge gaps within climate systems and processes are that spatially explicit climate data is lacking.



In a rapidly changing environment, increased knowledge about the relative role of shifting seasonality on individuals and populations is of great importance. Photo: Lawrence Hislop/NPI.

Specific research needs include:

- Process-oriented studies of how the physical processes interact (e.g., precipitation, snow depth, snow water equivalents, temperature etc.) to understand the formation and spatial extent of ice both within the snow-pack and on the ground.
- Modelling of the spatio-temporal variation of snow in the landscape using state-of-the-art modelling techniques at ecological relevant scales that match the fine resolution spatial and temporal reindeer data.
- Development of techniques that use remote sensing data to identify the extent of basal ground ice and snow cover in the landscape at ecologically relevant scales.
- Understanding the non-linear effects of rain-on-snow events on population growth rates in combination with other climate induced changes affecting e.g., forage resources and habitat use.

Harvest management

General knowledge gaps within harvest management relate to consequences on current and future harvest and the interaction with climate change on age and sex composition of Svalbard reindeer populations.

Specific research needs include:

- Eco-evolutionary implications from the excessive harvest and local extinction in the late 1800s / early 1900s on population distribution and population genetics, possibly in interaction with other anthropogenic stressors.
- Does the current harvest operate within the framework of the regulations? This includes evaluation of the current quota system, including the spatial distribution of the harvest, and the potential impacts on sex and age composition of the harvested populations.

Disturbances and environmental pollution

General knowledge gap within disturbance and environmental pollution relates to the sum of the increased human activity on the archipelago.

Specific research needs include:

- Cumulative or interactive effects from several environmental stressors (e.g., human disturbances, climate change etc.) on individuals and their fitness components, population dynamics and behaviour.
- Levels of new contaminants in reindeer and their effects on reindeer health, such as plastic pollution.

8 References

The ENDNOTE library Svalbardrein.enl is available with the electronic report at the web-pages of the Norwegian Polar Institute (www.npolar.no) and Svalbard Environmental Protection Fund (www.sysselmannen.no/Svalbards-miljovernfond).

- Aanes, R., B. E. Saether, and N. A. Øritsland. 2000. Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. *Ecography* 23:437-443.
- Aanes, R., B. E. Saether, F. M. Smith, E. J. Cooper, P. A. Wookey, and N. A. Øritsland. 2002. The Arctic Oscillation predicts effects of climate change in two trophic levels in a High Arctic ecosystem. *Ecology Letters* 5:445-453.
- Aanes, R., B. E. Saether, E. J. Solberg, S. Aanes, O. Strand, and N. A. Øritsland. 2003. Synchrony in Svalbard reindeer population dynamics. *Canadian Journal of Zoology* 81:103-110.
- Aas-Hansen, Ø., L. P. Folkow, and A. S. Blix. 2000. Panting in reindeer (*Rangifer tarandus*). *American Journal of Physiology: Regulatory, Integrative and Comparative Physiology* 279:R1190-R1195.
- Adamczewski, J. Z., P. F. Flood, and A. Gunn. 1997. Seasonal patterns in body composition and reproduction of female muskoxen (*Ovibos moschatus*). *Journal of Zoology* 241:245-269.
- Åhman, B., and R. G. White. 2019. Rangifer diet and nutritional needs. Pages 107-134 in M. Tryland and S. J. Kutz, editors. *Reindeer and caribou: health and disease*. CRC Press, Boca Raton, FL.
- Albon, S. D., A. Stien, R. J. Irvine, R. Langvatn, E. Ropstad, and O. Halvorsen. 2002. The role of parasites in the dynamics of a reindeer population. *Proceedings of the Royal Society B-Biological Sciences* 269:1625-1632.
- Albon, S. D., R. J. Irvine, O. Halvorsen, R. Langvatn, L. E. Loe, E. Ropstad, V. Veiberg, R. van Der Wal, E. M. Bjørkvoll, E. I. Duff, B. B. Hansen, A. M. Lee, T. Tveraa, and A. Stien. 2017. Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. *Global Change Biology* 23:1374-1389.
- Alendal, E., and I. Byrkjedal. 1976. Population size and reproduction of the reindeer (*Rangifer tarandus platyrhynchus*) on Nordenskiöld Land, Svalbard. *Årbok Norsk Polarinstittut, Norwegian Polar Institute, Tromsø, Norway*.
- Alendal, E., S. d. Bie, and S. E. van Wieren. 1979. Size and composition of the wild reindeer *Rangifer tarandus platyrhynchus* population in the Southeast Svalbard Nature Reserve. *Holarctic Ecology* 2:101-107.
- Andersøn, C. H. 1863. Om Spetsbergenrenen, *Cervus tarandus forma spetsbergensis*. *Öfversigt af Kongl. vetenskaps-akademiens förhandlingar* 19:457-461.
- Andersen, M. S., E. Fuglei, M. König, I. Lipasti, Å. Ø. Pedersen, A. Polder, N. G. Yoccoz, and H. Routti. 2015. Levels and temporal trends of persistent organic pollutants (POPs) in arctic foxes (*Vulpes lagopus*) from Svalbard in relation to dietary habits and food availability. *Science of the Total Environment* 511:112-122.
- Anon. 1827. "Stockholm, den 12te November". *Den Norske Rigstidende* 13 (94): p. 2
- Arnold, W., T. Ruf, L. E. Loe, R. J. Irvine, E. Ropstad, V. Veiberg, and S. D. Albon. 2018. Circadian rhythmicity persists through the Polar night and midnight sun in Svalbard reindeer. *Scientific Reports* 8:14466.
- Bandy, P. J., I. Cowan, and A. J. Wood. 1970. Comparative growth in four races of black-tailed deer (*Odocoileus hemionus*). *Canadian Journal of Zoology* 48:1401-1410.
- Benberg, B., and T. Punsvik. 2016. Forvaltning av svalbardreinen. Pages 379-383 in T. Punsvik and J. H. Frøstrup, editors. *Villreinen: biologi - historie - forvaltning*. Friluftslaget, Arendal, Norway.
- Bergerud, A. T., and M. J. Nolan. 1970. Food habits of hand-reared caribou *Rangifer tarandus* L. in Newfoundland. *Oikos* 21:348-350.
- Beumer, L. T., O. Varpe, and B. B. Hansen. 2017. Cratering behaviour and faecal C:N ratio in relation to seasonal snowpack characteristics in a High-Arctic ungulate. *Polar Research* 36:1286121.
- Bie, S. 1977. Survivorship in the Svalbard reindeer (*Rangifer tarandus platyrhynchus* Vrolik) on Edgeøya. *Årbok 1976, Norwegian Polar Institute, Tromsø, Norway*.
- Bjørkvoll, E., B. Pedersen, H. Hyttborn, I. S. Jønsdøttir, and R. Langvatn. 2009. Seasonal and interannual dietary variation during winter in female Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Arctic Antarctic and Alpine Research* 41:88-96.
- Blix, A. S. 2016. Adaptations to polar life in mammals and birds. *Journal of Experimental Biology* 219:1093-1105.
- Blix, A. S., and H. K. Johnsen. 1983. Aspects of nasal heat exchange in resting reindeer. *The Journal of Physiology* 340:445-454.
- Blix, A. S., L. Walløe, and L. P. Folkow. 2011. Regulation of brain temperature in winter-acclimatized reindeer under heat stress. *Journal of Experimental Biology* 214:3850-3856.
- Blix, A. S., P. H. Kvasdheim, M. V. Kholodova, V. E. Sokolov, E. B. Messelt, and N. J. C. Tyler. 2015. Superb winter fur insulation in the small Siberian musk deer (*Moschus moschiferus*). *Rangifer* 35:53-60.
- Bye, K. 1985. Cestodes of reindeer (*Rangifer tarandus platyrhynchus* Vrolik) on the Arctic islands of Svalbard. *Canadian Journal of Zoology* 63:2885-2887.
- CAFF Arctic Flora and Fauna. 2001. CAFF Map No.28 - Distribution of wild reindeer, caribou, and domestic reindeer in the Arctic. [Image]. Arctic Council, Conservation of Arctic Flora and Fauna Working Group, Akureyri, Iceland.

- Carlsson, P. 2012. POP-jakt i skolen: sluttrapport til Svalbard miljøvern-fond, november 2010–desember 2012. Svalbard Miljøvern-fond, Longyearbyen, Norway.
- Carlsson, A. M., K. J. Irvine, K. Wilson, S. B. Piertney, O. Halvorsen, S. J. Coulson, A. Stien, and S. D. Albon. 2012. Disease transmission in an extreme environment: Nematode parasites infect reindeer during the Arctic winter. *International Journal for Parasitology* 42:789-795.
- Carlsson, A. M., R. J. Irvine, K. Wilson, and S. J. Coulson. 2013. Adaptations to the Arctic: low-temperature development and cold tolerance in the free-living stages of a parasitic nematode from Svalbard. *Polar Biology* 36:997-1005.
- Carlsson, A. M., S. D. Albon, S. J. Coulson, E. Ropstad, A. Stien, K. Wilson, L. E. Loe, V. Veiberg, and R. J. Irvine. 2018. Little impact of over-winter parasitism on a free-ranging ungulate in the high Arctic. *Functional Ecology* 32:1046-1056.
- Colman, J. E., B. W. Jacobsen, and E. Reimers. 2001. Summer response distances of Svalbard reindeer *Rangifer tarandus platyrhynchus* to provocation by humans on foot. *Wildlife Biology* 7:275-283.
- Cooper, E. J., and P. A. Wookey. 2001. Field measurements of the growth rates of forage lichens, and the implications of grazing by Svalbard reindeer. *Symbiosis* 31:173-186.
- Côté, S. D., J. F. Dallas, F. Marshall, R. J. Irvine, R. Langvatn, and S. D. Albon. 2002. Microsatellite DNA evidence for genetic drift and philopatry in Svalbard reindeer. *Molecular Ecology* 11:1923-1930.
- Cuylar, C., and N. A. Øritsland. 2002. Effect of wind on Svalbard reindeer fur insulation. *Rangifer* 22:93-99.
- Cuylar, C., and J. B. Østergaard. 2005. Fertility in two West Greenland caribou *Rangifer tarandus groenlandicus* populations during 1996/97: Potential for rapid growth. *Wildlife Biology* 11:221-227.
- Danielsen, P. 2016. Climate trends, weather fluctuations and calving phenology in Svalbard reindeer (*Rangifer tarandus platyrhynchus*). M.Sc. NTNU, Trondheim, Norway.
- Derocher, A. E., O. Wiig, and G. Bangjord. 2000. Predation of Svalbard reindeer by polar bears. *Polar Biology* 23:675-678.
- Douhard, M., L. E. Loe, A. Stien, C. Bonenfant, R. J. Irvine, V. Veiberg, E. Ropstad, and S. Albon. 2016. The influence of weather conditions during gestation on life histories in a wild Arctic ungulate. *Proceedings of the Royal Society B-Biological Sciences* 283:20161760.
- Eckert, C. G., K. Samis, and S. Loughheed. 2008. Genetic variation across species' geographical ranges: The central-marginal hypothesis and beyond. *Molecular Ecology* 17:1170-1188.
- Eide, N. E., J. U. Jepsen, and P. Prestrud. 2004. Spatial organization of reproductive Arctic foxes *Alopex lagopus*: responses to changes in spatial and temporal availability of prey. *Journal of Animal Ecology* 73:1056-1068.
- Eide, N. E., A. Stien, P. Prestrud, N. G. Yoccoz, and E. Fuglei. 2012. Reproductive responses to spatial and temporal prey availability in a coastal Arctic fox population. *Journal of Animal Ecology* 81:640-648.
- Førland, E. J., R. Benestad, I. Hanssen-Bauer, J. E. Haugen, and T. E. Skaugen. 2011. Temperature and precipitation development at Svalbard 1900–2100. *Advances in Meteorology* 2011:1-14.
- Forman, S. L., D. Lubinski, and R. R. Weihe. 2000. The Holocene occurrence of reindeer on Franz Josef Land, Russia. *Holocene* 10:763-768.
- French, C. E., L. C. McEwen, N. D. Magruder, T. Rader, T. A. Long, and R. W. Swift. 1960. Responses of white-tailed bucks to added artificial light. *Journal of Mammalogy* 41:23-29.
- Fuglei, E., N. A. Øritsland, and P. Prestrud. 2003. Local variation in arctic fox abundance on Svalbard, Norway. *Polar Biology* 26:93-98.
- Gjertz, I. 1995. Reindeer on Prins Karls Forland, Svalbard. *Polar Research* 14:87-88.
- Gravlund, P., M. Meldgaard, S. Paabo, and P. Arctander. 1998. Polyphyletic origin of the small-bodied, high-arctic subspecies of tundra reindeer (*Rangifer tarandus*). *Molecular Phylogenetics and Evolution* 10:151-159.
- Gregorini, P. 2012. Diurnal grazing pattern: its physiological basis and strategic management. *Animal Production Science* 52:416-430.
- Gunn, A. 2016. *Rangifer tarandus*. The IUCN Red List of Threatened Species 2016: e.T29742A22167140. <http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T29742A22167140.en>. Accessed on 01 July 2019.
- Hallanger, I. G., E. Fuglei, N. G. Yoccoz, A. O. Pedersen, M. König, and H. Routti. 2019. Temporal trend of mercury in relation to feeding habits and food availability in arctic foxes (*Vulpes lagopus*) from Svalbard, Norway. *Science of the Total Environment* 670:1125-1132.
- Halvorsen, O., and K. Bye. 1999. Parasites, biodiversity, and population dynamics in an ecosystem in the High Arctic. *Veterinary Parasitology* 84:205-227.
- Halvorsen, O., A. Stien, J. Irvine, R. Langvatn, and S. Albon. 1999. Evidence for continued transmission of parasitic nematodes in reindeer during the Arctic winter. *International Journal for Parasitology* 29:567-579.
- Hansen, B. B., and R. Aanes. 2015. Habituation to humans in a predator-free wild ungulate. *Polar Biology* 38:145-151.
- Hansen, B. B., R. Aanes, I. Herfindal, B.-E. Sæther, and S. Henriksen. 2009a. Winter habitat–space use in a large arctic herbivore facing contrasting forage abundance. *Polar Biology* 32:971-984.
- Hansen, B. B., I. Herfindal, R. Aanes, B.-E. Sæther, and S. Henriksen. 2009b. Functional response in habitat selection and the tradeoffs between foraging niche components in a large herbivore. *Oikos* 118:859-872.
- Hansen, B. B., R. Aanes, and B.-E. Sæther. 2010a. Feeding-crater selection by high-arctic reindeer facing ice-blocked pastures. *Canadian Journal of Zoology* 88:170-177.
- Hansen, B. B., R. Aanes, and B. E. Sæther. 2010b. Partial seasonal migration in high-arctic Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Canadian Journal of Zoology* 88:1202-1209.

- Hansen, B. B., R. Aanes, I. Herfindal, J. Kohler, and B. E. Saether. 2011. Climate, icing, and wild arctic reindeer: past relationships and future prospects. *Ecology* 92:1917-1923.
- Hansen, B., V. Veiberg, and R. Aanes. 2012. Material from harvested Svalbard reindeer: evaluation of the material, the data and their areas of application for research and management. Brief Report Series 24, Norwegian Polar Institute, Tromsø, Norway.
- Hansen, B. B., V. Grotan, R. Aanes, B. E. Saether, A. Stien, E. Fuglei, R. A. Ims, N. G. Yoccoz, and A. O. Pedersen. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the high Arctic. *Science* 339:313-315.
- Hansen, B. B., K. Isaksen, R. E. Benestad, J. Kohler, Å. Ø. Pedersen, L. E. Loe, S. J. Coulson, J. O. Larsen, and Ø. Varpe. 2014. Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. *Environmental Research Letters* 9:e114021.
- Hansen, B. B., M. Gamelon, S. D. Albon, A. M. Lee, A. Stien, R. J. Irvine, B.-E. Sæther, L. E. Loe, E. Ropstad, V. Veiberg, and V. Grøtan. 2019a. More frequent extreme climate events stabilize reindeer population dynamics. *Nature Communications* 10:1616.
- Hansen, B. B., J. R. Lorentzen, J. M. Welker, Ø. Varpe, R. Aanes, L. T. Beumer, and Å. Ø. Pedersen. 2019b. Reindeer turning maritime: Ice-locked tundra triggers changes in dietary niche utilization. *Ecosphere* 10:e02672.
- Hansen, B. B., Å. Ø. Pedersen, B. Peeters, M. Le Moullec, D. S. Albon, V. Grøtan, I. Herfindal, B.-E. Sæther, and R. Aanes. 2019c. Spatial heterogeneity in climate change decouples the long-term dynamics of wild reindeer populations in the high Arctic. *Global Change Biology* 00:1-13.
- Hanssen-Bauer, I., E. J. Førland, H. Hisdal, S. Mayer, A. B. Sandø, and A. Sorteberg. 2019. Climate in Svalbard 2100 – a knowledge base for climate adaptation. NCCS Report no. 1/2019, Norwegian Environment Agency (Miljødirektoratet), Oslo, Norway.
- Hansson, R., P. Prestrud, and N. A. Øritsland. 1990. Assessment system for the environment and industrial activities in Svalbard. Rapport nr. 68, Norwegian Polar Institute, Oslo, Norway.
- Hazlerigg, D., A. S. Blix, and K.-A. Stokkan. 2017. Waiting for the Sun: the circannual programme of reindeer is delayed by the recurrence of rhythmical melatonin secretion after the arctic night. *Journal of Experimental Biology* 220:3869-3872.
- Heatta, M. J. 2009. The mating strategy of female Svalbard reindeer (*Rangifer tarandus platyrhynchus*). M.Sc. The Arctic University of Norway, Tromsø, Norway.
- Henriksen, S., R. Aanes, B. E. Saether, T. H. Ringsby, and J. Tufto. 2003. Does availability of resources influence grazing strategies in female Svalbard reindeer? *Rangifer* 23:25-37.
- Hogg, C., M. Neveu, K.-A. Stokkan, L. Folkow, P. Cottrill, R. Douglas, D. M. Hunt, and G. Jeffery. 2011. Arctic reindeer extend their visual range into the ultraviolet. *Journal of Experimental Biology* 214:2014-2019.
- Holand, O., A. B. Leifseth, and E. Persen. 1981. Nyetablering av rein på Brøggerhalvøya, Svalbard: En beiteøkologisk undersøkelse. M.Sc. Norges Landbrukshøyskole, Ås, Norway.
- Hung, H., R. Kallenborn, K. Breivik, Y. Su, E. Brorström-Lundén, K. Olafsdottir, J. M. Thorlacius, S. Leppänen, R. Bossi, and H. Skov. 2010. Atmospheric monitoring of organic pollutants in the Arctic under the Arctic Monitoring and Assessment Programme (AMAP): 1993–2006. *Science of the Total Environment* 408:2854-2873.
- Ims, R. A., J. U. Jepsen, A. Stien, and N. G. Yoccoz. 2013. Science plan for COAT: Climate-ecological Observatory for Arctic Tundra. Fram Centre Report Series 1, Tromsø, Norway.
- Irvine, R. J., A. Stien, O. Halvorsen, R. Langvatn, and S. D. Albon. 2000. Life-history strategies and population dynamics of abomasal nematodes in Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Parasitology* 120:297-311.
- Irvine, R. J., A. Stien, J. F. Dallas, O. Halvorsen, R. Langvatn, and S. D. Albon. 2001. Contrasting regulation of fecundity in two abomasal nematodes of Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Parasitology* 122:673-681.
- Irving, L., and J. Krog. 1955. Temperature of skin in the Arctic as a regulator of heat. *Journal of Applied Physiology* 7:355-364.
- Iverson, M., J. Aars, T. Haug, I. Alsos, C. Lydersen, L. Bachmann, and K. Kovacs. 2013. The diet of polar bears (*Ursus maritimus*) from Svalbard, Norway, inferred from scat analysis. *Polar Biology* 36:561–571.
- Jenkins, D. A., N. Lecomte, J. A. Schaefer, S. M. Olsen, D. Swingedouw, S. D. Côté, L. Pellissier, and G. Yannic. 2016. Loss of connectivity among island-dwelling Peary caribou following sea ice decline. *Biology Letters* 12:e20160235.
- Jepsen, J. U., N. E. Eide, P. Prestrud, and L. B. Jacobsen. 2002. The importance of prey distribution in habitat use by arctic foxes (*Alopex lagopus*). *Canadian Journal of Zoology* 80:418-429.
- Johansen, B., and H. Tømmervik. 2014. The relationship between phytomass, NDVI and vegetation communities on Svalbard. *International Journal of Applied Earth Observation and Geoinformation* 27:20-30.
- Johansen, B., S. R. Karlsen, and H. Tømmervik. 2012. Vegetation mapping of Svalbard utilising Landsat TM/ETM+ data. *Polar Record* 48:47-63.
- Johnsen, H. K., and L. P. Folkow. 1988. Vascular control of brain cooling in reindeer. *American Journal of Physiology* 254:R730-R739.
- Johnsen, H. K., A. S. Blix, L. Jørgensen, and J. B. Mercer. 1985a. Vascular basis for regulation of nasal heat exchange in reindeer. *American Journal of Physiology* 249:R617-R623.
- Johnsen, H. K., A. Rognmo, K. J. Nilssen, and A. S. Blix. 1985b. Seasonal changes in the relative importance of different avenues of heat loss in resting and running reindeer. *Acta Physiologica Scandinavica* 123:73-79.
- Johnsen, H. K., A. S. Blix, J. B. Mercer, and K.-D. Bolz. 1987. Selective cooling of the brain in reindeer. *American Journal of Physiology* 253:R848-R853.

- Joo, S., D. Han, E. J. Lee, and S. Park. 2014. Use of length heterogeneity polymerase chain reaction (LH-PCR) as non-invasive approach for dietary analysis of Svalbard reindeer, *Rangifer tarandus platyrhynchus*. *Plos One* 9:e91552.
- Josefsen, T., A. Oksanen, and B. Gjerde. 2014. Parasitter hos rein i Fennoskandia - en oversikt. *Norsk Veterinærtidsskrift* 126:185-201.
- Kinck, C. 2014. Reduced forage access affects home range size and site fidelity of Svalbard reindeer (*Rangifer tarandus platyrhynchus*). M.Sc. Norwegian University of Life Sciences, Ås, Norway.
- Klein, J., and M. Tryland. 2005. Characterisation of parapoxviruses isolated from Norwegian semi-domesticated reindeer (*Rangifer tarandus tarandus*). *Virology Journal* 2:79.
- Kohler, J., and R. Aanes. 2004. Effect of winter snow and ground-icing on a Svalbard reindeer population: Results of a simple snowpack model. *Arctic, Antarctic and Alpine Research* 36:333-341.
- Krogstad, J., O. A. Ødegaard, R. Aabakken, and A. Borset. 1981. Rabies på Svalbard våren 1980. Infeksjonen diagnostisert på polarrev, reinsdyr og ringsel. *Norsk Veterinærtidsskrift* 93:5-10.
- Kutz, S. J., J. Ducrocq, G. G. Verocai, B. M. Hoar, D. D. Colwell, K. B. Beckmen, L. Polley, B. T. Elkin, and E. P. Hoberg. 2012. Parasites in ungulates of Arctic North America and Greenland: A view of contemporary diversity, ecology, and impact in a world under change. *Advances in Parasitology* 79:99-252.
- Kvie, K. S., J. Heggenes, D. G. Anderson, M. V. Kholodova, T. Sipko, I. Mizin, and K. H. Røed. 2016. Colonizing the high Arctic: mitochondrial DNA reveals common origin of Eurasian archipelagic reindeer (*Rangifer tarandus*). *Plos One* 11:1-15.
- Langvatn, R., S. D. Albon, R. J. Irvine, O. Halvorsen, and E. Ropstad. 1999. Parasitter, kondisjon og reproduksjon hos Svalbardrein. Pages 139-148 in S. A. Bengtson, F. Mehlum, and T. Severinsen, editors. *Svalbardtundraens økologi*. Meddelelser 150. Norwegian Polar Institute, Tromsø, Norway.
- Laperriere, A. J., and P. C. Lent. 1977. Caribou feeding sites in relation to snow characteristics in Northeastern Alaska. *Arctic* 30:101-108.
- Larsen, T. S., N. O. Nilsson, and A. S. Blix. 1985. Seasonal changes in lipogenesis and lipolysis in isolated adipocytes from Svalbard and Norwegian reindeer. *Acta Physiologica Scandinavica* 123:97-104.
- Le Moullec M., Å. Ø. Pedersen, A. Stien, J. Rosvold, and B.B. Hansen. 2019a. A century of recovery from overharvest in a warming high-arctic: the successful conservation story of endemic Svalbard reindeer. *The Journal of Wildlife Management*. DOI: 10.1002/jwmg.21761
- Le Moullec, M. 2019b. Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony. Ph.D. Norwegian University of Science and Technology, Trondheim, Norway.
- Le Moullec, M., Å. Ø. Pedersen, N. G. Yoccoz, R. Aanes, J. Tufto, and B. B. Hansen. 2017. Ungulate population monitoring in an open tundra landscape: distance sampling versus total counts. *Wildlife Biology* 2017:1-11.
- Lee, A. M., E. M. Bjørkvoll, B. B. Hansen, S. D. Albon, A. Stien, B. E. Sæther, S. Engen, V. Veiberg, L. E. Loe, and V. Grøtan. 2015. An integrated population model for a long-lived ungulate: more efficient data use with Bayesian methods. *Oikos* 124:806-816.
- Lentz, C. P., and J. S. Hart. 1960. The effect of wind and moisture on heat loss through the fur of newborn caribou. *Canadian Journal of Zoology* 38:679-688.
- Letcher, R. J., J. O. Bustnes, R. Dietz, B. M. Jenssen, E. H. Jorgensen, C. Sonne, J. Verreault, M. M. Vijayan, and G. W. Gabrielsen. 2010. Exposure and effects assessment of persistent organohalogen contaminants in arctic wildlife and fish. *Science of the Total Environment* 408:2995-3043.
- Lincoln, G. A., I. J. Clarke, R. A. Hut, and D. G. Hazlerigg. 2006. Characterizing a mammalian circannual pacemaker. *Science* 314:1941-1944.
- Loe, L. E. 1999. Habitat selection and site fidelity in Svalbard reindeer. M.Sc. University of Oslo, Norway.
- Loe, L. E., R. J. Irvine, C. Bonenfant, A. Stien, R. Langvatn, S. D. Albon, A. Mysterud, and N. C. Stenseth. 2006. Testing five hypotheses of sexual segregation in an arctic ungulate. *Journal of Animal Ecology* 75:485-496.
- Loe, L. E., B. B. Hansen, A. Stien, S. D. Albon, R. Bischof, A. Carlsson, R. J. Irvine, M. Meland, I. M. Rivrud, E. Ropstad, V. Veiberg, and A. Mysterud. 2016. Behavioral buffering of extreme weather events in a high-Arctic herbivore. *Ecosphere* 7.
- Loe, L. E., G. Pigeon, S. D. Albon, P. E. Giske, R. J. Irvine, E. Ropstad, A. Stien, V. Veiberg, and A. Mysterud. 2019. Antler growth as a cost of reproduction in female reindeer. *Oecologia* 189:601-609.
- Lønø, O. 1959. Reinen på Svalbard. *Meddelelser* 83. Særtrykk av Fauna nr 2, 1959. Norsk Polarinstitut, Tromsø, Norway.
- Loudon, A. S. I., J. A. Milne, J. D. Curlew, and A. S. McNeilly. 1989. A comparison of the seasonal hormone changes and patterns of growth, voluntary food intake and reproduction in juvenile and adult red deer (*Cervus elaphus*) and Père David's deer (*Elaphurus davidianus*) hinds. *Journal of Endocrinology* 122:733-745.
- MacDonald, E., K. Handeland, H. Blystad, M. Bergsaker, M. Fladberg, B. Gjerset, O. Nilsen, H. Os, S. Sandbu, E. Stokke, L. Vold, I. Orpetveit, H. G. Amot, and O. Tveiten. 2011. Public health implications of an outbreak of rabies in arctic foxes and reindeer in the Svalbard archipelago, Norway, September 2011. *Eurosurveillance* 16:2-5.
- Malmgren, A. J. 1865. Iakttagelser och anteckningar till Finmarkens och Spetsbergens Däggdjursfauna. Öfversigt af Kongl. vetenskaps-akademiens förhandlingar. 21:127-155.
- Markussen, K. A., A. Rognmo, and A. S. Blix. 1985. Some aspects of thermoregulation in newborn reindeer calves (*Rangifer tarandus tarandus*). *Acta Physiologica Scandinavica* 123:215-220.
- Mathiesen, S. D., C. G. Orpin, and A. S. Blix. 1984. Rumen microbial adaptation to fiber digestion in Svalbard reindeer. *Canadian Journal of Animal Science* 64:261-262.
- Mathiesen, S. D., C. G. Orpin, Y. Greenwood, and A. S. Blix. 1987. Seasonal changes in the cecal microflora of the high-arctic

- Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Applied and Environmental Microbiology 53:114-118.
- Mathiesen, S. D., W. Sormo, O. E. Haga, H. J. Norbert, T. H. A. Utsi, and N. J. C. Tyler. 2000a. The oral anatomy of Arctic ruminants: coping with seasonal changes. Journal of Zoology 251:119-128.
- Mathiesen, S. D., M. A. Vader, V. B. Rædergard, W. Sørmo, O. E. Haga, N. J. C. Tyler, and R. R. Hofmann. 2000b. Functional anatomy of the omasum in High Arctic Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and Norwegian reindeer (*Rangifer tarandus tarandus*). Acta Veterinaria Scandinavica 41:25-40.
- Mathiesen, S. D., R. I. Mackie, A. Aschfalk, E. Ringø, and S. M. A. 2005. Microbial ecology of the digestive tract in reindeer: seasonal changes. Pages 75-101 in W. H. Holzapfel and P. J. Naughton, editors. Microbial Ecology in Growing Animals. Elsevier Limited.
- Meland, M. 2014. Partial migration as a response to ground icing events in a high arctic ungulate. M.Sc. Norwegian University of Life Sciences, Ås, Norway.
- Melien, K. H. 2014. A quantitative analysis of organochlorine pesticides in Svalbard reindeer (*Rangifer tarandus platyrhynchus*). M.Sc. Norwegian University of Life Sciences, Ås, Norway.
- Mercer, J. B., H. K. Johnsen, A. S. Blix, and R. Hotvedt. 1985. Central control of expired air temperature and other thermoregulatory effectors in reindeer. American Journal of Physiology 248:R679-R685.
- Mørk, T., J. Bohlin, E. Fuglei, K. Åsbakk, and M. Tryland. 2011. Rabies in the arctic fox population, Svalbard, Norway. Journal of Wildlife Diseases 47:945-957.
- Mørk, T., M. Sund, and T. Josefsen. 2014. Bakterieinfeksjoner hos rein. Norsk Veterinærtidsskrift 126:222-228.
- Mortensen, A., S. Unander, M. Kolstad, and A. S. Blix. 1983. Seasonal changes in body composition and crop content of Spitzbergen Ptarmigan *Lagopus mutus hyperboreus*. Scandinavian Journal of Ornithology 14:144-148.
- Nilssen, K. J., H. K. Johnsen, A. Rognmo, and A. S. Blix. 1984a. Heart rate and energy expenditure in resting and running Svalbard and Norwegian reindeer. American Journal of Physiology 246:R963-R967.
- Nilssen, K. J., J. A. Sundsfjord, and A. S. Blix. 1984b. Regulation of metabolic rate in Svalbard and Norwegian reindeer. American Journal of Physiology 247:837-841.
- Norheim, G., K. J. Nilssen, and J. Låg. 1990. Cadmium in Svalbard reindeer. Pages 215-216 in J. Låg, editor. Excess and deficiency of trace elements in relation to human and animal health in Arctic and sub-Arctic regions. The Norwegian Academy of Science and Letters, Oslo, Norway.
- Nowosad, R. F. 1973. Twinning in Reindeer. Journal of Mammalogy 54:781-781.
- Orpin, C. G., and S. D. Mathiesen. 1988. *Microcetus lappus* gen. nov. sp. nov.: new species of ciliated protozoon from bovine rumen. Applied and Environmental Microbiology 52:527- 530.
- Orpin, C. G., and S. D. Mathiesen. 1990. Microbiology of digestion in the Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Special issue Rangifer. Pages 187-199 Proceedings. UiT Arctic University of Norway, Tromsø, Norway.
- Orpin, C. G., S. D. Mathiesen, Y. Greenwood, and A. S. Blix. 1985. Seasonal changes in the ruminal microflora of the high-arctic Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Applied and Environmental Microbiology 50:144-151.
- Overrein, Ø. 2003. Reinsjakt på Svalbard: mye vassing og tunge bærer, men en fantastisk naturopplevelse. Villreinen 1:7-10.
- Øvstedal, D. O., T. Tønsberg, and A. Elvebakk. 2009. The lichen flora of Svalbard. Sommerfeltia. Vol. 33. Natural History Museum, Oslo, Norway.
- Parker, K. L., M. P. Gillingham, T. A. Hanley, and C. T. Robbins. 1993. Seasonal patterns in body mass, body composition, and water transfer rates of free-ranging and captive black-tailed deer (*Odocoileus hemionus sitkensis*) in Alaska. Canadian Journal of Zoology 71:1397- 1404.
- Paulsen, I. M. G. 2018. Calving site characteristics and habitat use in Svalbard reindeer. M.Sc. UiT – Arctic University of Norway, Tromsø, Norway.
- Pedersen, Å., T. Josefsen, T. Mørk, K. Åsbak, C. das Neves, B. Hansen, and M. Tryland. 2014. Svalbardreinen –økologi, parasitter og sjukdommer. Norsk Veterinærtidsskrift 2:262-268.
- Pedersen, Å. Ø., B. B. Hansen, L. E. Loe, E. Ropstad, J. Irvine, A. Stien, S. Albon, I. M. G. Paulsen, L. T. Beumer, I. Eischeid, M. L. Moullec, B. Peeters, E. Soininen, R. Aanes, and V. Ravolainen. 2018. When ground-ice replaces fjord-ice: results from a study of GPS-collared Svalbard reindeer females. Kortrapport 049, Norwegian Polar Institute, Tromsø, Norway.
- Peeters, B., V. Veiberg, Å. Ø. Pedersen, A. Stien, R. J. Irvine, R. Aanes, B.-E. Sæther, O. Strand, and B. B. Hansen 2017. Climate and density-dependence cause changes in adult sex ratio in a large Arctic herbivore. Ecosphere 8:e01699.
- Peeters, B. 2019. On the dynamics of populations under climate change and harvesting – Results from the High Arctic Svalbard reindeer. Ph.D. Norwegian University of Science and Technology, Trondheim, Norway.
- Peeters, B., A. O. Pedersen, L. E. Loe, K. Isaksen, V. Veiberg, A. Stien, J. Kohler, J. C. Gallet, R. Aanes, and B. B. Hansen. 2019. Spatiotemporal patterns of rain-on-snow and basal ice in high Arctic Svalbard: detection of a climate-cryosphere regime shift. Environmental Research Letters 14:e015002.
- Persen, E., O. Holand, A. B. Leifseth, and H. Staaland. 1983. Reindeer grazing on Brøggerhalvøya, Svalbard. Acta Zoologica Fennica 175:35-37.
- Pigeon, G., L. E. Loe, S. D. Albon, C. Bonenfant, D. A. Elston, R. Justin Irvine, E. Ropstad, V. Veiberg, and A. Stien. 2018. Biased estimation of trends in cohort effects: the problems with age-period-cohort models in ecology. Ecology 99:2675-2680.

- Poikolainen, J. 2004. Mosses, epiphytic lichens and tree bark as biomonitors for air pollutants - specifically for heavy metals in Regional surveys. Ph.D. University of Oulu, Oulu, Finland.
- Pond, C. M., C. A. Mattacks, R. H. Colby, and N. J. C. Tyler. 1993. The anatomy, chemical composition and maximum glycolytic capacity of adipose tissue in wild Svalbard reindeer (*Rangifer tarandus platyrhynchus*) in winter. *Journal of Zoology* 229:17-40.
- Pope, P. B., A. K. Mackenzie, I. Gregor, W. Smith, M. A. Sundset, A. C. McHardy, M. Morrison, V. G. H. Eijsink, and M. R. Liles. 2012. Metagenomics of the Svalbard reindeer rumen microbiome reveals abundance of polysaccharide utilization loci. *Plos One* 7:e38571.
- Prestø, T., M. Lüth, and K. Hassel. 2014. Bryophytes of the Longyearbyen area. Naturhistorisk notat 2014-10. NTNU Vitenskapsmuseet, Trondheim, Norway.
- Prestrud, P. 1992. Food habits and observations of the hunting behaviour of Arctic foxes, *Alopex lagopus*, in Svalbard. *Canadian field-naturalist* 106:225-236.
- Punsvik, T. 2009. Plan for forvaltning av svalbardrein, kunnskaps- og forvaltningsstatus. Rapport 1/2009. Sysselmannen på Svalbard. Longyearbyen, Norway.
- Reimers, E. 1982a. Body composition, mortality and population regulation of Svalbard reindeer. Ph.D. University of Oslo, Oslo, Norway.
- Reimers, E. 1982b. Winter mortality and population trends of reindeer on Svalbard. *Arctic and Alpine Research* 14:295-300.
- Reimers, E. 1983. Mortality in Svalbard Reindeer. *Holarctic Ecology* 6:141-149.
- Reimers, E., T. Ringberg, and R. Sørungard. 1982. Body composition of Svalbard reindeer. *Canadian Journal of Zoology* 60:1812-1821.
- Reimers, E., S. Lund, and T. Ergon. 2011. Vigilance and fright behaviour in the insular Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Canadian Journal of Zoology* 89:753-764.
- Reimers, E., and S. Eftestøl. 2012. Response behaviors of Svalbard reindeer towards humans and humans disguised as polar bears on Edgeøya. *Arctic Antarctic and Alpine Research* 44:483-489.
- Røed, K. H. 2005. Refugial origin and postglacial colonization of holarctic reindeer and caribou. *Rangifer* 25:19-30.
- Røed, S. B. 2018. Detection of trace elements in Svalbard reindeer (*Rangifer tarandus platyrhynchus*) faeces in Longyearbyen, Adventdalen and Kapp Linné. M.Sc. NTNU, Trondheim, Norway.
- Routti, H., J. Aars, E. Fuglei, L. Hanssen, K. Lone, A. Polder, Å. Ø. Pedersen, S. Tartu, J. M. Welker, and N. G. Yoccoz. 2017. Emission changes dwarf the influence of feeding habits on temporal trends of per- and polyfluoroalkyl substances in two Arctic top predators. *Environmental Science & Technology* 51:11996-12006.
- Severinsen, T., and J. U. Skaare. 1997. Arctic Monitoring and Assessment Programme. Levels of heavy metals and persistent organic components in some terrestrial animals from Svalbard. Pages 407-409 in *Extended Abstracts. The International Symposium on Environmental Pollution in the Arctic*, Tromsø, Norway.
- 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* 106:357-370.
- Skogland, T. 1989. Comparative social organisation of wild reindeer in relation to food, mates and predator avoidance. *Advances in Ethology* 29:3-74.
- Solberg, E. J., P. Jordhoy, O. Strand, R. Aanes, A. Loison, B. E. Saether, and J. D. C. Linnell. 2001. Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. *Ecography* 24:441-451.
- Soppela, P., M. Nieminen, S. Saarela, and R. Hissa. 1986. The influence of ambient temperature on metabolism and body temperature of newborn and growing reindeer calves. *Comparative Biochemistry and Physiology* 83:371-386.
- Soppela, P., R. Sormunen, S. Saarela, P. Huttunen, and M. Nieminen. 1992. Localization, cellular morphology and respiratory capacity of "brown" adipose tissue in newborn reindeer. *Comparative Biochemistry and Physiology* 101:281-293.
- Sørmo, W., Ø. E. Haga, R. G. White, and S. D. Mathiesen. 1997. Comparative aspects of volatile fatty acid production in the rumen and distal fermentation chamber in Svalbard reindeer. *Rangifer* 17:81-95.
- Sørmo, W., Ø. E. Haga, E. Gaare, R. Langvatn, and S. D. Mathiesen. 1999. Forage chemistry and fermentation chambers in Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Journal of Zoology* 247:247-256.
- Staaland, H. 1986. Svalbardreinenens ernæring. Pages 72-91 in N. A. Øritsland, editor. *Svalbardreinen og dens livsgrunnlag*. Universitetsforlaget, Oslo, Norway.
- Staaland, H., and K. H. Røed. 1986. Om Svalbardreinenens slektskapsforhold og opprinnelse. Pages 61-71 in N. A. Øritsland, editor. *Svalbardreinen og dens livsgrunnlag*. Universitetsforlaget, Oslo, Norway.
- Staaland, H., and R. G. White. 1991. Influence of foraging ecology on alimentary tract size and function of Svalbard reindeer. *Canadian Journal of Zoology* 69:1326-1334.
- Staaland, H., J. O. Scheie, F. A. Grondahl, E. Persen, A. B. Leifseth, and O. Holand. 1993. The introduction of reindeer to Brøggerhalvøya, Svalbard: grazing preference and effect on vegetation. *Rangifer* 13:15-19.
- Stien, A. 2009. Ekle cyster i kjøttet til Svalbardrein (4 September). *Svalbardposten* 61:18.
- Stien, A., R. J. Irvine, R. Langvatn, S. D. Albon, and O. Halvorsen. 2002a. The population dynamics of *Ostertagia gruehneri* in reindeer: a model for the seasonal and intensity dependent variation in nematode fecundity. *International Journal for Parasitology* 32:991-996.
- Stien, A., R. J. Irvine, E. Ropstad, O. Halvorsen, R. Langvatn, and S. D. Albon. 2002b. The impact of gastrointestinal nematodes on wild reindeer: experimental and cross-sectional studies. *Journal of Animal Ecology* 71:937-945.

- Stien, A., L. E. Loe, A. Myrsetrud, T. Severinsen, J. Kohler, and R. Langvatn. 2010. Icing events trigger range displacement in a high-arctic ungulate. *Ecology* 91:915-920.
- Stien, A., B. J. Bårdsen, V. Veiberg, R. Andersen, L. E. Loe, and Å. Ø. Pedersen. 2012. Jakt på svalbardrein – kunnskapsstatus og evaluering av aktuelle forvaltningsmodeller. Svalbards Miljøvern-fond, Longyearbyen, Norway.
- Stokkan, K.-A., L. Folkow, J. Dukes, M. Neveu, C. Hogg, S. Siefken, S. C. Dakin, and G. Jeffery. 2013. Shifting mirrors: adaptive changes in retinal reflections to winter darkness in Arctic reindeer. *Proceedings of the Royal Society of London* 280:20132451.
- Stuen, S., J. Krogsrud, B. Hyllseth, and N. J. C. Tyler. 1993. Serosurvey of three virus infections in reindeer in northern Norway and Svalbard. *Rangifer* 13:215-219.
- Sundset, M. A., K. E. Praesteng, I. K. O. Cann, S. D. Mathiesen, and R. I. Mackie. 2007. Novel rumen bacterial diversity in two geographically separated sub-species of reindeer. *Microbial Ecology* 54:424-438.
- Sundset, M. A., J. E. Edwards, Y. F. Cheng, R. S. Senosiain, M. N. Fraile, K. S. Northwood, K. E. Praesteng, T. Glad, S. D. Mathiesen, and A. D. G. Wright. 2009. Rumen microbial diversity in Svalbard reindeer, with particular emphasis on methanogenic archaea. *Fems Microbiology Ecology* 70:553-562.
- Suttie, J. M., E. D. Goodall, K. Pennie, and R. N. B. Kay. 1983. Winter feed restriction and summer compensation in red deer stags (*Cervus elaphus*). *British Journal of Nutrition* 50:737-747.
- Sysselmannen. 2018. Reinsdyr med rabies utenfor Ny-Ålesund. Sysselmannen, Longyearbyen, Svalbard. <https://www.sysselmannen.no/Nyheter/2018/07/reinsdyr-med-rabies-utenfor-ny-alesund/> (accessed 1. April 2019).
- Tandberg, A. 2016. Svalbardrein (*Rangifer tarandus platyrhynchus*) og snøskuterløyper. Kvantifisering av unntakelsesadferd i tid og rom. M.Sc. Norwegian University of Life Sciences, Ås, Norway.
- Thomson, B. 1977. The behaviour of wild reindeer in Norway. Ph.D. University of Edinburgh, Edinburgh, Scotland.
- Timisjärvi, J., M. Nieminen, and A.-L. Sippola. 1984. The structure and insulation properties of the reindeer fur. *Comparative Biochemistry and Physiology* 79:601-609.
- Tryland, M. 2013. Are we facing new health challenges and diseases in reindeer in Fennoscandia? *Rangifer* 32:35-47.
- Tryland, M., and S. J. Kutz (eds.). 2018. Reindeer and caribou health and disease. CRC Press, Boca Raton, USA.
- Tryland, M., C. Das Neves, and D. R. Klein. 2014. Virusinfeksjoner hos reinsdyr. *Norsk Veterinærtidsskrift* 126:230-241.
- Tyler, N. J. C. 1986a. Reinen i Adventdalen. Pages 142-159 in N. A. Øritsland, editor. Svalbardreinen og dens livsgrunnlag. Universitetsforlaget, Oslo, Norway.
- Tyler, N. J. C. 1986b. The relationship between the fat content of Svalbard reindeer in autumn and their death from starvation in winter. *Rangifer* 1:311-314.
- Tyler, N. J. C. 1987a. Body composition and energy balance of pregnant and non-pregnant Svalbard reindeer during winter. Pages 203-229 in A. S. I. Loudon and P. A. Racey, editors. *Symposia of the Zoological Society of London*. The Zoological Society of London, London, England.
- Tyler, N. J. C. 1987b. Natural limitation of the abundance of the High Arctic Svalbard reindeer. Ph.D. Cambridge University, Cambridge, United Kingdom.
- Tyler, N. J. C. 1991. Short-term behavioural responses of Svalbard reindeer *Rangifer tarandus platyrhynchus* to direct provocation by a snowmobile. *Biological Conservation* 56:179-194.
- Tyler, N. J. C. 2010. Climate, snow, ice, crashes, and declines in populations of reindeer and caribou (*Rangifer tarandus L.*). *Ecological Monographs* 80:197-219.
- Tyler, N. J. C., and N. A. Øritsland. 1989. Why don't Svalbard Reindeer migrate? *Holarctic Ecology* 12:369-376.
- Tyler, N. J. C., P. Fauchald, O. Johansen, and H. R. Christiansen. 1999. Seasonal inappetence and weight loss in female reindeer in winter. *Ecological Bulletin* 47:105-116.
- Tyler, N. J. C., M. C. Forchhammer, and N. A. Øritsland. 2008. Nonlinear effects of climate and density in the dynamics of a fluctuating population of reindeer. *Ecology* 89:1675-1686.
- Tyler, N. J. C., G. Jeffery, C. R. Hogg, and K.-A. Stokkan. 2014. Ultraviolet vision may enhance the ability of reindeer to discriminate plants in snow. *Arctic* 67:159 – 166.
- Tyler, N. J. C., P. Gregorini, M. C. Forchhammer, K.-A. Stokkan, B. E. H. Van Oort, and D. G. Hazlerigg. 2016. Behavioral timing without clockwork: photoperiod-dependent trade-off between predation hazard and energy balance in an arctic ungulate. *Journal of Biological Rhythms* 31:522-533.
- Van der Knaap, W. O. 1986. On the presence of reindeer (*Rangifer tarandus L.*) on Edgeøya, Spitsbergen, in the period 3800-5000 BP. *Circumpolar Journal* 1:1-9.
- Van der Wal, R. 2006. Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos* 114:177-186.
- Van der Wal, R., and R. Brooker. 2004. Mosses mediate grazer impacts on grass abundance in arctic ecosystems. *Functional Ecology* 18:77-86.
- Van der Wal, R., and D. O. Hessen. 2009. Analogous aquatic and terrestrial food webs in the High Arctic: The structuring force of a harsh climate. *Perspectives in Plant Ecology, Evolution and Systematics* 11:231-240.
- Van der Wal, R., and M. J. J. E. Loonen. 1998. Goose droppings as food for reindeer. *Canadian Journal of Zoology* 76:1117-1122.
- Van der Wal, R., and A. Stien. 2014. High-arctic plants like it hot: a long-term investigation of between-year variability in plant biomass. *Ecology* 95:3414-3427.
- Van der Wal, R., N. Madan, S. M. J. van Lieshout, C. Dormann, R. Langvatn, and S. D. Albon. 2000. Trading forage quality for quan-

- tity? Plant phenology and patch choice by Svalbard reindeer. *Oecologia* 123:108-115.
- Van der Wal, R., R. Brooker, E. J. Cooper, and R. Langvatn. 2001a. Differential effects of reindeer on high Arctic lichens. *Journal of Vegetation Science* 12:705-710.
- Van der Wal, R., S. M. J. van Lieshout, and M. J. J. E. Loonen. 2001b. Herbivore impact on moss depth, soil temperature and arctic plant growth. *Polar Biology* 24:29-32.
- Van Oort, B. E. H., N. J. C. Tyler, M. P. Gerkema, L. Folkow, A. S. Blix, and K.-A. Stokkan. 2005. Circadian organization in reindeer. *Nature* 438:1095.
- Van Oort, B. E. H., N. J. C. Tyler, M. P. Gerkema, L. Folkow, and K. A. Stokkan. 2007. Where clocks are redundant: weak circadian mechanisms in reindeer living under polar photic conditions. *Naturwissenschaften* 94:183-194.
- Veiberg, V., A. Myrsetrud, E. Bjørkvoll, R. Langvatn, L. E. Loe, R. J. Irvine, C. Bonenfant, F. Couveleers, and N. C. Stenseth. 2007. Evidence for a trade-off between early growth and tooth wear in Svalbard reindeer. *Journal of Animal Ecology* 76:1139-1148.
- Veiberg, V., P. Danielsen, L. E. Loe, A. Stien, B. Peeters, B. B. Hansen, R. J. Irvine, E. Ropstad, S. D. Albon, T. Tveraa, and Ø. Varpe. 2017a. Klimaeffektar på svalbardreinenens kalvingstidspunkt. NINA Rapport 1311, Norsk institutt for naturforskning (NINA), Trondheim, Norway.
- Veiberg, V., L. E. Loe, S. D. Albon, R. J. Irvine, T. Tveraa, E. Ropstad, and A. Stien. 2017b. Maternal winter body mass and not spring phenology determine annual calf production in an Arctic herbivore. *Oikos* 126:980-987.
- Vestues, G. 2009. The mating system of Svalbard reindeer. Effects of male age and antler size on harem size, behaviour during the rutting season and reproductive effort. M.Sc. Norwegian University of Science and Technology, Trondheim, Norway.
- Vickers, H., K. A. Høgda, S. Solbø, S. R. Karlsen, H. Tømmervik, R. Aanes, and B. B. Hansen. 2016. Changes in greening in the high Arctic: insights from a 30 year AVHRR max NDVI dataset for Svalbard. *Environmental Research Letters* 11:105004.
- Vrolik, W. 1829. Over eene vermoedelijk tweede soort van Rendier. *Nieuwe Verhandelingen der Eerste Klasse van het Koninklijk-Nederlandsche Instituut van Wetenschappen, Letterkunde en Schoone Kunsten* 2:153-160, 239-240.
- Weber, M. L., and J. M. Thompson. 1998. Seasonal patterns in food intake, live mass, and body composition of mature female fallow deer (*Dama dama*). *Canadian Journal of Zoology* 76:1141-1152.
- Wegener, C., and A. M. Odasz-Albrigtsen. 1998. Do Svalbard reindeer regulate standing crop in the absence of predators? A test of the "exploitation ecosystems" model. *Oecologia* 116:202-206.
- West, A. C., and S. H. Wood. 2018. Seasonal physiology: making the future a thing of the past. *Current Opinion in Physiology* 5:1-8.
- Westerling, B. 1970. Rumen ciliate fauna of semi-domesticated reindeer (*Rangifer tarandus L.*) in Finland: composition, volume and some seasonal variations. *Acta Zoologica Fennica* 127:1-76.
- White, R. G., and J. R. Luick. 1984. Plasticity and constraints in the lactational strategy of reindeer and caribou. Pages 215-232 in *Symposia of the Zoological Society of London* (Vol. 51), London, England.
- Wollebæk, A. 1926. The Spitsbergen reindeer (*Rangifer tarandus spetsbergensis*, Andersén 1862). *Norges Svalbard- og Ishavsundersøkelser - Skrifter om Svalbard og Ishavet*. Norske Videnskaps-Akademi, Oslo, Norway.
- Worden, K. A., and P. J. Pekins. 1995. Seasonal change in feed intake, body composition, and metabolic rate of white-tailed deer. *Canadian Journal of Zoology* 73:452-457.
- Yannic, G., L. Pellissier, J. Ortego, N. Lecomte, S. Couturier, C. Cuyler, C. Dussault, K. J. Hundertmark, R. J. Irvine, D. A. Jenkins, L. Kolpashikov, K. Mager, M. Musiani, K. L. Parker, K. H. Røed, T. Sipko, S. G. Pórisson, B. V. Weckworth, A. Guisan, L. Bernatchez, and S. D. Côté. 2013. Genetic diversity in caribou linked to past and future climate change. *Nature Climate Change* 4:132.
- Ødegaard, O. A., and J. Krogsrud. 1981. Rabies in Svalbard: infection diagnosed in Arctic fox, reindeer and seal. *Veterinary Record* 109:141-142.
- Øritsland, N. A. 1986. Svalbardreinen og dens livsgrunnlag. Universitetsforlaget, Oslo, Norway.

9 Appendix

Summary of methods and results from the literature searches

To identify studies related to Svalbard reindeer, different sources of published literature (peer-reviewed and non-peer-reviewed) were searched. The following two terms were used as search statements on English websites: 'Svalbard reindeer' and/or '*Rangifer tarandus platyrhynchus*'. The following three terms were used as search statements on Norwegian websites: 'Svalbardrein' and/or 'rein' and/or '*Rangifer tarandus platyrhynchus*'.

1. The ISI Web of Science (<http://apps.webofknowledge.com>, 1945–2017; accessed May 2017 and October 11 2018; = 135 identified studies).
2. The peer-reviewed journal Rangifer (<http://septentrio.uit.no/index.php/rangifer>; 1981–2017; accessed 25 October 2018).
3. The Norwegian library system BIBSYS-Brage (<https://brage.bibsys.no/xmlui/>; accessed 4 January 2018).
4. The Norwegian BIBSYS Oria (https://bibsys-almaprimo.hosted.exlibrisgroup.com/primo-explore/search?query=any,-contains,%22Rangifer%20tarandus%20platyrhynchus%22&-search_scope=default_scope&vid=NPOLAR&lang=no_NO; accessed 31 October 2018).
5. The popular science magazine Villreinen annual book edition (<http://vr.villrein.no/utgaver/>, 1986–2015; accessed 26 October 2018; = 22 articles).
6. Reports from Svalbard Environmental Protection Fund (<https://www.sysselmannen.no/Svalbards-miljovernfond/Rapportar/>; accessed 12. December 2018).
7. Rolf Langvatn, associate professor at the University Centre in Svalbard (UNIS; 1996–2005), initiated a comprehensive compilation of literature on Svalbard reindeer up to 2003. From 1999 to 2003 the literature was compiled by Elke Lindner and Lars Guren, who worked at the UNIS library. This database included at that time 402 entries of scientific articles and grey literature. The search terms for this extensive collection included all forms of Latin names of Svalbard reindeer and common names in several languages. The following reference databases were searched:
 - Dialog - bibliotekarbruk, GeoSearch, Arctic & Antarctic Regions
 - ISI – Web of Science
 - FirstSearch
 - Biological Abstracts
 - Zoological Records
 - GeoRef
 - SciFinder
 - Scopus
8. Additional articles by authors (published and/ or accepted) after the ISI Web of Science search (November 2018 till June 2019) are included in the EndNote library published with the report.
9. Additional published literature, known to the authors, which contain sections and / or paragraphs about the Svalbard reindeer, but is not identified by the search terms listed above.

The ENDNOTE library Svalbardrein.enl is available with the electronic report at the web-pages of the Norwegian Polar Institute (www.npolar.no) and Svalbard Environmental Protection Fund (www.sysselmannen.no/Svalbards-miljovernfond). If any references are lacking please email aashild.pedersen@npolar.no.

