

Norwegian University  
of Life Sciences

Master's Thesis 2017

30 ECTS

Faculty of Environmental Sciences and Nature Resource  
Management

**USING VARIATION IN ANTLER GROWTH TO  
IDENTIFY SHORT- AND LONG-TERM ENERGY  
ALLOCATION TRADE-OFFS IN FEMALE  
SVALBARD REINDEER (*RANGIFER TARANDUS  
PLATYRHYNCHUS*)**

**BRUK AV VARIASJON I GEVIRVEKST TIL Å  
IDENTIFISERE KORT- OG LANGSIKTIGE  
PRIORITERINGER I ENERGIINVESTERING HOS  
SIMLER AV SVALBARDREIN (*RANGIFER  
TARANDUS PLATYRHYNCHUS*)**

Pernille Andrine Eriksdatter Giske  
Natural Resource Management



USING VARIATION IN ANTLER GROWTH TO IDENTIFY SHORT- AND  
LONG-TERM ENERGY ALLOCATION TRADE-OFFS IN FEMALE  
SVALBARD REINDEER (*RANGIFER TARANDUS PLATYRHYNCHUS*)

BRUK AV VARIASJON I GEVIRVEKST TIL Å IDENTIFISERE KORT- OG  
LANGSIKTIGE PRIORITERINGER I ENERGIINVESTERING HOS SIMLER  
AV SVALBARDREIN (*RANGIFER TARANDUS PLATYRHYNCHUS*)



PERNILLE ANDRINE ERIKSDATTER GISKE  
MASTER THESIS IN NATURAL RESOURCE MANAGEMENT  
MAY 2017



---

## PREFACE

This master thesis is the final product of my MCs in Natural Resource Management at the Norwegian University of Life Sciences, NMBU. Writing this thesis has helped me learn about ungulates' fascinating antler development and the ecology of Svalbard reindeer. It has increased my interest in natural resource management, ecology and scientific methods and writing.

I wish to thank my great supervisor, professor Leif Egil Loe at NMBU for his excellent guidance, help and for supplying me with time-series data. Big thanks to researcher Vebjørn Veiberg at the Norwegian Institute for Nature Research (NINA) for reviewing the thesis and for helpful responses. Thank you Audun Stien (NINA), Justin Irvine (The James Hutton Institute) and Steve Albon (The James Hutton Institute) for constructive and useful feedback on the results. Thanks to my fieldwork companion Wibke Peters for memorable days and river crossings and for guidance with technical gear and safety equipment during the field trip at Svalbard. And a big thanks to Mathilde Tomine Eriksdatter Giske, Helle Giske and Erik Uggen for proofreading and loads of motivation.

To my fellow NMBU students Kristin Hornset, Johanne Bratfoss Sørensen, Ingrid Verne, Ida Kessel Nordgård and Signe Bergum: without you this process would have been endless, you are the best ever. Finally, a special thanks to Espen Larsen Mikkeltborg for supporting me through the whole process, giving me motivation and being patient with me.

Norwegian University of Life Sciences

Ås, May 12<sup>th</sup> 2017

---

Pernille Andrine Eriksdatter Giske



---

## ABSTRACT

In environments where resources are limited, trade-offs are made to allocate resources optimally between growth, maintenance, storage and reproduction. Trade-offs can manifest themselves as both short-term processes and over the life span of individuals. In iteroparous animals, the short-term effects can be seen as reduced reproductive success or reduced survival. For long-lived species, environmental factors experienced early in life can influence trajectories throughout the life span, and alter resource allocation tactics. Investigating such processes requires long-term time series. In this thesis, I take advantage of a long-term, individual-based dataset of female Svalbard reindeer (*Rangifer tarandus platyrhynchus*) to investigate how variation in antler growth could identify short- and long-term energy allocation trade-offs. Svalbard reindeer is the most northerly living herbivorous mammal, facing harsh environments and great variations in seasonality and access to resources. Reindeer is the only species of ungulates where females develop antlers.

To determine antler size, number of tines were used as a proxy. Antler size increased with age without any clear pattern of senescence. Antler size was negatively affected by a short-term trade-off in which females with a calf during the summer of antler growth produced smaller antlers than those without a calf (average of 1 tine less per beam). Females born after winters with major ground-icing events (a result of rain with subsequent freezing during winter causing ice-locked pastures) were affected by the energy allocation trade-off experienced by their mothers when resources were scarce. The females produced smaller antlers their entire life span compared to those born in years with benign winter conditions (average of ½ tine less per beam). This cohort effect neither amplified nor converged with age. The amount of resources available was measured through July temperature, plant phenology in spring and population size, but did not impact antler size significantly.

These results provide understanding of resource-allocating processes in Svalbard reindeer, and is, to my knowledge, the first to show that variation in antler growth can be used to identify short- and long-term energy allocation trade-offs in female reindeer.

*Key words: Svalbard reindeer – Rangifer tarandus platyrhynchus – Arctic – antler size – trade-off – resource allocation – senescence – life-history*





---

## SAMMENDRAG

I miljøer der ressurser er begrenset, foretar et individ avveininger for å fordele ressurser optimalt mellom vekst, vedlikehold, reserver og reproduksjon. Avveininger kommer til syne gjennom både kortsiktige kostnader og gjennom hele levetiden til individet. Hos iteropare dyr, kan de kortsiktige kostnadene være redusert reproduksjon eller redusert overlevelse påfølgende år etter oppfostring av et avkom. For lengelevende arter kan miljøfaktorer som inntreffer tidlig i livet ha langsiktige effekter og endre ressursallokeringstaktikker senere i livet. For å undersøke slike prosesser, kreves lange tidsserier. I denne avhandlingen drar jeg nytte av en lang tidsserie av individbasert data av simler av svalbardrein (*Rangifer tarandus platyrhynchus*) for å undersøke hvordan variasjon i gevirvekst kan brukes til å identifisere kortsiktige og langsiktige prioriteringer i energiallokering. Svalbardrein er det nordligst levende herbivore pattedyret, og erfarer til tider svært krevende miljøforhold med store sesongmessige variasjoner i ressurstilgang. Rein er det eneste hjortedyret der hunndyra utvikler gevir.

For å bestemme gevirets størrelse ble antall takker brukt som indikator. Gevirstørrelse økte med alder uten noe klart mønster av avtagende vekst med alderdom. Gevirstørrelse var negativt påvirket av kortsiktige investeringer. Simler som hadde kalv gjennom sommeren da geviret vokste, produserte mindre gevir enn simlene uten kalv (gjennomsnittlig én takk mindre per gevirstang). Simler født etter vintre med mye bakkeising (et fenomen forårsaket av regn etterfulgt av minusgrader vinterstid, som fører til utilgjengelige vinterbeiter), ble påvirket av prioriteringen i energiinvestering deres mor gjorde som følge av ressursbegrensning. Simlene produserte mindre gevir gjennom hele livsløpet enn simler født i ikke-isings år (gjennomsnittlig ½ takk mindre per gevirstang). Denne kohorteffekten hverken økte eller ble utvisket med alder. Ressurstilgang ble målt gjennom julitemperatur, plantefenologi om våren og populasjonsstørrelse, men ingen av disse påvirket gevirstørrelse signifikant.

Dette studiet gir forståelse av ressursallokerings-prosesser hos svalbardrein, og er, så vidt jeg vet, det første til å vise at variasjon i gevirvekst kan brukes til å identifisere kort- og langsiktige prioriteringer i energiallokering hos reinsimler.

*Stikkord: Svalbardrein – Rangifer tarandus platyrhynchus – gevirstørrelse – Arktis – kost-nytte avveininger - ressursallokering – livshistorie*



---

# CONTENTS

---

<b>CONTENTS .....</b>	<b>XI</b>
<b>1 INTRODUCTION .....</b>	<b>1</b>
AIMS OF INVESTIGATION .....	4
<b>2 MATERIALS AND METHODS .....</b>	<b>5</b>
2.1 STUDY AREA .....	5
2.2 STUDY SPECIES .....	6
2.3 DATA COLLECTION .....	8
SVALBARD REINDEER DATA .....	8
METEOROLOGICAL DATA .....	9
2.4 STATISTICAL ANALYSIS.....	10
<b>3 RESULTS .....</b>	<b>11</b>
3.1 NUMBER OF ANTLER TINES AND ANTLER SIZE .....	11
3.2 DRIVERS OF VARIATION IN ANTLER SIZE .....	12
<b>4 DISCUSSION .....</b>	<b>14</b>
4.1 THE COST OF REPRODUCTION REFLECTED THROUGH SMALLER ANTLER SIZE.....	14
4.2 COHORT EFFECTS AFFECT INDIVIDUAL ANTLER SIZE THROUGHOUT LIFETIME .....	15
4.3 VARIATION IN RESOURCES FAILED TO EXPLAIN VARIATION IN ANTLER SIZE .....	18
<b>5 CONCLUSION .....</b>	<b>20</b>
<b>6 REFERENCES.....</b>	<b>21</b>



---

# 1 INTRODUCTION

---

The expression of life-history traits is closely associated with, and strongly influenced by individual priorities related to life-history trade-offs. A benefit realized through a change in one trait is linked to a cost paid through a change in another (Stearns 1992). Energy and time are limited factors which leads to competition of internal resources, and important trade-offs occur to allocate resources optimally between growth, maintenance, storage and reproduction (Zera & Harshman 2001). A core element in life-history theory is the principle of resource allocation and trade-offs (Stearns 1992). These principles are essential to understanding patterns of variation in life-history traits. Trade-offs can manifest themselves within an individual as short-term processes between one year and another (Clutton-Brock et al. 1982; Côté et al. 1998), or as long-term processes over the entire life span of an individual (Gaillard et al. 2003; Lindström 1999). The trade-off may also be visible across generations, where the mother makes a trade-off in energy for own survival at the expense of her foetus (Bernardo 1996), e.g. due to scarcity of resources when environmental conditions are harsh. This intergenerational trade-off, made while an individual is *in utero*, will affect the offspring during the entire lifespan (Douhard et al. 2016; Thalmann et al. 2015).

Short-term trade-offs between life-history traits are commonly reported. When resources are scarce, the amount of internal energy is limited, often leading to a trade-off between current and future reproduction (Harshman & Zera 2007). In long-lived iteroparous mammals, the typical reproductive strategy is to produce a relatively low number of offspring per reproductive event, but to have a long reproductive lifespan. Hence, the lifetime reproductive success depends primarily on own survival and longevity (Clutton-Brock 1988, as cited in Erikstad et al. 2008). To maximize reproduction, mothers adopt a conservative strategy favoring own survival, body mass recovery and future reproductive potential over current offspring, which have a lower chance of surviving harsh environmental conditions (Festa-Bianchet & Jorgenson 1998; Gaillard & Yoccoz 2003). Therefore, the cost of reproduction in ungulates is rarely reflected as a reduction in own reduced survival, but rather detected as a relatively short-term cost in terms of a temporary reduction in reproductive performance (Clutton-Brock et al. 1983; Hamel et al. 2009; Testa 2004).

Evidence of trade-offs that affects the entire life spans of individuals are more limited, primarily because it requires long-term, individual based data. Variation in early life shaped by environment (Lindström 1999), and variation in population density often lead to phenotypic variation among cohorts (Thalmann et al. 2015), which may alter long-lasting life-history characteristics and trajectories of that group (Douhard et al. 2016; Hamel et al. 2016). Whether the alteration is for the benefit or to the disadvantage for the individuals in a given cohort depends on the environmental condition. Together with genotype and ontogenetic processes of the individual, these factors set the phenotypic starting point of individual life-history traits (Hamel et al. 2016). In interaction with environmental conditions later in life, all these variables influence life-history traits on a long-term scale and affects performance traits in adulthood (Crowley & Hopper 2015; Descamps et al. 2008; McNamara 1998). Recent evidence found by Douhard et al. (2016) suggests that the pattern of energy allocation in ungulates throughout life can be determined by environmental conditions at birth. They found that females of cohorts experiencing bad environmental conditions while *in utero*, had lower body mass compared to the females of cohorts experiencing beneficial environmental conditions while *in utero*. They also found that reproductive output among young females was equal between females belonging to good and bad cohorts. However, the cost of early-life environmental conditions was paid later in life, with a decrease in reproductive success for females aged 7 years and older. The altered reproductive tactic reflects trade-offs between allocation to early reproduction and late-life performance.

The annual antler growth within ungulate species is a most remarkable example of rapid bone formation (Goss 1983). The yearly replacement of these bone structures follows the photoperiodic cycle as they impose high needs for mineral- and energy resources, and they are energetically costly to produce (Myserud et al. 2005; Price et al. 2005). Thus, antlers are considered as honest signals of phenotypic quality and body condition (Festa-Bianchet 2004; Vanpé et al. 2007) and therefore affected by both short-term and long-term energy allocation strategies. The cost associated with the production of antlers indicate that if antlers did not provide the individual some important advantage, selection would quickly suppress them. While the bulk of scientific studies primarily have analyzed causes of variation in antler production (Myserud et al. 2005; Prichard et al. 1999; Thomas & Barry 2005; Vanpé et al. 2007), no studies, to my knowledge, have used variation in antler growth to investigate short- and long-term trade-offs in energy allocation.

Reindeer and caribou (*Rangifer tarandus*) is unique among the *Cervidae* as females normally possess antlers (Cronin et al. 2003; Holand et al. 2004). As antler size in females do not directly relate to reproductive success in the form of access to mates as do in males, the mechanisms behind the production of antlers is even more striking. Females carry the costs of gestation, lactation and provisioning of a calf and faces additional trade-offs between energy allocation both in somatic growth including antler production, offspring reproduction and own survival. The amount of energy allocated to antler growth depends on available amount of resources (Festa-Bianchet 2004; Mysterud et al. 2005; Thalmann et al. 2015), and the length of the summer season and plant quality and quantity are important factors affecting resource availability. Together with this, increased population size limits the amount of resources per capita (Stewart et al. 2005; Weladji et al. 2005), increasing the level of intraspecific competition. Several studies of ungulates have reported a negative effect of increasing population density on antler size (Prichard et al. 1999; Schmidt et al. 2001; Vanpé et al. 2007), suggesting that reindeer antlers are highly sensitive to the amount of available resources.

The northernmost of ungulates, Svalbard reindeer (*Rangifer tarandus platyrhynchus*), lives at 78°N and face an unpredictable environment and a great seasonal periodicity in food availability. Apart from the short summers, access to forage is restricted. Svalbard reindeer has developed a remarkable capacity to store energy reserves for the winter (Nilssen 1986). Winter resource availability is affected by variation in rain-on-snow (ROS) events (Hansen et al. 2013; Reimers 1982). Such extreme events are caused by the combination of precipitation and above freezing temperatures, causing the formation of ground ice, or impenetrable ice layers within the snow-pack, subsequently restricting the access to winter forage. Variation in winter forage access affects how much energy reserves a mother has, and determine how much she can afford to invest in foetal growth and early lactation. Individuals born in years with major ground-icing events will suffer from less maternal care while *in utero*, and this intergenerational trade-off will cause lower birth weight for these individuals than for those individuals born after winters with less ground ice and more forage available for the mother. This starting point will affect the individual throughout life, and such early-life conditions causes variations in body conditions between years, cohort effects, which will have a long-lasting influence on individual performance. The cohort effects caused by ROS events have been found in the Svalbard reindeer population (Douhard et al. 2016), and there is a good understanding that these events are the main cause of variation in body mass (Albon et al. 2016).

## AIMS OF INVESTIGATION

In this thesis, I will investigate variation in antler growth in female Svalbard reindeer to identify short- and long-term energy allocation trade-offs using a long-term (15 years) individual-based dataset. As antlers in female reindeer are produced between the calving season and the rut, the trade-off of how much resources an individual should allocate towards antler growth happen in this time frame. Within the same time frame, the female allocates resources to lactation, and to recover from depleted body mass stores after winter. Importantly, after the antlers are produced in summer and once the bone has hardened and the velvet is cleaned, the antlers are fixed over the following winter until cast the following early summer. Therefore, antler measurements taken in the winter (year  $t$ ) can be used to explore processes of energy allocation the previous summer (year  $t-1$ ). The following predictions are investigated:

I predict **H1** that antlers are reduced size in years when females had a calf during the summer of antler production, i.e. a short-term cost of reproduction. Regarding long-time trade-offs in energy allocation there are two mutually exclusive hypotheses. Hamel et al. (2016) found that cohort effects in ungulates fade out with age. If the same pattern is reflected in antler size, this predicts **H2a** that antler size of poor-cohort and good-cohort individuals converge as they age. Conversely, Douhard et al. (2016) reported that individuals born after a bad winter (poor-cohorts) with high amount of ROS, had as high fitness as those born after benign winters (good-cohorts) until mid-life, upon which the reproductive success of poor-cohort females dropped relatively to good-cohorts females. This predicts **H2b** a more rapid senescence (i.e. a decline in performance with increasing age) in antler production in poor-cohort females than good-cohort females.

Finally, I expect that antler production is dependent on annual resource base as a function of degree of competition. I predict that antler size is larger **H3a** after warm summers (due to a strong correlation ( $r = 0.92$ ) between July temperature and summer plant biomass; Van der Wal & Stien 2014), **H3b** when plant phenology in spring comes early (due to extended summer season with sufficient forage and reduced time where resources are limited in winter) and **H3c** when population size is low (decreased intraspecific competition for resources).



---

## 2 MATERIALS AND METHODS

---

### 2.1 STUDY AREA

The study was carried out in Nordenskiöld Land at Spitsbergen, Svalbard. The study area (77°50'N-78°20'N, 15°00'E-17°30'E) includes the three interconnected valleys Reindalen, Semmeldalen and Colesdalen with adjoining side valleys, covering about 150 km<sup>2</sup> (Fig. 1). The Svalbard archipelago (63 000 km<sup>2</sup>), with Spitsbergen as the largest island, is located in the western Barents Sea, between 74°N-81°N. Longyearbyen, the largest settlement at the archipelago, is situated 20-40 km northeast of the study area. The study area's landscape is mountainous with peaks up to 1000 m, wide, U-shaped valleys and steep hillsides.

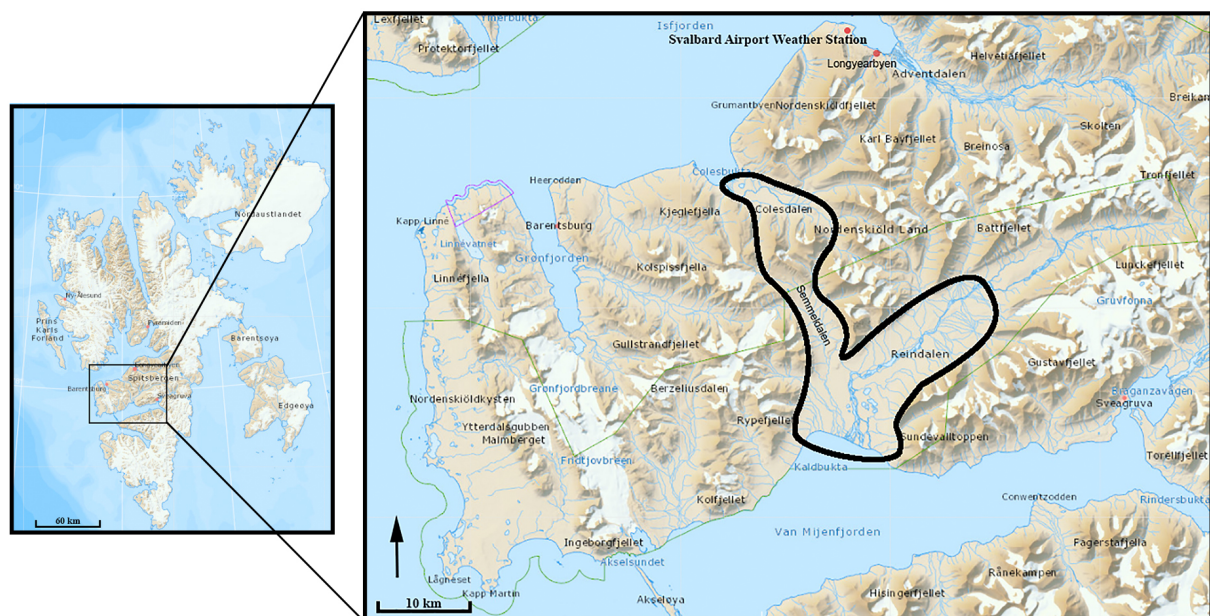


Figure 1. Svalbard archipelago (left) and the study area (right, delimited by the black line): The Reindalen-Semmeldalen-Colesdalen valley system in Nordenskiöld Land, Spitsbergen. Weather data were collected from Svalbard Airport Weather Station, north of the study system.

The vegetation in the area is classified as middle Arctic tundra zone (Elvebakk 2005). The valley floors are mainly vegetated by acidic mires bryophytes, graminoids and herbs (Solberg et al. 2001), while Arctic bell-heather and non-vegetative landslips cover the valley slopes (Elvebakk 2005). Ridge habitats, often wind-blown and exposed in winters and snow-free early in spring, are dominated by the dwarf shrubs *Dryas octopetala* and *Salix polaris* (Van der Wal & Stien 2014). Vegetation cover the valleys up to 50 m altitude (Brattbakk 1986). The vegetation growing season, defined as the time between green-up and 50 % senescence, begins

in early July and lasts only 9-10 weeks (Cooper et al. 2011), and is closely linked to the melt of snow (Mehlum 1999). Above-ground live vascular plant biomass in vegetated areas are low, average is only 35 g/m<sup>2</sup>, but varies twofold (23-46 g/m<sup>2</sup>) as a response to summer temperature (Van der Wal & Stien 2014). Trees and shrubs are absent.

Light conditions in Svalbard vary during the course of a year, with midnight sun from April 20<sup>th</sup> to August 21<sup>st</sup>, and dark season from October 26<sup>th</sup> to February 16<sup>th</sup> (Barr & Thuesen 2016). Mean air temperature (1981-2010) for the warmest month July is 5.8 °C and for the coldest month February is -13 °C (Nordli et al. 2014). The precipitation rates are low (Øseth 2010), annual average between 190 mm and 440 mm (Nordli et al. 2014). The study area, as most of Svalbard, can be described as cold desert, due to low temperatures and precipitation (Førland et al. 1997). Despite the Arctic climate and the high latitude, Svalbard has relatively mild winters compared to other areas of the Arctic owing to The North Atlantic Current (Førland et al. 1997). There is evidence for increased temperatures in Svalbard. Since 1901, the mean annual temperature has increased by 2.6°C, and it is Svalbard which has experienced the greatest temperature increase in Europe during the three latest decades (Nordli et al. 2014). Snow covers the area from October/November until mid-June, but varies considerably between years (Hansen et al. 2014). In winter, warm spells with above-zero temperatures and rain occasionally occur, and there is evidence of increased frequency of these events (Albon et al. 2016; Hansen et al. 2011). When temperatures return to below zero, ROS events are created. Hansen et al. (2010) suggests that such icing may substantially restrict access to winter grazing, causing reduced survival (Albon et al. 2016; Solberg et al. 2001), fecundity (Albon et al. 2016; Stien et al. 2012), and population growth (Albon et al. 2016; Hansen et al. 2013) in Svalbard reindeer.

## 2.2 STUDY SPECIES

Svalbard reindeer is a sub species of reindeer (*Rangifer tarandus*) endemic to Svalbard (Stien et al. 2010). Svalbard reindeer has several adaptations to the high Arctic environment and the large seasonal variability. This includes a compact body shape with a small head, short legs, ears and muzzle, a thick pelt (Wollebæk 1926) and physiological characters such as the ability to utilize mosses as fodder (Staaland 1986). The reindeer accumulate large amounts of fat in summer, used for over-winter survival and for gestation and lactation in spring (Parker et al. 2009). The species is considered a capital breeder rather than an income breeder (Festa-Bianchet et al. 1998). Capital breeders should adopt a conservative reproduction strategy, where

individuals secure a sufficient amount of body reserves to ensure their own survival during harsh winters (Erikstad et al. 1998). In addition, by being a capital breeder, the animal has a buffer against unpredictable environmental conditions in late gestation (Stephens et al. 2009), and are able to breed ahead of spring green-up (Veiberg et al. 2016).

The main rutting activity peaks in early October, with a polygynous mating system. A highly synchronized calving season takes place in early June (Tyler 1987). The females are iteroparous, potentially giving birth to a single calf each year from 2 years of age onwards (Douhard et al. 2016). The annual antler cycle tends to vary dependent on sex, age and fertility status (Espmark 1971). Female antler cycle is delayed compared with prime-aged males, which clean their antlers in August, and cast them shortly after the rut (Wika 1982). Females possess their antlers through the winter and if pregnant, cast the antlers a week or two after giving birth. Non-pregnant females normally cast their antlers a few weeks earlier (Espmark 1971; Weladji et al. 2005). Antler growth starts immediately after the old ones are cast, and the velvet is cleaned after the rutting season (Nieminen 1985).

As the only large herbivore on the archipelago, the Svalbard reindeer is exposed to minimum interspecific competition (Tyler & Øritsland 1999). The only other resident herbivores are the Svalbard rock ptarmigan (*Lagopus muta hyperborea*), and the sibling vole (*Microtus levis*), the latter only occurring locally in the study area. In summer, three species of geese, pink-footed goose (*Anser brachyrhynchus*), barnacle goose (*Branta leucopsis*) and pale-bellied brant (*Branta bernicla hrota*) are present, where the first two species graze in the same areas as the reindeer (Tyler & Øritsland 1999). Two other large mammals are present: Arctic fox (*Vulpes lagopus*), and polar bear (*Ursus maritimus*). None of them are considered a predatory threat to reindeer (Derocher et al. 2000; Reimers 1983a), although a few predatory events are known. Survival is largely dependent on food availability and weather (Albon et al. 2016).

Svalbard reindeer's habitat is limited to the ice-free areas with a minimum of plant production (Staalnd 1986). They have evolved a highly sedentary behavior (Staalnd et al. 1983) which forces the animals to rely on energy and nutrients from a few square kilometers throughout their whole life (Staalnd et al. 1983). The diet varies dependent on forage availability and quality, and the presence of snow cover (Bjørkvoll et al. 2009). Reindeer selectively forage in areas with early snow melt and high plant biomass (Van der Wal et al. 2000). Dominant species in their winter diet are *Salix polaris*, *Luzula confusa*, *Dryas octopetala* and various mosses

(Bjørkvoll et al. 2009; Staaland 1986). During summer, forage species of high quality and large biomass, such as various grasses, sedges and forbs are preferred choice (Bjørkvoll et al. 2009).

Unlike other subspecies of *Rangifer*, Svalbard reindeer do neither undertake long seasonal migrations, nor are they nomadic within seasons (Tyler & Øritsland 1989). In addition, they live in small, unstable groups and use small, traditional, seasonal home ranges (Tyler & Øritsland 1989), except in icy winters (Loe et al. 2016; Stien et al. 2010). The main area for reindeer on Svalbard is Nordenskiöld Land. It includes about 45 % of the total population of approximately 11 000 individuals, and has also the highest density of reindeer (2.2 animals per square kilometer ice-free lowland; Theisen & Brude 1998). Despite lack of effort to census the whole population of reindeer at the Svalbard archipelago, annual monitoring in Adventdalen suggest an increase in population size (Norwegian Polar Institute 2017) since the last population estimate was done in the 1970s (Tyler 1987). Within the study area, Albon et al. (2016) estimated an increase in population size, with more than a doubling between 1996 and 2014.

## 2.3 DATA COLLECTION

### SVALBARD REINDEER DATA

The Svalbard reindeer population at Nordenskiöld Land have been monitored by capture-mark-recapture since 1995. Annual population size estimates (all female adults plus calf of both sexes) has ranged between 733 in 1996 and 1758 in 2014 (Albon et al. 2016). Population size in the year of antler production was included (referred to as population size  $t-1$ ). Registration of number of antler tines on left and right beam began in 2002, and the last year of data was 2016. Thus, 15 years of data was included in this analysis. From year 2014, length of antlers was also recorded with a soft tape measure following the outer curve of the main antler beam. The practical field definition of an antler tine is that it needs to be long, and pointed enough to be able to hold a thin camera strap.

During the study period, female adults, yearlings and calves of both sexes were captured using two snowmobiles and a net stretched out in between (see Omsjoe et al. (2009) for detailed description of the methodology). When captured and recaptured in subsequent years, the reindeer were manually restrained, weighed, measured and blood-sampled. The animals were caught from late March to early May, and the females were fitted with numbered plastic collars and ear tags. All individuals were of known age, because they were either captured as calves (at 10-11 months of age) or as yearlings (22-23 months of age), or aged after death based on

counts of cementum annuli (Reimers & Nordby 1968). When age is referred to in this study, it corresponds to the individual age in June, one or two months after capture and around the normal timing of birth. Animals captured at age 1 year and 10 months are referred to as 2 year olds etc. Only females 2 years or older were included in the analysis, and is referred to as adults. In addition to the winter captures, reindeer summer census in July and August were conducted by observers walking through the study area, registering marked females and whether they had a calf or not (referred to as calf t-1; Albon et al. 2016).

A total of 1767 captures of individuals were done, with a median of 119 per year: range 83-160. Of the individuals observed three times or more as adults, 440 individuals were observed with antlers at all times, while 104 individuals were observed without antlers at one or several occasions. Despite the high number of observations of individuals without antlers, only 11 individuals (2.5 %) were permanently antlerless. This suggests that being antlerless one or a few years is rather common, and varies between individuals.

#### METEOROLOGICAL DATA

July temperature data were collected at Svalbard airport (78°25'N, 15°46'E, 28 m altitude) approximately 20-40 km north of the study area, and were available from the Norwegian Meteorological institute ([www.eklima.no](http://www.eklima.no); Fig. 1). Mean July temperature in the year of antler growth (referred to as July temperature t-1) was included based on daily measurements. I calculated ROS as the amount of precipitation that fell at temperatures above 1 °C between November 1<sup>st</sup> and April 30<sup>th</sup> (Stien et al. 2012). ROS events occurring in the winter in the birth year of one individual (ROS *in utero*) was entered in all models, as a two-level factor variable separating low ROS *in utero* (less than 15 mm) from high ROS *in utero* (more than or equal to 15 mm). To test for an effect of length of the growing season, the timing of the spring onset in the area was included. The Enhanced Vegetation Index (EVI) was used as a proxy for spring onset (referred to as plant phenology t-1). Between 2002 and 2014, the EVI values were available from the MODIS Terra platform (Huete et al. 2002) collected by NASA, available at <https://modis-land.gsfc.nasa.gov/vi.html> (Tveraa et al. 2013; Veiberg et al. 2016).

## 2.4 STATISTICAL ANALYSIS

All statistical analysis were performed using R version 3.3.2 (R Core Team 2016).

Both number of antler tines (Clutton-Brock et al. 1982; Mysterud et al. 2005) and antler length (Vanpé et al. 2007) have been found to be a good proximate for total antler mass. For this study, number of antler tines sampled over 15 years and antler length sampled over 2 years were available. To evaluate the relationship between these proxies of antler size, I investigated the linear relationship by fitting a Generalized Additive Model (GAM) using the *mgcv* package in R (Wood 2006). Antler length was used as response variable, and number of tines as predictor variable. GAM were chosen because a possible non-linear relationship would have appeared, and a linear relationship appears only if there is one. If a close to linear effect is found, number of tines can be used directly as a reliable proxy for antler size.

Linear mixed Poisson regressions fitted with the *glmer*-function in the R package *lme4* (Bates et al. 2015) was used to explore variation in individual antler production. The response variable was number of antler tines (average of left and right beam) in April in year  $t$  (produced in the summer of year  $t-1$ ). The regression was fitted with family Poisson because number of tines are counts. The variable individual was included as random effect *a priori*. Individual was included to account for the expected tendency that one individual sets up the same antlers every year. The start model included the following candidate predictor variables: age category as a five-level factor variable (2, 3, 4-9, 10-12 and 13+ years; following Lee et al. (2015)), calf  $t-1$ , plant phenology  $t-1$ , ROS *in utero*, population size  $t-1$ , July temperature  $t-1$ , and July temperature residuals  $t-1$ . The latter was included to investigate the effect of July temperature after accounting for variation in population size. Selection of fixed factors was done in a backwards selection procedure, testing main variable effects and first-order interactions. Statistical significance was assessed by likelihood ratio tests with cut-off value  $p = 0.05$  (Pinheiro & Bates 2000). All continuous predictor variables were standardized at mean 0 and variance 1 to facilitate model convergence and direct comparison of effect sizes. Lastly, to investigate whether or not there was an unexplained annual variation in antler size, the best model with and without including year as a predictor variable was compared by likelihood ratio test.

---

## 3 RESULTS

---

### 3.1 NUMBER OF ANTLER TINES AND ANTLER SIZE

Number of antler tines correlated strongly ( $r = 0.58$ ,  $p < 0.001$ ) with antler length in the subset of data where both measures were recorded (Fig. 2). Number of tines was therefore a suitable measure of antler size. Average number of tines per beam in female reindeer was 3.25 and the average predicted length of the antlers was 32.2 cm.

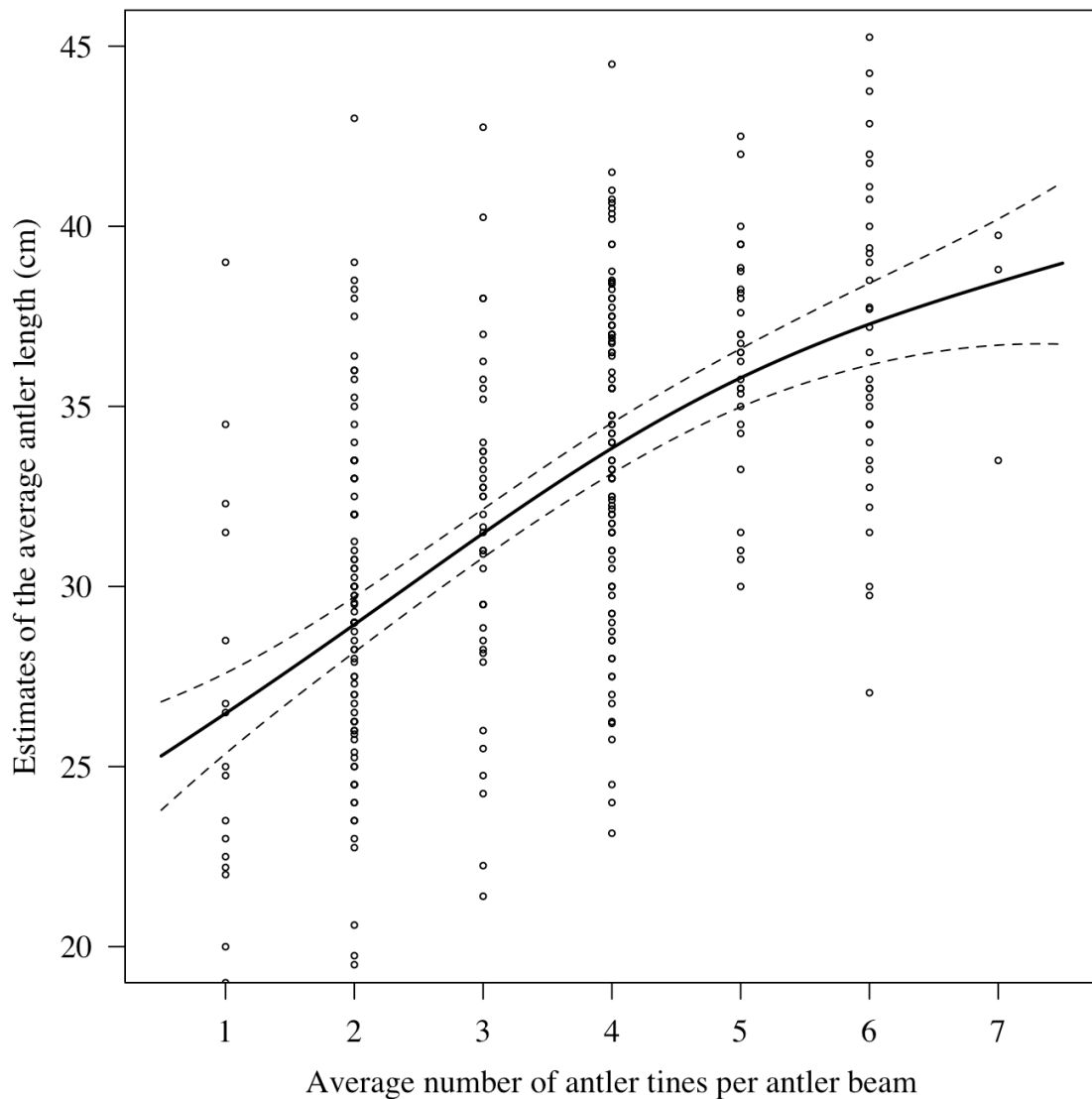


Figure 2. Relationship between average number of antler tines (rounded to the closest whole number) per antler beam and antler size in female Svalbard reindeer given as a predicted antler length in cm. The dashed lines represent 95 % CI.

### 3.2 DRIVERS OF VARIATION IN ANTLER SIZE

The selected model contained the main effects of age category, calf t-1, and ROS *in utero* (Table 1). No two-way or three-way interaction was supported (likelihood ratio tests always  $p > 0.05$ ). As expected, there was a strong age-effect on antler growth. Antler size increased with age without any clear pattern of senescence (Table 1; Fig. 3).

In support of **H1** there was a short-term cost of reproduction in antler growth as females with calf t-1 had about 1 tine less per antler beam than females without a calf t-1 (Table 1). There was a long-term cohort effect on antler size. Individuals born in high ROS *in utero* had about ½ tine less per antler beam compared to individuals born in low ROS *in utero* (Table 1). However, this cohort effect was not amplified nor converged with age, as a significant interaction effect between age and ROS *in utero* lacked. Hence, there was no statistical support of either **H2a** or **H2b**. When plotting a model including up to three-way interaction between age, calf t-1 and ROS *in utero*, antler size in individuals born in years with high ROS *in utero* tended to senesce faster than in individuals born after benign winters (Fig. 3). This result provides some support for **H2b** over **H2a**, despite no statistical significant support.

Regarding environmental factors describing resource limitation, neither July temperature, July temperature residuals, plant phenology or population size (all in year t-1) entered the final model. Thus I found no support of **H3 a, b** and **c**. However, some of the residual variation in number of antler tines was explained by variation among year ( $\chi^2 = 25.8$ ,  $df = 14$ ,  $p = 0.028$ ). The effect of year remained significant after re-entering all the resource variables, confirming that there was unexplained annual variation in antler size.



Table 1. Generalized linear mixed-effect model explaining variation in antler size in female Svalbard reindeer as a function of age, calf t-1 and ROS *in utero*. The variable individual was included as random effect. The standard deviation of the id random effect was 0.28. Two-year olds are the reference level of the age effect.

<b>Final model: antler tines ~ age category + calf t-1 + high ROS <i>in utero</i> + 1   id</b>				
Variable	Estimate	SE	Z	p
Intercept	-0.44	0.14	-3.06	< 0.01
age category 3	1.46	0.16	9.29	< 0.001
age category 4-9	1.82	0.15	12.6	< 0.001
age category 10-12	1.88	0.15	12.3	< 0.001
age category 13+	1.84	0.18	10.3	< 0.001
calf t-1	-0.27	0.05	-5.42	< 0.001
high ROS <i>in utero</i>	-0.15	0.07	-2.27	0.023

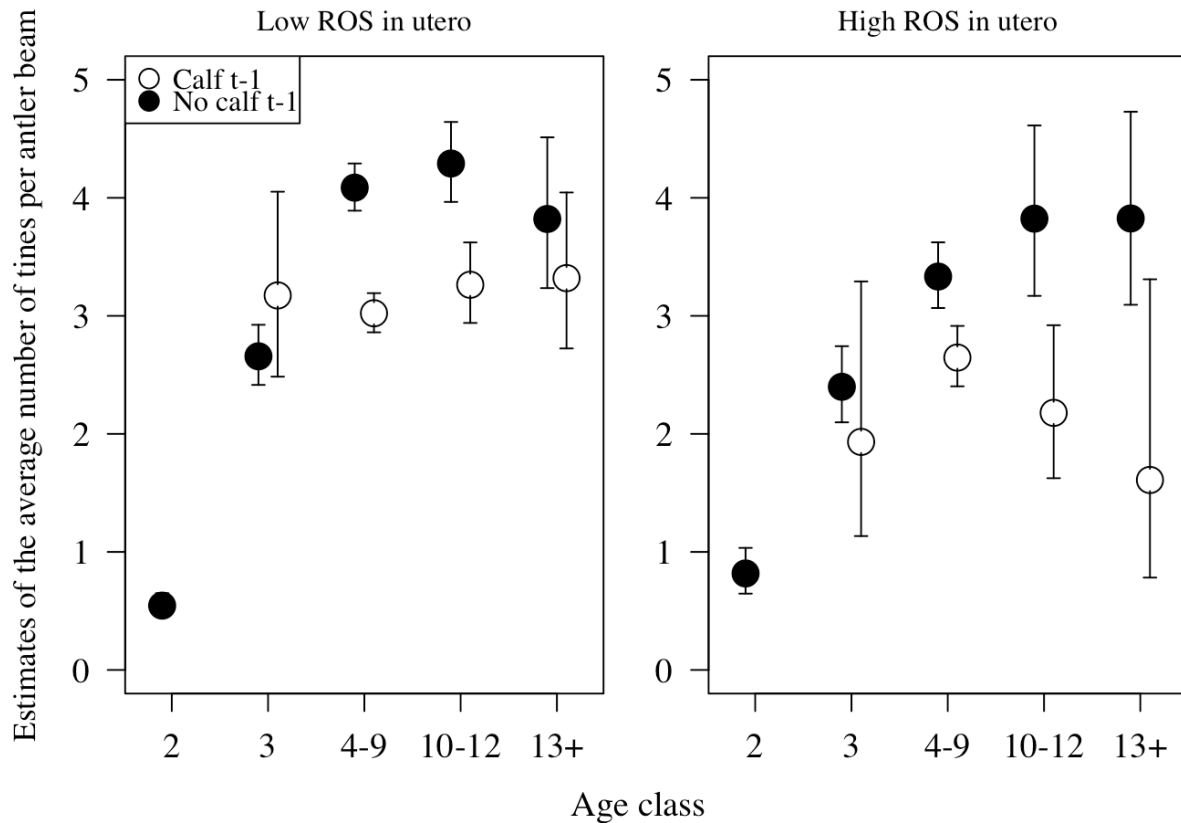


Figure 3. Estimates of the average number of antler tines per antler beam for all combinations of age, calf t-1 and ROS *in utero* in female Svalbard reindeer between 2002 and 2016 at Nordenskiöld Land, Svalbard. Error bars represent  $\pm 1$  standard error from the means. No 2 year olds had a calf last summer, explaining the missing data point for this age category.

---

## 4 DISCUSSION

---

This study is the first to report that female Svalbard reindeer were affected by a short-term cost of reproduction in reduced antler size the years the females had a calf, and that environmental conditions encountered while the animals were *in utero* influenced antler size negatively for the rest of their lives, which demonstrated that the trade-off experienced by a nutritionally stressed mother had long-term consequences for her calf. Further and surprisingly, the production of antlers was not affected by the resource abundance proxies used. This study implies that both short- and long-term life-history traits affect investment in antlers, and that number of antler tines can be used as an indicator for trade-offs in energy allocation.

### 4.1 THE COST OF REPRODUCTION REFLECTED THROUGH SMALLER ANTLER SIZE

In support of **H1**, antlers were reduced in size in years when females had a calf. Thus, a short-term cost of reproduction was reflected in antler production. This is in line with the traditional view on physiological trade-offs in life-history theory. When two traits compete directly with one another for limited resources within a single individual, allocation decisions occur (Stearns 1992). The reduced antler size could be a result of two things. First, reproduction is energetic costly and an investment in a calf is at the expense of an investment in the individual's own somatic growth including antler production. Energy requirements have been shown to be 50 % higher for pregnant than non-pregnant females (Pekins et al. 1998), and lactation is the state when daily energy costs are highest for females (Parker et al. 2009). Melnycky et al. (2013) found that female reindeer reaches a plateau in antler growth at age 3 years, which coincides with the beginning of prime-age and first pregnancy (Reimers 1983b). Côté et al. (1998) found a significant decrease in horn growth in lactating female mountain goats (*Oreamnos americanus*) aged 4 or 5 years. These results reflect the high energetic requirement of gestation and lactation (Hamel & Côté 2009), and indicate a trade-off in energy allocation towards offspring and hence reduced somatic investment. Second, as pregnant females have a higher energy expenditure during late gestation and lactation than non-pregnant, they are of higher need to reestablish their body reserves during the short period of access to sufficient forage. This situation indicates that rather to invest in antler production, they shift towards a heavier investment in somatic growth and accumulation of body reserves. Both winter survival and the reproductive strategy of female reindeer is dependent on body reserves to a larger extent than antler size. Thus, resources allocated towards body mass and fat deposits rather than to antler

growth will increase their own survival and subsequent future reproduction. In addition, there are increased chances that their single offspring will survive (Weladji et al. 2010), due to increased maternal resources to the calf when the female is heavier (Hamel et al. 2009). The demand for resources to multiple processes in pregnant females and priority of body growth rather than antler growth are mirrored in smaller antlers.

A contribution to explain the smaller antler size in females with a calf is the antler growing cycle, which depends on whether the female is pregnant or not. Pregnant females cast their antlers a few weeks after the non-pregnant ones, and thus, they have a delayed date of initiation of the new antler growth (Thomas & Barry 2005). By the time the pregnant females cast their 11-months-old antlers in mid to late June, non-pregnant females may have new-grown, velvet antlers up to 5 cm long (Thomas & Barry 2005). Both lactating and non-lactating females clean their antlers at the same time in autumn (Nieminen 1985), meaning that lactating females have a shorter period available to antler production. In addition to the abbreviated time for antler growth for lactating females, they have to split the energy between their own somatic growth, including antlers and nursing for the offspring. This energy trade-off is complicating the interpretation of individual quality reflected in antler size and requires consideration. The heaviest females are those who can afford to spend energy on reproduction, but their energy surplus is not fully reflected in antler size, due to the cost of reproduction. The females without a calf are of lower quality as they cannot afford to bear the costs of reproduction. The lack of reproductive expenditure leads to greater body and antler size, and all available summer forage can be allocated for own use. Thus, it must take into consideration whether or not the female has a calf when considering the quality of the individual reflected in antler size. If not, by looking at antler size isolated, this may give a wrong picture of the quality of the individual.

#### 4.2 COHORT EFFECTS AFFECT INDIVIDUAL ANTLER SIZE THROUGHOUT LIFETIME

The predictions in **H2** addressed how cohort effects affected antler size. The effect of variable environmental conditions in early life stages affected antler size in female Svalbard reindeer, but these cohort effects did not change with age (providing no support for **H2a** or **H2b**). Cohorts of females born in high ROS *in utero* had smaller antlers throughout life compared to females born in low ROS *in utero*, due to the allocation decision her mother made under resource limitation. Thus, this intergenerational trade-off (Stearns 1989), resulted in a long-term effect regarding energy allocated towards antler production in poor-cohort females. Due to less maternal energy reserves of the mothers of poor-cohorts, poor-cohort females were smaller,

and they have relatively higher metabolic rate and limited body reserves compared to good-cohorts. Hence, they may be more vulnerable to harsh environmental conditions experienced during winter (Parker et al. 2009), and to secure own survival, the poor-cohorts may invest in body size and fat stores at the cost of antler size. Opposite, the good-cohort females experienced long lasting benefits of being born during a favorable year. Permanent advantages caused by initial conditions corresponds to what is called the “silver spoon effect”, which operates through cohort variation (Grafen 1988). Consequently, cohort effects have long-lasting effects on antler size in female Svalbard reindeer, and that poor-cohorts undergo a trade-off between allocation of energy to soma rather than to antlers.

Despite the long-lasting negative cohort effects, an interaction between ROS *in utero* and age lacked, which was opposite of what was predicted in **H2a**. This implies that I found no cohort effects on how much animals invested in antlers in early and late life (my interpretation of long-term trade-off in energy allocation). Hamel et al. (2016) analyzed cohort variation body mass in 11 species of large herbivores (including Svalbard reindeer). They reported lower cohort variation in long-lived species with a slower pace of life. The decrease in cohort variation with increasing age was a result of both higher survival of large individuals and compensatory (increasing growth rate) or catch-up (extending the growth period) growth by smaller cohorts, which partly made up for the poor start they experienced (Hamel et al. 2016). Reindeer can be ranged at the middle in the “slow-fast” continuum of life-histories among the species included by Hamel et al. (2016). As a result, the poor-cohort females may not have had enough time available for compensating/catch-up growth before reaching prime age, which leads to lack of evidence for dissipated cohort variation in antler size with age.

Nor did I find any evidence of a more rapid senescence in antler production for poor-cohorts as predicted in **H2b**. This is contrary to what was discovered by Douhard et al. (2016), where reproduction success in female Svalbard reindeer were maintained at high levels in both good- and poor-cohorts, despite differences in body weight. However, a negative influence on reproductive success for poor-cohorts was reported after the age of 7. A possible explanation may lie in the differences between time of antler growth and pregnancy. Pregnancy in reindeer is highly dependent on maternal energy reserves accumulated months before needed (Barboza & Parker 2008). The female is pregnant throughout the winter and must trade resources to own survival with resources to growth of the foetus in a period of strong food restriction. Antlers, on the other hand, are grown in summer when energy is immediately accessible through forage

and thus is a more direct investment. Thus, it may seem that the requirement for good condition of the mother is of less importance when producing antlers than for bringing a foetus to term. As a result, the senescence is to a lesser extent pronounced in antler growth than reproduction. In addition, while pregnancy is traded against body fat deposits for own survival, antler growth is traded against lactation. Antler growth is a less important activity to secure own survival compared to storage of body fat, and the differences may explain the absence of interaction.

The lack of evidence of senescence in female reindeer antlers found in my study is different from what was found by (Melnycky et al. 2013). They argued that senescence in antlers was a response of increased demands for energy to gestation and lactation in older individuals compared to younger. Apart from this, evidence of senescence in female antler size is scarce. However, senescence in male antler size is commonly reported (Myysterud et al. 2005; Sæther & Haagenrud 1985; Vanpé et al. 2007; von Hardenberg et al. 2004). As antler growth is most common in males, the literature on antler and horn growth is heavily male-biased. In males, antlers act as a secondary sexual trait and contributes to breeding success (Clutton-Brock et al. 1982; Thomas & Barry 2005). The heavy investment males afford in antlers early in life is paid by a cost of earlier senescence. The function of antlers in females is to increase the female's social rank (Espmark 1964; Espmark 1971; Reimers 1993; Roberts 1996), so that she is able to take part in interference competition for feeding sites in winter. Hence, antlers in female reindeer act more as a weapon than a secondary sexual trait, and the effect of senescence may to a lesser extent be pronounced. Despite the intersexual differences in strategies and purposes for energy allocation to antlers, literature on male antler production should be transferrable when investigating female antler production. Antlers of both sexes reflect an honest signal of fight strength, individual condition and energy surplus.

Nevertheless, and despite no statistical significance, the raw data plot (Fig. 3) may reveal a tendency for an interaction with age on females with a calf and cohort effects. It appears that the differences in antler size for females with and without a calf were greater later in the lifespan than early, indicating an amplified effect with age. Similarly, high ROS *in utero* females seemed to suffer from the early-life conditions by producing smaller antlers than good-cohorts. This difference also increased with age. In addition, the raw data gives the impression that the differences in antler size in females with and without a calf were larger for high ROS *in utero* females than low ROS *in utero* females. This indicates that old, poor-cohort females with a calf experience the heaviest cost of them all. These results serve to give some support to **H2b** over

**H2a**, and suggest that for senescent females with a calf, antler production is somewhat costlier for poor-cohort than good-cohort females. The lack of interactions in this study is likely not due to too few observations. The dataset consists of long-term data with a large sample size. However, some combinations of categories, such as individuals aged 13 years and older, born in a high ROS year, contains few individuals. This shortcoming may be a cause of missing interaction between the predictor variables. However, the biology of Svalbard reindeer this has to be taken in consideration. Individuals aged 13 years and older are rare, and especially will individuals born in high ROS years struggle to reach to the highest year classes due to earlier senescence. In addition, fewer individuals were born in a high ROS year than a low ROS year, due to fewer high ROS years during the study period, and generally lower calving rate and calf survival in such years (Solberg et al. 2001; Stien et al. 2012).

#### 4.3 VARIATION IN RESOURCES FAILED TO EXPLAIN VARIATION IN ANTLER SIZE

None of the available variables describing resource availability's effect on antler size in prediction **H3** received support, which is contrary to what other studies have found (Festa-Bianchet 2004; Mysterud et al. 2005; Schmidt et al. 2001; Thomas & Barry 2005). Further, the Svalbard reindeer population have doubled during the study period (Albon et al. 2016), and the study system has had a twofold variation in annual plant biomass (Van der Wal & Stien 2014). These increases indicate an altered situation in the resource availability for Svalbard reindeer, but the factors could contradict each other. Increased plant productivity in time and space improves the individual's resource availability. Contrary, as the ecosystem in Svalbard is to a large extent controlled by bottom-up processes, an increase in resources generates higher carrying capacity in the system. This results in an increase in population size, causing less forage available per capita. It may seem that these conflicting impacts have caused a situation where resource availability impacting antler size is hard to reveal. However, when tested for contradictory effects (including July temperature after accounting for variation in population size), no significant relationship was found. Consequently, it may be winter forage and winter survival that constitutes a bottleneck in this study system. Bad winters results in mortality of juveniles and weak, old individuals (Albon et al. 2016; Lee et al. 2015), creating densities below carrying capacity during the summers. This situation leaves enough resources for all individuals in the population during summer (Wegener & Odasz-Albrigtsen 1998). As a result, Svalbard reindeer in the study area may still be far from the carrying capacity, with limited resource competition during the summers, indicating that production of antlers are not resource limited.

Although this study included a variable explaining variation in plant biomass (including Svalbard reindeer's dietary species) effectively, I cannot be sure that it provides any direct measure of mineral content within the forage species. In addition, there was residual variation in number of antler tines explained by variation among year, even after accounting for resource variables. The unexplained annual variation indicates that the resource proxies used in this study, were unable to detect variation in antler size. As found in earlier studies, producing antlers is a mineral-demanding activity (Hyvärinen et al. 2007; Suttie & Kay 1982, as cited in Markusson & Folstad 1997; Ullrey 1982, as cited in Markusson & Folstad 1997). Hence, the Svalbard reindeer may have limited access to minerals through forage, which could possibly affect antler growth. Calcium content and density of the skeleton in female reindeer has been shown to significantly decrease during antler development due to reabsorption and transfer to use in antlers (Baksi & Newbrey 1989). Muir et al. (1987) found that red deer (*Cervus elaphus*) stags only obtained 25-40 % of the calcium needed to grow antlers from the forage. These findings suggest that minerals used in the production of antlers are of limited availability in the forage, and the animals compensate by draining mineral resources from their skeleton. The fact that reindeer frequently chew on cast antlers during summer (Wika 1982), contributes to indicate that minerals in the diet are restricted. However, the casted antlers are included in the maintenance of the calcium balance (Wika 1982). This way, the minerals stored in the antlers represent a mineral reserve to be used during lactation, and compensates for the possible mineral restriction in forage. Staaland (1986) supports this assumption as he reported little interest from the reindeer into salt stones placed in the terrain, and concluded that minerals are not a shortage in the diet of the animals. Thus, the conflicting points of view on whether or not antler production is mineral limited remains unexplained in this study.

---

## 5 CONCLUSION

---

In this study, I show that antlers in female Svalbard reindeer are reduced in size if the female had a calf during the summer of antler growth, or if the female had experienced harsh winter condition while *in utero*. The intergenerational trade-off between the female and her mother affected the female antler production throughout her lifetime. Antler size increased with age without any clear pattern of senescence. This study provides understanding of resource-allocating processes in an Arctic herbivore, and is the first, to my knowledge, to demonstrate that variation in antler growth can be used to identify short- and long-term energy allocation trade-offs in female Svalbard reindeer.

The indicator is an applicable approach for other studies of reindeer, as the method is non-invasive, e.g. number of antler tines can be counted from a distance. In addition, these results reflect energy-allocation processes in a time of year when direct measures of body weight were unavailable to us, as would be the case in many other studies.



---

## 6 REFERENCES

---

- Albon, S. D., Irvine, R. J., Halvorsen, O., Langvatn, R., Loe, L. E., Ropstad, E., Veiberg, V., van der Wal, R., Bjørkvoll, E. M., Duff, E. I., et al. (2016). Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. *Global Change Biology*, 23 (4): 1374–1389.
- Baksi, S. N. & Newbrey, J. W. (1989). Bone metabolism during antler growth in female reindeer. *Calcified Tissue International*, 45 (5): 314-317.
- Barboza, P. & Parker, K. (2008). Allocating protein to reproduction in Arctic reindeer and caribou. *Physiological and Biochemical Zoology*, 81 (6): 835-855.
- Barr, S. & Thuesen, N. P. (2016). *Svalbard*. Store norske leksikon. Available at: <https://snl.no/Svalbard> (accessed: 11.01.2017).
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67 (1): 1-48.
- Bernardo, J. (1996). Maternal effects in animal ecology. *American Zoologist*, 36 (2): 83-105.
- Bjørkvoll, E., Pedersen, B., Hytteborn, H., Jónsdóttir, I. S. & Langvatn, R. (2009). Seasonal and interannual dietary variation during winter in female Svalbard reindeer (*Rangifer arandus platyrhynchus*). *Arctic, Antarctic, and Alpine Research*, 41 (1): 88-96.
- Brattbakk, I. (1986). Flora og vegetasjon. In Øritsland, N. A. (ed.) *Svalbardreinen og dens livsgrunnlag*, pp. 15-34. Oslo: Universitetsforlaget.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. (1982). *Red deer: behavior and ecology of two sexes*. Wildlife behavior and ecology. Chicago: University of Chicago Press.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. (1983). The costs of reproduction to red deer hinds. *Journal of Animal Ecology*, 52 (2): 367-383.
- Clutton-Brock, T. H. (1988). *Reproductive success: studies of individual variation in contrasting breeding systems*. Chicago, Illinois, USA: University of Chicago Press. (Cited after Erikstad et al. 1998).
- Cooper, E. J., Dullinger, S. & Semenchuk, P. (2011). Late snowmelt delays plant development and results in lower reproductive success in the high Arctic. *Plant Science*, 180 (1): 157-167.
- Côté, S. D., Festa-Bianchet, M. & Smith, K. G. (1998). Horn growth in mountain goats (*Oreamnos americanus*). *Journal of Mammalogy*, 79 (2): 406-414.
- Cronin, M. A., Haskell, S. P. & Ballard, W. B. (2003). The frequency of antlerless female caribou and reindeer in Alaska. *Rangifer*, 23 (2): 67-70.
- Crowley, P. H. & Hopper, K. R. (2015). Mechanisms for adaptive cohort splitting. *Ecological Modelling*, 308: 1-13.
- Derocher, A. E., Wiig, Ø. & Bangjord, G. (2000). Predation of Svalbard reindeer by polar bears. *Polar Biology*, 23 (10): 675-678.
- Descamps, S., Boutin, S., Berteaux, D., McAdam, A. G. & Gaillard, J.-M. (2008). Cohort effects in red squirrels: the influence of density, food abundance and temperature on future survival and reproductive success. *Journal of Animal Ecology*, 77 (2): 305-314.
- Douhard, M., Loe, L. E., Stien, A., Bonenfant, C., Irvine, R. J., Veiberg, V., Ropstad, E. & Albon, S. (2016). The influence of weather conditions during gestation on life histories in a wild Arctic ungulate. *Proceedings. Biological sciences*, 283 (1841).
- Elvebakk, A. (2005). A vegetation map of Svalbard on the scale 1:3.5 mill. *Phytocoenologia*, 35 (4): 951-967.
- Erikstad, K. E., Fauchald, P., Tveraa, T. & Steen, H. (1998). On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology*, 79 (5): 1781-1788.

- Espmark, Y. (1964). Studies in dominance-subordination relationship in a group of semi-domestic reindeer (*Rangifer tarandus* L.). *Animal Behaviour*, 12 (4): 420-426.
- Espmark, Y. (1971). Antler shedding in relation to parturition in female reindeer. *The Journal of Wildlife Management*, 35 (1): 175-177.
- Festa-Bianchet, M., Gaillard, J.-M. & Jorgenson, J. T. (1998). Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *The American Naturalist*, 152 (3): 367-379.
- Festa-Bianchet, M. & Jorgenson, J. T. (1998). Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behavioral Ecology*, 9 (2): 144-150.
- Festa-Bianchet, M. (2004). Relative allocation to horn and body growth in bighorn rams varies with resource availability. *Behavioral Ecology*, 15 (2): 305-312.
- Førland, E. J., Hanssen-Bauer, I. & Nordli, P. Ø. (1997). Climate statistics & longterm series of temperature and precipitation at Svalbard and Jan Mayen. Oslo. 73 pp.
- Gaillard, J.-M., Loison, A., Toïgo, C., Delorme, D. & Van Laere, G. (2003). Cohort effects and deer population dynamics. *Écoscience*, 10 (4): 412-420.
- Gaillard, J. M. & Yoccoz, N. G. (2003). Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, 84 (12): 3294-3306.
- Goss, R. J. (1983). Deer antlers, regeneration, evolution and function. *Academic, New York*: 133-147.
- Grafen, A. (1988). On the uses of data on lifetime reproductive success. In Clutton-Brock, T. H. (ed.) *Reproductive success: studies of individual variation in contrasting breeding systems*, pp. 454-471. Chicago: IL: University of Chicago Press.
- Hamel, S. & Côté, S. D. (2009). Foraging decisions in a capital breeder: trade-offs between mass gain and lactation. *Oecologia*, 161 (1): 421.
- Hamel, S., Côté, S. D., Gaillard, J. M. & Festa-Bianchet, M. (2009). Individual variation in reproductive costs of reproduction: high-quality females always do better. *Journal of Animal Ecology*, 78 (1): 143-151.
- Hamel, S., Gaillard, J. M., Yoccoz, N. G., Albon, S., Côté, S. D., Craine, J. M., Festa-Bianchet, M., Garel, M., Lee, P., Moss, C., et al. (2016). Cohort variation in individual body mass dissipates with age in large herbivores. *Ecological Monographs*, 86 (4): 517-543.
- Hansen, B. B., Aanes, R. & Sæther, B.-E. (2010). Feeding-crater selection by high-Arctic reindeer facing ice-blocked pastures. *Canadian Journal of Zoology*, 88 (2): 170-177.
- Hansen, B. B., Aanes, R., Herfindal, I., Kohler, J. & Sæther, B. E. (2011). Climate, icing, and wild Arctic reindeer: past relationships and future prospects. *Ecology*, 92 (10): 1917-1923.
- Hansen, B. B., Grøtan, V., Aanes, R., Sæther, B.-E., Stien, A., Fuglei, E., Ims, R. A., Yoccoz, N. G. & Pedersen, Å. Ø. (2013). Climate events synchronize the dynamics of a resident vertebrate community in the high Arctic. *Science*, 339 (6117): 313.
- Hansen, B. B., Isaksen, K., Benestad, R. E., Kohler, J., Pedersen, Å. Ø., Loe, L. E., Coulson, S. J., Larsen, J. O. & Varpe, Ø. (2014). Warmer and wetter winters: characteristics and implications of an extreme weather event in the high Arctic.
- Harshman, L. G. & Zera, A. J. (2007). The cost of reproduction: the devil in the details. *Trends in Ecology & Evolution*, 22 (2): 80-86.
- Holand, Ø., Gjøstein, H., Losvar, A., Kumpula, J., Smith, M. E., Red, K. H., Nieminen, M. & Weladji, R. B. (2004). Social rank in female reindeer (*Rangifer tarandus*): effects of body mass, antler size and age. *J. Zoology*, 263 (4): 365-372.
- Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X. & Ferreira, L. G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, 83 (1): 195-213.

- Hyvärinen, H., Kay, R. N. B. & Hamilton, W. J. (2007). Variation in the weight, specific gravity and composition of the antlers of red deer (*Cervus elaphus* L.). *British Journal of Nutrition*, 38 (3): 301-311.
- Lee, A. M., Bjørkvoll, E. M., Hansen, B. B., Albon, S. D., Stien, A., Sæther, B. E., Engen, S., Veiberg, V., Loe, L. E. & Grøtan, V. (2015). An integrated population model for a long-lived ungulate: more efficient data use with Bayesian methods. *Oikos*, 124 (6): 806-816.
- Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, 14 (9): 343-348.
- Loe, L. E., Hansen, B. B., Stien, A., Albon, S. D., Bischof, R., Carlsson, A. M., Irvine, J., Meland, M., Rivrud, I. M., Ropstad, E., et al. (2016). Behavioral buffering of extreme weather events in a high-Arctic herbivore. *Ecosphere*, 7 (6): e01374.
- McNamara, J. (1998). Phenotypic plasticity in fluctuating environments: consequences of the lack of individual optimization. *Behavioral Ecology*, 9 (6): 642-648.
- Mehlum, F. (1999). Tilpasninger hos arktiske organismer til kort sommersesong. Tiden som begrensende faktor. In Bengtson, S.-A., Mehlum, F. & Severinsen, T. (eds) *Terrestrisk økologisk forskningsprogram på Svalbard. Svalbardtundraens økologi*, pp. 161-169. Tromsø: Norsk Polarinstitutt.
- Melnycky, N. A., Weladji, R. B., Holand, Ø. & Nieminen, M. (2013). Scaling of antler size in reindeer (*Rangifer tarandus*): sexual dimorphism and variability in resource allocation. *Journal of Mammalogy*, 94 (6): 1371-1379.
- Muir, P. D., Sykes, A. R. & Barrell, G. K. (1987). Calcium metabolism in red deer (*Cervus elaphus*) offered herbage during antlerogenesis: kinetic and stable balance studies. *The Journal of Agricultural Science*, 109 (2): 357-364.
- Mysterud, A., Meisingset, E., Langvatn, R., Yoccoz, N. G., Stenseth, N. C. & Benton, T. (2005). Climate-dependent allocation of resources to secondary sexual traits in red deer. *Oikos*, 111 (2): 245-252.
- Nieminen, M. (1985). Reinens gevir - vekst og betydning. En oversikt. *Rangifer*, 5 (1): 26-32.
- Nilssen, K. J. (1986). Svalbardreinens energetikk. In Øritsland, N. A. (ed.) *Svalbardreinen og dens livsgrunnlag*, pp. 92-102. Oslo: Universitetsforlaget.
- Nordli, Ø., Przybylak, R., Ogilvie, A. E. J. & Isaksen, K. (2014). Long-term temperature trends and variability on Spitsbergen: the extended Svalbard Airport temperature series, 1898-2012. *Polar Research*, 33.
- Norwegian Polar Institute. (2017). *Reindeer population size, Adventdalen. Environmental monitoring of Svalbard and Jan Mayen (MOSJ)*. Available at: <http://www.mosj.no/en/fauna/terrestrial/svalbard-reindeer-population.html> (accessed: 29.03.17).
- Omsjoe, E. H., Stien, A., Irvine, J., Albon, S. D., Dahl, E., Thoresen, S. I., Rustad, E. & Ropstad, E. (2009). Evaluating capture stress and its effects on reproductive success in Svalbard reindeer. *Canadian Journal of Zoology*, 87 (1): 73-85.
- Parker, K. L., Barboza, P. S. & Gillingham, M. P. (2009). Nutrition integrates environmental responses of ungulates. *Functional Ecology*, 23 (1): 57-69.
- Pekins, P. J., Smith, K. S. & Mautz, W. W. (1998). The energy cost of gestation in white-tailed deer. *Canadian Journal of Zoology*, 76 (6): 1091-1097.
- Pinheiro, J. C. & Bates, D. M. (2000). *Mixed-effects models in S and S-PLUS*. Statistics and computing. New York: Springer.
- Price, J. S., Allen, S., Faucheux, C., Althnaian, T. & Mount, J. G. (2005). Deer antlers: a zoological curiosity or the key to understanding organ regeneration in mammals? *Journal of Anatomy*, 207 (5): 603-618.

- Prichard, A. K., Finstad, G. L. & Shain, D. H. (1999). Factors affecting velvet antler weights in free-ranging reindeer in Alaska. *Rangifer*, 19 (2): 71-76.
- R Core Team. (2016). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Reimers, E. & Nordby, Ø. (1968). Relationship between age and tooth cementum layers in Norwegian reindeer. *The Journal of Wildlife Management*, 32 (4): 957-961.
- Reimers, E. (1982). Winter mortality and population trends of reindeer on Svalbard, Norway. *Arctic and Alpine Research*, 14 (4): 295-300.
- Reimers, E. (1983a). Mortality in Svalbard reindeer. *Holarctic Ecology*, 6 (2): 141-149.
- Reimers, E. (1983b). Reproduction in wild reindeer in Norway. *Canadian Journal of Zoology*, 61 (1): 211-217.
- Reimers, E. (1993). Antlerless females among reindeer and caribou. *Canadian Journal of Zoology*, 71 (7): 1319-1325.
- Roberts, S. C. (1996). The evolution of hornedness in female ruminants. *Behaviour*, 133 (5/6): 399-442.
- Schmidt, K., Stien, A., Albon, S. & Guinness, F. (2001). Antler length of yearling red deer is determined by population density, weather and early life-history. *Oecologia*, 127 (2): 191-197.
- Solberg, E. J., Jordhøy, P., Strand, O., Aanes, R., Loison, A., Sæther, B. E. & Linnell, J. D. C. (2001). Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. *Ecography*, 24 (4): 441-451.
- Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, 3 (3): 259-268.
- Stearns, S. C. (1992). *The evolution of life histories*: Oxford University Press Oxford.
- Stephens, P. A., Boyd, I. L., McNamara, J. M. & Houston, A. I. (2009). Capital breeding and income breeding: their meaning, measurement, and worth. *Ecology*, 90 (8): 2057-2067.
- Stewart, K. M., Bowyer, R. T., Dick, B. L., Johnson, B. K. & Kie, J. G. (2005). Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. *Oecologia*, 143 (1): 85-93.
- Stien, A., Loe, L. E., Mysterud, A., Severinsen, T., Kohler, J. & Langvatn, R. (2010). Icing events trigger range displacement in a high-Arctic ungulate. *Ecology*, 91 (3): 915-920.
- Stien, A., Ims, R. A., Albon, S. D., Fuglei, E., Irvine, R. J., Ropstad, E., Halvorsen, O., Langvatn, R., Loe, L. E., Veiberg, V., et al. (2012). Congruent responses to weather variability in high Arctic herbivores. *Biology Letters*.
- Staaland, H., Brattbakk, I., Ekern, K. & Kildemo, K. (1983). Chemical composition of reindeer forage plants in Svalbard and Norway. *Holarctic Ecology*, 6 (2): 109-122.
- Staaland, H. (1986). Svalbardreinenens ernæring. In Øritsland, N. A. (ed.) *Svalbardreinen og dens livsgrunnlag*, pp. 72-91. Oslo: Universitetsforlaget.
- Suttie, J. M. & Kay, R. N. B. (1982). The influence of nutrition and photoperiod on growth of antlers of young red deer. In Brown, R. D. (ed.) *Antler development in Cervidae*, pp. 61-71. Kingsville: Caesar Kleberg Wildlife Research Institute. (Cited after Markusson, E. & Folstad, I. 1997).
- Sæther, B.-E. & Haagenrud, H. (1985). Geographical variation in the Antlers of Norwegian moose in relation to age and size. *The Journal of Wildlife Management*, 49 (4): 983-986.
- Testa, J. W. (2004). Population dynamics and life history trade-offs of moose (*Alces alces*) in south-central Alaska. *Ecology*, 85 (5): 1439-1452.
- Thalmann, J. C., Bowyer, R. T., Aho, K. A., Weckerly, F. W. & McCullough, D. R. (2015). Antler and body size in black-tailed deer: an analysis of cohort effects. *Advances in Ecology*, 2015: 11.

- Theisen, F. & Brude, O. W. (1998). Evaluering av områdevernet på Svalbard - Representativitet og behov for ytterligere vern. Oslo: Norsk Polarinstitutt. 144 pp.
- Thomas, D. & Barry, S. (2005). Antler mass of barren-ground caribou relative to body condition and pregnancy rate. *Arctic*, 241-246.
- Tveraa, T., Stien, A., Bardsen, B.-J. & Fauchald, P. (2013). Population densities, vegetation green-up, and plant productivity: impacts on reproductive success and juvenile body mass in reindeer. *PLoS ONE*, 8 (2): e56450.
- Tyler, N. J. C. (1987). *Natural limitation of the abundance of the high Arctic Svalbard reindeer*: University of Cambridge. 321 pp.
- Tyler, N. J. C. & Øritsland, N. A. (1989). Why don't Svalbard reindeer migrate? *Holarctic Ecology*, 12 (4): 369-376.
- Tyler, N. J. C. & Øritsland, N. A. (1999). Varig ustabilitet og bestansregulering hos svalbardrein. In Bengtson, S.-A., Mehlum, F. & Severinsen, T. (eds) *Svalbardtundraens økologi*, pp. 125-138. Tromsø: Norsk Polarinstitutt.
- Ullrey, D. E. (1982). Nutrition and antler development in white-tailed deer. In Brown, R. D. (ed.) *Antler development in Cervidae*, pp. 49-59. Kingsville: Caesar Kleberg Wildlife Research Institute. (Cited after Markusson, E. & Folstad, I. 1997).
- Van der Wal, R., Madan, N., van Lieshout, S., Dormann, C., Langvatn, R. & Albon, S. D. (2000). Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. *Oecologia*, 123 (1): 108-115.
- Van der Wal, R. & Stien, A. (2014). High-Arctic plants like it hot: a long-term investigation of between-year variability in plant biomass. *Ecology*, 95 (12): 3414-3427.
- Vanpé, C., Gaillard, J.-M., Kjellander, P., Mysterud, A., Magnien, P., Delorme, D., Laere, G. V., Klein, F., Liberg, O. & Mark Hewison, A. J. (2007). Antler size provides an honest signal of male phenotypic quality in roe deer. *The American Naturalist*, 169 (4): 481-493.
- Veiberg, V., Loe, L. E., Albon, S. D., Irvine, R. J., Tveraa, T., Ropstad, E. & Stien, A. (2016). Maternal winter body mass and not spring phenology determine annual calf production in an Arctic herbivore. *Oikos*.
- von Hardenberg, A., Bassano, B., Arranz, M. D. P. Z. & Bogliani, G. (2004). Horn growth but not asymmetry heralds the onset of senescence in male Alpine ibex (*Capra ibex*). *Journal of Zoology*, 263 (4): 425-432.
- Wegener, C. & Odasz-Albrigtsen, M. A. (1998). Do Svalbard reindeer regulate standing crop in the absence of predators? *Oecologia*, 116 (1): 202-206.
- Weladji, R. B., Holand, Ø., Steinheim, G., Colman, J. E., Gjøstein, H. & Kosmo, A. (2005). Sexual dimorphism and intercohort variation in reindeer calf antler length is associated with density and weather. *Oecologia*, 145 (4): 549-555.
- Weladji, R. B., Holand, Ø., Gaillard, J.-M., Yoccoz, N. G., Mysterud, A., Nieminen, M. & Stenseth, N. C. (2010). Age-specific changes in different components of reproductive output in female reindeer: terminal allocation or senescence? *Oecologia*, 162 (1): 261-271.
- Wika, M. (1982). Antlers - a mineral source in Rangifer. *Acta Zoologica*, 63 (1): 7-10.
- Wollebæk, A. (1926). The Spitsbergen reindeer (*Rangifer tarandus spetsbergensis*). Det Norske Videnskapsakademi Oslo. Resultater av de norske statsunderstøttede Spitsbergenekspeditioner. 71 pp.
- Wood, S. (2006). *Generalized additive models: an introduction with R*. New York: Chapman & Hall/CRC press.
- Zera, A. J. & Harshman, L. G. (2001). The physiology of life history trade-offs in animals. *Annual Review of Ecology and Systematics*, 32: 95-126.
- Øseth, E. (2010). Klimaendringer i norsk Arktis – Konsekvenser for livet i nord. Tromsø: Norsk Polarinstitutt. 134 pp.







Norges miljø- og biovitenskapelig universitet  
Noregs miljø- og biovitenskapelige universitet  
Norwegian University of Life Sciences

Postboks 5003  
NO-1432 Ås  
Norway