Preface

This Master thesis completes my study in Natural Resource Management at the Norwegian University of Life Sciences (UMB), Ås.

First of all I would like to thank my supervisor Leif Egil Loe at UMB for all help and guidance regarding this thesis and for memorable fieldwork at Svalbard. I would also like to thank Elisabeth Iversen for all her help, coffee breaks and good comments, Lars Østbye Hemsing for all his help and GIS help, and my neighbor at the reading room, Jørgen Remmen for always being there to help me. Thank you, Peter Doley, Maren Grindstad and Sara B. Zambon for useful comments and to Anja Carlsson who was very helpful during the final writing process. Last but not least, my dear Maarten Slangen deserves a huge thank for help during the fieldwork and for being patient with me during the whole process.

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Ås, 11. May 2012

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Abstract

Arctic winter weather is unstable with winter temperatures that can increase to above 0 °C. This warm spells lead to changed snow pack properties and precipitation falling in this period falls as rain-on-snow (ROS) and create a layer of ice. Such events locks the winter pastures of arctic herbivores and may cause mass mortalities. There is a concern that the current global warming may lead to an increased frequency of icing events.

In my thesis I used detailed spatial (GPS) data from Svalbard reindeer (*Rangifer tarandus platyrhynchus*) for the first time to investigate the effects of icing on Svalbard reindeer space use and habitat selection. I document by use of ground temperature loggers and field validation that the two winters 2009/10 and 2010/11 differed strongly in amount and spatial extent of icing. The reindeer responded immediately to icing by increased movement rates and by that increasing the size of their winter home range. The space shifts following the mid-winter warm spell in 2010 occurred along specific gradients. The reindeer moved rapidly closer to the coastline and, as a more delayed response, to latitudinal higher areas. There were no differences in selection of vegetation types between the two years. Field validation documented decreasing thickness of ice along the coast and at high latitudes. It is therefore clear that reindeer searched for, and found, areas with less ground ice. My thesis contribute to the understanding of how behavior can buffer the effect of extreme climate events in population dynamics, and for the first time demonstrate that excursions to avoid icing occurs along geographical gradients such as elevation and distance to coast.

Sammendrag

Den arktiske vinteren er preget av ustabile værforhold der temperaturen kan øke til over frysepunktet. Disse mildværsperiodene fører til endrede egenskaper til snødekket og nedbør faller som regn på snø (rain on snow, ROS). Nedbøren renner gjennom snølaget, fryser på bakkenivå og lager et isdekke over vegetasjonen. Slike isingshendelser fører til utilgjengelige vinterbeiter for arktiske planteetere og kan føre til svært høy dødelighet. Det er bekymringsverdig at den globale oppvarmingen kan føre til økt frekvens av slike isingshendelser.

I min masteroppgave har jeg brukt detaljerte GPS data fra Svalbardrein (*Rangifer tarandus platyrhynchus*) for å undersøke effektene av bakkeising på Svalbardreinens arealbruk og habitatseleksjon. Dette er det første studiet på om temaet. Ved bruk av bakketemperaturloggere og feltvalidering har jeg dokumentert at vintrene 2009/10 og 2010/11 var svært ulike i forhold til mengde og utbredelse av bakkeis. Reinen viste en umiddelbar reaksjon på bakkeising ved økt forflytning og økt størrelse på hjemmeområde vinterstid. Den endrede områdebruken etter mildværsperioden midtvinteren 2010, skjedde langs spesifikke gradienter. Reinen flyttet seg raskt nærmere kysten, og med en mer forsinket respons, til høyereliggende områder. Det var ingen forskjeller i valg av vegetasjonstyper de to årene. Feltvalidering dokumenterte at isen langs kysten og i høyereliggende områder hadde en minkende istykkelse. Det er derfor klart at reinen søkte etter, og fant, områder med mindre bakkeis. Denne oppgaven kan bidra til å forstå hvordan endret adferd kan minke effekten av ekstreme klimahendelser i og viser, for første gang at vandring for å unngå ising oppstår langs geografiske gradienter som høyde og avstand til kysten.

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1. Introduction

Climate in Arctic is harsh and highly seasonal (Ferguson & Messier 1996). The ground is frozen and snow-cowered from October-November until June, which leaves a short season for plant growth. The vegetation if affected by climate and is expected to change with a changing climate (Moen et al. 1999). Climate change is particularly pronounced in this area and with the rapid warming of the Arctic, an increase of extreme events, changes in precipitation pattern and temperature are expected to occur (IPCC 2007).

The Arctic winter conditions are particularly unpredictable (Ferguson & Messier 1996). Winters can be severe with large amounts of snow and high wind velocities, resulting in hard wind-packed snow. Furthermore, temperatures may rise above 0 °C during the winter, and precipitation during these warm spells (rain-on-snow events, hereafter called ROS) can lead to the formation of a layer of ice on the ground. This ice layer and hard wind-packed snow is impenetrable for ungulates, and limits the access to forage, a phenomenon called "locked pastures" (Solberg et al. 2001). Even though arctic ungulates are adapted to this extreme environment, winter conditions are believed to have a limiting effect on the ungulate populations due to restricted access to forage (Reimers 1983).

Restricted forage access reduces the ungulates fitness (Gunn 1995), and can lead to increased mortality, especially for calves, weak or old individuals (Reimers 1983). Mass mortalities of caribou (*Rangifer tarandus*) were reported in the Northwest Territories, Canada, after winters with heavy snowfall (Caughley & Gunn 1993). Further, increased mortality due to ground icing were also reported in studies on other arctic ungulates such as muskoxen (*Ovibos moschatus*) (Forchhammer & Boertmann 1993), Peary caribou (*Rangifer tarandus pearyi*) (Miller & Gunn 2003) and semi-domesticated reindeer (*Rangifer tarandus tarandus*) (Tveraa et al. 2007). The effect of ground icing on population dynamics in the Arctic is therefore well known.

On the arctic archipelago of Svalbard, the only large herbivore found is the endemic Svalbard reindeer (*Rangifer tarandus platyrhynchus*) (Bengtson 1999). They are known to be fairly sedentary (Tyler & Øritsland 1989), and live within small home ranges (sensu Burt 1943). The reindeer have adapted to food restriction during winter particularly by accumulation of fat reserves during the summer (Tyler 1986a). This fat reserves is sufficient to meet parts of the energy needs during winter (Tyler 1987). Nevertheless, the fat reserves functions more as

an emergency energy reserve. The reindeers cannot survive on stored energy alone (Tyler 1986b), they are still dependent on foraging during winter (Loe et al. 2007).

During winters with extensive icing it has been observed high mortality rates for calves and old animals due to starvation during "locked pastures" (Reimers 1977; Reimers 1982). The subsequent summer, fewer calves are born due to reduced female fecundity because of scares food availability (Solberg et al. 2001). The increased mortality rate and decreased birth rate leads to a reduction in population size (Tyler & Øritsland 1999). Hansen et al. (2011) were the first to document that ROS events lead to extensive ground icing with a subsequent population decline of Svalbard reindeer in the Brøgger peninsula. Following an icing event an immediate increase in reindeer movement was documented, which was suggested to be excursions in search for new and ice-free grounds (Stien et al. 2010). Due to the increased movement, dispersion to neighboring areas is assumed to be contributing to the population decline in winters with extensive icing (Stien et al. 2010). Depending on winter conditions, the dispersion rates are highly variable among years which contribute to the variation in population size between years (Tyler & Øritsland 1999).

Ground icing and behavioral responses of Svalbard reindeer are poorly studied. Stien et al. (2010) studied reindeer's response to icing effect. However, from what I know, no study has combined field observation of ground ice formation with detailed animal movement data to investigate the behavioral response to locked pasture events. This master thesis will use detailed data from GPS-marked Svalbard reindeer to document behavioral responses to registered icing events from ground temperature the 2009/10 and 2010/11 winters. Further, I will examine the impact of icing on home range size and habitat selection. I will specifically investigate how Svalbard reindeer respond to ground icing and how their space use differs between the two contrasting winters. I will test the following predictions:

P1. Svalbard reindeer attempts to avoid locked pastures by increasing their movement rates

P2. By increasing their movement they increase the size of their home range compared to ice-free winters

P3. They move along geographical gradients that correspond with spatial variation in icing to improve their access to food:

      P3a). Reindeer will seek towards the coast

      P3b). Reindeer will seek higher elevated areas

      P3c). Icing will influence use of habitat types

2. Material and methods

2.1 Study area

This study was carried out in Reindalen, Colesdalen and Semmeldalen valleys, (including adjoining valleys) in Nordensköld land, Svalbard (78° 0´ N, 16° 0´ E) (Figure 1). Wide valleys, large plateaus and steep hillsides characterize the area. Due to variation in snow-depth and the process of wind-packing the snow, snow and ice conditions often vary between the valleys and plateaus. Human activity during the summer is rare. However, during the long winter season a snowmobile track runs through the area. Longyearbyen is the largest Norwegian settlement on Svalbard, and it is located approximately 20 km northeast of the study area.
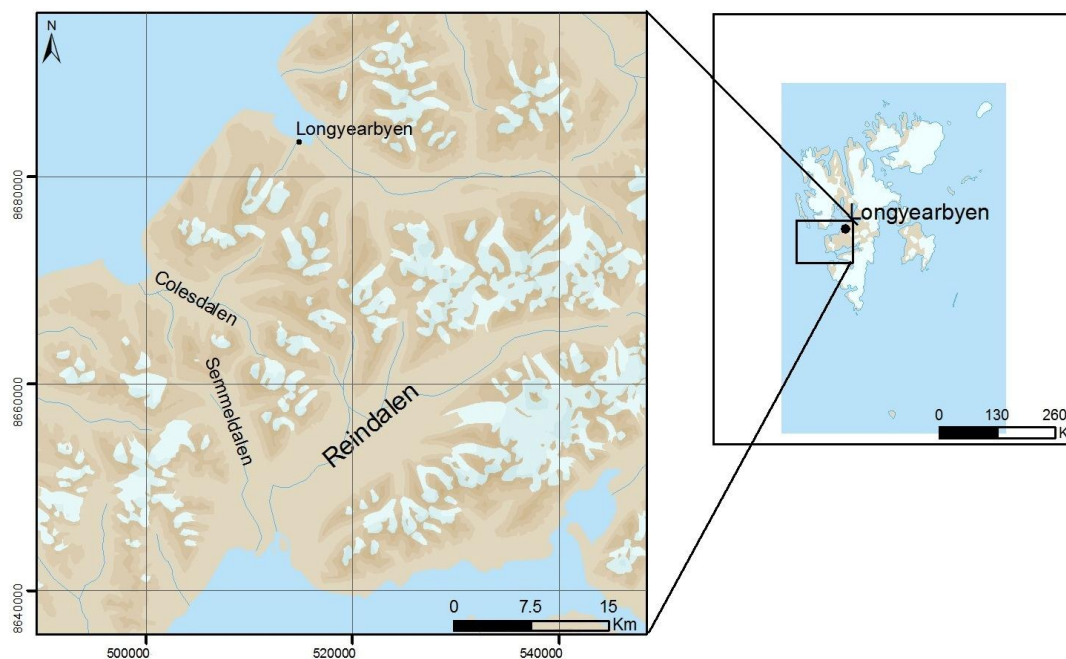
Figure 1: Study area is located on Nordenskiöld land, Svalbard (78° 0´ N, 16° 0´ E), encompasses the Reindalen, Colesdalen and Semmeldalen valleys and the adjoining valleys (WGS 1984, UTM 33).

Svalbard has an arctic climate (Rudberg 1988) and snow covers the area from October or November to mid-June. In this latitude light conditions are extreme (Bengtson 1999), as one moves northward, the annual variation in light conditions becomes more distinct and the diurnal variation becomes less distinct. From the 6th of April to the 7th of September there is constant daylight, and from the 15th of November to the 28th of January, there is no daylight at all. Annual precipitation in Spitsbergen is low, 200-440 mm per year (Hanssen-Bauer et al. 1990) which makes it a so-called polar desert. February is the coldest month and the average

temperature is – 16 °C, while during the warmest months, July and August, the average temperature is between 2°C and 6°C (Bengtson 1999).

Despite the high latitude, the temperatures in winter can increase above freezing point. When the air temperature is high and the ground temperature is low, an ice crust forms on the ground. Further, if rain falls on the snow, it penetrates the snow pack, freezes on the ground and covers the vegetation (Rennert et al. 2009). The ice layer makes the vegetation inaccessible for the reindeer, and the already depleted winter pasture becomes even more depleted (Aanes et al. 2000). These icing events are irregular, in some years there are several icing events, and in other years there are none (Isaksen, K. pers. comm.). Icing events have caused the reindeer population to significantly decline because of lack of food (e.g. winter 1993/94) (Kohler & Aanes 2004; Putkonen & Roe 2003). There is a concern that the climate on Svalbard is getting warmer (Førland et al. In press) and that the frequency of ROS events will increase. Such events may contribute to the continued decline in the reindeer population with possible negative trends in future population sizes (Hansen et al. 2011).

On Svalbard trees and shrubs are absent, but there is a continuous vegetation cover in the lowlands close to the coast and in the ice-free valleys. The growing season is short, and because of large temperature fluctuations, limited nutrient supply and wind exposure, the plant growth is limited (Bengtson 1999). In a couple of busy summer months the top layer of the permafrost thaws and makes it possible for plants to grow (Moen et al. 1999). However, temperature, bedrock, wind exposure and topography are critical for what types of plants that can survive and how they are distributed (Rønning et al. 1996). In addition, the variation in terrain, the thickness of snow cover and the duration of snow cover are also critical for plant survival and distribution. Despite the harsh artic climate, the vegetation close to the sea and below 200-300 m.a.s.l. is diverse. In the large ice-free valleys the vegetation ranges from dry and exposed ridges to moist mires, marshes and lush meadows (Rønning et al. 1996). The vegetation in open areas forms a mosaic with gravel and vegetation (Langvatn et al. 1999). For the ridge vegetation there is little snow protection during the winter, and the plants are exposed to wind, dry weather and temperature fluctuations. However, because there is little snow cover the growing season is long (Rønning et al. 1996). In areas where snow cover is thicker, the growing season is considerably shorter due to the late snow melting. The plants that grow there have snow protection during the winter but face a short and hectic growing season.

2.2 Study species

Svalbard reindeer are the only herbivorous large mammal on Svalbard (Bengtson 1999) (Figure 2). The total number of reindeer on Svalbard was estimated to approximately 11 000 individuals 1984 (Øritsland & Alendal 1986). No full-scale census has been conducted since then. Within my study area the estimated number of reindeer has fluctuated between 238 and 1129 animals since 1979 (population census conducted by NINA; V. Veiberg pers. comm.). There are large annual fluctuations due density dependent and climate dependent variation in calf production and survival (Solberg et al. 2001). The endemic Svalbard reindeer has special adaptions for surviving in the arctic environment (Nilssen 1986). During the summer and autumn they are capable of storing energy as fat reserves along the spine, sides and around the skeletal muscles (Tyler 1986a). The stored fat can comprise as much as 20 % of their body weight (Reimers & Ringberg 1983), and meet their energy needs for about 25 % of the winter (Tyler 1987).

The Svalbard reindeer have evolved without the presence of predators for more than 5000 years (van der Knaap 1989). They are sedentary and do not migrate long distances, in contrast to other sub-species of the *Rangifer*-genus (Tyler & Øritsland 1989). They are sedate and calm and are not easily affected by humans. In most places in Svalbard, reindeer are

Figure 2: Svalbard reindeer (*Rangifer tarandus platyrhynchus*) grazing in the Colesdalen valley. Photo: Dag Ringstad

seldom visited by humans, except for areas close to human settlements. Svalbard reindeer are the smallest *Rangifer*, with short legs and compact bodies (Gravlund et al. 1998). Thick fur keeps the reindeer warm under extreme conditions. Even in temperatures below -30 °C they do not have to use any extra energy to regulate their body temperature (Nilssen 1986). They have a varied diet and graze on most available plant species (Staaland et al. 1993). During the summer the reindeer most commonly graze in the bottom of the valleys and on lush tundra areas where the vegetation is rich and moist. In the winter these areas are mostly covered

with hard, wind packed snow so the reindeer seek out wind-swept ridges, slopes and higher plateaus (Langvatn et al. 1999; Reimers & Ringberg 1983). Because they graze on sparse vegetation, the reindeer often ingest gravel and soil together with plants, which leads to dental wear (Veiberg et al. 2007). The most common cause of death among adult animals is starvation in winter (Tyler 1986b).

2.3 Meterological data

2.3.1 Ground temperature

In August 2009, 144 temperature loggers (ibuttons) were placed out in the study area. The temperature loggers were arranged in a spatial hierarchical setup with levels at 5, 50, 500 and 5000 meters. This arrangement covers the winter habitat of the reindeer in Colesdalen-Semmeldalen-Reindalen and measures the temporal variation in ground temperature in an attempt to detect where and when icing takes place (winter temperatures above zero degrees followed by sub-zero periods). The temperature loggers were placed in a waterproof capsule and pressed 5 mm into the soil. Therefore the measurements acquired from them reflect soil surface temperatures. The capsules were marked above ground by a 10x10 cm aluminum plate located about 20 cm from the logger in order to not affect temperature. Data were retrieved in August 2010 and 2011. From the retrieved data warm spells were interpreted as a longer period with temperatures of 0 °C and above. Data from the 15th of October to the 1st of May in each year were used in my study.

2.3.2 Ice and snow cover

In April 2010, February 2011 and April 2011 snow and ice layer was measured the at the location of each temperature logger. The position of the temperature loggers was determined by handheld GPS, which means that the snow and ice measurements most of the time was very close, but in rare occasions may have been up to 20 meters away from the temperature loggers (due to GPS error). On the position of every logger all snow was dug away, an axe was used to penetrate the ground ice, and the thickness of ground ice was measured by a ruler. Other measures such as snow depth and number of ice layers in the snow pack were also measured.

2.3.3 Air temperature and precipitation

Air temperature and precipitation were measured at Longyearbyen Airport and retrieved from Norwegian Meteorological Institute (www.met.no). The air temperature and precipitation

measurements were used to evaluate if conditions during the warm spells could lead to icing.

2.4 Reindeer positioning data

In February and April of 2009 and 2010 female reindeer were captured using snowmobiles and catching nets (Omsjoe et al. 2009). A total of 41 reindeer (n = 20 in 2009 and n = 21 in 2010) were collared with Vectronics aerospace GPS collars (weight 850 gram, approximately 1-2 % of the animals winter weight). The age of the GPS marked animals were known due to marking with ear tags and plastic collars as calves. The GPS collars were programmed to record the animals positions every second hour with a precision of about 12 meters (Godvik et al. 2009). In February and April of 2010 and 2011 reindeer were captured and data from the GPS units were downloaded (n = 15 in 2010 and n = 20 in 2011). Hence, I do not have any data later than April 2011, so the 2010/11 winter ends earlier than the 2009/10 winter in my results. I did a screening of the data to remove outlying locations (GPS-errors) using the method described by Bjørneraas et al. (2010). After a visual inspection I manually removed one obvious outlier that was not removed in the automated screening procedure. In my thesis I use the data from the winter months (the 15th of October to the 1st of May).

2.5 Vegetation

Data for vegetation types were obtained from the Norwegian Institute for Nature Research`s (NINA) vegetation map from 2009 (Johansen et al. 2009). The vegetation map is based on Landsat satellite photos with a 30 x 30 meter resolution. The original vegetation types were grouped to identify important grazing areas for the reindeer, specifically ridge and meadow vegetation (Table 1). Ridge vegetation contains four vegetation types. These types are all typical ridge vegetation, with little snow cover, a long growing season and plants that tolerate temperature fluctuations. The meadow vegetation consists of six types of wet and moist vegetation dominated by mosses and meadow species.

Table 1: Selected vegetation types included in the analyses. Vegetation classes as defined by Johansen et al. (2009).

Veg. type	Veg.class	No. of reindeer plots	Description
Ridge vegetation	25	9016	Dry ridge, open vegetation. *Potentilla pulchella, Poa abbreviate, Poa hartzii*
	21	3068	Ridge. *Dryas octopetala, Carex rupestris,* Cassiope tetragona ssp. tetragona
	18	1213	Ridge. *Dryas octopetala*
	22	1217	Heath. *Dryas octopetala, Carex rupestris*
Moss tundra/ Meadow community	13	7511	Moss tundra. *Tomentypnum nitens, Dupontia fisheri, Eriophorum scheuchzeri* ssp. *arcticum, Carex parallela, Carex saxatilis*
	12	6476	Moss tundra. *Tomentypnum nitens, Warnstorfia sarmentosa, Alopecurus magellanicus*
	20	11055	Meadow. Lush vegetation and bird cliff vegetation
	19	2915	Lush meadow and grasses. Often in combinition with moss tundra in dry areas.
	17	879	*Luzula confuse* often in combination with *Flavocetraria nivalis* and *Cladonia mitis*
	16	170	Open vegetation. *Luzula confuse*

2.6 GIS-analyses

All GIS-analyses were run in ESRI`s ArcMap version 9.3 (ESRI 2009) including Hawth`s Analysis Tools version 3.27 (Hawthorne 2010). Standard overlay and spatial join procedures were used to calculate the distance from all reindeer GPS-plots to the coastline, the nearest elevation contour line, and to identify the vegetation type. The same procedure was applied for the localization of the temperature loggers. Graphical presentation of home ranges was done in GIS by using Hawth`s tools fixed Kernel Density Estimator (KDE) with 95 % and 50 % isopleths.

2.7 Statistical analyses

Temporal and spatial distribution of ice

I used General Additive Models (GAM) (Wood 2006) fitted with the "mgcv" package in R (R Development Core Team 2011) to estimate the probability of temperatures of 0 °C or higher during each winter. By using ground temperature data (binomial distributed) as the response and date as the predictor, I determined when ground temperatures increased which indicates icing. Additive models allow a non-linear relationship between the response variable and the explanatory variable (Zuur et al. 2009). In practice a GAM fits a number of segmented curved lines along the x-axis that is connected and smoothed in a final step. The more segments in a model, the better the line will fit the data points. However, according to the principle of parsimony there is also a value in keeping the model as simple as possible (i.e. with fewer segments). The GAM function in package "mgcv" uses cross validation to automatically set the degrees of freedom (number of segments) of the spline function. If the outcome of the cross validation still appears too complex for biological realism, the user can reduce the degrees of freedom manually. This is common practice (Stien et al. Submitted) and in some cases I restricted the degrees of freedom to 5 (K = 5) or 3 (K = 3). This is reported in text and figure legends.

Spatial variation in icing was analyzed with a Generalized Linear Mixed effects Model (GLMM) using the function lmer in the R library lme4 (Bates et al. 2011). Ice thickness (1 = thicker; 0 = thinner than a threshold of 2 cm) was the response variable. Elevation (in meter), distance to coast (in km) and vegetation category (ridge and meadow; see Table 1) and snow cover (in cm) was used as predictor variables. Each spatial cluster (on approximately 500 m scale) was treated as a random intercept to account for spatial autocorrelation in the ice measures.

Reindeer movement

I also used a GAM approach when analyzing the reindeer data. If reindeer responded to icing by first increasing and then decreasing movement rates, this will be well represented as a non-linear effect of date (predictor) on movement (response). By using additive models I could therefore flexibly detect increases and decreases in step length in critical icing periods. Because repeated locations are sampled for each individual I used a mixed-GAM with individual identity as the random intercept (Zuur et al. 2009).

Separate mixed GAMs were run for each winter to investigate change in movement rate and habitat use over time. Julian date was always used as the single predictor in all models. The response variables and assumed error distribution in the different analyses consisted of 1) reindeer step length per two hours (family negative binomial), 2) elevation (m.a.s.l.; family poisson), 3) distance to coast (km; family gaussian) and the two vegetation types a) ridge and b) meadow (both family binomial). For the two vegetation analyses, I manually reduced the degrees of freedom to 3 and 5 for ridge and meadow vegetation to approach a more biologically realistic curve fitting of the model (see above). Significance was assessed directly from predicted confidence limits in the figures. If the confidence interval of the lines from two years does not overlap, it is a significant result. This is a very conservative measure on statistical significance between years.

The calculation of home range sizes for the 13 GPS-collared females that had data from both winters were performed by the package adehabitat (Calenge 2006) in R. I used fixed kernel where I calculated the smoothing factor h using the reference method (Worton 1989). To avoid extreme effect of large home ranges and reduce heteroschedasticity, I log-transformed the home range sizes before statistical analyses. I used a t-test to test the differences between the winters.

3. Results

3.1 Contrasting ice conditions the two winters

Ground ice thickness was significantly different between the two winters (t-test: $p < 0.0001$; Figure 3). Average ice thickness for the 2009/10 winter was 3.2 cm (± SE; 0.2), considerably higher than to 0.2 cm (± SE; 0.06) for the 2010/11 winter. In the 2009/10 winter 76 % of the sites were covered by ground ice, whereas 6 % in the 2010/11 winter.

Data from the ground temperature loggers indicate differing conditions between the winters, and most likely show when ground icing occurred in the 2009/10 winter. The 2009/10 winter had two warm spells with temperatures above 0 °C and precipitation, the late autumn spell in November-December (11.3 mm precipitation) and, the mid-winter spell in January (48.7 mm precipitation). During the 2010/11 winter, temperature was stabile below 0 °C. There were no warm spells during the winter after the temperature dropped below 0 °C in late October, except for one short period in late March.

There were systematic differences in ground ice along geographical gradients in the 2009/10 winter. The probability of development of a thick ice cover (> 2 cm) decreased with increasing elevation (Table 2). There was a strong trend that ice thickness increased with increasing distance from the coast. I found no support for more ice on ridge compared to in meadow vegetation. Finally ice thickness decreased with the depth of the snow layer (Table 2).
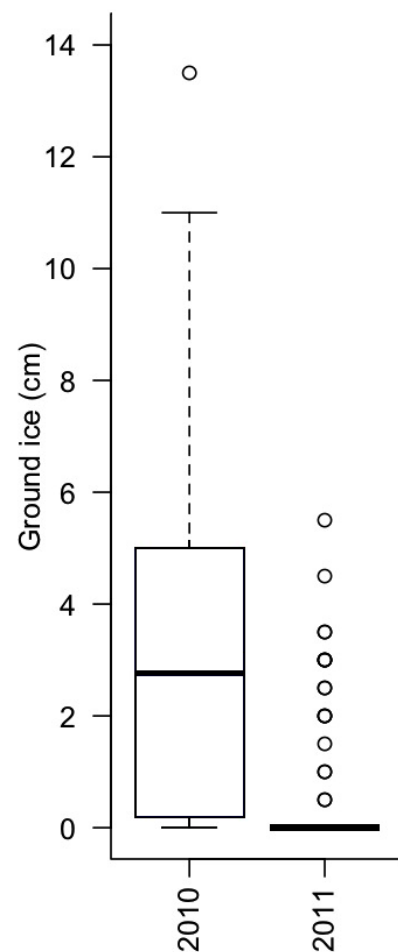

Figure 3: Ground ice measured by field validation. Average ice thickness the 2009/10 winter was 3.2 cm (± SE; 0.2) and 0.2 cm the 20010/11 winter (± SE; 0.06).

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Table 2: Logistic Mixed Model explaining variation in the probability of thick ice cover (thicker or thinner than 2 cm) occurring after the icing event in winter 2009/10. Subarea (500 m scale) was treated as a random intercept to account for spatial dependency in ice measures.

	Estimate	SE	z	p
Intercept	3.12	1.32	2.37	0.017999
Elevation (m)	-0.02	0.01	-3.45	0.00057
Distance to coast (km)	0.21	0.12	1.79	0.073608
Vegetation (ridge-meadow)	1.11	0.70	1.58	0.115326
Snow (cm)	-0.05	0.01	-3.71	0.00021

3.2 Increased reindeer movement during warm spells

As predicted from P1, reindeer step lengths were longer and much more variable in the icing winter of 2009/10 when compared to the ice-free winter 2010/11 (Figure 4). In the 2010/11 winter the step length decreased in late autumn to a stable baseline level of about 70 meter per two hours. The reindeer step lengths in the 2009/10 winter started along the same way as it decreased in the beginning of the winter from 130 meters to 70 meters. Then there was a slight increase to about 90 meters per day in late November, with subsequent decrease back to the previous level. This corresponded with the time of the late autumn warm spell. In January there was a marked increase in step length from less than 70 meters per day to about 200 meters in a short period. This increase occurred at the same time as the mid-winter warm spell. The response of the warm spell in mid-winter was thus much larger than the effect of the late autumn warm spell.
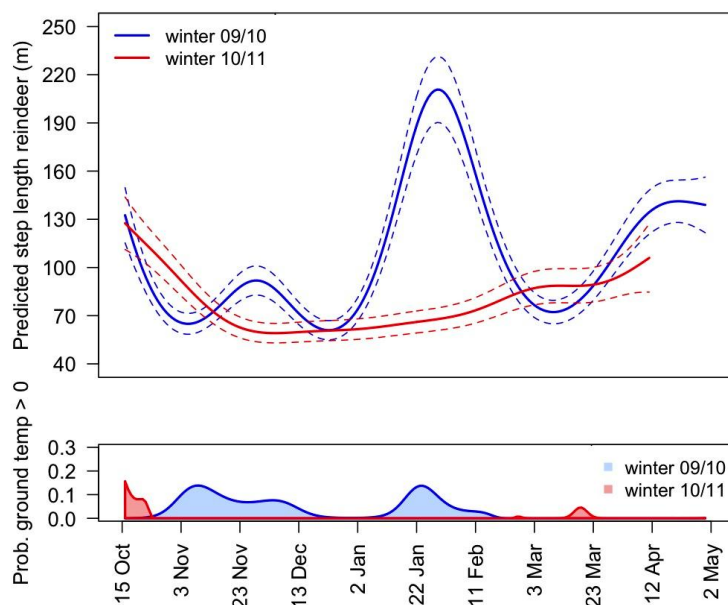

Figure 4: Predicted step length (meter per two hours) for Svalbard reindeer (*Rangifer tarandus platyrhynchus*) the 2009/10 winter (blue) and the 2010/11 winter (red) from the 15th of October to the 1st of May (average ± SE, dotted lines).

3.3 Increased home range size as result of icing

As predicted from P2, home ranges of reindeer were significantly larger during the 2009/10 winter as compared to the 2010/11 winter (log estimate for size difference = 1.33, SE = 0.3984, t = 3.35, p = 0.00578). The median home range size in the 2009/10 winter was 29 km^2, and in the 2010/11 winter it was 13 km^2. The median home ranges were 2.2 % larger in the icing winter of 2009/10 compared to the ice-free winter of 2010/11 (Table 3, Figure 5) but the difference between years differed largely among individuals. Three individuals conducted long-distance excursions following the icing event and thus show extreme differences in home range size between years (reindeer with id's W91, W72 and Y112; Table 3).

Table 3: Home range size (km^2) of the 13 individuals that were GPS-collared both years, and the difference between home range sizes between the two years. Kernel home ranges calculated in R.

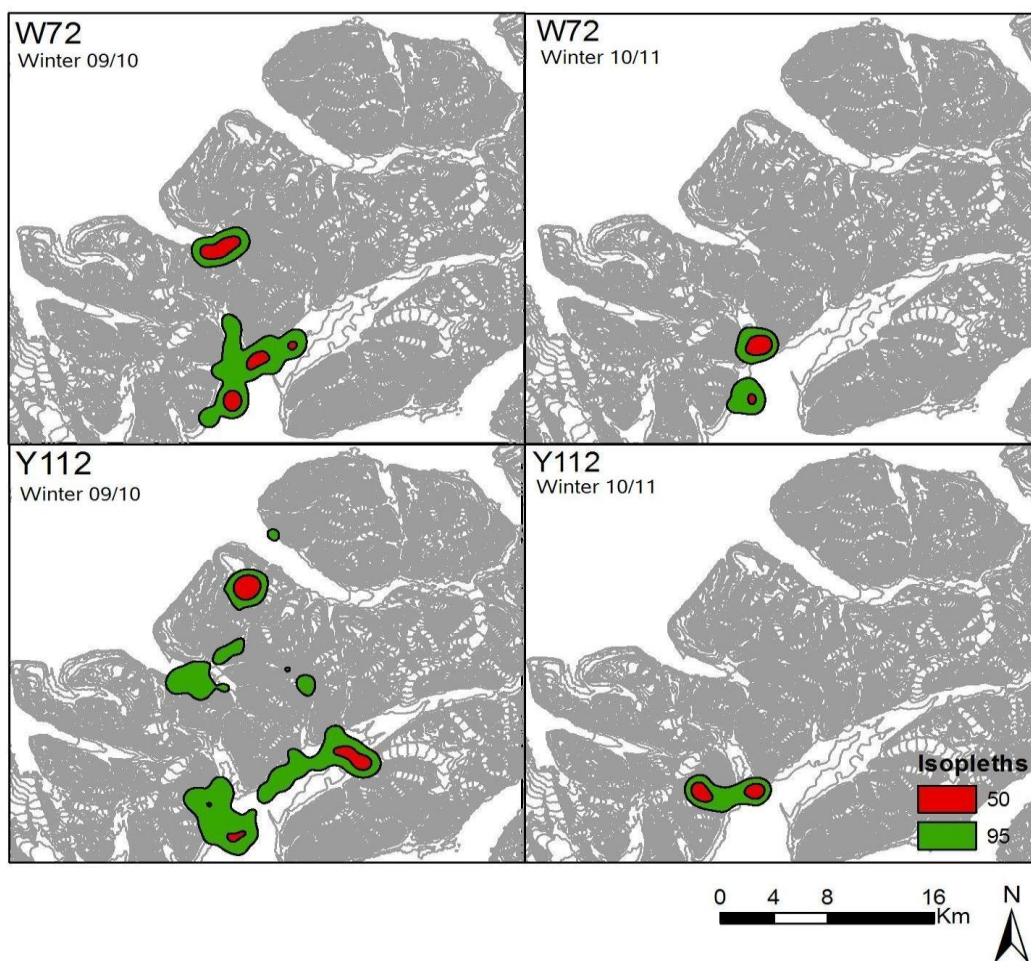| Reindeer ID	Areal km^2 w 2009/10	Areal km^2 w 2010/11	Differance areal km^2
B100	45.06	27.63	17.43
B123	20.06	3.87	16.18
B93	45.77	3.13	42.65
B96	28.76	47.51	-18.74
G39	14.47	16.12	-1.65
R240	15.13	11.49	3.65
W64	3.13	4.15	-1.02
W72	218.73	7.61	211.12
W74	78.49	14.74	63.74
W91	788.50	18.77	769.73
Y105	14.15	4.93	9.22
Y112	566.18	33.77	532.14
Y117	21.59	13.00	8.59
Median	28.76	13.00	16.18
Average	143.08	15.90	127.18

Figure 5: Home range of Svalbard reindeer (*Rangifer tarandus platyrhynchus*), exemplified by individuals W72 and Y112, the 2009/10 winter (left) and the 2010/1 winter 1 (right) with 95 % isopleths (green) and 50 % isopleths (red). The remaining 11 individuals are presented in Appendix.

3.4 Movement along geographical gradients

3.4.2 Distance to coast

The Svalbard reindeer's use of areas with respect to distance to the coast vary throughout the winter in both years, but I did not find support for P3a. In both years reindeer tended to move closer to the coastline as the winter progressed. The largest difference between the two years was that the reindeer in the 2009/10 winter rapidly moved on average approximately 3 km closer to the coast following the second warm spell (Figure 6). This did not occur in the ice-free winter.

Figure 6: Predicted distance to coast (km) for Svalbard reindeer (*Rangifer tarandus platyrhynchus*) the 2009/10 winter (blue) and the 2010/11 winter (red) from the 15th of October to the 1st of May (average ± SE, dotted line).
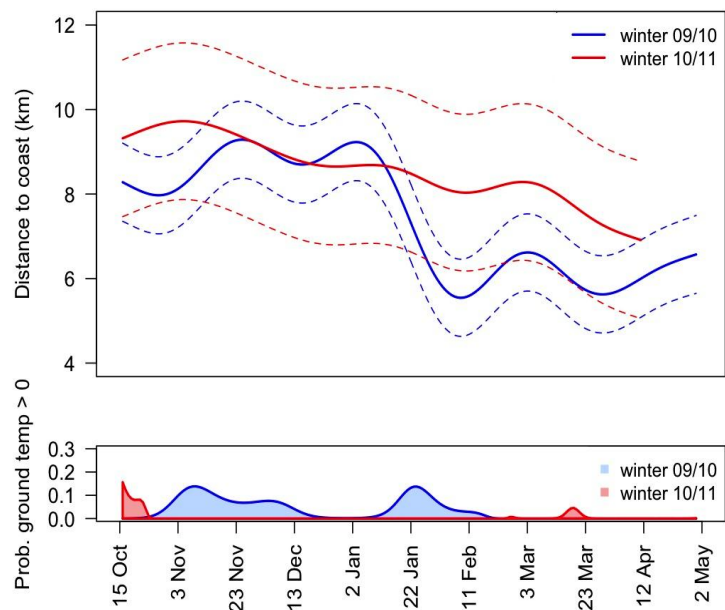
3.4.1 Elevation

The reindeer stayed in higher elevated areas in the beginning of the winter and then relocated to lower elevations for while in November both years (Figure 7). In the beginning of the 2009/10 winter the reindeer stayed in lower elevated areas as compared to the 2010/11 winter. The reindeer's use of elevated areas varies through both winters. Corresponding with P3b, after the mid-winter warm spell the reindeer moved from about 90 m.a.s.l. to about 270 m.a.s.l. in a short period after the mid-winter warm spell. The subsequent month they returned to the lowlands. The response seemed to be delayed compared to the movement towards the coast. For the same period the 2010/11 winter there was an increased use in higher elevated areas, but when compared to the same time in 2009/10 winter, they were used to a much smaller extent.


Figure 7: Predicted elevation (m.a.s.l.) for Svalbard reindeer (*Rangifer tarandus platyrhynchus*) the 2009/10 winter (blue) and the 2010/11 winter (red) from the 15th of October to the 1st of May (average ± SE, dotted line).
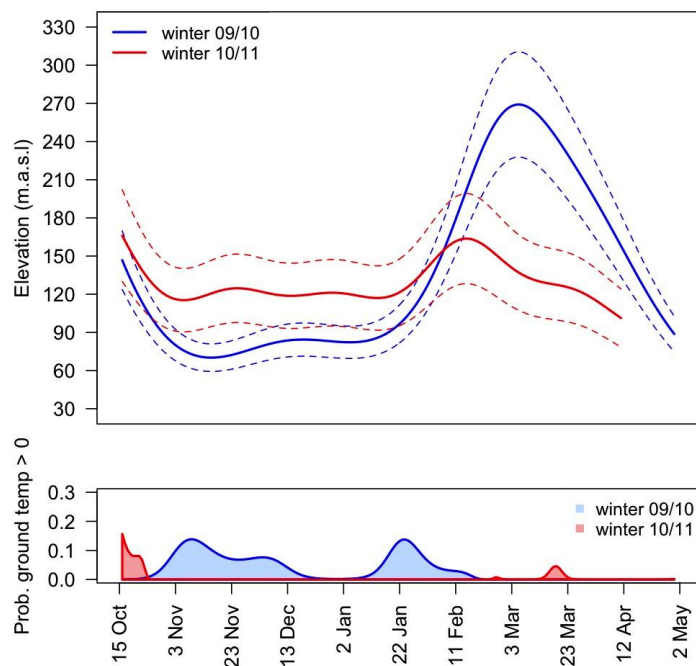
3.4.3 Vegetation

There was a seasonal trend both years that the reindeer used progressively more ridge vegetation later in the winter season but with no differences between the two years (Figure 8).

Figure 8: Probability of Svalbard reindeer´s (*Rangifer tarandus platyrhynchus*) use of ridge vegetation winter 2009/10 (blue) and winter 2010/11 (red) from the 15th of October to the 1st of May (average ± SE, dotted line). K=5
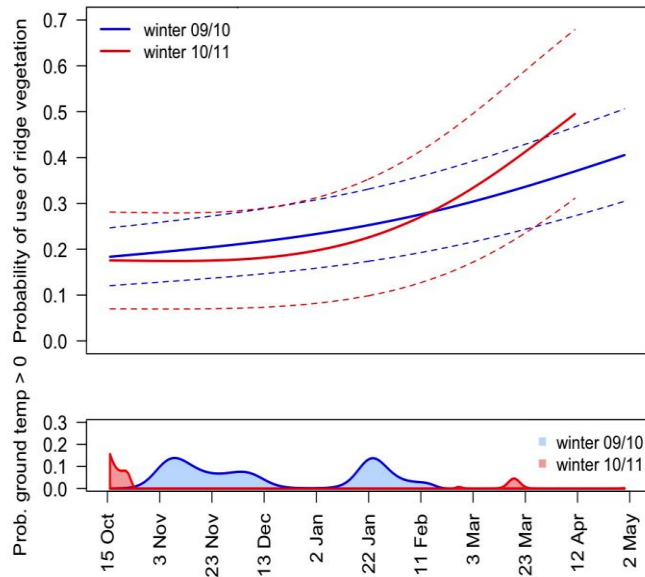
Corresponding with the increased use of ridge vegetation, there was a reduced use of meadow late in the winter also with no obvious difference between the two years (Figure 9).

Figure 9: Figure 9: Probability of Svalbard reindeer´s (*Rangifer tarandus platyrhynchus*) use of meadow/ moss tundra vegetation winter 2009/10 (blue) and winter 2010/11 (red) from the 15th of October to the 1st of May (average ± SE, dotted line). K=3
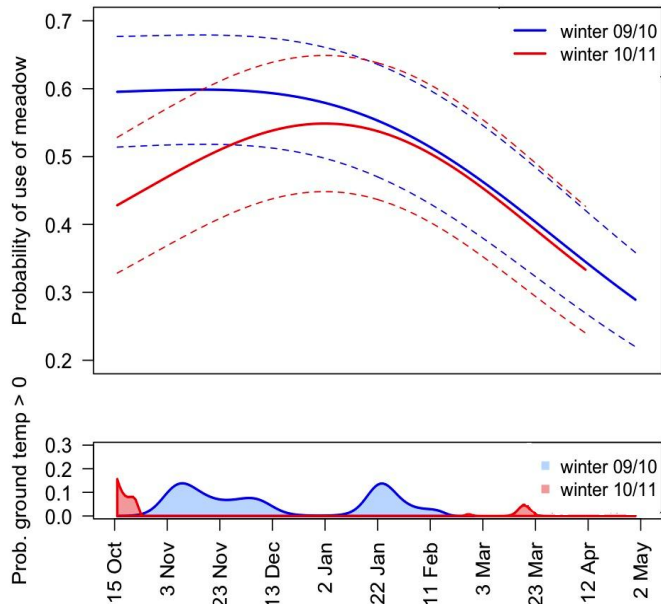
4. Discussion

This study document by the use of ground temperature loggers and field validation that the two winters 2009/10 and 2010/11 differed strongly in amount and spatial extent of icing. The reindeer responded immediately to ground icing by increasing movement rates and by that increasing the size of their winter home range. The space shifts following the mid-winter warm spell in 2010 occurred along specific gradients. The reindeer moved rapidly closer to the coastline and, with a more delayed response, to higher elevated areas. There were no differences in selection of vegetation types in the two years. Field validation documented decreasing thickness of ice along the coast and at high elevations. It is therefore clear that reindeer searched for, and found, areas with less ground ice

4.1. Estimating annual difference in icing and timing of icing events

Field validation measurements demonstrated that the extent of icing differed between the two winters, where ground ice was found in 76% of the measured winter habitat in the 2009/10 winter compared to only 6% in 2010/11 winter. This finding was the outset for contrasting how reindeer behave in an icing winter compared to an ice-free winter. Two warm spells that may induce icing events the 2009/10 winter, one late autumn spell in November and one midwinter spell in January were detected from the ground temperature loggers. The autumn warm spell lasted eight days form the 10th to the 28th of November, while the warm spell in late winter lasted nine days between the 15th and the 25th of January. During the 2010/11 winter no warm spells were detected and this finding coincides well with expected results i.e. no warm spells, no icing.

My study is the second ungulate study, only preceded by Hansen et al. (2011) to document the effects of ground icing on the Svalbard reindeer, based on field validation. Other studies have discussed the effect of warm spells and icing (Solberg et al. 2001; Tyler 2010) but only using meteorological data as proxies for icing events. This study is, to my knowledge, the first one to use ground temperature data to study the development of ground ice. Ground temperature data form the loggers coincides well when compared to the measured air temperatures at Longyearbyen Airport. It is possible that by using the air temperatures as a measurement for temperature change, the result would be the same. However, a few days increase in air temperature might not be detected in the loggers that are located under the

snow pack. A combination of the two temperature measurements might be a good solution. The field validation of ice and snow is an important measure to validate the temperature measurements and to verify if icing did occur. During the 2009/10 winter the field validation confirmed that ground ice had developed during the winter. The weakness of this measurement is that the results can only confirm that ice developed during the winter, it is not possible to determine when ice developed in case of multiple warm spells during the winter. However, by comparing ice measurements, ground temperature, air temperature and precipitation measures, it is possible to estimate when ground icing occurred.

4.2. Increased movement during warm spells

As predicted in P1 the reindeer responded to icing by increasing their movement from 70 meters to 200 meters moved per two hours during and after the midwinter warm spell. A similar increase was also documented by Stien et al. (2010). It was expected that the reindeer would respond the same way to both warm spells, but surprisingly they did not respond to the late autumn spell with increased movement.

The difference in response to warm spells could be due to varying amounts of precipitation during this period. It is possible that the autumn warm spell the 2009/10 winter did not lead to development of ground ice. There is no field validation to verify ground icing the autumn warm spell, and it is thus possible that this warm spell did not lead to development of ground ice. However, an evaluation from a meteorologist (Isaksen, K. pers. comm.) indicates that the temperature and precipitation associated with this particular warm spell is expected to create a layer of ground ice. Previous studies have shown that air temperatures above 0 °C during the winter season or light rain would result in unfavorable conditions for ungulates (Rennert et al. 2009). The two warm spells in the 2009/10 winter lasted about the same amount of days, but considerable amount of rain fell during the mid-winter spell (~ 50 mm) compared with the late autumn spell (~ 11 mm). It has been suggested that the number of heavy ROS events is the best explanation for annual variation in ground-ice presence (Hansen et al. 2011). Consequently it is reasonable to believe that the majority of the ground ice found during the field validation the 2009/10 winter, developed during the mid-winter warm spell. The late autumn warm spell may have led to a thin ice-layer, which the reindeer could penetrate. While the second ROS event with large amounts of precipitation probably lead to an increase in the thickness of the ground ice, triggering the observed increased movement.

Another possibility is that reindeer were able to locate ice-free patches in autumn, without the need for increased movement. Ground ice develops unevenly in the landscape, depending on topography. There is better run-off in slopes, thus water will drain more effectively in these areas than what you will find in flat areas, and less ice will develop. This creates a patchy ice covered landscape, and it is possible for reindeer to find ice-free microhabitat. Hansen et al. (2010) studied reindeer feeding craters the winter of 2006, a very icy winter, and found no craters covered with ground ice, but many control sites in between craters were covered with ice. Mechanistically, this is believed to be caused by reindeer's ability to smell plant forage under the snow. By using their sense of smell they only crater in places with little or no ice and less snow (Bergerud & Nolan 1970; Bergerud 1974).

Finally, it is also possible that the reindeer had sufficient amount of body fat during the autumn warm spell and hence could rely on their energy reserves to avoid starvation during the first icing period. When choosing to rely on saved energy reserves the reindeer can remain inactive. By reducing activity the reindeer spend less energy (Nilssen 1986). Starving reindeer constantly need to make a trade-off between staying where they are and try to find ice-free microclimate or to wander off to the unknown in search for ice-free grounds (Stien et al. 2010). Increased movement rates costs energy and increase the reduction of body fat reserves (Rennert et al. 2009). It is possible that in cases of extensive icing, excursions results in reindeer spending more energy in food search than what they will spend if they do not wander. This was probably the case in the 1975/76 winter on Edgeøya where many individuals died of starvation when trying to escape the ice locked pastures (Reimers 1982).

Stien et al. (2010) was the first to document the reindeer's response to icing events. However, their study was based on only six individuals, marked with satellite collars, which recorded the animals` position every fifth day. Air temperatures were uses as proxies for icing, but there were no actual measurements of icing. My study is based on detailed GPS-data from 35 female Svalbard reindeer, which record the animals` position every second hour. Additionally, when combined with ground temperatures and filed validation data of ice development a more detailed and reliable result concerning the animals' responses occurs.

4.3 Increased home range sizes as a result of icing

Following the increased movement rates I also document that home range size was larger in the icing winter compared to the non-icing winter, as predicted in P2. The GPS-collared individuals were marked as known aged adults (3-5 years), with no previous knowledge about their space use. Therefore, the data obtained from the GPS collars could not be used to establish if individuals moved out of their previously known range in response to icing events. Findings from Stien et al. (2010) indicate that this was indeed the case. If this is the case, icing events leads to expansion of home ranges into new areas. This may be beneficial in later icing years. Recent studies in spatial ecology focuses on the role that memory has in space use (e.g. van Moorter et al. 2009). Potentially, it can be very important for fitness to remember locations that can increase the likelihood for survival following a critical event. For example, to remember the location of an area that tends to have less ice after an icing event can increase the individual's change to survive.

In other ungulates species, the calf learns migration behavior from its mother (Hjeljord 2008). In future studies it could be interesting to investigate if such a behavioral attribute also exists among the Svalbard reindeer. If this were the case, one would expect that resident mother would raise resident calves, while calves from mothers that tend to migrate learn this behavior from its mother. Further, if calves are exposed to an icy winter the first year one could speculate that they would have larger home ranges than calves that are not exposed to extra-ordinary conditions.

4.4 Movement along geographical gradients

4.4.1 Distance to coast

During the mid-winter warm spell in winter 2009/10, the reindeer showed a marked movement towards the coast, as was predicted in P3a. This movement is likely a direct response to the ground icing following the warm spell. However, even during the ice-free 2010/11 winter, the reindeer tended to seek towards the coastline during the winter season, but in a more stable trend than in the 2009/10 winter. It is possible that the observed pattern of moving towards the coastline the non-icing winter is an unusual event. However, it might also be common behavior for reindeer.

It is possible that the reindeer have adapted to a life in an unpredictable environment. Thus they may have built-in mechanism to wander toward the coastline as a buffer for unexpected icing events.

I documented a relation between the thickness of snow cover and the probability of ground ice development. In the inland the snow cover was thinner than near the coast and thus the probability of icing was higher. In coastal areas the situation was reversed, there is more snow, but lower probability for development of an ice cover and thus better conditions for reindeer to find food. Further, it is possible that in winters with severe icing conditions that the reindeer utilize marine resources. Hansen & Aanes (2012) reported that especially calves and young animals feed on kelp and seaweed to avoid starvation. This contributes to the explanation of why reindeer moved toward coastal areas after an icing event and it support my prediction (P3a).

4.4.2 Elevation

As predicted in P3b the reindeer showed a distinct increase in the use of higher elevated areas after the mid-winter warm spell in the 2009/10 winter. However, in the 2010/11 winter the reindeer seemed to stay at a stable elevation of approximately 120 m.a.s.l. The movement up the elevation gradient was delayed compared to the movement towards the coast. It is possible that the reindeer followed the valleys when moving towards the coast, and thereafter moved towards higher lying areas. Reindeer might have moved up to the plateaus, which would explain the marked increase within elevation in a period of decreasing step length. The movement from the valley towards the plateau is not a long walk in meters, but represent a marked change in elevation.

The movement up the elevation gradient was delayed compared to the movement towards the coast. There was less thick ice in high-elevated areas, possibly due to lower temperatures (Isaksen. K. pers. comm.). Migrations are common among ungulates i.a. to escape areas with thick snow cover (Nelson 1995) or following the snow melt to find nutrient rich vegetation (Albon & Langvatn 1992). These migrations are often towards lower elevations in the autumn, whereas Svalbard reindeer move the opposite way (Tyler & Øritsland 1989). In Svalbard the snow and ice layer in the low land grow thicker and wind is packing the snow dense and hard, therefore the reindeer seek towards wind-swept areas where vegetation is

available (Langvatn et al. 1999; Reimers 1983). During extensive ground icing, parts of the Svalbard reindeer population have been found in search for food in exposed areas with little snow cover e.g. ridges and mountainous habitat (Hansen et al. 2010). This movement in search for food can, even though it is small scale, be compared to other ungulates wandering that is driven by snow conditions e.g. roe deer (*Capreolus capreolus*) (Mysterud 1999), moose (*Alces alces*) (Gundersen et al. 1998) and mule deer (Garrott et al. 1987).

4.4.3 Vegetation

The reindeer did not show any difference in use of vegetation types in the 2009/10 winter compared to the 2010/11 winter, which did not support P3c. However, they did show a progressively increased use of ridge vegetation, but a decreased use of meadow vegetation in late season both winters. It is possible that snow accumulation in the valley force the reindeer to seek towards ridge vegetation. Due to wind exposure, the ridges have a thin snow cover. Where snow cover is thin the probability of development of ice is higher. The increase in use of ridge vegetation may be explained by more difficult snow and ice conditions in less wind exposed areas, forcing the reindeer to utilize exposed ridges with sparse, but available vegetation.

5. Conclusion

Ice conditions vary along coast-inland and high-low elevation gradients. This study is the first to demonstrate that when ground icing occurs, Svalbard reindeer undertake excursions along these gradients in search for ice-free habitat where vegetation is available. There is a concern that in the future, the winters in Svalbard will be warmer and rainier with following ground icing and non-favorable conditions for reindeer. My study contributes to the debate on the future viability of Svalbard reindeer by pointing at behavior as an important buffer towards small and intermediate scaled ground icing.

This study is based on data from two winters. The ice conditions were very different these two winters, leading to differences in reindeer's response to icing events. Part of my study has previously been investigated and my results were in accordance with earlier results. However, it would have been interesting to have access to data from several years. Long-term data could give a more complete and better understanding of the reindeer´s response on icing events.

However, it is expected that reindeer will show the same response on icing events during successive years.

6. References

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Appendix

Home ranges for 13 individuals of Svalbard reindeer that was GPS-collared winter 2009/10 and 2010/11.

B100
Winter 09/10

B100
Winter 10/11

B93
Winter 09/10

B93
Winter 10/11

R240
Winter 09/10

R240
Winter 10/11

N

0 5 10   20   30
Km

Isopleths
50 %
95 %

III

G39
Winter 09/10

G39
Winter 10/11

N

0 5 10   20   30
Km

Isopleths

50 %

95 %

IV