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# **Effects of spatio-temporal weather conditions in autumn and winter on body mass and behaviour of the high Arctic Svalbard reindeer (*Rangifer tarandus platyrhynchus*)**

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## **Preface**

This thesis constitutes the final product of my Master's Degree in Natural Resource Management at the Norwegian University of Life Science (NMBU). I have spent the last year acquiring knowledge about the process of writing a scientific paper. This process has provided me with fascinating insight to the world of science and furthermore increased my knowledge substantially about Svalbard reindeer ecology and the effects of weather and snow conditions on body mass and behavior.

Several people deserves credit for helping me throughout the process of completing this thesis. Firstly, I want to give special thanks to my primary supervisor and professor at NMBU, Leif Egil Loe. He has provided my with reindeer-data and indispensable help with the statistical analysis, as well as encouragement, support, motivation and high-quality feedback throughout the entire process. I also want to tribute my co-supervisor, Åshild Pedersen, for valuable feedback and corrections. Moreover, I must give credit to professor Steve Albon, for valuable comments and feedback. I appreciate you all investing your time and effort in quick responses and providing me with guidance. Furthermore, I am grateful to Glen Liston for supplying me with spatio-temporal weather data necessary to conduct the analysis, in addition to Stein Tore, Vebjørn, Monica, Alina, Steve, Leif Egil, Øystein and Linda for unforgettable experiences and memories during the field work at Svalbard, which was funded by the Research Council of Norway.

Finally, I want to give thanks to my personal psychologist, who throughout this process has provided me with support, encouragement and proof reading, as well as therapy-sessions free of charge. In the end, I also want to credit my own effort and achievements. Before I started the writing process, I was in doubt of my abilities to write a thesis in a foreign language. Thus, the composition of this thesis has been a journey with moments of frustration, as well as utter excitement and feelings of accomplishment.

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## Abstract

There exists large consensus within the research community that climatic changes have a world-wide impact on ecosystems, which is further expected to be most prominent in the Arctic. In these strongly seasonal environments, one key aspect is that global warming affects the duration of seasons. The focus on climate research has principally been directed towards the earlier coming of spring, meanwhile autumn is perhaps a neglected season. A natural consequence of warmer autumn seasons, is a delay in the onset of winter snow cover. This may in turn cause beneficial effects for herbivores, due to a prolonged period with good foraging conditions. In contrast, the increase in rain-on-snow events due to warmer winters may restrict access to forage as the rain refreezes on the ground or inside the snow pack. This may lead to contrasting effects on body mass, which responds continuously to changes in environmental conditions and influence both survival and recruitment parameters in herbivores.

In this study, GPS-data of marked adult Svalbard reindeer (*Rangifer tarandus platyrhynchus*), were combined with spatio-temporally explicit maps of air temperature, snow density and snow depth to increase our mechanistic understanding of climate change effects in Svalbard reindeer. I followed 35 individual female reindeer, which resulted in 96 individual reindeer years through 7 winter seasons between 2009 and 2016. The aim was to investigate the impact of these weather conditions on movement behaviour and April body mass, which constitutes the main driver of the population dynamics.

The main findings demonstrated that April body mass decreases with increasing amount of snow on reindeer GPS-track in the preceding October, after accounting for weather conditions during the rest of the winter. The predicted mass difference was about 7 kg between the lowest and highest recorded amount of October snow. In this case, the results would strongly emphasize the importance of autumn conditions on Svalbard reindeer population dynamics. Furthermore, the amount of October snow outperformed the temperature estimates as predictors, which indicates that the previously reported positive effect of warm Octobers on April body mass likely is caused by a shorter winter season. In contrast to the prediction and previously reported negative effects of rain-on-snow, both snow density on the reindeer GPS-track and the annual variation in rain-on-snow during winter had no significant negative effect on April body mass. Moreover, snow depth outperformed both snow density and rain-on-snow as predictors, which is emphasizing the importance of snow depth as a hitherto unexplored mechanism behind variation in April body mass in Svalbard reindeer. In addition, I explored behavioral responses, which demonstrated increased movement of the reindeer in warm Octobers with less snow. In winter, increasing snow density appeared as probable causal explanation for increased movement and surprisingly, reduced time spent on ridges. Overall, this study provides important contributions towards increasing the mechanistic understanding of the environmental factors driving the population dynamics in Svalbard reindeer in a rapidly warming Arctic.



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# 1. Introduction

Climate change has a well-known impact on ecosystems and animal populations world-wide (Scheffers et al. 2016), caused by a variety of mechanisms such as short-term draughts (Saatchi et al. 2013) and wildfires (Isaak et al. 2010). Although global warming involves profound consequences for tropical and temperate ecosystems, the warming effects are most pronounced in the Arctic (Snow, Water, Ice and Permafrost in the Arctic (AMAP) 2017), with considerable impacts on ecosystems and species living in these areas (Ims et al. 2013; Post et al. 2009). Here, the timing and nature of the seasons are expected to change, and a key aspect in these regions is that summers become longer (i.e. greater proportional lengthening of summer compared to more temperate regions) and winters become shorter (Cooper 2014; Ernakovich et al. 2014). Currently, we have poor mechanistic understanding of the consequences of these changes in seasonality for the animals inhabiting the Arctic regions (Cooper 2014).

Animals are adapted to a certain timing of seasonal change (Futuyma 2008; Roff 2002), and disruptions in this phenology might cause substantial impact on populations living in seasonal environments through changes in recruitment parameters (Durant et al. 2007). Increasingly earlier springs have received a lot of attention due to the potential for mismatch between breeding phenology and food abundance (Kerby & Post 2013; Post & Forchhammer 2008; Post 2013; Tveraa et al. 2013). Conversely, autumn is somewhat a neglected season, probably due to the complexity of autumn drivers on phenology and a more gradual transition compared to the more pronounced change between winter and spring (Gallinat et al. 2015). Nonetheless, a change in timing of autumn may hold significant implications for the influence of climatic changes on ecosystems in the Arctic (Olsson et al. 2003).

Given warmer summers and the associated increase in available forage (van der Wal & Stien 2014), a lengthening of the growing season due to warmer autumns (Garonna et al. 2014) may be beneficial for temperate and Arctic herbivores because of a continued productivity and/or delays in senescence and continued forage availability in the absence of snow (Albon et al. 2017; Forchhammer et al. 2008; Hurley et al. 2014). On the other hand, warmer and more humid periods in an otherwise cold winter may lead to increased icing causing severe negative consequences for both animals (Forchhammer et al. 2002; Hansen et al. 2013; Kausrud et al. 2008; Stien et al. 2012) and plants (Milner et al. 2016). Thus, climate change comes as a suite of factors affecting both the summer, autumn and winter conditions, which hamper our

mechanistic understanding of population dynamics of herbivores living in such strongly seasonal environments (see Krebs & Berteaux 2006).

On Svalbard, the endemic Svalbard reindeer (*Rangifer tarandus platyrhynchus*) is the only large herbivore present. The population is limited by bottom-up processes (Solberg et al. 2001) in a predator-free environment (but see Derocher et al. 2000), likely operating through the food base in winter (Albon et al. 2017). The reindeer gain mass during summer and build up extensive fat stores for use during the food-limited and unpredictable winter (Reimers et al. 1982). Furthermore, they are considered a good indicator of environmental change due to their sensitivity to changes in environmental conditions (Conservation of Arctic Flora and Fauna (CAFF) 2010). Body mass responds continuously to changes in environmental conditions through the effects on food intake rates and energy expenditures (Bårdsen & Tveraa 2012) and are considered a good indicator of body condition, which in turn affects survival and recruitment parameters in ungulates (Parker et al. 2009). Consequently, body mass is considered a good variable for investigating the integrative effects of seasonally varying environmental drivers (Taillon et al. 2011).

Warmer summers have a positive impact on the autumn body mass (Albon et al. 2017) and population growth of Svalbard reindeer (Hansen et al. 2013; Aanes et al. 2002), due to an increase in primary production (van der Wal & Stien 2014). On the other hand, one consequence of warmer winters is an increase in rain-on-snow events (Putkonen & Roe 2003; Rennert et al. 2009), a proxy for the extent of ground ice formation and food availability (Albon et al. 2017; Gilg et al. 2009; Ims & Fuglei 2005). Annual variation in late winter body mass, other fitness traits and population growth have been explained by the amount of rain-on-snow in winter (Albon et al. 2017; Hansen et al. 2011; Kohler & Aanes 2004; Stien et al. 2012). Additionally, a positive effect of warm Octobers on April body mass has recently been demonstrated (Albon et al. 2017). As autumns are becoming increasingly warmer in Svalbard (Førland et al. 2011) the mechanism of this factor may be either a positive “summer effect” resulting in more available forage throughout the autumn and/or a positive effect of a shorter period of winter snow cover.

In general, landscapes are heterogeneous and animals may respond to negative events by moving to areas with more favorable conditions (Figuerola 2007; Lea et al. 2009; Loe et al. 2016; Stien et al. 2010). Obtaining spatial data through animal-borne global positioning systems

(GPS) from individuals in a population has therefore been considered a promising tool to enhance our mechanistic understanding of climate effects on animal populations (Morales et al. 2010; Tomkiewicz et al. 2010). However, linking habitat use to fitness consequences in heterogeneous seasonal landscapes has proven surprisingly challenging (Galliard et al. 2010) due to the extensive space use of animals and the seasonally varying environmental drivers (i.e. later winter onset, earlier springs) affecting various aspects of fitness and spatial ecology (Garshelis 2000). Thus, a common obstacle is the lack of temporally explicit geographic maps for the main environmental factors affecting the population (Garshelis 2000).

In Svalbard, there is large annual and spatial variation in environmental conditions. Although most winters have few and insignificant rain-on-snow events, some years are characterized by mild spells with heavy rainfall with large geographical variation in the spatial extent of icing (Loe et al. 2016). Similarly, snow conditions are highly variable in space because of wind distribution and topography (Loe et al. 2016), and is known to be a considerable behavioral constraint for ungulates through the effect on food availability (Skogland 1984), and energy expenditures (Fancy & White 1987; Fancy & White 1985; Parker et al. 1984). Moreover, Svalbard reindeer is known to be behaviorally responsive to changes in environmental conditions affecting food availability (Hansen & Aanes 2012; Loe et al. 2016; Stien et al. 2010), and the main behavioral driver behind movement decisions is likely related to search for forage (Loe et al. 2016). In sum, this provides an ideal system to test if spatial animal data increase our mechanistic understanding of how altered seasonality affect fitness.

The aim of my thesis is to combine GPS-data of marked adult female Svalbard reindeer with spatio-temporally explicit maps of snow conditions (Liston & Elder 2006a) and air temperature (Liston & Elder 2006b) to increase our mechanistic understanding of climate change effects on fitness and behaviour of Svalbard reindeer. I will focus on the effect on April body mass, which constitutes the key fitness trait, explaining nearly 90 % of the annual variation in population growth (Albon et al. 2017). My main hypothesis postulates that spatio-temporal variation in key environmental traits (i.e. air temperature, snow density and snow depth) on reindeer GPS-tracks will explain more of the variation in April body mass than the annual variation in the metrological metrics of October degree-days and rain-on-snow (cumulative precipitation on days when mean temperature > 0 degrees Celsius) found in Albon et al (2017).

First, I expect that the positive effect of October degree-days (Albon et al. 2017) is caused by a shorter winter season due to a delay in the onset of winter snow cover in autumn. I therefore predict that **(P1)** the amount of snow on the individual GPS-track in October will outperform October degree-days as a predictor for variation in April body mass (low April mass after snow rich Octobers). Second, I expect that the mechanism behind the negative effect of rain-on-snow events in winter on April body mass (Albon et al. 2017) is through the formation of ground-fast ice and crusty ice-layers inside the snow-pack (Putkonen & Roe 2003; Rennert et al. 2009). Additionally, strong wind events may create hard/icy layers in the snow pack (Benson & Sturm 1993). I therefore predict that **(P2)** the snow density on the individual GPS-track from November to March will outperform the annual variation in the meteorological metrics of rain-on-snow as a predictor for April mass (low April body mass in winters with high snow density). Thirdly, I will for first time investigate the impact of snow depth during winter on April body mass in Svalbard reindeer. I expect the amount of snow experienced by the reindeer to be an index reflecting the severity of the winter conditions. Consequently, I predict that **(P3)** the April body mass will decrease with increasing snow depth on reindeer GPS-track during winter (November to March).

In addition, I will explore effects of snow and temperature conditions on movement behavior (total distance moved) and habitat use (time spent on ridge vegetation) in autumn (October) and winter (November to March) by using GPS-data and a static vegetation map made from satellite photos (Johansen et al. 2009).

## **2. Materials and methods**

### **2.1 Study area**

The study area is located at Nordenskiöld Land in Svalbard (78° N, 15° E), ca. 20-40 km from Longyearbyen (Fig. 1). Three large valleys, Colesdalen, Reindalen and Semmeldalen with adjoining side valleys, constitute the study area, about 150 km<sup>2</sup> in total. The distance between Colesdalen in north-west and Reindalen in south-east is approximately 20 km. The larger valleys are interconnected by smaller valleys, enclosed by higher elevation passes and steep mountains with peaks up to 1000 m above sea level (m.a.s.l.).

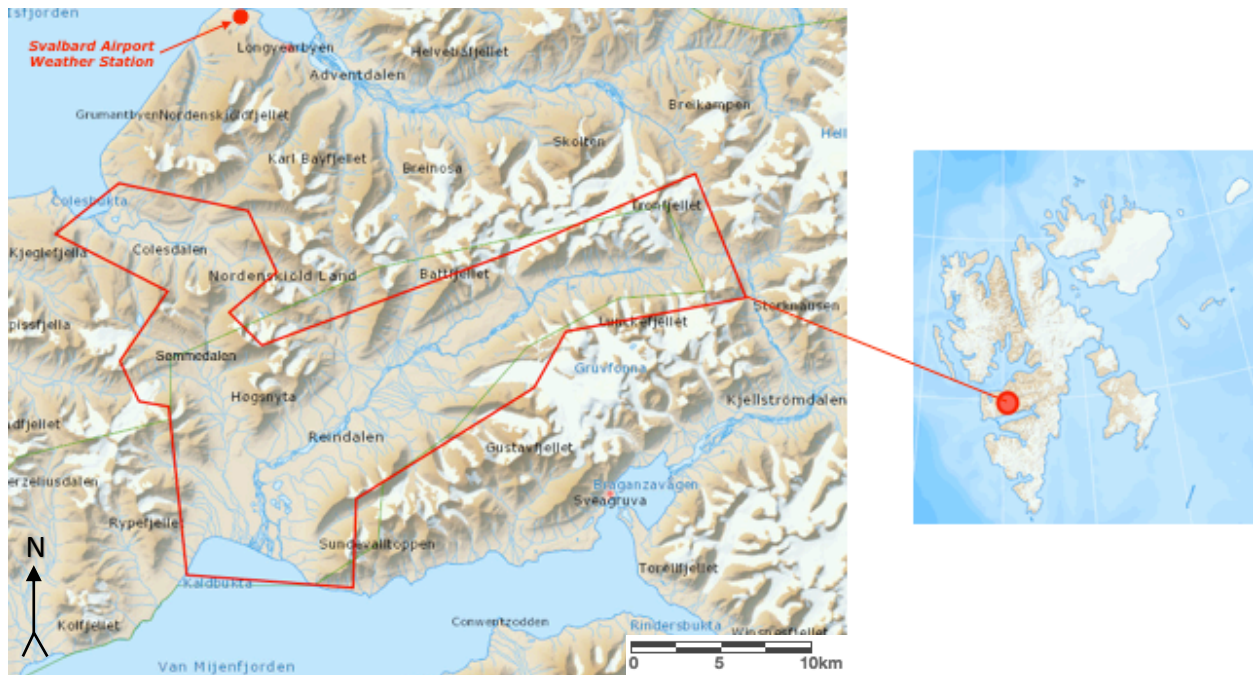


Fig. 1. The study area is located at Nordenskiöld Land at Svalbard, south of Longyearbyen. Reindalen, Colesdalen and Semmeldalen with adjoining side valleys constitute the main parts of the study area. Svalbard airport weather station is located north-west of Longyearbyen, approximately 20-30 km north of the study area. The map is from: <http://www.toposvalbard.npolar.no> (Norwegian Polar Institute).

The vegetation in the area is characterized by low field-layer (5-10 cm) (Jónsdóttir 2005), dominated by graminoids, mosses and herbs (Elvebakk 1994). The vegetation covers the ground up to about 100 m.a.s.l. and becomes increasingly patchy further up to 250 m.a.s.l., where the vegetation becomes sparse (van der Wal & Stien 2014). During winter, from early November to early in February, the polar night results in complete darkness (26.10 – 16.02), in stark contrast to the midnight sun between late April (19.04) and late August (20.08). The plant growing season typically lasts from the start of June to the start of August, but there is large variation between years due to large annual variation in environmental conditions affecting plant growth (Karlsen 2013). The period of senescence usually starts in early August (Parmentier et al. 2011), and plant growth has stopped and little photosynthesis is carried out by the start of September (Parmentier et al. 2011). Snow typically covers the ground in October (Albon et al. 2017; van der Wal & Stien 2014), but with large annual variations (Tyler et al. 2008). The tundra is almost totally covered by snow during November to March/April (Albon et al. 2017), except from some wind-blown ridges that remain partially snow-free (Hansen et al. 2010). While the precipitation during most winters comes as snow, warm spells may occur in some winters, with heavy rainfall resulting in extensive icing of the tundra vegetation when the rain refreezes (Hansen et al. 2014; Putkonen & Roe 2003).

## 2.2 Study species

There are large fluctuations in the Svalbard reindeer population dynamic between years due to density dependent food-limitation in winter and high variation in climatic factors affecting mortality and recruitment rates during winter (Solberg et al. 2001; Aanes et al. 2003). The study area sustains a higher density of reindeer compared to other areas at Svalbard (Van der Wal & Brooker 2004) and the population size has increased by nearly thousand individuals (about 800 to 1800) the last two decades (Albon et al. 2017). The population size increased steadily during the period of this study, with no large population crashes (Albon et al. 2017).

Although the amount of fat obtained during the growing season is crucial for winter survival (Reimers et al. 1982), and reproduction the subsequent spring (Barboza & Parker 2008), foraging through the autumn and winter is critical too (Albon et al. 2017). Nonetheless, nearly all of the resources allocated to reproduction in reindeer come from maternal body stores gained through summer (Parker et al. 2009) suggesting reindeer as highly «capital» breeders (Stephens et al. 2009). Currently, the Svalbard reindeer in the study area seem to reset their reproductive potential during summer, independently of the previous winter conditions (Albon et al. 2017). However, despite that the warmer summers have a positive effect on the autumn body mass (October), no “carry-over” effect on the subsequent April body mass have been documented (Albon et al. 2017). Moreover, the positive effect of warmer Octobers on April body mass imply that the body mass in the end of winter likely is affected by conditions in autumn/winter.

The Svalbard reindeer is adapted to minimize energy expenditure in winter. They are well insulated and do not increase metabolic rates for heat production within the thermal neutral zone ranging from about 10 °C to -40 °C (Nilssen et al. 1984). In winter, they enters a lethargic state where food intake rates decreases by more than 50 % of the corresponding summer levels (Nilssen et al. 1984). The metabolic rates for standing at rest are higher than for lying at rest (Cuyler & Øritsland 1993), and reduced activity levels and movement in winter are considered energy saving mechanisms for winter survival (Cuyler & Øritsland 1993). Furthermore, they are considered sedentary and to have small seasonal home ranges (Tyler & Øritsland 1989) (i.e. the reindeer do not show nomadic behavior or undertake longer regularly migration distances in winter, but see; Loe et al. 2016; Stien et al. 2010). Moreover, they are non-territorial and live alone or together in small groups consisting of 2-5 individuals (Loe et al. 2006; Tyler 1987) in

an almost predator-free environment (only a few kills by polar bears (*Ursus Maritimus*) are documented; Derocher et al. 2000). Movement decisions are consequently taken at the individual level and are also unlikely to be influenced by social barriers or anti-predation behavior. The traffic from snowmobiles is also expected to be of minor importance on movement, as the reindeer seem to habituate to the potential disturbance relatively fast (Hansen & Aanes 2015; Tyler 1991). Thus, the main behavioral driver behind Svalbard reindeer movement behaviour is primarily related to search for forage, besides from calving in June (Skogland 1989; Tyler 1987) and rut in October (Skogland 1989).

During summer, the Svalbard reindeer utilize plant species (e.g. various grasses, sedges and forbs) with high quality and high biomass, often growing in wet to mesic sites at lower altitudes close to the valley (Bjørkvoll et al. 2009; Punsvik et al. 1980; Van der Wal et al. 2000). In autumn/early winter, wet land species are less frequently grazed, while plant species growing in mesic sites still are prevalent in the diet (Bjørkvoll 2009). While these pastures are grazed during summer (and partly during early winter), snow cover in late winter tend to make them less accessible due to deep or hard snow. Consequently, during winter the reindeer tend to forage on ridge and sub ridge vegetation with less snow cover (Hansen et al. 2010).

### 2.3 Reindeer data

The individuals (n=35) included in this study are a subsample of a larger marked population (ca 800 individuals) of female Svalbard reindeer at Nordenskiöld land. All of the 35 individuals included were of known age (birthday June 1<sup>st</sup> by definition) ranging from 2-12 yr. with an average of 6.3 yr. They were captured and weighted to the nearest 0.5 kg in April each year between 2009 and 2016 (Omsjoe et al. 2009). The 35 adult females were equipped with store-on-board GPS-collars (Vectronic Aerospace, Berlin, Germany) recording bihourly positions and GPS-data were downloaded annually during recapture events in April and/or February. All GPS-locations obtained during capture in April were removed from the analysis, while locations from capture days in February were included to avoid problems when calculating cumulative snow measures during winter. Not all individuals were captured every year, resulting in periods of missing GPS-data (if the battery run out before recapture) and missing April weights. I only included individual-years of known April body mass and full winter trajectories running from October 1<sup>st</sup> in year t-1 to 31 March in year t. Together, they

contributed with 96 individual reindeer years through seven winters (09/10 – 15/16) between October 2009 and April 2016.

Using bihourly positions, I calculated the mean time difference between positions within individuals to check for how often a GPS-animal lost a position (a value of 2.0 means no loss). All values were well below 2.5, implying that GPS-success rate was well above 80 %. GPS-failures were consequently not accounted for when calculating the summed values of environmental data (below) on the reindeer GPS-track (below). Movement rate measured as bihourly step length in meters was extracted with the `ltraj` function found in the R-package «`adehabitatLT`» (R Core Team 2017). The total distance moved by the reindeer in October was calculated to investigate the impact of weather conditions in October on activity levels. Similarly, the total movement distance between November and March were calculated to investigate the impact of different weather conditions on movement in winter. To obtain environmental data at each of the reindeer GPS-locations, I combined the GPS-data with the environmental data (below) from raster maps using the `extract` function in the R package “`raster`” (R Core Team 2017). This was done by merging the data with dates that were both represented in the raster maps and the reindeer data, running from October 2009 to April 2016.

## 2.4 Environmental data

The environmental variables included to test for effects on April adult female body mass and movement behaviour were October degree-days, air temperature in October, snow depth in October, snow depth during November to March, snow density during November to March and rain-on-snow between November and march (Table 1).



Table 1: Summary of the weather variables included to test for effects on April body mass, their units, descriptions, location and biological meaning.

Predictor variables	Units	Description	Location	Biological meaning
October degree-days	°C	Sum of mean daily degrees above 0	Modelled estimates at the individual GPS-track	An indicator of the end of summer/start of winter. The duration of the autumn season (Albon et al. 2017).
Air temperature (October)	°C	Sum of mean daily air temperature	Modelled estimates at the individual GPS-track	An indicator of the end of summer/start of winter. The duration of the autumn season.
Snow depth (October)	m	Summed vertical amount of snow	Modelled estimates at the individual GPS-track	An indicator of the end of summer/start of winter. The duration of the autumn season. Affecting food availability and foraging conditions in autumn.
Snow depth (November-March)	m	Summed vertical amount of snow	Modelled estimates at the individual GPS-track	An indicator of the severity of the winter. Affecting food availability and energy expenditures.
Snow density (November-March)	kg/m <sup>3</sup>	Summed mass per unit volume of snow between November and March	Modelled estimates at the individual GPS-track	An indicator of the formation of ground ice and crusty ice layers inside the snow pack, that affect food availability in winter.
Rain-on-snow (November-March)	mm	The amount of rain falling at air temperatures higher than zero	Values measured at Svalbard airport (Longyearbyen) weather station	A proxy for the extent of ground ice formation and food availability in winter (Albon et al. 2017).

### Temperature data

The October degree-days (Table 1) were chosen because of earlier findings of positive effect of October degree-days on April body mass (Albon et al 2017). In addition, I included an air temperature variable (Table 1) that also took into account the degrees below zero (thus including both negative and positive degrees in October). This was done to test for whether including degrees below zero in October affected April mass and behavior to a greater degree than including the positive temperatures only (as is done when calculating October degree days). The October degree-days and summed mean daily air temperature in October were first calculated based on temperature values recorded 2 meters above ground level from Svalbard airport (Longyearbyen) weather station (located 20-30 km north of the study area. Fig. 1), and downloaded from the Norwegian Meteorological Institute (<http://www.eklima.met.no>).

Moreover, a spatio-temporal raster map containing modelled estimates of daily air temperature within grid increments of 100 x 100 m simulated by the metrological model MicroMet (Liston & Elder 2006b), were coupled with the reindeer GPS-data to obtain temperature measures at the individual level in time and space. I calculated the October degree-days and sum of mean daily air temperature on reindeer GPS-locations in October (Table 1) to compare them with the temperature measures from Svalbard airport weather station. Weather data from the weather stations may not be representative of the actual conditions in the landscape due to large spatial variation in weather. Combining weather data from different weather stations surrounding the study area (Longyearbyen airport and Svea) has been found to explain more of the variation in populations dynamic than using data from separate weather stations only (Solberg et al. 2001; Aanes et al. 2003). In accordance with this, the modelled temperature estimates from the individual GPS-tracks were better predictors of April body mass than the temperature measures from the Svalbard airport weather station (Table S1), and was consequently used in the analyses. Using temperature from the individual GPS-locations also made it more comparable to the snow estimates, which also are based on modelled estimates from the individual GPS-locations (below).

#### Rain-on-snow data

The rain-on-snow measure (Table 1) was chosen because of the negative effect of rain-on-snow events on April body mass found in Albon et al. (2017). Temperature and precipitation data from Longyearbyen airport weather station were used to calculate the amount of rain-on-snow between November and March and these values were downloaded from the Norwegian Meteorological Institute (<http://www.eklima.met.no>). The rain-on-snow index is found to be positively correlated with total winter precipitation (Aanes et al. 2000).

#### Snow data

Spatio-temporal raster maps containing modelled estimates of snow depth and snow density were obtained from a spatially distributed snow-evolution modelling system that includes meteorological forcing conditions, surface energy exchanges, snow depth and water equivalent evolution, in addition to snow redistribution by wind (Liston & Elder 2006a). The SnowModel (Liston & Elder 2006a) simulated snow depth and snow density values within grid increments of 100 x 100 meters on a daily basis. The summed snow depth on individual GPS-locations in October were calculated to make it comparable to the previously reported positive effect of

October degree-days found in Albon et al. (2017). Similarly, the summed snow depth and snow density on individual GPS-locations from November to March were calculated to make it comparable with the time period for the rain-on-snow measure used in Albon et al (2017).

## 2.5 Vegetation variables

The vegetation data used to investigate the proportion of reindeer on ridge vegetation in response to snow and temperature conditions were based on a vegetation map from 2009 obtained from the Norwegian Institute for Nature Research (Johansen et al. 2009), described in (Johansen et al. 2012). The map was made from Landsat satellite photos, with a resolution of 30 x 30 meters (Johansen et al. 2009). I extracted the vegetation classes that contained the ridge vegetation (Table 2), because ridge vegetation constitute the main winter feeding habitat of Svalbard reindeer (Hansen et al. 2010) and is more likely to be snow-free when other vegetation types are covered by snow. Furthermore, I calculated the proportion of reindeer positions on ridges by dividing the number of reindeer GPS-locations on ridge vegetation by the number of GPS-locations in other vegetation classes. This was done to test if the reindeer spent less time on ridges in years with warm Octobers with little snow, and to test if reindeer spent more time on ridges in winters with much snow and ice. I chose to focus on annual rather than individual variation in use of ridge vegetation. The rationale for this is that variation in snow-cover along the ridge-subridge is expected to be shared by large areas and that individuals are behaviorally responsive to environmental conditions (Loe et al 2016).

Table 2. Vegetation classes included as the ridge vegetation from the classification system described in Johansen et al (2009). Vegetation class refers to their numbering in Johansen et al (2009).

Vegetation class	Description
21	Ridge with <i>Dryas octopetala</i> and <i>Carex rupestris</i> as well as <i>Cassiope tetragona</i> on heath.
22	Open heath with <i>Dryas octopetala</i> and <i>Carex rupestris</i> , as well as <i>Saxifraga oppositifolia</i> .
25	Dry ridge, open vegetation with <i>Potentilla pulchella</i> , <i>Poa abbreviate</i> and <i>Poa hartzii</i> .

## 2.6 Data analyses

There was a strong correlation between capture date and some of the environmental conditions in the study period (2009-2016) that could have resulted in a confounded effect of environment and late date of capture (e.g. captured late in icy winters). To mitigate this, the April body mass

was adjusted by regressing the effect of capture date on body mass from the entire data set (1995-2017), resulting in an estimated mass loss of 254 g per day. Adjusted mass was centered at mean capture date (mass at later capture dates were added and mass at earlier captures were reduced by 254 g per day). Moreover, the individuals were divided into two different age groups (1-2 yr. and 3-12 yr.) to account for differences in body mass between age classes.

Linear regression models (Seber & Lee 2012) were used to test for the effect of weather variables on capture-date adjusted April body mass (response variable). Age class was included as a covariate in all models to account for body mass differences in young and adult individuals. To compare which environmental variable explained most variation in mass, only one environmental variable at a time was added to the model and the Akaike's information criterion (AIC) value computed (Burnham & Anderson 2003). Initially I ran separate models for autumn effect and mid-winter effects on body mass. Candidate autumn predictor variables were October degree-days, summed air temperature and summed snow depth in October. Candidate winter variables were rain-on-snow (log transformed), summed snow depth and summed snow density from November to March. Linear regression models were also used to test for the effect of weather variables on total distance moved in October and in winter (i.e. Temperature and snow depth in October and snow depth and snow density during winter). All continuous variables were scaled (mean zero and variance 1) to facilitate direct comparison of effect sizes. I also computed the correlation values between time spent on ridges and weather variables (i.e. temperature and snow depth in October, and snow density and snow depth during winter) to test for relationships between use of ridge vegetation and weather conditions.

Model comparisons were made by comparing AIC values (Burnham & Anderson 2003). Clear support for a single best model occurs if the second best model had a  $\Delta$ AIC of 2 or higher. Some environmental variables were correlated and I therefore provide the correlation coefficient between all variable pairs (Fig. s2). In a final step, predictor variables from the best autumn model (snow depth and age class) was included in the best winter model (snow depth and age class) to investigate if there was a residual effect of autumn after accounting for winter conditions.

All the statistical analysis carried out in this study were done using R software version 3.4.2 (R Core Team 2017).

### 3. Results

#### 3.1 Correlation between weather variables

The daily snow depth on the reindeer GPS-track in October was negatively correlated with both October degree-days ( $r=-0.24, p=0.02$ ) and summed mean air temperature in October ( $r=-0.44, p<0.001$ ) on the reindeer GPS-track, implying that there is less snow present in warm Octobers (see Fig. s2 for correlation values between all of the weather variables). Moreover, the summed snow depth in October were positively correlated with the summed snow depth on reindeer GPS-locations from November to March ( $r=0.44, p<0.001$ ), implying that early snow predisposes for a snow rich winter. Furthermore, the snow depth and snow density estimates between November and March were positively correlated ( $r=0.52, p<0.001$ ), and there was a positive correlation between the snow depth estimate and the rain-on-snow measure ( $r=0.49, p<0.001$ ) during the same period, indicating that much of the precipitation in years with high snow comes as rain. Additionally, there was a strong correlation between the snow density estimate and rain-on-snow measure ( $r=0.82, p<0.001$ ).

#### 3.2 The effect of autumn conditions on April body mass

April body mass decreased significantly with increasing sum of snow depth on GPS-locations in October ( $\beta= -1.49 \pm 0.47, t=-3.14, p=0.00$ ) after accounting for age class ( $\beta= 7.31 \pm 1.95, t=3.76, p=0.00$ ), with a predicted mass difference of about 7 kg between the lowest and highest recorded amount of October snow (Fig. 1a). The summed snow depth on GPS-locations in October explained more of the variation in April mass than both measures of October temperature (Table 2), supporting the prediction that the mechanism of the previously reported October degree day effect is a negative effect of early snow fall. Although explaining less variation, the summed mean daily air temperatures on GPS-locations in October had a significant positive impact of April body mass ( $\beta= -1.09 \pm 0.48, t=2.27, p=0.03$ ; Fig. 1b). Surprisingly no significant effect of October degree-days on April mass ( $\beta= -0.35 \pm 0.49, t=-0.72, p=0.47$ ; Fig. 1c) was observed, contrary to the effect seen for a larger data set including more years and individuals (Albon et al 2017).

Table 2. Comparison of three linear models explaining variation in capture-date adjusted April body mass in adult female Svalbard reindeer. Explanatory weather variables in October included the summed snow depth on reindeer GPS-track, the summed mean daily air temperature on the reindeer GPS-track and the October degree-days on the reindeer GPS-track. Model comparisons were made using relative differences in AIC ( $\Delta AIC$ ) compared with the model with the lowest AIC.

Autumn models explaining variation in April body mass	$R^2$	AIC	$\Delta AIC$
Summed snow depth (October) + age class [2,20]	0.23	569.39	0.00
Summed mean daily air temperature (October) + age class [2,20]	0.19	573.89	4.50
October degree-days + age class [2,20]	0.15	578.54	9.15

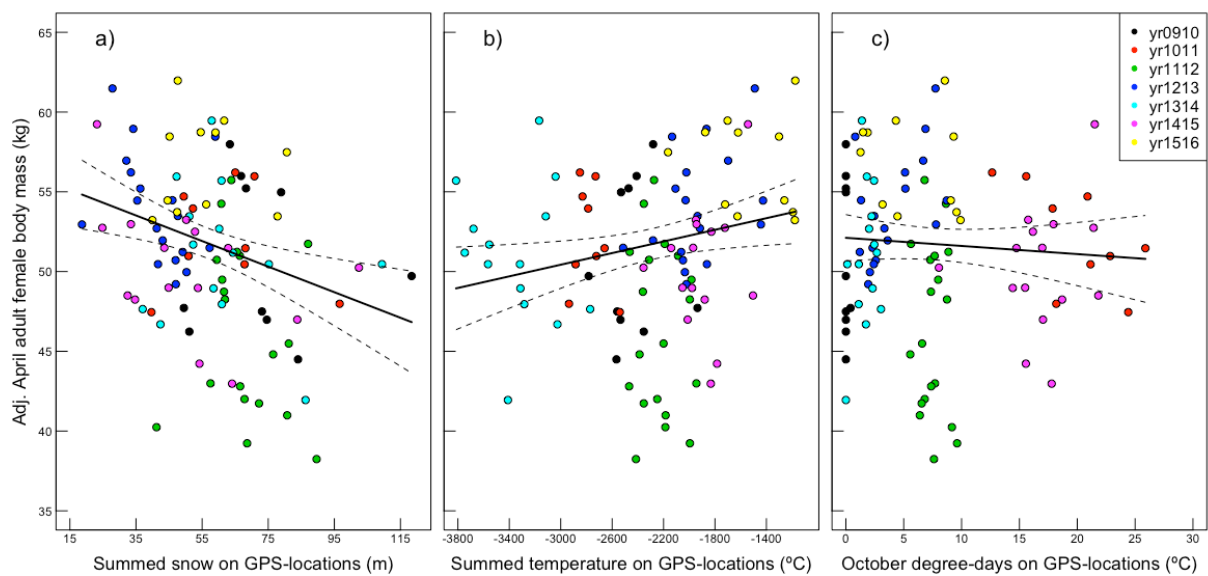


Fig. 2. Capture-date adjusted April body mass of adult female Svalbard reindeer as a function of a) the summed snow depth on reindeer GPS-locations in October, b) the summed mean daily air temperature on reindeer GPS-locations in October and c) October degree-days on reindeer GPS-locations for each individual winter-year between 2009/2010 and 2015/2016. The solid line represent the predicted regression line and dashed lines represent the associated  $\pm 95$  confidence intervals. Effects are adjusted for variation in age class.

### 3.3 The effect of autumn conditions on reindeer behaviour

In a given year the median use of ridge vegetation ranged from less than 10% to about 35% of locations. At the annual level there was a negative non-significant correlation between use of ridge vegetation and temperature sum in October ( $r = -0.65$ ,  $p = 0.12$ ; Fig 3a), with a tendency for a threshold effect for the two warmest years were the use of ridges was lower. Conversely, there was a positive non-significant correlation between use of ridge vegetation and snow in

October ( $r=0.41$ ,  $p=0.36$ ; Fig 3b). The proportion of time spent on ridges was very low, however only for the two warmest years with nearly no snow in October (Fig. 3), implying that many individuals do not start utilizing ridges until the landscape is snow covered.

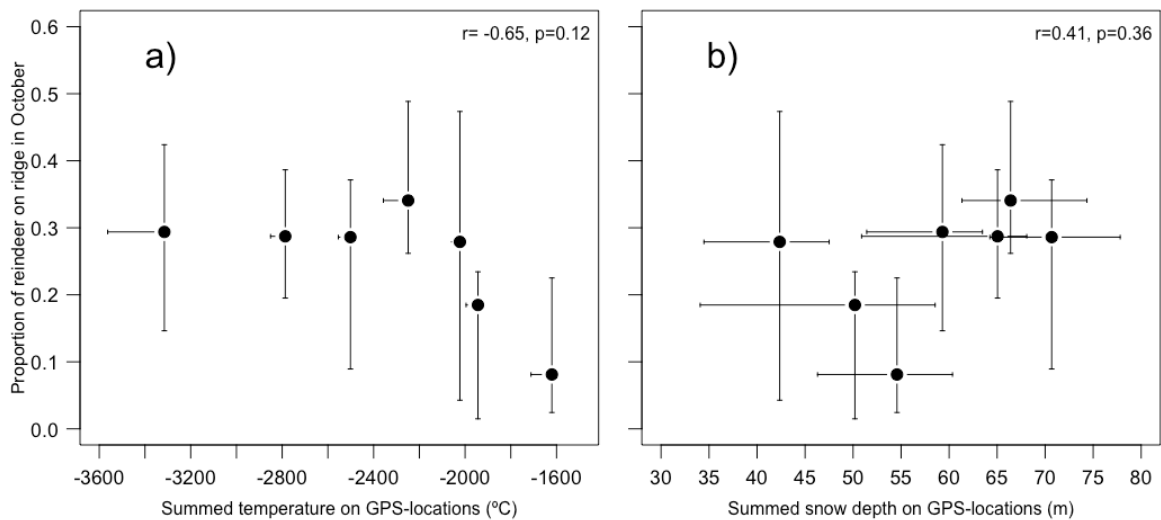


Fig. 3. Proportion of reindeer GPS-locations on ridge vegetation in October each year from 2009 to 2015 as a function of a) summed mean daily air temperature on GPS-locations in October and b) summed snow depth on GPS-locations in October. The solid points represent median values each year. The vertical (proportion of reindeer on ridge) and horizontal lines (temperature/snow depth) represent the upper and lower 75 percentile of the median values for each of the 7 years. Correlation values and the associated p-values are given in the upper right corner.

The movement distance in October increased significantly with increasing air temperature on GPS-locations ( $\beta = 4.24 \pm 0.95$ ,  $p < 0.001$ ,  $R^2 = 0.17$ ; Fig. 4a), with a predicted difference of about 20 km (645 meters per day) between the lowest and highest recorded sum of air temperature. In contrast to the increased movement distance of individuals in warm Octobers, there was a non-significant tendency towards less movement in October with increasing snow depth on individual GPS-locations ( $\beta = -1.84 \pm 1.03$ ,  $p = 0.08$ ,  $R^2 = 0.03$ ; Fig. 4b). However, the model explained very little of the variation in movement ( $R^2 = 0.03$ ).

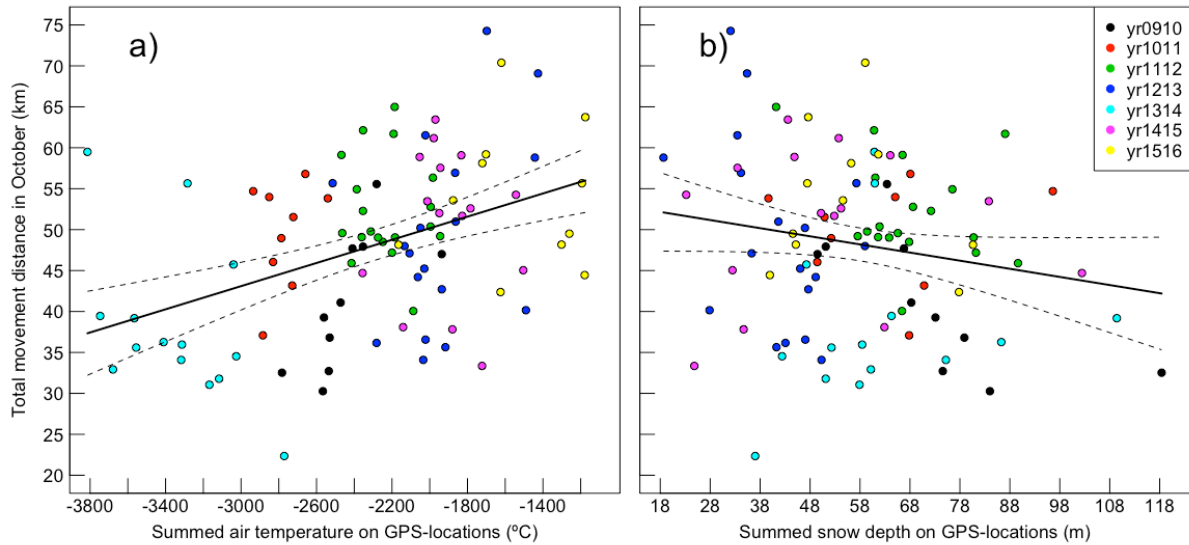


Fig. 4. Total movement distance (km) in October as a function of a) summed air temperature on reindeer GPS-locations in October and b) summed snow depth on reindeer GPS-locations in October, for each individual winter-year between 2009/2010 and 2015/2016. The solid line represent the predicted regression line and the dashed lines represent the associated  $\pm 95$  confidence intervals.

### 3.4 The effect of winter conditions on April body mass

April body mass decreased significantly with increasing sum of snow on GPS-locations between November and March ( $\beta = -1.38 \pm 0.47$ ,  $t = -2.9$ ,  $p = 0.00$ ) after accounting for age class ( $\beta = 8.07 \pm 1.94$ ,  $t = 4.15$ ,  $p = 0.00$ ), with a predicted mass difference of about 7 kg between the lowest and highest recorded amount of snow through winter (Fig. 5a). The summed snow density on the individual GPS-track had no significant effect on April mass ( $\beta = -0.53 \pm 0.51$ ,  $t = -1.04$ ,  $p = 0.30$ ; Fig 5b) and there was only a non-significant tendency towards a negative effect of log transformed rain-on-snow on April mass ( $\beta = -0.68 \pm 0.41$ ,  $t = -1.64$ ,  $p = 0.10$ ). Again, the non-significant effect size of rain-on-snow is in stark contrast to the strong negative effect seen for a larger data set including years back to 1995 (Albon et al 2017).



Table 3. Comparison of linear models explaining variation in capture-date adjusted April body mass in adult female Svalbard reindeer. Explanatory weather variables (between November and March) included the sum of estimated snow depth and snow density on reindeer GPS-track, in addition to the annual variation in the meteorological measure of amount of rain-on-snow from Svalbard airport weather station. Model comparisons were made using relative differences in AIC ( $\Delta AIC$ ) compared with the model with the lowest AIC.

Winter models explaining variation in April body mass	$R^2$	AIC	$\Delta AIC$
Snow depth (Nov-Mar) + age class [2,20]	0.22	570.63	0.00
Rain-on-snow (Nov-Mar) + age class [2,20]	0.17	576.32	5.69
Snow density (Nov-Mar) + age class [2,20]	0.16	577.95	7.32

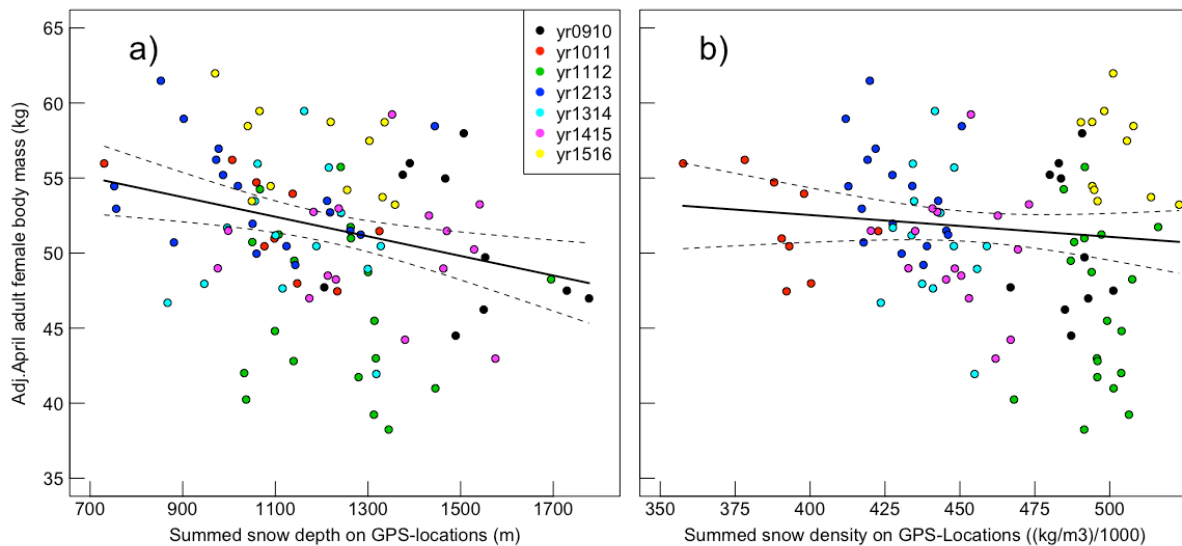


Fig. 5. Capture-date adjusted April body mass of adult female Svalbard reindeer as a function of a) the summed snow depth on GPS-locations from November and March and b) the summed snow density on GPS-locations from November to March each individual winter-year between 2009/2010 and 2015/2016. The solid line represent the predicted regression line and dashed lines represent the associated  $\pm 95$  confidence intervals. Effects are adjusted for variation in age class.

### 3.5 The effect of winter conditions on reindeer behaviour

There were some annual variation in individuals' use of ridge vegetation in winter (November to March). The median individual ranged from less than 10% to about 40% of locations in ridge vegetation. At the annual level there was no significant correlation between use of ridge vegetation and summed snow depth in winter ( $r = -0.26$ ,  $p = 0.57$ ; Fig 6a). In contrast, there was a strong negative significant correlation between use of ridge vegetation and summed snow

density on GPS-locations ( $r=-0.85, p=0.02$ ; Fig 6b), opposite to what expected if icing leads to reindeer aggregating on ridges.

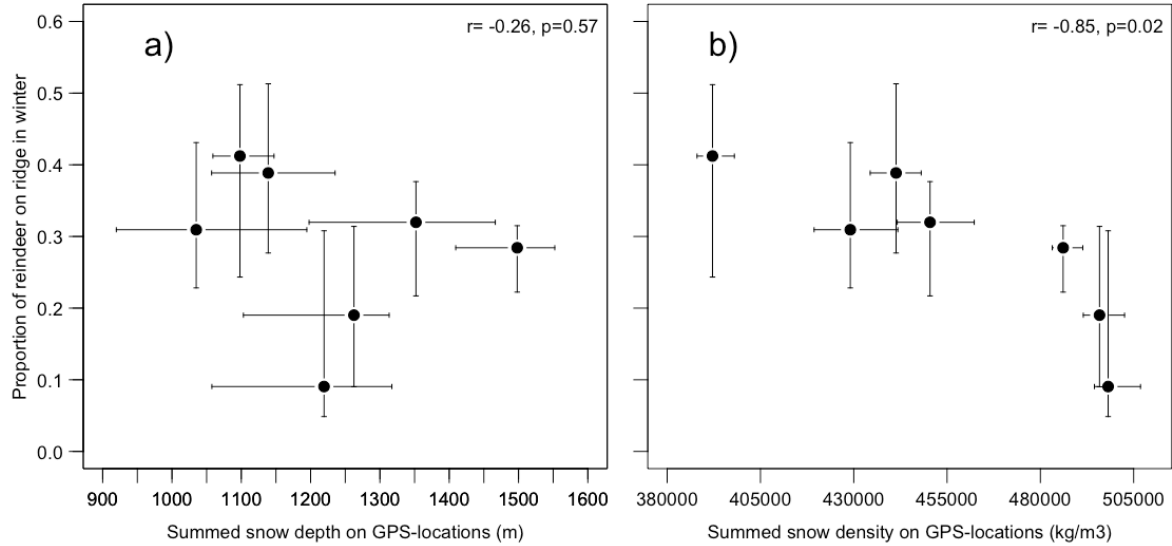


Fig. 6. Proportion of reindeer GPS-locations on ridge vegetation from November to March each year from 2009 to 2015 as a function of a) summed snow depth on GPS-locations and b) summed snow density on GPS-locations in the same time period. The solid points represent median values each year. The vertical (proportion of reindeer on ridge) and horizontal lines (snow depth/snow density) represent the upper and lower 75 percentile of the median values for each of the 7 years. Correlation values are given in the upper right corner.

Total movement distance in winter from November to March increased with increasing rain-on-snow ( $\beta= 25.34 \pm 3.93$ ,  $p<0.001$ ,  $R^2=0.31$ ). Similarly, increased snow density on reindeer GPS-locations also led to an increase in winter movement ( $\beta= 16.67 \pm 4.40$ ,  $p<0.001$ ,  $R^2=0.13$ ). The predicted difference in total movement between the lowest and highest summed snow density on GPS-locations were about 70 km (about 470 meter per day). In contrast, the snow depth had no significant impact on total distance moved in winter ( $\beta= 3.41 \pm 4.71$ ,  $p=0.47$ ,  $R^2=0.00$ ).

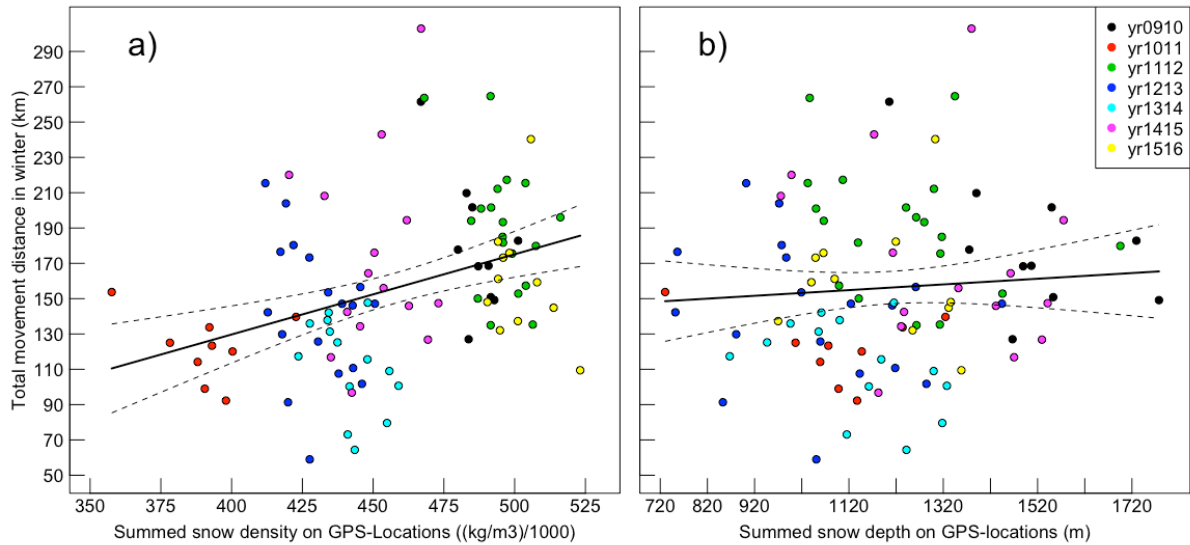


Fig. 7. Total movement distance (km) from November to March as a function of a) summed snow density on reindeer GPS-locations and b) summed snow depth on reindeer GPS-locations for each individual winter-year between 2009/2010 and 2015/2016. The solid line represent the predicted regression line and the dashed lines represent the associated  $\pm 95$  confidence intervals.

### 3.6 Comparing the autumn and winter effects

Despite that early snow predisposes for a snow rich winter ( $r=0.44$ ,  $p<0.001$ ), the effect of snow depth in October on capture-date adjusted April body mass was still significant after accounting for the effect of snow depth from November to March and age class (Table 4). Nevertheless, the effect of snow depth from November to March became insignificant after controlling for snow depth in October (Table 4). Furthermore, the model with only snow depth in October had a slightly lower AIC-value ( $\Delta AIC = -1.24$ ) than the model with only snow depth from November to March. Thus, although the  $\Delta AIC$  of less than 2, this indicates that the time for the onset of winter was more decisive for April mass than the conditions during the main winter during my study period.

Table 4. Linear regression model comparing autumn and winter effects on capture-date adjusted April body mass after accounting for age class. The variables are scaled (mean zero and variance 1) to facilitate direct comparison of effect sizes.

Comparing autumn and winter effects on April mass	<i>Estimate</i>	<i>S.E.</i>	<i>t</i>	<i>p</i>	<i>R</i> <sup>2</sup>
Snow depth (October) + Snow depth (Nov-Mar) + age class					0.25
Intercept	44.18	1.87	23.68	0.00	
Snow depth (October)	- 1.08	0.52	- 2.06	0.04	
Snow depth (November-March)	- 0.90	0.52	- 1.74	0.09	
Age class	7.51	1.93	3.90	0.00	

## 4. Discussion

My findings of how spatio-temporal weather data explained variation in April body mass (adjusted for capture date) increases our current comprehension of how climate-induced changes in the autumn may affect the population dynamics of a herbivore facing a rapidly warming Arctic. Here, I demonstrated that the previously reported positive effect of warmer autumns on April body mass (Albon et al. 2017) is most likely caused by a shorter winter season due to a delay in the onset of winter snow cover (**P1**). Furthermore, the absence of a significant negative effect of the snow density estimate (**P2**) and the rain-on-snow measure during winter (November to March) is in stark contrast to the previously reported negative effect of rain-on-snow on April body mass (Albon et al. 2017). Moreover, the negative effect of snow depth (**P3**) outperformed both snow density and rain-on-snow as predictors. Thus, these findings enhances the importance of snow depth as a hitherto unexplored mechanism behind variation in April body mass, which in turn affect the population dynamics of Svalbard reindeer (Albon et al. 2017).

### 4.1 The strong effect of autumn on April body mass and behaviour

Despite that the growing season is lengthening due to a delay in the timing of senescence as much as advances in spring “green-up” (Garonna et al. 2014), the impact of warmer autumns and the associated delayed onset of winter has received considerable less attention than the corresponding impact of warmer springs on phenology (Gallinat et al. 2015). In a recent study from a semi-arid environment in Idaho, the impact of foraging conditions in autumn on body mass of mule deer (*Odocoileus hemionus*) fawns was found to be much stronger than the foraging conditions during spring (Hurley et al. 2014). Moreover, in capital breeders (Stephens

et al. 2009) such as Svalbard reindeer (Albon et al. 2017), conditions long before spring are expected to be important for reproduction and calf survival (Veiberg et al. 2017). Consequently, it has been proposed that the window of time to investigate the match-mismatch framework (Durant et al. 2007) in Arctic ungulates is in late summer-autumn, and not at parturition in spring (Gustine et al. 2017). My findings of how weather conditions in October greatly affect behaviour (Fig 3 and Fig 4) and the subsequent April body mass (Fig 2) after accounting for the weather conditions during the rest of the winter (Table 4), strongly fortifies the importance of autumn conditions on Svalbard reindeer population dynamics.

#### 4.1.1 Warmer autumns: a prolonged period with snow-free grazing conditions?

Although a delay in the timing of senescence is likely to contribute to a prolonged growing season in more temperate areas (Garonna et al. 2014), this might not be the case for Arctic regions (Cooper et al. 2011). Here, the timing of senescence is mainly determined by the light conditions in August (Nilsen 1985), and the growing season is therefore improbable to change with warmer autumns and the associated delayed onset of winter snow cover (Cooper et al. 2011; Parmentier et al. 2011; Rumpf et al. 2014). In October, the plant growth have already stopped and withering processes have commenced (by the start of September; Parmentier et al. 2011). Thus, other factors affecting the foraging conditions, such as snow (Beumer et al. 2017), may be of importance for food availability in autumn/early winter. Here, the amount of snow on reindeer GPS-track outperformed both temperature estimates (Table 2) and strongly affected body mass the following April (Fig. 2a). This is indicating that the positive effect of warm Octobers is related to less snow (**P1**) resulting in a prolonged period with snow-free grazing conditions and consequently a shorter period with over-winter mass loss.

Noteworthy, the slightly negative effect size of October degree-days on April body mass reported here (Fig 2c) was not expected, as opposed to the positive effect reported in Albon et al. (2017). One explanation for this contradictive result might be the considerably smaller data set utilized in this study (including fewer years and individuals). However, the temperature sum in October (taking into account degrees below zero) resulted in a significant positive effect on April body mass (fig 2b). This effect indicates that including all temperatures probably reflect the snow conditions in a greater degree than including the positive temperatures only (as is done when calculating October degree days). This assumption is supported by the comparatively stronger negative correlation between snow depth and all air temperatures in October (Fig s2).

Hence, the positive effect of the temperature sum in October could possibly be explained through the presence of less snow.

Plant species utilized during summer are also present in the diet during early winter, in October (Bjørkvoll et al. 2009). Thus, more biomass during summer (van der Wal & Stien 2014) may increase the amount of forage available for the reindeers through an extended period in autumn. However, at some point during the transition from autumn to winter, the increasing snow cover will eventually lead to a reduction in diet quality or food intake rates, as plant species with lower quality or lower biomass (Hansen et al. 2010) are selected (Beumer et al. 2017; Bjørkvoll et al. 2009). Accordingly, my findings indicates that many individuals do not start utilizing ridges until the landscape is snow covered (Fig 3). Thus, in warm Octobers with almost no snow, reindeer may employ plant species with higher quality and/or higher biomass for an extended period in autumn, which in turn will reduce the over-winter mass loss due to a shorter winter season. However, there was no significant correlation between the use of ridge vegetation and weather conditions in October (Fig 3). A possible explanation for this could be that some of the key forage plants, especially *Salix*, are also present in other vegetation types (Johansen et al. 2009), and there might be gradual transitions between vegetation types present in the vegetation map. Additionally, the vegetation map is found to have limited validation statistics (Johansen et al. 2012) and a substantial amount of errors appear in the map (pers. comm. V. Ravolainen).

#### 4.1.2 Less movement as an energy-saving strategy in snow rich Octobers?

Reduced movement in winter is considered an energy saving mechanism for winter survival (Cuyler & Øritsland 1993), which is demonstrated by the steady decrease in monthly activity levels between the seasons of late summer and winter (Loe et al. 2007; Loe et al. 2016). At the same time, the food intake rates decreases (Nilssen et al. 1984). Thus, given the assumption that an increase in snow cover in October affect the food availability, and thereby reducing the quality and quantity of utilized plant species (Beumer et al. 2017; Johansen et al. 2009), one might expect that the movement distance will decrease with increasing snow cover in autumn as an energy saving behavioral strategy for the upcoming winter. However, the non-significant tendency towards less movement with increasing amount of snow in October (Fig 4b) explained little of the variation in total movement distance, and the effect of air temperature were far greater than the amount of snow (Fig 4a).

Despite the fact that cold Octobers will, to some extent, hold increased amount of snow (Fig s2), it is still surprising that air temperature displayed a better predictor than snow for movement. One possible explanation for this could be that plant senescence has occurred earlier in years with cold Octobers and that the poor-quality diet triggers energy-saving in the reindeer. This mechanism is most probable if October temperatures are correlated with temperatures earlier in autumn, when plant senescence occurs (August/September; Cooper et al. 2011; Parmentier et al. 2011). However, there was no significant correlation between temperatures in October and September ( $r=0.35$ ,  $p=0.40$ ) or between October and August ( $r=-0.27$ ,  $p=0.52$ ). In addition, the increase in movement with increasing temperatures in October are unlikely to be related to the rut (Skogland 1989), because the time of gestation in reindeer is constant and the important thing is the timing of parturition in spring (Reimers et al. 1983; Tveraa et al. 2013). Thus, there probably exists other not yet revealed mechanisms behind the increase in movement with increasing temperatures in October.

#### 4.2 Snow conditions and forage availability in winter

The strong correlation between the rain-on-snow measure and the snow density estimate from the reindeer GPS-track ( $r=0.82$ ,  $p<0.001$ ) support the assumption that snow density indeed forms a reasonable index of winter rain, and thus a reliable proxy for the extent of ground ice formation and food availability (Albon et al. 2017). Thus, the absence of a significant negative effect of snow density ( $\beta= -0.53 \pm 0.51$ ,  $p=0.30$ ) and rain-on-snow ( $\beta= -0.68 \pm 0.41$ ,  $p=0.10$ ) on April body mass reported here was surprising, and in contrast to the prediction (**P2**) and previously reported negative effects of rain-on-snow on Svalbard reindeer fecundity (Stien et al. 2012), population growth (Hansen et al. 2013; Kohler & Aanes 2004) and April body mass (Albon et al. 2017).

However, the strong negative effect of rain-on-snow on April body mass found in Albon et al. (2017) were based on a larger data set including more years and individuals. In that period (1995-2014), three critical years with large crashes in population occurred in the winters 1995/1996, 2001/2002 and 2007/2008 (Albon et al. 2017). During the timeframe of this study (2009-2016), none of the winters with significant rain-on-snow events and high snow density estimates (2009/2010, 2011/2012, 2014/2015 and 2015/2016) resulted in large population crashes (Albon et al. 2017; Environmental Monitoring of Svalbard and Jan Mayen (MOSJ)), despite that all these winters had more rain-on-snow than any other winter since 1995/1996. Interestingly, one of the winters with highest snow density during this study (winter 2015/2016)

were also one of the winters with highest recorded April body mass (Fig. 5b). Hence, these findings may imply that the reindeer during the recent winters have succeeded in finding areas with available forage, and thus avoided starvation and large die-offs of individuals. Moreover, the amount of snow had a greater impact of April body mass in these winters (Table 3).

#### 4.1.2 Snow density versus snow depth

During icing events, patches of food may still be accessible, and the reindeer may buffer the negative consequences of icing by moving to areas with less ice (i.e. improved foraging conditions) (Loe et al. 2016; Stien et al. 2010). Individuals in the study area (Fig. 1) who relocated from Reindalen (much ice) to Colesdalen (less ice) in icy winters had lower over-winter body mass loss than individuals staying in Reindalen (Loe et al. 2016). In accordance with this, the movement distance increased significantly with both snow density ( $\beta=16.67 \pm 4.40, p<0.001$ ) and rain-on-snow ( $\beta=25.34 \pm 3.93, p<0.001$ ), implying that snow density indeed is affecting forage availability, which in turn triggers movement (Fig 7a).

In contrast to the large geographical variation in the spatial extent of icing that may occur in the study area, snow may in many years be more uniformly distributed (Loe et al. 2016). In addition, as the formation of ground ice may restrict the access to forage completely (Hansen & Aanes 2012), the reindeer could still have access to forage beneath the snow pack in areas where no ice is present (Beumer et al. 2017). This may explain why no effect of snow depth on movement was found ( $\beta= 3.41 \pm 4.71$ ,  $p=0.47$ ). However, the slightly positive effect size (Fig 7b) was surprising, as the energy expenditures when moving in snow increase with increasing snow depth (Fancy & White 1987; Parker et al. 1984). The positive correlation between snow depth and snow density ( $r=0.52, p<0.001$ ; Fig s2) constitutes a possible explanatory factor for this effect, implicating that icing conditions are more likely to occur in winters with much snow due to an increase in precipitation that falls as rain (Aanes et al. 2000; This study: Fig s.2). Additionally, the Svalbard reindeer are adapted to little movement in winter (Cuyler & Øritsland 1993), and less snow in a given winter may not change this “default” behavior (i.e. movement and activity levels are already reduced in October (Loe et al. 2007; Loe et al. 2016), despite the relatively thin snow cover compared to later in winter).

Moreover, the snow distribution, snow depth and snow density are the main factors affecting the use of different vegetation types of Svalbard reindeer in winter (Lindner 2003). My findings



of how snow density strongly correlates with the use of ridge vegetation in winter (Fig. 6b), imply that icing conditions affect Svalbard reindeer habitat use. Behavioral responses to changes in snow-pack characteristics (snow density) is documented also in a coastal population of Svalbard reindeer at Brøggerhalvøya. Here the reindeer started utilizing marine habitats (i.e. feeding on kelp and seaweed) or relocated to higher altitudes when faced with ice-locked pastures (Hansen & Aanes 2012). However, the strong negative correlation between use of ridge vegetation and snow density reported here ( $r=-0.85, p=0.2$ ) was astonishing and contradictive to what should be expected if ridges constitutes the main winter feeding habitat in icy winters (Hansen et al. 2010). One possible explanation could be that the reindeer have succeeded finding forage resources other places than ridges in recent winters (e.g. snow in the valley bottoms are washed away during heavy rainfall, and thus exposing mossy tussocks/hummocks sticking out above the ice which the reindeer can feed). Alternatively, there probably exists other not yet revealed mechanisms behind this pattern.

#### 4.3 Duration of snow cover most important for over-winter mass loss?

As predicted (**P3**), more snow in winter (November to March) had a negative effect on April body mass (Fig.5a). This is in accordance with other studies showing negative effects of much snow on ungulate populations (Garrott et al. 2003; Garroway & Broders 2005; Keech et al. 2011; Willisich et al. 2013). However, the timing of onset of winter (snow in October) was likely to be more decisive for April body mass than the conditions during the main winter ( $\Delta AIC = -1.24$ ; Table 4). This result further implies that the duration of winter snow cover (i.e. the length of the winter season) was more important than the direct negative effect of much snow on forage availability during main winter. However, there was still a tendency towards a negative effect of snow depth on April body mass after accounting for autumn conditions (Table 4), which suggest that snow depth in main winter also have an impact on late winter body mass. In conclusion, these results provides considerable support for the assumption that factors affecting the duration of the winter season are of special importance for mass loss during winter, and thus body mass in April.

## 5. Conclusion and future perspectives

Few studies have used GPS-data and spatio-temporal maps of weather data to explain individual variation in fitness (Gaillard et al. 2010; Morales et al. 2010). This study managed to establish a link between movement behaviour and the seasonal varying environmental factors affecting resource acquisitions, and in turn link this to individual performance through the effect on April body mass. Thus, by combining temporally explicit maps of weather conditions with the individual reindeer GPS-track, this study have constructed a commonly missing link (Morales et al. 2010) between animal movement behaviour and fitness (April body mass), that in turn affect population dynamics (Albon et al. 2017). Furthermore, this study is the first to investigate the impact of snow depth on April body mass in Svalbard reindeer. An extended period with snow-free grazing conditions in autumn presumably led to a shorter period of over-winter mass loss. Hence, I have substantiated the assumption that changes in autumn seasonality may have beneficial consequences for the population dynamics of a high Arctic herbivore. Furthermore, the absence of a negative effect of snow density indicates that the reindeer in recent winters have succeeded in finding areas with accessible forage despite periods with significant rain-on-snow events. In sum, these findings contribute to elucidate our current mechanistic understanding of climate change effects in Svalbard reindeer.

Currently, the population of Svalbard reindeer at Nordenskjold land seems to benefit from the warmer climate (MOSJ), despite the increase in rain-on-snow events during winter (Rennert et al. 2009). However, the positive population growth at Nordenskjold land is in stark contrast to the Svalbard reindeer population at Brøggerhalvøya, which is likely to be more strongly affected by the negative effect of the increase in rain-on-snow events during winter (pers. comm. Å. Pedersen). Thus, the effects of the environmental factors on Svalbard reindeer that I have investigated may affect distinct populations of Svalbard reindeer differently, depending on geographic areas. As climatic changes are expected to proceed (AMAP 2017; Hansen et al. 2014), one future aspect is therefore to investigate the net effects (Tews et al. 2007) of improved foraging conditions during summer (Albon et al. 2017) and autumn (Albon et al. 2017; This study), as well as the reduced forage accessibility associated with an increase in rain-on-snow during winter (Albon et al. 2017; Hansen & Aanes 2012) on different populations of Svalbard reindeer. This will hopefully aid in prospective predictions of how Svalbard reindeer will persist in an rapidly changing Arctic environment.

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## 7. Appendix

**Table s1.** Comparison of four linear models explaining variation in capture-date adjusted April body mass in adult female Svalbard reindeer. Temperature variables included were summed mean daily air temperature in October from the individual GPS-track, October degree-days from the individual GPS-track, summed mean daily air temperature from Svalbard airport weather station and October degree-days from Svalbard airport weather station. Temperatures from the individual GPS-track are modelled estimates, while temperatures from Svalbard airport weather station are recorded two meters above ground level. Model comparisons were made using relative differences in Akaike's information criterion ( $\Delta AIC$ ) compared with the model with the lowest AIC.

<b>Models of temperature in October explaining variation in April body mass</b>	<b><i>AIC</i></b>	<b><i><math>\Delta AIC</math></i></b>
Summed air temperature in October (individual GPS-track) + age class	573.89	0.00
Summed air temperature in October (Svalbard airport weather station) + age class	577.17	3.28
October degree-days (individual GPS-track) + age class	578.54	4.65
October degree-days (Svalbard airport weather station) + age class	579.07	5.18

**Table S2.** Correlation coefficients between capture-date adjusted April body mass and potentially explanatory weather variables. The rain-on-snow measure is log transformed. Variables from the individual GPS-track are modelled estimates, while variables from Svalbard airport weather station are recorded measures. The lower left side of the matrix shows correlation values between the weather variables within and between seasons (green shading = autumn, beige shading = autumn/winter and blue shading = winter). Significant correlation values at the 0.05 level are indicated by bold values marked with \*.

	October degree-days (Svalbard airport weather station)	October degree-days (individual GPS-track)	Summed mean daily air temperature (Svalbard airport weather station)	Summed mean daily air temperature in October (individual GPS-track)	Summed snow depth in October (individual GPS-track)	Rain-on-snow > 0°C (Nov-Mar, individual GPS-track)	Summed snow depth (Nov-Mar, individual GPS-track)	Summed snow density (Nov-Mar, individual GPS-track)
April body mass	0.04	-0.07	0.11	0.19	-0.33*	-0.30*	-0.27*	-0.20*
October degree-days (Svalbard airport weather station)	1							
October degree-days (individual GPS-track)	<b>0.89*</b>	1						
Summed mean daily air temperature (Svalbard airport weather station)	<b>0.69*</b>	<b>0.51*</b>	1					
Summed mean daily air temperature in October (individual GPS-track)	<b>0.36*</b>	<b>0.24*</b>	<b>0.82*</b>	1				
Summed snow depth in October (individual GPS-track)	-0.19	-0.24*	-0.23*	-0.44*	1			
Rain-on-snow > 0°C (Nov-Mar, individual GPS-track)	-0.19	-0.16	0.19	<b>0.27*</b>	<b>0.37*</b>	1		
Summed snow depth (Nov-Mar, individual GPS-track)	0.00	-0.08	0.00	-0.03	<b>0.44*</b>	<b>0.49*</b>	1	
Summed snow density (Nov-Mar, individual GPS-track)	-0.35*	-0.36*	<b>0.23*</b>	<b>0.30*</b>	<b>0.35*</b>	<b>0.82*</b>	<b>0.52*</b>	1





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