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Partial migration as a response to ground icing events in a high arctic ungulate

Delvis migrasjon som respons til bakkeising for et arktisk hovdyr

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Preface

This thesis is written as a part of my master degree in Natural Resource Management at the Norwegian University of Life Sciences (NMBU) in 2014. Several people deserve credit for helping me complete this thesis.

First I would like to thank my supervisor Prof. Leif Egil Loe at NMBU for his guidance, good discussions and encouragement throughout the whole process of writing this thesis. I want to thank The Research Council of Norway who funded my fieldwork on Svalbard through the Arctic field grant. I also would like to thank to Brage B. Hansen who gave helpful comments to my thesis.

A special thank goes to Kristine Våge for supporting me when writing this thesis. Finally I would like to thank Are Endal Rognes and Knut Åge Meland for helpful input and for revealing mistakes during the writing process.

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Abstract

Partial migration – a phenomenon where only part of a population performs annual migrations, is common in ungulates. Despite partial migration being well documented, little is known about the annual partial migration frequency in ungulates and if individuals perform the same strategy (migratory or stationary) every year. Additionally, few studies have investigated if variations in weather conditions have an impact on the degree of partial migration.

The endemic Svalbard reindeer (*Rangifer tarandus platyrhynchus*) live under extreme climatic conditions on the island of Svalbard in the Arctic. During winter, temperatures may rise above 0° C and precipitation fall as rain, an occurrence known as rain-on-snow events (ROS). Such warm spells lead to the formation of ground ice, creating locked pastures, inhibiting foraging thus potentially leading to starvation and death for Svalbard reindeer.

In this thesis I analyzed patterns of partial migration in Svalbard reindeer. I used GPS data from 36 females of a Svalbard reindeer population in the period 2009-2013. The GPS data of Svalbard reindeer were related to field validated data of ground ice, snow depth, ground temperature and air temperature. I found that winter conditions and amount of ground ice clearly differed between years and valleys. Years were thus distinguished as icing years (two years) and non-icing years (two years) in this thesis. Warm spells followed by ground icing affected migratory behavior of Svalbard reindeer by increasing the probability of migration and increasing migration distance. I also show that the warm spells corresponded with the timing of migration from summer to winter range, as well as causing most migrants to seek ranges with less ground ice nearer the coast. Furthermore, 41% of the Svalbard reindeer monitored for at least two years changed annual movement strategy when facing differing ground ice conditions, i.e. adopted a migratory strategy in icing years and stationary strategy in non-icing years. To my knowledge, this has rarely been documented for any ungulate.

This study provides rare evidence of what drives partial migration in ungulates by showing how a partially migratory population responds to climate and extreme weather events, in turn affecting the annual portion of migrants in a wild ungulate population.

Sammendrag

En populasjon der bare deler av populasjonen er migrerende blir omtalt som delvis migrasjon, og er vanlig blant hovdyr. Selv om delvis migrasjon er godt dokumentert vet man mindre om frekvensen av delvis migrasjon varierer mellom år og individ. I tillegg er det få tidligere studier som har undersøkt hvordan værforhold kan påvirke andel migrerende dyr i en delvis migrerende populasjon.

Den endemiske svalbardreinen (*Rangifer tarandus platyrhynchus*) lever under ekstreme klimatiske betingelser på øygruppen Svalbard i Arktis. Selv om den arktiske vinteren vanligvis er kald kan nedbøren falle som regn i perioder når temperaturen overstiger 0° C. Slike regn-på-snø hendelser fører til at det dannes et islag mellom bakken og snøen. Islaget reduserer beitetilgangen til svalbardrein og kan potensielt medføre utsulting og høy dødelighet for svalbardrein.

I min masteroppgave har jeg analysert delvis migrasjon hos svalbardrein. Jeg har brukt GPS-data fra 36 simler fra en populasjon av svalbardrein i perioden 2009-2013. GPS-dataene ble sammenlignet med feltvaliderte data av bakkeis, snødybde samt bakke- og lufttemperatur. Jeg har vist at mengden bakkeis varierer signifikant mellom år og daler. Basert på dette ble år definert som enten isingsår (to år) eller ikke-isingsår (to år). Mildværsperioder med dannelse av bakkeis påvirket migreringsmønstre hos svalbardrein gjennom økt sannsynlighet for migrering og økt migrasjonsavstand i isingsår. Jeg har også vist at mildværsperiodene samsvarte med tidspunktet for vintermigrering og at de fleste migrantene søkte områder med mindre bakkeis nærmere kysten. Individuelle svalbardrein fulgt i minst to år byttet strategi - migrerende strategi i år med mye bakkeis og stasjonær strategi i år med lite bakkeis. Dette har så vidt meg bekjent sjeldent blitt dokumentert hos hovdyr.

Mitt studie dokumenterer mekanismene som driver delvis migrasjon hos hovdyr gjennom å vise hvordan en delvis migrerende populasjon responderer til klima og ekstreme værforhold, og med det påvirkning på den årlige migrasjonsandelen i en vill hovdyrbestand.

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1 Introduction

Resources such as food tend not to be randomly distributed in the landscape. Consequently, spatial-temporal variation in resource quality, resource availability, access to shelter and risk of predators lead to seasonal variation in habitat selection (Hebblewhite & Merrill 2009; Krebs & Davies 1993). This is often the case in temperate and arctic areas where resources are scarce in the winter months. As a result of this, several species migrate between summer- and winter ranges (Bischof et al. 2012). One of the most impressive migrations are seen for the seasonally nomadic caribou (*Rangifer tarandus*) capable of travelling hundreds of kilometers between summer and winter ranges (Fancy et al. 1989). For temperate ungulates such as moose (*Alces alces*), red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) seasonal migration between high-elevation summer ranges and low-elevation winter ranges are most common (Baskin & Danell 2003). The seasonal migration pattern for ungulates are thus closely related to food quality and accessibility as shown for roe deer (Mysterud 1999) and red deer (Albon & Langvatn 1992), or snow depths as reported in moose (Ball et al. 2001).

Not all animals are completely migratory. In some populations of temperate ungulates only a portion of the population perform annual migrations, a phenomenon called partial migration. (Chapman et al. 2011; Kaitala et al. 1993). Partial migration is well documented for many ungulates, e.g. in populations of red deer (Mysterud et al. 2011), roe deer (Mysterud 1999), moose (Bunnefeld et al. 2010), elk (*Cervus canadensis*) (Hebblewhite et al. 2006) and pronghorn (*Antilocapra americana*) (White et al. 2007). The frequency of partial migration differs both between species (Mysterud et al. 2012) and populations (Mysterud et al. 2011). Difference in physiological, morphological and behavioral traits may be important cues in order to explain underlying ecological mechanisms that promote the preferred movement strategy (Chapman et al. 2011). Additionally, a combination of the factors above may induce partial migration, i.e. tradeoffs between foraging and predation avoidance as observed in elk (Hebblewhite & Merrill 2009; Hebblewhite & Merrill 2011). Despite partial migration being well documented in ungulates, few studies have investigated if the partial migration frequency varies among years and if individuals repeat the same strategy year after year. In addition, few studies have investigated if variations in weather conditions have an impact on the degree of partial migration.

Svalbard reindeer (*Rangifer tarandus platyrhynchus*) is an endemic species of reindeer living on the Arctic island of Svalbard (Tyler & Øritsland 1989). In this predator-free arctic environment, seasonal climatic conditions are extreme and highly variable. The ground is normally frozen solid and snow-covered in the period mid-October until June, limiting plant growth. Consequently, winter is the limiting season for the population of Svalbard reindeer (Aanes et al. 2000; Reimers 1983). Although the mean monthly winter temperatures on Svalbard are well below freezing, temperatures may relatively frequently rise above 0 °C. These conditions, in combination with rain-on-snow events (hereby called ROS), may cause the formation of ground ice (Kohler & Aanes 2004; Putkonen & Roe 2003). During such events rain percolates through the snow, forming a layer of ice between the ground and the snow (Rennert et al. 2009). Alternatively, ice may also occur in warm spells (without ROS-events) when air temperature is above 0° C and ground temperature is below 0° C, creating a crust of ice on the ground. Formation of ground ice may create a “locked pasture”-situation, thereby largely limiting forage availability resulting in increased winter mortality of Svalbard reindeer due to starvation (Reimers 1977).

It is well known that Svalbard reindeer are relatively sedentary and do not perform annual large-scale seasonal migrations compared to other species of *Rangifer* (Tyler & Øritsland 1989). Nevertheless, partial migration in a Svalbard reindeer population has already been documented (Hansen et al. 2010b). In this study, female reindeer with radio- and plastic collars that migrated from a summer range with depleted lichen resources to a rich-lichen winter range had improved calving success compared with stationary Svalbard reindeer in the poor summer range. It is also known that Svalbard reindeer respond to ground icing of winter pastures by increasing movement (Stien et al. 2010). By using a simple snowpack model (Kohler & Aanes 2004), Stien et al. (2010) showed that animals increased home range-use and performed erratic movements following ground icing events. Additionally, a study of habitat use of Svalbard reindeer in relation to ground ice reported that some individuals used high altitude ranges with sparse vegetation while others fed on snow free ridges or other local snow covered pastures free of ground ice following an icing event (Hansen et al. 2010a). Hansen et al. (2010a) suggested that there was large individual variation in the behavioral response to extreme winter feeding conditions.

In this study I investigate migration dynamics of Svalbard reindeer in response to ground icing events to test if the population is partially migratory. In contrast to previous studies, I

will combine detailed movement data with measurements of temperature and ground ice formation to investigate if the degree of partial migration is affected by ground ice formation. I will for the first time examine if individual reindeer change strategy between winters with and without ice. I have data from 36 GPS-marked female Svalbard reindeer followed for up to four years in the period of 2009-2013. This is the first time GPS-data over several years in combination with field validated data of ground ice and ground temperature have been available for any ungulate. With this, I will shed light on weather events as a mechanism of migration in ungulates.

I test the following predictions:

P₁: Svalbard reindeer can be termed partially migratory meaning that a portion of the marked individuals will migrate annually.

P₂: Warm spells followed by ground icing:

- a) increase the probability of reindeer migration.
- b) closely match the timing of reindeer migration.
- c) increase reindeer migration distance.
- d) cause migrants to seek ranges with less ground ice near the coast.

P₃: Individual movement strategy change between years depending on ground ice conditions: individuals are migratory in years with ground ice and stationary in years with no ground ice.

2 Materials and methods

2.1 Study area

The study was conducted in Reindalen, Semmeldalen and Colesdalen including adjoining valleys in Nordenskiöld Land, at Svalbard (78 ° 0 ' N, 16 ° 0 ' E) (Fig. 1) in the Arctic. The terrain is characterized by wide valleys, slow running rivers and large plateaus, with mountains ranging up to 1700 m.a.s.l (Bengtson 1999). The vegetation zone is arctic tundra. Mosses, lichens and fungus along with approximately 170 vascular plants make up the vegetation (Bengtson 1999). Close to no human settlements and very little human activity are related to the study area except for rare occasions of hikers. A snowmobile track runs through the study area (across Reindalen) during late winter/spring. The largest settlement on

Svalbard, Longyearbyen is located approximately 20 kilometers northeast of the study area.

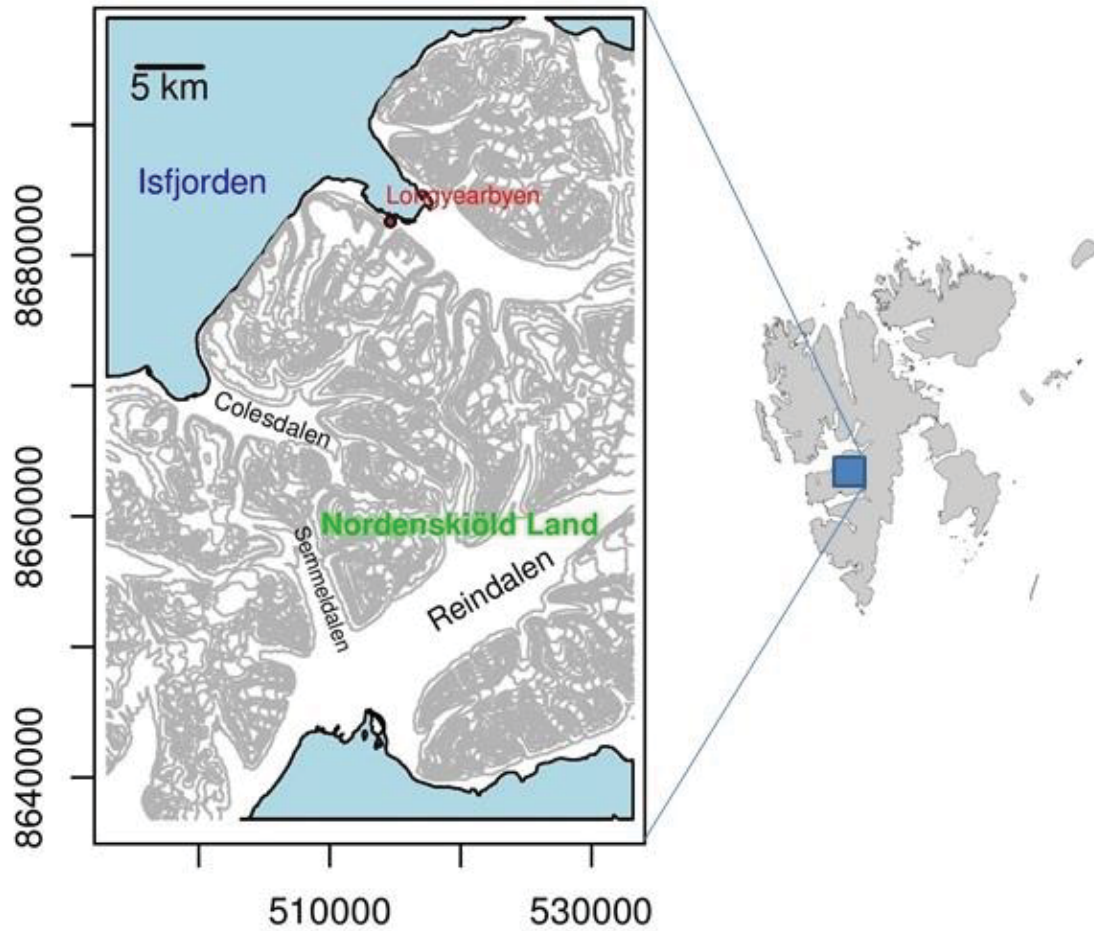


Figure 1: Reindalen, Semmeldalen and Coledalen and adjoining valleys in Nordenskiöld Land at Svalbard make up the study area.

Svalbard reindeer is the only ungulate at Svalbard. Common mammals are arctic fox (*Vulpes lagopus*) and polar bear (*Ursus maritimus*). Svalbard also has populations of geese, seabirds, Svalbard rock ptarmigan (*Lagopus muta hyperborea*) and arctic tern (*Sterna paradisaea*) among others (Bengtson 1999). Svalbard is defined as an arctic desert with annual precipitation ranging between 200-440 mm (Førland et al. 2012). Mean annual temperature is generally low with temperatures in July and August averaging between 2 °C and 6 °C and winter temperatures in the period January-March averaging between -12 °C and -14 °C (Bengtson 1999).

2.2 Study species

The Svalbard reindeer is a subspecies of *Rangifer* that can only be found on Svalbard. Svalbard reindeer exhibits low genetic variation due to being geographically isolated for a long time (Yannic et al. 2014). Glaciers, fjords and mountains (natural barriers) further limit gene flow and have resulted in isolated populations of reindeer on Svalbard (Yannic et al. 2014). The total population size of Svalbard reindeer remains unclear. Annual counts in the study area have the last ten years fluctuated around 800 annual individuals with considerable variation in numbers, the amount of calves per female and number of carcasses found (Solberg et al. 2012). Their diet consists of lichens, mosses and grass and animals are characterized by an opportunistic grazing behavior (Staaland et al. 1993). Svalbard reindeer are generally thought of as sedentary, in sharp contrast to mainland reindeer that concentrate in large wide-ranging herds (Skogland 1989). Svalbard reindeer have partly lost their anti-predation strategies due to the lack of effective predators on the island of Svalbard (Øritsland 1986). Despite Svalbard having large numbers of polar bear and arctic fox, neither species predate on reindeer in particular, other than on carcasses (Reimers 1983). Since 1983 around 150 individuals of reindeer have been shot each year (Stien et al. 2012a) of which approximately 40% of harvest off-take is within my study area. Svalbard reindeer may reach old age with individuals up to 17 years recorded (Hindrum et al. 1995), but most individuals die much earlier. The primary cause of death is starvation during the winter (Tyler 1986). There is large annual variation in reproduction (Stien et al. 2012b) and population growth rate (Hansen et al. 2011; Hansen et al. 2013) caused by a combination of density dependence and starvation in late winter in years with harsh weather conditions and icing.

2.3 Data collection

2.3.1 Ground temperature loggers

I used temperature data obtained from ground temperature loggers in field. In 2009, 128 temperature loggers (Ibuttons) were put into the ground surface in the Reindalen-Semmeldalen-Colesdalen area. The temperature loggers were distributed in a spatial hierarchical setup with replicates at the levels of 5, 50, 500 and 5000 meters (Nedberg 2012). There are a total of eight clusters of temperature loggers in the study area with each cluster containing 16 temperature loggers. During field work, every logger was located using handheld GPS. Temperature loggers are marked with a 10 x 10 cm aluminum plate to make

them easier to locate. All temperature loggers were collected from its capsule, replaced with a new one and put back into the ground surface.

2.3.2 Weather data

Weather data was obtained from a local weather station at Longyearbyen airport situated approximately 20 km northeast from the study area (www.met.no). Information on daily precipitation and mean air temperature was used.

2.3.3 Ground ice and snow depth data

I used data from measurements of snow depth and ground ice thickness that have been collected at the 128 logger sites every April in the period 2009 to 2013. Snow was removed with a shovel and ice was removed with an axe, before measuring snow depth and ice layers using a ruler. In 2011 and 2012 snow and ice were measured in both February and April. In 2010 and 2013 measurement were only conducted once. The loggers were not marked in any way that made them visible above the snow layer and hence the match between the measurement site and true logger locations is affected by precision of the GPS-coordinates (margin of error: approx. +/- 10 meters).

2.3.4 Reindeer GPS-data

Data from GPS-marked Svalbard female reindeer was used, some individuals were followed up to four years. Animals were captured with nets using snowmobiles (Omsjoe et al. 2009) and fitted with Vectronics aerospace GPS collars weighing 850 gram (~1-2 % of animals winter weight). A total of 36 adult female reindeer (age: 2-11 years) have been fitted with GPS collars in the period 2009-2013. Marked individuals were then recaptured every February or April in the period from 2010 to 2013 in order to obtain annual GPS-data. This has given me a total of 119 animal years available for analysis. The collars update and register their location every second hour with a margin of error of approximately 12 meters (Nedberg 2012). All the marked reindeer are of known age because they were originally marked with plastic collars and earmarks as calves.

2.4 Statistical analysis

All the following statistical analyses have been conducted using the R project for statistical computing program, version 3.0.2 (R Development Core Team 2013).

2.4.1 Ground temperature loggers

Ground temperature data of the 128 temperature loggers were analyzed in the period of 2009 to 2013. The aim of the ground temperature logger data is to investigate in what periods of the winter ground temperature exceed 0 °C (so called warm spells). Such temperatures often indicate ROS-events and the possible formation of ground ice (Putkonen & Roe 2003). I defined winter season as running from 15.October to 30.April. I was particularly interested in detecting temperatures above freezing. Therefore I first extracted the sign of each temperature measurement (negative for < 0 C, positive for ≥ 0 C). Thereafter, I fitted generalized additive models (GAMs) with temperature sign (1/0) as the binomially distributed response variable and date as the predictor variable, using the function “gam” in the mgcv-package in R. GAMs are non-linear models that fit curves to particular number of segments along the x-axis of the dataset and smoothing the fitted curves to a final model (Wood 2006). The outcome of my models is the smoothed probability of temperatures ≥ 0 C on each day during winter. Separate models were fitted for each winter.

2.4.2 Weather data

I examined air temperature and precipitation data by visually inspecting the weather data during winter. Here I searched for periods where average daily air temperature exceeded 0 °C. When combined with precipitation, such periods of warm spells indicate ROS-events and the formation of ground ice. In cases where warm spells were discovered, I calculated average air temperature and amount of precipitation in the period of the warm spell. Weather data and ground temperature data were then compared to examine if they coincided.

2.4.3 Ground ice and snow depth data

Measurements of ground ice data and snow depth data were grouped based on valley (spatial scale) and month (February or April) for visual inspection and presentation (boxplots). I used t-tests to test annual differences in mean ice thickness and snow depth between years and

valleys (spatial scale), enabling me to distinguish between years in addition to examine the spatial distribution of ice and snow throughout the study area.

2.4.4 Reindeer GPS-data

GPS-data were first screened for GPS-errors (Bjørneraas et al. 2010), of which none were found. I used the model fitting approach used by Bischof et al. (2012), which in turn is based on Bunnefeld et al. (2010) in order to investigate movement strategies. The approach of Bunnefeld et al. (2010) fits various functions to the net squared displacement (NSD) profile of subsequent relocations from the starting point. This makes it possible to distinguish movement patterns from another, i.e. separate migration from other movement patterns. The NSD measures the distance in a straight line between the point of departure and subsequent relocations for the movement tracks of a random individual (Bunnefeld et al. 2010). Due to highly variable space-use patterns in the dataset of the Svalbard reindeer, the automatic fitting approach of Bunnefeld et al. (2010) can lead to incorrect categorization of movement patterns as proposed by Bischof et al. (2012). Therefore, final designation of movement patterns were done by manually inspecting each net displacement profile (ND) in relation to its respective spatial distribution as done by Bischof et al. (2012). Here I refitted the logistic curves for the period of winter and spring migration in the ND profiles. This was done to eliminate poor fits generated by the automated model fitting approach of Bunnefeld (2010). The logistic migration segments of the ND profiles were then interpreted using the asymptote parameter as distance travelled, inflection point defined as the midpoint of migration and the scale value $\times 5$ equal to the duration of the migration (Bischof et al. 2012). The model fitting approach of Bischof et al. (2012) were then slightly modified so that it would better fit the Svalbard reindeer movement patterns. This was done by rearranging the timeframe of each ND-plot so that I could investigate movement strategies during the winter months. Here I displayed each ND plot from the 1st of July (Juliandate: 182) the first year running to the 30th of June the latter year (Juliandate: 181).

All 119 ND-reindeer plots were categorized to be either “migratory”, “dispersal”, “stationary”, “other” or “incomplete”. The ND pattern of a typical migrating individual will have a hat-like shape, meaning it moved away from the starting location and returned to the starting location after staying in another area for a given time (Bischof et al. 2012) (Fig. 2). For Svalbard reindeer such movement behavior may be due to winter icing events, meaning

the animals started migrating sometime during winter, before returning to the summer range in the months of April/May (spring migration). Erratic movements during the winter months were also included in the migration-category. Although such movements didn't last long (4-14 days) they may indicate movement behavior as a response to icing events. I defined winter migration to be movement at least five km from the summer range. ND-plots termed "dispersal" were defined as individuals migrating during winter and not returning to their summer ranges (Fig. 3). Individuals in this category were most likely migratory, but because they were recaptured in February/April (before having returned to their summer range) they were categorized as dispersers. However, of all ND-plots followed for a complete year, none showed signs of dispersal without returning to their previous range. It is therefore highly probable that animals in this category truly are migratory and these are thus included as migrants in the statistical analysis. ND-plots of stationary individuals were defined as individuals residing in an area no more than five kilometers from the starting location in July (Fig. 4). Excursions during calving and rutting seasons were discarded when classifying individuals to be migratory or stationary since such movement have little relevance for movement behavior during the winter season. ND-plots fitting the "other" category were individuals with movement behavior that suggested neither migratory nor stationary movement behavior, so called irregular individuals (Fig. 5). Reindeer placed in the category "incomplete" were individuals with GPS-data of a very short time frame (i.e., no information of mid-winter movement) and such data were thus excluded from the statistical analysis.

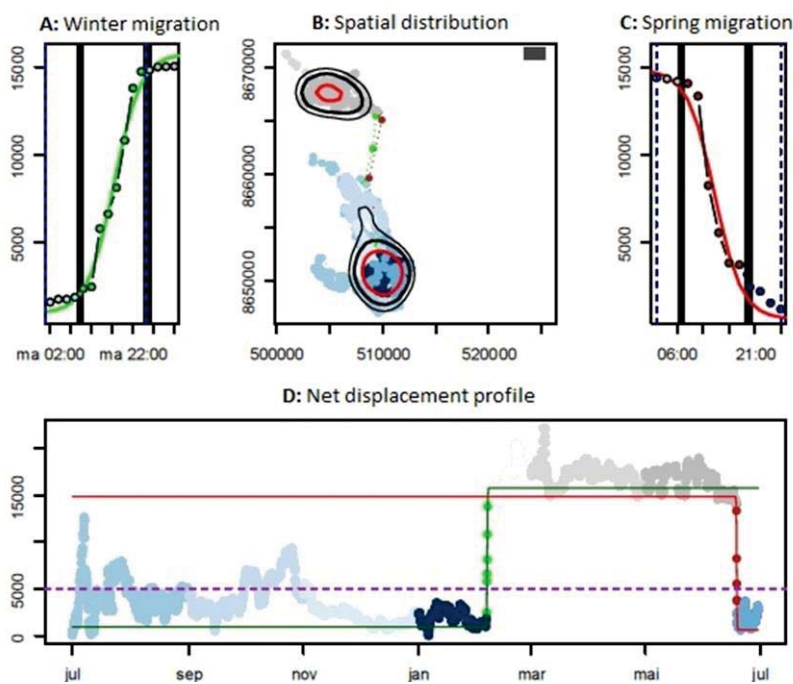


Figure 2: A typical migratory Svalbard reindeer, showing movement strategy of individual B101 followed in the period 01.07.2011 to 30.06.2012. The best fitting logistic curves of winter migration (A) are displayed as a green line and spring migration (C) are displayed as a red line. Detailed information of point of migration is included on the X-axis in A and C. Spatial distribution plot show annual spatial movement (B) with a 2 km scale bar in the top right corner of the plot. The color coding in the spatial distribution plot is identical to that of the total net displacement profile (D). Here the Y-axis show the distance moved away from the point of origin (in meters). The horizontal purple dashed line represents the five km gap from starting point of the marked individual (minimum migration distance).

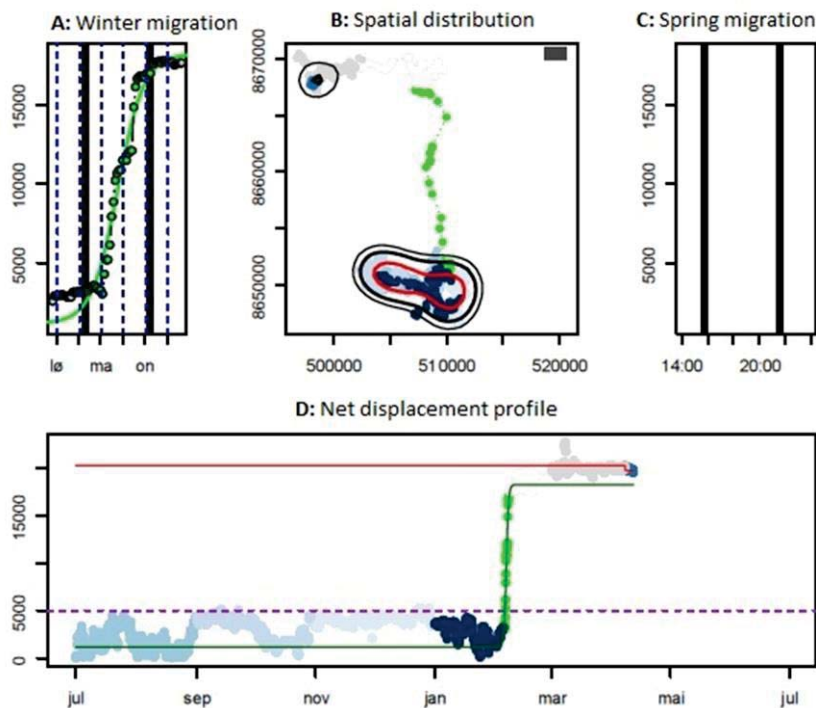


Figure 3: Svalbard reindeer that was termed “dispersal”, showing movement strategy of individual Y112 followed in the period 01.07.2011 to point of recapture in mid-April the following year. Animals in this category are included as “migratory” in the statistical analysis, assuming that a return during spring would have occurred if data collections were not interrupted before time of spring migration.

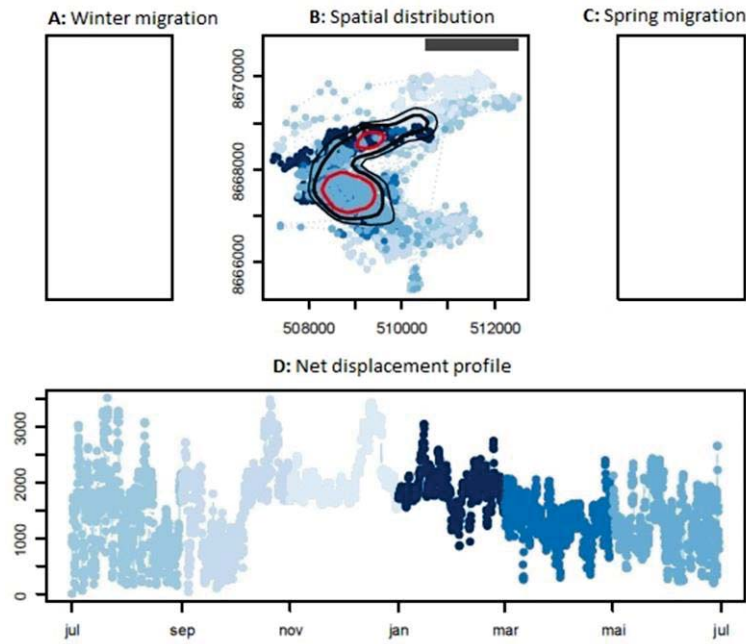


Figure 4: A typical stationary Svalbard reindeer, showing movement strategy of individual Y120 followed in the period 01.07.2011 to 30.06.2012. No logistic migration curves were fitted (A and B blank) as no migration took place.

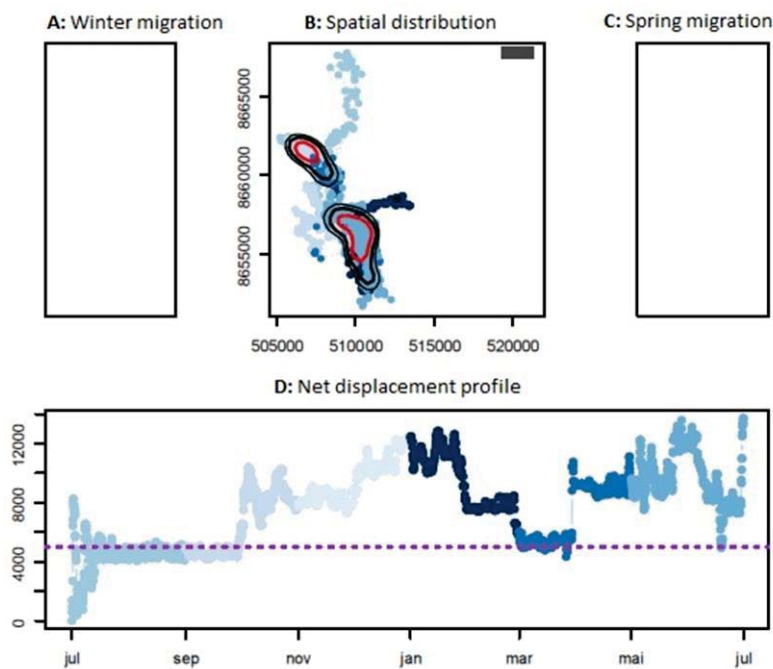


Figure 5: Svalbard reindeer that was termed as other/irregular, showing movement strategy of individual W103 followed in the period 01.07.2010 to 30.06.2011. Individuals placed in this category were typically animals with irregular movement pattern, i.e. neither migratory nor stationary individuals.

Output of the analysis of reindeer movement data were organized into a final worksheet containing movement strategy, timing of winter migration, migration distance and time spent on winter range for each individual in each year (July to July). All statistical analysis of reindeer data are based on this final worksheet. When determining if a significant portion of marked reindeer perform annual migrations, I based my findings on the portion of ND-profiles that could be termed as migrants (category: migratory and dispersal) compared to the portion of stationary animals and those that were termed “other” (P_1). Reindeer in the “other”-category were excluded in the rest of the statistical analysis. I used a generalized linear mixed model (GLMM) using the function `lmer` in the R package “lme4” when examining the effect of icing (predictor variable; 1=icing, 0=no icing) on migration behavior of reindeer (response variable; 1=migratory and 0=stationary). Individual was used as a random factor due to dependence among individual reindeer (P_{2a}). To test if timing of migration from summer- to winter range were linked to timing of warm spells in icing years, I visually compared the data of temperature loggers with mean date of winter migration of marked individuals in icing years to examine if they coincided. Additionally, I compared these data with air temperature data and precipitation data from Longyearbyen Airport to qualitatively evaluate the weather regime during the mild spells (in particular the association with rain) (P_{2b}). A linear mixed-effects model was used to test if migrants wandered further in years with ground ice. The annual migration distances were log-transformed due to several short and few long registered migration distances (P_{2c}). When testing if warm spells followed by ground icing events caused migrants to seek ranges near coast with less ground ice, I first determined migration departure and destination locations of migrants. I then investigated if the location of migration destinations were closer or not closer to the coast than the location of migration departures by using spatial measurements. Then I compared ice thickness data of migration departure locations with the ice thickness data of migration destinations. A t-test was used to test differences in amount of ground ice between migration departure and destination locations (P_{2d}). To test if individual movement strategy changed between years depending on ground ice conditions, I executed a chi-squared test. Here I compared the portion of individuals with GPS-data of at least two years that changed movement strategy according and contrary to P_3 , i.e. animals that were migratory in icing years and stationary in non-icing years compared to animals that were migratory in non-icing years and stationary in icing years (icing years occurred every second year)(P_3).

3 RESULTS

3.1 Ground temperature loggers and weather data

GAMs of winter season 2009-2013 are shown below with the probability of ground temperature exceeding 0 °C as a function of date for each winter season separately (Fig. 6). Increase in probability of ground temperature exceeding 0 °C is apparent for winter seasons 2009/10 and 2011/12 in particular. Here, a peak of temperature increase is evident during a period from mid-November to December and in a period from mid-January to February for both years. In contrast, the winters 2010-11 and 2012-13 have few and very short periods when loggers exceed zero degrees indicative of winters without any substantial warm spells.

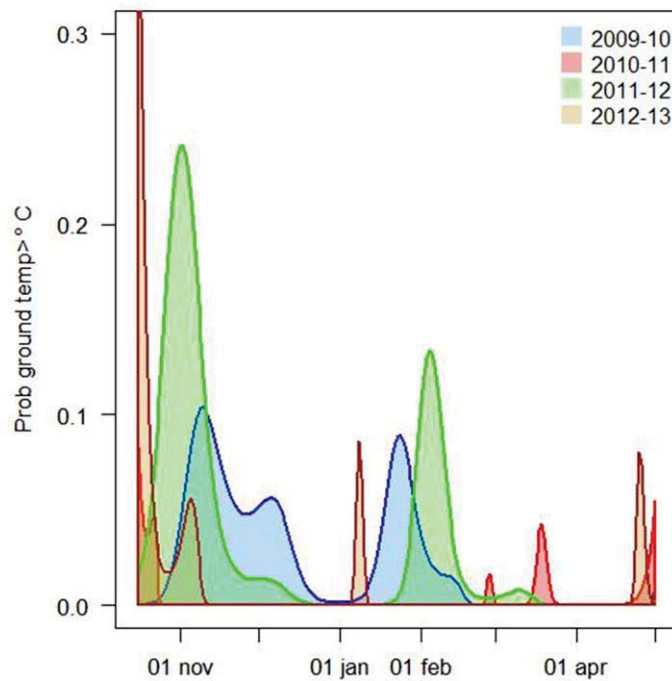


Figure 6: Probability of ground temperature exceeding 0 °C based on GAMs of the winter season of 2009-10 (filled blue curve), 2010-11 (filled red curve), 2011-12 (filled green curve) and 2012-13 (filled light brown curve). Winter season is defined as running from the 15th of October to the 15th of May.

As detected by the ground loggers, the weather data corroborate that several periods of warm spells took place during winter 2009/10 and 2011/12. The winter of 2009/10 had two warm spells. A short period in mid-November with little precipitation associated with it (< 7mm).

The more extensive warm spell in the period 15-25.01.10 had a total of 43.8 mm precipitation with an average air temperature of +1.9 °C. Winter season of 2011/12 had one extensive warm spell in the period 27.01-08.02.10 with a total of 59.5 mm precipitation and average air temperature of +0.5 °C. Additionally, several shorter warm spells occurred in November (8.7mm) and March (2.8mm). In accordance with data of ground temperature loggers (Fig. 6), winter season of 2010/11 and 2012/13 had no warm spells except for very short periods with little precipitation (<7mm).

3.2 Ground ice and snow depth data

Average ground ice thickness in the winter seasons of 2009/10, 2010/11, 2011/12 and 2012/13 was 3.2cm (range: 0-17cm), 0.3cm (range: 0-5.5cm), 5.2 cm (range: 0-21 cm) and 0.1 cm (range: 0-3 cm) respectively (Fig. 7a). The amount of ground ice was significantly higher in winter of 2009/10 and 2011/12 compared to that of 2010/11 and 2012/13 ($t=22.29$, $p<0.001$; Fig. 7a). Average snow depth in the winter of 2009/10, 2010/11, 2011/12 and 2012/13 was 30.6 cm, 29.1 cm, 23.6 cm and 26.8 cm respectively. Snow depth did not differ between winter of 2009/10 and 2011/2012 compared to winter of 2010/11 and 2012/13 ($t= -1.0565$, $p= 0.291$) (Fig. 7b).

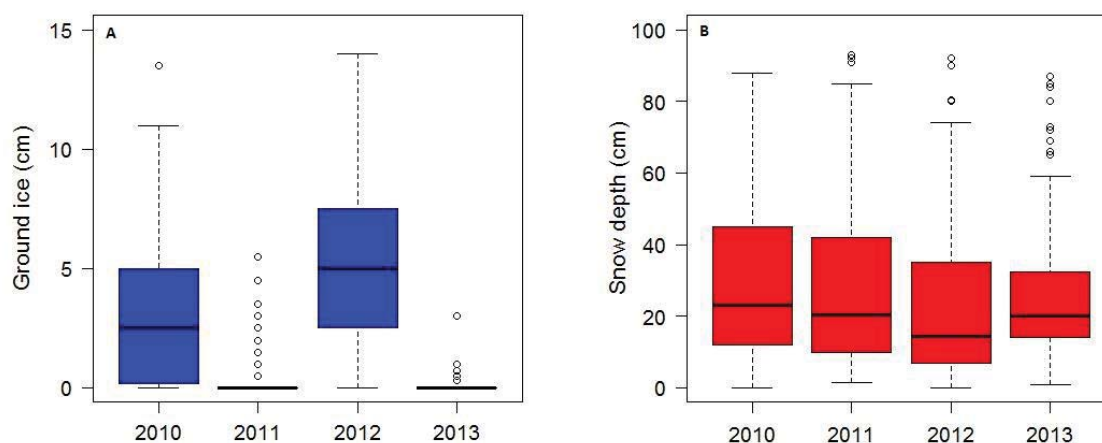


Figure 7a and 7b: Box plot with annual field validated measurements of ground ice (A) and snow (B) (in centimeters).

Average ice thickness varied significantly between several valleys for years 2009/10 (range: 0.1-6.9cm) and 2011/12 (range: 2.2-7.6cm) (Fig. 8a and 8b). Coastal valleys (Colesdalen,

Fardalen/Bødalen and Medalen) had combined significantly less ground ice than inland valleys (remaining valleys; $t = -4.2135$, $p < 0.001$). In contrast, average ice thickness did not vary between valleys for years 2010/11 and 2012/13 due to little ground ice measured (Fig. 7a).

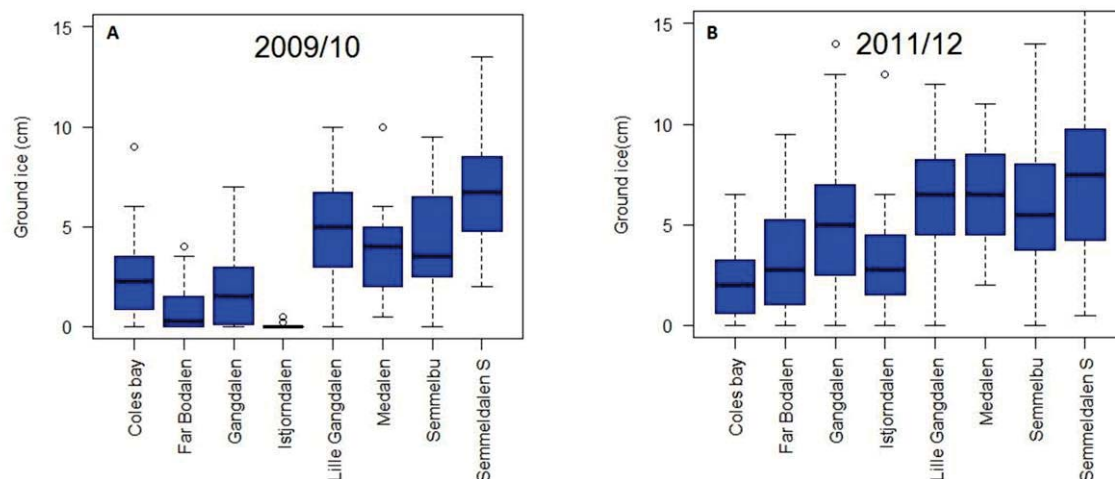


Figure 8: Box plot with field validated measurements of ground ice (in centimeter) for eight connecting valleys in the study area for icing years 2009/10 (A) and 2011/12 (B).

Average snow depth varied significantly between several valleys for years 2009/10 and 2011/12 (years with ground ice ; Fig. 9a and 9b). Coastal valleys (Colesdalen, Fardalen/Bødalen and Medalen) had significantly less snow than inland valleys (remaining valleys; $t = -6.957$, $p < 0.001$) although considerable variation between valleys were apparent. The higher elevated Istjorndalen had significantly more snow than other valleys for all years.

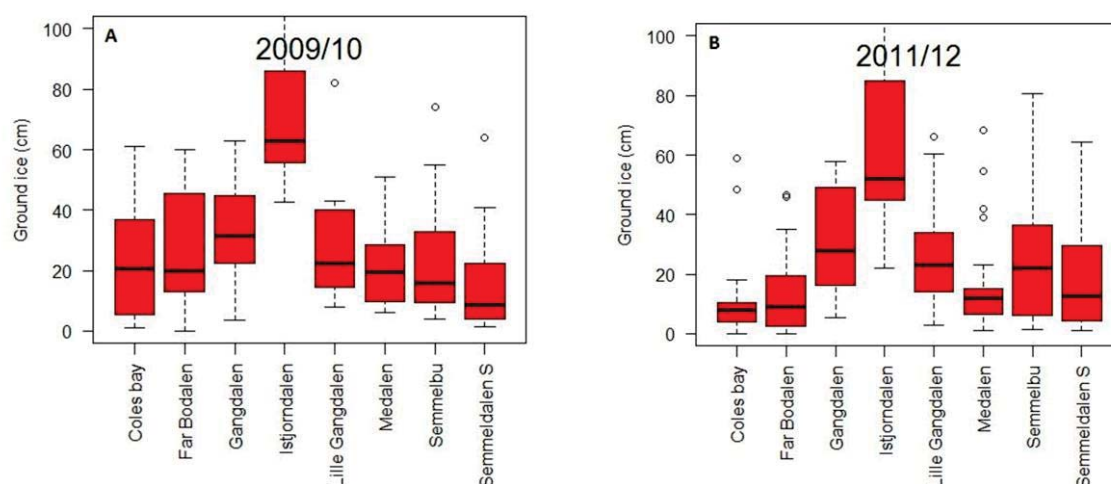


Figure 9: Box plot with field validated measurements of snow depth (in centimeter) for eight connecting valleys in the study area for icing years 2009/10 (A) and 2011/12 (B).

3.3 Combining ground temperature data, weather data and ground ice data

The combination of ground temperature data, weather data and field measures of ground ice clearly discriminate among years with respect to warm spells causing ice formation. Winter seasons of 2009-10 and 2011-12 are thus termed “*icing years*” and winter seasons of 2010-11 and 2012-13 are termed “*non-icing years*”.

3.4 Reindeer GPS-data

3.4.1 Partial migration in Svalbard reindeer

Of the available ND reindeer profiles, 20 (24.1%) were defined as migratory, 10 (12%) were termed dispersal (i.e. first half of migration, see materials and methods), 27 (32.5%) were stationary, and 26 (31.3%) were termed “other” (Table 1). The remaining 36 profiles contained too little GPS-data and were thus termed incomplete and left out of the analysis. Supporting P₁, about 1 out of 3 of the individuals (36.1%; the sum of individuals classified into the migrants and dispersal categories) show clear patterns that indicate migratory behavior.

Table 1: Movement strategy (migratory, dispersal, stationary, other or incomplete) of the analyzed 119 ND-profiles.

Movement strategy	# Ind.	%	In icing-years	In non icing-years
Migratory	20	24.1	16	4
Dispersal	10	12	8	2
Stationary	27	32.5	8	19
Other	26	31.3	11	15
Incomplete	36	-	-	-

3.4.2 Probability of performing annual migrations depend on ground ice

Consistent with P_{2a} , marked individuals of Svalbard reindeer show a significant higher probability of migrating in icing years (75%) compared to years with no icing (25%) ($z = -3.624$, $p=0.002$; Fig.10).

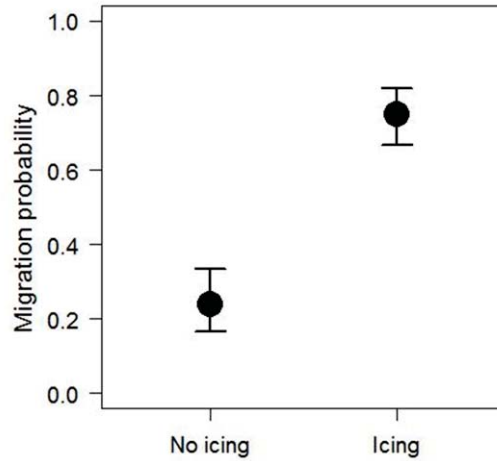


Figure 10: Predicted probability of migrating in icing years (2009/10 and 2011/12) and non-icing years (2010/11 and 2012/13). Error bars represent one standard error from the mean ($\pm SE$: 0.085).

3.4.3 Timing of migration in relation to warm spells

In accordance with P_{2b} , median date of migration from summer to winter range follows shortly after peaks in ground temperature (probability of ground temperature exceeding 0 °C; Fig. 11) and occurrences of ROS-events in icing years. In icing year 2009/2010 median date of migration was January 29 ($n=11$), corresponding with the second warm spell of 2009/10 peaking the January 22 (8.9% probability of ground temperature exceeding 0 °C) (Fig.11a) and in accordance with weather data (Fig.11c). In icing year 2011/2012 median date of migration was February 6 ($n=12$), also corresponding with the second warm spell of 2011/12 peaking February 3 (13.4% probability of ground temperature exceeding 0 °C) (Fig. 11b) and in accordance with weather data (Fig. 11d).

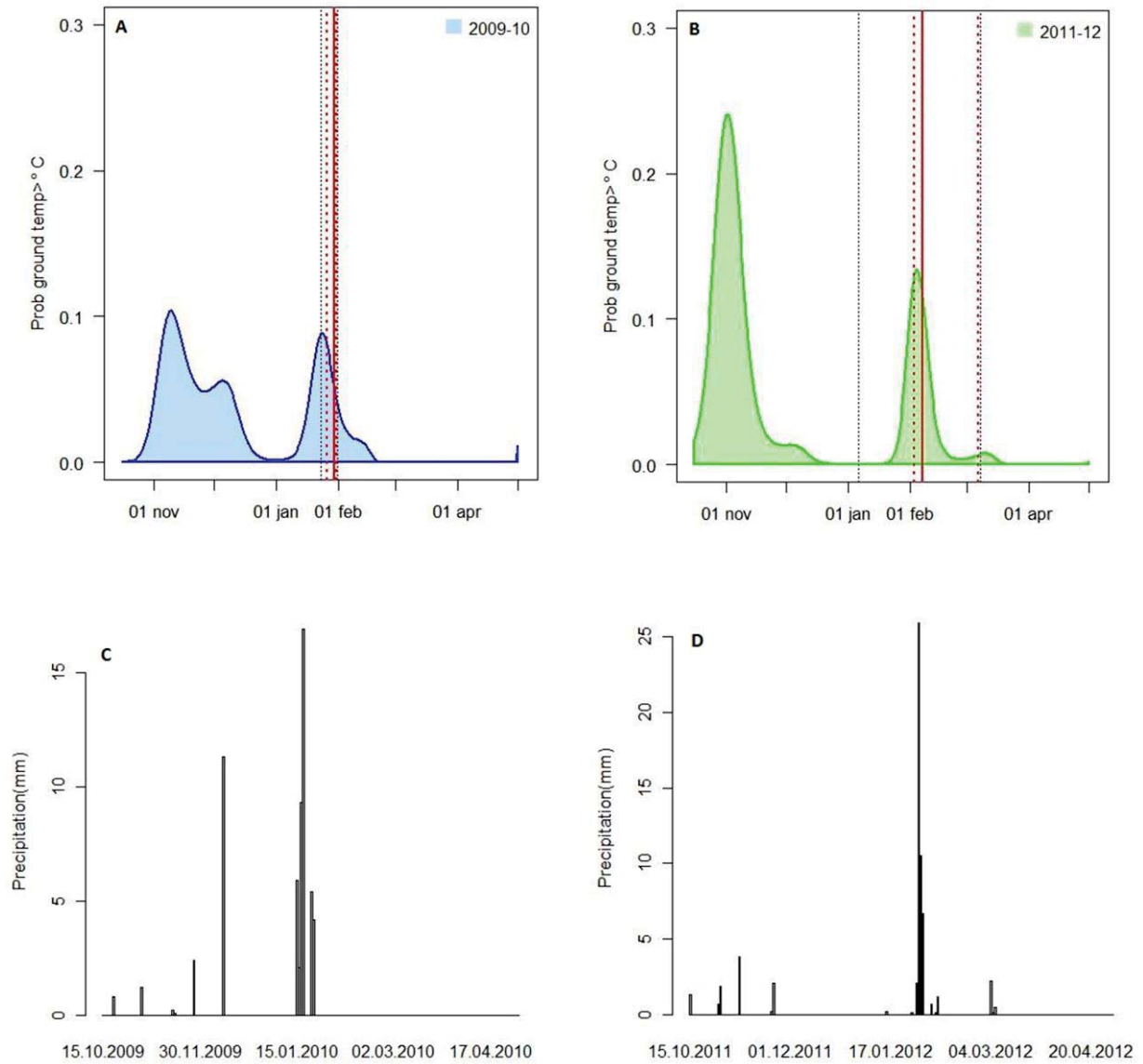


Figure 11: Probability of ground temperature exceeding 0 °C based on GAMs of winter season 2009-10 (A) and 2011-12 (B). The median dates of migration are illustrated as solid vertical red lines. Dashed vertical red lines represent 25% and 75% quantiles and black dashed lines represent 10% and 90% quantiles for each year. Daily precipitation (mm) in days where mean air temperatures > 0 °C are displayed for the same years in the bar graphs below (C: 2009-10 and D: 2011-12).

3.4.3 Migration distances

Supporting P_{2c} , migrants (dispersing animals included) move significantly further between summer and winter range in icing years than in non-icing years ($t = -2.36$, $p = 0.027$). Here,

migrants in the winters of 09/10 and 11/12 (icing years; n=24) travelled further than migrants in winters of 10/11 and 12/13 (non-icing years; n=6; Fig. 12).

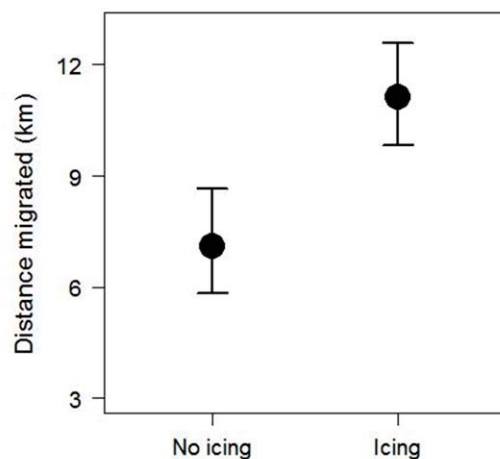


Figure 12: Precited mean distance migrated (in km) for marked female individuals in icing years (2009/10 and 2011/12) and non-icing years (2010/11 and 2012/13). Error bars represent one standard error from the mean.

None of the other migration parameters i.e. mean date of winter/spring migration, average duration of winter/spring migration and average time spent on winter range differed between icing years and non-icing years (Table 2).

Table 2: Svalbard reindeer migration dynamics in icing (n=24) and non-icing years (n=6). Sample size is small in non-icing years because few individuals migrated.

	Icing years			Non-icing years			
	Mean	SD	Range	Mean	SD	Range	T-test, p-values
Mean date of winter migration (date)	Jan 30		Oct 24-March 9	Jan 24		Nov 27-March 22	t= 0.298, p= 0.776
Average migration distance (km)	13.6	7.3	5.3-35.9	8.7	3.2	5.4-14	t= -2,36, p= 0,027*
Average duration of winter migration (days)	8.2	7.7	0.5-25	13.5	17.1	0.1-49.7	t= -0.72, p= 0,496
Average time spent on winter range (days)	74.8	58.4	4.1-197.6	86.9	48.9	14.7-149.1	t= -0.37, p= 0.721
Average duration of spring migration (days)	4.8	5.6	0.4-16.1	3.9	2.9	0.7-8.6	t= 0.41, p= 0.695
Mean date of spring migration (date)	Apr 13		Jan 28-June 18	Apr 15		Jan 7-June 12	t= -0.0548, p= 0.959

3.4.4 Migrants seek ranges near the coast with less ground ice

Migrants showed strong tendencies to travel from inland valleys to coastal areas in northwestern parts of the study area (Fig. 14). Of migrants in icing years, all individuals moved nearer the coast (26 out of 26; 100%). It was only some migrants in non-icing years (2 out of 6; 33%) that travelled the opposite way (away from the coast). These coastal areas had significantly less ice and snow than the inland valleys of which most reindeer migrated from (Fig. 8).

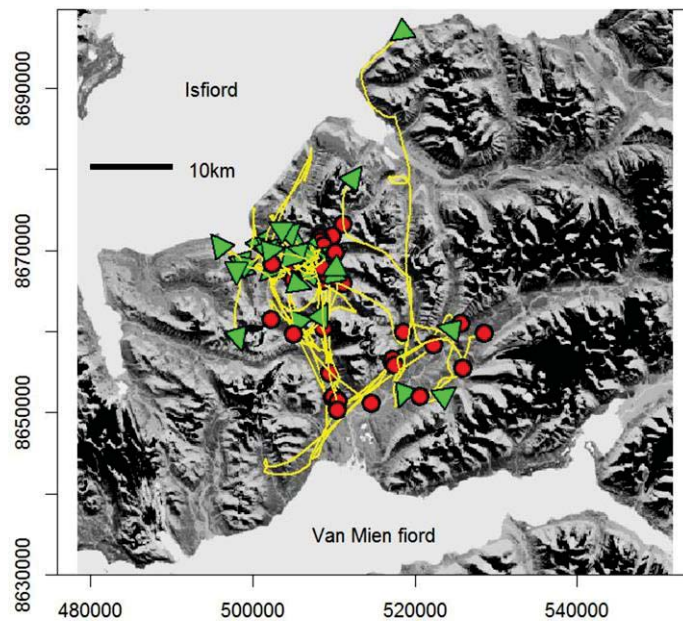


Figure 14: Migration patterns of GPS-collared reindeer. Red circles and green triangles represent migration departure and migration destination points, respectively. The yellow solid-drawn line equals the smoothed movement path between migration departure and migration destination points.

In icing years, migrants generally moved from ranges with ground ice (mean ice thickness: 5.8 cm) to ranges with significantly less ground ice (mean ice thickness: 2.3 cm), supporting P_{2d} ($t= 7.46$, $p<0.001$; Fig. 13). Here, 71.4% migrants moved to areas with significantly less ground ice, 23.8% migrated to areas with less ground ice (but not significantly) while only one individual (4.8%) moved to an area with more ground ice compared to the migration start location. Three migrants were excluded due to the fact that they migrated towards coastal

areas north of the study area, i.e. no ground ice data were obtained in the winter range of these individuals.

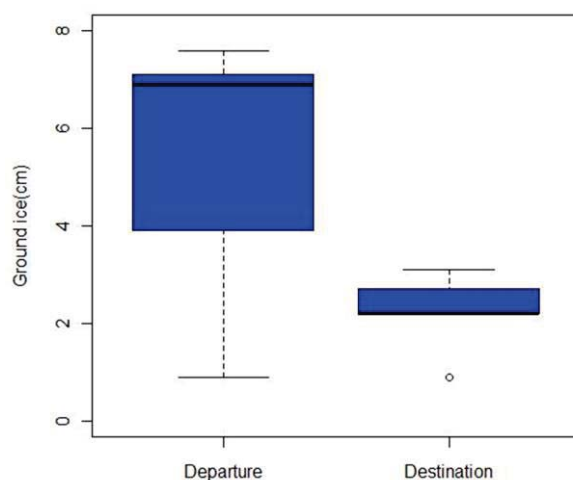


Figure 13: Ice thickness (in centimeter) in departure and destination locations of migrants in icing years.

3.4.5 Individual flexibility in migration strategy

As expected of P_3 , as much as 41% of individuals followed for at least two years, switched movement strategy; staying migratory in icing years and stationary in non-icing years, thus confirming that a large part of the population adjust movement strategy depending on ground ice conditions. This was in strong and significant contrast to that no individuals switched strategy in the opposite direction, contrary to P_3 ($\chi^2=11$: $p < 0.001$) (Table 3). The remaining individuals did not change strategy, i.e. always stationary (33.3% or always migratory (25.9%).

Table 3: The change in movement strategy of marked individuals followed for at least two years (n=27).

Choice of strategy	n	%
Always stationary	9	33.3
Always migratory	7	25.9
Changed strategy according to P_3	11	40.7
Changed strategy contrary to P_3	0	0

4 DISCUSSION

In this study I have shown that the Svalbard reindeer exhibit clear patterns of partial migration in relation to ground icing events. Warm spells followed by ground icing affected migratory behavior of Svalbard reindeer by increasing the probability of migration and increasing migration distance. I have also documented that migration from summer- to winter ranges seem to coincide with warm spells in icing years, as well as causing migrants to seek ranges with less ground ice near the coast. Furthermore, Svalbard reindeer changed movement strategy when facing differing ground icing conditions between years, i.e. adopted a migratory strategy in icing years and stationary strategy in non-icing years. My study provides rare evidence of annual variation in weather events affecting individual migration strategies, in turn influencing the annual portion of migrants in a wild ungulate population.

4.1 Partial migration in Svalbard reindeer

By using field validated data of ground ice, ground temperature and meteorological data in combination with detailed GPS data, I have investigated the effects of warm spells followed by ground icing on migration dynamics of Svalbard reindeer. I have shown that a portion of the adult female Svalbard reindeer population (36%) in my study area perform annual migrations. This is in close accordance with studies of Hansen (2010b) where about every third collared reindeer migrated. Populations of other ungulates that exhibit partial migration often show higher frequencies, i.e. red deer (38-100%) (Mysterud et al. 2011), elk (60%) (Hebblewhite & Merrill 2007), pronghorn (70%)(White et al. 2007). Consequently, the tendency to migrate depends on several factors, i.e. temporal variation in forage conditions, predation risk or density dependent factors. The fairly low overall portion of migrants in my study compared to other ungulate populations may be due to the lack of strong large scale environmental gradients in ice-free winters. Shifts between summer and winter habitat in such winters typically occur at a local scale, from grazing on lush snow-bed vegetation in summer to ridge-vegetation in winter (Hansen et al. 2010a).

4.2 Probability of performing annual migrations depend on ground ice

My study is one of the first to demonstrate that the frequency of partial migration varies among years for ungulates, with a high probability of migration (75%) in icing years and a

much lower probability of migration (25%) in years with no ice. The variation in migration frequency between years strongly suggests that it is beneficial to migrate in icing years and beneficial to remain stationary in years with little icing as proposed in P_{2a} . Hansen et al. (2010b) suggests that abundance of lichen is an important factor for the migration dynamics of Svalbard reindeer at Brögger peninsula. It may be possible that both forage and weather are important factors of migration as lichen has shown to be important for winter survival of reindeer (Boertje 1990; Skogland 1984). However, my study has a longer grazing history than in Brögger peninsula and lichen is thus virtually non-existing and does consequently not drive winter migration in my study area.

Previous studies have examined how weather and snow depth affects migration in ungulates. Winter migrations may be delayed due to absence of snow cover, documented for several ungulates including moose (Ballard et al. 1991). Ungulates may also remain stationary or almost stationary when there is less snow, as seen in mule deer (*Odocoileus hemionus*) (Brown 1992). In similar fashion, such behavior is apparent in my study with a higher portion of migrants in icing years, supporting P_{2a} . However, my results indicate that snow depth is less crucial than ice thickness for the movement behavior of Svalbard reindeer due to the fact that snow on ridges rarely is deep and can be dug away while ice is impenetrable. This interpretation may be caused by the fact that I had fairly low variation in snow depth during the cause of my study. Very large amount of snow would obviously also present an obstacle for reindeer feeding during winter and increase the locomotion costs between feeding areas.

4.3 Timing of migration in relation to warm spells

As expected of P_{2b} , the timing of migration corresponds with the occurrences of warm spells and formation of ground ice in icing years. The majority of migrants in icing years (91%) migrated instantly or shortly after the peak of the warm spell. There were only two animals in icing year 2011/12 that migrated prior to the warm spell (Fig. 11b), but these animals also performed migrations in years with no ground ice and thus do not reflect the common pattern of my study.

Icing years 2009/10 and 2011/12 both had two warm spells. The migration period is linked to the second warm spell for both icing years. There might be several reasons for this. First of all, the first warm spells for both icing years occurred early in the season (November) and

with little precipitation ($<7\text{mm}$) compared to the second warm spells (44 mm and 56 mm respectively). Also, the duration of the warm spells were short. These factors combined indicate that little ground ice was formed during the first warm spell for both icing years. It is also possible that reindeer were able to penetrate a layer of ice if only a thin layer of ice was created in the early warm spells.

In general, the median date of migration occurred shortly after the warm spells in my study. Animals might be able to buffer such icing events by minimizing energy consumption (Nilsen 1986) and remain stationary, instead wearing down the built up fat content in the body (Tyler 1986). In this way they might evaluate the extent of the warm spell before starting migration. There seems to be a tradeoff between staying and searching for local ice free patches (Hansen et al. 2010a) or searching for new ice-free ranges (Stien et al. 2010). A simple explanation for the short delay between the peak warm spell and migration may also be due to that animals delay migration until ice starts to form. Still my results indicate that migration is a direct response of ground icing events following a warm spell.

4.4 Migrants increase migration distance and seek ranges near the coast with less ice

I have shown that migrants moved significantly further in icing years than in years with no or less ground ice, supporting P_{2c} . I have also shown that migratory individuals (71.4%) moved from ranges with ground ice to ranges with significantly less ground ice near the coast as a response to warm spells, as predicted in P_{2d} .

Two previous studies have documented increased movement after warm spells in Svalbard reindeer (Nedberg 2012; Stien et al. 2010). Stien et al. (2010) indicate that migration is a result of opportunistic behavior due to harsh ice conditions, strengthening the idea that migrants are forced to move further in years with ground ice due to the lack of suitable forage. However, the study of Stien et al. (2010) did not use field validated weather data and his study was based on fewer radio collared animals with no data of seasonal movement patterns. The study of Nedberg (2012) only had one icing winter available, fewer GPS-marked animals and lacked the migration model of my study. In contrast, my study combined weather data with field validated data of ground ice, hereby increasing the accuracy of the data. My study gives further and stronger support to the belief that migration in Svalbard reindeer is directly related to warm spells and degree of ground ice (Stien et al. 2010).

No previous studies have documented how spatial distribution of ground ice affects migration patterns of Svalbard reindeer. Tyler and Øritsland (1989) argued that Svalbard reindeer could satisfy their nutritional requirements without the need to wander far due to the large variation in hydrological and micro climatic conditions in the landscape. Hansen et al. (2010a) further suggested that these small scale mosaic variations of the landscape normally enable Svalbard reindeer to seek out local ice-free patches. This might be the case in semi-icing years where the spatial distribution of ice are less severe, but this alone does not fully explain why migrants in my study move to relatively distant areas with significantly less ground ice. The maximum limit for cratering activity for reindeer lie around snow depth of 50-70 cm, although cratering in much deeper snow have been reported (Brown & Theberge 1990). The snow depth threshold for smelling forage has been suggested to be 25 cm (Bergerud & Nolan 1970) and it is known that reindeer avoid deep or hard snow when foraging (Skogland 1984). Cratering sites in the study of Hansen et al. (2010a) on Svalbard reindeer lie around the proposed smelling threshold of Bergerud & Nolan (1970). In my study, only 5% of logger sites of snow depth less than 25 cm in inland valleys were available for foraging due to ground ice (>2cm) in icing years. Furthermore, only 10% of all control sites (n=225) in inland valleys had 2 cm or less ground ice. In contrast, 34% of all control sites (n=151) in coastal valleys had 2 cm or less ground ice, 27% of these control sites in snow depths less than 25 cm (n=41). I suggest that both ice thickness and snow depth limit foraging and that the availability of feeding patches are higher nearer the coast due to less ground ice and snow, leading to migration towards coastal ranges with less ground ice (coast-inland gradient). It is also documented that reindeer feed on kelp and seaweed following an icing event which could be another plausible explanation of migration nearer coast in particularly severe icing years (Hansen & Aanes 2012).

4.5 Individual flexibility in migration strategy

Of individuals followed for at least two years, nearly half of the individuals (41%) changed movement strategy (i.e. adopted a migratory strategy in icing years and stationary strategy in non-icing years) when facing differing ground ice conditions supporting P_3 , while about a third remained stationary (33%) or migratory (26%). In contrast, none switched in the opposite direction contrary to P_3 .

Previous studies have found evidence for that ungulates tend to return to the winter range they inhabited as calves, documented both in white-tailed deer (*Odocoileus virginianus*) (Tiersen et al. 1985) and moose (Sweanor & Sandegren 1988). Migratory behavior, or the absence of it, is thus explained as a result of distinctive learning behavior from mother to offspring (migratory and stationary mothers give birth to migratory and stationary calves, respectively). The default is therefore to conservatively do as your mother, or use the same strategy used in previous year. In line with this, my study shows that some individuals maintained their default stationary strategy. Here, seven of the eight individuals that were stationary in icing years, inhabited the Colesdalen-area (closer to coast, less ice) indicating that a portion of the stationary individuals (87.5%) already reside the “best” range and thus have no need to migrate. Both Hansen et al. (2010b) and White et al. (2007) suggest that preferred movement strategy of ungulates is a result of tradeoff between safe and risky behavior. Consequently, migration may be risky in that it requires a lot of energy with possibly little cumulative gain in reproductive success or forage. In contrast, a stationary strategy is less energy consuming (Nilsen 1986) but can prove fatal under locked pastures leading to starvation (Reimers 1983). Stationary animals may have adjusted to a niche by exploiting the few remaining ice-free patches available, instead of performing risky migrations. This might be the case for weaker individuals that do not have the extra energy to migrate or have no experience of other ranges (Van Moorter et al. 2009).

The main pattern was that individuals switched strategy and that they are successful in detecting areas with less ice than the departure location. My study is one of the first studies that demonstrate that the annual portion of migrants in a population of ungulates depend on the winter conditions, only previously mentioned by White et al. (2007). Here it was suggested that some individuals (20%) in North-American pronghorn migrated in some years but not others by monitoring radio collared animals using aerial telemetry. However, White et al. (2007) had no field validated data of winter conditions but rather proposed that there was an individual assessment of conditional variables such as environmental suitability and behavior of fellow pronghorn before pronghorn decided to migrate or not. Similar environmental assessments prior to migration have been proposed in other ungulates (Ball et al. 2001; Bergerud et al. 1990). A dynamic migration behavior in response to critical events, as seen in Svalbard reindeer, is likely adaptive in terms of increasing winter survival and reproductive success in the following year.

The possibility that animals remember ranges that are more favorable (Van Moorter et al. 2009) , i.e. remember ranges that tend to have less ground ice from year to year, have been debated for Svalbard reindeer (Hansen et al. 2009). Past experience of icing may serve beneficial for the winter survival of “experienced” animals, and explain why most individuals of my study do not “scan” the area but instead start migration to ranges with less ground ice almost instantly following a warm spell. The number of years with repeated GPS-data from the same individuals is still too low to investigate this idea.

In theory, coexistence of migratory and stationary strategies within a partially migratory population should only occur if they result in equal fitness (Hansen et al. 2010b; Lundberg 1988), under the assumption of ideal free distribution. Previous studies have examined demographic tradeoffs between movement strategies (stationary or migratory) of partial migratory populations of ungulates. Scandinavian moose evidently benefited from migration by reducing risk of being hunted at the expense of lowered forage quality (Andersen 1991). In a Canadian elk population, Hebblewhite & Merrill (2011) documented tradeoffs between forage and predation between migratory and stationary strategies. Hansen et al. (2010b) documented a positive effect of improved winter foraging conditions for migratory Svalbard reindeer. Negative fitness consequence could be that migration is energetically costly (Parker et al. 1984), and that individuals move out of previously known areas (Stien et al. 2010), with a risk of ending up in even worse locations with an increased risk of starvation. How partial migration and individual flexibility is expressed in terms of fitness and reproductive success for ungulates still remains to be fully understood.

5 Conclusion

This study contributes to the understanding of how ungulates respond to variation in climate and extreme weather events. I have documented that Svalbard reindeer is partially migratory and that the annual frequency of partial migration depend on ground ice conditions. Further, I have shown that animals may switch movement strategy between years depending on icing events and that they are able to track areas with less ice.

It is likely to assume that icing events may occur more frequently and possibly on an increased spatial extent in the future arctic environment (Putkonen & Roe 2003), under the

assumption of rising temperatures (Hansen et al. 2011; Stien et al. 2012b). Given the complex behavioral flexibility of Svalbard reindeer, it is difficult to interpret how the climatic effects will influence migration patterns in the future. Mass mortalities for high arctic ungulates may be possible if the spatial distribution of ice exceed the spatial scale of realistic migration ranges following an icing year (Gunn 1995). In terms of migration, the theoretical expectation would be that decreased population density may increase stationary behavior due to lower food competition (Lundberg 1988). Still, I expect future icing to have a more important effect than density because it may completely block the access to forage and potentially also have a stronger local gradient (coast-inland) than reindeer density. Despite this, small-scale migrations might still counterbalance some of these future climatic events to a certain extent, especially for more local icing events (Stien et al. 2010).

In future studies it would be interesting to further examine how the patterns of partial migration frequency influence the fitness of stationary and migratory individuals and if the individual fitness varies between years and movement strategy, as predicted from the theory of partial migration. Continued monitoring over several icing years with variable spatial extent, as well as the use of satellite collars to detect mortality of reindeer migrating beyond the study area borders, will be necessary in order to document both survival and spatial movement patterns.



Two curious male Svalbard reindeer in Colesdalen

6 References

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