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Calving site characteristics and habitat use in Svalbard reindeer

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Abstract

Migrating reindeer and caribou tend to return to traditional calving locations every spring with specific environmental conditions and protection of calving grounds is a central part of *Rangifer* conservation. In contrast, the non-migratory Svalbard reindeer inhabit an environment free of predators, insect stressor and human disturbance during calving season making them ideal as a reference population. Little is known about habitat characteristics within calving locations for Svalbard reindeer. The objectives of this study were therefore to first, identify the calving day and location of Svalbard reindeer using GPS relocation data, second, to describe the habitat characteristics in the estimated calving locations, and third, to investigate if females with multiple calving seasons return to the same calving location. Using recursive partitioning and first passage time to estimate calving day, I found that Svalbard reindeer in northern locations calve significantly later in June compared to reindeer located 100 km south, in Nordenskiöld Land. Individual habitat selection analysis demonstrated little difference in habitat selection for females with and without calves during the immediate calving period in any of the study areas. Nordenskiöld Land females tended to select for calving locations with higher than average proportion of moss tundra, flatter and lower elevated areas, while females in northern locations tended to select calving locations with more heath cover and high NDVI. The Svalbard reindeer returned to the same valley or adjacent areas (i.e. side-valleys) to calve for the next calving season, and the distance between the first and second calving location was on average 3.3 km. Although, not statistically significant, such short distances between consecutive calving sites indicates site fidelity to the calving area. This thesis provides knowledge on important habitat characteristics for reindeer calving locations and can provide management with information to restrict human activity within areas critical for Svalbard reindeer reproduction.

Keywords: *GPS, remote sensing, habitat selection, ecology, niche, reindeer, ungulates, calving, spring, vegetation, calving site fidelity, Svalbard.*

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1 Introduction

Calf survival is one of the main factors that affect population dynamics in many ungulate species, including reindeer and caribou (Vors and Boyce 2009), elk (Lukacs et al. 2018) and moose (Testa 1998). Due to this, the calving period is considered a critical stage in the life history of ungulates, and the decisions about calving locations are often influenced by experience and memory in large herbivores, where ungulates select calving locations based on perceived risk and foraging conditions (Tremblay et al. 2007, Van Moorter et al. 2009). In recent years, ungulate populations such as *Rangifer* species have experienced large population declines related to e.g. climate change, anthropogenic landscape changes and increased human disturbances, and a better understanding of the factors contributing to this decline is of increased interest (Vors and Boyce 2009).

The immediate calving period, defined as the stage when parturition takes place and the female needs to recover from calving, is often the time-period when predation risk is also highest (Nobert et al. 2016). Fear of predators affect the habitat choice during this stage because the females are less mobile and the calves highly vulnerable to predation. The predation-risk hypothesis states that ungulates are more likely to select sites with less optimal foraging conditions if there is high predation-pressure in the area (Kie and Bowyer 1999). Selecting for areas with lower food quality is possible because many ungulates are capital breeders. This means that they use their own energy reserves during the immediate stage of the calving period, but eventually need to replenish their energy stores as the calf grows older and needs more milk (Veiberg et al. 2016). As the calf grows older, there is an increase in nutritional requirements for the cow due to lactation and a relative decrease in predation risk (Nobert et al. 2016). Thus, the food quality and quantity are playing an increasing role in female habitat selection, and the choice of the calving location will be influenced by a trade-off between foraging conditions and predation risk (Loe et al. 2006, Gustine et al. 2010, Nobert et al. 2016). Understanding this trade-off and the habitat characteristics of calving locations can aid management in conserving landscapes important for ungulate reproduction.

1.1 Habitat selection during calving in *Rangifer*

The main driver for choice of calving locations for *Rangifer* populations is often predation-risk. *Rangifer* females tend to separate from the rest of the herd during parturition to minimize the risk of detection by predators such as bears or wolves (Gustine et al 2010). Reindeer and caribou populations have developed anti-predator strategies to minimize the risk of detection during the critical calving stage. One of the preferred habitat types for woodland caribou during the immediate calving period are suboptimal habitat types, such as barren landscapes, higher elevated areas with limited food availability (McCarthy et al. 2011), or dense vegetation that gives protection from predators (Carr et al. 2008). These landscapes are selected because predator density is often lower in these vegetation types (Gustine et al. 2010) (Table 1). In woodland caribou, the pregnant females move up in elevation close to the alpine zone, but below the treeline outside of the predators' home range, while the males keep a lower elevation (Wood 1994, Jones et al. 2006). Similarly, wild reindeer in Hardangervidda, Norway, select relatively nutrition-poor, rocky areas for calving locations (Strand et al 2006). *Rangifer* are also known to distance themselves from other perceived risks such as human activity and infrastructure (Vistnes and Nelleman 2006). In mainland Norway, wild reindeer in Beitostølen avoid human settlements (houses and cabin areas) and roads during the calving period (Strand et al. 2015). In addition, females avoid wet areas during the parturition period as the newborn is susceptible to getting cold and wet the first days after birth (Tyler pers.comm, October 2017). These examples of calving location characteristics and strategies contribute to increase the chance for calf survival during the critical calving stage of *Rangifer* reproduction.

Foraging availability, both quality and quantity, plays an increasing role as the calf grows older. In reindeer, the nutritional requirements from forage other than milk begin when the calf is strong enough to walk and occurs around week 2 for reindeer on mainland Norway (Rognmo et al. 1983). This is a critical period where the mother also needs to replenish her energy reserves from lactation. For instance, calving sites of woodland caribou in Northern Ontario (Canada) were characterized by having high foraging quality with mineral-rich plants, such as lichens and *Ericaceans* that are important for lactating females in mid-July, compared to locations where females without calves were observed (Lantin 2001). While wild reindeer in Setesdal Ryfylke (Norway) and British Columbia (Canada) preferred calving sites on south-facing slopes that became early snow-free (Jones et al. 2006, Strand et al. 2011). The latter demonstrates the importance of landscape features and terrain variability in reindeer selection of calving areas. During the post-parturition stage reindeer habitat with higher food quality and

quantity become increasingly important because the *Rangifer* females need to replenish energy reserves from lactation.

If the foraging conditions and predation-risk are assessed to be adequate the herd will return to the same calving locations for multiple years (Hazell and Taylor 2008). The strong site fidelity for calving locations are well documented in many reindeer and caribou herds in both Europe and North-America (Schaefer et al. 2000, Popp et al. 2008). For instance, in mainland Norway wild reindeer return to the same calving ranges in most ranges (e.g. Setesdalheiene, Beitostølen and Hardangervidda) (Strand et al. 2005,2011,2015). Similarly, GPS collared boreal caribou in Northern Ontario used the same core areas for calving during multiple years (Hazell and Taylor 2008) and in British Columbia, 6 out of 10 reindeer returned to the same area to calve the next year (Wood 1994). The scale of the calving location is important to consider when investigating calving location fidelity. For example, migratory and sedentary caribou display high calving site fidelity for the post-calving ranges, but fidelity to calving locations on a smaller spatial scale such as for the immediate calving site can vary (Schaefer et al. 2000). High calving location fidelity indicates that appropriate habitat characteristics exist in the calving locations and can be used as an indication for habitat suitability.

Although reindeer and caribou return to approximately the same calving ranges these areas are also known to shift. Particularly if habitat conditions in the calving site changes, such as predation-risk or human disturbance in the given year. If predator abundance increases the caribou will improve fitness by shifting their calving ranges to an area with less predation-risk (Lafontaine et al. 2017). Humans are perceived as a threat for reindeer, and historical calving sites of wild reindeer in Beitostølen shifted due to habitat fragmentation from increased cabin- and road building (Strand et al. 2006). Shifts in calving ranges highlight the importance of identifying the factors responsible for the changes in calving locations and the impact on reindeer reproduction from such human disturbances.

1.2 Habitat use and calving locations in Svalbard reindeer

The high-Arctic Svalbard archipelago houses the endemic Svalbard reindeer (*Rangifer tarandus platyrhunchus*), which is a key herbivore and a main driver of vegetation community dynamics (Hansen et al. 2007). In contrast to most other *Rangifer*, the Svalbard reindeer is solitary, non-migratory and not subject to predation, insect harassment or interspecific competition (Reimers 1977, Tyler and Øritsland 1989). Despite being an attractive species for

research over many decades, very little is known about their choice of calving locations and the habitat characteristics within these sites.

The Svalbard reindeer use small traditional home ranges (Tyler and Øritsland 1989), and they appear to show site fidelity to their home ranges (Hansen et al. 2010, Kinck 2014). For example, Kinck (2014) showed that the winter and summer home ranges of reindeer in Nordenskiöld Land overlapped as much as 70%, likely due to adequate foraging availability in both seasonal home ranges. In the same study, females with calves also tended to have a smaller home range compared to females without calves. There are also indications that Svalbard reindeer females show site fidelity to their former calving locations (Tyler and Øritsland, Hansen et al. 2010). In central Spitsbergen (Adventdalen), females were observed walking long distances right before calving, which indicate preference towards specific calving areas (Tyler and Øritsland 1989). Likewise, in coastal populations further north, females were returning across the sea from winter to summer ranges to calve (Hansen et al. 2010). Yet, no study has taken advantage of investigating calving location characteristics, selection and site fidelity using the accumulated pool of high-quality spatial data derived from GPS collars females in Svalbard.

Svalbard reindeer have few natural predators, although polar bears, Arctic foxes and glaucous gulls are known to occasionally kill adult reindeer and calves (Brattbakk and Øritsland 1986, Prestrud 1992, Derocher et al. 2000). Only a handful of observations exist of polar bears preying on adult Svalbard reindeer (Derocher et al. 2000). Similarly, Arctic foxes have terrorized reindeer mothers and calves in the past (Brattbakk and Øritsland 1986) but only one successful kill by Arctic fox is documented (Prestrud 1992). Since predation on Svalbard reindeer is rare, it is therefore likely that the reindeer females perceive predation-risk as low during the calving period, despite the calves being vulnerable to predation and less mobile during the calving period. The unique, almost predator-free environment of the high-Arctic archipelago makes it interesting to study Svalbard reindeer' choice of calving locations in relation to other ungulates where calving site selection is mostly driven by predation.

The factors contributing to the selection of calving locations for Svalbard reindeer are currently mostly unknown. There are also some indications that the Svalbard reindeer show remnants of anti-predatory behavior during the calving period although predation is almost non-existent in this high-Arctic environment. VHF collared Svalbard reindeer seasonally migrated between the lichen-rich Sarsøyra in the winter to the adjacent overgrazed peninsula Brøggerhalvøya in

the summer possibly owing to high site fidelity towards calving locations (Hansen et al. 2010). The tendency to return to the same summer home range although the location was classified as resource-poor indicated that the reindeer displayed high site fidelity. However, the hypothesis about remnants of this type of anti-predatory behaviour in Svalbard reindeer has not been explored further.

Food resources are scarce in early spring in Svalbard and are likely to play an important role (Van der Wal et al. 2000). Svalbard reindeer are often observed in areas becoming early snow-free in the spring, and these patches are often in southern aspects and sloped hills (Pedersen pers. comm, May 2018), which are also the areas that receive the most heat load during the day (Parker 1988). The snow-free areas are also the areas where plants begin to sprout first in the spring. The Svalbard reindeer are opportunists, but are known to select food quality over quantity during the first part of spring/summer (Van der Wal et al. 2000) and then switch to food quantity in the later part of summer/fall (Henriksen et al. 2003). Food availability, both quality and quantity, may play a main role in habitat use, site selection and fidelity during the calving period (Loe et al. 2006). Such conditions are impacted by the fast-changing natural environment (SWIPA 2017) and the plasticity in foraging behavior of the reindeer – thus being the key to calf survival (Hansen et al. 2009).

1.3 Identification of calving time, habitat characteristics and site fidelity using GPS data

It can be challenging to investigate reindeer calving site habitat characteristics, selection and fidelity because it can disturb and stress the females during a critical stage of their life history and interfere with the calving process (Overrein 2002, DeMars et al. 2013). Tracking animals equipped with GPS devices to record their movement patterns is therefore one way to overcome this challenge because it records space use at fixed time intervals without human interference that stresses the animals.

Identification of calving time, which is a prerequisite to study habitat characteristic and selection of calving sites, has earlier been done using GPS data by taking advantage of reindeer and caribou's distinct movement patterns before, during and after calving (Rudolph and Drapeau 2010, DeMars et al. 2013, Le Corre et al. 2014). The pre-calving period is characterized by a general restlessness as the female try to find a suitable calving site (Strand et al. 2011, Veiberg et al. 2017). This can be identified as an increase in movement rate on GPS relocation data (Rudolph and Drapeau 2010, Danielsen 2016, Veiberg et al. 2017). Then, the

pre-calving period is followed by parturition and resting after birth, which can be observed as a decrease in movement rate. The mother cannot move far with her calf so she maintains a slower speed until the calf is able to maintain adult speed at about 4 weeks of age (DeMars et al. 2013). This distinct movement behaviour can help to identify the parturition time for individual reindeer.

Different methods have been developed to estimate calving time using GPS data. Rudolph and Drapeau (2012) estimated calving patterns based on changes in movement rate and net displacement over time for reindeer populations in Ontario, Canada. First passage time (FPT) is another metric used to detect differences in movement patterns (Le Corre et al. 2014). It was originally derived to estimate habitat selection using foraging patch theory and aids in distinguishing movement patterns related to foraging and traveling activities (Fauchald and Tveraa 2003). FPT has previously been used successfully to identify calving grounds based on the time spent in one area (Le Corre et al. 2014), but has never been tested on smaller spatial scales to identify calving locations for other more sedentary animals. Since Svalbard reindeer are non-migratory they may not display as large differences in movement patterns across seasons compared to migrating caribou or reindeer. It is, however, likely that the Svalbard reindeer show similar anomalies in movement patterns during parturition time as other subspecies (Veiberg et al. 2017). Thus, making it possible to identify the exact calving time to further study habitat characteristics, selection and fidelity of this high-Arctic reindeer species.

1.4 Goals and hypotheses

Calving time for Svalbard reindeer has previously been estimated using data from GPS collared females in Nordenskiöld Land during the period from 2009 till 2015. Yet no study has taken the advantage of the pool of GPS data from several Svalbard reindeer populations across 9 years (2009-2017) and two different bioclimatic zones to study and compare calving location habitat characteristics, selection and site fidelity. This thesis addresses these knowledge gaps by focusing on three main goals with the following hypotheses:

- 1) *Estimate calving day and location of female Svalbard reindeer by using GPS data from four reindeer populations, and review the quality of the method.* I hypothesize that northern and southern populations have differing calving days because the northern locations become later snow-free compared to southern locations due to climatic and latitudinal differences. The climatic difference can play a role in the calving time in the spring because food resources become later available for females in northern locations.
- 2) *Identify habitat characteristics in calving sites and compare habitat selection of females with and without calves during the same period.* I predict that Svalbard reindeer females with calves select for the same habitat compared to females without calves due to that both experience the similar low predation risk. Therefore, all females select for areas with high forage quality, likely on south-facing slopes with high terrain ruggedness that become earlier snow-free (Table 1).
- 3) *Investigate calving site fidelity by evaluating the distance to previous calving site and potential overlap for females calving multiple years.* Hansen et al. (2010) demonstrated site fidelity in female reindeer on Brøggerhalvøya based on a small sample of VHF collared females. Based on this I predict that female reindeer return to the same calving area in consecutive years due to favourable habitat characteristics in these areas.

These predictions will be explored by estimating calving day from existing GPS data from female reindeer between 2009 and 2017 in four Svalbard reindeer study populations in the Svalbard archipelago. Individual habitat characteristics and selection within estimated calving locations will be analysed for females with and without calves using the K-select analysis. The results from this thesis can enhance the knowledge base for the management and conservation

of the endemic Svalbard reindeer, which live in a natural environment that is under pressure from climate conditions and human activities (Nordli et al. 2014, SWIPA 2017).

Table 1. Overview of predictor variables for analysis of habitat selection in calving locations for Svalbard reindeer. The table is based on a literature review of studies of reindeer and caribou calving site selection in their circumpolar ranges. Hypothesis and justifications important to other *Rangifer* populations (AR=All *Rangifer*) and predictions specifically for Svalbard reindeer (SR=Svalbard reindeer) are separated in individual columns. All original spatial data layers are static layers (i.e. average across several years or from individual satellite image scenes) meaning that they do not capture any annual variation.

| Predictor variable | Digital spatial data layer | Hypothesis and justifications (AR) | Prediction (SR) | Original spatial resolution (m) | Reference |
|--------------------------|------------------------------------|--|--|---------------------------------|--|
| Food quality | <i>Moss tundra</i> | Nnutritious plants are important during the calving period due to greater energy needs during the calving period. Moss tundra includes presence of the important plants for lactating females in calving site. | Females will select calving sites with higher proportion of moss tundra than the average availability in the landscape. | 30 x 30 | Johansen et al. (2012), Lantin et al (2001). |
| | <i>Heath</i> | Heath is a vegetation class that includes important foraging plants for reindeer. | Northern female reindeer select more heath compared to southern reindeer female due to differences in availability of these two types. | 30 x 30 | Johansen et al (2012). Lantin et al (2001). |
| | <i>Barren</i> | The reindeer will select barren areas instead of areas with high food quality due to predation-risk. | Females will not select barren locations due to low predation-risk. | 30 x 30 | Gustine et al (2010). Lantin et al (2001). |
| Food quantity | <i>NDVI</i> | High biomass is important due to greater energy needs and lower mobility in calving period. NDVI is a measure of foraging quantity. | Females select calving sites with high NDVI. | 250 x 250 | Johansen and Tømmervik (2014) |
| Terrain variables | <i>Topographical Wetness Index</i> | Females choose areas that are drier for calving. | Females select areas with low wetness values. | 30 x 30 | Loe et al (2006) Hansen et al (2009). |
| | <i>Slope (DEM)</i> | Calving sites are in south facing slopes. Reindeer prefer slopes less than 30 degrees. | Females select areas with slopes 0 > 30 degrees. | 20 x 20 | Loe et al (2006) |
| | <i>Aspect (DEM)</i> | Calving sites are in south-facing slopes where snow melts faster and plants emerges earlier. | Females select areas with south-facing aspects. | 20 x 20 | Strand et al (2011) |
| | <i>Elevation (DEM)</i> | Calving sites are often at higher elevations which often are outside the range of the most common predators. | Females select areas at low elevation since predation is low during calving. | 20 x 20 | Wood (1994) Jones et al (2006) |
| | <i>Terrain Ruggedness Index</i> | Calving sites are often in less rugged terrain to ease detection of predators. The pregnant females want overview in the landscape, so they are not ambushed by predators. | Females seek terrain with high ruggedness values due to higher terrain heterogeneity leading to more diverse foraging resources. | 30 x 30 | Nelleman and Thomsen (1994) |
| | <i>Heat Load Index</i> | The amount of solar radiation (heat load) hitting the ground is an indicator of snow-melt. | Females select areas with high heat load values due to early snow melt | 30 x 30 | Parker 1988 |

2 Methods

2.1 Study areas

The study areas were located in the high-Arctic on the archipelago of Svalbard and consists of four locations in Brøggerhalvøya, Sarsøyra and Kaffiøyra (termed northern locations) and Nordenskiöld Land (termed southern location) (Fig. 1). Nordenskiöld Land (78°N, 15°E) is located in central parts of Spitsbergen and is approximately 3554 km². The main study areas on Nordenskiöld Land were found in Reindalen, Colesdalen and Semmeldalen, an area of approximately 150 km² (Loe et al. 2016). Nordenskiöld Land contains three small coastal settlements, including Longyearbyen (2000 inhabitants), Barentsburg (400 inhabitants) and Svea (closed down mining town) (Sysselmannen 2016). The landscape on Nordenskiöld Land is characterized by wide valleys, steep mountains and hillslopes and glaciers. The vegetation cover is dominated by dense vegetation in the lowlands, such as marshes or wetlands in the valleys or heaths on the hillslopes, but mostly polar desert (Johansen and Tømmervik 2014). Nordenskiöld Land is considered one of the most productive land areas in Svalbard (Karlsen et al. 2014).

About 100 kilometers north of Nordenskiöld Land are the northernmost study areas Brøggerhalvøya, Sarsøyra and Kaffiøyra located (78-79°N, 11°E). These are coastal areas with less vegetation and limited human disturbance compared to Nordenskiöld Land (Hansen and Aanes 2014). Brøggerhalvøya is a peninsula by Kongsfjorden, northwest on Spitsbergen, approximately 60 km². The peninsula is characterized by mountains, glaciers and coastal lowlands. The nearest town is Ny-Ålesund with 35 inhabitants on the northeast of the peninsula (Hansen and Aanes 2014). In contrast, Sarsøyra and Kaffiøyra are two smaller, coastal plains with almost no human activity. These study areas are located south of Brøggerhalvøya in Forlandsundet, of respectively 40 and 35 km². The three study areas are characterized by polar desert with patches of graminoid and shrub vegetation varying 5-10 cm (Johansen and Tømmervik 2014, Moullec et al. 2017).

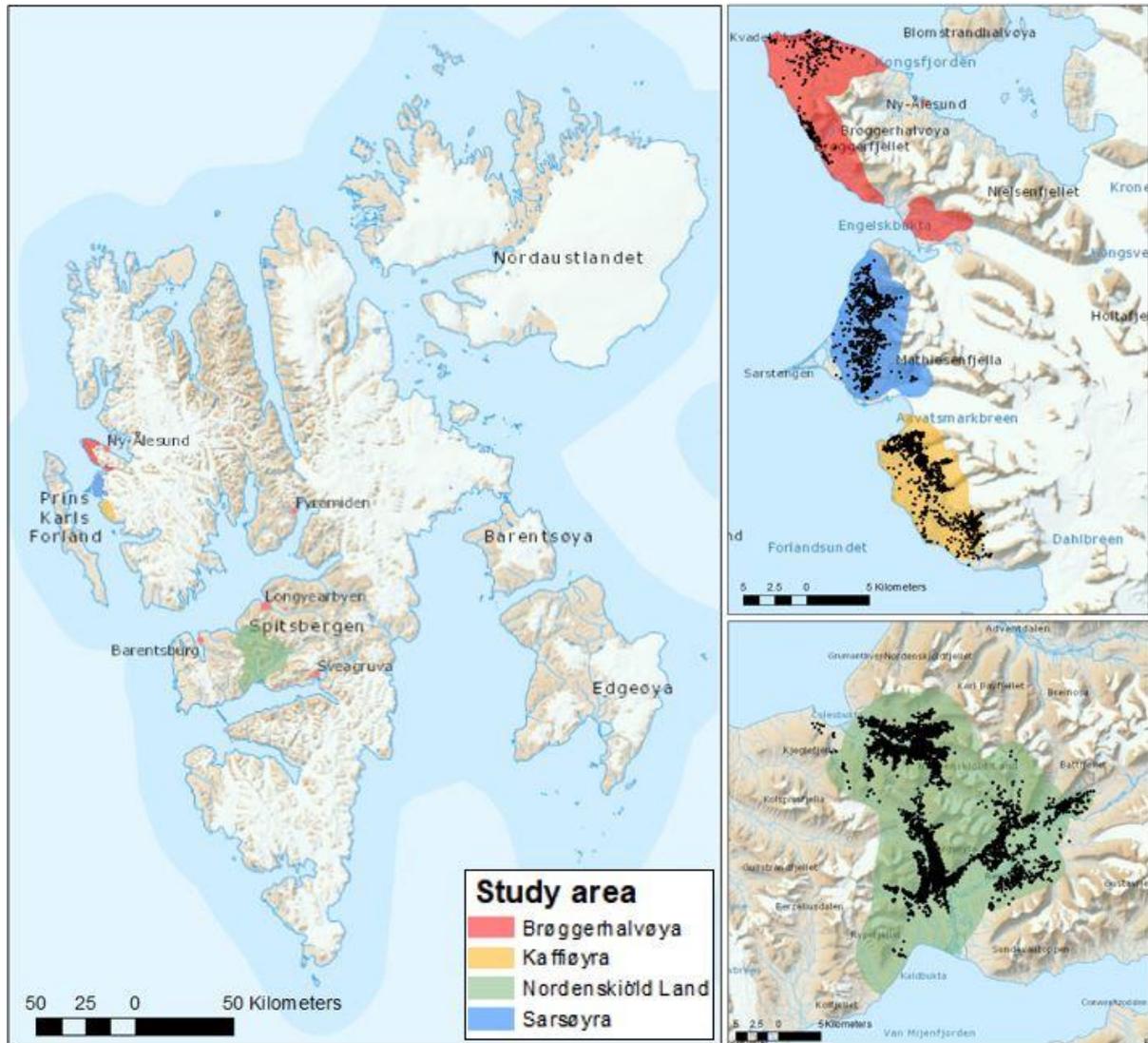


Figure 1. Map of the four study areas with GPS collared female Svalbard reindeer. The northern locations Brøggerhalvøya (red), Sarsøya (blue), Kaffiøya (yellow) and the southern location Nordenskiöld Land (green). The colored areas are merged spring home ranges (15 May to 30 June) for all females with calves during the study period 2009-2017. GPS positions for all females during the same period is shown on the left as black dots within the study areas.

The study areas are located within two bioclimatic zones (Elvebakk et al. 1999), and climatic differences govern the habitat conditions of Nordenskiöld Land and the northern locations Brøggerhalvøya, Sarsøya and Kaffiøya. The number of days with snow cover differ between the locations and both spring onset and snow-melt is later in the northern locations. Brøggerhalvøya has 41 days more with snow compared to Nordenskiöld Land (Fig. 2). Snowmelt tends to occur earlier in Nordenskiöld Land compared to the northernmost locations due to the latitudinal differences. Brøggerhalvøya and Nordenskiöld Land had most snow days in 2014 and least snow in 2016.

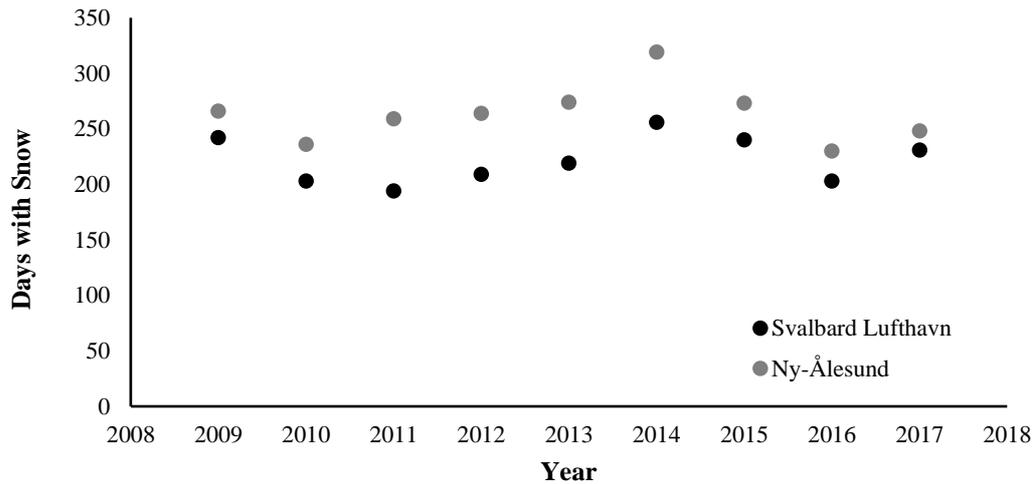


Figure 2. Number of days with snow cover in Svalbard. Nordenskiöld Land (Svalbard Lufthavn) and Brøggerhalvøya (Ny-Ålesund) between 2009-2017 (Meterologisk-Institutt 2018).

2.2 Study species and populations

The Svalbard reindeer are distributed across the entire Svalbard archipelago and have inhabited the island for at least 6000 years (Kvie et al. 2016). The reindeer colonized Svalbard by natural dispersal and are genetically linked to Eurasian reindeer. In contrast to other *Rangifer* they appear in small groups and are non-migratory (Tyler and Øritsland 1989). Nordenskiöld Land is the region in Spitsbergen with the densest population of reindeer (MOSJ 2017). The study population reside in the valleys of Colesdalen, Semmeldalen and Reindalen and can move freely between these interconnected valleys. Human activity is highest in the winter and early spring due to snowmobile traffic between small settlements between February-May, and the reindeer are likely to be disturbed during this period (Tandberg 2016). In the fall, reindeer hunting occurs in designated areas within the study area, selected by management authorities of Svalbard. The calving period coincide with late snow melt rendering the study largely inaccessible both by snowmobile, ski or by foot. The reindeer populations in Nordenskiöld Land have steadily increased since the 1990s and population counts in Adventdalen and Reindalen revealed the populations to be 1 282 (2017) and 1089 (2016) animals, respectively (MOSJ 2017). This makes Nordenskiöld Land the study area with the largest reindeer populations.

The three northern populations on Brøggerhalvøya, Kaffiøyra and Sarsøyra are isolated from each other by glaciers and fjords, but migrations between the three study areas are recorded in the past (Hansen et al. 2010). The reindeer population in Brøggerhalvøya was historically

eradicated from hunting and the current population is based on the genetic material of 12 reindeer from Adventdalen introduced to the island in 1978 (Aanes et al. 2000). The introduced reindeer quickly grew in population and experienced a population crash in 1996 due to insufficient forage resources after a rain event that led to formation of heavy ground ice. The population in Sarsøyra was established during the crash year before by reindeer that moved from Brøggerhalvøya across glacier or fjord ice in search for new foraging areas. In 1996 reindeer from Sarsøyra populated Kaffiøyra making it the most recent established population of the three northern study areas. Thus, the current northern populations have been in the study areas less than 40 years (Staaland et al. 1993). No hunting occurs in these areas and human activity is rare apart from field researchers in the spring and fall. The population in Brøggerhalvøya is now at a stable level of about 109 animals (MOSJ 2017), while Sarsøyra and Kaffiøyra have a higher reindeer population, with total counts equaling 221 and 144 reindeer during summer 2013 in Sarsøyra and Kaffiøyra, respectively (Le Moullec et al. 2017).

2.3 GPS reindeer data

2.3.1 Field protocols - capturing and handling

The animals were captured and handled each spring according to protocols approved by the Governor of Svalbard and the Norwegian Ethics Committee during the study period 2009-2017. The reindeer were captured with a handheld net from two snowmobiles and restrained while GPS collars were fitted or checked, and calf status by ultrasound and/or progesterone tests were recorded. The procedures were done by trained biologists each spring. The 51 GPS collared reindeer in Nordenskiöld Land recorded movement every 1-2 hours between 2009-2012 (Vectronic store-on-board collars), and every 8 hours between 2013-2016 (Follow-it satellite link collars). The GPS collared reindeer on Brøggerhalvøya (12 females), Kaffiøyra (11 females) and Sarsøyra (8 females) also wore satellite-link collars that recorded GPS locations every 8 hours between 2014-2017 (for more details on the methods see Loe et al. (2016)).

In the fall, population counts and calf status for the GPS collared females were recorded in all study areas (Table 2). Thus, it was possible to identify which of the GPS collared females captured in the spring and measured for pregnancy, had calves surviving the summer after birth. Only females observed with calf in the fall by trained personnel were considered in the study to make sure that the analysis did not include females that aborted the fetus in spring. In

total, 65 females from the four populations in Nordenskiöld Land, Brøggerhalvøya, Sarsøyra and Kaffiøyra that were captured and fitted with GPS collars had one or more calf over the study period. Thus, this dataset consisted of 189 animal years for GPS collared females (95 with calf, 94 with no calf) between 2009-2017 (Table 2).

Table 2. Summary of number of GPS collared females observed with calf (=1) or no calf(=0) during field surveys in the fall in the four study areas between 2009 and 2017. The GPS collar program started in 2014 for Brøggerhalvøya and Kaffiøyra, and 2016 for Sarsøyra.

| | 2009 | | 2010 | | 2011 | | 2012 | | 2013 | | 2014 | | 2015 | | 2016 | | 2017 | |
|----------------------|----------|----------|----------|----------|----------|----------|----------|-----------|----------|-----------|-----------|-----------|-----------|-----------|----------|-----------|----------|-----------|
| No calf (0)/Calf (1) | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| Nordenskiöld Land | 8 | 5 | 6 | 6 | 7 | 4 | 9 | 10 | 9 | 11 | 5 | 10 | 9 | 5 | 3 | 8 | 3 | 7 |
| Brøggerhalvøya | | | | | | | | | | | 10 | 0 | 8 | 5 | 1 | 4 | 2 | 2 |
| Kaffiøyra | | | | | | | | | | | 7 | 2 | 5 | 5 | 0 | 4 | 0 | 0 |
| Sarsøyra | | | | | | | | | | | | | | | 2 | 6 | 0 | 1 |
| TOTAL | 8 | 5 | 6 | 6 | 7 | 4 | 9 | 10 | 9 | 11 | 22 | 12 | 22 | 15 | 6 | 22 | 5 | 10 |

2.3.2 Filtering of GPS data for analysis

For estimating calving locations in spring home ranges, I included GPS fixes between May 15 and June 30 for GPS collared females from the four study areas. This temporal scale was selected because it covers the entire calving period (Veiberg et al. 2016). Before the analysis, the data was filtered for unrealistic movement patterns using a screening procedure (Bjørneraas et al. 2010) implemented in R. The filtering method was applied to the GPS datasets from Brøggerhalvøya (2014-2017), Sarsøyra (2016-2017), Kaffiøyra (2013-2017) and Nordenskiöld Land (2009-2017). The screening procedure applied from Bjørneraas et al. (2010) filtered out unrealistic movement distances and turning angles between consecutive GPS fixes based on established movement parameters and knowledge about the reindeer's movement pattern. All GPS fixes with a median distance >100 km, mean distance >10 km, and step lengths that exceeded 1.5 km/h with a turning angle between 166 and 194 degrees were excluded from the dataset. The conservative movement thresholds were chosen because they handle the trade-off between removing location errors and retaining sufficient GPS fixes in the dataset. After the screening procedure 3% of the GPS fixes were removed from the dataset. In addition, all GPS points with a Horizontal Dilution of Precision (HDOP) more than 10 meters were excluded. The HDOP measures the uncertainty of GPS coordinates in space and was applied to increase

the spatial precision of GPS fixes (Recio et al. 2011). 7% of GPS fixes was removed from the dataset after applying HDOP the threshold of 10 m,

Individual reindeer recorded a variable number of relocations per day, with the two most common schedules being 12 and 3 relocations per day. To standardise, individuals with high frequency of relocations were rarefied to three GPS fixes per day by sub-sampling the data set to the same (or close) times as the GPS dataset with 3 relocations per day. This was done to achieve similar precision across the four study populations (for effect of number of relocations on calving day estimation see appendix A). GPS collared females with calf and less than 60% successful fixes between 15. May and 30. June were excluded from the study (n=5). In average, the remaining 90 animal year movement trajectories had a mean successful fix rate of 97% (93% for Follow-it satellite link service, 98% for Vectronic store-on-board).

2.4 Processing environmental variables

Selection of environmental variables for analysis of calving home ranges and habitat selection were based on knowledge about important factors for habitat selection in calving ranges elsewhere, the ecology of Svalbard reindeer and availability of digital spatial layers for the study area (Table 1). The environmental variables outlined below were derived and processed from satellite layers using ArcMap 10.6.1 (ESRI 2011) and R Studio Version 1.0.143 (Rstudio 2015, Eischeid and Ravolainen pers.comm, November 2017). All layers were resampled to 30×30 meters spatial resolution, and the pixel values were recalculated for all vegetation variables using neighborhood analysis. In this neighbourhood analysis a nine-pixel moving window where the middle pixel gets the average value of the nine pixels (including the middle pixel) surrounding it. This analysis especially useful for seeing patterns in a patchy landscape (Turner 1990).

2.4.1 Vegetation variables

Forage quality. The vegetation layers were derived using unsupervised classification of Landsat 7 TM/ETM+ satellite imagery from 1987 to 2002 by Johansen and colleagues (2012). The vegetation map initially contained 18 vegetation groups, but was grouped into 3 main vegetation classes, moss tundra, heath and barren, to reflect the main foraging types and because several of the sub-classes were ambiguous when comparing the vegetation classes to ground truthing work (Pedersen et al. 2017) (Table 3). For example, moss tundra also includes moist vegetation classes such as swamps, marshes and wet tussock as satellite-based

classification of these were inconsistent with field observations that confirmed moss tundra (Ravolainen pers. comm. November 2017). Heath contained drier vegetation communities dominated by *Cassiope*, *Dryas* and *Carex rupestris*. On coastal flats such as in the northern study areas, the heath communities were dominated by *Saxifraga oppositifolia* and *Luzula spp.* The barren vegetation class was based on sub-classes such as sparsely vegetated flats, polar deserts and polygon fields. Barren landscapes are known as poor foraging areas for Svalbard reindeer, but reindeer elsewhere seek towards this landscape type during the calving period (Strand et al. 2006).

Table 3. Overview of the three main vegetation classes and the sub-vegetation classes from Johansen et al. (2012) that were re-grouped into the three main classes. The vegetation layers were originally created by Johansen et al. (2012) and re-classified by Isabell Eischeid and Virve Ravolainen.

| Vegetation classes | Sub-vegetation classes |
|--------------------|---|
| <i>Moss tundra</i> | Vegetated flats, moist/wet tussock, swamps, mires, marsh, moist moss tundra dominated by <i>Tomentypnum nitens</i> , <i>Alopecurus borealis</i> , <i>Eriophorum schueuchzeri</i> and <i>Dupontia fisheri ssp. Psilosantha</i> . Arctic meadows, bird cliff communities, open dry grass communities. |
| <i>Heath</i> | Open dryas communities with <i>Carex rupestris</i> , Dense <i>Dryas octopetala</i> heaths, <i>Cassiope tetragona</i> with elements of <i>Dryas</i> heaths, <i>Luzula</i> vegetation and lichens. |
| <i>Barren</i> | Wet, non-vegetated to sparsely vegetated flats, beaches, slopes and river fans, gravel, barren communities, polar-deserts and polygon fields. |

Forage quantity. The Normalized Difference Vegetation Index (NDVI) measures chlorophyll density in plants. The index can be used as a proxy for biomass and plant productivity (Johansen and Tømmervik 2014). The NDVI raster layer used in this analysis were based on average maximum NDVI from 2000-2014 (Karlsen et al. 2018). Max NDVI is a commonly used index for displaying seasonal vegetation dynamics in the Arctic. The NDVI layer was resampled from original spatial resolution of 250 × 250 m to 30 × 30 m.

2.4.2 Terrain variables

Terrain variables were derived from digital elevation models (DEM) with 20 x 20 meter original resolution and a standard error of 2-5 meters (Norwegian-Polar-Institute 2014). Elevation, slope and aspect were calculated in R studio using the raster package. Three

additional terrain variables were calculated, Vector Ruggedness Measure (VRM; Sappington et al. 2007), Topographical Wetness Index (TWI;(Beven and Kirkby 1979)) and Heat Load Index (HLI; Parker 1988) using geometric functions in ArcMap and R (ESRI 2011, Rstudio 2015). Vector Ruggedness Measure is different from other ruggedness indices in that it captures the 3-dimensional complexity of the landscape (Sappington et al. 2007). The index does this by using vector analysis of slope and aspect derived from DEM, and then applying a 3×3 moving window on the dataset. The values for the ruggedness ranges between 0 (no terrain variation) and 1 (complete terrain variation). Vector Ruggedness Measure was calculated using Terrain Tools toolbox in ArcMap (Eischeid pers.comm October 2017). Topographical Wetness Index is a measure of the water accumulation from upslope contributing areas and the slope value of the pixel. The upslope contributing area was calculated using Flow Accumulation derived from the DEM layer in ArcMap. High values represents drainage depression and low values means ridges or crests (Beven and Kirkby 1979). The Heat Load Index is a measure of how much solar radiation a location receives during a 24-hour period (Parker 1988, Pedersen et al. 2017). This index is used as a proxy for snowmelt in the landscape, which is important for forage access for the Svalbard reindeer during the spring. The Heat Load Index was calculated based on aspect and slope from the DEM layer using the raster package in R. High values account for high incoming radiation on the slopes, and low values represent low incoming radiation.

2.4.3 Habitat characteristics in study areas

The difference in availability of environmental variables in the study areas must be considered when making comparisons across study areas of habitat selection. To compare environmental characteristics between study areas, the spring home range for all individuals in all years was merged, and the vegetation and terrain raster layers were clipped. The pixel values for all above raster layers were summarized for each study area (Fig. 3). The environmental characteristics differed between the northern locations and Nordenskiöld Land for elevation and vegetation conditions, but other topographical variables were similar. For example, there is much more moss tundra in Nordenskiöld Land compared to the northern locations with almost none in Brøggerhalvøya. NDVI values are highest for Nordenskiöld Land with a median value of 0.5 and lowest for Brøggerhalvøya with a median of 0.24. Much of Brøggerhalvøya is characterized by polar desert and contain much more barren areas compared to Nordenskiöld Land. Slope, aspect, heat load and wetness had quite similar values across all four study areas.

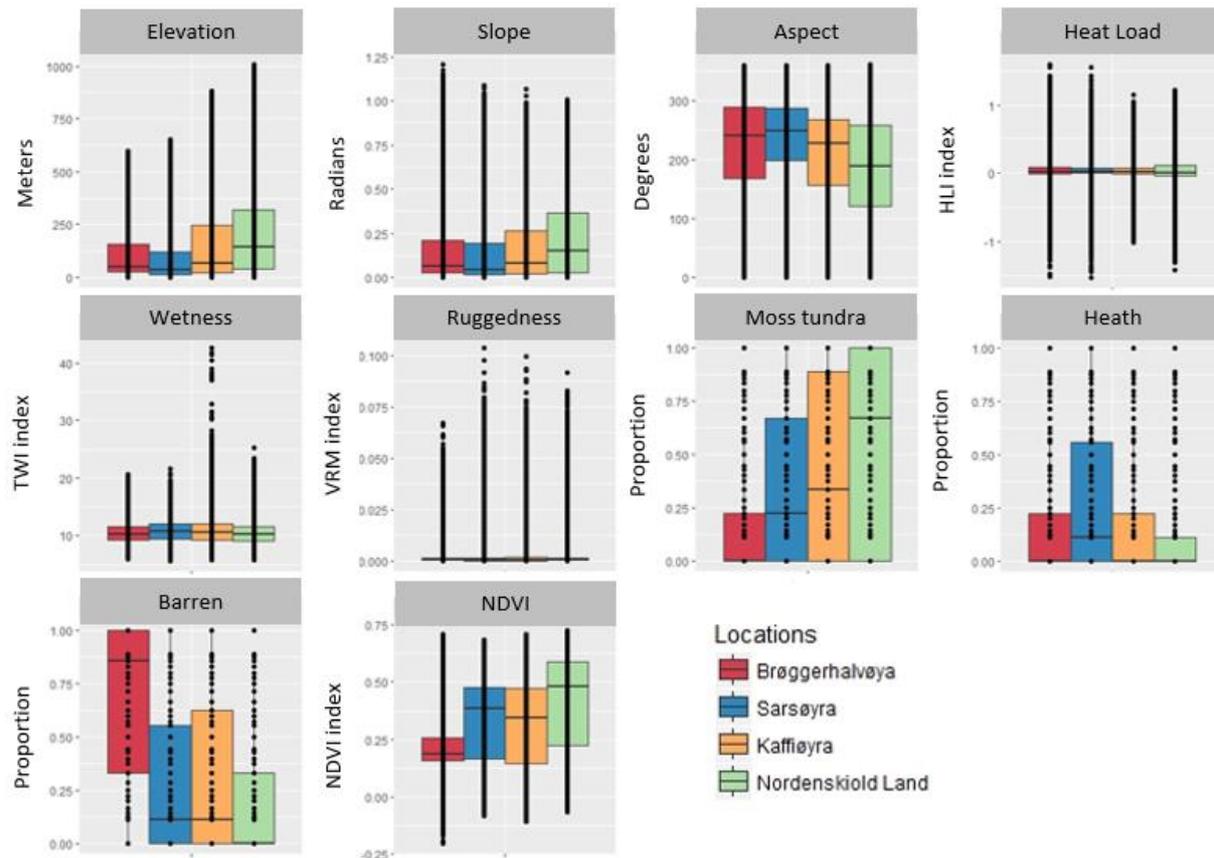


Figure 3. Median values of the spatial raster layers used for analysis of calving site selection of Svalbard reindeer females in the four study areas (extent=merged spring home range). The black line in the middle are the median values of each environmental raster layer for each study area, and the black dots are the individual pixels with minimum and maximum values. The top of the box shows the 75% quartile and the bottom of the box shows 25% quartile.

2.5 Data analysis

2.5.1 *Estimating calving day and location by recursive partitioning and first passage time*

To estimate the calving day from GPS relocation data I used recursive partitioning from Rudolph and Drapeau (2012), which identifies candidate breakpoints in the movement rate and net displacement over time. In addition, I used first passage time for a subset of animals (2014-2017, see below). The calving day estimated from recursive partitioning and first passage time are based on the behavioural patterns of reindeer before, during and after calving (see introduction 1.3).

Recursive partitioning produces candidate breakpoints for any significant change in movement rate and net displacement from high to low values using regression tree analysis and ANOVA (Rudolph and Drapeau 2010). This is advantageous because it produces individual calving day graphs that displays the movement behaviour before, during and after calving. The graphs show the movement rate, which is the step length per hour divided by the time between two consecutive GPS points, and the net displacement value, a measure of the distance between the first GPS fix of the study period and each successive GPS fix (Fig. 4a,b). The movement metrics were calculated using the AdehabitatLT package in R. Using the protocol developed by Rudolph and Drapeau (2012) the dataset was first log transformed to improve normality (Shapiro-Wilks Normality Test) and then a three GPS fix moving window was applied on the movement rate. Any significant changes in movement rate or net displacement from high to low values were split into candidate breakpoints, and the calving day was estimated based on classification criterias (Table 4). The calving breakpoint was defined as the point on the graph with the lowest drop in movement rate. For recursive partitioning analyses, I used the zoo package in R (Zeileis et al. 2018).

First passage time (FPT) rediscretizes the movement trajectory and makes circles at regular intervals of a certain radius, and measures the time of the animal at first passage out of the circle (Fauchald and Tveraa 2003). Thus, high first passage time values account for more time spent in an area. For identifying calving time, I hypothesized that during and after parturition the female with calf would be more likely to spend time in one area compared to the rest of the spring period. I therefore estimated calving day as the Julian day with highest FPT value after day 150 in a circle with radius 100 meters (Fig. 4c). Only females with Follow-it satellite collars (2014-2017) were checked for FPT because these had in average more missing GPS

fixes compared to females with Storeonboard collars. The FPT calving day estimation was therefore used as an extra measure for calving day for those females where calving was difficult to estimate by recursive partitioning. For Nordenskiöld females in 2017 only FPT was used to estimate calving day because this dataset was included at the end of the study. The FPT analyses was done using AdehabitatLT in R (Calenge 2016).

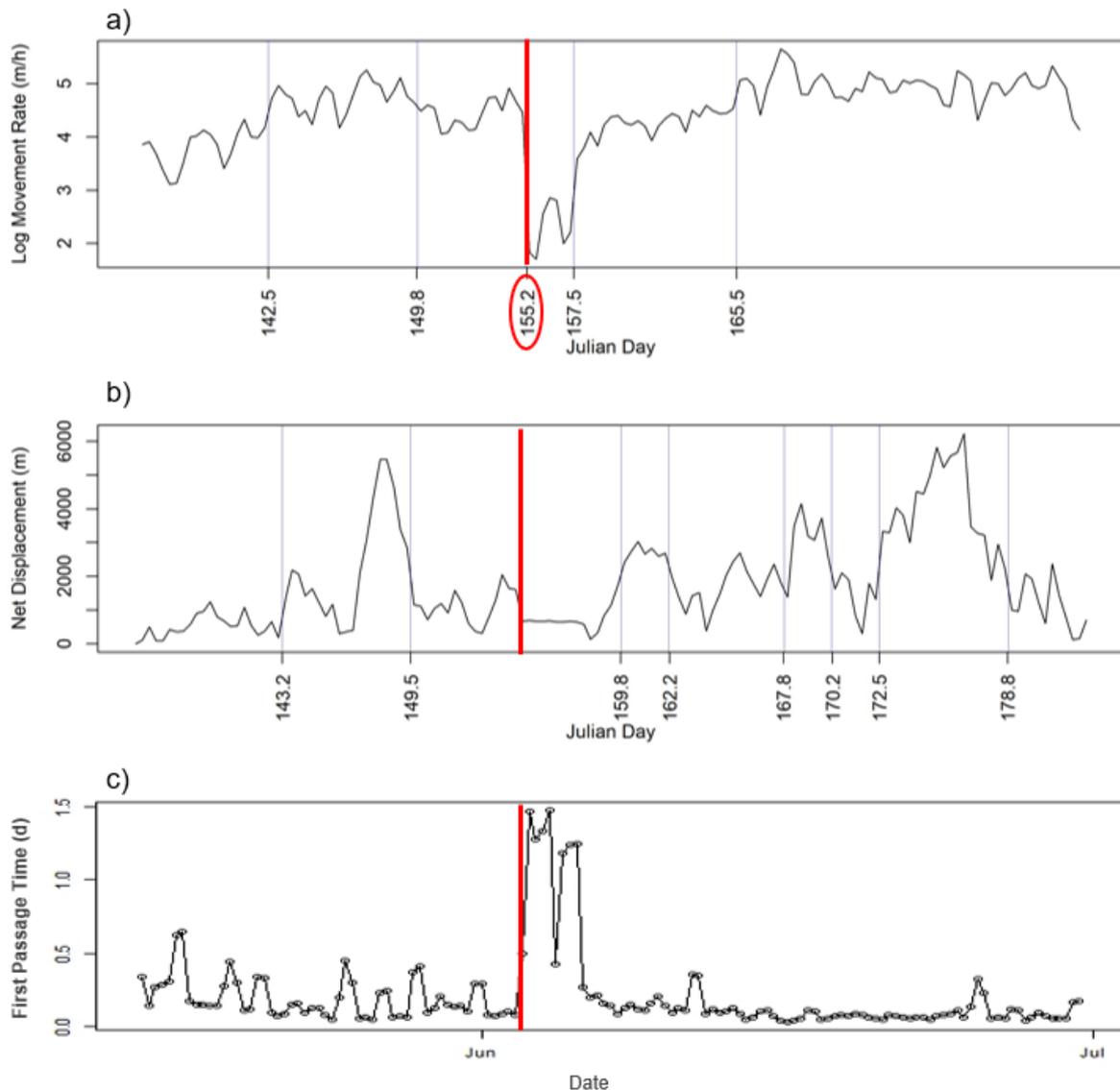


Figure 4. Estimated calving day based on the recursive partitioning and first passage time methods. The graphs show an example of recursive partitioning on **a)** movement rate, **b)** net displacement and **c)** a graph for first passage time for one female in the spring (15. May-30. June). Calving day, illustrated with the red line, was estimated to be Julian day 155 (4. June, regular years).

Classification criteria. A classification protocol was developed to standardize the calving day estimation and exclude individuals with ambiguous calving day from habitat analysis (Table

4). Females classified as 1 in the classification criteria had a clear calving pattern with only one decrease in the movement rate during the spring period and the highest FPT value on the same day as the recursive partitioning breakpoint. Females classified as criteria 2 had more than two substantial drops in movement rate during the calving period, but first passage time was the same as one of the two drops in movement rate. Females with classification 3 had no pronounced decrease in movement rate during the study period and/or the first passage time did not correspond with any of the drops in movement rate. Only females classified as 1 was considered in the habitat analysis.

Table 4. Classification criteria of calving day using recursive partitioning and first passage time. Both methods were used in estimating calving day between 2014-2017. Recursive partitioning was used for females between 2009-2013, and FPT was used for Nordenskiöld individuals only in 2017.

| Method for estimating calving day | | |
|-----------------------------------|--|---|
| Classification Criteria | Recursive partitioning | First passage time |
| 1 | Movement rate decreases to less than 2.5 m/h. Candidate breakpoint after Julian Day 150* is close to the minimum point in the graph. | The highest FPT value after day 150 is on the same day as the candidate breakpoint from recursive partitioning. |
| 2 | More than one pronounced decrease in movement rate during the study period, shown as two approximately equal drops in movement rates | First passage time date is the same as one of the two drops in movement rate |
| 3 | No pronounced decrease in movement rate during the study period. | The highest first passage time value does not correspond with a drop in movement rate. |

*Julian day 150 is 28. May There are few observations of calves before this date and snow may restrict movement of females (Danielsen 2016).

Statistical analysis. To test if calving day was different between the study areas and years, I applied Generalized Linear Models (GLMs). Since residuals from preliminary analyses deviated from a normal distribution, the dataset was transformed using z-score ($z = (x_i - \text{mean}(x_{\text{all}})) / \text{sd}(x_{\text{all}})$). The response variable was estimated calving day (classification criteria 1), and the explanatory factor variables were year (2014-2017) and study area (northern populations versus southern population). Due to small sample sizes no interaction effect between study area and year was applied.

2.5.2 *Identifying habitat selection by K-Select Analysis*

K-select analysis was used to estimate individual habitat selection in calving locations (Calenge et al. 2005). This is an exploratory resource selection analysis, which plots the habitat selection in a multidimensional niche space, where combinations of habitat variables represent dimensions. Habitat selection in K-select is defined by the marginality vector, which is the difference between the vector of average available habitat and the vector of average used locations. The marginality vector is then plotted for each female in a non-centered principal component analysis. The beginning of the arrow represents average available habitat for the female. The direction of the arrow indicates selection direction, and the length of the arrow represents the marginality strength. Habitat preference for individuals can then be interpreted visually by investigating the habitat variable loadings and eigenvalues, which shows the amount of marginality explained by each factorial axis. K-select analysis is advantageous because it does not have too strict underlying hypotheses. For example, the analysis is not affected by the autocorrelation of habitat variables. In addition, both categorical and qualitative data can be used as variable dimensions. The K-select analysis requires three different inputs, the habitat variables (as explained in section 1.8), the used GPS fixes and the available area for each individual. All K-select analyses were analysed using the AdehabitatHS package in R (Calenge 2011).

For the used calving area, I explored different spatiotemporal scales in the K-select analysis to investigate the spatial extent of the area considered to be relevant for habitat selection after calving. For females with calves, this turned into 4 different K-select analyses where the used area in the immediate calving location was defined as GPS fixes from individual females on: 1) estimated calving day, 2) three days post-calving, 3) five days post-calving, and 4) all GPS fixes within a 1 km buffer surrounding the calving breakpoint.

Since the four K-select analyses gave similar results for habitat selection, the 1-km buffer analysis is presented in the results section because this gave the maximum number of GPS fixes to compare to the available spring home ranges (see below and appendix B). The habitat selection results from the 1 km buffer analysis were compared to a K-select analysis for females without calves, where the used area was defined for each female as GPS fixes for each individual between minimum and maximum calving day (as estimated in section 2.5.1) in the same year and study area.

The available area for each female was defined as the spring home range between 15. May and 30. June, using the AdehabitatHR package (Calenge 2015). The home ranges were calculated using Kernel's Density Estimate (KDE). The KDE is defined as the minimum home range of where the female has a probability of being located given the position of its actual GPS coordinates. In this study, 95% probability was used as a threshold. The advantage of using KDE is that it gives an estimate of the probable locations between actual GPS position recordings. The smoothing parameter, which determines the probability width around each GPS coordinate, was determined by the default "ad hoc" method and assumes a bivariate normal kernel (Calenge 2016).

Randomization tests were performed to analyse whether the habitat selection was significant. The randomization test recomputes the marginality for a set of random GPS fixes for n=1000 times, and the predicted marginality is then compared to the observed marginality (Calenge et al. 2005). The main assumption behind this test is that all GPS fixes are equiprobable in space. Since the GPS fixes are part of a movement trajectory with 8 hours frequency it means that the fixes are temporally autocorrelated, and thus the assumption is violated. The better option is to perform random walks in the randomization test, but this was not an option in the current randomization test for the K-select analysis.

2.5.3 *Calving site fidelity*

To estimate calving site fidelity, the interannual distance between calving locations in each spring home range for females with two consecutive calving seasons was calculated. This distance was compared to a null hypothesis to standardize the comparison of observed and expected walking distances between spring home ranges. The null hypothesis was defined as the average interannual distance between pairwise GPS fixes on the same date and time, but different years between the two spring home ranges for each female. The observed interannual distance was the distance between two calving breakpoints for the same female in the two consecutive calving years. I expected that the interannual distance between calving points would be shorter compared to the interannual distances in spring home ranges if the reindeer displayed site fidelity. Site fidelity was tested by one-tailed paired t-test and any overlap between calving locations was noted. All analyses were performed with R Studio version 1.0.143 and ArcMap 10.6.

3 Results

3.1 Calving day and locations across years and study areas

Of the 90 calving seasons for GPS-collared females, 50 individuals displayed a clear calving pattern and was classified as 1 according to the classification criteria (Appendix A-3 and A-4). The generalized linear model showed that calving day was significantly earlier in Nordenskiöld Land compared to the three northern populations on Brøggerhalvøya, Sarsøyra and Kaffiøyra between 2014-2017. In this period, the northern populations had a predicted calving day of 16. June (Julian day 167, 95% C.I.=161-172, n=15), while Nordenskiöld had a predicted calving day 11 days earlier 5. June (Julian day 156, 95% C.I.=151-160, $F=7.0$, $p=0.023$, n=14). There was also a significant difference in calving day between study area and year. The predicted mean calving day for year 2016 was earlier than other years (95% C.I.=151-160, $F=17.9$, $p=0.024$). However, when excluding 3 outliers (individuals with calving days late in June) 2016 was not significantly different from other years anymore (appendix C-2). Due to small sample sizes, it was not possible to estimate calving day for the individual northern study populations.

Mean calving day varied across the four study populations and years. In the northern populations the mean calving date was 13. June (Julian day \pm SE = 164 ± 1.9 , n=14, 2014-2017) and 7. June for the southern population (Nordenskiöld Land) (Julian day \pm SE = 158 ± 1.1 , n=15, 2009-2017) (Table 5). For the southern population, the estimated calving day varied between 1. June to 20. June (Julian day 150-163, Table 5), while in the northern populations the calving period was much wider spread, varying between 3. June to 26. June (Julian day 155-177, Table 5). This difference was likely driven by the late calving in the northern populations in 2015 compared to the southern population, when mean calving day differed 13 days between study populations (Table 5).

Table 5. Summary of estimated Svalbard reindeer calving day (mean \pm standard error, minimum and maximum values and range) between Nordenskiöld Land (southern population; 2009-2017) and Brøggerhalvøya, Sarsøyra and Kaffiøyra (northern populations; 2014-2017). Calving day is estimated from recursive partitioning graphs and only females classified as 1 in the classification scheme are taken into account ($N = 50$).

| Mean estimated calving day (Julian day) | | | | | | | | | | |
|---|-----------------------------------|-----|-----|-------|---|-----------------------------------|-----|-----|-------|---|
| Nordenskiöld Land | | | | | | Northern populations | | | | |
| Year | Mean (\pm SE) | Min | Max | Range | N | Mean (\pm SE) | Min | Max | Range | N |
| 2009 | 158 (\pm 1.1) | 155 | 160 | 5 | 5 | | | | | |
| 2010 | 157 (\pm 1.8) | 153 | 162 | 9 | 5 | | | | | |
| 2012 | 162 (\pm 0.1) | 162 | 163 | 1 | 3 | | | | | |
| 2013 | 154 (\pm 1.3) | 150 | 159 | 10 | 8 | | | | | |
| 2014 | 160 (\pm 1.0) | 157 | 163 | 6 | 5 | 177 (NA) | 177 | 177 | 0 | 1 |
| 2015 | 156 (\pm 2.5) | 154 | 159 | 5 | 2 | 167 (\pm 2.5) | 159 | 177 | 18 | 7 |
| 2016 | 156 (\pm 1.5) | 153 | 161 | 8 | 5 | 158 (\pm 1.7) | 155 | 162 | 7 | 4 |
| 2017 | 164 (\pm 3.4) | 160 | 171 | 11 | 3 | 162 (\pm 0.2) | 162 | 162 | 0 | 2 |

Core calving areas for the southern population were located in the innermost parts of the valleys of Colesdalen, Bødalen, Ringdalen, and Semmeldalen (Fig. 5a). Females without calves tended to occupy similar locations as females with calves. Seven out of 36 pregnant females (all years pooled) in the southern population moved large distances one week before calving indicated by a higher than average net displacement before calving (Fig. 6). These females walked distances between 9 and 14 kilometers 2-3 days before the calving event. The average net displacement increased two days before calving and after the calving the female with calf kept within 2 kilometers of the calving location the next week. For the northern populations the core calving areas were located mostly on the flat, coastal plains (Fig. 5 b). Four out of five females calved on the coastal plains in the North of Brøggerhalvøya. Two of three females, calving on Sarsøyra in 2016, selected areas closer to side valleys, while the third calved on the coastal plains. In Kaffiøyra, three out of five calving locations were located in the same area on the plains in the north of the study area. In contrast to Nordenskiöld Land, only one female showed high net displacement (all years pooled) before calving in the northern populations (Fig. 7). For this female, there was an increase in average net displacement 2 days before the calving event and the female with calf kept a distance between 2-3 km away from the calving location the first week.

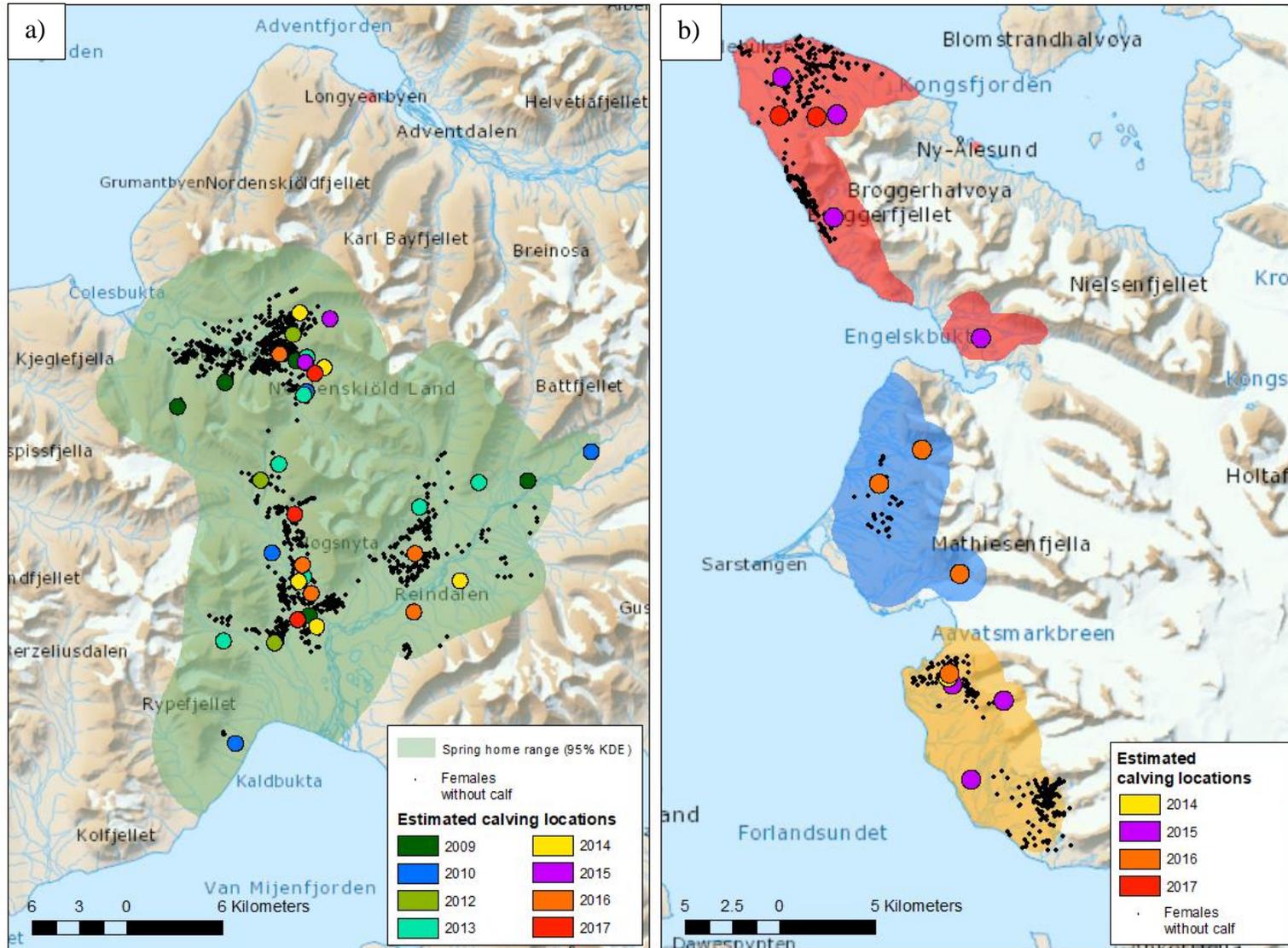


Figure 5. Estimated annual Svalbard reindeer calving locations for the four study populations calculated by recursive partitioning and first passage time (certainty criteria 1, see methods 2.5.1). **a)** Nordenskiöld Land (southern population; 2009-2017, N=36) and **b)** Brøgger Peninsula, Sarsøyra and Kaffiøyra (northern population; 2014-2017, N=14) Black points are GPS fixes from females without calves during the calving period. 1 km diameter buffer around the calving breakpoint is shown. The colored area is the merged spring home range for all females with calves during the study period.

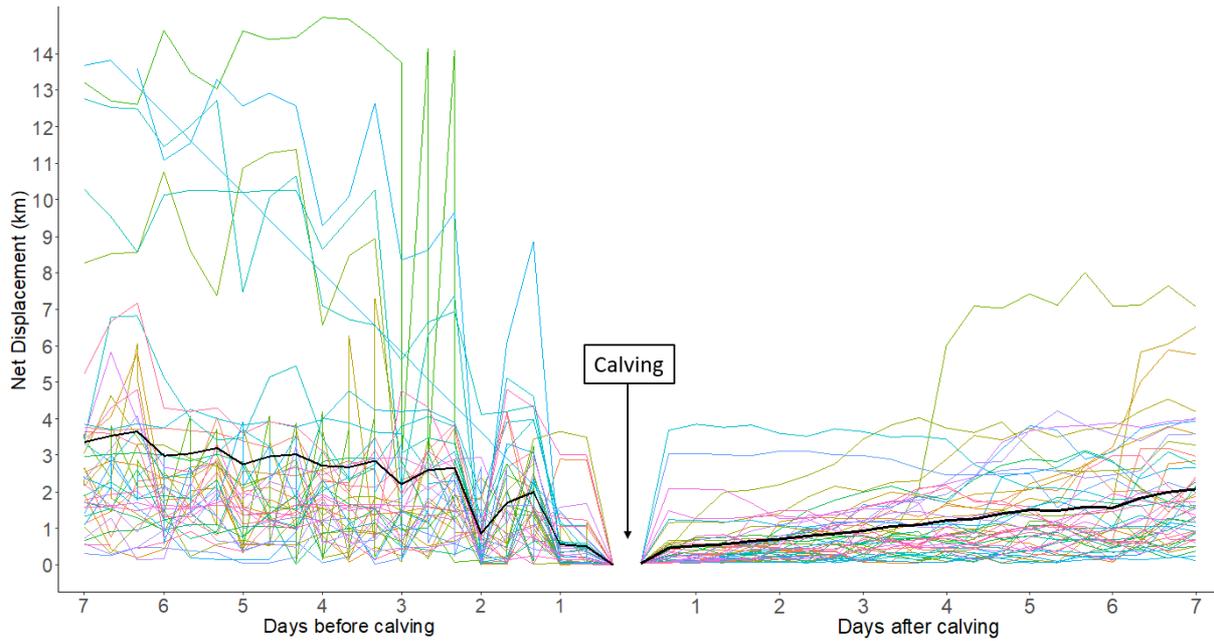


Figure 6. Net displacement one week before and after calving for individuals on Nordenskiöld Land classified with certainty 1 ($n=36$). The colored lines are net displacement for individuals and the black line represents mean of net displacement.

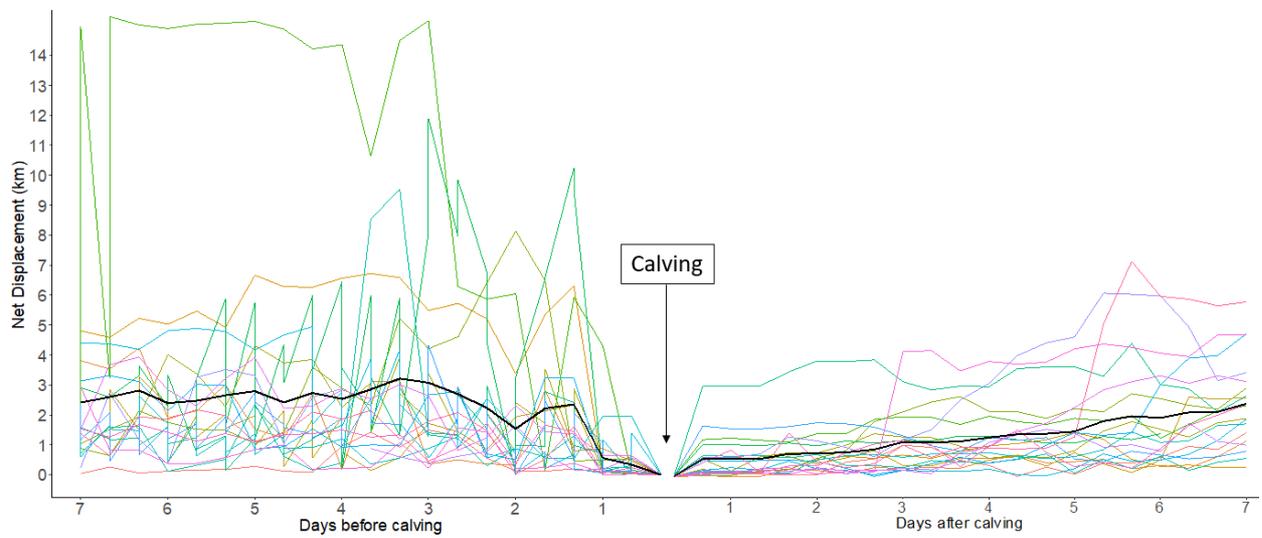


Figure 7. Net displacement one week before and after calving for individuals in northern populations (Brøggerhalvøya, Sarsøyra and Kaffiøyra) classified with certainty 1 ($n=14$). The colored lines are net displacement for individuals and the black line represents mean of net displacement.

3.2 Habitat use in calving locations

Females with calves. The K-select analysis for immediate calving locations (GPS fixes in 1 km buffer) showed that the first two axes of the eigenvalues explained a large proportion (64%) of the total marginality (Fig. 8a,b). The first factorial axis accounted for most of the variation (42.2 %), and indicated selection for areas with higher NDVI (17.8%), larger proportion of moss tundra (14.9%) and higher wetness (11.3%), while the negative correlation with this axis for slope (18%), elevation (17.5%) and barren (12.8%) indicated avoidance. The second factorial axis explained 21.8% of the total variation and accounted for selection of areas positively correlated with proportion of heath (50%) and negatively correlated with proportion of moss tundra (27.8%), barren (5.8%) and terrain ruggedness (4.2%). The K-select analysis identified three groups across the four study populations with similar habitat selection within the calving locations (Fig. 8c). The main group contained only females from Nordenskiöld Land, which selected for calving locations with higher proportions of moss tundra and NDVI, as well as flatter, less rugged and lower elevated areas compared to their average available spring habitat (8c, Appendix D).

The northern populations had higher individual habitat variability in habitat selection but could be divided into two distinct groups. Both northern groups selected for calving locations containing more heath compared to their average available habitat. The first group, consisting of 6 individuals (Kaffiøyra=3, Brøggerhalvøya=2, Sarsøyra=1) selected for areas that were flatter, less rugged and on lower elevations, while the second group, consisting of 7 individuals (Brøggerhalvøya=3, Sarsøyra=2, Kaffiøyra=2) selected for areas that were steeper and on higher elevations compared to their available spring home range. The first eigenvalue, after applying the randomization test, was larger than what would be expected under the null hypothesis ($\lambda=1.264, p\text{-value}<0.0001$), which means that at least one of the groups significantly selected for a specific habitat type in their calving location (Appendix B-6).

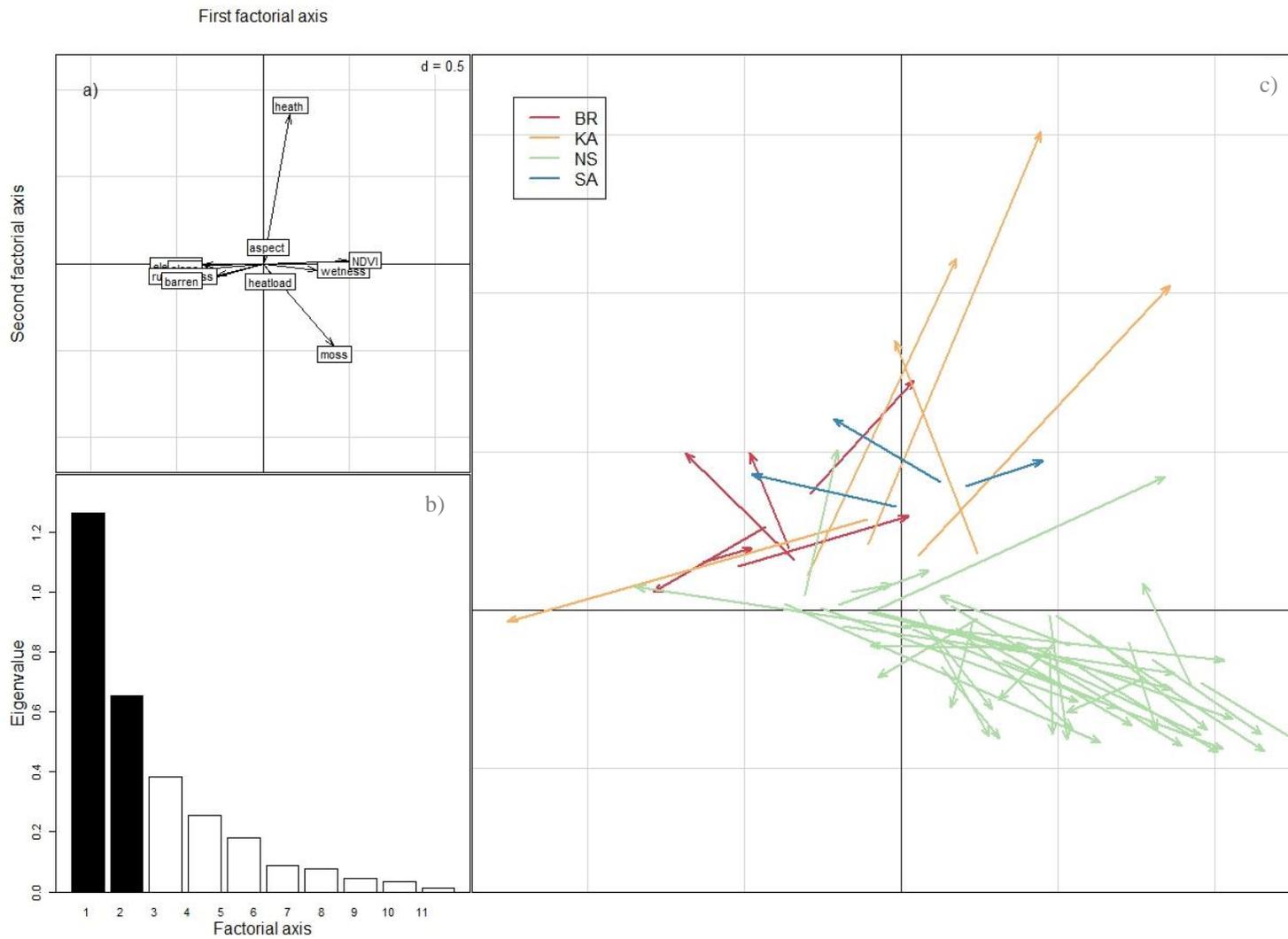


Figure 8. Non-centered K-select analysis for habitat selection of Svalbard reindeer females with calf. **a)** habitat variable loadings with proportion of heath, moss and barren, wetness, NDVI, aspect, heat load, ruggedness, elevation and slope according to Table 1. **b)** Eigenvalues for 11 factorial axes where the two black ones indicate that most variation is accounted for by these axes. **c)** K-select analysis for Brøggerhalvøya (BR), Kaffiøyra (KA), Nordenskiöld Land (NS), Sarsøyra (SA). Each arrow represents an individual female with calf. The origin of each arrow is the average available habitat for that female (95% KDE between 15.May-30.June) and the end of the arrow is the average used habitat conditions in the calving location (all GPS fixes within 1 km buffer).

Females without calves. Similarly to the K-select analysis for females with calves, females in the southern population selected the same type of habitat independent of reproductive status meaning that there was no difference in habitat selection between females with or without calves. In this analysis, the two first axis explained 75.6% of habitat selection. The first factorial axis explained 55.5% of the total variation among the habitat variables and indicated selection for areas with higher proportions of moss tundra, increased wetness and higher NDVI, in addition to flatter, less rugged areas (Fig. 9a,b). The second factorial axis explained 20.1% and represented areas with less heath, and more rugged steeper, terrain and higher elevation (Fig. 9ab).

The K-select plots show two main groups of females without calves as selecting for the same habitat during the calving period. The first group contained females from Nordenskiöld Land (n=27) (Fig. 9c), which selected for areas with high NDVI, moss tundra and increased wetness. The second group (Brøggerhalvøya n=4, Kaffiøyra n=3, Nordenskiöld Land n=1, Sarsøyra n=1) selected for a combination of high NDVI and heath. For females without calves, the first eigenvalue was larger than what would be expected under the null hypothesis in the randomization test ($\lambda=1.07$, p-value<0.0001), meaning that the non-reproductive groups also significantly selected for a specific habitat type during the calving period in June.

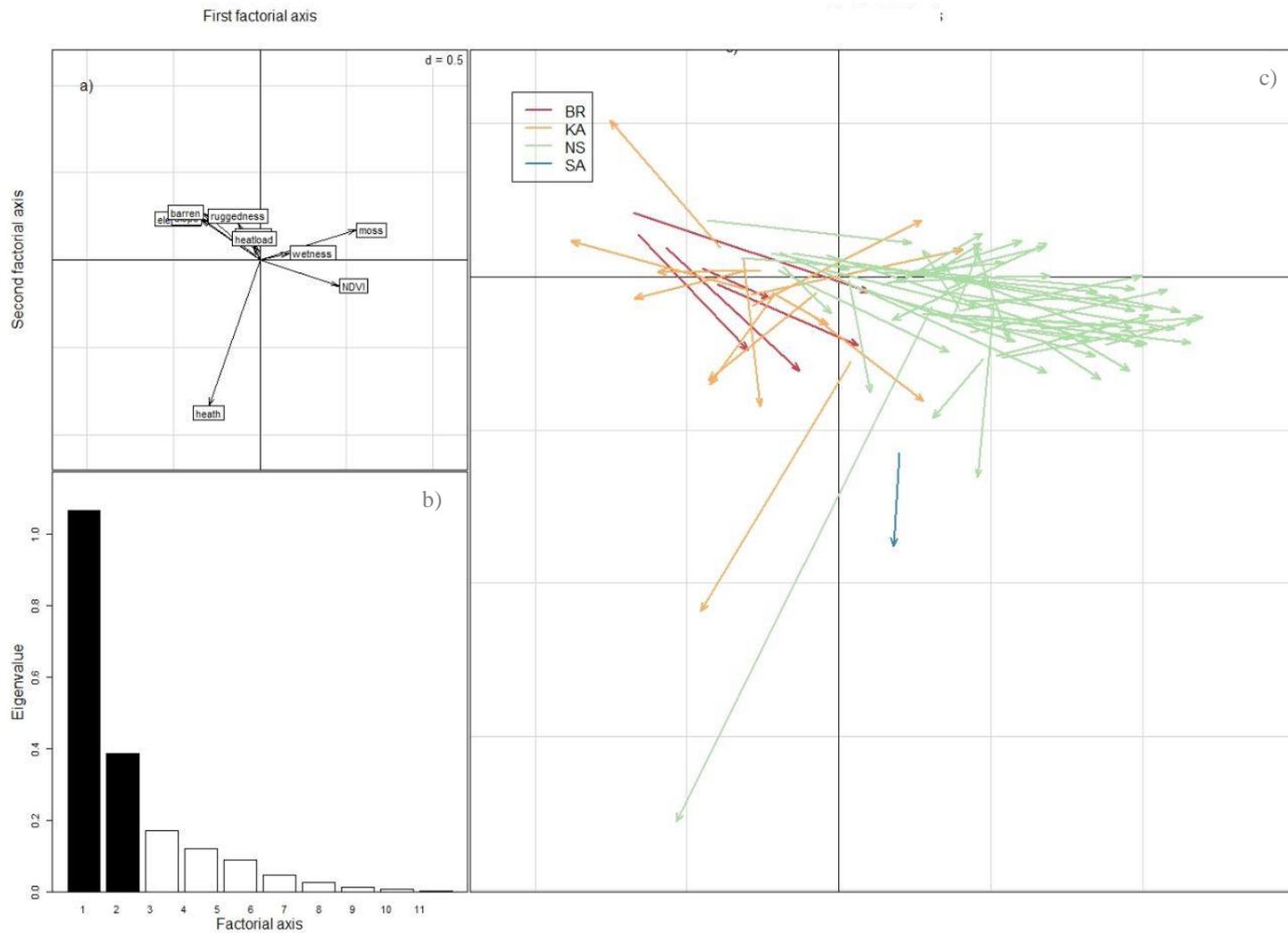


Figure 9. Non-centered K-select analysis for habitat selection of Svalbard reindeer females without calf. a) habitat variable loadings with proportion of heath, moss and barren, wetness, NDVI, aspect, heat load, ruggedness, elevation and slope according to Table 1. b) Eigenvalues for 11 factorial axes where the two black ones indicate that most variation is accounted for by these axes. c) K-select analysis for Brøggerhalvøya (BR), Kaffiøyra (KA), Nordenskiöld Land (NS), Sarsøyra (SA). Each arrow represents an individual female with calf. The origin of each arrow is the average available habitat for that female (95% KDE between 15.May-30.June) and the end of the arrow is the average used habitat conditions in the calving period (min-max) of females with calves for the same location and year.

3.3 Calving site fidelity

Only a small proportion of females (N = 13, 17 %) in Nordenskiöld Land had more than one consecutive calving season to evaluate calving site fidelity. The distance between the first and second calving location was on average 3.3 ± 2.6 km (median=2.5 km). This was not significantly closer compared to the null hypothesis, which was the average interannual spring home range distance of 2.9 ± 1.6 km ($p > 0.05$, $t_{28} = 2.04$, $n = 13$). However, there was large variance between females, 38%, 69% and 94% calved less than 2, 4 and 6 kilometres away from the first calving site, respectively (Appendix E-1). The females tended to calve the consecutive calving season in the same or adjacent valley (Fig. 10). A core calving area for the GPS collared females in Nordenskiöld Land appeared to be the innermost valleys of Colesdalen, specifically Ringdalen and Bødalen. Here, 6 out of 13 females selected the same calving site as from the previous seasons, which indicates site fidelity for calving locations among Svalbard reindeer.

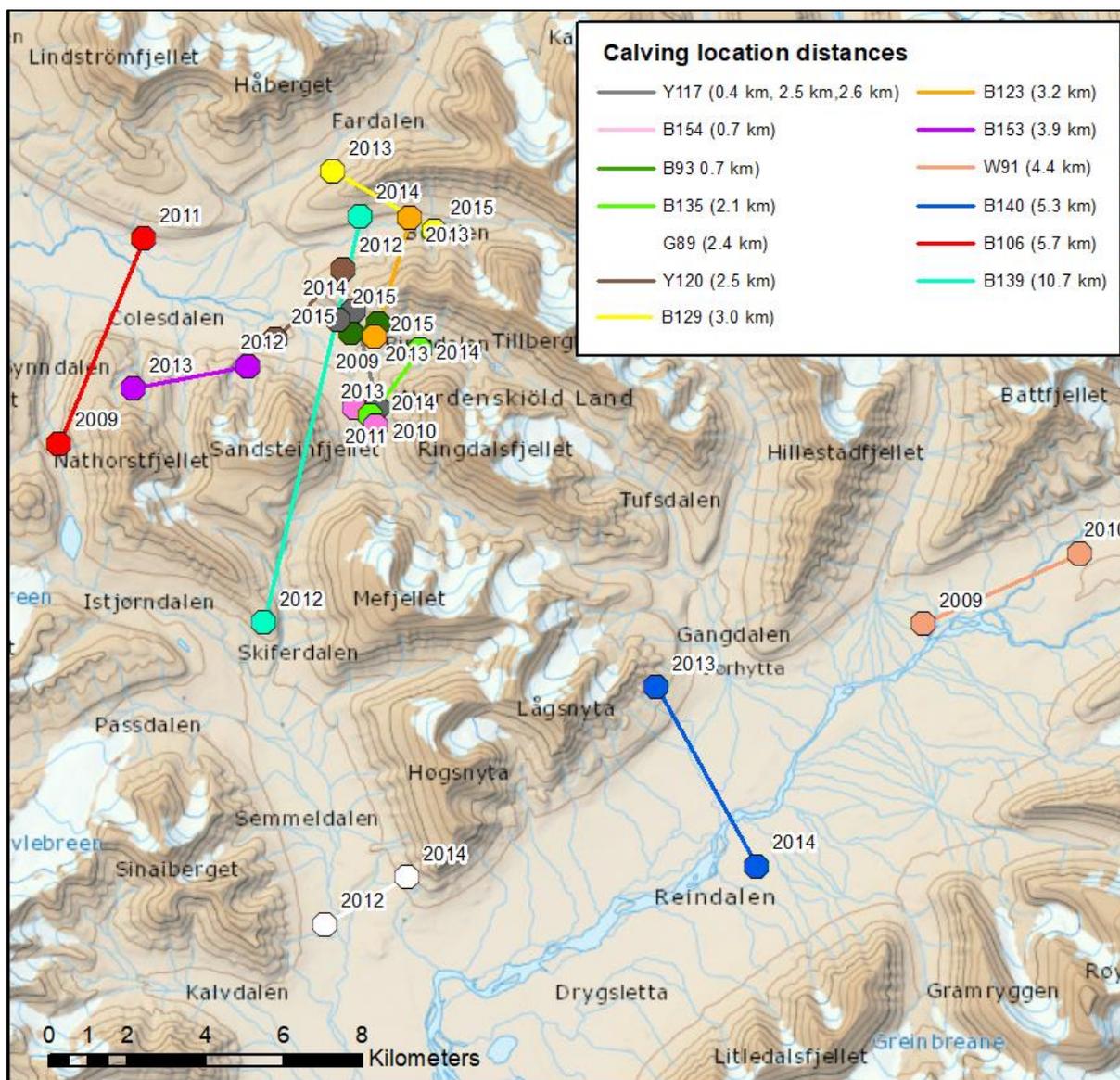


Figure 10. Distance (km, line) and location (coloured circle) between calving sites for 13 Svalbard reindeer females with two or three consecutive calving seasons in the southern population on Nordenskiöld Land. Each colour and letter/number combination indicate a female for a certain year and the line depicts the distance between the two calving locations.

4 Discussion

In this thesis I estimated calving day, location and habitat use for Svalbard reindeer using recursive partitioning and first passage time of GPS movement trajectories. I predicted that northern populations had later mean calving day compared to southern locations. My results support this hypothesis, which shows that on average, predicted calving day between 2014 and 2017 was 11 days later for northern populations compared to Nordenskiöld Land. The observed calving locations on Nordenskiöld Land were located in the innermost valleys in the study areas, while calving locations in the northern areas were more spread evenly out in the coastal flats. I expected that females with calves would select for calving sites in high food quality locations with early snow melt. My results found no difference in habitat selection during the study period (15 May – 30 June) between females with or without a calf. It appeared that females from Nordenskiöld Land selected for more moss tundra on flatter, lower elevation terrain compared to females in the northern populations, which selected for areas with heath, but had high individual variability in terrain selection. However, there was no difference between females with and without calves although both groups had strong habitat selection.

4.1 Calving day and locations across years and study areas

The estimated calving days varied between the study populations, but with little annual variability within the populations. For Nordenskiöld Land females, the estimated calving period was between 1. June and 20. June, and this period seemed to vary little across 2009-2017 (mean Julian day \pm SD = 158 ± 4.4 , n=36). Although it was not possible to obtain field validation of exact calving days, other studies estimating calving day found similar results (Danielsen 2016, Veiberg et al. 2017). In these studies, the calving days were estimated using activity sensors on the same GPS collared females for the study period 2009-2015. Here they found that the calving period varied between 3. and 12. June (mean Julian day \pm SD = 158 ± 9.5 , n=101). The estimated calving day derived from activity sensor data for 9 out of 10 Nordenskiöld Land females fell on the same Julian day as the estimated calving day using recursive partitioning with 12 GPS fixes per day (Appendix A-2). However, with 3 GPS fixes per day the estimated calving day using recursive partitioning tended to be 1-2 days later compared to the same individuals estimated with activity sensors. For future studies it is therefore recommended that the frequency of GPS fixes during the calving period should be at least 12 per day to estimate calving day, which is essential for understanding the habitat selection in this period.

Up to present, no studies have identified the calving day or location for Svalbard reindeer in other locations than on Nordenskiöld Land. In this study, the estimated calving period for the three northern study populations on Brøggerhalvøya, Sarsøyra and Kaffiøyra, was between 3. and 26. June in 2014-2017. This result supports the hypothesis that calving day was later in northern populations compared to Nordenskiöld Land (mean Julian day \pm SD = 164 ± 7.2 , $n=14$). This difference could be because of variation in environmental conditions, especially related to later snowmelt and spring onset in the northern locations (Post and Forchhammer 2008). For example, on Brøggerhalvøya, 100 km north of Nordenskiöld Land, the number of days with snow cover, a proxy used for spring onset, was on average 41 days longer than in Nordenskiöld Land between 2009-2017 (Meteorologisk-Institutt (2018), Fig. 2). Additionally, the onset of the growing season was estimated to be before 16. June for Nordenskiöld Land and to be after 26.-30. June for the northern study areas, a difference of more than 2 weeks (Karlsen et al. 2014).

Earlier hypotheses states that Svalbard reindeer are capital breeders and do not depend on spring onset for calf survival (Veiberg et al. 2016). This hypothesis is supported in my results for Nordenskiöld Land, which shows that the calving period varies little between years compared to the variation of number of days with snow cover between 2014-2017 (Fig. 2). Danielsen (2016) found a similar result with no correlation in calving day for Nordenskiöld Land reindeer and spring heat sum, another proxy for spring onset. This despite a significant increase in spring heat sum (2.2°C per year) the last 37 years. The results from this study gives additional support to the hypothesis stating that the high synchronization in calving period across years for Arctic reindeer is because of the reindeer being capital breeders, which means that they are not dependent on spring onset for calf survival (Veiberg et al. 2016). Instead the reindeer depends on body mass acquired from the summer before for the first stage of lactation.

The calving period for the northern populations differed more between years compared to the southern population. The earliest and latest mean calving day for northern populations was on 6. June 2014 and 25. June 2016 respectively. Therefore, it is interesting to note that 2014 was the year with least number of days with snow cover, while 2016 was the year with most snow days during the entire study period (Fig. 2). It is possible that with shorter growing season and longer winters in the northern study areas compared to Nordenskiöld Land, the females are not able to acquire the body mass needed for both winter survival and feeding of the calf once it is born (Post and Forchhammer 2008). Since the growing season is shorter, the period the reindeer

uses to gain body mass is also reduced. Thus, it is possible that the reindeer in northern populations rely more on spring onset timing for calving compared to reindeer in Nordenskiöld Land. However, due to the small sample sizes for northern populations, it was not possible to validate a potential relationship between mean calving day and number of days with snow cover, but future studies can explore this hypothesis further.

In this study, the calving locations on Nordenskiöld Land were located in the innermost valleys of Colesdalen, specifically Bødalen and Ringdalen, and in the end of Semmeldalen extending out towards Reindalen. This is consistent with findings from Øritsland and Alendal (1986) where female reindeer moved inland in the last weeks of May in Adventdalen. Colesdalen is also one of the areas with the highest densities of GPS collared reindeer. The consistent use of the innermost valleys of this area confirm the pattern of habitat use at this time of the year (Veiberg et al. 2017). Colesdalen is a popular area for scooter driving in the winter and spring but is likely undisturbed during the calving period in June. Despite this, many of the calving locations are located outside of valleys with main scooter trails, such as Fardalen (Tandberg 2016). The calving locations for northern populations were more spread in the terrain, and there was no pattern in habitat use. The latter may be related to more uniform environmental conditions in the flat coastal tundra plains and to low sample sizes. The calving locations were located 0.8-5.2 kilometers away from the ocean. In contrast to Nordenskiöld Land, 8 out of 13 calving locations were located on the coastal plains, which are characterized by flat, open tundra landscape with limited terrain variability.

4.2 Habitat use in calving locations

Up to date, this is the first study to identify habitat use in the immediate calving location for Svalbard reindeer. Contrary to my expectations, all habitat analyses on different temporal scales showed little variation in habitat selection during the calving period and no difference between females with and without calves. This is similar to the observational study by Loe et al. (2006) where both females with calves and without calves used similar habitat at small scales (i.e. immediate calving home range). The low segregation during calving may result from sparse and patchy foraging resources in the spring due to snow conditions, which might explain why all females, regardless of reproductive status, occupied similar locations during calving. However, at larger temporal scales (i.e. early summer) social and spatial segregation increased between the females with and without calves (Loe et al. 2006), which the researchers related to increasingly differences in nutritional requirements during the lactating period.

In Nordenskiöld Land, the calving locations were characterized by high proportions of moss tundra, high NDVI values, increased wetness and on flatter, less rugged and lower elevated terrains and with limited variability between females. Similarly, the calving locations in northern areas were in areas with higher food quality, such as heath-covered tundra which is the most common type of vegetation in this region (Johansen et al. 2012), but with high individual variability in terrain selection. Wild reindeer in Hardangervidda, Norway tended to select for calving areas in higher elevated, barren areas (Strand et al. 2006), areas with low vegetation biomass or on steep slopes in high predation pressure areas (Gustine et al. 2010). The Svalbard reindeer in this study rarely seek higher terrain or steeper slopes over higher food quality for calving. Trade-offs exist between predation-avoidance and high foraging quality areas, depending on predation-pressure and foraging availability (Gustine et al. 2010). Since the Svalbard reindeer have few natural predators and predation pressure is very low, it is likely the reindeer are missing an incentive to calve at locations that give the most predator protection and the least high-quality food availability. Furthermore, the fact that females without calves are in the same habitat types during the calving period support the hypothesis that predation does not affect the choice of calving location for Svalbard reindeer, but rather the foraging quality.

Although collinearity does not affect the assumptions of the K-select analysis, the results must be interpreted with caution when considering the biological significance. NDVI and wetness were correlated and this makes it challenging to interpret which variable is more important for reindeer calving location selection. In addition, many terrain variables were autocorrelated such as barren, elevation, terrain ruggedness and slope. Thus, it is not possible to identify which of these variables were most important for the selection of calving locations given the analytical framework I chose in my thesis. For future studies it is recommended to explore this further by using these predictor variables in generalized linear models and find best model fit. It was evident that regardless of study area or reproductive status, reindeer selected for locations with higher foraging quality as indicated by moss tundra (southern study location) or heath (northern study location) during the calving period, depending on the availability. These two vegetation classes are comprised by several smaller sub-vegetation classes with varying food quality. Moss tundra consisted of wet terrain such as swamps and marshes, but also drier terrain such as open dry-grass communities. Reindeer may use these vegetation covers differently depending on the season (Bjune 2000). For example, important foraging areas for Svalbard reindeer during the summer are wetlands and moss tundra (Øritsland and Alendal 1986).

However, it was necessary to combine these classes since field data showed varying degree of accuracy in the sub-vegetation classes derived from satellite layers (Ravolainen pers.comm, November 2017). Such lumping of vegetation classes into coarse classes may have removed more of the potential fine scale selection that the reindeer may display. For future studies it would be interesting to investigate the habitat in calving locations on a smaller scale through fieldwork or improvement in sub-vegetation class layers.

The K-select analysis demonstrated that the three northern populations had high individual variability in habitat selection for terrain variables in their calving locations, which is formerly suggested to be important to consider in such analyses (Mysterud and Ims 1998). The northern populations are isolated from each other by glaciers and fjords, but the habitat conditions within the spring home ranges are rather similar. Calenge et al. (2005) suggested that the selection of habitat conditions differs greatly depending on the individual's habitat availability in the spring home range, especially if there are physical barriers between animals. This might be the case for the northern reindeer populations. While in the case of female reindeer in Nordenskiöld Land that express high fidelity to summer home ranges and similar habitat conditions (i.e. meaning that they reside in the same main valleys, e.g. Colesdalen or Reindalen when they forage in summer; (Kinck 2014)), the selection for similar habitat conditions takes place.

The habitat variables used in the study were fixed for each year and it was not possible to calculate annual digital data layers of the environmental predictors, but the environmental conditions in the study areas varied across 9 years (i.e. snow melt, snow cover etc.). Vegetation, represented with average spatial data layers across several satellite image scenes (Johansen et al. 2012, Karlsen et al. 2014) such as NDVI, heath, moss tundra and barren lands are expected to have varied annually, but the Heat Load Index, terrain ruggedness, wetness, elevation, slope and aspect are likely to not vary much between years since they were derived from fixed topographical variables. However, since the heath and moss tundra comprised of several sub-vegetation classes it was more suitable to combine these variables in this multi-year study since sub-vegetation classes changes faster than major food quality classes. For future studies it is recommended that food quality and quantity data layers are treated separately for each year, but the K-select analyses does not allow for this for several years and such layers were not available for this study.

4.3 Calving site fidelity

The average distance between two calving locations for females with two calving seasons was 3.3 ± 2.6 km. This was a similar distance to the mean interannual distance between spring home ranges (15. May to 30. June) of 2.9 ± 1.6 km, which was defined as the null hypothesis. Although there was no significant difference between calving location and null hypothesis, the mean calving location distance was closer for Svalbard reindeer compared to *Rangifer* elsewhere (Schaefer et al. 2000, Popp et al. 2008). For sedentary mountain caribou in Labrador, Canada the distance between calving locations was high (15 km), but still displayed high site fidelity compared to the null hypothesis (Schaefer et al. 2000). For the Mealy Mountain caribou population in Labrador the closest distance to the previous year's calving location was 3.9 km (Popp et al. 2008). However, among other ungulates, Tremblay et al. (2007) found similar distances as this study between calving locations for moose. Moose cows on Vega Island, Norway had a site fidelity of 2.4 ± 2.0 km between consecutive calving locations for females with no loss in calves. This shows that although there was no significant difference between calving location and null hypothesis, the next year's calving location for the same female is still relatively close.

To define whether site fidelity is high or low for herbivores it is important to define the temporal and spatial scale (Owen-Smith and Martin 2015). For the null hypothesis in this study I used each individual's spring home range (15. May to 30. June). The spring home ranges were relatively small, and the females appeared to display high site fidelity towards the spring home range although this was not investigated statistically. Kinck (2014) found high site fidelity towards summer home ranges and it is likely that the Svalbard reindeer display high site fidelity towards spring home ranges as well. The average annual home range for females with two calving seasons was on average 83 km^2 for females in Nordenskiöld Land, and in comparison, the average distance between calving locations of 3.3 km is relatively close. If the interannual distance had been calculated for annual home ranges instead of spring home ranges, the distance between calving locations may have been significantly closer compared to null hypothesis. Additionally, females in Nordenskiöld Land calved in the same or adjacent valley in the following calving season and the defined calving location was based on 1 GPS fix. Thus, on a larger annual scale, the Svalbard reindeer shows high site fidelity towards calving locations, but on a seasonal scale (spring home range) the experimental design did not capture this fidelity.

5 Conclusion

This study showed that the calving period significantly differs across southern and northern Svalbard reindeer study populations likely related to different climate conditions within the study areas. It is recommended that the reasons for differences in calving period is investigated further especially by relating environmental predictors such as spring onset to the variation in calving day for study areas. Furthermore, the study suggests that to estimate calving day from GPS movement trajectories, the GPS fix frequency should be 12 GPS fixes per day during the calving period in June. As expected, the Svalbard reindeer appear to select calving locations based on foraging decisions as opposed to predation-risk, which is almost non-existent in this high-Arctic tundra landscape. This is demonstrated by the selection of calving locations in areas with high food quality on flatter, lower elevated grounds instead of higher elevated, barren areas. In addition, at this time of year females without calf selected the same type of habitat, which indicates that calving locations are selected independent of reproductive status in Svalbard reindeer. In addition, the Svalbard reindeer show high site fidelity at larger scales (e.g. annual home range) because they tend to calve in the same or adjacent valleys. At a smaller, seasonal scale (May-June) the calving locations were not statistically closer compared to the null hypothesis derived from spring home ranges. Overall, this study has successfully demonstrated the use of non-invasive methods to estimate calving day and habitat use for Svalbard reindeer during the calving period. The presented study can provide management with information on the type of habitat characteristics in reindeer calving locations to restrict human activity or infrastructure within the core calving areas as demonstrated by the space use of these GPS collared reindeer females. Such information is critical for the Svalbard reindeer reproduction and the long-term conservation of this endemic species.

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Appendix

A. Quality check for calving day estimation

This section includes three different methods I used to quality check the calving day estimation method, which is the background for the habitat analysis. In addition, it includes the result from the classification criteria and individual calving days.

A-1. Effect of 3 vs. 12 GPS fixes per day on calving estimations

To better understand how the number of GPS fixes affect the estimation of calving day, recursive partitioning graphs based on 3 and 12 GPS fixes were produced and calving day estimated separately for the same Nordenskiöld females (Fig. A-1). 65% (n=31) had the same calving day, while 29% (n=14) differed 1 day on the 3 and 12 GPS fix graphs. 8.3% (n=4) differed more than 1 day in calving day from the two different trials.

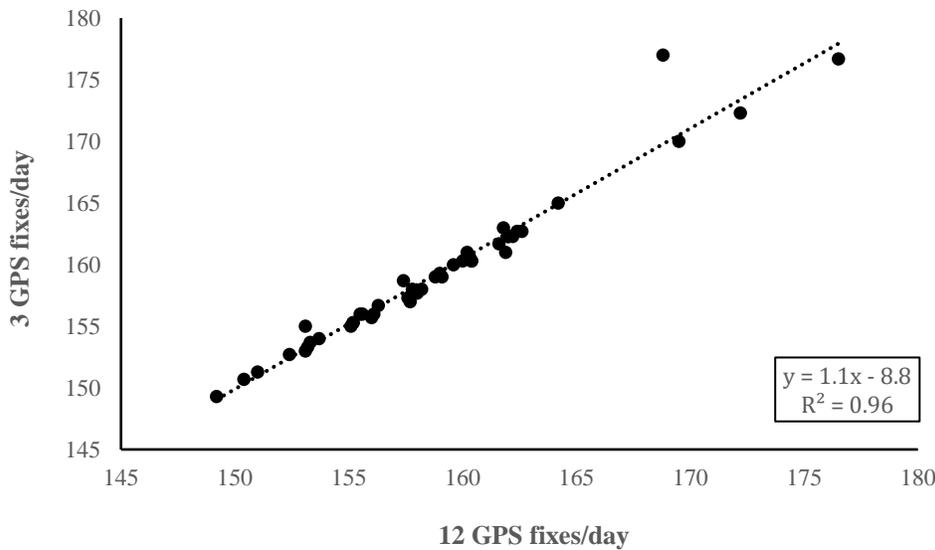


Figure A-1. Estimated calving day based on recursive partitioning plots showing 3 GPS fixes/day versus 12 GPS fixes/day. $R=R$ -squared.

A-2. Comparing calving day estimations with results from activity data

The calving dates from GPS data in Nordenskjöld Land were also compared with calving dates estimated by Vebjørn Veiberg based on activity sensor data (Veiberg et al. 2017). Ten individual calving dates were provided by V. Veiberg, and these were compared with calving dates from GPS data in Table A-2. Calculations of estimated calving dates from activity data is viewed as a better estimate of the actual calving date compared to GPS points since it has a higher temporal resolution with 1 activity point measured each minute. Only females from Nordenskiöld Land wa used for the quality check of method. The calving day differed between 0 and 1 days for all individuals. However, the GPS data with 12 GPS fixes/day corresponded more often to the activity data than the calving day estimations with 3 GPS fixes/day.

Table A-2. Comparison of calving dates estimated by recursive partitioning with 3 GPS fixes per day and 12 GPS fixes per day and results from activity data analysis from the same individuals. Matching dates are bolded and certainty classifications for 3 GPS fixes and 12 GPS fixes per day is in brackets. The estimation of calving dates from activity data is done by Vebjørn Veiberg (2017).

| Method comparison for calving day estimation (Julian day) | | | |
|--|----------------------|------------------------|-------------------------|
| Individuals | Activity data | 3 GPS fixes/day | 12 GPS fixes/day |
| NS_2009_B106 | 153 | 155 (1) | 153 (1) |
| NS_2009_B93 | 160 | 160 (1) | 160 (1) |
| NS_2010_B96 | 150 | 153 (2) | 150 (1) |
| NS_2012_B153 | 161 | 161 (2) | 161 (1) |
| NS_2012_G89 | 158 | 158 (2) | 158 (1) |
| NS_2013_B135 | 155 | 156 (1) | 155 (1) |
| NS_2013_B140 | 155 | 156 (1) | 156 (1) |
| NS_2013_B153 | 159 | 159 (2) | 159 (2) |
| NS_2014_B154 | 161 | 162 (2) | 161 (2) |
| NS_2014_G89 | 155 | 156 (2) | 155) |

A-3. Calving event detection in recursive partitioning graphs.

A manual test was carried out to make sure that the calving breakpoints were present for the females that calved and was not an artefact of the behaviour for all animals during the spring. The recursive partitioning graph of 93 individuals (50 females with calves and 43 females without calves) were selected and visually classified by myself as having calved/not calved during the May period without having this knowledge ahead of time.

In the manual test, 47% (n=44) were correctly identified as having calved based on the graph and field observations of calf at heel in the fall. 25% (n=23) of the females were correctly identified as not having calved in the spring and not observed with calf the same fall. 21.5% (n=20) females were identified as having calved on the graphs but not observed with a calf in the fall. However, 15 of these 20 females were identified as pregnant by ultrasound during the spring field surveys illustrating that the recursive partitioning graphs correctly identified the calving events, although the calf may have died during the summer and was not observed with a calf in the fall. Thus, only 5 out of 20 of these females were truly false negatives. 6.5% were classified as false positives, identified with calf on the recursive partitioning graph but not recorded with a calf the same fall.

A-4. Classification scheme of calving day estimations from recursive partitioning and first passage time.

Of the 95 calving seasons for GPS-collared females during 2009-2017, 50 showed a clear calving breakpoint on the recursive partitioning and first passage time graphs and were classified as 1 according to the classification scheme (Table A-4). For 16 calving season analyses, the graphs were too ambiguous to determine a calving day and were classified as 2 because they had two or more decreases in movement rate that could be identified as a calving breakpoint. For 10 calving season analyses, the graphs were determined as no calving breakpoint shown.

Table A-4. Certainty classification of estimated calving dates based on recursive partitioning graphs with 3 GPS fixes per day.

| Location | Classification scheme (n) | | | Total |
|-------------------|---------------------------|-----------|-----------|-----------|
| | 1 | 2 | 3 | |
| Brøggerhalvøya | 6 | 1 | 4 | 11 |
| Kaffiøyra | 5 | 1 | 2 | 11 |
| Nordenskiöld Land | 36 | 11 | 8 | 66 |
| Sarsøyra | 3 | 3 | 1 | 7 |
| Total | 50 | 16 | 10 | 72 |

A-4. Individual calving day estimations

Table A-4. Estimated calving day (in Julian Day) using recursive partitioning and first passage time for all GPS collared females observed with calves during the fall in the period 2009-2017. Certainty 1=clear calving pattern, 2=two or more possible calving breakpoints, 3=unclear pattern.

| ID | Calving day (FPT) | Calving day (rpart-3pts) | Calving day (rpart-12pts) | Certainty (3pts) | Certainty (12 pts) |
|--------------|-------------------|--------------------------|---------------------------|------------------|--------------------|
| BR_2015_21 | 170 | 170 | 170 | 1 | 1 |
| BR_2015_22 | 161 | 159 | 159 | 1 | 1 |
| BR_2015_24 | 167 | 165 | 165 | 2 | 1 |
| BR_2015_26 | 171 | 177 | 169 | 1 | 3 |
| BR_2015_32 | 165 | 165 | 164 | 1 | 1 |
| BR_2017_23 | 162 | 162 | 162 | 1 | 1 |
| BR_2017_Y80 | 162 | 162 | 163 | 1 | 1 |
| KA_2014_33 | 176 | 177 | 177 | 1 | 2 |
| KA_2014_40 | 176 | 176 | 175 | 2 | 2 |
| KA_2015_34 | 161 | 161 | 160 | 1 | 2 |
| KA_2015_36 | 163 | 163 | 162 | 1 | 1 |
| KA_2015_37 | 155 | 154 | 161 | 3 | 2 |
| KA_2015_38 | 172 | 172 | 172 | 1 | 1 |
| KA_2015_39 | 173 | 151 | 171 | 3 | 3 |
| KA_2016_33 | 153 | 155 | 155 | 1 | 1 |
| NS_2009_B106 | | 155 | 153 | 1 | 1 |
| NS_2009_B93 | | 160 | 160 | 1 | 1 |
| NS_2009_W91 | | 156 | 156 | 1 | 1 |
| NS_2009_Y105 | | 160 | 160 | 1 | 1 |
| NS_2009_Y112 | | 158 | 158 | 1 | 1 |
| NS_2010_B103 | | 157 | 156 | 1 | 1 |
| NS_2010_B96 | | 153 | 150 | 2 | 1 |

| ID | Calving day (FPT) | Calving day (rpart-3pts) | Calving day (rpart-12pts) | Certainty (3pts) | Certainty (12 pts) |
|---------------|------------------------------|-------------------------------------|--------------------------------------|-----------------------------|-------------------------------|
| NS_2010_R240c | | 153 | 152 | 1 | 1 |
| NS_2010_W72 | | 162 | 162 | 1 | 1 |
| NS_2010_W91 | | 160 | 160 | 1 | 1 |
| NS_2010_Y117 | | 153 | 153 | 1 | 1 |
| NS_2011_B106 | | 157 | 157 | 2 | 1 |
| NS_2011_B154 | | 154 | 158 | 3 | 2 |
| NS_2012_B139 | | 163 | 162 | 1 | 1 |
| NS_2012_B153 | | 161 | 161 | 2 | 1 |
| NS_2012_G89 | | 158 | 159 | 2 | 1 |
| NS_2012_R246 | | 162 | 162 | 1 | 2 |
| NS_2012_W64 | | 165 | 165 | 3 | 1 |
| NS_2012_Y120 | | 162 | 162 | 1 | 1 |
| NS_2013_B105 | | 151 | 150 | 1 | 1 |
| NS_2013_B123 | | 151 | 151 | 2 | 1 |
| NS_2013_B129 | | 155 | 155 | 2 | 1 |
| NS_2013_B135 | | 156 | 156 | 1 | 1 |
| NS_2013_B140 | | 156 | 156 | 1 | 1 |
| NS_2013_B153 | | 159 | 159 | 3 | 2 |
| NS_2013_B156 | | 151 | 151 | 1 | 1 |
| NS_2013_B157 | | 156 | 156 | 1 | 1 |
| NS_2013_B158 | | 149 | 149 | 1 | 1 |
| NS_2013_B93 | | 159 | 159 | 1 | 1 |
| NS_2013_R264 | | 157 | 158 | 1 | 1 |
| NS_2014_B101 | 159 | 157 | 158 | 1 | 1 |
| NS_2014_B135 | 162 | 163 | 163 | 1 | 1 |
| NS_2014_B139 | 160 | 161 | 160 | 1 | 1 |
| NS_2014_B140 | 157 | 158 | 158 | 1 | 1 |
| NS_2014_B154 | 156 | 162 | 162 | 2 | 2 |
| NS_2014_G89 | 162 | 156 | 156 | 2 | 1 |
| NS_2014_W103 | 160 | 160 | 160 | 1 | 1 |
| NS_2014_Y104 | 153 | 153 | 155 | 3 | 2 |
| NS_2014_Y117 | 155 | 155 | 155 | 3 | 1 |
| NS_2015_B123 | 154 | 154 | 153 | 1 | 1 |
| NS_2015_B129 | 158 | 159 | 157 | 1 | 2 |
| NS_2015_Y117 | 159 | 158 | 157 | 2 | 1 |
| NS_2015_Y120 | 161 | 161 | 159 | 3 | 2 |
| NS_2016_B137 | 158 | 159 | 159 | 1 | 1 |
| NS_2016_B151 | 154 | 155 | 155 | 1 | 1 |
| NS_2016_G123 | 160 | 161 | 162 | 1 | 1 |
| NS_2016_W127 | 153 | 154 | 154 | 1 | 1 |

| ID | Calving day (FPT) | Calving day (rpart-3pts) | Calving day (rpart-12pts) | Certainty (3pts) | Certainty (12 pts) |
|--------------|------------------------------|-------------------------------------|--------------------------------------|-----------------------------|-------------------------------|
| NS_2016_Y167 | 152 | 153 | 153 | 1 | 1 |
| NS_2017_G118 | 164 | 161 | | 1 | |
| NS_2017_G143 | 153 | 152 | | 3 | |
| NS_2017_R299 | 171 | 171 | | 1 | |
| NS_2017_R310 | 160 | 160 | | 1 | |
| NS_2017_W139 | 165 | 162 | | 2 | |
| NS_2017_Y136 | 159 | 154 | | 2 | |
| NS_2017_Y205 | 164 | 168 | | 3 | |
| SA_2016_Y81 | 160 | 160 | 160 | 2 | 1 |
| SA_2016_Y82 | 161 | 162 | 162 | 1 | 1 |
| SA_2016_Y83 | 154 | 155 | 155 | 1 | 1 |
| SA_2016_Y84 | 157 | 158 | 158 | 1 | 1 |
| SA_2016_Y88 | 165 | 165 | 165 | 2 | 2 |
| SA_2017_Y81 | 157 | 157 | 166 | 2 | 3 |

B. Results from K-select analysis

B-1. Habitat selection one day post-calving

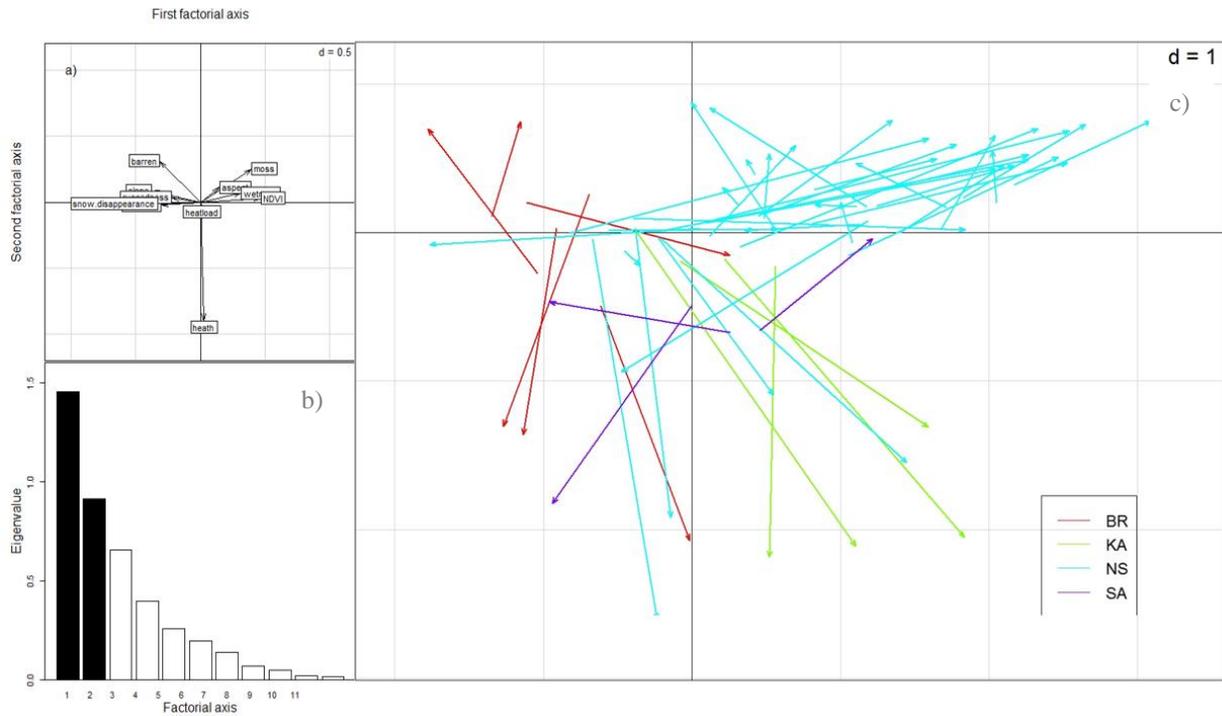


Figure B-1. Non-centered K-select analysis for habitat selection of Svalbard reindeer females the first day after calving. a) habitat variable loadings with proportion of heath, moss and barren, wetness, NDVI, aspect, heat load, ruggedness, elevation and slope according to Table 1. b) Eigenvalues for 11 factorial axes where the two black ones indicate that most variation is accounted for by these axes. c) K-select analysis for Brøggerhalvøya (BR), Kaffiøyra (KA), Nordenskiöld Land (NS), Sarsøyra (SA). Each arrow represents an individual female with calf. The origin of each arrow is the average available habitat for that female (95% KDE between 15.May-30.June) and the end of the arrow is the average used habitat conditions for the first day (3 GPS fixes) after calving.

B-2. Habitat selection three days post-calving

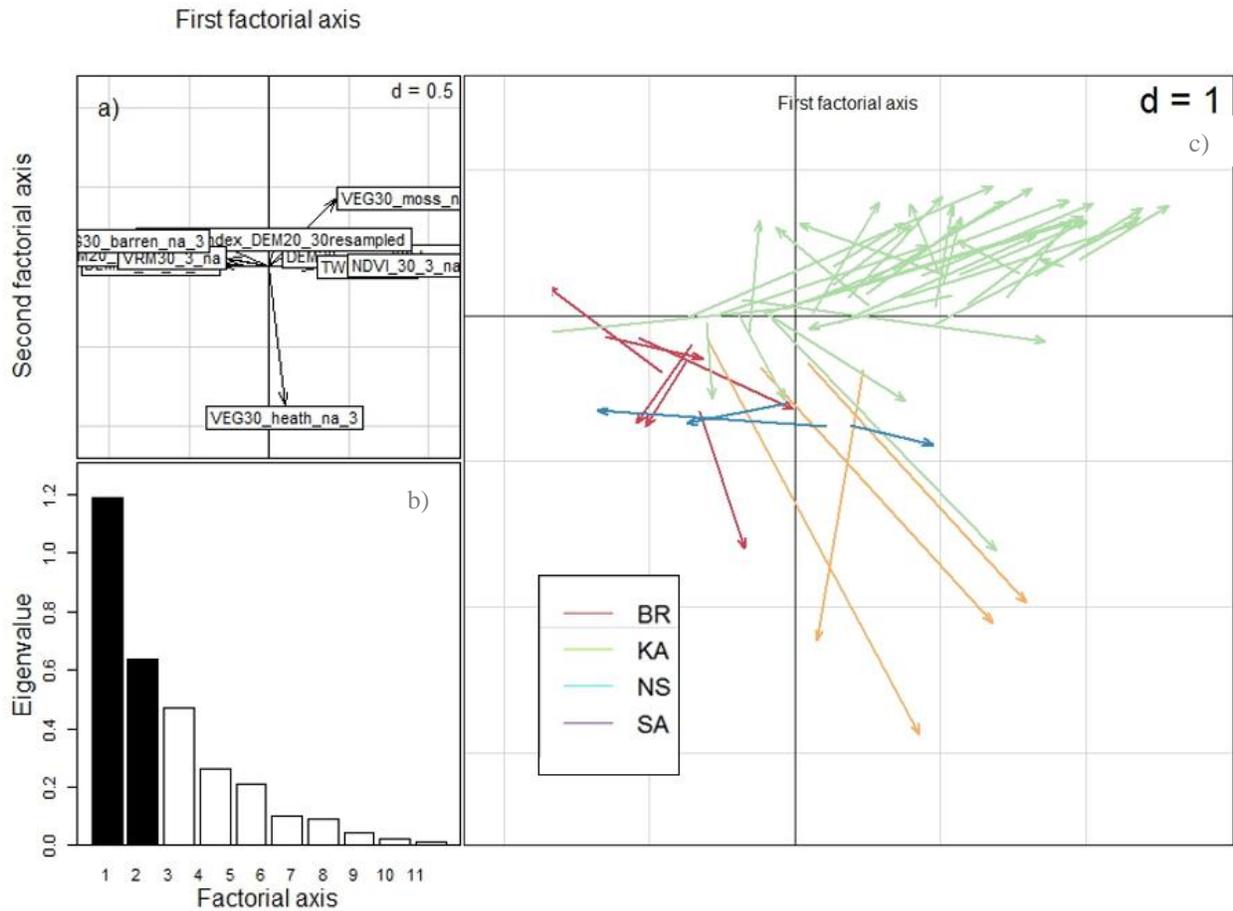


Figure B-2. Non-centered K-select analysis for habitat selection of Svalbard reindeer females the three first days after calving. a) habitat variable loadings with proportion of heath, moss and barren, wetness, NDVI, aspect, heat load, ruggedness, elevation and slope according to Table 1. b) Eigenvalues for 11 factorial axes where the two black ones indicate that most variation is accounted for by these axes. c) K-select analysis for Brøggerhalvøya (BR), Kaffiøyra (KA), Nordenskiöld Land (NS), Sarsøyra (SA). Each arrow represents an individual female with calf. The origin of each arrow is the average available habitat for that female (95% KDE between 15.May-30.June) and the end of the arrow is the average used habitat conditions for the three first days (9 GPS fixes) after calving.

B-3. Habitat selection four days post-calving

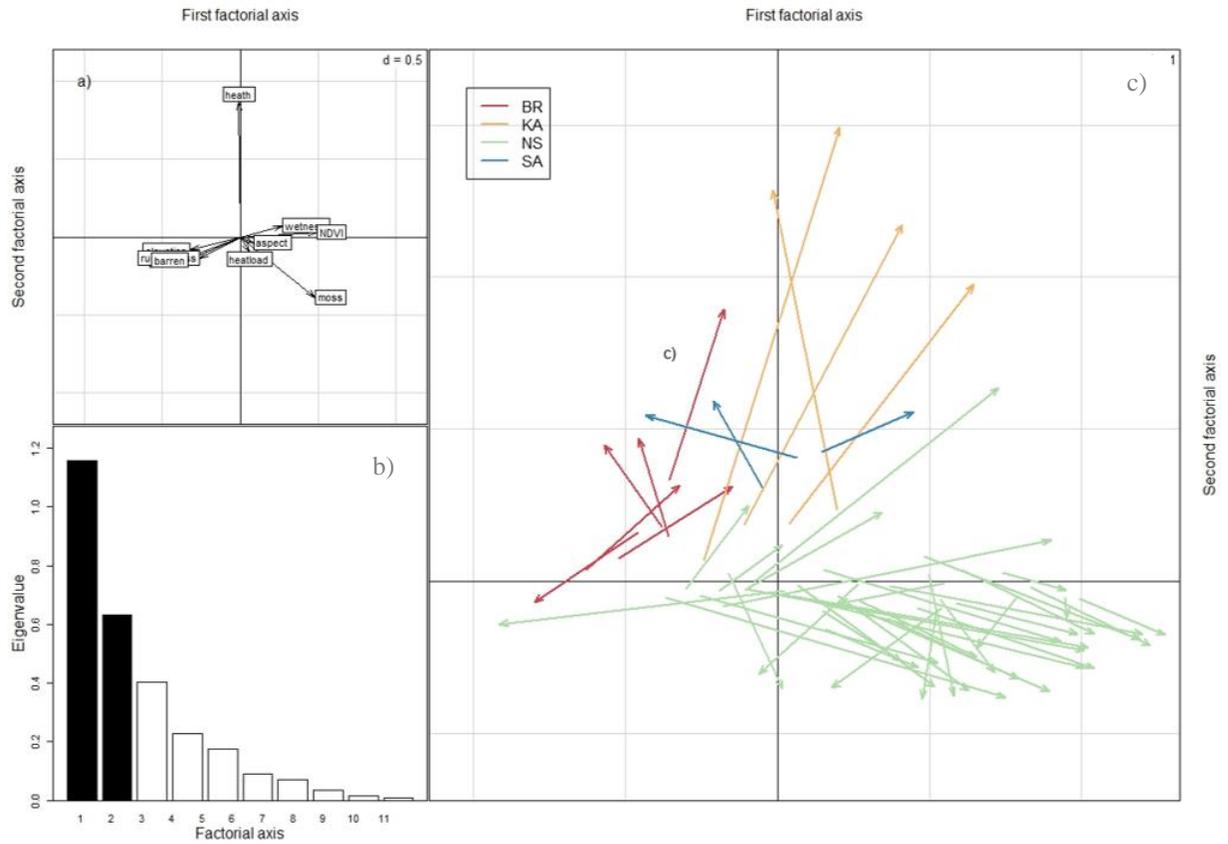


Figure B-3. Non-centered K-select analysis for habitat selection of Svalbard reindeer females the four first days after calving. a) habitat variable loadings with proportion of heath, moss and barren, wetness, NDVI, aspect, heat load, ruggedness, elevation and slope according to Table 1. b) Eigenvalues for 11 factorial axes where the two black ones indicate that most variation is accounted for by these axes. c) K-select analysis for Brøggerhalvøya (BR), Kaffiøyra (KA), Nordenskiöld Land (NS), Sarsøyra (SA). Each arrow represents an individual female with calf. The origin of each arrow is the average available habitat for that female (95% KDE between 15.May-30.June) and the end of the arrow is the average used habitat conditions for the four first days (12 GPS fixes) after calving.

B-5. Determining the 1 km buffer around calving location for habitat selection

The buffer width of 1 km diameter (radius=500 m) around the calving breakpoint was determined based on three different aspects.

- 1) Identifying calving length on the net displacement graphs based on the second candidate breakpoint after the calving breakpoint from recursive partitioning. Most females appeared to have a calving length between 1-4 days (Fig. B-4).
- 2) Average net displacement after the calving breakpoint for females showed that 4 days after calving the female was on average 1 km away from the calving breakpoint.
- 3) Earlier field observations indicate that the females with calves tend to be within 1 km of parturition location during the summer (Nick Tyler, pers.comm, February 2018).

All GPS fixes inside the buffer for each individual female were quality checked to ensure that every female had enough GPS fixes inside their 1 km buffer. This was due to varying times spent inside the buffer.

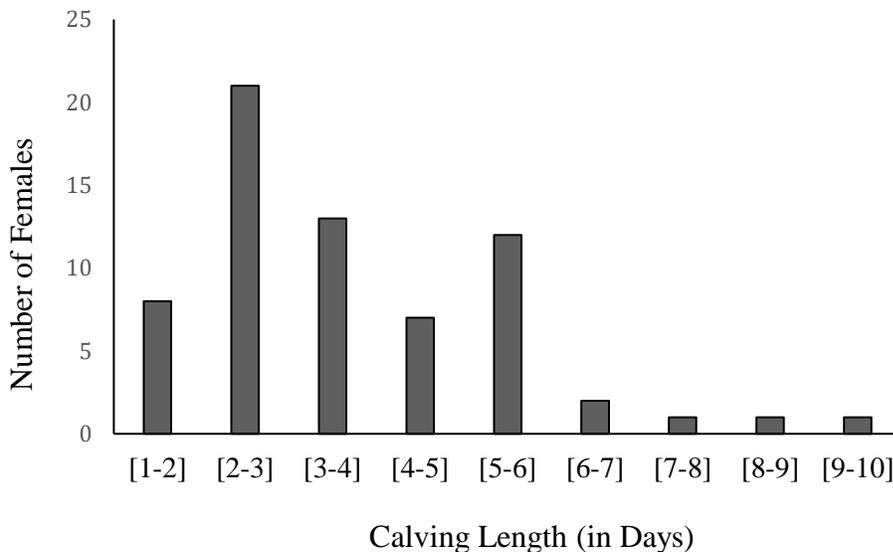


Figure B-5. Distribution of calving lengths for females. The calving length is derived from the second breakpoint after the calving breakpoint on the recursive partitioning graphs.

B-6. Results from marginality test

Figure B-6. Marginality and significance values for all females with calves in 1 km buffer as estimated by the randomization test for K-select. Number of replications $n=1000$. BR=Brøggerhalvøya, KA=Kaffiøyra, NS=Nordenskiold Land, SA=Sarsøyra.

| Location | ID | Marginality | P-value |
|----------|---------------|-------------|---------|
| BR | BR_2015_21 | 2.07 | 0.03 |
| BR | BR_2015_22 | 2.82 | 0.02 |
| BR | BR_2015_26 | 1.59 | 0.08 |
| BR | BR_2015_32 | 1.98 | 0.03 |
| BR | BR_2017_23 | 1.05 | 0.15 |
| BR | BR_2017_Y80 | 1.91 | 0.04 |
| KA | KA_2014_33 | 9.30 | 0.00 |
| KA | KA_2015_34 | 5.23 | 0.00 |
| KA | KA_2015_38 | 4.32 | 0.01 |
| KA | KA_2016_33 | 5.19 | 0.00 |
| NS | NS_2009_B106 | 5.64 | 0.00 |
| NS | NS_2009_B93 | 2.23 | 0.02 |
| NS | NS_2009_W91 | 1.37 | 0.08 |
| NS | NS_2009_Y105 | 2.33 | 0.02 |
| NS | NS_2009_Y112 | 1.52 | 0.06 |
| NS | NS_2010_B103 | 1.87 | 0.02 |
| NS | NS_2010_R240c | 1.41 | 0.08 |
| NS | NS_2010_W72 | 5.22 | 0.00 |
| NS | NS_2010_W91 | 1.90 | 0.04 |
| NS | NS_2010_Y117 | 1.79 | 0.04 |
| NS | NS_2012_B139 | 1.80 | 0.05 |
| NS | NS_2012_R246 | 4.62 | 0.00 |
| NS | NS_2012_Y120 | 1.26 | 0.10 |
| NS | NS_2013_B105 | 5.16 | 0.00 |
| NS | NS_2013_B135 | 6.48 | 0.00 |
| NS | NS_2013_B140 | 2.13 | 0.05 |
| NS | NS_2013_B156 | 0.89 | 0.25 |
| NS | NS_2013_B157 | 2.13 | 0.03 |
| NS | NS_2013_B158 | 1.72 | 0.04 |
| NS | NS_2013_B93 | 0.66 | 0.39 |
| NS | NS_2013_R264 | 8.00 | 0.00 |
| NS | NS_2014_B101 | 4.25 | 0.00 |
| NS | NS_2014_B135 | 2.59 | 0.01 |
| NS | NS_2014_B139 | 1.82 | 0.04 |
| NS | NS_2014_B140 | 1.07 | 0.18 |

| Location | ID | Marginality | P-value |
|-----------------|--------------|--------------------|----------------|
| NS | NS_2014_W103 | 4.71 | 0.01 |
| NS | NS_2015_B123 | 1.40 | 0.10 |
| NS | NS_2015_B129 | 1.19 | 0.11 |
| NS | NS_2016_B137 | 1.62 | 0.05 |
| NS | NS_2016_B151 | 0.54 | 0.46 |
| NS | NS_2016_G123 | 2.91 | 0.01 |
| NS | NS_2016_W127 | 5.29 | 0.00 |
| NS | NS_2016_Y167 | 2.89 | 0.01 |
| NS | NS_2017_G118 | 3.34 | 0.01 |
| NS | NS_2017_R299 | 0.28 | 0.75 |
| NS | NS_2017_R310 | 3.82 | 0.00 |
| SA | SA_2016_Y82 | 0.91 | 0.21 |
| SA | SA_2016_Y83 | 2.09 | 0.02 |
| SA | SA_2016_Y84 | 1.83 | 0.03 |

C. Generalized linear models

I used GLMs on the dataset to examine whether calving day was significantly different among study areas or year. For the first analysis I included the entire dataset with only calving days classified as 1 in the classification criteria (Table A-4). For the second analysis, three outliers were excluded to investigate the potential effect of these outliers on the results. There could be two possible reasons for these outliers 1) the calving day is a method estimated based on GPS fixes and one cannot be certain calving has taken place although a behavioral calving pattern is identified, and 2) there is natural individual variation between populations in calving day (especially for the three northern isolated populations) and the outliers are a result of this natural variation. The three outliers were identified based on being above the upper quartile for study area or year when plotted in boxplots and as observed in Cook's distance on the residuals vs. leverage plot (Fig. C-1).

Predictor variables:

- Study area (northern populations (Brøggerhalvøya, Kaffiøyra and Sarsøyra) vs southern population (Nordenskiöld Land).
- Year (2014-2017).

Response variable:

- Calving day (in Julian day).

C-1. Transformation with z-scores (complete dataset)

Glm (formula = scale(calving day) ~ area + year, family = gaussian(link = "identity"), data = dataset)

Deviance Residuals:

| Min | 1Q | Median | 3Q | Max |
|---------|---------|---------|--------|--------|
| -1.0350 | -0.6496 | -0.1614 | 0.3598 | 1.7811 |

Coefficients:

| | Estimate | Standard Error | T-value | P-value | |
|------------------|----------|----------------|---------|---------|---|
| (Intercept) | 0.86 | 0.45 | 1.91 | 0.07 | . |
| areaNordenskiöld | -0.85 | 0.35 | -2.43 | 0.02 | * |
| year2015 | -0.21 | 0.49 | -0.44 | 0.67 | |
| year2016 | -1.09 | 0.45 | -2.41 | 0.02 | * |
| year2017 | -0.08 | 0.52 | -0.16 | 0.87 | |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for gaussian family taken to be 0.7074888)

Null deviance: 28.00 on 28 degrees of freedom

Residual deviance: 16.98 on 24 degrees of freedom

AIC: 78.775

Number of Fisher Scoring iterations: 2

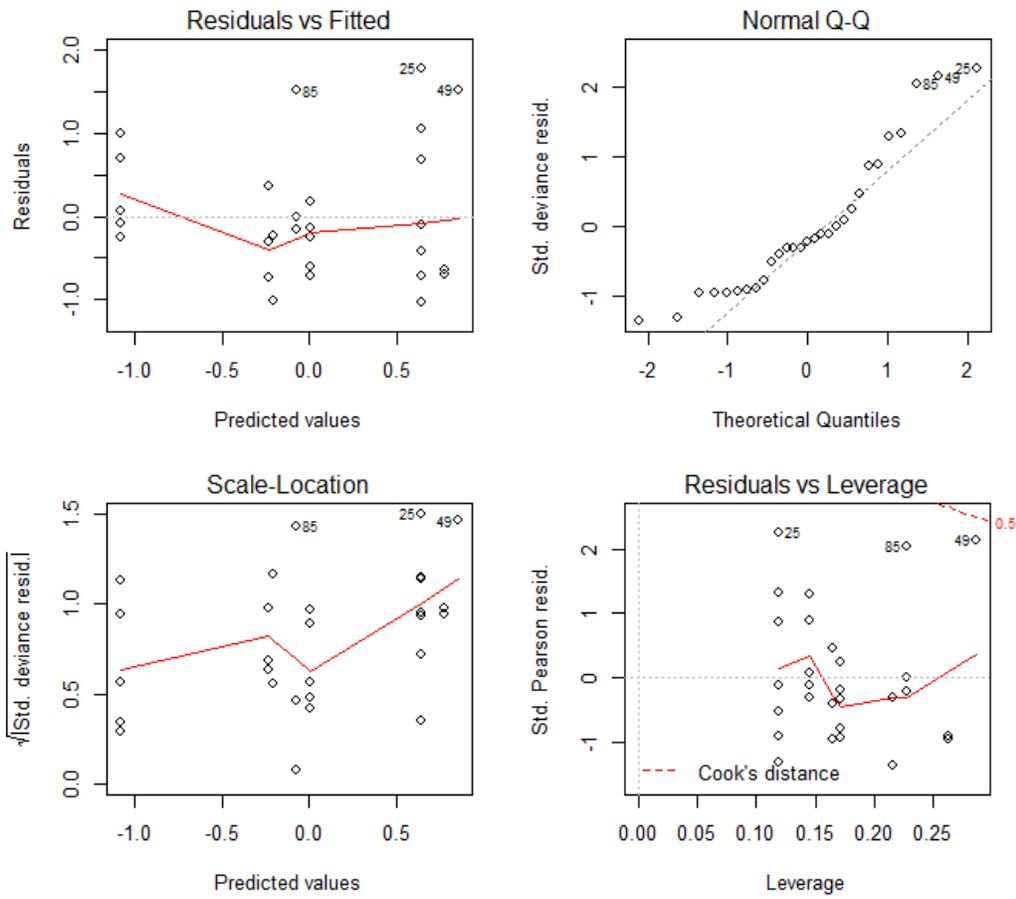


Figure C-1. Residual plots from regression analysis with z-score transformation. *formula = scale(calving day) ~ area + year, family = gaussian(link = "identity"), data = dataset.*

C-2. Transformation with z-scores (outliers excluded)

Call:

```
glm(formula = scale(calving day) ~ area + year, family = gaussian(link = "identity"), data = df3excl)
```

Deviance Residuals:

```
   Min      1Q  Median      3Q      Max
-1.3727 -0.4817 -0.1853  0.3224  1.8559
```

Coefficients:

| | Estimate | Standard Error | T-value | P-value |
|------------------|----------|----------------|---------|---------|
| (Intercept) | 0.75 | 0.53 | 1.41 | 0.17 |
| areaNordenskiold | -0.82 | 0.38 | -2.16 | 0.04* |
| year2015 | 0.08 | 0.55 | 0.15 | 0.89 |
| year2016 | -0.94 | 0.49 | -1.91 | 0.07. |
| year2017 | -0.04 | 0.60 | -0.07 | 0.94 |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for gaussian family taken to be 0.6899682)

Null deviance: 25.00 on 25 degrees of freedom

Residual deviance: 14.50 on 21 degrees of freedom

AIC: 70.583

Number of Fisher Scoring iterations: 2

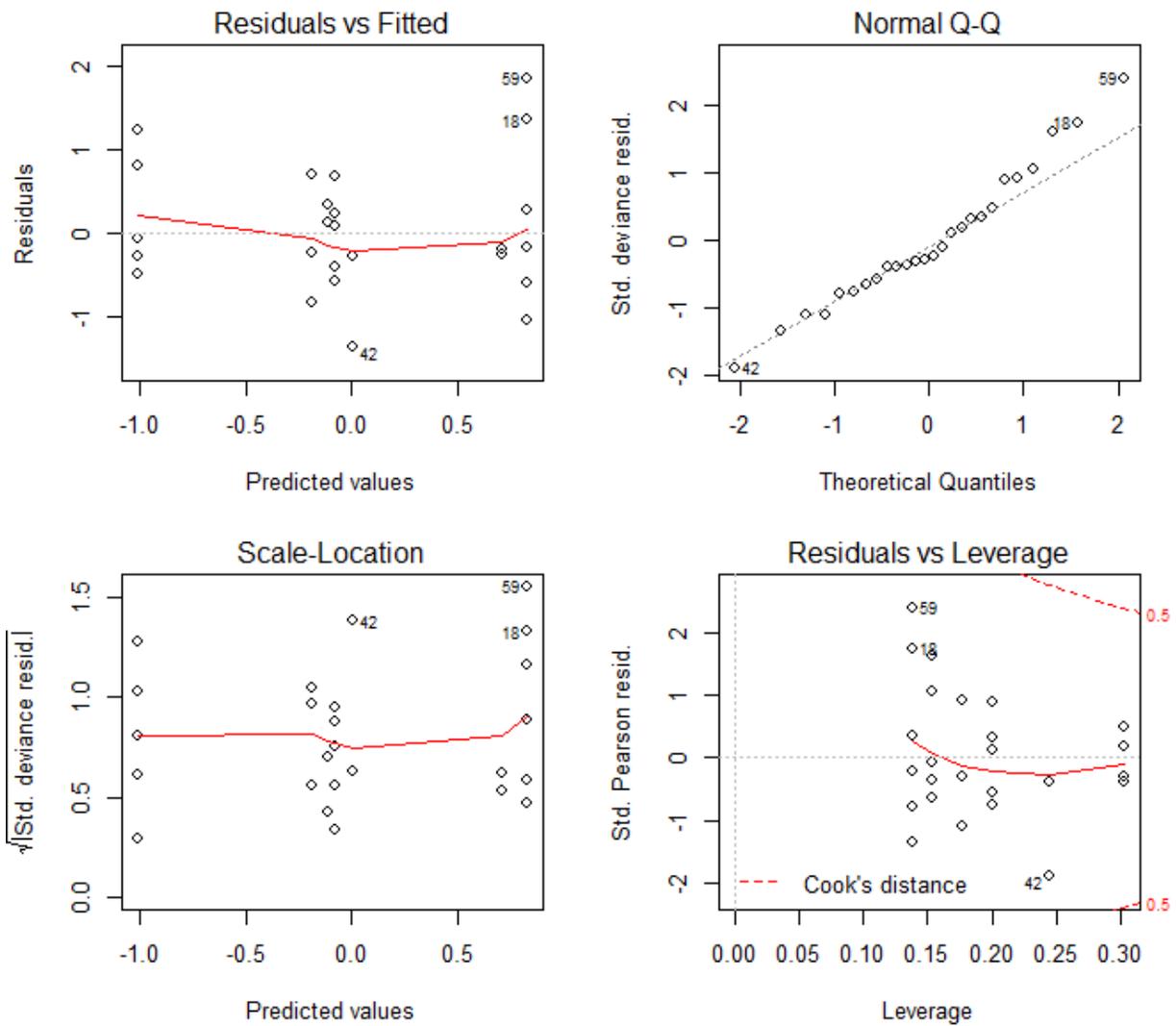


Figure C-2. Residual plots from regression analysis with z-score transformation and three outliers removed.
 Formula = `scale(calving day) ~ area + year, family = gaussian(link = "identity"), data = df3excl`

D. Average habitat selection

Table D-1. Number and % of females located below and above average mean available habitat in Nordenskiöld Land (n=36). The used available habitat was defined as the GPS fixes for each individual female inside the 1 km calving buffer. The mean available habitat was calculated based on the average value of each raster layer within the study area (defined as the merged spring home range (15. May to 30. June). The number of animals (n) were summarized as having above or below the mean habitat values in the study area from the randomization test.

| Nordenskiöld Land | | | | | |
|---|---|----------------------|------------|----------------------|------------|
| Number of females located in each habitat variable | | | | | |
| Habitat variables | Mean available habitat for all animals | Below average | | Above average | |
| <i>Elevation (m)</i> | 211 (1,1005) | 21 | 60% | 14 | 40% |
| <i>Slope (radians)</i> | 0.2 (0,1) | 23 | 66% | 12 | 34% |
| <i>Aspect (degrees)</i> | 187 (0,360) | 19 | 54% | 16 | 46% |
| <i>Heatload index</i> | 0.02 (-1.4,1.2) | 16 | 46% | 19 | 54% |
| <i>Wetness</i> | 10 (6,25) | 16 | 46% | 19 | 54% |
| <i>Ruggedness</i> | 0.001 (NA,0.9) | 28 | 80% | 7 | 20% |
| <i>Moss</i> | 0.5 (0,1) | 5 | 14% | 30 | 86% |
| <i>Heath</i> | 0.1 (0,1) | 26 | 74% | 9 | 26% |
| <i>Barren</i> | 0.2 (0,1) | 29 | 83% | 6 | 17% |
| <i>NDVI</i> | 0.4 (-0.07,0.7) | 6 | 17% | 29 | 83% |

Table D-2. Number and % of females located below and above average mean available habitat in the northern locations (n=14). The used available habitat was defined as the GPS fixes for each individual female inside the 1 km calving buffer. The mean available habitat was calculated based on the average value of each raster layer within the study area (defined as the merged spring home range (15. May to 30. June). The number of animals (n) were summarized as having above or below the mean habitat values in the study area from the randomization test.

| Northern locations | | | | | |
|--|-------------------------------|----------------------|------------|----------------------|------------|
| Selection of each habitat variable for individual females | | | | | |
| Habitat variables | Mean available habitat | Below average | | Above average | |
| <i>Elevation (m)</i> | 104 (7,362) | 8 | 57% | 6 | 43% |
| <i>Slope (radians)</i> | 0.1 (0,0.6) | 8 | 57% | 6 | 43% |
| <i>Aspect (degrees)</i> | 206 (4,354) | 8 | 57% | 6 | 43% |
| <i>Heatload index</i> | 0.06 (-0.2,0.5) | 9 | 64% | 5 | 36% |
| <i>Wetness</i> | 10 (7,16) | 9 | 64% | 5 | 36% |
| <i>Ruggedness</i> | 0.003 (0,0.02) | 11 | 79% | 3 | 21% |
| <i>Moss</i> | 0.12 (0,0.9) | 11 | 79% | 3 | 21% |
| <i>Heath</i> | 0.4 (0,1) | 3 | 21% | 11 | 79% |
| <i>Barren</i> | 0.5 (0,1) | 7 | 50% | 7 | 50% |
| <i>NDVI</i> | 0.2 (-0.03,0.6) | 9 | 64% | 5 | 36% |

E. Calving site fidelity

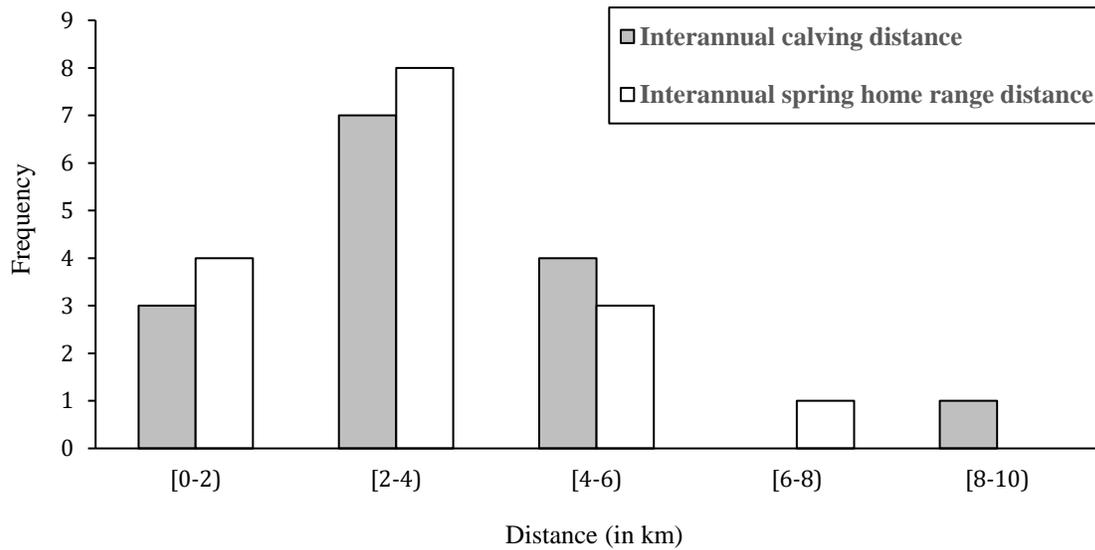


Figure E-1. Frequency distribution of females. The columns show the distances between interannual calving locations (shown in grey) and the null expectation (shown in white). The null expectation is the average pairwise distance between GPS fixes in each individual female's spring home range.