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Don't go chasing the ghosts of the past: habitat selection and site fidelity during calving in an Arctic ungulate

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Predator avoidance and food availability are both factors known to influence habitat selection and site fidelity around calving in caribou and reindeer. Here, we assess habitat selection and site fidelity during the calving period in the solitary, Arctic Svalbard reindeer *Rangifer tarandus platyrhynchus*, which is subject to limited predation risk and human disturbance. In this largely predator-free environment, we explore and discuss if habitat selection during the first week after calving is driven by food availability or remnants of anti-predatory behaviour. Based on GPS-collar data and ultrasound scanning (2009–2017; n = 134 individual-years) from two study areas, we estimated individual calving dates using recursive partitioning and first passage time and compared habitat selection and site fidelity of reproductive versus non-reproductive females. The K-select analysis suggested similar habitat selection during calving in reproductive and non-reproductive females. Female reindeer generally selected for lowland, flat habitats with high proportion of heath and moss tundra, i.e. habitats typically rich in terms of forage plants. Individuals producing a calf had significantly higher site fidelity in the calving period compared to the null model, and the mean distance between consecutive years' calving areas ranged between 1.5 and 3.9 km. Our study provides support for the prediction that in the absence of significant predation, ungulate calving site selection in the Arctic is mainly driven by the availability of spatially and temporally varying food resources.

Keywords: Arctic, calving, food availability, GPS, *Rangifer tarandus platyrhynchus*, remote sensing, site fidelity

Environmental conditions during gestation and after birth (Wolcott et al. 2015), including those affected by parental behavioural decisions, can influence reproductive success (McNamara and Houston 1986, Byers and Hogg 1995). For instance, choice of rearing habitat can be pivotal for offspring early survival (Refsnider and Janzen 2010). Animal habitat selection involves both responses in space and time to perceived risks and rewards and occur at multiple spatial and temporal scales (Mayor et al. 2009). For many female ungulates, the distribution of predators and the availability of forage resources are the two main factors explaining habitat selection in the calving period (Gustine et al. 2006). The 'predation risk hypothesis' states that females with dependent offspring trade good foraging locations for predator safe areas when the offspring is at its most sensitive stage to predation (Bowyer 1984, Brown et al. 1999), as seen in e.g. moose *Alces alces* (Tremblay et al. 2007), European red deer *Cervus elaphus* (Bonenfant et al. 2004) and reindeer and caribou *Rangifer tarandus* sp. (Mumma et al. 2017, Viejou et al. 2018). However, for many ungulates, predation risk alone cannot explain female habitat selection around the period of birth (Ruckstuhl and Neuhaus 2002). As the offspring grows, nutritional requirements increase (Cook et al. 2004), and access to foraging areas with high quality and quantity of forage is essential (Ruckstuhl and Neuhaus 2002). In predator-free environments, one could therefore anticipate that forage resources are the main determinant of habitat selection, and that the habitat selection patterns are independent of reproductive status. However, even in the absence of predators, relict anti-predator behaviour, has been observed to affect habitat selection in ungulates (Byers 1998, Mahoney and Schaefer 2002).

Site fidelity, i.e. the tendency of an individual to return to a previously used area, is often strong in ungulates (Gunn and Miller 1986, Tremblay et al. 2007). The past experience of spatial predation patterns, food resource distribution and positive reproductive outcomes may encourage females to return to the same calving area (i.e. philopatric behaviour) and thus help them maximize reproductive success (Switzer 1993, Mettke-Hofmann 2017). However, it is not clear whether calving site fidelity is mainly driven by predictability of reproductive success (i.e. the expectation that future outcomes will be the same as the current outcome, if you do the same) or by the assessment of environmental cues, i.e. temporally or spatially varying costs and benefits. In general, site fidelity may be weaker the less predictable resources are in space and time (Arthur et al. 2015). For instance, terrestrial Arctic ecosystems are characterized by long, harsh winters, short summers and large seasonal variability in forage availability. During spring and early summer, the landscape characteristics typically change from total snow cover to a mosaic of snow covered and exposed vegetation, and eventually, a 'greening' landscape. Because of large annual variation in timing of snowmelt and spring onset (Pedersen et al. 2016, Schmidt et al. 2019), the spatial distribution and availability of forage is likely to be highly variable both within and between years. Low spatiotemporal predictability of food availability in potential calving areas may therefore lead to reduced calving site fidelity in the Arctic compared to more predictable environments (Callaghan et al. 2011). Thus, particularly low calving site fidelity could be anticipated in Arctic ungulates experiencing low predation pressure, such as the wild Svalbard reindeer *Rangifer tarandus platyrhynchus* (Tyler 1987, Derocher et al. 2000). The medium sized predator, the Arctic fox *Vulpes lagopus* is a common scavenger of Svalbard reindeer (Prestrud 1992, Eide et al. 2005) and capable of killing new-born calves (Prestrud 1992), but there is very limited evidence of such predation events or attempts (Tyler 1986, 1987, Prestrud 1992). Polar bears *Ursus maritimus* occur on the Svalbard tundra during parts of the year but have very rarely been observed killing adult reindeer (and never calves; Derocher et al. 2000).

In this observational study, we used a GPS-collar dataset with 134 individual-years from Svalbard reindeer females (2009–2017) to estimate individual calving dates and analyse seasonal habitat selection and site fidelity patterns of reproductive versus non-reproductive individuals. We explored if, in an environment with negligible predation risk, habitat selection of female reindeer during the calving period is driven by selection for areas with high food availability (Hamel and Côté 2008) or remnants of anti-predatory behaviour during this most sensitive life stage for the Svalbard reindeer.

Material and methods

Study area

This study was conducted on Spitsbergen in the Arctic Svalbard archipelago, and included two study areas that differ in terrain and climate characteristics – Nordenskiöld Land (78°N, 15–16°E; middle Arctic tundra zone; Elvebakk 1999) and West-Spitsbergen (78°N, 11–12°E; High-Arctic tundra zone) (Fig. 1). The Nordenskiöld Land study area (hereafter 'inland area'; approx. 150 km^2) consists of wide u-shaped valleys connected by smaller valleys through high elevation passes. The area contains a wide variety of habitat types, ranging from continuous vegetation of different types in the valleys to barren ground at higher elevation. Marshes, wetlands and moist moss tundra dominate the lowland valley bottoms, while various types of moss tundra and heaths cover the foothills and slopes (Johansen et al. 2012). The West-Spitsbergen study area (hereafter 'coastal area'; approx. 296 km^2) consists of three peninsulas, which are separated by open sea and large tidewater glaciers. These peninsulas are characterized by coastal plains with an abrupt shift to steep and rugged terrain with alpine mountains. The vegetation cover in the coastal plains is discontinuous and consists of heath, open ridge communities and small pockets of different types of moss tundra (Johansen et al. 2012).

The study areas differ in terms of climate and weather variability, including length of the period with snow cover and the amount of precipitation. The coastal area (Ny-Ålesund weather station) has on average six weeks longer period of snow cover than the inland area (Svalbard airport weather station) (2009–2017; Norwegian Meterological Inst. 2018), and the timing of onset of the growing season is also overall later in Ny-Ålesund (Karlsen et al. 2014). Furthermore, the mean annual precipitation is more than double in Ny-Ålesund (541.9 ± 122.8 mm) than at Svalbard airport (209.7 ± 41.6 mm) (2009–2017; downloaded from <www.seklima.met.no>).

Study species

Svalbard reindeer are non-migratory and appear solitary or in small, often sexually segregated groups (Loe et al. 2006). Individuals occupy seasonal home ranges that are small compared to the migratory reindeer and caribou herds elsewhere in the Arctic (Tyler and Øritsland 1989). However, partial seasonal migration can occur, for instance in severe winters (i.e. with multiple icing events) and when forage resources are scarce (Hansen et al. 2010, Loe et al. 2016). The population fluctuations are mainly driven by winter weather variability and density-dependence, which operates through competition for food and gastrointestinal parasitism (Albon et al. 2002, Kohler and Aanes 2004, Tyler et al. 2008, Hansen et al. 2013).

Reindeer GPS-data

Reindeer capture

Female Svalbard reindeer were marked with GPS-collars to obtain data on their habitat and space use. The reindeer were captured during winter (February to April 2009–2017) using a handheld net from a pair of snowmobiles (Omsjoe et al. 2009). In total, 84 and 51 individual female reindeer from the inland and coastal areas, respectively, were fitted with GPS-collars (Vectronic 'store-on-board' collars in the inland study area (2009–2015), Followit satellite collars in the inland study area (2016–2017) and the coastal study area (2014–2017)) during the study period. All animals were

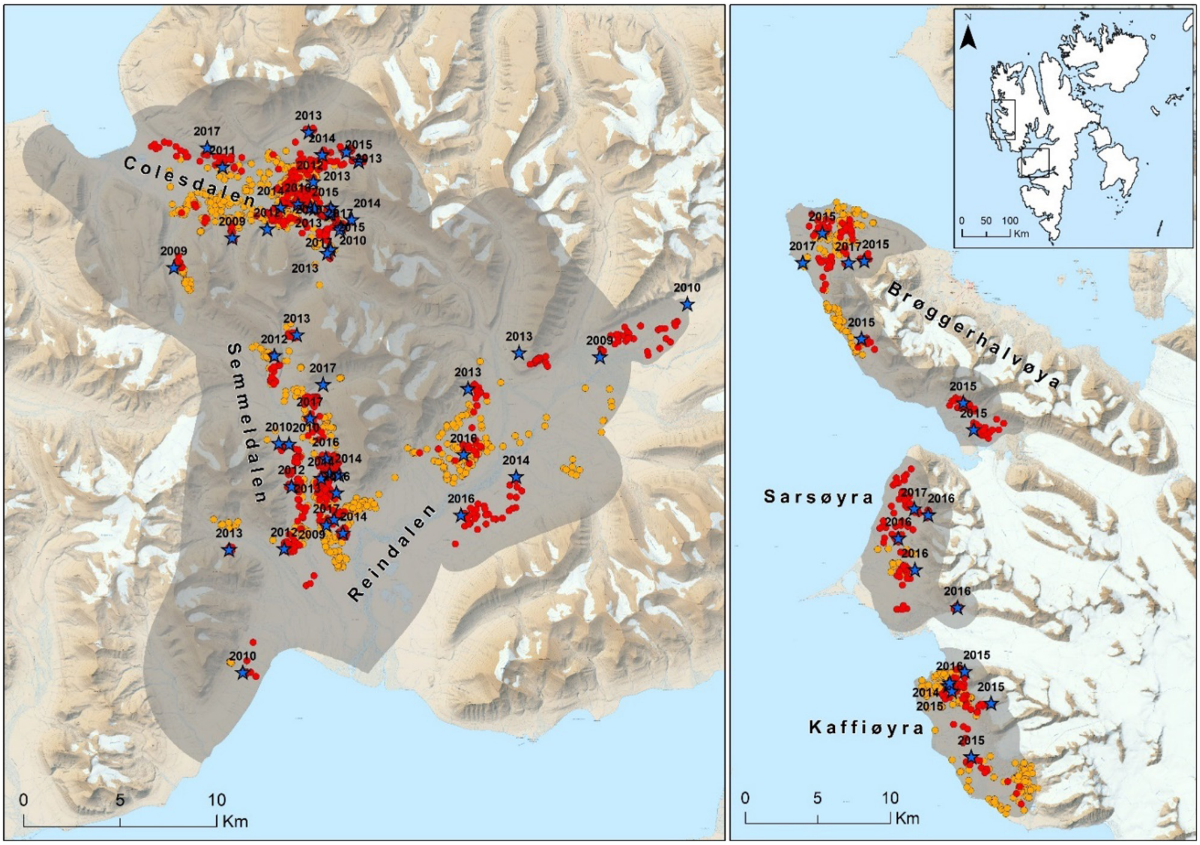

Figure 1. Locations of GPS-marked Svalbard reindeer females the seven days after calving in summers 2009–2017 in the inland study areas of Nordenskiöld Land (left panel) and coastal study areas of West-Spitsbergen (right panel). Light-grey areas are merged spring home ranges (95% KernelUD, 15 May–30 June) for all females with calves in the period 2009–2017. Blue stars = estimated individual calving sites from GPS movement metrics (RP and FPT). Circles = all GPS-positions seven days after calving for females with calves (red), and seven days after median calving day for females without calves (orange).

handled according to protocols approved by the Governor of Svalbard and the Norwegian Food Safety Authority.

Reproductive status

We recorded reproductive status of the GPS-collared females using ultrasound and/or progesterone blood sampling during capture and as the presence or absence of a calf at heel during late summer censuses in July and August (Albon et al. 2017 and Moullec et al. 2017 for description of protocols). Thus, reproductive females were defined as pregnant in spring and observed with a calf in the late summer census, while non-reproductive females were defined as not pregnant in spring and not observed with a calf in the summer census.

Pre-processing of GPS-data

To remove errors and outliers from the GPS-dataset, we followed the screening protocols by Bjørneraas et al. (2012), which reduced the number of unrealistic distances between GPS-positions (median > 100 km, mean > 10 km) and turning angles (> 1.5 km h^{-1}). The conservative movement thresholds were chosen because they handle the tradeoff between removing location errors and retaining sufficient GPS-positions in the dataset. In addition, all GPS-positions with a horizontal dilution of precision (HDOP) more than 10 m, were excluded to have similar spatial precision of GPS-positions (Recio et al. 2011). In total, these screening procedures removed 7% of the GPS-positions. The Vectronic 'store-on-board' collars recorded positions every 1–2 h, while the Followit satellite collars recorded positions once every eight hour. For consistency, all datasets were standardized to one position every eight hour (nearest GPS-position to 08:00, 16:00 and 00:00, Greenwich Mean Time). To reduce errors when estimating calving sites for females, we excluded individual-years if more than 60% of GPS-positions were missing in the pre- and post-calving period (15 May–30 June). On average, the remaining individual-year trajectories had a mean successful fix rate of 97% (93% for Follow-it satellite link service, 98% for Vectronic store-on-board). The resulting dataset contained data from 134 individual-years ($N_{inland} = 98$, $N_{coastal} = 36$) available for analysis (Table 1).

Environmental data

To study female habitat selection during the calving period, we selected 11 environmental variables based on literature about habitat selection in calving ranges elsewhere, the ecology of Svalbard reindeer and availability of digital spatial layers for the study areas (Table 2, for correlations among variables see Supporting information). We resampled all raster layers to the same spatial extent and resolution (30 × 30 m) using ArcMap 10.6.1 (ESRI 2011) and R Studio ver. 1.0.143 (<www.r-project.org>). For any raster layer with missing values within an individual's home range, missing values were replaced with the mean of existing values for the

Table 1. Sample size overview of GPS-collared Svalbard reindeer females for each study year and area (total $N_{inland} = 98$; $N_{coastal} = 36$; Fig. 1 for study areas) used in the habitat selection analyses. Calf status reflects the number of females with (1) and without (0) a calf at heel in late summer.

Study area	Location	Calf status	2009	2010	2011	2012	2013	2014	2015	2016	2017	Total
Coastal	Brøggerhalvøya	0	–	–	–	–	–	–	5	–	–	5
		1	–	–	–	–	–	–	5	–	2	7
	Kaffiøyra	0	–	–	–	–	–	7	5	–	–	12
		1	–	–	–	–	–	1	4	1	–	6
	Sarsøyra	0	–	–	–	–	–	–	–	1	–	1
		1	–	–	–	–	–	–	–	4	1	5
Inland	Nordenskiöld Land	0	8	6	6	8	6	4	3	2	7	50
		1	5	6	1	5	10	7	3	5	6	48
		Total	13	12	7	13	16	19	25	13	16	134

given home range. This way missing values were given less weight in the habitat selection analyses.

Vegetation variables

We extracted vegetation variables from the digital vegetation map by Johansen et al. (2012). Because several of the initial vegetation classes were ambiguous, based on the overall validation statistics, we regrouped the vegetation classes to three coarse habitat types reflecting available foraging habitats (termed 'moss tundra', 'heath' and 'barren'). Moss tundra (e.g. meadows, various types of wetlands and bird-cliff vegetation) reflects the most biomass-rich foraging habitats (mean biomass 330 g m^{-2}), while heath reflects less productive foraging habitats that constitute open heath communities and grasslands (mean biomass 225 g m^{-2}). Barren consist of areas with non-vegetated to sparsely vegetated areas, gravel and polar desert (mean biomass 28 g m^{-2}) (details in the Supporting information). All three habitat types are present in the inland and coastal areas in varying extents (Supporting information). When calculating the vegetation variables, we applied a moving average so that each 30 × 30 m pixel had the mean value based on the pixels in its immediate surroundings (3 × 3 pixels; 90 × 90 m).

Onset of the growing season

Annual raster maps describing the timing of the 'onset of the growing season' were available for the period 2009–2016 (Karlsen et al. 2014 for details). The onset of the growing season was defined as the day when the NDVI-value of a pixel first passed 70% of the same pixel's annual maximum NDVI-value (termed spring onset). This proxy for onset of growing season in Svalbard correlates well with the flowering of polar willow *Salix polaris* in Nordenskiöld Land, which is an important foraging plant for Svalbard reindeer (Bjørkvoll et al. 2009). For the habitat selection analyses, we calculated the mean onset of the growing season between 2009 and 2016 as we predicted reindeer to select calving areas with generally earlier growing season onset.

Terrain variables

Altitude, slope in radians and aspect in degrees were extracted from a Digital elevation model (DEM, 5–10 m estimated uncertainty, Norwegian Polar Inst. 2014). From the DEM, we also calculated three indices relevant to reindeer habitat selection: 1) terrain wetness, which represents an inverse measure of available dry habitat, was calculated following the 'the topographical wetness index' by Beven and Kirkby (1979). 2) The amount of incoming solar radiation, which affects snowmelt and plants' growing conditions (Pedersen et al. 2017), was calculated following the 'the heat-load index' by Parker (1988). 3) Terrain ruggedness, which is a measure of topographical heterogeneity, was calculated following the 'vector ruggedness measure' by Sappington et al. (2007).

Predation risk variable

Although predation by Arctic fox on reindeer calves is considered rare, observations of foxes harassing reindeer mothers and calves exist (Tyler 1986, 1987, Prestrud 1992). To investigate to what extent spatial variation in fox breeding den presence may influence Svalbard reindeer habitat selection in the calving period, we calculated a raster layer displaying the linear distance from each pixel to a known fox den in Svalbard (n = 81) and used this variable (termed foxdens) as a proxy for predation risk for reindeer calves. The position of fox breeding dens was obtained from the database 'Arctic fox dens on Svalbard' database that contain information on den sites from 1982 till today (Fuglei unpubl.). Arctic fox dens are used over generations and even for centuries (Prestrud 1992).

Statistical analyses

Estimation of calving day and site

To estimate calving day, and hence individual calving site from GPS-data, we used two methods based on movement metrics: 1) recursive partitioning, which uses movement rate and net displacement to capture distinct calving behaviours before, during and after birth in caribou (RP, Rudolph and Drapeau 2010), and 2) first passage time, which calculates time spent in a certain area, commonly applied in studies on foraging ecology of species (FPT, Fauchald and Tveraa 2003). For the RP method, we defined individual calving day as the day of the year where a recursive partitioning line (identifying a significant change from high to low movement rate) coincided with the minimum point in movement rate in the pre- and post-calving period (here defined as 15 May–30 June). This was followed by constant net displacement indicating that the female remained stationary. For the FPT method, we defined calving day as the date with the highest FPT value after 30 May, which corresponds to the date when females with calves required the longest time to move through a circle with radius 100 m, i.e. the date with most sedentary behaviour indicating calving. The RP and FPT

Table 2. Overview of environmental variables used to assess Svalbard reindeer calving habitat selection, with observed (reindeer/caribou in general) and expected effects on calving habitat selection given two main constraints (forage availability and predator avoidance). Prior to statistical analysis, all raster layers were re-sampled from their original resolution to a spatial resolution of 30 × 30 m to match the spatial resolution of the digital vegetation map by Johansen et al. (2012).

Constraint	Predictor variable	Original spatial resolution (m)	Unit of measure and range	Source	Observed or expected effects
Distribution of foraging resources	Heath	30 × 30	Proportion	Johansen et al. (2012)	Reindeer select for areas with high proportions of heath habitat because this vegetation type often consists of bare ridges where forage is accessible, even when much of the landscape still is snow covered (Henriksen et al. 2003, Hansen et al. 2009).
	Moss tundra	30 × 30	Proportion	Johansen et al. (2012)	Reindeer select areas with high quality and quantity of forage resources such as moss tundra because this vegetation type contains higher vascular plant biomass and important food items in early summer (Ruckstuhl and Neuhaus 2002, Henriksen et al. 2003, Pyare and Berger 2003).
	Onset of the growing season	240 × 240	Day of year	Karlsen et al. (2014)	Reindeer calve in areas with earlier onset of the growing season increases reproductive success (Tveraa et al 2013, Gustine et al. 2006).
	Aspect	20 × 20	0–360 degrees	DEM, NPI	Reindeer select southern aspects, which becomes earlier snow-free during calving (Jones et al. 2006, Loe et al. 2006)
	Elevation	20 × 20	Masl.	DEM, NPI	Reindeer select areas at low elevation since forage resources may be most abundant in the lowlands/foothills (Loe et al. 2006, Pinard et al. 2012, Nobert et al. 2016).
	Heatload index	20 × 20	0–1 (low – high)	DEM, NPI; Parker (1988); Pedersen et al. (2017)	Reindeer select snow-free, dry patches during the calving period, likely due to the abundance of emergent vegetation (Kelleyhouse 2001).
	Slope	20 × 20	0–90 degrees	DEM, NPI	Reindeer select moderate slopes because of generally less snow accumulation and earlier snowmelt than more flat terrain. Accordingly, forage will be available earlier during the calving season (Loe et al. 2006, Mårell and Edenius 2006).
	Terrain ruggedness index	20 × 20	0–1 (smooth–rugged)	DEM, NPI; Sappington et al. (2007)	Reindeer select for terrain with high ruggedness values due to higher terrain heterogeneity (e.g. various types of e.g. ridge habitats) leading to a more diverse foraging landscape (Nellemann and Thomsen 1994, Marell and Edenius 2006, Hansen et al. 2009).
	Topographical wetness index	20 × 20	0–1 (dry–wet)	DEM, NPI; Beven and Kirkby (1979)	Reindeer select dry areas because newborn calves are prone to hypothermia in wet conditions (Markussen 1983).
Predator avoidance	Barren	30 × 30	Proportion	Johansen et al. (2012)	Reindeer select for less optimal foraging habitats, often at higher elevations, at higher predation risks (DeCesare et al. 2014, Klaczek et al. 2015, Mumma et al. 2017, Viejou et al. 2018).
	Elevation	20 × 20	Masl.	DEM, NPI	Reindeer select calving sites on high-elevation ridgetops (Nobert et al 2016).
	Distance from foxdens	30 × 30	Meters	Eva Fuglei/NPI (pers. comm)	Reindeer select for calving locations with the least predation risk (DeCesare et al. 2014, Klaczek et al. 2015, Mumma et al. 2017, Viejou et al. 2018).
	Terrain ruggedness index	20 × 20	0–1 (smooth–rugged)	DEM, NPI; Sappington et al. (2007)	Reindeer select areas with high ruggedness values due to higher terrain heterogeneity, leading to better protection from predators (Nellemann and Thomsen 1994, Marell and Edenius 2006, Hansen et al. 2009).

analyses were computed using the Zoo and AdehabitatLT packages in R (Calenge 2016; see the Supporting information for an individual-year example). For both movement metrics, data for each individual-year were categorized according to how precisely calving day was determined. The categories were: 1) one-day certainty (n = 50), 2) 1–3 days certainty (calving day recorded as the first day of minimum movement rate after the recursive partitioning line, n = 16) and 3) no clear calving day (n = 14). Only data from females in category 1 was used in the subsequent habitat selection analyses. We found that the calving dates identified in the RP method correlated well with the calving dates identified from the FPT analyses in most cases (70%), but when these dates differed, recursive partitioning was used since this is a published calving day estimation method (Rudolph and Drapeau 2010).

Defining used and available habitats

We applied third-order habitat selection to investigate how habitat components within the home range are utilized in the calving period (Johnson 1980, Manly et al. 2002). Used and available habitat were defined for each individual-year separately to best match the calving period for each female (design III, Manly et al. 2002). For females with both a calf at heel in late summer censuses and an estimated calving day (n = 48), we defined the calving area as the location of all GPS-positions the first seven days after calving (Supporting information). We chose this period because the results of K-selection analyses on shorter time intervals after calving (location of females one, two, three and five-days post-parturition) appeared qualitatively similar. To compare habitat selection between reproductive and non-reproductive females, the used area for non-reproductive females in spring field surveys (n = 30) was defined as the location of all GPS-positions the first seven days after median calving day in the same population and year. For every individual-year in the two reproductive groups, the available habitat was defined as the spring home range (calculated using 95% Kernel's utilization distribution) from 15 May to 30 June, which also included the calving period.

Habitat selection in the calving area

To assess individual Svalbard reindeer calving habitat selection, we applied multivariate K-select analysis where environmental variables define a multi-dimensional niche space (Calenge et al. 2005). The K-select analysis is an exploratory factorial analysis that applies marginality vectors, i.e. the difference between vectors of an individual's mean utilised habitat and its mean available habitat in centred and non-centred principal component analyses. The size of the marginality vector for an individual is proportionate to the strength of habitat selection. The eigenvalues indicate the amount of mean marginality explained by each factorial axis. The K-select analysis is advantageous because correlation of habitat variables does not affect the results, both categorical and quantitative variables can be used, and the analysis graphically displays individual differences within populations. For each individual-year, the mean used habitat in the calving period is compared to mean available habitat. We separated individual-years into inland ($N_{with\_calf} = 36$, $N_{no\_calf} = 20$) and coastal study areas ($N_{with\_calf} = 12$, $N_{no\_calf} = 10$). To test whether habitat selected was non-random for these study populations and reproductive groups, we applied randomization tests on the marginality for each individual-year using a Bonferroni correction (n = 1000 repetitions, Calenge et al. 2005).

To summarize the importance of each of the 11 habitat variables across females of different reproductive status, we calculated the mean marginality vector length of each variable, i.e. the average across individuals of the difference between mean used and the mean available for the variable. The higher the absolute value of these mean marginality estimates, the further the reindeer departed on average from the mean available habitat of the given variable. A positive coefficient of a variable indicates that the females selected calving areas where the value of the variable is higher than the mean of the available habitat in spring home ranges, while negative coefficients indicate selection for areas with lower than the mean variable value. If the coefficient is close to zero, the mean variable value in the calving area is similar to the mean variable value in the spring home ranges (i.e. used is the same as available habitat). To test whether habitat selection differed significantly between reproductive and non-reproductive females, linear mixed effect models were performed on each environmental variable separately in R using the package *nlme*. We used the marginality coefficient of each habitat variable as the dependent variable, reproductive status as a predictor variable, while animal id were used as a random effect.

Site fidelity in the calving and rearing period

We analyzed site fidelity using the approach from Schaefer et al. (2000), where seasonal movement properties of the study animal define the scale of site fidelity. This allowed us to investigate how close Svalbard reindeer females is to a location that they occupied in previous years without setting an arbitrary spatial scale, an advantage when making comparisons between individuals. Distances between paired GPS-positions of a female obtained one year apart or more, but on the same day of year, were calculated for the whole year, and then aggregated into mean weekly distances for every individual. Data were available for 22 pairs of individual-years and the females had these possible reproductive outcomes in year t and year t >– 1: 1) calf–calf (n = 10), 2) no calf–no calf (n = 12), 3) no calf in one year and a calf in the other year (n = 8). To assess how site fidelity in the calving period differed from other seasons, the mean and 95% confidence intervals of individual distances were calculated for each week of the year for each reproductive group. We divided the spring and summer seasons into periods to ease group comparisons: calving (2–19 June) and rearing (early summer 20–30 June; mid-summer 1–31 July; late summer 1–31 August; following temporal scales defined by Loe et al. (2006). We combined inland and coastal study populations due to the low sample size from the coastal populations. To investigate differences in site fidelity during the calving and rearing period between reproductive groups, we used the non-parametric Wilcoxon rank-sum test to account for non-normality of the data.

To assess site fidelity in different seasons we developed a null model. First, we defined an individual's range as the space denoted by all GPS-positions in year t and year t > 1. Only pairs of individual-years with GPS-positions covering > 300 days per year were included to ensure all seasons were covered. Within this individual's annual range, we randomly sampled 1000 pairs of GPS-positions and calculated the distance between positions in each pair. These 1000 randomized distances were then averaged for pairs of individual-years to create the null model (representing the distribution of expected distance between any two GPS-positions). Significant site fidelity occurred in periods when the distance between the average of 'real pairs' of individual-years was lower than the lower 95% confidence limit of the average 'randomized pairs' of individual-years in the null model.

All statistical analyses were performed in R ver. 1.456 <www.r-project.org>.

Results

Estimation of calving day and site

Estimated calving dates for GPS-collared female Svalbard reindeer ranged from 5 to 17 June with median date of 8 June (Inland: median = 7 June, SD = 4 days, Coastal: median = 11 June, SD = 7 days). In the inland study area, most calving sites were aggregated in the innermost upland areas of Colesdalen (40%, n = 19) and Semmeldalen (34%, n = 16) (Fig. 1). In the coastal study area, no apparent pattern existed, all calving sites were distributed on the coastal flats and in the foothills (n = 18).

Habitat selection in the calving areas

In the inland area, the first axis of the K-select analysis explained 44.4% of the variation in average marginality, while the second and third axis explained 17% and 15% of the variation, respectively (Fig. 2a). The first factorial axis was positively related to variables associated with forage such as the proportion of moss tundra and terrain wetness, and negatively related to ruggedness, slope steepness, altitude

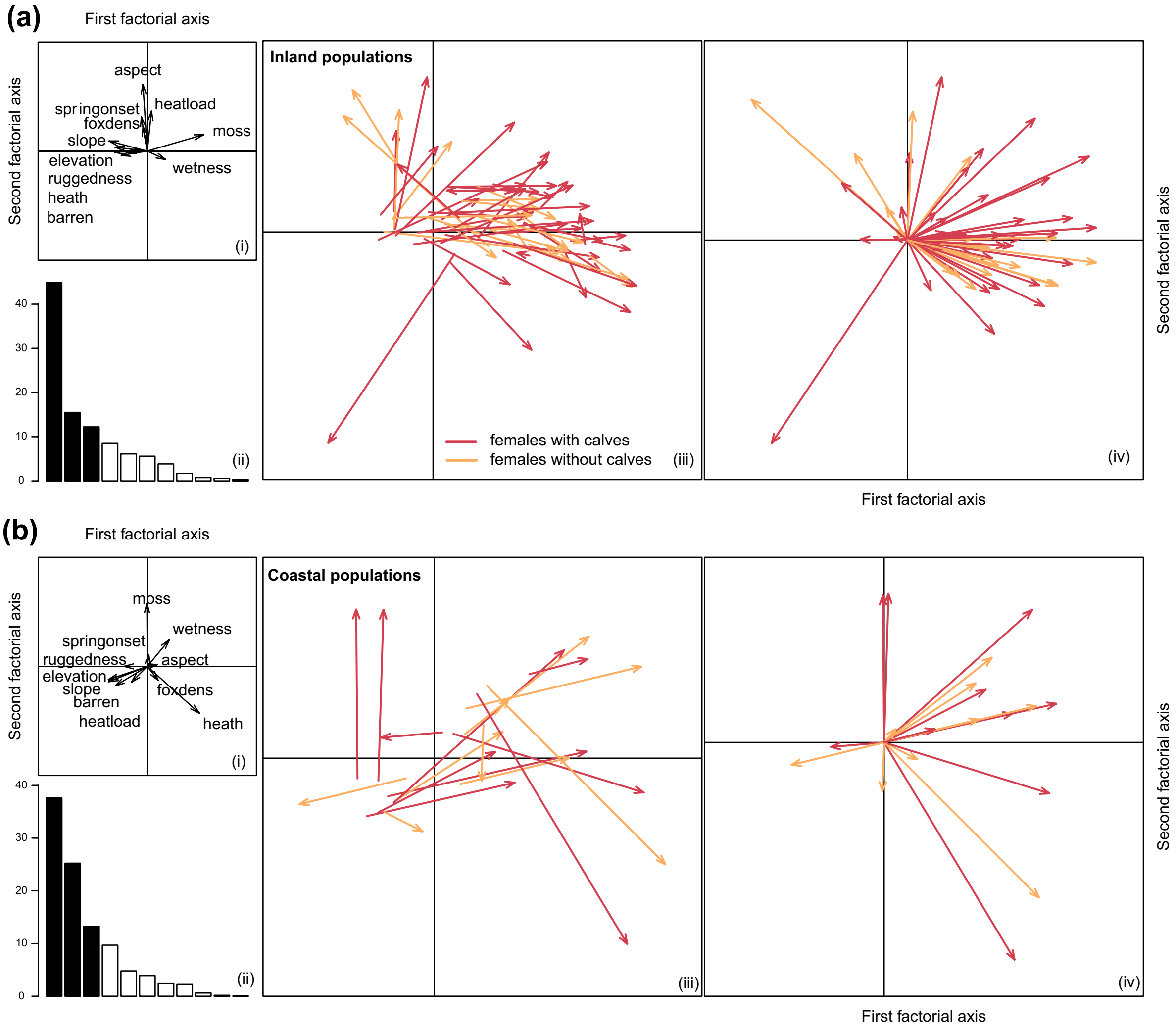

Figure 2. Results of the K-select analysis for Svalbard reindeer female habitat selection during the calving period in (a) inland and (b) coastal populations ($N_{coastal} = 22$, $N_{inland} = 56$). For both figures: 1) variable loadings on the first two factorial axes related to vegetation, terrain and calf predation predictor variables, 2) eigenvalues in % for 11 factorial axes (> 70% contribution shown in black), 3) uncentered (middle panel) and 4) centred (right panel) projections of the marginality vectors on the first and second factorial planes for individual females with calves (red arrows) and females without calves (orange arrows). In the diagrams, the tip of the arrow indicates used habitat (7 days post-calving for females with calves and 7 days after median calving day for females without calves), while the base of arrow indicates available habitat (individual spring home ranges, 15 May–30 June). The length of the arrow indicates marginality, i.e. the strength of habitat selection. The variable 'onset of the growing season' is denoted as 'springonset' on the figures. and the variable 'distance to fox dens' is denoted as 'foxdens' in the figures

and proportion of heath and barren areas. The second factorial axis was positively related to the onset of the growing season, heatload, aspect and distance to fox dens (Fig. 2a, Supporting information). Thus, as indicated by the direction of the arrows, most female reindeer in the inland populations selected areas in flat, lowland, moss tundra landscapes. Disproportionate use of habitat during the calving period, compared to available habitat, occurred for 14 females in the reproductive group and 7 females in the non-reproductive group, as indicated by the results of the randomization tests (Supporting information). Non-reproductive females selected significantly more frequently for heath in their used habitat during the calving period compared to reproductive females ($F_{1,54} = 4.30$, $p = 0.043$; Fig. 3a), while all other environmental variables were selected similarly for by both reproductive groups. In combination, this implies that the majority of females with calves select for calving habitat similar to their available area in the first week after birth, and that non-reproductive females are more frequently found on heath compared to reproductive females in the calving period.

In the coastal area, the first axis of the K-select analysis explained 39.9% of the variation in the total marginality, while the second and third axis explained 23.6% and 13.2% of the variation respectively (Fig. 2b). The first factorial axis was positively related to proportion of heath and terrain wetness, and negatively related to altitude, terrain ruggedness, slope steepness and barren areas. The second factorial axis indicated selection towards areas with high proportion of moss tundra and high wetness levels (Fig. 2b, Supporting information). Thus, most female reindeer in the coastal populations selected areas in flat, lowland, heath tundra landscapes. Habitat selection was significantly non-random for nine (four females with calves and five females without calves) out of 22 females during the calving period at both the 10% and 5% level (Supporting information). As for the inland females, the importance of environmental variables was similar for reproductive and non-reproductive females, but higher individual variability in habitat use during the calving period existed. Thus, there was a tendency for more consistent selection for habitats with high plant biomass production as indicated by high proportion of moss tundra in the inland than the coastal area.

Site fidelity in the calving and rearing period

Svalbard reindeer females displayed varying degrees of site fidelity to calving areas, contingent on time of the year and their reproductive status (Table 3, Fig. 4). After the onset of calving (2–19 June), females with a calf in two consecutive years displayed a significantly shorter distance between GPS-positions compared to both the null model than to females with calf in one year but not the other. This provides indicative evidence for site fidelity to calving areas. The mean distances between consecutive calving areas for females with calves in two consecutive years were 1.5–3.9 km, suggesting that calving site fidelity operated on a relatively coarse spatial scale relative to the annual home range

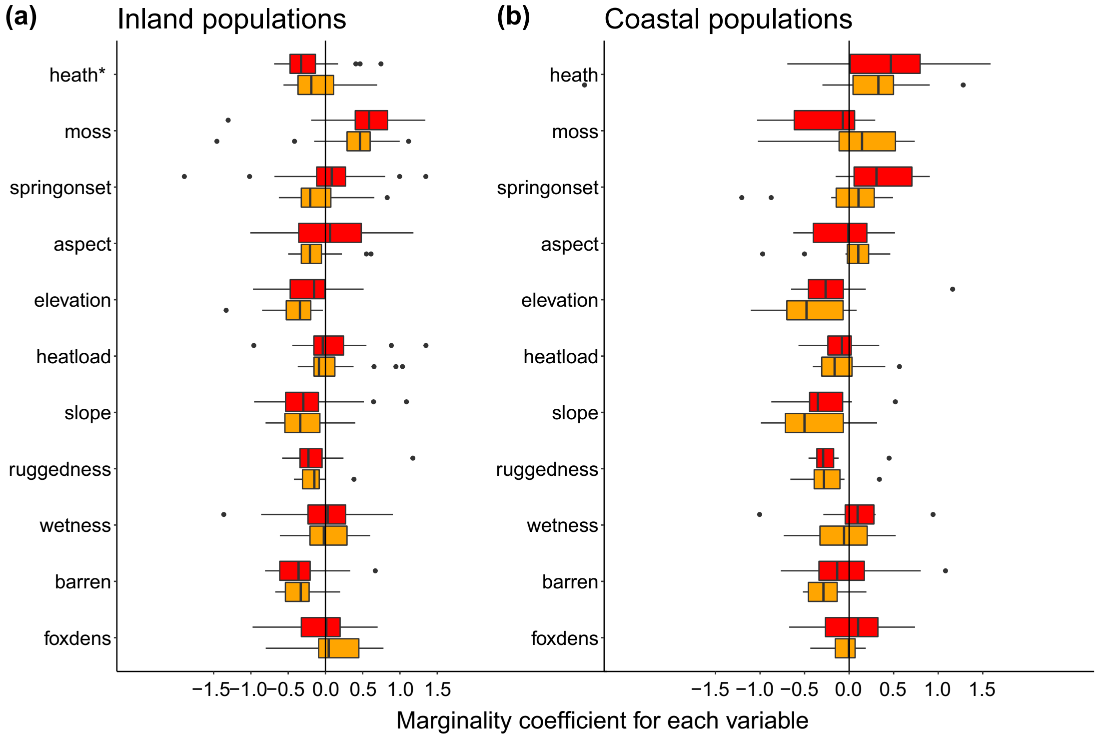

Figure 3. Mean marginality vector lengths from the K-select analysis of habitat selection in Svalbard reindeer females 7 days post-calving for females with calves (red boxes) and 7 days after median calving day for females without calves (orange boxes) in (a) inland and (b) coastal populations. The variable ‘onset of the growing season’ is denoted as ‘springonset’ on the figures. For the coastal populations, the variable springonset is marked with an asterisk because mixed effect models indicated a significant difference between reproductive and non-reproductive females.

Table 3. Mean distances (km) between paired GPS-positions of females, obtained one year apart on the same day of the year, during the summer season across Svalbard reindeer females of different reproductive status. Distances that are significantly shorter than the null model (5.3 km) are marked with *.

Reproductive class year t	Year t +1	Sample size	Calving period (2–19 June)	Early summer (20–30 June)	Mid-summer (1–31 July)	Late summer (1–31 August)
With calf	With calf	(n = 10)	2.7 ± 1.2*	2.3 ± 0.8*	3.8 ± 1.3*	2.8 ± 0.9*
With calf or no calf	With calf or no calf	(n = 8)	9.8 ± 6.8	3.6 ± 2.7	2.5 ± 1.2*	2.0 ± 1.2*
With no calf	With no calf	(n = 12)	4.1 ± 1.8	3.3 ± 1.3*	3.3 ± 1.1*	2.4 ± 0.9*

size of 50–65 km² (resembling a diameter of 8–9 km if circular, n = 134). Site fidelity remained high throughout the entire summer in females with calves in two consecutive years compared to the null model (Fig. 4). Females with no calf in either of the years, and females with no calves in one of the years displayed significant site fidelity, but later in the summer.

Discussion

In this study we demonstrated that habitat selection of female Svalbard reindeer during the calving period is largely independent of reproductive status. As expected in this virtually predator-free environment, individual reindeer generally selected for flat, lowland habitats associated with high forage availability. There was no evidence of selection for habitats assumed to reduce predation risk for calves (i.e. proximity to fox dens, terrain ruggedness or steep slopes). This indicates that low predation pressure allows females to choose their calving location based only on forage availability. Nevertheless, we found indications of site fidelity to the calving area, but at a coarse scale relative to the size of individual home ranges. The apparent paradox of a significant calving site fidelity despite similar habitat selection as non-reproductive females may be explained by remnants of anti-predatory behaviour or memory of rich summer foraging resources and past reproductive success (Byers 1998, Mahoney and Schaefer 2002).

Habitat selection in calving areas

Adult females selected moss and heath tundra during the calving period in the coastal and inland area, respectively (Fig. 2, 3). These habitat classes contain vegetation types characterized by high amounts of foraging plant biomass (Johansen and Tømmervik 2014; Supporting information) and food quality during the calving period (Bjune 2000, Peignier et al. 2019). Similar habitat selection is also observed in other High-Arctic caribou populations such as the

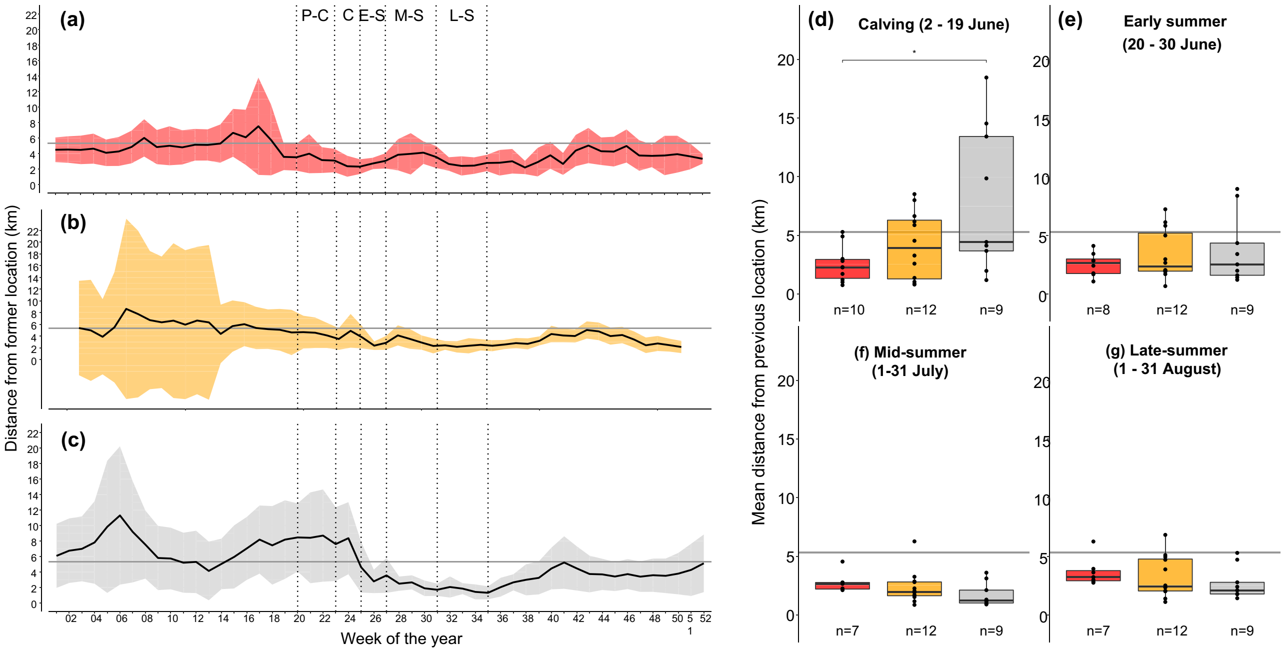

Figure 4. Left panel (A–C): the black line and coloured areas represent the mean weekly distances and 95% confidence intervals between GPS-positions obtained one year apart but in the same week for individual reindeer in the same reproductive group (red = females with calf at heel in both years, orange = females without calf in both years, grey = females with calf at heel in only one of the two consecutive years). The grey horizontal line is the null model (i.e. randomized paired GPS-positions for each female reindeer in year t and t + 1). The time-periods separated with stippled vertical lines are: P-C = pre-calving (15 May–2 June), C = calving (2–19 June), E-S = early summer (20–30 June), M-S = mid-summer (1–31 July), L-S = late summer (1–31 August) (Loe et al. 2006). Right panel (D–G): boxplot showing the group medians and null model for each reproductive group in the calving and rearing periods. Asterisk indicates a significant difference in mean between reproductive groups from Wilcoxon rank-sum test.

Alaskan barren-ground caribou *Rangifer t. granti* (Kelleyhouse 2001). Common for the barren-ground caribou' calving areas are that they contain high green biomass either during calving or peak lactation, and often provide better forage than elsewhere in their seasonal ranges (Russell et al. 2002). The selection for moss tundra and heath habitats in Svalbard reindeer likely reflect their nutritional requirements and the need to be in proximity to areas with good forage quality and quantity as the snow melts. In our study, heath was the only variable where habitat use significantly differed between reproductive and non-reproductive females (Fig. 2, 3). Energy cost during the calving period for reproductive females is higher than for non-reproductive females due to the additional need for lactation and calf nursing, which makes additional movement costly. Ridges with heath become earlier snow-free, but also contains less biomass of relevant foraging plants compared to foraging plants in moss tundra. This suggests that non-reproductive females can be more opportunistic in their foraging and movement behaviour, and thus use a larger foraging area during early spring compared to females with calves.

The slight differences in female habitat selection between our inland and coastal study areas (Fig. 2, 3), may reflect differences in available vegetation, snow melt patterns and onset of the growing season. Heath also becomes earlier snow-free on the coastal plains, which may explain why available pockets of nutrient-rich moss tundra near bird cliffs were not selected as calving areas. The inland study area becomes earlier snow-free, and patches of moss tundra can be exposed as early as the calving period. In addition, the onset of the growing season is more consistent between years in the foothills of the inland calving areas compared to the coastal plains (Karlsen et al. 2014). Therefore, the selection for heath in coastal areas and moss tundra in inland study area may simply reflect habitat availability during the snow melting period.

As assumed from the low predation pressure in Svalbard (Tyler 1986, 1987, Prestrud 1992), there was no evidence for selection of habitat variables associated with predation risks for reindeer calves (e.g. high elevations, steep slopes, rugged terrain and large distance from fox dens; Fig. 2, 3) at our study scale (i.e. foraging area). This contrast other reindeer and caribou populations that seek habitats with low predator-densities and high forage quality and quantity during the calving period to maximize calf survival (Nobert et al. 2016, Viejou et al. 2018). Our results correspond, however, to habitat selection patterns of other ungulates, such as the roe deer in the study of (Dupke et al. 2017), where food availability rather than lynx predation risk governs habitat selection on multiple scales. However, however, the Arctic is also experiencing altered predator–prey relations under climate change (Post et al. 2009), and both Arctic fox (Prestrud 1992) and polar bears (Derocher et al. 2000) are capable of killing reindeer (calves and adults, repectively), thus the current knowledge about predator–prey interactions in Svalbard (Tyler 1986, 1987, Prestrud 1992, Derocher et al. 2000) may change. The expected expansion of polar bear range use onto land (Rode et al. 2015) might lead to increased use of alternative prey resources, such as reindeer (Stempniewicz et al. 2013, Kavan 2018).

Site fidelity in the calving and rearing period

We found that parturient females had significantly higher site fidelity during the calving period (2–19 June) than females without calves in the same period (Fig. 4), which is supported by previous studies (Tyler 1986, Hansen et al. 2010). The distances between individual calving areas were of similar order of magnitude as for predator-free moose (Tremblay et al. 2007), but on average closer than for e.g. North-American migratory caribou *R. t. caribou* (8.7 km (Nobert et al. 2016); 3.6 km (Popp et al. 2008)) and sedentary caribou (6.7 km; Schaefer et al. 2000) in the post-calving period.

There was no significant difference in habitat selection between reproductive and non-reproductive females. Still, many of the reproductive females returned to the same calving areas the next year. This fidelity behavior, with no apparent benefit, is a paradox and could likely be explained by innate conservative traits, as seen in other ungulate populations without predators (Byers 1998) and populations with low incidental predation rates (Qin 2011, LaFontaine et al. 2017), or alternatively be associated with aspects of resources at a more detailed spatial level than what we could detect in our study. Remnants of anti-predatory behavior in predator-free or nearly predator-free environments can persist for thousands of years (Byers 1998), especially if these innate conservative traits are not too costly to maintain (Neill 1990). For instance, caribou in Newfoundland continues to migrate in the absence of wolves (Mahoney and Schaefer 2002), and bed-site selection of roe deer with fawns was still influenced by anti-predatory strategies for decades after eradication of predators (Qin 2011).

Previous reproductive success could also play a role in calving site selection in subsequent years for Svalbard reindeer, and may explain the variation in site fidelity between individuals in different reproductive groups. Reproductive success is influenced by food availability in the calving site, and the slight difference in site fidelity between reproductive groups during calving suggests that relying on prior knowledge of foraging resources may be especially important for females with calves. Remembering where the best foraging areas are located and being adjacent to these can therefore be energetically advantageous (Gunn and Miller 1986). The increasing site fidelity pattern over the summer aligns with studies from North American caribou populations (Schaefer et al. 2000, Popp et al. 2008) and the fact that site fidelity is linked to predictability in resource availability (Switzer 1993), which increases after snowmelt and over the growing season. The foraging landscape during the summer rearing period is more predictable than during calving, and it is possible that females are 'homing in' on an area that are important in foraging resources once the snow disappears. Although memory of rich summer foraging patches and previous reproductive success may be a plausible contender to the 'ghost of predators past' hypothesis we cannot rule out one over the other. More research needs to be done to effectively evaluate these hypotheses, for instance by investigating the role of reproductive success in selection and fidelity of calving sites.

Conclusion

We demonstrate that female reindeer in this High-Arctic environment select habitats associated with good forage conditions over predation-risk during the critical stage after calving. It is possible that the reindeer rely on former knowledge of the best food patches and place themselves accordingly before the onset of the growing season. The apparent paradox of a significant calving site fidelity, despite similar habitat selection among females with different reproductive status, may be explained by innate conservative traits (Byers 1998) or relict anti-predatory behaviour (Mahoney and Schaefer 2002). This explorative study provides a baseline for the continuation of hypothesis-based studies on calving habitat selection where individual fitness components are linked to habitat selection and site fidelity at the critical stage of calving.

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