

Sea or summit? Wild reindeer spatial responses to changing high-arctic winters

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Abstract. Because of climate change, wildlife is facing altered environments, including profound shifts in temperature and precipitation regimes. In snow-dominated ecosystems, winter warming and resulting changes in snowpack properties impact forage accessibility for ungulates—often for the worse. The potential of individuals and populations to buffer negative fitness effects of harsh winters with “basal ice” (i.e., ice on the ground) and/or a harder or deeper snowpack depends on their ability to adjust behaviorally through changes in diet, dispersal, or small-scale habitat use. Here, we use ten years of late winter snowpack monitoring and population census data from three neighboring, semi-isolated coastal populations of high-arctic wild Svalbard reindeer to explore small-scale space use responses to annual variation in late winter-foraging conditions. Based on location data from the population censuses, we roughly classified individuals’ spatial foraging strategy (i.e., habitat use) during late winter into “tundra” (foraging on tundra plains), “mountain” (foraging at high elevations, with low plant biomass but less snow and ice), or “shore” (foraging along the seashore, subsidizing terrestrial food with kelp and seaweed). Using multinomial logistic regression, we modeled the probability of reindeer adopting either of these strategies as a function of density-dependent winter severity. Our results suggest that effects of winter severity on habitat use are density-dependent and that snowpack depth and hardness (excluding basal ice, measured as “integrated ram hardness,” IRH) have stronger influence on reindeer foraging behavior than basal ice, at least at such spatial scales. Particularly, high IRH increased the probability of reindeer seeking high-elevation and steep terrain instead of tundra lowlands, but not at low population density, that is, when competition for food is negligible. This strategy was most pronounced among adult males, possibly reflecting their risk-prone behavior and/or reduced competitiveness related to lack of antlers during winter. This study demonstrates important patterns of temporal, spatial, and demographic variation in reindeer’s winter-foraging strategies, adding novel, nuanced insights into how climate change affects spatial processes in isolated ungulate populations. The results add to the impression of considerable behavioral flexibility, which may aid buffering the negative fitness effects of complex changes in foraging conditions due to environmental changes.

Key words: adaptation; Arctic; behavioral plasticity; climate change; rain-on-snow; *Rangifer tarandus platyrhynchus*; Svalbard; ungulate.

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INTRODUCTION

Throughout the arctic tundra and the boreal forests of the Northern Hemisphere, snow is a dominating and structuring feature of ecosystems for up to 9–10 months of the year. During the last decades, however, the Arctic has experienced rapid and pronounced shifts in temperature and precipitation regimes (Vikhamar-Schuler et al. 2016, Bintanja and Andry 2017, Peeters et al. 2019), changing not only the spatial extent, seasonal timing, and duration of snow cover but also the physical properties of the snowpack (Callaghan et al. 2011, Box et al. 2019). In particular, more frequent episodes of rain during mild winter spells (Vikhamar-Schuler et al. 2016, Bintanja and Andry 2017) lead to changes in snowpack hardness and may, in extreme cases, cause the formation of thick basal ice (Peeters et al. 2019) or complete ablation of the snow (Tyler 2010), blocking or exposing the vegetation, respectively. While vertebrates inhabiting these snow-dominated landscapes have developed various snow-specific morphological, physiological, and behavioral adaptations, their survival and reproduction, and thereby population viability, nonetheless seem to depend on favorable snow conditions (e.g., Miller and Gunn 2003, Kausrud et al. 2008, Tyler 2010, Forbes et al. 2016, Albon et al. 2017, Berteaux et al. 2017, Boelman et al. 2019, Hansen et al. 2019a). Yet, a general lack of in situ snow data at relevant spatial and temporal scales has so far hampered our understanding of wild animals' adaptive capacity in responding to rapidly changing winter conditions (Boelman et al. 2019).

The climate-induced alterations of arctic winter conditions may be particularly impactful for large herbivores, that is, muskoxen (*Ovibos moschatus*) and reindeer/caribou (*Rangifer tarandus*), because their tundra forage plants are typically short-growing and snow-covered for most of the year (Tyler 2010). Deeper and/or harder snow with ice layers within the snowpack may increase time and energy investments required for foraging, while solid basal ice can fully encapsulate the forage plants (Rennert et al. 2009, Hansen et al. 2010a). Correspondingly, several studies have indicated that "rain-on-snow" (ROS) events may reduce skeletal growth of

juveniles (Berger et al. 2018), as well as body mass, survival, fecundity, and population growth rates in arctic ungulates (Miller and Gunn 2003, Rennert et al. 2009, Stien et al. 2012, Forbes et al. 2016, Albon et al. 2017, Hansen et al. 2019c). For such species with long generation times (i.e., little capacity for fast evolutionary adaptation), the extent to which individuals and populations can adapt to winter climate warming will likely depend on their behavioral plasticity, for example, through changes in dispersal, migration, or small-scale habitat use. Behavioral plasticity has indeed been shown to buffer negative impacts of extreme weather events in both terrestrial mammals and plants (Boutin and Lane 2014, Franks et al. 2014).

In wild Svalbard reindeer (*R. t. platyrhynchus*), recent studies have demonstrated changes in small-scale space use through local movements (Stien et al. 2010, Loe et al. 2016) and an expansion of the dietary niche (Hansen and Aanes 2012, Hansen et al. 2019b) in response to constrained winter-foraging conditions, especially basal ice. Female reindeer have been observed to respond through partial seasonal migrations between inland valleys with high landscape connectivity or across sea ice in coastal areas, with an apparent positive net fitness effect (Hansen et al. 2010b, Stien et al. 2010, Loe et al. 2016). In coastal populations, utilization of kelp and seaweed along the shoreline has been shown to supplement tundra foraging (Hansen and Aanes 2012, Hansen et al. 2019b). These findings suggest that behavioral plasticity and adaptive landscape use may at least in part buffer increasingly severe winter-foraging conditions, counteracting negative fitness consequences at the individual level.

However, arctic terrestrial wildlife's ability to respond to environmental change is increasingly limited by habitat fragmentation, either directly or indirectly caused by human activity (Mallory and Boyce 2018). The rapid loss of arctic sea ice (Onarheim et al. 2014), an important corridor for seasonal migrations (Miller 2002, Hansen et al. 2010b, Poole et al. 2010, Mathieu et al. 2013) and dispersal (Post et al. 2013, Jenkins et al. 2016, Peeters et al. 2020) in some reindeer and caribou populations, increases the level of spatial isolation. For instance, Jenkins et al. (2016) found a

negative temporal trend in landscape connectivity for island-dwelling caribou populations in the Canadian Arctic Archipelago, predicting a further decrease due to future loss of sea ice (see also Mallory and Boyce 2018). In both Svalbard reindeer and arctic island-dwelling caribou (*R. t. groenlandicus*, *R. t. pearyi*), there are strong links between sea-ice dynamics and the level of genetic isolation among populations (Jenkins et al. 2018, Peeters et al. 2020). This highlights the importance of behavioral plasticity at small spatial scales for population viability in arctic island ungulates.

Here, we use ten years of spatially explicit population census data and in situ snow monitoring to explore small-scale spatial responses to varying winter-foraging conditions in three semi-isolated coastal populations of Svalbard reindeer. Because of the severely restricted dispersal opportunities due to the recent lack of sea ice, these data sets provide a unique opportunity to improve our understanding of isolated arctic island ungulates' small-scale capacity to adapt behaviorally to current and future climate change. Recent studies have focused on the impact of increasingly frequent ROS events and resulting basal ice (e.g., Stien et al. 2010, Hansen and Aanes 2012, Hansen et al. 2019b). However, winter warm spells and rain may also impact snowpack conditions beyond basal ice formation, for instance through snowpack hardening (Beumer et al. 2017), while fluctuations in the amount of annual winter rain- and snowfall affect snow depths. These effects should likewise not be ignored (Hansen et al. 2019c). Thus, we expanded on Hansen et al. (2019b) by examining how both basal ice and snowpack depth and hardness impact foraging strategies in interaction with population density, across populations and demographic groups. We expected that restricted forage accessibility as a result of basal ice and/or hard/deep snow reduces the probability of reindeer utilizing their "normal" lowland tundra habitat and instead increases the probability of reindeer to forage at the shore (Hansen et al. 2019b) or at high elevations (as indicated anecdotally in Hansen et al. 2010a). Given that population-dynamic effects of winter severity are clearly density-dependent (Kohler and Aanes et al. 2004, Hansen et al. 2019a, c), we also anticipated the effect of winter harshness on habitat

use to be particularly pronounced at high population densities. Furthermore, we tested whether demographic groups differ in their prevalence for these alternative—possibly energetically costly and risky—foraging strategies since, for instance, female adult reindeer keep their antlers throughout most of the winter, providing a competitive advantage over antlerless male adults (Schaefer and Mahoney 2001), and because females are less risk prone than males in many species (Miquelle et al. 1992, Jolles et al. 2015).

MATERIAL AND METHODS

Study area

The Svalbard archipelago is located in the Arctic Ocean north of Norway (76–81° N, 10–35° E; Fig. 1). Around 60% of the land surface is glaciated and only 15% is vegetated, while the remaining part is barren ground. The study area is located at 78° N and 11–12° E along the west coast of Spitsbergen and consists of three semi-isolated peninsulas: Brøggerhalvøya (area with continuous vegetation cover = 105 km²), Sarsøyra (40 km²), and Kaffiøyra (35 km²) (Fig. 1). These peninsulas are dominated by flat tundra lowlands in between the shore and steep alpine mountains. Brøggerhalvøya has a more rugged terrain and higher terrain heterogeneity compared with the open tundra plains of Sarsøyra and Kaffiøyra. Flat beaches, typically providing access to washed-ashore kelp and seaweed, are common along parts of Brøggerhalvøya and Sarsøyra, but less common in Kaffiøyra. Large tidewater glaciers and open fjords isolate the peninsulas from each other. Plants are short-growing and dominated by mosses, dwarf willow *Salix polaris*, purple saxifrage *Saxifraga oppositifolia*, and graminoids, while lichens are scarce due to past grazing and trampling (Hansen et al. 2007).

Svalbard has a relatively mild climate, with humid, oceanic weather patterns in the western parts, including our study area. Total annual winter precipitation and mean winter temperature (December–February, 1971–2000) were on average 110 mm and –12.9°C in Ny-Ålesund, Brøggerhalvøya (Hanssen-Bauer et al. 2019). However, a strong winter warming has been identified during the last decades (Førland et al. 2012) and warm spells with above-zero

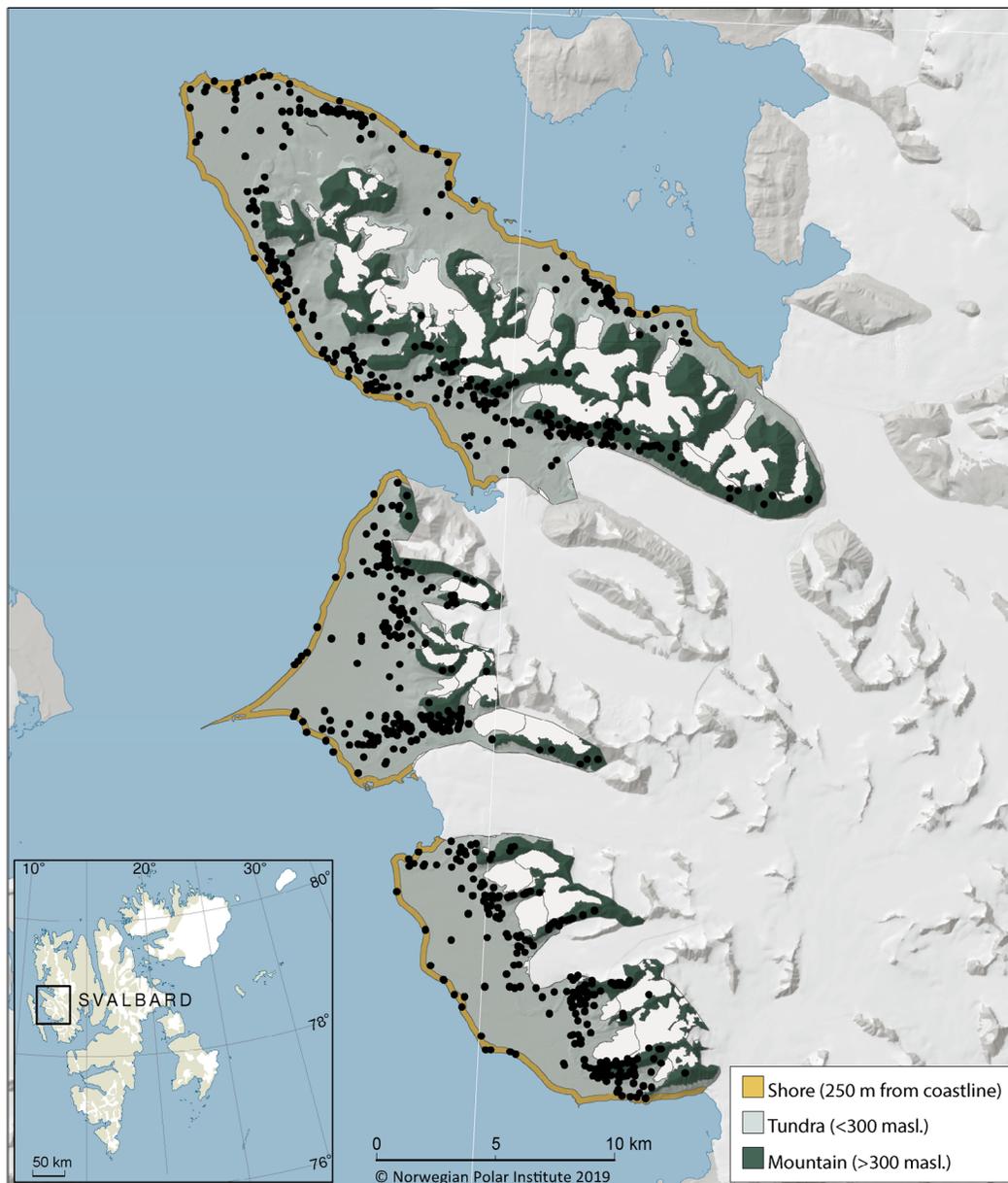


Fig. 1. Location of the Svalbard archipelago (lower left) and the three study areas at the north-western coast of the Spitsbergen (Brøggerhalvøya = upper, Sarsøyra = middle, Kaffiøyra = lower), where annual Svalbard reindeer population abundance censuses have been conducted during the study period (2006–2016). The colored areas delineate the shore, tundra, and mountain habitats (see *Methods*), and the small black dots are individual Svalbard reindeer observations pooled across year per study area. Map: Oddveig Øien Ørvoll/NPI.

temperatures now occur more frequently with a particularly strong increase in winter temperatures and winter rain since the 1990s (Vikhamschuler et al. 2016, Peeters et al. 2019). Sea ice

extent usually reaches its maximum in late winter (March–April), but reductions of 5–20% per decade have resulted in several fjords along the west coast being virtually ice free in recent

winters (Muckenhuber et al. 2016, Dahlke et al. 2020). In our study area, fjord ice between the peninsulas has been absent since 2006, except in 2011 (B. B. Hansen, *personal communication*), limiting options for dispersal or seasonal movements of reindeer.

Study species and populations

Svalbard reindeer are the only large herbivores inhabiting the archipelago. While predominantly solitary (Tyler 1987), they can also occur in small assemblages of around 2–5 individuals, typically sexually segregated (Loe et al. 2006). Compared to other *Rangifer* subspecies, they have small seasonal and annual home ranges and are non-migratory (Tyler and Øritsland 1989). However, partial seasonal migrations may occur, for instance in severe winters when forage resources are scarce or depleted due to overgrazing, high population densities, “ice-locked” pastures, or adverse snow conditions (Hansen et al. 2010b, Loe et al. 2016), or a combination of these factors (Kohler and Aanes 2004, Stien et al. 2010). Svalbard reindeer are not subject to significant predation (but see Derocher et al. 2000 for reports on rare killings by polar bear *Ursus maritimus* and Prestrud 1992 for arctic fox *Vulpes lagopus*), insect harassment, or interspecific competition (Øritsland and Alendal 1986). Instead, annual population fluctuations are mainly driven by density-dependent effects caused by winter weather variability, especially fluctuations in the amount of rain- and snowfall (e.g., Aanes et al. 2000, Albon et al. 2002, Hansen et al. 2011, Albon et al. 2017, Hansen et al. 2019c).

Data collection

Meteorological data.—We obtained daily mean air temperature and daily total precipitation data from the Norwegian Meteorological Institute’s weather station in Ny-Ålesund (seklima.met.no/observations/). Following the protocols of Peeters et al. (2019), we defined winter precipitation as rain when falling at air temperatures $\geq 1^{\circ}\text{C}$ between 1 November and 30 April.

Reindeer data.—We obtained reindeer positional data for the three study populations (Brøggerhalvøya, Sarsøyra, and Kaffiøyra; Fig. 1) from annual total population count censuses (Appendix S1: Table S1) conducted in late March or April during 2006–2016. The data thus

represent a “snapshot” in time, assumedly representative of the late winter period when snow accumulation is usually at its maximum and weather conditions are typically cold and stable (Hanssen-Bauer et al. 2019, Peeters et al. 2019). Each individual reindeer observation included the geographic position and, in most cases, information regarding the sex and age of the animal. Besides an overall lack of data for 2009, reindeer data were not collected in Sarsøyra in the period 2013–2016 and in Kaffiøyra in the period 2014–2016. Two persons on snowmobiles conducted the total population censuses on sunny days with no wind. Each location was covered in one day, except Brøggerhalvøya, which was covered in two days. We detected reindeer by systematic scanning of the study area, using hand-held binoculars (Swarowski/Zeiss binoculars; 10 × 42). Based on Le Moullec et al. (2017), we assumed detection rates to be highly accurate and to remain similar between censuses. Reindeer positions were marked on a map (1:100,000 or 1:50,000) using a hand-held GPS as guidance.

Each reindeer was classified into one of three sex-age classes: calves (C), female adults (FA, including yearlings), and male adults (MA, including yearlings). If the distance was too far for age and sex determination, individuals were classified as unknown (U). Due to the rather poor resolution of the map, several individuals may be recorded at the same location (Appendix S1: Table S1). This, however, does not necessarily imply social group bonds, but could just as well reflect spatial aggregations (i.e., up to ca. 50–100 m distances) due to spatial clustering of accessible foraging spots. Consequently, and because Svalbard reindeer are known to be largely solitary (especially during this time of the year; Tyler 1987), we chose to use individuals, and not “groups,” as unit for statistical analyses. As calves are largely independent of their mothers in late winter, and because we were not able to determine whether calves and adult females observed in close proximity were indeed mother–calf pairs, we also considered calves and adult females as independent observations.

After initial exploration of the spatial distribution of reindeer in the landscape, we assigned each individual reindeer one out of three spatial foraging strategies: “tundra” (foraging on tundra plains), “mountain” (foraging at high elevations

[>300 m asl] with scarcer food abundance but less snow and ice), or “shore” (foraging along the seashore [within 250 m from the coastline], subsidizing terrestrial food with kelp and seaweed; Hansen et al. 2019b) (Fig. 2, Appendix S2: Figs. S1 and S2). We extracted elevation (m asl) of each reindeer position using a digital elevation model (spatial resolution 20 × 20 m, Norwegian Polar Institute).

To account for potential density-dependent effects of winter severity in statistical analyses, we included a density proxy based on the scaled absolute number of observed animals per area from the winter population census (see Fig. 4E for sample sizes across location).

Snowpack data.—Two different data sets provided information on snowpack properties, such as snow depth, snow hardness, and basal ice thickness. For the first data set (2006–2012), described in Hansen et al. (2010a), parameters were measured in snow pits ($n = [54–84]$) in late

March to early May in a fixed grid design (900 × 1800 m). In 2013, we replaced this study design with a spatial-hierarchical design of 40 snow pits, sampled in each April (2013–2016), that cover two main reindeer winter habitats (i.e., *Salix polaris* dominated ridge and *Luzula confusa* or *Poa* sp. dominated sub-ridge; see Loe et al. 2016 and Peeters et al. 2019) along an elevational gradient (range [3–475 m asl]). Due to logistical challenges related to winter access after 2013, snow sampling was not established in two of the peninsulas (Sarsøyra and Kaffiøyra). To check whether the change in study design influenced the data, we extracted winter median values for basal ice and snow depth (responses) and ran a regression against the amount of precipitation as winter rain and snow (predictors). We particularly checked if model residuals differed significantly between the period 2006–2012 and 2013–2016, which was not the case (model residuals against year for model median basal ice

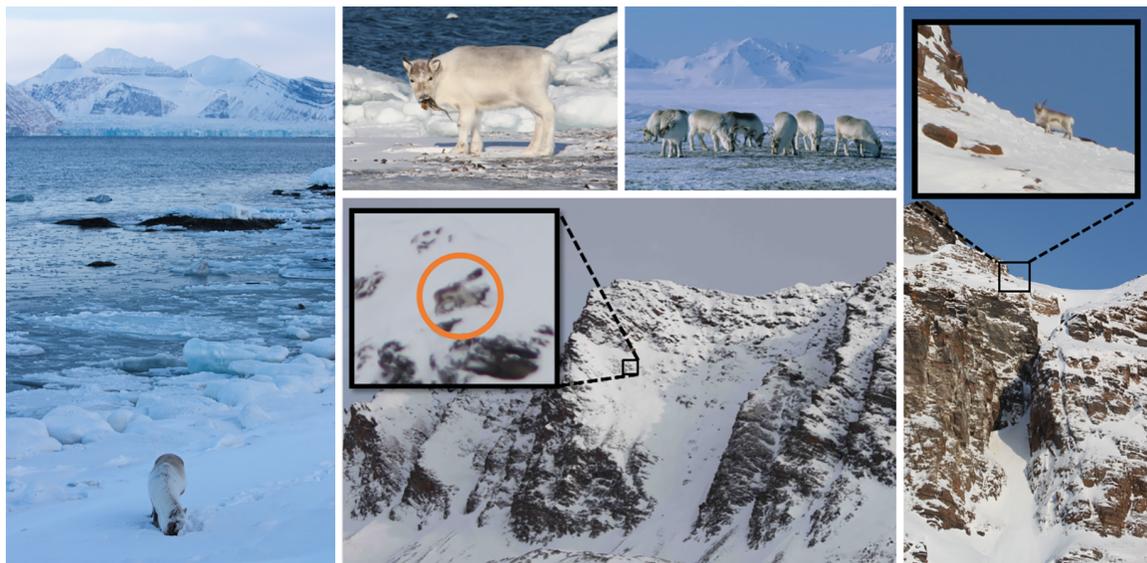


Fig. 2. Photographs showing the different spatial foraging strategies by Svalbard reindeer in winter. *Left panel:* Adult male foraging at the seashore in Brøggerhalvøya (Photo: Larissa T. Beumer). *Left upper middle panel:* Calf foraging on seaweed and kelp in Colesbukta, Central Spitsbergen (Photo: Malin Daase). *Right upper middle panel:* Adult reindeer foraging in lowland tundra landscapes in Brøggerhalvøya (Photo: Ronny Aanes). *Lower middle panel:* Adult reindeer (inset, orange circle) foraging at high elevations in alpine mountains in Kaffiøyra, West-Spitsbergen (Photo: Brage B. Hansen). Note also the slab avalanche edge, only vaguely seen, right above the depicted reindeer. *Right panel:* Adult reindeer (unknown sex) foraging at high elevations in the vicinity of Ny-Ålesund, Brøggerhalvøya (Photo: Brage B. Hansen).

vs. rain: $y = -0.22 + 0.00 x$, $P = 1$, adjusted $R^2 = -0.14$; for snow depth vs. snowfall: $y = -3584.22 + 1.78 x$, $P = 0.37$, adjusted $R^2 = 0.37$). Thus, we concluded that the change in study design did not affect the annual estimates and ignored this issue in the following statistical analyses.

In both data sets, snow depth and basal ice thickness were measured to the nearest 0.5 cm to calculate measures of winter severity (Appendix S1: Table S1). However, basal ice thickness was only measured up to 10 cm during some of the study years, while the exact thickness of the ice was measured in the remaining years. To ensure comparability between all years, we set estimates to 10 cm if measurements exceeded this value. To measure snowpack hardness, we used a ramsonde penetrometer (Skogland 1978; Hansen et al. 2010). With a conical tip, the ramsonde penetrates the snow cover in response to a load (1 kg), which is dropped from a defined standard height (55 cm). The depth of penetration into the snow is noted for each time the load is dropped until the ramsonde reaches the ground (or basal ice, which is usually impenetrable). Following the protocols detailed in Beumer et al. (2017), we calculated integrated ram hardness (IRH; kgcm), a measure of the total force needed to penetrate the entire snowpack (i.e., an integrated measure of snow depth and hardness). Snowpack surveys were conducted in close temporal proximity to reindeer censuses (Appendix S3: Fig. S1).

Data analyses

Initial data explorations.—Due to differences in sampling effort (i.e., snow-ice variables were not collected in all areas in all years; Appendix S1: Table S1) and change in study design in 2013, initial data preparation steps (detailed in Appendix S4) were required to generate proxies characterizing annual winter severity across study locations. IRH, which was only measured in the field from 2005 to 2008, was predicted for the remaining years, and estimated predictions for all study years were used subsequently. As candidate predictor variables representing winter severity, we initially considered annual median values of snow depth, basal ice thickness, thickness of ice layers within the snowpack, and IRH. The IRH measure integrates snow depth and hardness (i.e., accounting for ice layers

within the snowpack) and has previously been demonstrated to capture snow properties that affect the foraging conditions of herbivores (Skogland 1978, Beumer et al. 2017). Hence, we decided to use IRH and basal ice thickness as predictor variables in the subsequent statistical analyses, as they reflect different properties and components of the snowpack that are relevant in terms of forage accessibility. Because weather and associated conditions are highly correlated across these three nearby study locations (Appendix S4), we used annual median values from Brøggerhalvøya, where measurements were performed in all but one year (using both study designs), to represent winter severity across all study locations. Both IRH and basal ice were rescaled by centering on their mean and dividing by their standard deviation to reduce model convergence issues and to allow for the comparison of effect sizes of these two continuous explanatory variables. Pearson's correlation between annual median IRH and basal ice thickness was considerable ($r = -0.63$, $P = 0.05$). To avoid collinearity effects as well as overparametrization of models, we thus decided to not include basal ice thickness and IRH in the same candidate models. However, to somehow account for both severity measures, we also tested for the effects of summed (annual) scaled IRH and basal ice values and used this variable as a third alternative measure of winter severity (hereafter termed "IRHice").

Statistical modeling.—All analyses were performed in R (version 4.0.3; R Core Team 2020). We used mixed-effects multinomial logistic regression to investigate how the choice of spatial foraging strategies (shore, tundra, or mountain; see Fig. 2 for photo documentation) was influenced by predictor variables describing winter severity (basal ice thickness, IRH, or their additive effect (IRHice)) and population density, and their interaction. Year was included as a random intercept effect to account for residual variation due to year effects and data dependencies within years. Because of the collinearity issues, we built three alternative global models with basal ice (scaled), IRH (scaled), or IRHice in interaction with population density, as well as sex-age class (as factor, with levels MA, FA, C, U) and area (as factor, with levels Brøggerhalvøya, Sarsøyra, Kaffiøyra) as fixed predictor variables.

Models were fitted via penalized quasi-likelihood maximization using the “mblogit” function in the “mclogit” R package. For each global model, we tested all different possible subsets of candidate models. Model selection was performed using Akaike’s information criterion (AIC) corrected for small sample sizes (AICc), where the candidate model with the lowest AICc value is regarded the best-fitting model, but all models within $\Delta\text{AIC}_c < 2$ of the top-ranked model are generally considered to have equal support (Burnham and Anderson 2002). The final (top-ranked) model was re-fitted using the restricted maximum-likelihood estimator (Elff et al. 2021).

RESULTS

Annual variation in winter severity

Mean winter temperatures and the amount of annual winter rain have increased in Ny-Ålesund since the 1990s (Fig. 3). However, large fluctuations in the amount of precipitation, as well as in the proportion of precipitation falling as rain vs. snow, caused considerable annual variation in basal ice thickness and IRH also during our study period (Fig. 4; see also Peeters et al. 2019). The highest amounts of total precipitation occurred in winters 2006 and 2012 (Fig. 4). Basal ice was present in all years, but particularly thick in 2010 and 2012, that is, two rainy winters characterized by intermediate amounts of snow (Fig. 4; see Peeters et al. 2019 for snow-rain interaction effects on basal ice). Annual IRH, which was negatively correlated with basal ice thickness (see Initial data explorations), was highest in winters characterized by high snowfall (e.g., 2011 and 2014; Fig. 4) or by intermediate and mixed precipitation combined with relatively little basal ice formation (e.g., 2007; Fig. 4).

Spatial behavioral responses to winter severity

The full (i.e., global) model with IRH representing winter severity (i.e., including IRH in interaction with population density, as well as area and sex–age class) was by far the top-ranked model (ΔAIC_c of 17.34 to second-best model; Table 1, Appendix S5: Table S1) to explain the variation in spatial foraging strategies among the observed reindeer (total of 269 calves,

1165 female adults, 514 male adults, and 356 unknowns; Appendix S1: Table S1). According to this model, the probability of mountain vs. tundra feeding increased with IRH, but only at high population density (Table 2, Fig. 5). Individuals of unknown sex–age (interpreted as predominantly adult males, see Appendix S2: Fig. S3) exhibited the highest probability of mountain feeding, followed by adult males, calves, and adult females (Fig. 6). All between-class differences were statistically significant, except between male adults and calves ($P = 0.20$) as well as female adults and calves ($P = 0.17$). The probability of adapting the mountain foraging strategy (as opposed to tundra feeding) was highest on Kaffiøyra and lowest on Sarsøyra; all area differences were statistically significant (Table 2).

According to the top-ranked model, the probability of shore vs. tundra feeding appeared to decrease with increasing IRH, but not when population density was high (Table 2, Fig. 5), that is, when competition for food is substantial. Adult males were most likely to be shore feeding, although the difference was only statistically significant between males and females ($P < 0.001$) as well as males and unknowns ($P < 0.01$). All other between-class differences were not significant. Shore feeding (as opposed to tundra feeding) was most prevalent on Brøggerhalvøya and least common on Sarsøyra (Appendix S6: Table S1).

Especially at high population densities, there was also an increasing probability of reindeer adopting the mountain as opposed to the shore feeding strategy when IRH increased (Table 2).

DISCUSSION

This study demonstrates important patterns of temporal, spatial, and demographic variation in high-arctic reindeer’s winter-foraging strategies. In particular, our results show that the probability of individuals “heading for the hills” increased under severely restricted forage accessibility combined with high population density (Table 2, Fig. 5). Also, the more severe the conditions, the more likely reindeer were to choose mountain habitat over shore habitat as alternative to tundra foraging, especially when population densities were high. Adult males were more

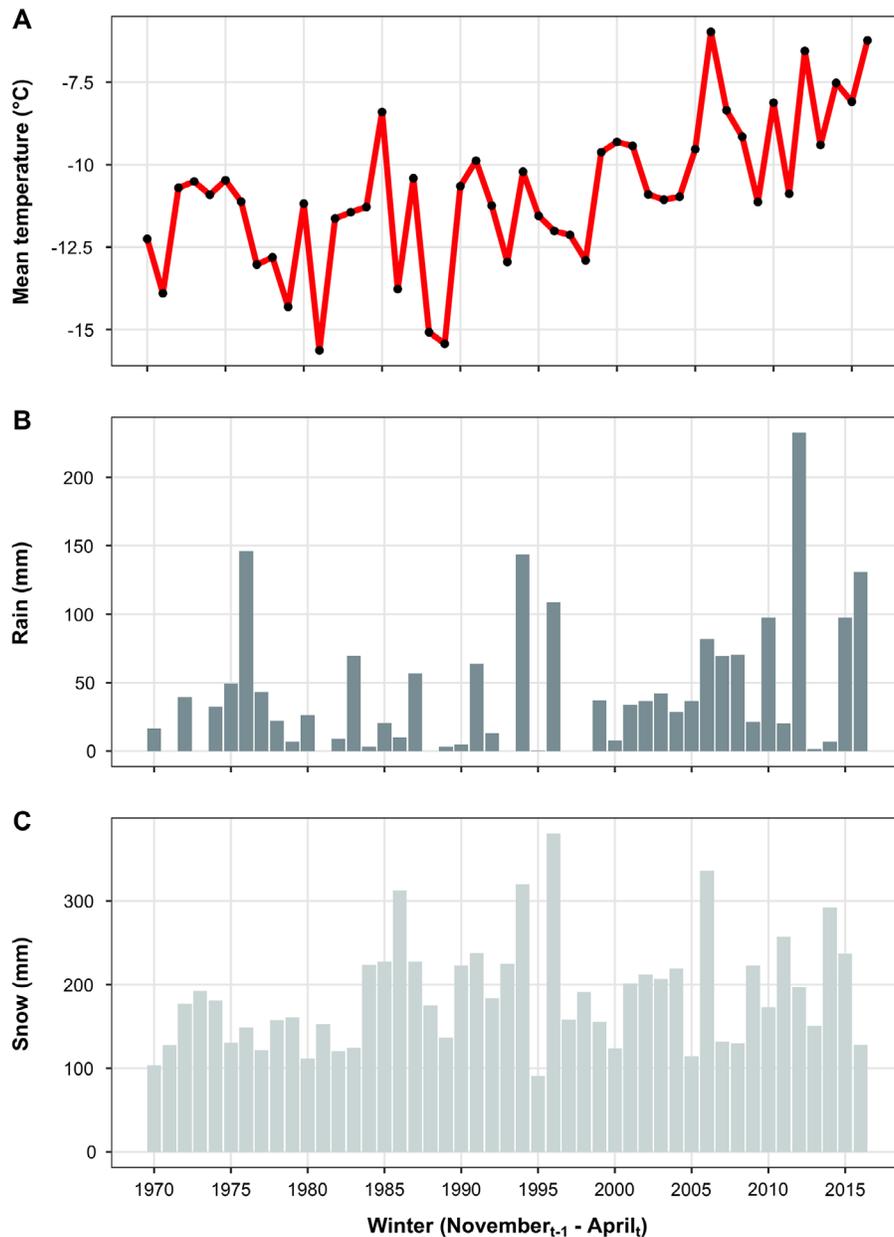


Fig. 3. Fluctuations in (A) mean temperature (degrees Celsius), (B) precipitation as rain (mm), and (C) precipitation as snow (mm) over the winter months (November–April) from 1970 to 2016 (data obtained from Norwegian Meteorological Institute’s weather station in Ny-Ålesund, www.seklima.met.no). Note that winter was defined as 1st of November in year $t - 1$ to 30th of April in year t .

likely to resort to mountain (or shore) feeding than adult females (Table 2). Importantly, and in contrast to recent studies highlighting basal icing as the main determinant of winter resource selection and vital rates of Svalbard reindeer (Albon

et al. 2017, Hansen et al. 2019c), we found that the integrated effect of snow depth and hardness (IRH) appeared to explain variation in foraging strategies much better than basal ice thickness or the sum of IRH and basal ice (IRHice) (Table 2).

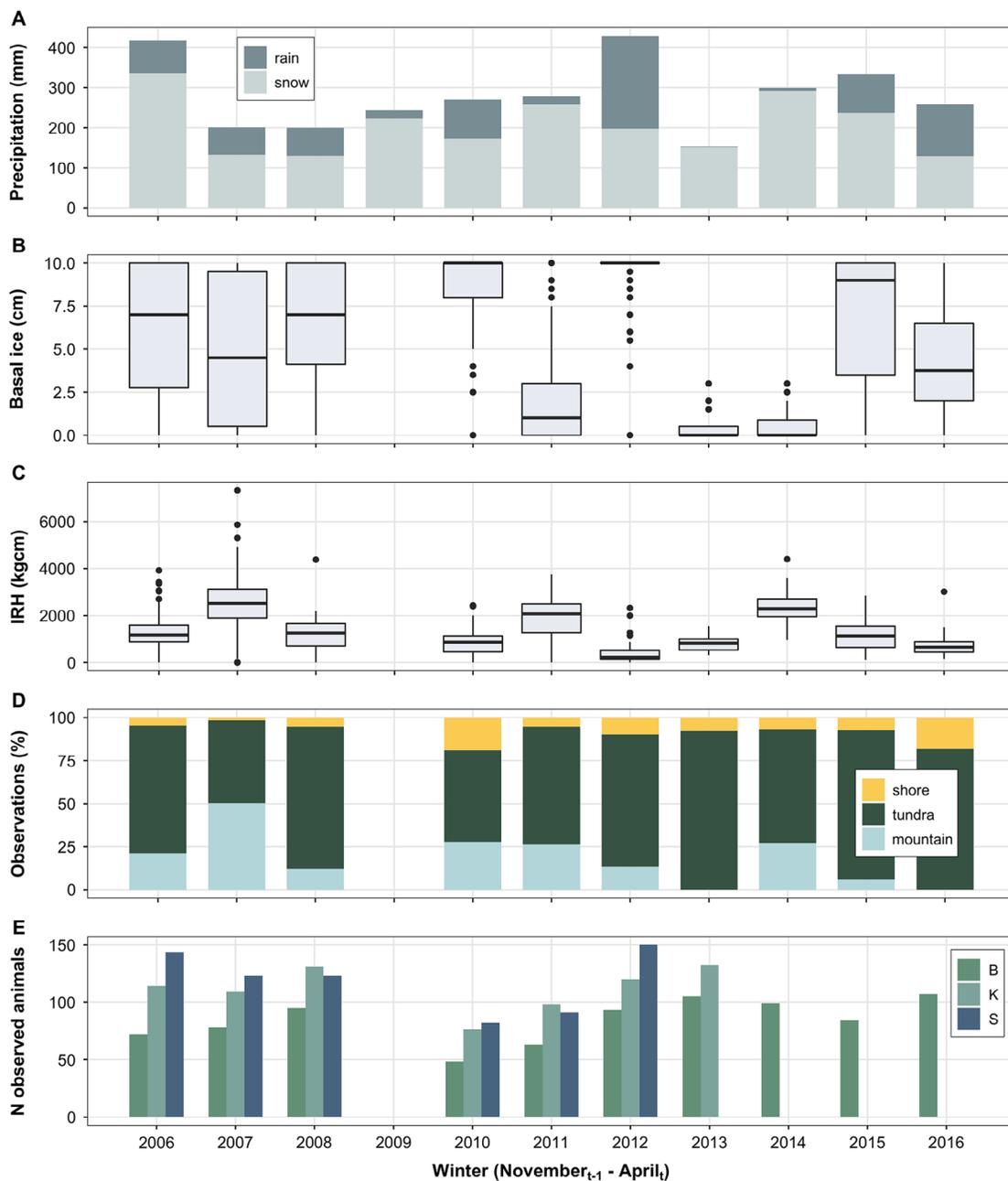


Fig. 4. Annual fluctuations in precipitation, snow-ice conditions, reindeer observations in different habitat types, and total number of observed animals per study area during the study period (2006–2016, but no reindeer or snow-ice data for 2009). (A) Annual precipitation (mm) falling as rain (dark color) or snow (light color) recorded at the Ny-Ålesund weather station, Svalbard. (B–C) Annual changes in thickness of basal ice (cm) and integrated ram hardness ($\text{kg} \times \text{cm}$) in the study area. (D) Percentage of reindeer observed in mountain (dark green), tundra (light blue), or shore (yellow) habitat during the annual population count (pooled across the three different areas). (E) Total number of observed animals per study area (B = Brøggerhalvøya, K = Kaffiøyra, S = Sarsøyra). Note that winter was defined as 1st of November in year $t - 1$ to 30th of April in year t (e.g., winter 2006 is November 2005–April 2006).

Table 1. Results of model selection for mixed-effects multinomial logit models assessing the probability of reindeer adopting either the shore, tundra, or mountain foraging strategy as function of winter severity, population density, sex–age class, and study area.

Model rank	Winter severity			Winter severity × Density	Density	Sex–age class	Area	K	AIC _c	ΔAIC _c	AIC _c weights
	Basal ice	IRH	IRHice								
1	–	×	–	×	×	×	×	18	2720.19	0.00	1
2	–	–	×	×	×	×	×	18	2737.53	17.34	0
3	×	–	–	×	×	×	×	18	2739.31	19.12	0
4	–	×	–	–	–	×	×	14	2744.83	24.64	0
5	–	–	–	–	–	×	×	12	2745.11	24.92	0
6	–	–	×	–	–	×	×	14	2745.14	24.95	0
7	×	–	–	–	–	×	×	14	2747.21	27.02	0
8	–	–	–	–	×	×	×	14	2747.25	27.06	0
9	–	×	–	–	×	×	×	16	2747.61	27.42	0
10	–	–	×	–	×	×	×	16	2747.76	27.57	0

Notes: Models are ranked according to Akaike’s information criterion (AIC) corrected for small sample size (AIC_c) (Burnham and Anderson 2002). To avoid collinearity issues and model over-parametrization, we fitted three global models, with winter severity represented by either basal ice thickness, integrated ram hardness (IRH), or their additive effect (“IRHice”). In addition, global models included population density (in interaction with the respective measure of winter severity), sex–age class, and area as fixed explanatory variables and year as a random intercept effect. For each global model, all different possible subsets of candidate models were tested (note though that eight candidate models did not converge and were therefore excluded from model selection). Explanatory variables included in each candidate model are marked with ×. K = number of parameters estimated. The candidate model given in bold was chosen. Shown here are the results for the 10 best-ranked models; for the full model selection results, see Appendix S5: Table S1.

Spatial foraging strategies

Starving animals tend to expose themselves to greater risks than those in good condition (Sinclair and Arcese 1995). Correspondingly, in harsh winters with high IRH, up to 50% of the reindeer were found in mountainous terrain above 300 m elevation (Fig. 4), and the predicted probability of mountain feeding approached 70% under high IRH and at high population densities (Fig. 5). The observation that mountain foraging was a generally less prevalent strategy under good winter conditions, and even in harsh winters with low population densities, indicates that there might be fitness costs associated with this strategy. Climbing steep mountains is likely energetically costly, that is, in contrast to the overall energy-saving behavior of Svalbard reindeer (Tyler 1987, Loe et al. 2007). It is also potentially dangerous due to the risks of injury or sudden death (e.g., by falling or triggering an avalanche, see example photograph in Appendix S7: Fig. S1). As forage abundance is also lower at high elevations due to limited plant productivity (Johansen and Tømmervik 2014), the mountain foraging strategy must provide some benefits in terms of forage accessibility, that is, less deep/hard snow and less basal ice.

Demographic variation

We found clear indications of different spatial responses between demographic classes (Fig. 6). Female adults were least likely to be mountain or shore feeding, whereas these strategies appeared to be prevalent among adult males. The “unknown” class, that is, the most common class among the mountain foraging animals, is also very likely dominated by adult males, which are typically antlerless at this time of the year and therefore less distinguishable from a distance (see Appendix S2: Fig. S3 and its figure caption for further details). Adult females generally keep their antlers throughout winter, although they may occasionally also be without antlers (Jacobsen et al. 1998). Given this competitive advantage of antler-bearing adult females, which are often observed chasing away males from foraging hotspots at low elevations (Schaefer and Mahoney 2001; authors’ personal observations), males may more often have to resort to alternative—and possibly suboptimal—behavioral strategies. In many species, males are also the more risk-prone sex (see, e.g., Miquelle et al. 1992 for moose, King et al. 2013 for sticklebacks, Jolles et al. 2015 for rats), which may include a higher propensity for seeking unsafe, steep terrain in search for food.

Table 2. Effects of integrated ram hardness (IRH), population density, sex–age class, and study area on the probability of reindeer foraging in shore, tundra, or mountain habitat.

Model	Parameter	Estimate	SE	z	P
Mountain vs. tundra	Intercept	−2.57	0.78	−3.28	<0.01
	IRH	0.43	0.81	0.53	0.60
	Density	−0.33	0.26	−1.28	0.20
	IRH * density	1.70	0.38	4.50	<0.001
	Sex–age calf	0.31	0.23	1.37	0.17
	Sex–age male adult	0.62	0.17	3.76	<0.001
	Sex–age unknown	2.06	0.16	12.60	<0.001
	Area Kaffiøyra	0.42	0.18	2.36	<0.05
	Area Sarsøyra	−1.53	0.23	−6.59	<0.001
Shore vs. tundra	Intercept	−2.21	0.21	−10.79	<0.001
	IRH	−0.75	0.20	−3.68	<0.001
	Density	0.04	0.18	0.19	0.85
	IRH * density	0.78	0.26	3.05	<0.01
	Sex–age calf	0.45	0.25	1.78	0.08
	Sex–age male adult	0.84	0.19	4.46	<0.001
	Sex–age unknown	−0.19	0.36	−0.52	0.60
	Area Kaffiøyra	−0.56	0.21	−2.67	<0.01
	Area Sarsøyra	−1.16	0.23	−5.0	<0.001
Mountain vs. shore	Intercept	−0.38	0.83	−0.46	0.65
	IRH	1.21	0.86	1.42	0.16
	Density	−0.23	0.30	−0.79	0.43
	IRH * density	1.08	0.42	2.56	<0.05
	Sex–age calf	−0.18	0.32	−0.57	0.57
	Sex–age male adult	−0.22	0.23	−0.93	0.35
	Sex–age unknown	2.22	0.37	6.04	<0.001
	Area Kaffiøyra	1.0	0.25	4.04	<0.001
	Area Sarsøyra	−0.39	0.30	−1.23	0.19

Notes: Parameter estimates are shown for the best-ranked multinomial mixed-effects model (binomial family, logit link) of the three assigned foraging strategies of individual reindeer mapped during annual population censuses in late winter ($n = 2304$ reindeer observations over 10 winters). Year was included as a random intercept effect. Estimates are given as log odds. IRH values were standardized. For factor variables, the intercept was set to “female adult” (sex–age) and “Brøggerhalvøya” (area). SE = standard error. Statistically significant P values (with alpha level = 0.05) are given in bold.

Sea or summit?

While previously observed anecdotally (Hansen et al. 2010a), our study demonstrates for the first time the extensive use of steep mountain habitat by Svalbard reindeer, particularly pronounced in winters with constrained forage access and high population densities. Combining our results with previous studies (Hansen and Aanes 2012, Hansen et al. 2019b), it appears that isolated coastal populations of Svalbard reindeer exhibit a bimodal spatial response—that is, they are forced toward “sea or summit”—when faced with harsh winter-foraging conditions. Hansen et al. (2019b) recently showed that reindeer supplemented “normal” tundra forage with marine food (i.e., washed-ashore kelp and seaweed) in years when access to terrestrial food patches was

restricted due to basal ice. Such “maritime behavior” is known to occur also in several other terrestrial herbivores, including sheep *Ovis aries* (Hall 1975, Novoa-Garrido et al. 2014), red deer *Cervus elaphus* (Conradt 2000), black-tailed deer *Odocoileus hemionus* (Parker et al. 1999), and other reindeer/caribou populations (Leader-Williams 1988). The nutritious value and digestibility of consuming marine biomass is uncertain (see Makkar et al. 2016 for a review). However, a relatively high prevalence of diarrhea symptoms (Hansen and Aanes 2012) combined with the tendency for lower occurrence of shore feeding under normal conditions suggests that kelp and seaweed provide only supplementary and probably suboptimal forage (Hansen et al. 2019b). As for mountain feeding, our modeling results also

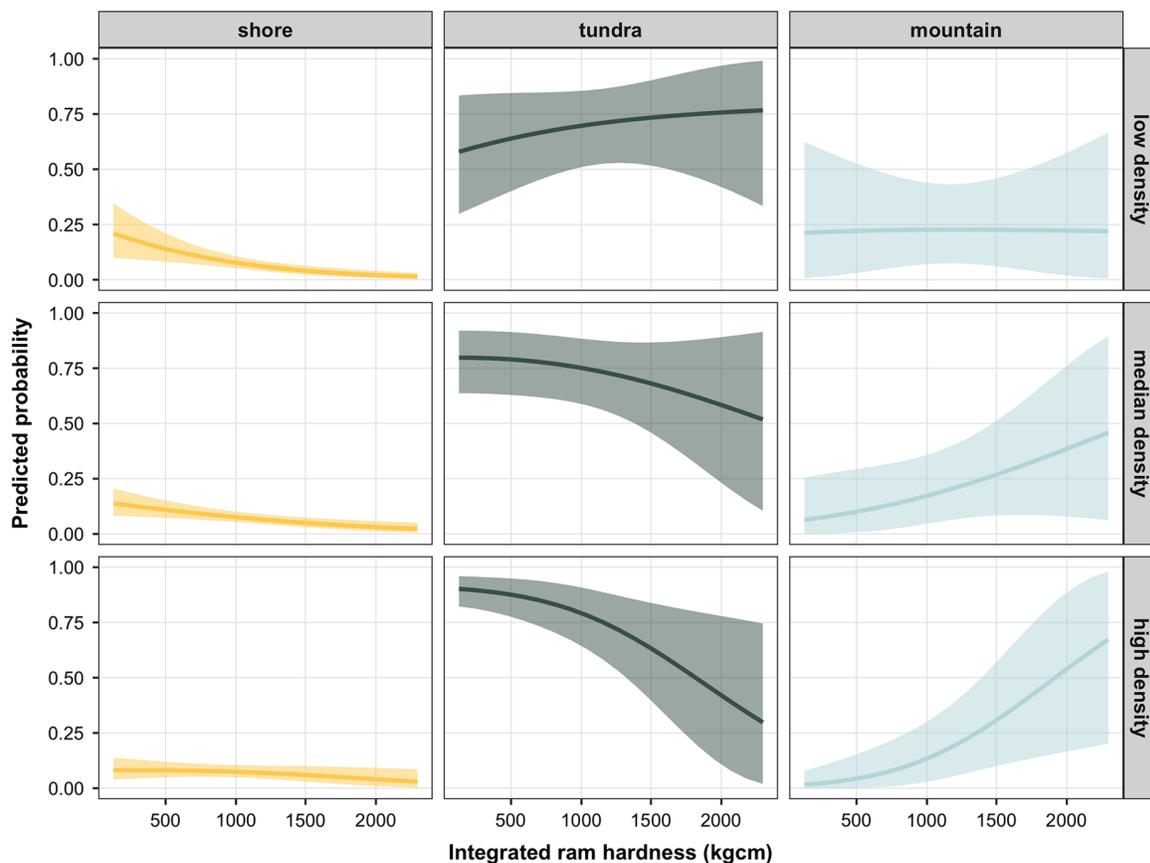


Fig. 5. Predictive margins plot for the fitted multinomial mixed-effects model (binomial family, logit link) assessing the probability of Svalbard reindeer utilizing shore, tundra, or mountain habitat in response to integrated ram hardness, for low (25th quantile), median, and high (75th quantile) levels of population density. Effect sizes are shown by shaded 95% confidence intervals, with “female adults” as reference level for the categorical variable “sex–age class,” “Brøggerhalvøya” as reference level for the categorical variable “area,” and random effects (year) set to zero. Predictive margins were calculated using the “predmarg” function in the R package “mpred.”

indicated a density-dependent effect of deeper and harder snow (i.e., increased IRH) on the probability of choosing shore feeding as opposed to tundra feeding (Table 2). However, sample size was very low for this spatial strategy, also reflecting that shore feeding is a much less common strategy to escape poor foraging conditions than mountain feeding (Fig. 4D, Fig. 5). Moreover, reindeer were increasingly likely to adopt the mountain feeding vs. shore feeding strategy when competition for food increased. This may be related to the observation that marine biomass seems to only supplement terrestrial forage

(Hansen et al. 2019b). As conditions get worse and population density is high, extreme competition for the very few accessible lowland tundra food patches may prevent sufficient supplements of terrestrial food to support the population, forcing (mainly adult male) individuals to seek forage at high altitudes, which are hard to combine with shore feeding.

Winter severity

Snow is a major determinant of northern ungulates’ space use (Tyler 2010) and winter ecology (Pruitt 1959), affecting forage accessibility

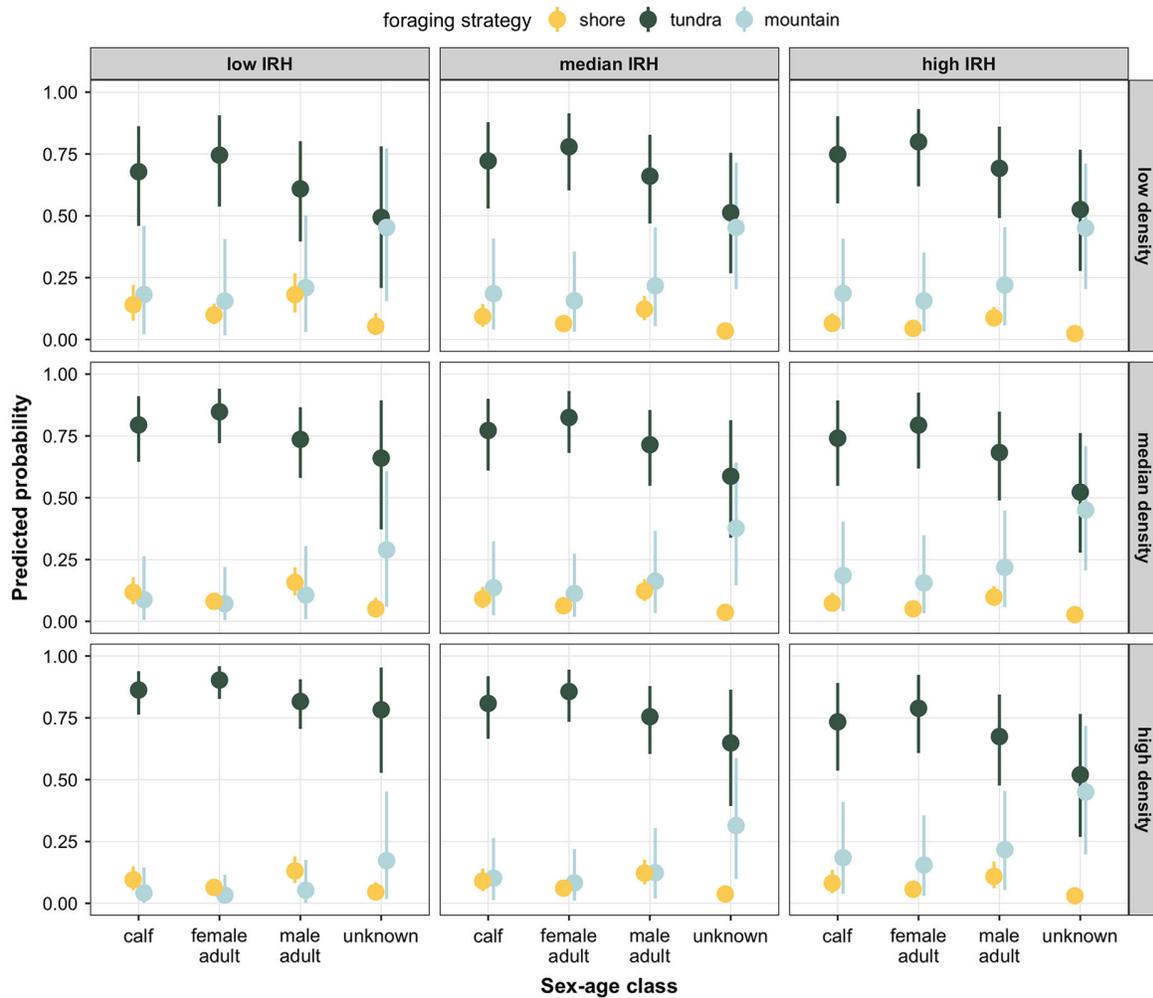


Fig. 6. Predictive margins plot for the fitted multinomial mixed-effects model (binomial family, logit link) assessing the probability of Svalbard reindeer utilizing shore, or tundra, or mountain habitat as a function of sex-age class and in response to low (25th quantile), median, and high (75th quantile) levels of integrated ram hardness (IRH) and for low (25th quantile), median, and high (75th quantile) levels of population density. Estimates are shown with 95% confidence intervals, with “Brøggerhalvøya” as reference level for the categorical variable “area,” and random effects (year) set to zero. Predictive margins were calculated using the “predmarg” function in the R package “mpred.”

(Collins and Smith 1991, Johnson et al. 2001, Robinson and Merrill 2012), diet (Laperriere and Lent 1977, Saether and Andersen 1990, Beumer et al. 2017), costs of movement and foraging (Fancy and White 1985, 1987, Lundmark and Ball 2008), habitat selection (Adamczewski et al. 1988, Mayor et al. 2009, Gilbert et al. 2017), home range size (van Beest et al. 2011), vital rates (Hurley et al. 2017), and population dynamics

(Hansen et al. 2019c, Desforages et al. 2021, Loe et al. 2021). During recent decades, however, there has been increased focus on the role of rain-on-snow events and subsequent basal ice formation in shaping climate change impacts on the performance of arctic ungulates (Miller and Gunn 2003, Putkonen and Roe 2003, Kohler and Aanes 2004, Hansen et al. 2011, 2019a, 2019c, Stien et al. 2012, Forbes et al. 2016, Loe et al.

2016, Albon et al. 2017). While these studies demonstrate that ice-locked pastures have a major impact on both survival and reproduction, and thereby population dynamics, other properties of the snowpack, such as its hardness and depth, may be just as important (Tyler 2010). Here, the model with IRH representing winter severity ranked by far the highest (Table 1). Our results from three Svalbard reindeer coastal populations therefore imply that the combined effect of snow depth and hardness (not including basal ice) may, overall, be a stronger constraint on the choice of foraging strategy than annual variation in basal icing (see also Beumer et al. 2017). In this system, both thick and extensive basal ice and very high IRH are often a result of extreme warm spells and rain events, and their negative correlation probably occurs because ice layers in the snowpack (causing high IRH) are formed when rain and melted snow do not percolate to the ground, which can even prevent later basal ice formation. Importantly, this suggests that negative impacts of warmer and rainier winters on reindeer may operate through either basal ice formation or a harder snowpack, with some winters characterized by a combination of both (e.g., in 2007; Fig. 4). Snowpack dynamics and the effects of weather on formation of ice layers are clearly complex, involving the interplay between snow depth, temperature, amount of precipitation as rain, and timing (Peeters et al. 2019). To assess ecological responses to changing snow conditions, our results emphasize the need for improved in situ, remotely sensed, and/or modeled snow data products that capture wildlife-relevant snow properties at appropriate spatial and temporal resolution (Boelman et al. 2019).

Conclusions and outlook

Although our “snapshot-in-time” data call for cautious interpretation, this study adds novel and nuanced insights into how a variety of behavioral strategies may potentially buffer negative effects of a changing winter climate in isolated arctic ungulate populations. The increasing isolation of some coastal reindeer populations, inhabiting islands and peninsulas separated by landscape barriers and a lack of sea ice (Poole et al. 2010, Jenkins et al. 2018, Peeters et al. 2020), makes them particularly vulnerable to changes in snowpack conditions and forage accessibility.

Under such isolation, seasonal migration and larger-scale range displacement, as observed in more inland populations of Svalbard reindeer (Loe et al. 2016), as well as more mobile reindeer and caribou populations (e.g., Cameron et al. 2020, Joly et al. 2020) are virtually impossible. Thus, individuals and populations must cope with severe foraging conditions at relatively small spatial scales, potentially expanding their realized foraging niche to include previously unused and possibly risky habitat and food sources, such as steep and mountainous habitat as demonstrated here. However, the degree to which such alternative foraging strategies can buffer potential negative fitness impacts of winter climate change remains largely unknown. By, for instance, combining individual-based behavioral data, such as GPS tracking and biologging data, with mark–recapture and population census time-series and extensive snowpack monitoring, future studies should therefore explore habitat–fitness relationships across demographic groups and populations (see, e.g., Loe et al. 2016 for fitness effects of icing-induced range displacement and Loe et al. 2021 for fitness effects of warmer autumns). Such studies will allow assessments of whether and how negative impacts of more frequent severe winters can be buffered by behavioral plasticity (see Beever et al. 2017 for a review), over time providing a tool to predict both behavioral responses and population dynamics under future environmental change.

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DATA AVAILABILITY

Data are available from Zenodo: <https://doi.org/10.5281/zenodo.5634124>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3883/full>