












## ARTICLE

## Animal Ecology

# Get it while it's hot: Benefits of a large herbivore exploiting stochastic resource pulses in a time of food scarcity

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**Funding information**

Norwegian Research Council,  
 Grant/Award Numbers: 12/115, 13/49,  
 18/19, 267613, 315454, 343398; Svalbard  
 Science Forum, Grant/Award Numbers:  
 322516, RIS-ID 2909; Climate-Ecological  
 Observatory for Arctic Tundra

**Handling Editor:** Joseph D. Holbrook

**Abstract**

To persist in seasonal environments, animals track, exploit, and store energy when food is plentiful. Seasonal changes in plant phenology that are predictable allow animals to track abundant food resources. However, little is known about how animals use and benefit from ephemeral and unpredictable food pulses during times when food is scarce. Climate change is altering the timing, abundance, and spatial distribution of food releases, emphasizing the ongoing need for understanding how unseasonal weather conditions influence access to food. Using 12 years of GPS-location data and annual measures of body mass in 72 adult female Svalbard reindeer (*Rangifer tarandus platyrhynchus*), we tested whether individuals with greater use of nutritionally beneficial resource pulses in autumn and early winter are heavier going into parturition in spring. Additionally, we evaluated how stochastic weather conditions influence the use of food resources. Reindeer that foraged most in marshes during autumn and early winter gained a positive carryover effect of up to 5 kg heavier body mass in late winter, with previously demonstrated benefits to both survival and reproduction. Marsh use was rare, brief, and intense, which is the expected response to a pulsed resource. The extent to which marshes

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were used varied greatly among years and was associated with stochastic mild spells that relaxed constraints of snow depth for a few days. Compared with other habitats used, marshes offered superior quantity and quality of below-ground plant biomass that may be accessed more easily under milder autumn and winter conditions. Our findings demonstrate the individual benefits of exploiting stochastic food pulses and showcase how resource tracking during periods of food scarcity may be a behavioral trait that could enhance population resilience in a rapidly warming climate.

#### KEYWORDS

Arctic, body mass, carryover effects, climate change, fitness-related trait, habitat selection, movement behavior, nutrition, plant quality, *Rangifer tarandus*, Svalbard reindeer

## INTRODUCTION

To persist in environments of extreme seasonality, long-lived animals must be able to exploit and store energy from food resources when they are abundant (Barboza et al., 2008). Across taxa, mobile consumers track seasonal food resources of varying predictability in space, time, and abundance (Yang et al., 2008). Recurring releases of seasonal resources generate predictable patterns in resource exploitation that are well documented—for example, migratory cervids “surf the green wave” of emerging vegetation in spring (Aikens et al., 2020; Albon & Langvatn, 1992; Bischof et al., 2012), grizzly bears “ride the crimson tide” of salmon spawning (Schindler et al., 2013), and blue whales undergo trans-Pacific migration following upwelling of phytoplankton blooms (Abrahms et al., 2019). However, little attention has been given to less predictable, fleeting resource pulses occurring in seasons of food shortage, despite clear fitness benefits for individuals capable of exploiting such ephemeral resource pulses (Bogdziewicz et al., 2016; Maute et al., 2019; Touzot et al., 2020; Yang et al., 2008).

In general, reproductive cycles are timed such that energetically costly aspects of reproduction (e.g., provisioning newborn offspring) coincide with seasonally predictable releases of food (Stearns, 1992). Yet, seasonal interactions with carryover effects from previous foraging conditions, including during food-limited seasons, can have significant influence on reproductive success (Cook et al., 2004; Merems et al., 2020; Monteith et al., 2014; Norris & Marra, 2007; Rockwell et al., 2012). In times of dwindling food supply, or overall food scarcity, such as during autumn and winter, there are benefits of accessing pulses of food during the brief times they are available (Yang et al., 2008). This is because incremental increases in access to nutritious food are likely to slow loss of fat reserves (Dwinnell et al., 2021) in a similar way that

selective feeding has multiplicative effects on assimilation of energy stores (White, 1983). Nonetheless, carryover effects of use of ephemeral resource pulses during food-limited seasons at the individual level are largely unexplored.

Evidence is growing that current changes in climate will not only alter the timing and length of seasons, but also increase variability of weather patterns within seasons, which may have ecological and evolutionary impacts (Vázquez et al., 2017). In seasonally cold environments, the use of foraging habitats during winter is often constrained by climate-related factors, influencing presence, depth, and hardness of snow and ice (Beumer et al., 2019; Hansen et al., 2010; Mysterud et al., 1997; Pedersen et al., 2021). Shifts in weather patterns in autumn and winter that influence previously predictable patterns of forage availability may have both negative and positive effects on populations. For example, extreme accumulation of snow or ground icing can limit access to forage, impacting population dynamics by way of accelerated loss of energy stores (Albon et al., 2017; Desforges et al., 2020; Hurley et al., 2017; Simard et al., 2010). Conversely, unusually warm conditions in autumn can delay onset of winter, providing prolonged access to food with positive carryover effects that promote population growth (Loe et al., 2021). Less explored, however, is the possibility of unseasonal and stochastic warm spells during snow-covered seasons, temporarily releasing resources with nutritional benefits that can be exploited by animals, like the exploitation of stochastic food pulses caused by rainfall in arid environments (Fryxell et al., 2005; Maute et al., 2019). The ability of individuals to exploit seasonally unexpected food is potentially an important indicator of population resilience to climate change (Yang et al., 2008).

We examined the nutritional benefits of individuals exploiting food resources in times of overall food

scarcity and how weather conditions in the seasonally extreme environment of the High Arctic constrain use of available resources in foraging habitats. Using 12 years of data combining GPS tracking and measurements of a fitness-related trait (i.e., body mass) of female Svalbard reindeer (*Rangifer tarandus platyrhynchus*), we first evaluated seasonal patterns in habitat use, within known key foraging habitats, to identify whether animals were preferentially using in on a specific resource during the food-limited seasons of autumn and early winter. Second, we evaluated whether there were nutritional benefits for individuals exploiting specific resources that carried over to body condition in late winter. Third, we characterized the ephemerality and stochasticity of use of key resources by quantifying the frequency, duration, and magnitude of habitat use. Finally, we evaluated the environmental conditions that limit forage availability and thus regulate use of ephemeral food resources. This approach allowed us to test the hypothesis that individuals with greater use of nutritionally beneficial resource pulses in autumn and early winter would have fitness benefits.

## MATERIALS AND METHODS

### Study area

Our study area encompasses three main valleys, Colesdalen, Semmeldalen, and Reindalen, in Nordenskiöld Land, Svalbard (78° N, 15° E; 182 km<sup>2</sup>). Vegetated habitats are typically found below 250 m. Mosses make up much of the tundra with cover varying among habitats. Vascular plants rarely cover >35% of the ground (Van der Wal & Stien, 2014). The short growing season from snow melt in June to peak biomass in late July/early August is immediately followed by rapid senescence (Van der Wal & Stien, 2014), which limits the duration of access to high-quality food.

Typical of High Arctic systems, summer temperatures are cool (mean July temperature: 7.3 ± 1.8°C, 2009–2021), while winters are much colder (mean January temperature: −11.6 ± 7.8°C, 2009–2021). Consistent snow cover usually spans October–June, but the onset of snow in autumn is increasingly delayed and spring melt-out is increasingly advanced due to recent temperature increases (Cooper, 2014). Mean snow depths were 54 ± 10 cm (2009–2021) in our study area in March, predicted from SnowModel (Liston & Elder, 2006). Although rain-on-snow events resulting in accumulation of ground ice are increasing in frequency (Peeters et al., 2019), these events do not occur consistently across years (Hansen et al., 2019; Loe et al., 2016).

### Study species

Svalbard reindeer are distributed across non-glaciated land of the archipelago, and their numbers have doubled since the early 1980s (Le Moullec et al., 2019). Despite the increase, effects of density dependence are only apparent in years with significant rain-on-snow events (Hansen et al., 2019). Foraging behavior of Svalbard reindeer is not influenced by predation because of few natural predators; however, there are rare incidents of polar bear predation (Derocher et al., 2000; Stempniewicz et al., 2021) and limited hunting (Peeters et al., 2022). Svalbard reindeer are mostly found in small groups of two to five individuals with low group cohesion (Loe et al., 2006). They are mostly nonmigratory but have been observed to move distances of 20–60 km to seek out better foraging conditions in severe winters (Loe et al., 2016).

### Reindeer life-history and GPS location data

Female reindeer were initially captured as 9- to 10-month-old calves marked with unique collar bands in late winter and therefore of known age. When recaptured as adults each subsequent late winter (March–April), we measured body mass to the nearest 0.5 kg using a spring scale (Salter Industries, West Bromwich, UK). Starting in 2009, a subset of marked adult females was fitted with GPS collars ( $n = 20$ ; Vectronic Aerospace GmbH), and we maintained a sample of up to 46 animals equipped with GPS collars in the following years, amounting to a total of 72 different individuals (ages 3–13, mean = 7.6, 2009–2021). GPS collars remained on individuals for 1–7 consecutive years, recording locations at rates ranging between 2 and 10 h, depending on the year. Additionally, collars were equipped with activity sensors recording mean values of acceleration along two axes every 5 min.

### Vegetation data

Using the best available vegetation-classification map of Svalbard, derived from Landsat data at 30 m resolution (Johansen et al., 2012), we extracted vegetation data for each reindeer GPS-location and randomly selected locations at home range and landscape scale. We reclassified the original 37 spectral classes into five groups (Appendix S1: Table S1): (1) grass swards dominated by *Poa* sp., *Festuca rubra* ssp. *richardsonii*, *Alopecurus ovatus*, and various forb species; (2) *Luzula* heaths dominated by *Luzula confusa* and *Salix polaris*; (3) marshes dominated by *Dupontia fisheri* and *Eriophorum*

*scheuchzeri*; (4) ridges characterized by sparse vegetation, primarily of *S. polaris* and *Dryas octopetala*; and (5) all other habitats, largely moss-dominated but also including sparsely vegetated gravel and polar desert (see Van der Wal & Stien, 2014 for further detail). Vegetation classes 1–3 are largely composed of plant species known to be prevalent in early-winter diets of Svalbard reindeer (Bjørkvoll et al., 2009), while class 4 (ridges) is used when more biomass-rich classes are covered under deep snow. All vegetation classes of interest are geographically available to reindeer throughout the year and all our study animals had GPS locations in each of the vegetation classes in most months.

To characterize quantity and quality of forage in autumn and winter, we sampled live and dead plant biomass above and below ground in three focal habitats—grass sward, *Luzula* heath, and marsh—during peak production in August (2–8) and after full senescence in October (6–8) 2022. We were particularly interested in evaluating belowground parts of plants, because this is where nutrients are stored in autumn and winter (Chapin et al., 1980), and reindeer have been observed to target roots following senescence (Staaland, 1986; unpublished field observations by SPH Dwinnell in autumn 2022). Within each focal habitat, we collected whole plants by digging up 20–30 individual plants (with all connected ramets), to include aboveground foliage and belowground roots, from three sites <100 m from known GPS locations of reindeer. We collected samples of graminoid species most abundant in reindeer diets in autumn and early winter (Bjørkvoll et al., 2009), including *D. fisheri* and *E. scheuchzeri* in marshes, *Poa arctica*, *F. rubra* ssp. *richardsonii*, and *A. ovatus* in grass swards, and *L. confusa* in *Luzula* heaths.

Live plant material from August was dried at 60°C and subsequently weighed for mean above and belowground biomass of each species during peak plant production in summer. Next, using samples collected in October, we measured the percentage of dry matter of acid-detergent fiber (% ADF), neutral-detergent fiber (% NDF), and the ratio of percent carbon relative to nitrogen (C:N ratio; an inverse measure of diet quality) per species and separated by above and belowground plant parts to capture nutrition following senescence (see Appendix S1 for methods). When material mass allowed, we used three subsamples to calculate means of metrics of plant quality.

## Weather, snow, and ice data

At each reindeer GPS location, we extracted ambient air temperature (in degrees Celsius), snow depth (in meters),

and snow density (in kilograms per cubic meter) from a spatially explicit and temporally dynamic snow-evolution model, available at daily temporal and 100-m spatial resolution (SnowModel; Liston & Elder, 2006). Using these data, we calculated three additional indices: (1) snow water equivalent (SWE = snow density  $\times$  snow depth, in millimeters); (2) daily difference in snow depth (in meters) to estimate snow accumulation and depletion; and (3) cumulative degree days above freezing, derived by summing the mean daily temperature for all previous days above 0°C, starting from October 1. Also, we defined onset of snow as the day-of-year when SWE exceeded 15 mm (Loe et al., 2021).

Precipitation and ground temperature were not available as outputs from SnowModel. Measures of precipitation were provided by the Norwegian Centre for Climate Services (<https://seklima.met.no/>) from an automated weather station 20 km from our study area (Svalbard Airport, station number SN99840). Precipitation was classified as rain when falling at mean daily ambient temperatures >0°C, and we calculated the daily cumulative amount of rain from October 1, because rain accumulation during seasons with consistently below-freezing temperatures can lead to ground icing (Loe et al., 2021). Ground temperature was represented by mean daily temperatures recorded by 128 iButtons (DS1921G; Maxim Integrated, San Jose, California, USA) in winter foraging habitats distributed across all main valleys. Each year in March or April, using an axe and ruler, we measured ground ice thickness to the nearest 5 mm at each iButton location and calculated annual mean thickness for each main valley. As it is possible that habitat use is influenced by previous environmental conditions, we also calculated the maximum ambient and ground temperatures, snow depth difference, and cumulative rain (in millimeters) across the 3 days prior to the date of the GPS location.

## Statistical analyses

All analyses were done in R version 4.1.3. We used GPS data from 72 females to evaluate seasonal shifts in population-level habitat selection by comparing habitat composition within monthly ranges in each year (for 347 animal-years, 2009–2021) to habitat composition across the landscape (second-order selection; Johnson, 1980). We evaluated second-order habitat selection to capture the higher order selection process, identifying which habitats reindeer prefer at different times of the year, including rarer habitats that only occur in parts of the landscape. We used the animal's range estimation (i.e., utilization distribution) as the sample unit to best evaluate second-order habitat selection when using varying fix rates that include



coarse temporal scales (Northrup et al., 2022). We delineated monthly ranges for each animal in each year using 95% autocorrelated kernel density estimators (AKDE; Fleming et al., 2015) using the package “ctmm” (Calabrese et al., 2016). This method in home range estimation accounts for pseudoreplication and bias in parameter estimates of resource selection functions by applying a likelihood weight to animal locations based on autocorrelation among GPS positions (Alston et al., 2023). To represent available habitat composition at the landscape level, we randomly sampled 7000 locations from a composite range boundary, delineated by the perimeter of the aggregated monthly ranges of all individuals across years (Appendix S1: Figure S1). Glaciers, moraines, ice, and open water were excluded from available habitat types. To identify habitat compositions of monthly ranges, we randomly sampled 1400 locations within each monthly range and extracted habitat type at each location, thus maintaining a sample ratio of 1:5 home range to landscape locations. We estimated habitat selection by fitting generalized linear regression models (function “glm”) with a binomial error distribution. Covariates included habitat type, month, and their interaction. We opted to run separate models for each year to allow for unconstrained annual variation in monthly habitat selection.

Next, we compared the effects of habitat selection and habitat use on body mass. We evaluated both habitat selection and use at the monthly and season (combining October–February) scales, because search for and utilization of resources can manifest at multiple spatiotemporal scales in selection and use (Gaillard et al., 2010; Johnson, 1980). We focused on selection and use in October–February to capture animal behavior after full senescence of vegetation, marking the onset of the food-limited season (Loe et al., 2021) and before animals were recaptured in late winter (March–April). To obtain estimates for individual habitat selection, we extracted selection coefficients from month and season models fitted for each individual, separately. Similarly, month and season estimates of habitat use at the individual level were calculated as proportion of GPS locations recorded in each of the focal habitats. Since we were most interested in understanding the forage benefits of habitat use, we used only GPS locations of individuals deemed to be active. Here, we used activity data collected from GPS collars and censored all locations with mean acceleration values less than  $50 \text{ m/s}^2$  at the 5-min interval matching the GPS location, because those are known to be associated with “resting” behavior (Trondrud et al., 2021).

We used generalized linear mixed-effects regression models (GLMM) and the Akaike information criterion ( $\text{AIC}_c$ ) corrected for small sample sizes to evaluate the influence of habitat selection and use on the adjusted

late-winter body mass. We adjusted the response variable, body mass in late winter (March and April), to account for date of capture, effects of reproduction, and age using a generalized additive model (following Loe et al., 2021). All competing models included animal ID as a random effect to account for dependency in body mass over time ( $n = 64$ , because not all animals with GPS data were successfully recaptured, nor were all monthly selection coefficients available). Included fixed effects were annual onset of snow, ground ice thickness, and population size, because of their known influence on late-winter body mass of Svalbard reindeer (Hansen et al., 2019; Loe et al., 2021). Population size was estimated using an integrated population model, combining individual mark–recapture data with population counts and harvest data (Lee et al., 2015). All models containing selection coefficients derived from individual resource selection models were weighted by the inverse variance of the selection coefficient to account for errors in model estimates (Dwinnell et al., 2021). We used  $\Delta\text{AIC}_c$  for selecting the variables that most influenced body mass in late winter. We standardized all covariates to allow for direct comparisons of effect size and considered the simplest model within  $2.0 \Delta\text{AIC}_c$  of the top model to be the best model (Arnold, 2010).

We used ANOVA to compare the nutritional value of vegetation within each focal habitat, including biomass at peak production (August) and quality of below and aboveground plant material after complete senescence (October). We used % ADF to compare the digestibility of above and belowground plant material (Danell et al., 1994), noting that it was highly correlated with % NDF ( $r = 0.96$ ). We used C:N ratios as a proxy for nutritional quality of species (Leslie & Starkey, 1985), because low sample quantities limited our ability for replicate measures of the digestibility indicators of % ADF and % NDF for all plant parts sampled. C:N ratios were highly correlated with % ADF ( $r = 0.73$ ) and % NDF ( $r = 0.65$ ) affirming use of C:N ratios as a sufficient proxy for nutrition in this analysis.

Our evaluation of the ephemerality and stochasticity of resource use was guided by the definition of a pulsed resource as low frequency, short duration, and high magnitude, *sensu* Yang et al. (2008). We calculated the frequency, duration, and magnitude of focal habitat use, as well as the interval between use, for each individual. To diminish the effect of differing positioning frequency of collars and vegetation map misclassifications, we assumed that a focal habitat was used on a given day if at least one GPS location classified as “active” was recorded in that habitat and day. For each individual and year, we calculated *frequency* as the number of days individuals used each focal habitat. We calculated *duration* as mean

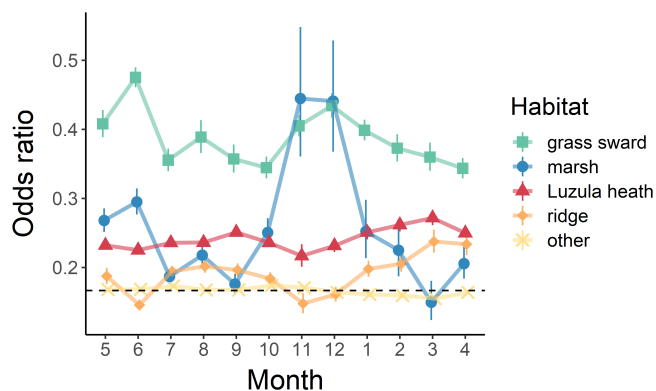
bout length, where bouts are defined as a string of days with consecutive use (including single days), and *interval* as the mean number of days between bouts. We quantified *magnitude* of use as the proportion of points that fell within each focal habitat during a bout divided by overall use of the respective habitat throughout the season (i.e., magnitude = mean proportion of use in bouts/mean proportion of overall use in a season).

Finally, we used mixed-effects multinomial logistic regression to determine the weather and snow variables that most influenced the probability of reindeer moving into and staying in the focal habitat for which selection or use affected body mass (according to  $AIC_c$  ranking from GLMM analysis outlined above). We used all GPS locations, reflecting accessibility of habitat regardless of foraging, to determine transitions between moving into the focal habitat and staying in the focal habitat. We used animal ID as a random effect, and fixed effects included all weather and snow metrics described above (see *Weather, snow, and ice data*) and days since October 1 (i.e., day of season). GPS location rates varied widely among individuals and years, so locations with greater than 24 h between acquisition times were considered a break in the movement step. All models were fit with quasi-likelihood maximization (using the “mblogit” function; “mclgfit” package). Like our modeling approach above, all covariates were standardized to allow for direct comparisons of effect size and  $\Delta AIC_c$  was used to select the final model. Many weather and snow variables were strongly correlated with day of season, including all metrics related to ground temperature, snow, accumulated rain, and degree days above freezing (Appendix S1: Table S2), potentially giving spurious effects if included in the same model. Thus, we evaluated day of season, weather, and snow variables in univariate model comparisons, and compared their ability to predict probabilities of animals moving into and staying in the focal habitat.

## RESULTS

### Monthly habitat selection

At the population level, monthly ranges of female Svalbard reindeer always contained more *Luzula* heath and grass sward habitat than expected based on availability at the landscape scale (Figure 1; Appendix S1: Table S3). *Luzula* heath was consistently selected for throughout the year. Similarly, grass sward was selected throughout the year, but with relative peaks in June, and again in November and December. Seasonal selection for ridge habitats indicated some avoidance in



**FIGURE 1** Mean and SE of odds ratios of monthly (May [5] through April [4]) population-level habitat selection of grass sward, marsh, *Luzula* heath, ridge, and all other habitats by Svalbard reindeer 2009–2021. Ratios of used to available locations was 1:5; thus, all odds ratios above 0.17 (dashed line) indicate selection for the habitat type. Habitat selection is assessed for the second-order scale (i.e., habitat composition of the used range relative to habitat composition in the available landscape; Johnson, 1980).

summer and autumn but relatively strong selection in late winter (March–April). Small confidence limits for *Luzula* heath, grass sward, and ridge habitats across all months suggest that seasonal trends are consistent among years (Figure 1). In contrast, the selection of marsh habitat was much more variable throughout the year, with seasonal trends in both avoidance and selection but a marked peak in selection in November and December, along with a weaker increase in June. Also, large confidence limits of marsh selection suggest variability in selection among years—especially in autumn and early winter (October–December).

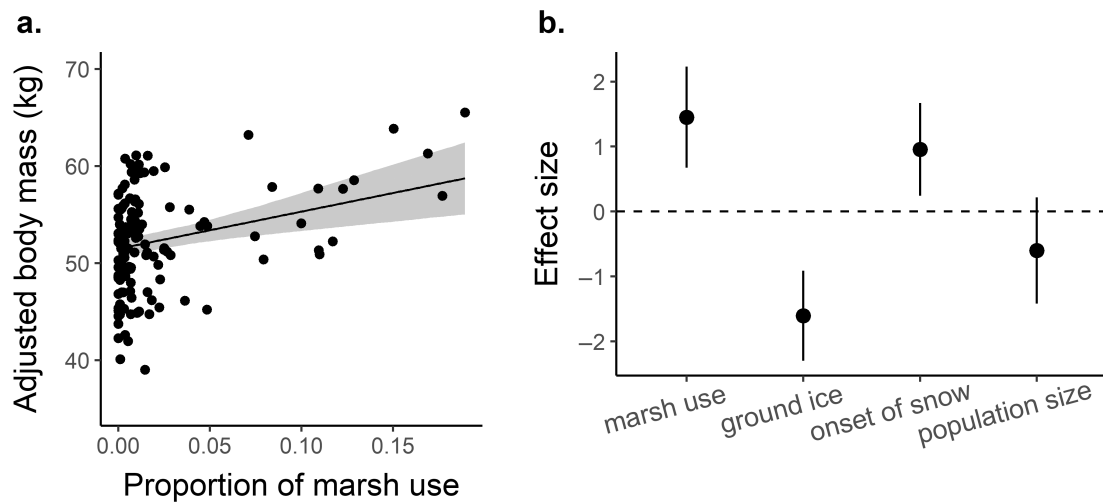
### Carryover effects of marsh use

Late-winter body mass increased 0.38 kg for every 1% increase in marsh use throughout a season (October–February; Figure 2a;  $\beta_{\text{marshuse}}$ : 38.3; 95% CI: 17.5, 59.7). Marsh use in February had the greatest effect on body mass, increasing the mass by 0.50 kg for every 1% increase in February use ( $\beta_{\text{Feb.marshuse}}$ : 49.9; 95% CI: 23.8, 76.5). The use of marsh habitat (both throughout the season and in February) was included in the best-ranked models explaining variation in late-winter body mass, together with onset of snow, ground ice accumulation, and population size, but the influence of population size was not significant (Figure 2b; Appendix S1: Table S4). The selection or use of no other habitats was included in the top ranked models ( $\Delta AIC_c > 3.5$ ).

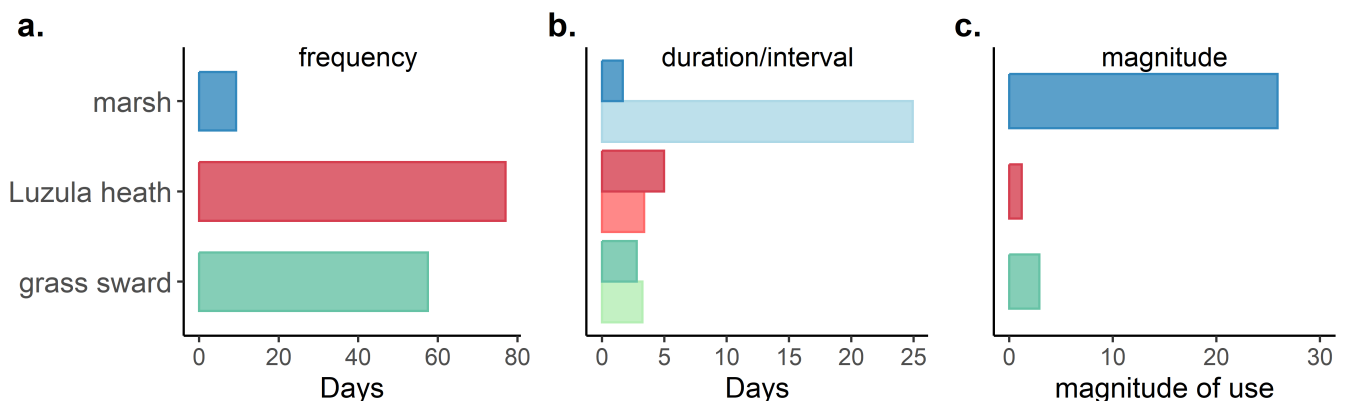
## Frequency, duration, interval, and magnitude of use

Grass sward, *Luzula* heath, and marsh habitats were selected for in autumn and early winter and, thus, were the focus for evaluating ephemerality of resource use. Among focal habitats, marsh had the lowest *frequency* of use (mean  $9.3 \pm 1.8$  days in the period October–February; Figure 3a). *Luzula* heath had the greatest *frequency* of use ( $77.0 \pm 5.5$  days), followed by grass sward ( $57.5 \pm 5.4$  days; Figure 3a). Correspondingly, mean bout length (*duration*) was shortest for marsh ( $1.76 \pm 0.1$  consecutive days) with the longest intervals

between bouts ( $24.9 \pm 2.1$  days). Conversely, the *duration* of use was longest ( $5.0 \pm 0.4$  days) and *intervals* shortest ( $3.5 \pm 0.2$  days) for *Luzula* heath, followed by grass sward ( $2.9 \pm 0.1$ ;  $3.4 \pm 0.3$ , respectively; Figure 3b). The *magnitude* of use was the greatest in marsh habitat, with a 26.2-fold increase in use during bouts relative to overall use throughout autumn and early winter ( $47.2 \pm 2.0\%$  and  $1.8 \pm 0.4\%$  of locations, respectively), compared with other habitats (*Luzula* heath = 1.2-fold increase [ $43.7 \pm 4.6\%$  vs.  $35.9 \pm 1.4\%$ ]; grass sward = 2.9-fold increase [ $53.7 \pm 2.4\%$  vs.  $18.4 \pm 0.8\%$ ]; Figure 3c). Mean daily proportions of marsh use of all individuals from October to February were variable within and between



**FIGURE 2** (a) Adjusted late-winter body mass of adult female Svalbard reindeer as a function of marsh use (proportion of locations in marsh habitat, October–February 2009–2021), and (b) effect sizes with 95% CIs of scaled fixed variables in the generalized linear mixed model of adjusted body mass, including marsh use, ground ice thickness, timing of onset of snow, and population size. Late-winter body mass was adjusted using a generalized additive model to account for date of capture, effects of reproduction, and age.



**FIGURE 3** Characterization of use of resource pulses (sensu Yang et al., 2008) in three focal habitats (marsh, *Luzula* heath, and grass sward) used by GPS-collared female Svalbard reindeer (2009–2021), including (a) mean *frequency* of use in a season (October–February), (b) mean *duration* of habitat use during a bout (dark hue) and interval between bouts (light hue), and (c) *magnitude* of use (mean proportion of GPS locations in each habitat during a bout divided by mean proportion of locations during the entire October–February season).

years—considerably more so than use of other habitats (Figure 4; Appendix S1: Figures S2 and S3). This was also the case at the individual level (range 0%–14% of GPS locations were in marshes; Appendix S1: Figure S4), with 10% of individuals never using marshes and several individuals using marshes frequently in some years but not in others.

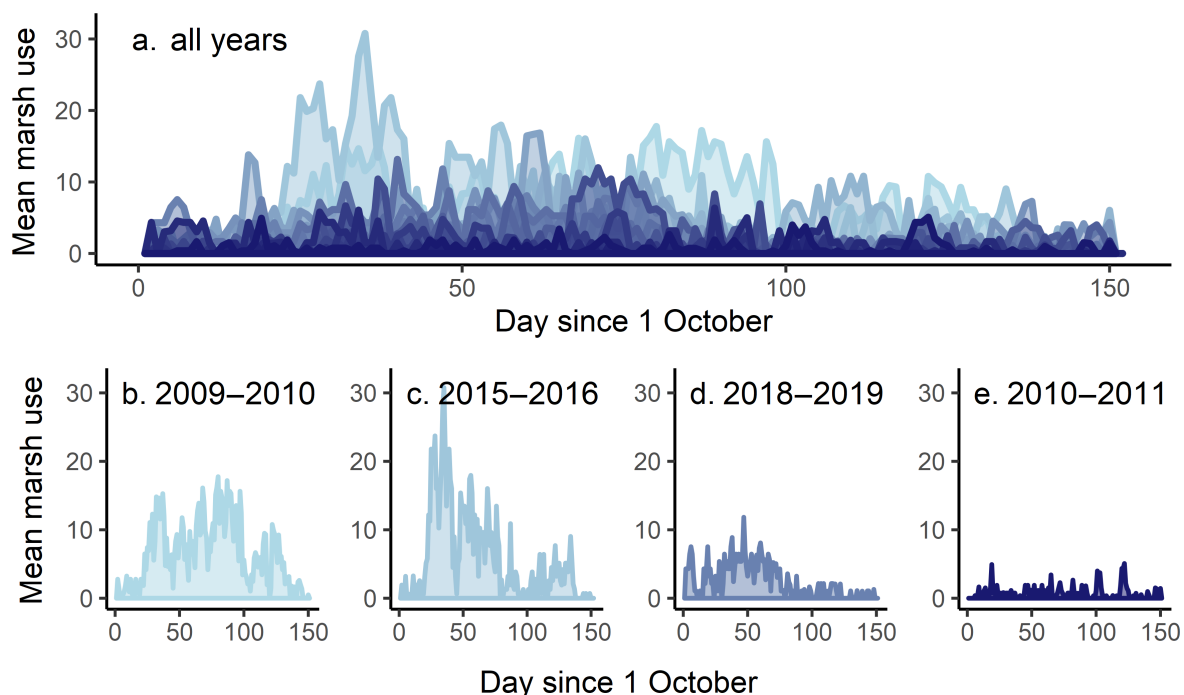
### Biomass and quality of forage among key habitats

In October, aboveground plant material among all habitats was mostly dead and of low quality, but the quality of live belowground plant material was considerably better (mean C:N ratios belowground were  $34.8 \pm 5.0$  vs.  $52.9 \pm 3.6$  aboveground;  $F_{1,34} = 12.7$ ,  $p = 0.001$ ) and with lower fiber content (% ADF;  $F_{1,10} = 5.09$ ,  $p = 0.048$ ). Belowground material of graminoid species in marshes had greater quality (Appendix S1: Table S5), especially *E. scheuchzeri*, compared to all other species, except for *P. arctica* ( $F_{5,12} = 22.97$ ,  $p < 0.001$ ; Figure 5). The belowground biomass of our samples was significantly greater than aboveground biomass already from summer ( $F_{1,62} = 12.61$ ,  $p < 0.001$ ; Figure 5), with *D. fisheri* in marshes having the greatest proportions of

belowground biomass (i.e., greater root and rhizome mass available per individual plant; illustrated in Appendix S1: Figure S5). In combination, belowground plant material in marshes stands out by being of high quality and high biomass.

### Constraints on marsh use

Since marsh use in autumn and early winter had the greatest effect on body mass in late winter, we were most interested in environmental constraints on movements into and continuous stays within marshes (e.g., Appendix S1: Figure S6). Snow depth was the most influential variable for explaining variation in the probability of reindeer moving into and staying in marshes (Appendix S1: Table S6) and had substantially more support than the second highest ranking model, including SWE;  $\Delta AIC_c$ : 67.1. Snow depth and SWE were the only variables that outperformed the effect of day of season. The probability of entering and remaining in marsh habitat decreased as snow depth increased ( $\beta_{\text{intomarsh}}$ :  $-1.90$ ; 95% CI:  $-2.07$ ,  $-1.72$  and  $\beta_{\text{stay in marsh}}$ :  $-1.98$ ; 95% CI:  $-2.11$ ,  $-1.84$ ). Although overall movements into marshes, and stays in marshes, were few (1.1% and 1.8% of all movement steps, respectively), the probability of

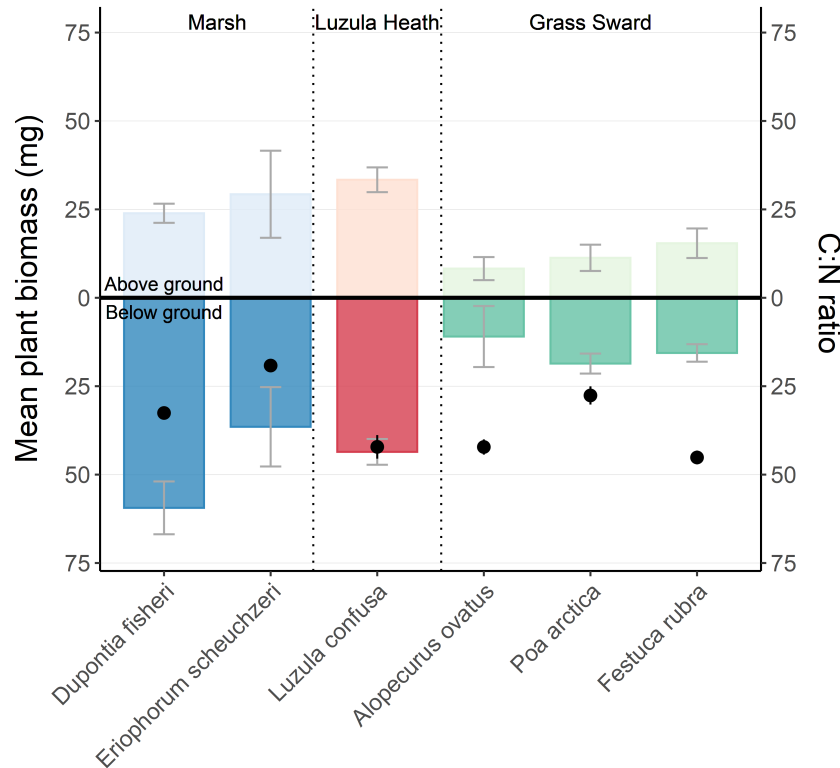


**FIGURE 4** (a) Mean daily use of marshes (percent of locations in marsh habitat) for each season 2009–2021, with color gradient across all 12 years and ordered by years of high cumulative (sum October–February) use (light blue) to low cumulative use (dark blue). (b–e) Individual years are highlighted, including (b) the year with greatest overall use (2009–2010), (c) the year with greatest peak in use (2015–2016), (d) the year with median overall use (2018–2019), and (e) the year with minimum overall use (2010–2011).

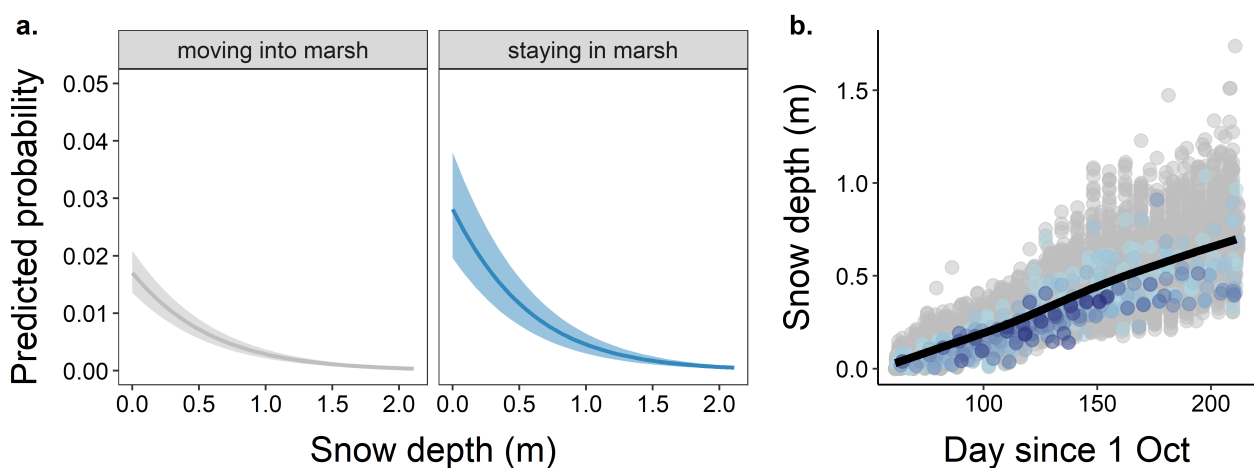


staying in marshes was two times greater where there was no snow (0 m snow depth) when compared to mean snow depth at a location used by reindeer (0.36 m;

Figure 6a,b), and marsh use typically occurred when and where snow depth was lower than the predicted mean throughout the season (Figure 6c). When fitted



**FIGURE 5** Biomass (bars; mean  $\pm$  SE) during peak production (August) of above- (light hue; increasing values upward) and belowground (dark hue; increasing values downward) plant materials per shoot of graminoid species dominating marsh, *Luzula* heath, and grass sward habitats in 2022, and mean C:N ratios (black dots) of belowground plant material following complete senescence (October).



**FIGURE 6** (a) The influence of local snow depth on the probability of an adult female Svalbard reindeer moving into a marsh from any other habitat and staying in marsh habitat and (b) the seasonal predicted mean of snow depth (black line; derived from a generalized additive model) with the mean snow depth of GPS locations for an individual in each week (blue and gray dots; October–February, 2009–2021). The proportional use of marsh habitat by an individual in a week is ordered by light blue hues indicating low proportion of use and dark blue indicating high proportions of use; weekly proportions with zero marsh use are marked in gray. Thus, points below the black line indicate weekly snow depth values of used locations below the predicted average snow depth among all locations of that week.

alone, ground temperature, especially maximum ground temperature in the previous 3 days, also significantly influenced marsh use, with animals more likely to move into, and stay within, marshes at warmer temperatures ( $\beta_{\text{intommarsh}}$ : 0.06; 95% CI: 0.05, 0.07 and  $\beta_{\text{stayinmarsh}}$ : 0.06; 95% CI: 0.05, 0.07), but due to collinearity, the effect was reduced when including snow and day of season (Appendix S1: Table S6, Figure S7).

## DISCUSSION

Our findings demonstrate how fleeting use of a resource in times of food scarcity can influence a fitness-related trait in a grazing large herbivore through the nutritional benefits it provides. Although marsh use was generally rare and brief, we revealed strong positive carryover effects from exploiting this resource. Reindeer that used marshes in autumn and early winter were up to 5 kg heavier in late winter than individuals that did not use this habitat—despite the resource being used with low frequency and short duration, but with high magnitude of use when accessible (characteristic of a resource pulse; Yang et al., 2008). The use of marshes was limited by snow but occasionally facilitated by stochastic mild spells that relieved constraints of snow conditions. Since late-winter body mass influences survival (Albon et al., 2017) and successful calving (Veiberg et al., 2017), our findings emphasize the importance of considering nutritional benefits of ephemeral food resources across stages of the reproductive cycle when evaluating mechanisms driving population dynamics.

The timing of marsh use within seasons was highly variable among years, and some years had overall low use compared to others, suggesting that the timing of marsh use is less predictable, compared with other habitats with consistent seasonal use. Indeed, this is expected of a resource where accessibility is dependent on weather conditions. In our study, we did not have measurements of the resource availability that were independent of the consumer. Even so, in our food-limited and predator-free system, it is extremely likely that variation in marsh use was driven by variation in accessibility of the resource. There is some evidence of large-bodied, long-lived mammals exploiting weather-constrained resource pulses with variable predictability (Fryxell et al., 2005; Ryan et al., 2022), but these behavioral observations can rarely be tied to fitness (but see Touzot et al., 2020). For other taxa, however, the importance of resource pulses for population abundance in times of constraint is well documented, such as short-lived invertebrate responses to intensive rain in warm deserts (Maute et al., 2019) or responses of small mammals to seed masting

(Bogdziewicz et al., 2016; Wolff, 1996). Our study provides a critical link between pulsed exploitation of a rare resource and a fitness-related trait of a large-bodied, long-lived mammal—reinforcing the multiplicative effects of incremental advantages that come with selective feeding (White, 1983).

Some individuals apparently never used marsh habitat, even when conditions were conducive for exploitation. This finding was surprising given the observed benefits of using marshes, and the ability of Svalbard reindeer to undergo larger movements (>20 km) to reach better forage following rain-on-snow events that inhibit access to vegetation locally (Loe et al., 2016). Such varied use of marshes suggests that some individuals may be limited by knowledge of the locale or occurrence of the resource pulse. With rapid warming in the High Arctic (Hanssen-Bauer et al., 2019), it is possible that marsh availability has become a relatively new resource in autumn and winter and some animals have learned to exploit this novel resource, while others have not. Cultural knowledge, memory, and familiarity with benefits of resources are recognized as playing an important role in resource use of large herbivores (Jesmer et al., 2018; Merkle et al., 2019; Ranc et al., 2020). Knowing where and when to find ephemeral food pulses is a possible mechanism driving varied use of marshes by reindeer that warrants more explicit evaluation.

In the absence of external constraints, the use of food resources should be shaped by the quality and abundance of that resource. For most vertebrate herbivores, the prime food supply is located aboveground, but our study points to belowground resources of marshes to be a potential treasure trove for reindeer during autumn and winter. The quality of dead aboveground vegetation was low among habitats, but live belowground vegetation in marshes did differ from other habitats by having both higher quality and biomass. It is possible that reduced snow density and depth, prompted by warm spells, allow reindeer to access extensive food resources in the form of belowground plant parts, located in moss and soil layers (e.g., Bardgett et al., 2007) that are otherwise inaccessible. Nutrients of deciduous plants in Arctic systems typically shift into stem bases, rhizomes, and roots in autumn and remain there until spring (Chapin et al., 1980), and other herbivores, such as pink-footed geese (*Anser brachyrhynchus*), exploit these belowground nutrients through grubbing in spring—primarily in marsh habitat while live aboveground biomass is still very low (Anderson et al., 2012; Speed et al., 2009). Reindeer dig for food throughout winter by cratering in patches with snow conditions that allow for easier digging (Beumer et al., 2017) and use their olfactory sense to select for patches with vascular plants (Hansen et al., 2010).

Although it is unknown whether they are accessing belowground food while cratering in winter, Svalbard reindeer have been observed selecting for roots following senescence in early autumn (Staaland, 1986; SPH Dwinnell, unpublished observations). Long-standing notions of belowground forage being inaccessible in the frozen soil over winter may be challenged under warming Arctic conditions that increase the frequency of temporary thawing and release of such resources. Further exploration into the ability of Svalbard reindeer to access nutritious, belowground food resources in winter is needed.

A primary prediction of climate change is that extreme weather events will occur more frequently, and seasonal patterns will likely be less predictable (Walsh et al., 2020). Predictability of food availability may therefore decrease with climate change, making it harder for animals to track food pulses. At the same time, it is possible that shifts in frequency or duration of food releases, associated with both temperature increases and longer snow-free seasons, may make nutritionally beneficial habitats more available. As such, increases in marsh accessibility may have contributed to the recent phase of increased numbers of Svalbard reindeer (Le Moullec et al., 2019) and could carry on to do so into the future. In the High Arctic, herbivores will continue to be affected by shifts in food available to them, with population-level consequences. Behavioral traits of individuals, exploiting largely unpredictable food resources with nutritional benefits, may increase population resilience to the effects of climate change.

#### AUTHOR CONTRIBUTIONS

Samantha P. H. Dwinnell, Leif Egil Loe, René van der Wal, Åshild Ø. Pedersen, and Steve D. Albon developed and designed the study. Leif Egil Loe, Steve D. Albon, Åshild Ø. Pedersen, and Brage B. Hansen secured funding. Samantha P. H. Dwinnell performed statistical analysis with assistance from Larissa T. Beumer and Leif Egil Loe. Øystein Holand facilitated and conducted lab analyses. Samantha P. H. Dwinnell, Leif Egil Loe, René van der Wal, Steve D. Albon, R. Justin Irvine, Erik Ropstad, Vebjørn Veiberg, Åshild Ø. Pedersen, and Larissa T. Beumer collected data, and Leif Egil Loe and Samantha P. H. Dwinnell managed data. Samantha P. H. Dwinnell wrote the manuscript and all coauthors provided revisions.

#### ACKNOWLEDGMENTS

This long-term study was possible with combined funding from the Research Council of Norway (RCN; grant numbers 267613, 315454, and 343398), Svalbard Environmental Fund (grants 12/115, 13/49, and 18/19),

US Norway Fulbright Foundation for Educational Exchange, Svalbard Science Forum (Arctic Field Grant RIS-ID 2909, 322516), and the Climate-Ecological Observatory for Arctic Tundra (COAT; [www.coat.no](http://www.coat.no)). We thank the Governor of Svalbard and the Norwegian Food Safety Authority for permission to conduct our research. A special thanks to Stein Tore Pedersen and other technical staff at the Norwegian Polar Institute and the University Centre in Svalbard for supporting fieldwork. Thanks to numerous field assistants for help with capture of reindeer and other data collection from the field and to Hanne Kolsrud Hustoft at NMBU for assistance with plant analyses. We thank Glen E. Liston and Adele K. Reinking for providing needed technical support in using SnowModel and Atle Mysterud for providing the first 20 GPS collars used in the project. Finally, a very special thanks to the late Mads Forchhammer for his many contributions to the field of Arctic biology, support in this research, and excellent cooking in the field.

#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

GPS location data (Dwinnell et al., 2024) are available from Dryad: <https://doi.org/10.5061/dryad.4qrfj6qkx>. Svalbard reindeer capture data (Dwinnell, 2024) are available from the NIRD Research Data Archive: [10.11582/2024.00158](https://doi.org/10.11582/2024.00158).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Dwinnell, Samantha P. H., Larissa T. Beumer, René van der Wal, Steve D. Albon, Åshild Ø. Pedersen, Øystein Holand, Brage B. Hansen, et al. 2024. “Get it while It’s Hot: Benefits of a Large Herbivore Exploiting Stochastic Resource Pulses in a Time of Food Scarcity.” *Ecosphere* 15(12): e70080. <https://doi.org/10.1002/ecs2.70080>