UiT The Arctic University of Norway

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Nutritious and delicious?

A non-invasive study of food plant choices by Svalbard reindeer in Summer and late Autumn

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Cover photo: Picture of a female Svalbard reindeer.
Shot by Morgan Heim, September 2022, Reindalen

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Abstract

Seasonality affects growing patterns of vegetation and habitat use by herbivores. Short growing seasons make plants grow quickly through phenological stages which alters their nutrient levels and thus habitat use of herbivores that depend on energy assimilation in summer. Selective foraging that increases intake of high-quality forage can be highly advantageous and is usually a trade-off between forage quantity and quality. In the high Arctic, characterised by extreme seasonality, I examined 1) what plant species and plant functional groups were selected by Svalbard reindeer on a fine patch-level scale, 2) how selectivity changed from summer (when available plant biomass is at its highest) to autumn (when most plants are senescing and animals are at their fattest), and 3) how forage selectivity tied to plant nutrients and plant antiherbivore defences over the season. Svalbard reindeer displayed preference of specific plant functional groups consisting of certain key forage species, and forage selection changed throughout the study period. Selectivity was not found to be affected by concentrations of the plant nutrients nitrogen and phosphorus. Surprisingly, grazing selectivity related positively to silicon which is thought to be a herbivore deterrent in plants. Phenolics had a net negative effect on selectivity, whereas the phenolics to nitrogen ratio did not affect grazing preference in summer, and only later in the season showed a negative effect.

1 Introduction

1.1 Variation in availability, quantity, and quality of forage

Vegetation and herbivores in terrestrial Arctic ecosystems have adapted to extreme seasonality. In the short summers, plants grow quickly through different phenological stages (Bliss, 1971). This affects habitat use and feeding patches of ungulates, oftentimes linked to trade-off mechanisms between forage quality and quantity (Fryxell, 1991). Finding enough nutritious food in summer is especially important to ungulates in seasonal environments where available food is scarce and of poorer quality in winter (Parker et al., 2009).

Vascular plants in Arctic ecosystems span a range of plant functional groups (PFGs; sensu growth forms), from forbs and graminoids to woody shrubs, that often link with different nutrient content and hence expected quality to herbivores (Aerts and Chapin, 1999). Common measures of plant quality include nitrogen (N), which is fundamental for protein synthesis and thus growth, and phosphorus (P), which is essential for bony structures and ATP synthesis (Sterner and Elser, 2002). PFGs often vary consistently in their concentrations of N and P (forbs > graminoids > deciduous shrubs > evergreen shrubs; Thomas et. al., 2019), yet the most nutritious forage is usually not the most abundant and frequently even inversely correlated to one another (Fryxell, 1991). Selective feeding by northern ungulates can therefore be highly advantageous, where small changes in quality or forage intake can cause big, or so called multiplier, effects on animal productivity (White, 1983). Additionally, shifts in selectivity from high digestible nitrogen in early summer to high biomass in late summer has been observed as a response to the plants phenology over the growing season (Johnson et al., 2021).

Besides plant nutrient content (N and P), plant defence content such as phenolics and silicon (Si) can also affect herbivore forage selection by reducing palatability and digestibility (Coley et al., 1985, Vicari and Bazely, 1993). However, accumulation of phenolics and silicon vary widely among plant species, and resource limitations and environmental factors can affect phenolic and silicon-based leaf defences in different ways (de Tombeur et al., 2021). In general, phenolics are accumulated in slow growing plants such as shrubs, whereas Si concentrations are usually higher in the faster growing graminoids. Both tend to accumulate over the growing season, which might affect plant-herbivore interactions.

1.2 The Svalbard reindeer

Svalbard reindeer (*Rangifer tarandus platyrhynchus*) is an endemic subspecies of reindeer living on the High-Arctic Svalbard archipelago. Big seasonal differences in food availability make the accumulation of fat during the growing season essential for the survival of these animals (Reimers, 1984). In order to do so, more time is allocated to feeding during the short summer (van Oort et al., 2007), when there is a buffet of various plant growth emerging as the snow retreats (Beumer et al., 2017). The foodscape of the Svalbard reindeer is a mosaic of different habitats due to fine-scaled variations in topography and soil moisture (Sjögersten et al., 2006). These habitats are characterised by different compositions of plant species which differ in their nutrient concentrations. The vascular plants on Svalbard are generally small in size and biomass is relatively low, yet leaf quality has been found to be higher in Svalbard than globally (van der Wal and Hessen, 2009). From spring to autumn, the use of vegetation types by the Svalbard reindeer changes (Loe, 1999), and is likely due to mixed effects of accessibility, and selection for high plant biomass (van der Wal et al., 2000). Little research is done on fine-scale forage selection in relation to plant nutrient levels, yet graminoids have been found to constitute the largest proportion of the summer and early winter diet (Bjørkvoll et al., 2009). Summer diets also include forbs, whereas in winter dwarf shrubs and mosses play an important part. Wetland habitats are frequently used in summer, whereas drier windblown ridges are utilised in winter where the snow cover tends to be smaller (Pedersen et al., 2019).

Several trademarks of the Svalbard reindeer make them unique and suitable for studies on resource selection. Firstly, due to a lack of natural predators and harassing insects, “the Svalbard reindeer mainly selects habitats based on seasonal energy and nutrient requirements” (Pedersen et al., 2019). Secondly, they are non-migratory and live in generally small home ranges (Hansen et al., 2009, Tyler and Øritsland, 1989) with high seasonal overlap in winter and summer habitat suitability (Pedersen et al., 2023) Thus, forage selection is done on a small geographical scale. Finally, due to the lack of natural enemies these wild animals are not particularly afraid of people allowing for close-up studies of forage selection at the patch level.

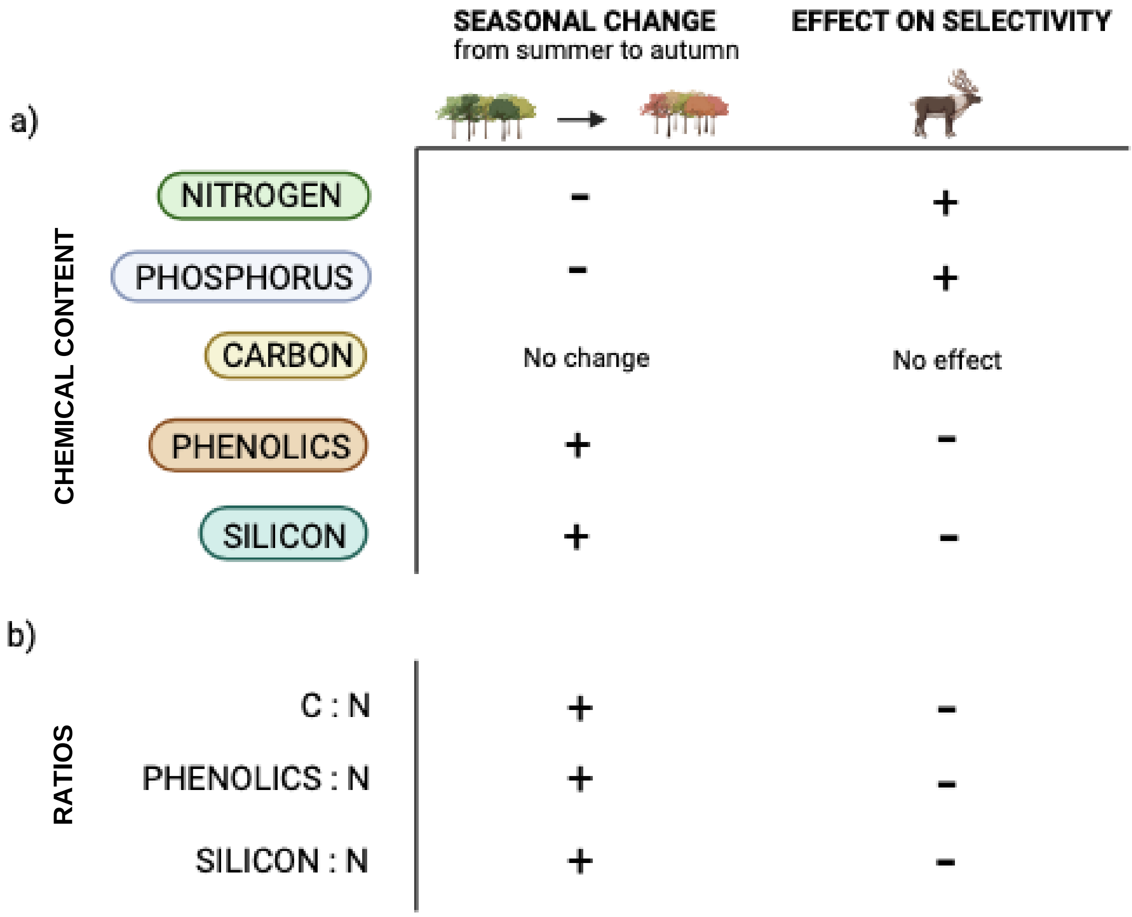
Understanding resource selection in a key herbivore species such as the reindeer on Svalbard can be important for conservation management, especially in High-Arctic environments where temperatures are rising fast (Rantanen et al., 2022). As climate is getting warmer, reindeer foodscapes are changing. Plant cover and aboveground biomass is increasing while, in experimental setups, concentrations of plant nutrients like nitrogen and phosphorus are decreasing (Bon et al., 2023).

1.3 Objectives

Fine-scale studies on forage selection at the patch level might provide complementary and useful information on Arctic vegetation and herbivores to large-scale studies using remote sensing techniques and NDVI-data (see Hansen et al., 2009; Pedersen et al., 2023).
The objectives of this study are to

1) explore grazing selectivity by Svalbard reindeer by describing availability and use of plant species and PFGs on a fine geographical scale
2) investigate how grazing selectivity is affected by seasonal change between summer and autumn in an environment of extreme seasonality
3) probe the effects of plant nutrients (N and P-concentration) and plant herbivore-deterrents (Si and phenolics-concentration) on grazing selectivity in summer versus autumn

With near-infrared reflectance spectroscopy (NIRS) it is possible to measure concentrations in % dry weight (dw) of N, P, Si, phenolics, and carbon (C), all from the exact same leaf (Petit Bon et al., 2020), and hence evaluate if and at what level there is a trade-off in selectivity between plant nutrient content and compounds that deter herbivory. Since different PFGs often vary consistently in their nutrient and defence contents (Cornelissen et al., 2004, Thomas et al., 2019) grazing selection is analysed at both species and growth-form level. The leaves analysed in this study were collected from actual grazing spots and chemical content parameters were measured all from the same leaf. Furthermore, count-data of plant species available and grazed was retrieved from plots where reindeer chose to graze. This allows for a high-resolution, bite-size scale analysis of forage selection and its potential drivers. I would expect reindeer to select nutritious forage plants rich in N and P, and oppositely, avoid plants with high concentrations of the defensive contents phenolics and Si (Figure 1). Since young plant leaves are generally rich in nitrogen and low in phenolics (Jones and Hartley, 1999), I also expect that there might be shifts in forage selection as the growing season progresses.



a)

CHEMICAL CONTENT	SEASONAL CHANGE from summer to autumn	EFFECT ON SELECTIVITY
NITROGEN	-	+
PHOSPHORUS	-	+
CARBON	No change	No effect
PHENOLICS	+	-
SILICON	+	-

b)

RATIOS	SEASONAL CHANGE from summer to autumn	EFFECT ON SELECTIVITY
C : N	+	-
PHENOLICS : N	+	-
SILICON : N	+	-

Figure 1: *Expected trends in a) the seasonal change in concentrations of plant chemical content, and effects of concentration on selectivity, and b) the seasonal change in selected nutrient ratios considered to be of biological importance, and how selectivity associates with these ratios. Carbon is abbreviated to "C", nitrogen is "N". Note that the expected effect on selectivity is not necessarily an outcome of the anticipated seasonal change but should be read as a standalone variable in response to levels of plant chemical contents and ratios. E.g.,I expect the relationship between C:N ratio and forage selectivity to be negatively correlated.*

2 Material and Methods

2.1 Study system

Field work was conducted by foot within a 10 km range from the cabin Tarandus in Reindalen (77°56'N, 15°28'E), on the west coast of Spitsbergen, Svalbard. The study area included the valleys Semmeldalen, Kalvdalen, and Istjørndalen in addition to Reindalen. The vegetation in these valleys is ranging from sparsely vegetated ridges and moraines to heaths and lusher swards, mires, and marshes. The study period lasted a total of 58 days between end of July 2022 (peak plant biomass period, see Van Der Wal and Stien, 2014), and middle of October 2022 (period of peak reindeer fatness, see Tyler, 1987). Average monthly temperatures during the study period decreased from July (8.5°C), through August (5.7°C) and September (2.1°C) to October (-3,1°C), measured at the weather station in Istjørndalen (within the study area, by Norwegian Centre for Climate Services, retrieved from https://seklima.met.no). The first snow fell in the beginning of September. There is little human infrastructure and disturbance in Reindalen and mentioned side valleys. Although the study period overlapped with the hunting season of reindeer (15. August – 20. September) and ptarmigan, no hunters were observed during our time in the field.

2.2 Field observations and grazing plots

The data was collected from actual feeding spots where female GPS-marked Svalbard reindeer (n=23) grazed. Individuals were located by means of GPS-data and telemetry, and repeated observations were carried out on the same 23 animals with an average of 4.5 (median = 3) observations per animal. Closing in on a focal animal, we would walk carefully to not disturb the reindeer, and typically finding a slope or a butte with a good overview to do our observations from. When the animal was grazing without any signs of stress, a "spotter" would zoom in on a grazing spot while looking through a spotting scope (Swarovski with up to 60x magnification). Distance between the spotter and the animal was measured with range-finding binoculars (mean=330m; range 64-610m). The spot fixated had to be grazed for a minimum of 4 seconds (measured by counting to 4), while the reindeer stood still with all 4 legs. A "runner" would then locate the grazing spot as guided by the spotter through walkie-talkie communications. When the exact grazing spot was reached, a flag would be planted at the spot, and the ground carefully searched for newly grazed plants, i.e., plants with fresh bitemarks on them. A 10x10cm square was placed as close to the flag as possible where newly grazed shoots were found. If there were multiple alternatives on where to lay down the square, the spot with the highest number and diversity of grazed plant shoots was selected. A shoot is here defined as any singular above ground / above moss-layer live stem with associated appendages like leaves and flowers. All shoots in the square were counted and identified to species level or, when in doubt, to genus level. Additionally, shoots with green or fresh cuts (i.e., bitemarks) were counted and identified in a similar manner. Plant species were sorted to PFGs according to Table 1. “Graminoids” include sedges, rushes, and grasses. “Forbs” were defined as herbs with soft stems. “Horsetails” included only one fern species. Graminoids growing in wet marshland habitats were assigned to a separate functional group, “marsh graminoids”, due to an observed shift in habitat use during the study period. “Shrubs” were categorised by having a woody stem.

Table 1: *Overview of sortings of plant species and genus to plant functional groups.*

PLANT FUNCTIONAL GROUP	PLANT SPECIES / GENUS
Graminoids	*Alopecurus ovatus* *Calamagrostis spp* *Deschampsia spp* *Festuca rubra richardsonii* *Hierochloe alpina* *Luzula confusa* *Poa alpigena* *Poa alpina* *Poa arctica* *Trisetum spicatum*
Forbs	*Bistorta vivipara* *Cardamine bellidifolia* *Cerastium arcticum* *Cerastium regelii* *Coptidium spitsbergense* *Koenigia islandica* *Oxyria digyna* *Minuartia biflora* *Micranthes hieraciifolia* *Polemonium boreale* *Ranunculus hyperboreus* *Ranunculus pygmaeus* *Stellaria longipes*
Horsetails	*Equisetum arvense*
Marsh graminoids	*Carex spp* *Dupontia fisheri* *Eriophorum scheuchzeri*
Shrubs	*Dryas octopetala* *Salix polaris* *Saxifraga oppositifolia*

Count-data of plant shoots available and grazed were retrieved from a total of 103 grazing plots. The grazing plots and associated leaf sampling were spatially and temporally distributed over three sampling periods, further referred to as seasons labelled “summer”, “shoulder-season”, and “autumn” (Figure 2).

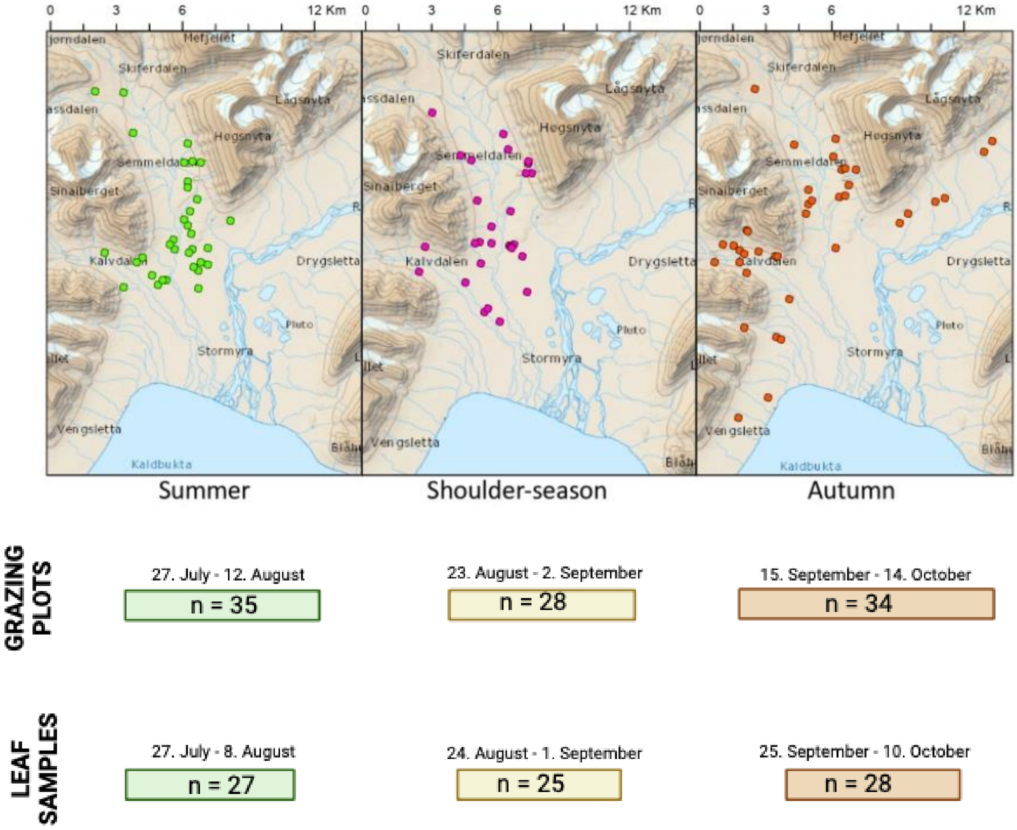


Figure 2: *Map of spatial distribution of grazing plots in the first "summer" sampling period (n=35), the second "shoulder-season" period (n=28), and third "autumn" period (n=40). Leaf samples were collected opportunistically in and (when necessary) around grazing plots in summer (n=27), shoulder-season (n=25), and autumn (n=28).*

2.3 Leaf sampling and NIRS-analysis

Leaf samples from 19 species thought to be important food plants for Svalbard reindeer (see (Bjørkvoll et al., 2009) were collected opportunistically during the three seasons at the same locations as the grazing plots. To get enough plant material, and since the actual foraged leaves were gone with the reindeer, leaves were cut from plant shoots in and around the grazing plot. To capture a species' average spatiotemporal chemical content for a given grazing plot, leaves were cut from approximately 5 shoots and placed together in a tea bag. More cuttings were needed for particularly small species (e.g., *Koenigia islandica*). At the end of the day, samples were pressed between thick, moisture-absorbing paper in a dry spot. After the field period, all samples where oven dried for a minimum of 24 hours at 60 °C and cooled in desiccators with silica gel. Leaves with visible soil or clay stains were rinsed in tap water and oven dried for 48 hours. An overview of species collected is presented in Table 2. A few species were absent from all grazing plots in the shoulder-season and/or autumn and were therefore not collected. *Poa alpigena* was not collected in the first period despite being grazed and was later included due to apparent popularity among reindeer.

Table 2: *A total of 78 samples were collected from 19 plant species in the sampling periods of summer, shoulder-season, and autumn. Plant functional groups are represented by the following amount of species: forbs, n=7; graminoids, n=5; horsetails, n=1; marsh graminoids, n=3; and shrubs, n=3.*

Species	**Summer**	**Shoulder-season**	**Autumn**	**Total**
Alopecurus ovatus	3	2	3	8
Bistorta vivipara	1	1	1	3
Carex subspathacea	2	1	0	3
Cerastium arcticum	1	1	1	3
Coptidium spitsbergense	2	2	0	4
Dryas octopetala	1	1	1	3
Dupontia fisheri	2	2	2	6
Equisetum arvense	2	1	2	5
Eriophorum scheuchzeri	2	1	1	4
Festuca rubra richardsonii	1	2	3	6
Koenigia islandica	1	0	0	1
Luzula confusa	3	1	2	6
Oxyria digyna	1	2	0	3
Poa alpigena	0	1	2	3
Poa arctica	1	2	2	5
Ranunculus sulphureus	1	1	0	2
Salix polaris	2	2	1	5
Saxifraga oppositifolia	1	0	2	3
Stellaria longipes	1	2	2	5

After drying, each sample was analysed with NIRS FieldSpec 3; ASD Inc. in a 350-2500 nm range. Samples of species with particularly small leaves (*Equisetum arvense*, *Koenigia islandica*, and *Saxifraga oppositifolia*) were milled, pressed into tablets, and scanned 3 times. Remaining species were analysed in leaf-form with a 4 mm adapter (according to practice, see Petit Bon et al., 2020). These samples were scanned 25 times each to get measures of the entire surface of all leaves. Results from the NIRS spectra were extracted with open source models using the “pls” and “prospectr” packages in R statistical program (Murguzur et al., 2019). Leaf scans where corrected using correction factors described in Petit Bon et al. (2020). Means were calculated per sample for each measurement of plant chemical content.

2.4 Statistical analysis

All statistical analysis were performed in R statistical program version 4.2.2. Predictions of grazing selectivity according to season and plant chemical content were done with generalized linear models (GLM) and generalized linear mixed-effects models (GLMER) respectively, using the “lme4” package. I used an information theoretic approach for model selection and evaluation of variable importance (Anderson and Burnham, 2002). Since aspects of plant chemical content are often colinear, I first tested the collinearity of all currencies ([N], [P], [C], [Si], and [phenolics]) and the selected ratios considered to be of ecological importance (C:N, Si:N, and phenolics:N) using Pearson’s correlation coefficient. Any variables with $|r| > 0.5$ were considered colinear. Nitrogen is an ecologically important measure of plant nutrition, so I first evaluated which variables were colinear with nitrogen and removed them from the competing model sets. Next, I used Akaike Information Criterion corrected for small sample size (AICc) to select the most parsimonious model among the remaining variables (Anderson and Burnham, 2002). I considered any model within 2.0 ΔAICc of the top model to be a potential alternative, and then selected the best model based on the ecological insight it provided. All competing models contained plant species as a random effect and season as a fixed effect, with proportion of grazed shoots as the response variable. The models were fitted with a logit link function, meaning that the outcome of the model is interpreted as the probability of a shoot being grazed. I then tested all possible combinations (Doherty et al., 2012) of the remaining variables. Predictors were standardized to evaluate the relative effect size. Since season may affect grazing pressure both alone and in interaction with nutritional variables, I tested both additive and interactive effects of season.

3 Results

3.1 Count data from grazing plots

The plant shoot density (availability of shoots per plot) was highest in the summer and decreased throughout the shoulder-season and autumn (Figure 3). In a linear model relating the number of available and grazed shoots through the study period (Figure 3), the estimate of the slope decrease for available shoots over time was -0.21 per day (equivalent to 1 shoot less per five days per $10cm^2$; p=0.02), and the number of grazed shoots per plot had a slight decrease with an estimate of -0.08 per day equivalent to one less per 12 days; p<0.001). Additionally, the greatest variability of species available and grazed occurred in the summer (Table 3). The total count data from all grazing plots in the three study periods show that some species were more available than others (e.g. *Salix polaris*), yet some species were grazed at higher rates (e.g. *Festuca rubra richardsonii*). Graminoids were the most grazed PFG in all three seasons by number of grazed shoots. Forbs and shrubs were highly available in the summer but seemingly less used. Note that the number of field observations varied between seasons (summer=35; shoulder-season=28; autumn=34), thus comparisons of total use and availability should be made within seasons.

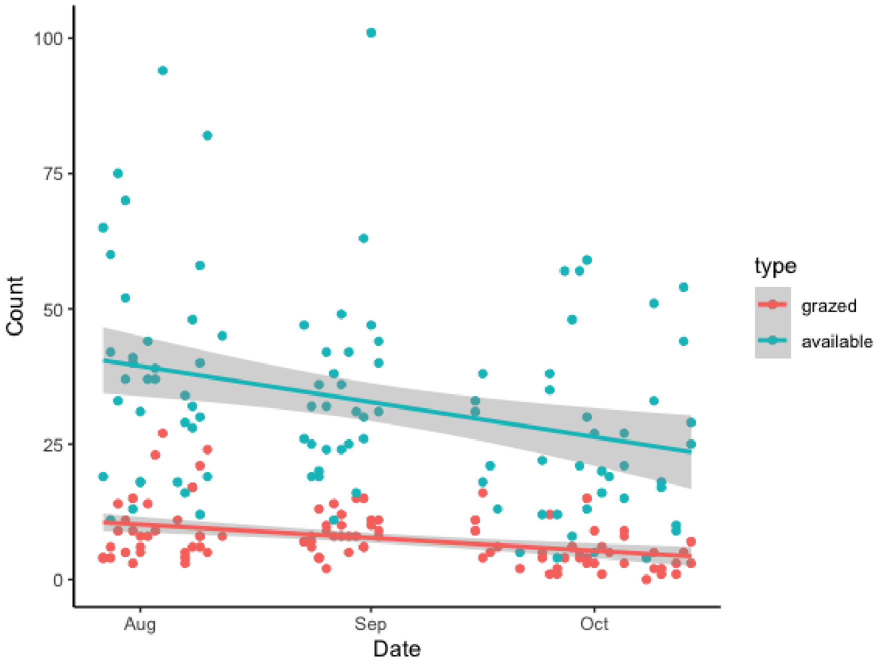


Figure 3: *Number of grazed and available shoots in each plot as a function of time (dots). The lines are estimated slopes from a linear model, with confidence bands in grey. Available shoots decreased over time with an estimate of -0.21 (p=0.02). Number of grazed shoots decreased slightly over time with an estimate of -0.08 (p<0.001).*

***Table 3**: Sum of grazed and available shoots by plant species in the summer, shoulder-season, and autumn. The species are sorted to the following plant functional groups: forbs, graminoids, horsetails, marsh graminoids, and shrubs. Sum of grazed and available shoots by functional group and season is displayed at the bottom of each group.*

SPECIES	**FUNCTIONAL GROUP**	**GRAZED / AVAILABLE**		
		Summer	**Shoulder-season**	**Autumn**
Bistorta vivipara	Forb	2 / 28	0 / 12	0 / 0
Cardamine bellidifolia	Forb	0 / 6	0 / 0	0 / 14
Cerastium arcticum	Forb	6 / 16	0 / 15	0 / 23
Cerastium regelii	Forb	0 / 0	5 / 79	6 / 43
Coptidium spitsbergense	Forb	20 / 65	10 / 42	0 / 0
Koenigia islandica	Forb	1 / 10	0 / 0	0 / 0
Oxyria digyna	Forb	0 / 0	0 / 8	0 / 0
Minuartia biflora	Forb	0 / 30	0 / 0	0 / 0
Micranthes hieraciifolia	Forb	0 / 0	0 / 0	1 / 3
Polemonium boreale	Forb	0 / 0	0 / 0	1 / 2
Ranunculus hyperboreus	Forb	0 / 16	0 / 0	0 / 0
Ranunculus pygmaeus	Forb	2 / 69	0 / 39	0 / 0
Stellaria longipes	Forb	0 / 0	0 / 6	0 / 15
Sum		**31 / 240**	**15 / 193**	**8 / 100**
Alopecurus ovatus	Gramionoid	17 / 41	41 / 92	37 / 100
Calamagrostis spp	Gramionoid	0 / 0	0 / 0	0 / 4
Deschampsia spp	Gramionoid	0 / 0	5 / 34	0 / 0
Festuca rubra richardsonii	Gramionoid	64 / 104	67 / 201	66 / 205
Hierochloe alpina	Gramionoid	21 / 47	0 / 0	0 / 0
Luzula confusa	Gramionoid	14 / 45	9 / 28	0 / 4
Poa alpigena	Gramionoid	11 / 23	11 / 28	30 / 88
Poa alpina	Gramionoid	0 / 0	0 / 0	1 / 3
Poa arctica	Gramionoid	30 / 88	19 / 95	17 / 68
Trisetum spicatum	Gramionoid	7 / 10	0 / 0	0 / 6
Sum		**164 / 365**	**152 / 478**	**151 / 478**
Equisetum arvense	Horsetail	16 / 78	0 / 27	23 / 146
Sum		**16 / 78**	**0 / 27**	**23 / 146**
Carex spp	Marsh graminoid	20 / 40	0 / 0	4 / 27
Dupontia fisheri	Marsh graminoid	32 / 55	59 / 140	0 / 0
Eriophorum scheuchzeri	Marsh graminoid	19 / 54	8 / 19	0 / 0
Sum		**71 / 169**	**67 / 159**	**4 / 27**
Dryas octopetala	Shrub	2 / 15	0 / 0	0 / 0
Salix polaris	Shrub	68 / 517	7 / 114	30 / 226
Saxifraga oppositifolia	Shrub	0 / 0	0 / 0	6 / 101
Sum		**70 / 532**	**7 / 114**	**36 / 327**

3.2 Grazing selectivity between seasons

From GLM-analysis, the grazing selectivity (number of grazed versus ungrazed shoots per plot) was significantly different between plant functional groups ($p<0.001$) and seasons (Table 4). Graminoids that were growing in drier habitats (not in marshes) were overall selected for with a relatively high probability of being grazed in all three seasons, but with the highest grazing pressure in summer. Graminoids growing in marsh habitats were treated as an individual functional group, and these were grazed significantly less in autumn compared to the summer and shoulder-season (Figure 4). Both horsetails and shrubs decreased in preference from summer into the shoulder season, but then increased again in autumn. A high proportion of the horsetails (*Equisetum arvense*) grazed in the third season came from gravel patches where the reindeer were digging and grazing on roots from this species, as well as roots from *Salix polaris*.

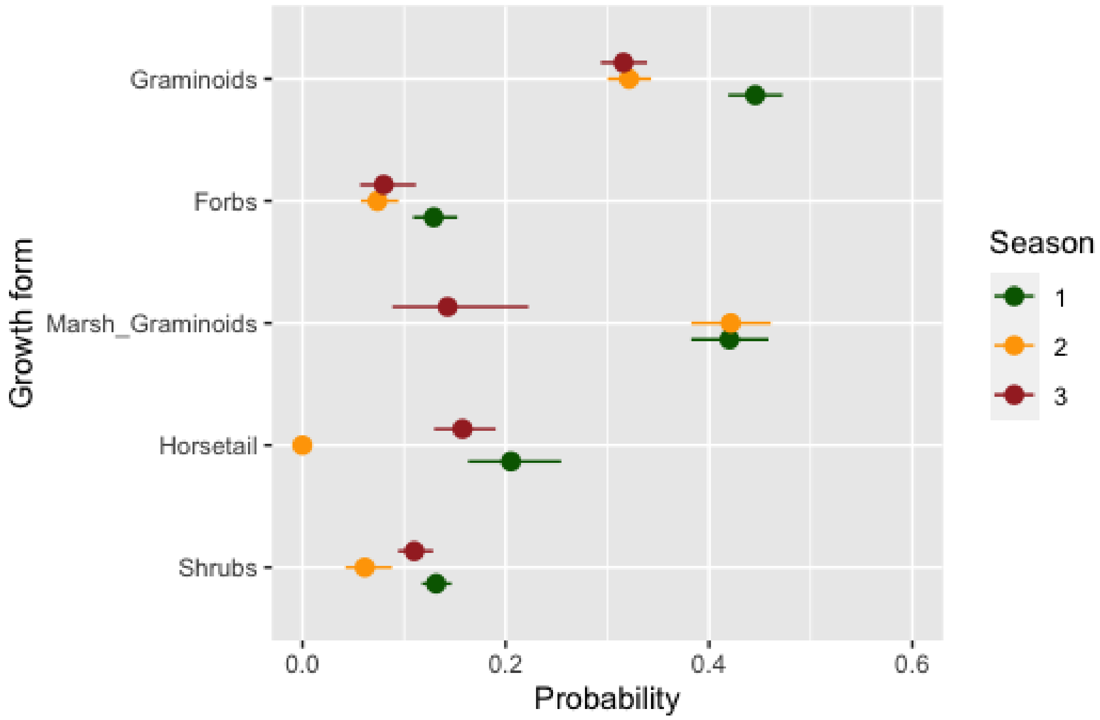


Figure 4: *Estimates (dotted) and standard error (lines), from a generalized linear model describing grazing selectivity (number of grazed versus number of ungrazed shoots per plot) as a function of plant functional group and season and their interaction. The estimates and standard error are transformed to probabilities from logit scale. Season 1 = summer (27. July – 12. August), season 2 = shoulder-season (23. August – 2. September), and season 3 = autumn (15. September – 14. October).*

Table 4: *A generalized linear model describing grazing selectivity (number of grazed versus number of ungrazed shoots per plot) as a function of plant group and season and their interaction. The plant groups are graminoids, forbs, marsh graminoids, horsetails and shrubs. The seasons are summer (27. July – 12. August), shoulder-season (23. August – 2. September), and autumn (15. September – 14. October). The p-values represent a global test for the variables where the interaction effects resemble a seasonal change in grazing preference of plant functional groups.*

	df	**Deviance**	**Resid. df**	**Resid. dev.**	***p***
Null			309	919.0	
Plant group	4	301.8	305	617.3	<0.001
Season	2	24.1	303	593.1	<0.001
Plant group x Season	8	22.6	295	570.6	0.004

To shed light on which species drive the patterns of the functional group, results are also shown at the species level. Some specific plant species were frequently grazed by reindeer in all three seasons, including the graminoids *Alopecurus ovatus*, *Festuca rubrua richardsonii*, *Poa arctica*, and the shrub *Salix polaris.* Figure 5 displays the raw data points of grazed shoots as a function of available shoots. The slope steepness refers to the ratio of grazed shoots based on availability, and there is a clear difference between some species. *Festuca rubra richardsonii* was grazed at a higher proportion per plot in all seasons compared to *Salix polaris* which was high in availability but lower in number of grazed shoots. An observed shift in selection occurred between shoulder-season and autumn. Some graminoids that grow in wet marshland habitats (*Dupontia fisheri* and *Eriophorum scheuchzeri*) were frequently grazed in the summer and shoulder-season, and not at all in the autumn. A similar pattern was found for the marshland forb *Coptidium spitsbergense*. Many species were only occasionally grazed and some only in one season.

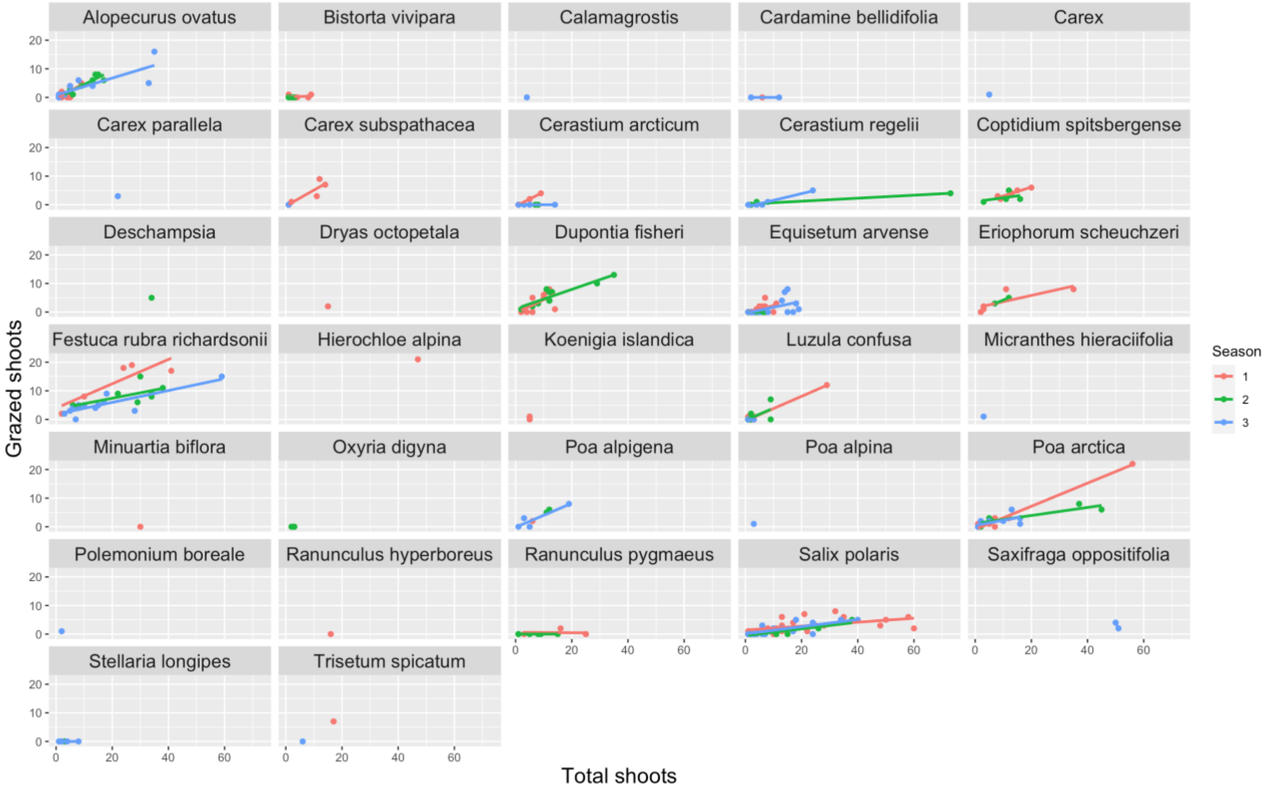


Figure 5: *Scatter plots showing all datapoints from the grazing plots, separated by species or genus (Calamagrostis, Carex, and Deschampsia), and color-coded by season. Season 1 (orange) represents datapoints in summer, season 2 (green) is the shoulder-season, and season 3 (blue) shows the autumn. The x-axis refers to the count of available shoots, and the y-axis represents grazed shoots. Lines are drawn with a linear model where there was enough datapoints. Flat lines indicate little to no grazing, even if the specie was available. Oppositely, steep lines indicate high rates of grazing.*

3.3 Predicting grazing selectivity from plant chemical currencies

All PFGs contained higher N concentrations in summer and shoulder-season than in autumn (Figure 6a). Forbs, marsh graminoids and shrubs contained significantly higher P-concentrations in summer versus autumn (Figure 6b). In summer, forbs contained the highest concentrations of N and P of all tested PFGs, yet outliers indicate variability among samples (Figure 6a; 6b).

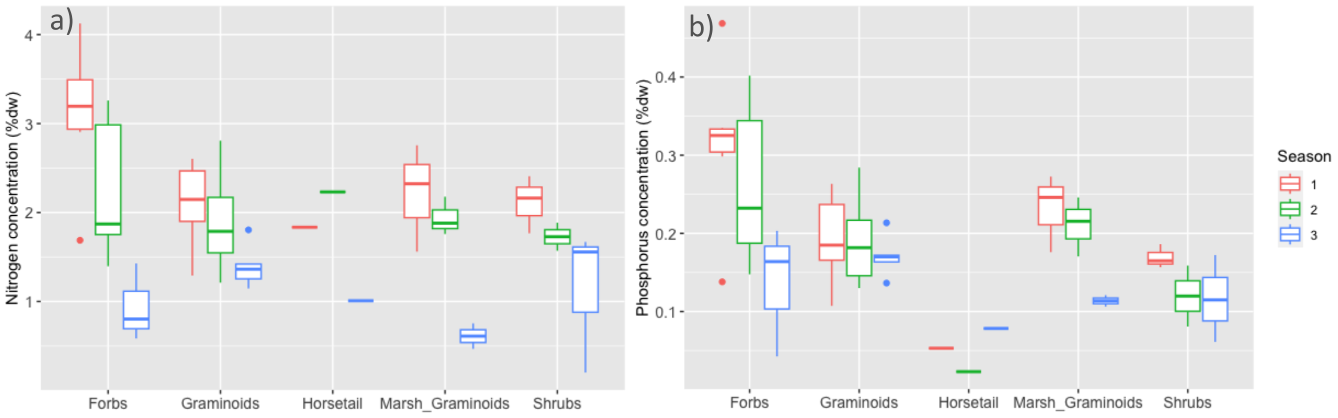


__Figure 6:__ Measured concentrations of the plant nutrients a) nitrogen, and b) phosphorus. Season 1 (orange) is summer (27. July – 8. August), season 2 (green) is shoulder-season (24. August – 1. September), and season 3 (blue) is autumn (25. September – 10. October). The medians are displayed as thick horizontal lines, and the boxes represent the interquartile range (25-75% of the data).

Si concentrations increased from summer to autumn among forbs, graminoids, and marsh-graminoids (Figure 7a). The big variability among seasons in horsetail Si concentrations might be due to small sample size (n=1). Shrubs had a higher concentration of phenolics in all seasons compared to graminoids, horsetails, and marsh-graminoids (Figure 7b), and the overall tendency seems to be a decrease of phenolics concentration from shoulder-season to autumn.

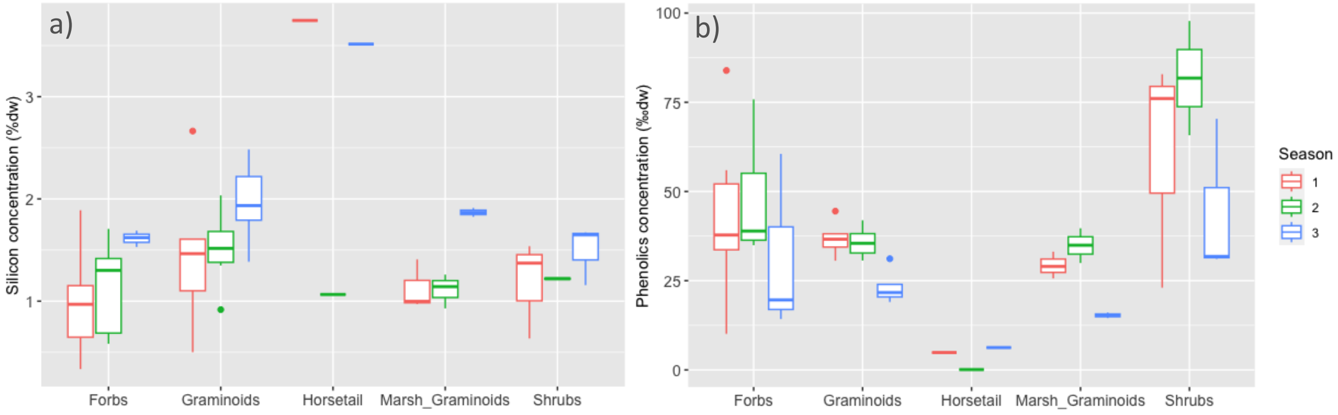
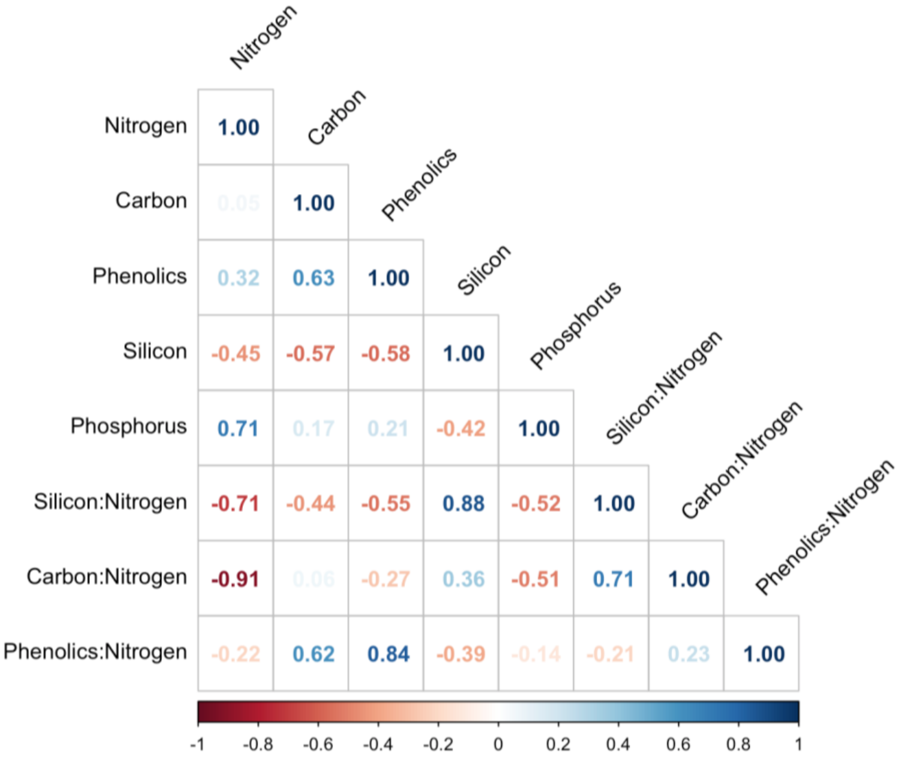


__Figure 7:__ Measured concentrations of plant herbivore-deterrents a) silicon, and b) phenolics. Season 1 (orange) is summer (27. July – 8. August), season 2 (green) is shoulder-season (24. August – 1. September), and season 3 (blue) is autumn (25. September – 10. October). The medians are displayed as thick horizontal lines, the boxes represent the interquartile range (25-75% of the data).

In preliminary testing, no significant effects of N or P concentration on grazing selectivity were found using general linear mixed effects models. Explorative figures of these relationships and average N concentration by plant species are displayed in the Appendix (Figures 11;12;13;14). Further model selection to predict grazing selectivity included combinations of the variables [N], [C], [Si], [phenolics], and phenolics to nitrogen ratio, all of which had a correlation coefficient less than |0.5| (Figure 8).



	Nitrogen	Carbon	Phenolics	Silicon	Phosphorus	Silicon:Nitrogen	Carbon:Nitrogen	Phenolics:Nitrogen
Nitrogen	1.00							
Carbon	0.05	1.00						
Phenolics	0.32	0.63	1.00					
Silicon	-0.45	-0.57	-0.58	1.00				
Phosphorus	0.71	0.17	0.21	-0.42	1.00			
Silicon:Nitrogen	-0.71	-0.44	-0.55	0.88	-0.52	1.00		
Carbon:Nitrogen	-0.91	0.06	-0.27	0.36	-0.51	0.71	1.00	
Phenolics:Nitrogen	-0.22	0.62	0.84	-0.39	-0.14	-0.21	0.23	1.00

Figure 8: *Correlation matrix of all measured plant chemical contents and the ratios considered to be of ecological importance. In pairs with correlations higher than |0.5| one variable was left out in the subsequent model selection.*

The most parsimonious generalized linear mixed effects model for grazing selectivity contained the additive effects of Si content and season, with plant species as a random effect. Surprisingly, reindeer preferred species with higher Si concentrations. The seasonal effect constituted of a reduced probability of a shoot being newly grazed as the season progressed. I opted for presenting the second-most parsimonious model for grazing preference because it was highly competing (ΔAICc only 0.5 higher) and considered to have additional ecological insight. In addition to the effects in the very best model, this model also included the phenolics to nitrogen ratio with season as an interactive variable. In this model, grazing preference was still positively correlated with Si concentration in the plants (Table 5; Figure 9). The phenolics to nitrogen ratio affected grazing preference negatively in the last two seasons but did not affect grazing in the earliest season (Table 5; Figure 10). However, when testing the additive effects of only phenolics and season (with plant species as a random effect) grazing selectivity correlated negatively with phenolics (p=0.04; Figure 15 in Appendix). Models with plant functional group as a random effect returned overall similar results as models with species as the random effect.

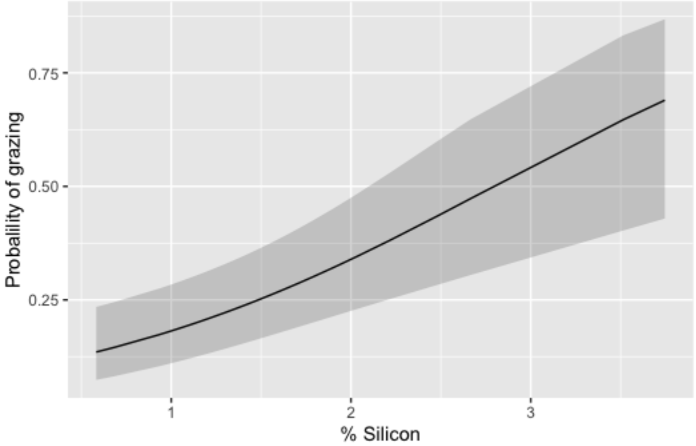


Figure 9: *Grazing selectivity (probability (0-1) of number of grazed vs ungrazed shoots per plot) as a function of plant silicon concentration (in %dw) with season as a covariate. Plant species was included in the model as a random effect. p<0.001.*

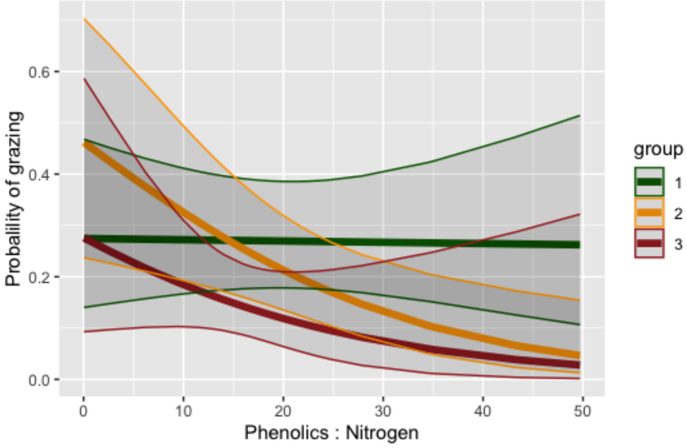


Figure 10: *Grazing selectivity (probability (0-1) of number of grazed vs ungrazed shoots per plot) as a function of plant phenolics to nitrogen ratio in interaction with season (group 1 = summer, p<0.1; group 2 = shoulder-season, p=0.009; and group 3 = autumn, p=0.1). Plant species was included in the model as a random effect.*

Table 5: *Fixed effects from the second-most parsimonious generalized mixed effects model for grazing selectivity (number of grazed versus number of ungrazed shoots of each species per plot) as a function of nutritional and defence components of plants grazed by female Svalbard reindeer. Plant species was included as a random intercept (SD=1.02). The reference season is summer (27. July – 12. August). Shoulder-season is defined as 23. August – 2. September, and autumn as 15. September – 14. October.*

	Estimate	**SE**	**Z-value**	***p***
Intercept	-2.3	0.6	-3.7	<0.001
Silicon	0.8	0.2	3.8	<0.001
Phenolics:Nitrogen	-0.001	0.02	-0.08	0.1
Shoulder-season vs Summer	0.8	0.5	1.7	0.09
Autumn vs Summer	0.008	0.5	0.02	0.1
Phenolics:Nitrogen / Shoulder-season	-0.06	0.02	-2.6	0.009
Phenolics:Nitrogen / Autumn	-0.05	0.03	-1.6	0.1

No alternative model within 2.0 ΔAICc of the top model contained C concentration as a factor, see Appendix for explorative figure of grazing selectivity predicted by [C] (Figure 16).

4 Discussion

Grazing selection is an important process for Arctic herbivores which have a very short time window for positive energy assimilation. In my study I have found that Svalbard reindeer display seasonal variation in grazing selectivity of PFGs consisting of certain key forage species. Marshland graminoids (*Carex spp, Dupontia fisheri,* and *Eriophorum scheuzheri*) and the forb *Coptidium spitsbergense* were frequently grazed in summer and significantly less in autumn. Several species of graminoids, forbs and shrubs were only occasionally observed grazed, and occurred seldom in the grazing plot. This might be due to low availability, or that the animals foraged in habitats that did not hold these plants. Some species were frequently grazed in all three seasons (*Festuca rubra richardsonii* and *Salix polaris)* but were grazed at different intensities. *Salix polaris* was highly available but less selected than *Festuca rubra richardsonii.*

Using NIRS analysis I detected a positive association between grazing selectivity and Si concentration, possibly because preferred graminoid species were also relatively rich in Si. Although Si is referred to as an anti-herbivore defence (Soininen et al., 2013, Vicari and Bazely, 1993), there might be a certain threshold of tolerance by herbivores to Si concentration. The plant species I measured were not particularly high in Si concentration compared to findings in northern Norway where concentrations reached up to 10%dw (Smis et al., 2014). Svalbard reindeer further switched from a neutral preference of a phenolics-to-nitrogen ratio to a negative one. The strongest effect was found in the shoulder-season when concentrations of phenolics were at their highest. In explorative testing, phenolics alone had a significant negative effect on grazing selectivity according to expectations. Due to complex variation in the functional properties of Si and phenolics and their variable effectiveness as antiherbivore defences, more research is needed to determine the impact on grazing selectivity in Arctic ecosystems.

Concentrations of plant N and P followed an expected decline in concentration from summer to autumn but no effect of plant nutrient concentrations were found on grazing selectivity, concurrent with previous studies on Svalbard reindeer (van der Wal et al., 2000). However, my study is limited by the lack of resource quantity measures. I found that forbs had the highest concentration of N among all PFGs in summer, yet selection of forbs by reindeer was low. A possible explanation might be that forbs can be generally small in size (e.g. *Koenigia islandica* and *Ranunculus pygmaeus*) resulting in lower resource quantity than a larger graminoid with slightly lower N concentration. It is likely that optimal forage selection is multifaceted and that a broader approach including both N concentration and N pool would give more insight.

In this study, I have had an explorative approach to the effects of plant nutrient and defence on grazing selectivity. There are multiple ways of assessing plant quality, and the chemical content described in this study is a brief representation of a larger ecological picture. The study design has favoured a high resolution in terms of forage selectivity on the patch level where the animals are grazing, which has resulted in a detailed description of plant species used by Svalbard reindeer in a critical period of energy assimilation. Faced with rapid warming affecting plant cover and nutrient concentrations (Bon et al., 2023) in addition to more unpredictable and harsher winter conditions (Hansen et al., 2014) further research on how climate change will affect specific key forage species can be essential to our understanding of the Svalbard reindeer.

5 Conclusion

Svalbard reindeer exhibit grazing selectivity of specific plant functional groups consisting of certain key forage species, and forage selection changed throughout the study period from end of July to mid-October. Grazing selectivity related positively to silicon concentrations, and negatively to a phenolic-to-nitrogen ratio when the phenolics were at peak concentration levels. Determining selection based on plant chemical content is a complex matter with multiple explanatory variables that has baffled the author and needs further research.

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Appendix

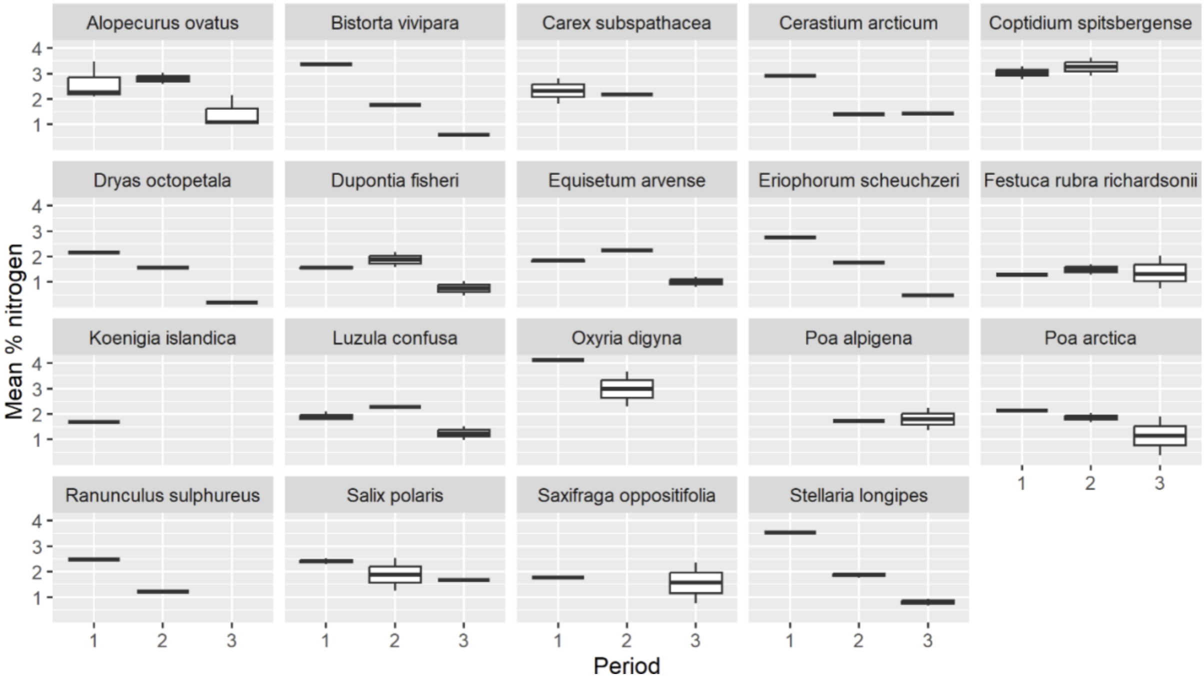

Figure 11: *Mean nitrogen %dw per species in period 1 (summer), 2 (shoulder-season), and 3 (autumn).*

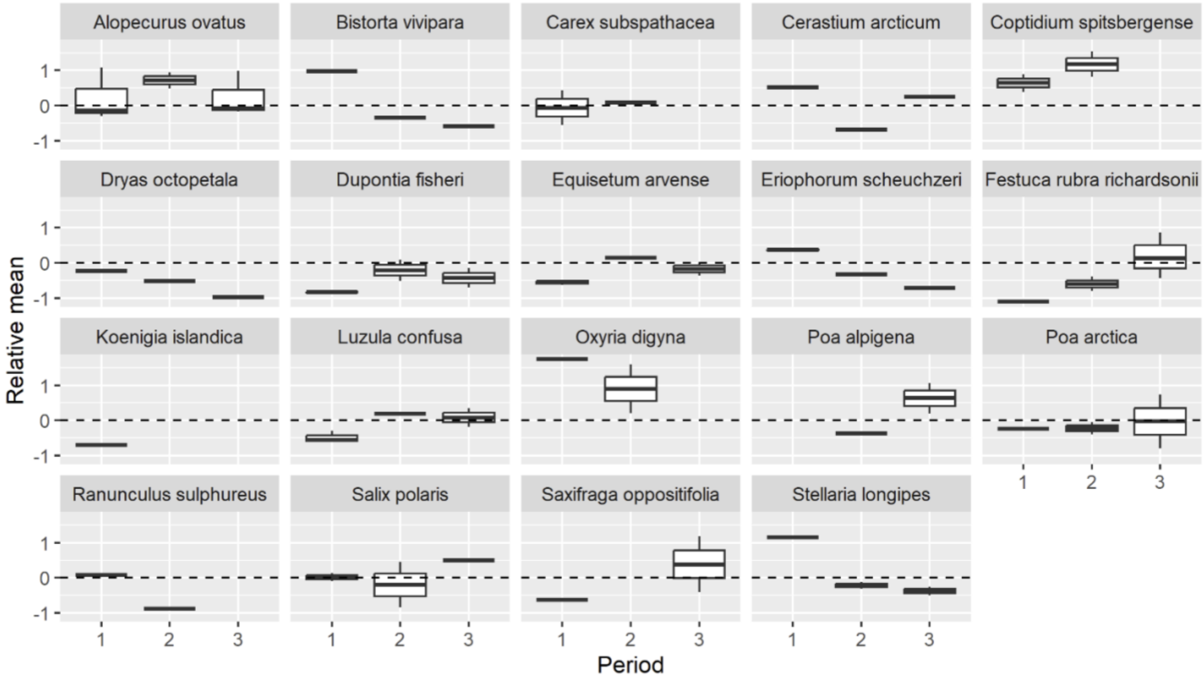

Figure 12: *Relative mean of nitrogen %dw per species to mean nitrogen %dw of all plants sampled in that period. Period 1=summer, 2=shoulder-season, and 3=autumn.*

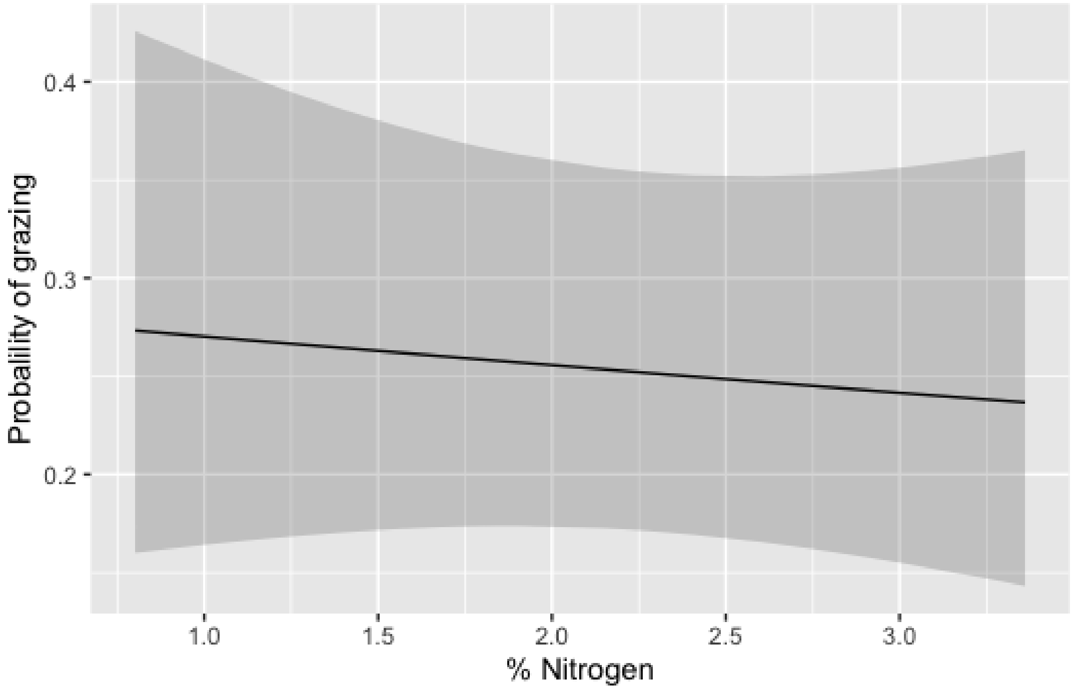

Figure 13: *Grazing selectivity (probability (0-1) of number of grazed vs ungrazed shoots per plot) as a function of plant nitrogen concentration (in %dw) with season as a covariate, p=0.66. Plant species was included in the model as a random effect.*

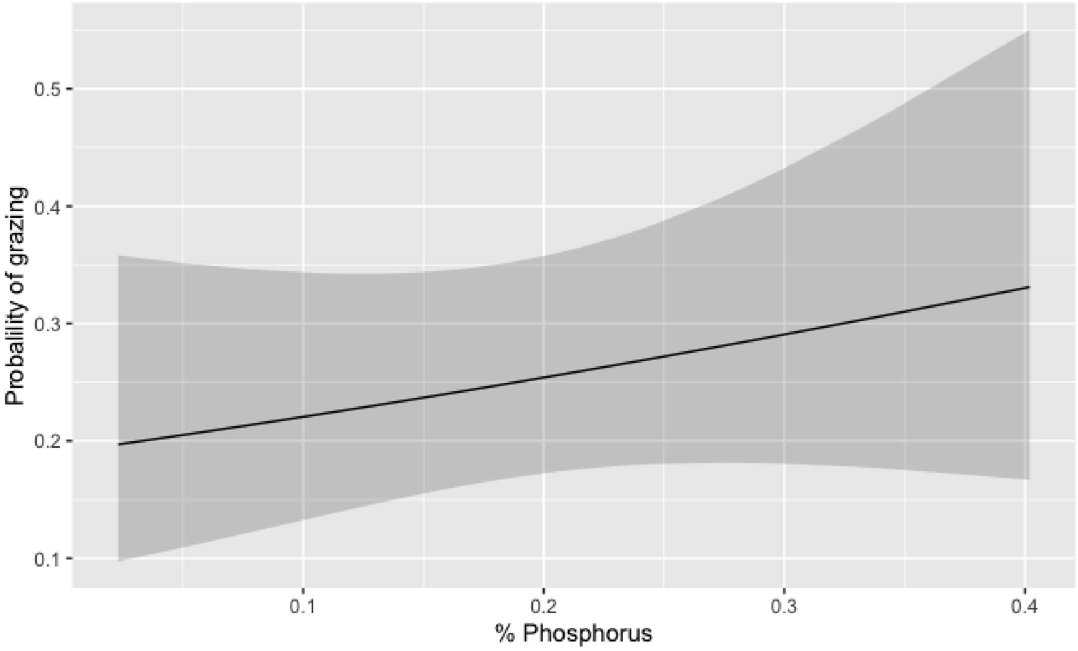

Figure 14: *Grazing selectivity (probability (0-1) of number of grazed vs ungrazed shoots per plot) as a function of plant phosphorus concentration (in %dw) with season as a covariate, p=0.33. Plant species was included in the model as a random effect.*

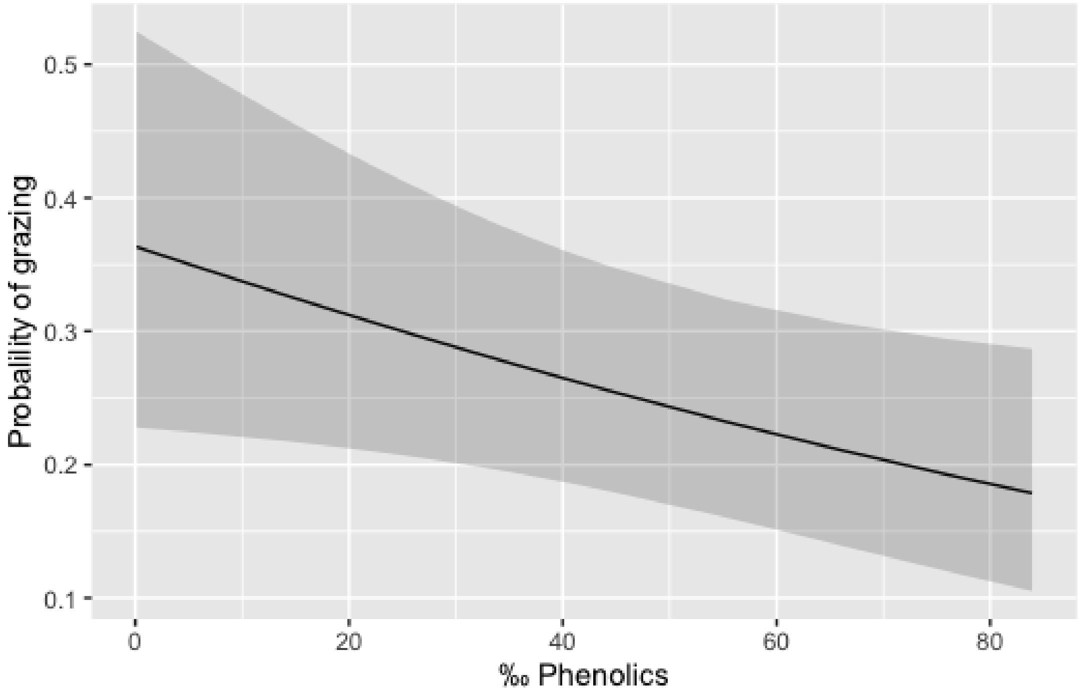

Figure 15: *Grazing selectivity (probability (0-1) of number of grazed vs ungrazed shoots per plot) as a function of plant phenolics concentration (in %dw) with season as a covariate, p=0.04. Plant species was included in the model as a random effect.*

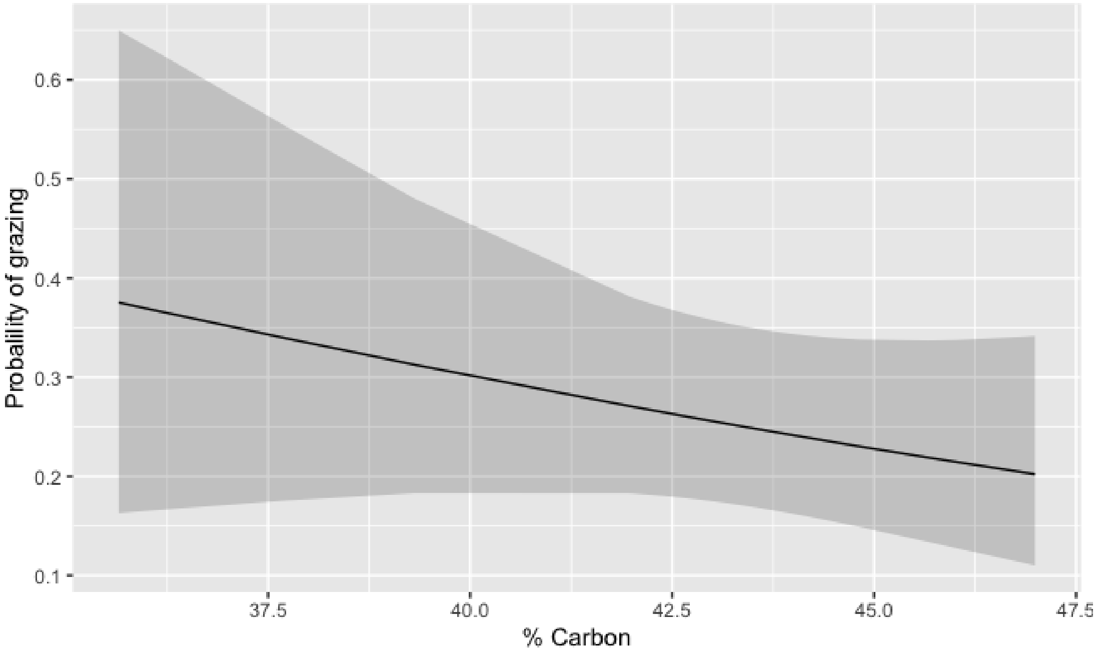

Figure 16: *Grazing selectivity (probability (0-1) of number of grazed vs ungrazed shoots per plot) as a function of plant phenolics concentration (in %dw) with season as a covariate, p=0.27. Plant species was included in the model as a random effect.*