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Greater biomass from Arctic greening absorbs increased grazing pressure from a large herbivore

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Abstract

Arctic warming is causing widespread “greening” of tundra ecosystems. What this means for plant–herbivore relations, including the grazing pressure herbivores exert on increasingly productive tundra ecosystems, is poorly understood. Svalbard is one of the fastest warming places on Earth, with concomitant increases in both forage biomass and reindeer numbers. In 11 years between 1998 and 2023, we measured grass biomass and the proportion of shoots grazed in mesic grass-dominated tundra to evaluate whether increased forage biomass of grass absorbed the grazing pressure of more reindeer. Also, we used GPS data from adult female reindeer (2009–2023) to identify if grazing pressure was relieved by spillover into other habitats. During the study period, reindeer abundance, estimated by annual capture-mark-recapture, tripled, while grass biomass only doubled. Grazing pressure increased from 4% to 8%, which was lower than expected from the increased reindeer density. This discrepancy was not caused by spillover into other habitats, but rather by increased grazing in higher-biomass patches that have emerged with summer warming. Our findings support the notion that increased summer forage has contributed to Svalbard reindeer population growth, notably by making available higher biomass grass swards that allow for greater food offtake.

Key words: forage offtake, functional response, habitat use, population growth, *Rangifer tarandus platyrhynchus*, Svalbard reindeer

Introduction

“Arctic greening” is a widespread response to climate change, affecting ecological processes across tundra ecosystems (Berner et al. 2020). Warmer summer temperatures and lengthened growing seasons are among the most important drivers of increases in primary production (Post et al. 2009; Myers-Smith et al. 2020). Increased primary production can, in turn, raise the nutritional plane for large herbivores, prompting population growth through improved body condition and associated higher reproduction and survival (Parker et al. 2009). In “bottom-up” regulated systems, more food ought to result in more herbivores, because they are not regulated by “top-down” factors, such as predators (Gotelli 2008), but environmental factors, such as winter conditions, may still be limiting (LaSharr et al. 2023). However, the ways in which Arctic greening and the responsive consumers alter grazing pressure across a landscape is not straightforward, because plant–herbivore interactions are shaped by mechanisms at multiple scales, such as foraging among habitats (habitat scale) and within a habitat (patch scale; Senft et al. 1987; Shipley 2007). Thus, to better understand landscape-level impacts of plant–herbivore interactions under Arctic greening, one must carefully consider the scales of use that influence grazing.

At the habitat scale, free-roaming animals can move among habitats in response to animal density—to avoid competition and meet energetic and nutritional needs to promote net-positive fitness consequences (in accordance with the ideal free distribution theory; Fretwell 1969; Morris 1987). Density-dependent processes of the consumer can thus diminish selection of typically productive and preferred habitats, while increasing selection of others (Ramp and Coulson 2002; Mobæk et al. 2009). Such “spillover” in habitat use in response to animal density could mask trends in increased grazing pressure across the landscape if other alternative habitats are used, but the possibility of habitat use spillover has not been investigated. Within-habitats, at the patch scale, foraging that is dependent on plant biomass typically results in functional responses where consumption rates increase with food density (Spalinger and Hobbs 1992), until leveling off at a point of food saturation where consumption rate no longer increases because food is unlimited (typical of hyperbolic

Type II or sigmoidal Type III functional responses; Holling 1959). Functional responses can serve as a good framework for evaluating grazing pressure within natural gradients of available food because the accumulation of individual intake rates should translate into greater consumption in patches with relatively high food biomass that leaves little or no need to forage in relatively low-biomass patches (Rowcliffe et al. 1999; Kalinkat et al. 2023). It is possible that Arctic greening from warming provides a wider gradient of biomass patches, resulting in even greater consumption of food in patches of higher biomass. However, there remains little information of these dynamics of herbivory from areas, such as the High Arctic, where effects of climate change are most drastic (Soininen et al. 2021).

Of tundra ecosystems, the Northern Barents region is one of the fastest warming places globally (Isaksen et al. 2022). Over the last four decades warmer summers have been associated with a marked increase in remote-sensed greening (NDVI) in Svalbard, a part of this Barents region (Vickers et al. 2016; Karlsen et al. 2024), providing higher forage production for its only large herbivore, the Svalbard reindeer (*Rangifer tarandus platyrhynchus*, Grinnell, 1908; Van der Wal and Stien 2014; Karlsen et al. 2018). Grasses are an important summer dietary item for Svalbard reindeer (Bjørkvoll et al. 2009), and typically respond more strongly to temperature increases and fertilization than other plant growth forms (Arft et al. 1999; Dormann and Woodin 2002), with greater grass abundance mediated through warmer soils from moss removal (Van der Wal and Brooker 2004). Additionally, with climate warming, reindeer diets have shifted toward greater use of grasses in winter (Hiltunen et al. 2022). At the same time, there has been a marked population increase of Svalbard reindeer (Le Moullec et al. 2019), with populations in Nordenskiöld Land more than doubling in abundance in just over two decades (Hansen et al. 2019a; Loe et al. 2021). This increase is driven by “bottom-up” processes (Albon et al. 2017; Loe et al. 2021), because typical “top-down” effects, such as predation (Derocher et al. 2000), human harvesting (Peeters et al. 2022), and insect harassment (Williamsen et al. 2019), are negligible. Higher grazing pressure naturally results from more herbivores, but the ensuing impacts of increased herbivory, trampling, and fertilization (from urine and feces) on plant communities and ecosystem function (McNaughton et al. 1997; Olofsson et al. 2004; Van der Wal and Brooker 2004) can vary widely across the Arctic and is dependent on local conditions (Bernes et al. 2015; Ravolainen et al. 2020). Therefore, there is an ongoing need to empirically investigate shifts in herbivory at local scales throughout different Arctic regions (especially in the High Arctic; Soininen et al. 2021) to better forecast if increased grazing can approach levels that prompt landscape-level shifts in vegetation.

We aimed to evaluate how the influence of a warming Arctic on grass biomass affects grazing pressure under increasing densities of Svalbard reindeer. We used longitudinal data on summer temperatures, grass biomass, reindeer abundance, and grazing pressure collected between 1998 and 2023. Since spillover to other habitats can ameliorate grazing pressure in preferred grass-dominated habitats, we used location data from GPS-collared Svalbard reindeer to evaluate if habitat use has shifted since 2009. Considering the almost continually warmer summer temperatures contributing to an increasing trend in available grass biomass (Van der Wal and Stien 2014) and the continued increase in reindeer abundance beyond what was previously documented (reindeer population trends up to 2019; Loe et al. 2021), we expected one of two competing outcomes. Herein, we hypothesized that the increase in animal abundance under current conditions would result in an additive effect on grazing pressure, elevating grass consumption across the gradient of all available biomass (H_1; Fig. 1). Alternatively, it is possible grazing pressures remained similar where biomass overlapped historic levels (1998–2010) of available forage, but extended to relatively higher levels of consumption in the most productive patches reflecting the current (2021–2023) wider gradient of biomass available (H_2; i.e., the shape of the functional response remained the same but extended to include higher grass biomass values attracting higher use). Since tundra ecosystems are typically of low biomass, we expected that no scenario would result in food consumption reaching a point of saturation and thus would not expect to see an asymptote characteristic of a functional response at high biomass values as seen in other grassland ecosystems.

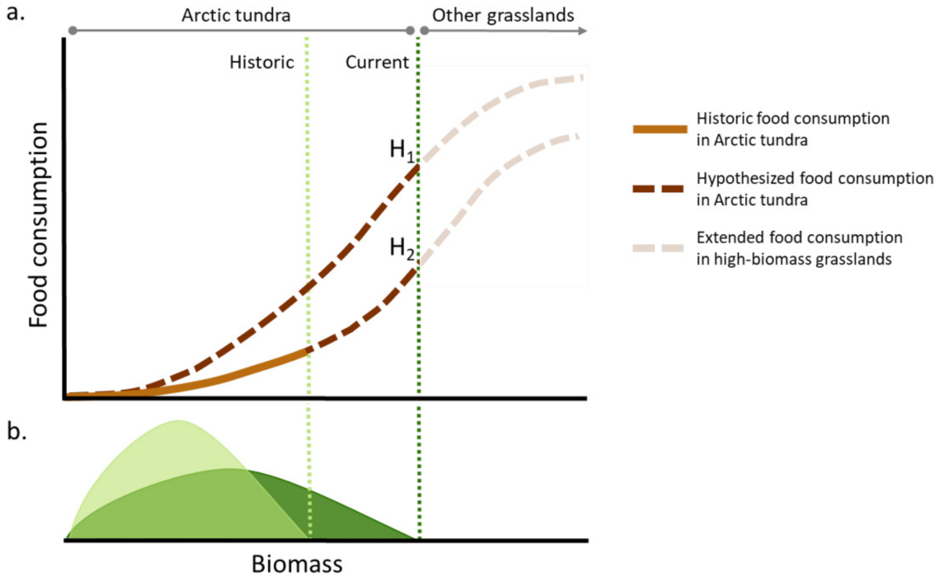
Materials and methods

Study area

We conducted the study in Nordenskiöld Land, Svalbard, within three main valleys, Semmeldalen, Reindalen, and Colesdalen (78°N, 15°E; 182 km^2). Most vegetation occurs below 250 m and is composed of moss carpets of different depths in which vascular plants grow interspersed (Ravolainen et al. 2020). During summer, Svalbard reindeer feed primarily on vascular plants (Bjørkvoll et al. 2009); therefore, classification of habitats used by them is based on vascular plants, rather than on bryophytes. *Luzula* heath (dominant species including *Salix polaris* and *Luzula confusa*) and wet moss (including *Equisetum arvense* and *Alopecuris borealis*) are the most abundant types (collectively over 60% landcover). Grass sward, a mesic grass-dominated habitat, is less abundant (ca. 6% landcover) but important to reindeer during summer when mixed swards, including *Poa* sp., *Festuca rubra* subsp. *richardsonii*, and *A. borealis*, form high-quality forage. Other notable reindeer habitats are marsh (including *Dupontia fisheri*, *Eriophorum scheuchzeri*, and *Carex subspatacaea*) and ridge (including *S. polaris* and *Dryas octopetala*), with <10% landcover.

Winters are cold (mean January temperature -9.4 ± 0.3 °C, 1998–2023; Svalbard airport weather station) and summers are relatively cool (mean July temperature: 7.5 ± 0.1 °C, 1998–2023). Since 1981, rapid warming of up to 1.6 °C per decade has occurred across seasons in Svalbard (Isaksen et al. 2022). Although consistent snow cover usually spans October–June, spring melt-out is increasingly advanced due to trending temperature increases (Karlsen et al. 2014). Advanced spring melt-out can affect the duration of forage available for reindeer during the short growing season that is initi-

Fig. 1. Competing predictions in comparing historic (solid orange line) and current (dashed brown line) trends in consumption of food (e.g., offtake of grass) in response to increased biomass from historic (light green polygon) to current (dark green polygon) distributions, with an assumed increase animal abundance under current conditions (*a*), and respective maximum gradient ranges (light green and dark green vertical dotted lines) in observed available biomass in an Arctic tundra system (*b*). H_1 predicts that the assumed increase in animal abundance would result in an elevated consumption of food relative to historic consumption, due to an additive effect of more animals. Alternatively, H_2 predicts sufficient biomass to feed more animals, resulting in greater food consumption along a wider gradient of available biomass, without an additive of animal abundance on food consumption at biomass values at the historically shorter gradient of available biomass. Due to the overall low biomass of Arctic systems, neither outcome should reach the asymptote of a functional response (e.g., a Type III functional response here for illustrative purposes) that could be expected in other high-biomass grassland systems (light-brown dashed extension of the functional response to the right of the dark green vertical dotted line marking the extent of potentially available biomass in a future Arctic system).



ated following snow melt until peak biomass in late July/early August (Van der Wal and Stien 2014).

Summer weather data

We obtained daily July temperatures from the aforementioned automated weather station 20 km from our study area (Svalbard Airport, station number SN99840), via the Norwegian Centre for Climate Services (https://seklima.met.no/). From these weather-station data, we calculated mean temperatures in July to assess the influence of July temperature on available biomass across time.

Measurements of grass biomass and grazing pressure

In September 1997, we established 13 plots (5 m × 5 m) in grass sward habitats in Semmeldalen to monitor grazing pressure on grasses (Van der Wal et al. 2000). We focused on grass swards due to their known selection by Svalbard reindeer in summer (Van der Wal et al. 2000). Plots were randomly selected among separate patches of varying shoot density of grasses and were >20 m apart from each other. In 2021 an additional 15 plots were established in grass sward habitat near the original plots to increase sample size and allow assessment of potential preferential shifts in grazing into neighboring grass sward patches that may have occurred since 1998 in the originally established plots. Although we could not assess conditions of the newly established plots prior to 2021, there were no significant differences between the originally and newly established plots in biomass ($F_{1,69} = 0.04$; $p = 0.85$) or grazing ($F_{1,69} = 2.53$; $p = 0.12$) when compared during 2021–2023. In late July and August (median date of measurement: August 4; range: July 29–August 24), we measured density of shoots and number of shoots grazed (only measuring true grasses and, thus, excluding rushes and sedges). Within each 5 m × 5 m plot, we sampled shoot density by randomly selecting 15 subplots of 10 cm × 10 cm where we counted the number of grass shoots and the number of shoots grazed. Subplots were selected by tossing a 10 cm × 10 cm frame and counting the number of grazed and ungrazed grass shoots where it landed; thus, locations of subplots varied during each sampling period. To estimate the available grass biomass of a plot, we determined average shoot mass by collecting 25 randomly selected, ungrazed, grass shoots from within each 5 m × 5 m plot at each time of measurement. We dried shoot samples at 60 °C and placed them in a desiccator for a minimum of 48 h before weighing them to the nearest mg to get the average mass per shoot. Mean shoot mass was then multiplied by shoot density and then multiplied by 100 (since measurements were taken at the 10 cm × 10 cm subplot) to estimate grass biomass within each plot (g/m^2; biomass = shoot count × mean shoot mass × 100). Plots were monitored annually in 1998–2005 (except in 2003), 2010, and 2021–2023, for a total of 170 plot-level observations of grass biomass and grazing. We considered measurements taken between 1998 and 2010 to be "historic" conditions in biomass and grazing, while measurements taken in 2021–2023 were considered "current" conditions.

We calculated proportions of shoots grazed for the whole plot (i.e., proportion grazed = sum of grazed shoots/sum of total shoots among all 15 subplots sampled from each plot). Since date of measurement influenced the proportion of shoots grazed, we used a generalized linear model (function "glm" in the "stats" package in R) with a binomial error distribution to adjust the measured proportion grazed relative to the date of measurement (i.e., Julian date; $\beta = 0.08 \pm 0.02$, $p < 0.001$).

Reindeer population estimates and GPS-collar data

Since 1995, a sample of calves and adult female reindeer were captured and marked with a unique collar band and ear tags each spring (March–April; for details see Albon et al. 2017). All capture and handling was performed under licenses and permits issued by the Norwegian National Research Authority (license nr. 22/5068) and the Governor of Svalbard (license nr. 16/01632-25). In late July and early August, an annual census of reindeer abundance was conducted. by observers walking through the valleys to record marked and unmarked animals (Albon et al. 2017). Population estimates were derived from an integrated population model using these capture–mark–recapture data in winter and observations from the annual summer population census, while also accounting for measurement error and demographic stochasticity (Lee et al. 2015; Bjørkvoll et al. 2016). We used population estimates from Loe et al. (2021) through 2019, and updated estimates through 2023, following their method.

Since 2009, between 12 and 48 captured adult females were fitted with GPS collars (Vectronic Aerospace GmbH) during capture events (see for details Loe et al. 2016), resulting in GPS data from 135 different individuals. GPS collars remained on individuals for 1–7 consecutive years ($n = 419$ animal years), recording locations at rates ranging between 1 and 10 h. We screened for errors in GPS relocations (following Bjørneraas et al. 2010). In total, 319 774 GPS locations were recorded from 2009 to 2023.

We extracted information on reindeer use of habitat during July and August (2009–2023) from a 30 m × 30 m resolution map of vegetation classifications, based on Landsat data (Johansen et al. 2012), using the function "extract" from the "raster" package (Hijmans and van Etten 2020). We reclassified the original 37 vegetation types into five groups (e.g., grass sward (our focal habitat), *Luzula* heath, marsh, ridge, and other, which was mostly composed of wet moss) depicting habitat types that are of seasonal importance for Svalbard reindeer (see Dwinnell et al. 2024 for further details). We only had GPS data for adult female reindeer, and therefore, adult male habitat use could not be evaluated.

Statistical analyses

All analyses were done in R version 4.1.3. We assessed the longitudinal trends in mean July temperature, grass biomass, the relationship between temperature and biomass, and reindeer population size (i.e., reindeer abundance). We used a linear regression model (function "lm" in the "stats" package in R), with Gaussian distribution, to evaluate mean July temperature and biomass as a function of year across the period 1998 to 2023. Similarly, we used a linear regression model to evaluate biomass as a function of mean July temperature. To evaluate long-term trends in reindeer abundance between 1998 and 2023, we used a Poisson regression model (standard for count data) with year as a predictor of population size estimates from the integrated population model. We assessed goodness of fit using R^2 and model significance based on $p < 0.05$.

Next, we evaluated longitudinal trends in grazing pressure, measured as proportion of shoots grazed and also estimated an index of grass biomass offtake (hereafter referred to as "offtake") at the 5 m × 5 m plot scale ($n = 170$). We used our estimation of offtake as an index reflecting biomass consumed by reindeer, which was calculated by multiplying the adjusted proportion of grazed shoots (accounting for date of measurement) in a plot times the estimated biomass of that plot (i.e., offtake = proportion of shoots grazed × mean biomass (g/m^2)). Our index of biomass offtake assumed consistent bite depth along a shoot (complete consumption of a shoot), as we did not acquire measures of bite depth after the shoot had already been grazed. This overestimated offtake where reindeer took shallow bites, with less biomass consumed. We used the adjusted proportion grazed in a linear regression model, predicting proportion of grasses grazed based on median date of measurement (4 August), to evaluate temporal trends in grazing as a function of year between 1998 and 2023, including trends in proportion of shoots grazed and offtake.

We evaluated reindeer habitat use by calculating the proportion of GPS locations over the study period that were within areas classified as grass sward habitat. We used a linear mixed model with Gaussian distribution ("lme4" package in R; Bates et al. 2015), to evaluate whether there was a change in the use of grass sward habitat as a function of year between 2009 and 2023. Animal ID was included as a random effect to account for differences in sample size among individuals in each year as well as bias in habitat use an individual reindeer may have.

To reveal mechanisms underlying trends in grazing pressure, we evaluated how biomass and reindeer abundance influenced "proportion of grass shoots grazed" and "grass biomass offtake". These analyses were performed at the 5 m × 5 m plot scale. First, we used a generalized linear mixed model with a quasi-binomial distribution (accounting for over-dispersion) to evaluate the influence of biomass and reindeer abundance on proportions of grass shoots grazed (note, when back-transformed to normal scale, a quasi-binomial model distribution fits a logistic curve akin to functional response curves). Next, we used a linear mixed model with a Gaussian distribution to explore how biomass and reindeer abundance may influence estimated offtake.

Year and plot ID were included in all models as a random effect to account for unexplained variation among years and plots. For all models, we used backward stepwise model selection, eliminating insignificant predictor variables based on *p*-values ($\alpha = 0.05$; Burnham and Anderson 2003), to test support for fixed effects of reindeer abundance and biomass on offtake and proportion of grass shoots grazed. Predictor variables were considered not significant if the 95% confidence intervals overlapped zero. We included Julian day as a fixed effect in all models to account for any potential bias in grazing pressure based on how late in the season measurements were taken as well as accounting for any potential influence of compensatory growth on biomass from grazing that has already occurred. All variables were standardized to compare effect sizes of the predictor variables of interest. Cook's distance was used to evaluate leverage of outliers and removed all observations with a Cook's distance that exceeded 0.05. There were four statistical outliers (2% of data), including two with the greatest biomass (46.8 and 50.2 g/m^2), that were removed in modeling both proportion of shoots grazed and offtake due to leverage (Cook's distance > 0.05). Removal allowed us to critically test H1 versus H2 (Fig. 1) across the gradient of biomass values for which the two time periods overlapped substantially.

Results

Longitudinal trends in summer temperature, grass biomass, and population size

Between 1998 and 2023, mean daily July temperature (°C), biomass of grasses (g/m^2), and population size of Svalbard reindeer increased significantly (Fig. 2). Mean daily July temperature varied annually, but nonetheless increased by 2 °C over the period 1998 to 2023 ($R^2 = 0.08$; $F_{1,792} = 71.12$, $p < 0.001$; Fig. 2*a*). Mean grass biomass across all years was 13.0 ± 0.7 g/m^2 (annual means ranged from 7.5 ± 1.1 to 19.5 ± 2.4 g/m^2; Fig. 2*a*), and only 21% of plots had biomass that exceeded 19.5 g/m^2 in the 11 years of observations, most of which (69%) occurred under current conditions (2021–2023). Over this 26-year period, the estimated biomass of grasses (g/m^2) increased by 86% ($R^2 = 0.11$, $F_{1,168} = 22.15$, $p < 0.001$; Fig. 2*b*). Mean biomass of grasses increased with mean daily July temperature by 2.5 g/m^2 for every 1 °C increase, between 1998–2023 ($R^2 = 0.14$, $F_{1,168} = 27.65$, $p < 0.001$; Supplementary Materials Fig. S1). Overall, the estimated population size of Svalbard reindeer in our study area increased by 3.5-fold during the 26-year period ($R^2 = 0.95$; $p < 0.001$), and with the most substantial increase in the last decade (Fig. 2*c*).

Longitudinal trends in grazing pressure and habitat use

Annual means of proportion of grazed grass shoots among all plots remained low, never exceeding 0.1, but increased linearly over the 26 years, as did our index of grass biomass offtake (g/m^2) ($p < 0.05$; Fig. 3). The estimated linear trend in mean proportion of grass shoots grazed increased from 0.04 to 0.08 ($R^2 = 0.37$, $F_{1,9} = 6.99$, $p = 0.026$; Fig. 3*a*), while the index of biomass offtake increased by 66% ($R^2 = 0.37$, $F_{1,9} = 6.86$, $p = 0.03$; Fig. 3*b*). Finally, GPS-derived use of grass sward did not change significantly between 1998 and 2023 ($p = 0.60$; Fig. 3*c*), implying no spillover into other habitat types.

Influence of grass biomass and reindeer abundance on proportion of grass shoots grazed and biomass offtake

Reindeer abundance had no significant effect on proportion of shoots grazed among plots (95% confidence interval overlapped zero: Table 1). However, the proportion of shoots grazed in a plot increased significantly with biomass (Fig. 4) and Julian day. The random effect of year accounted for minimal variance and more variance was accounted for by plot ID (σ^2 <0.01 and $\sigma^2 = 0.74$, respectively). Offtake of biomass (an index of g/m^2 of grass consumed) among plots was also most influenced by biomass and Julian day (Table 1), while reindeer abundance had no significant effect at the plot level (95% confidence interval overlapped zero). As biomass increased, offtake increased nonlinearly (biomass^2; Fig. 5). Similarly, more variance was accounted for by plot ID ($\sigma^2 = 0.11$) than year ($\sigma^2 = $ <0.01) as random effects.

Discussion

In the last 26 years Arctic greening from climate warming has almost doubled available grass forage while Svalbard reindeer abundance has increased 3.5-fold over the same period. Proportion of shoots grazed and our index of biomass offtake among foraging patches increased over the study period, but even still, we found that grazing pressure in a preferred summer habitat remained low (below 10%) across patches. Reindeer targeted the most biomass-rich patches both historically and currently. After accounting for the strong biomass effect, we found no additive effect of reindeer abundance on grazing pressure. Also, there was no evidence for spillover into other habitats; hence, reindeer did not appear to relieve grazing pressure in grass sward habitat by shifting use into other habitats. These findings support our alternative hypothesis (H_2), because consumption of grasses by reindeer remained similar in patches where historic and current levels of available biomass overlapped but reached to higher levels of consumption under current conditions of patches with higher biomass. This indicates that the increase in grass biomass from higher summer temperatures was sufficient to meet the energetic needs of the increased population of reindeer.

We showed that reindeer targeted patches with higher grass biomass and foraged very little in patches with low grass biomass—characteristic of a functional response (Holling 1959). Typically, natural plant–herbivore systems follow a Type II functional responses in foraging (Gross et al. 1993; Wilmshurst et al. 1995; Augustine et al. 1998), where the rate of increase in consumption is steadily decelerating with increasing biomass and reaching an asymptote at a point of food saturation (providing a hyperbolic curve; Holling 1959). A functional response of food intake rates of an individual is a temporal process, but the cumulative ef-

Fig. 2. Annual means and 95% confidence intervals of (*a*) mean daily July temperature (°C) in Nordenskiöld Land (collected from Longyearbyen airport weather station), (*b*) biomass of grass (g/m^2) of plots in Semmeldalen, and (*c*) estimates of population size of Svalbard reindeer among three core valleys, Semmeldalen, Reindalen, and Colesdalen, in Nordenskiöld Land, including fitted linear and logistic trends (grey solid line) with 95% confidence bands (grey dashed line) of change over time, 1998–2023. Years when grazing data were collected are highlighted for historic years (1998–2010; light green points) and current years (2021–2023; dark green points).

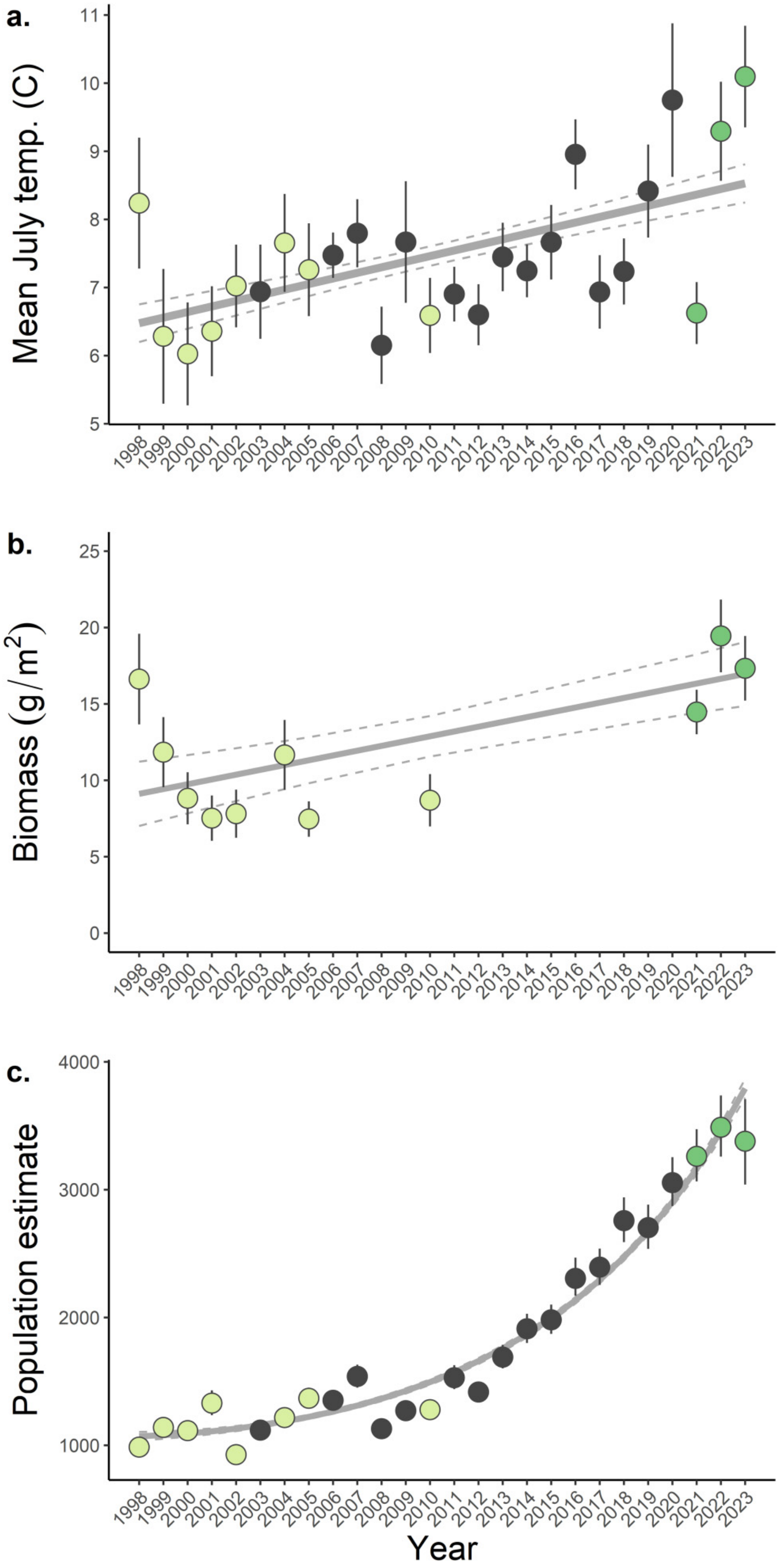


Fig. 3. (*a*) Mean proportion of grass shoots grazed (points) and (*b*) an index of offtake of biomass (g/m^2) adjusted to account for date of measurement (Julian day), for 11 years of observations between 1998 and 2023 in Semmeldalen, Svalbard. Highlighted are years when historic (1998–2010; light green points) and current (2021–2023; dark green points) grazing measurements were collected. (*c*) Adjusted mean proportion of GPS locations falling in grass swards (i.e., proportion of use), accounting for variation among animal IDs (as a random effect), in 2009–2023 in three core valleys, Semmeldalen, Reindalen, and Colesdalen, of Nordenskiöld. The grey solid line indicates the linear trend of proportions grazed, offtake, and proportion of use of grass swards estimated over time with a 95% confidence band (grey dashed line).

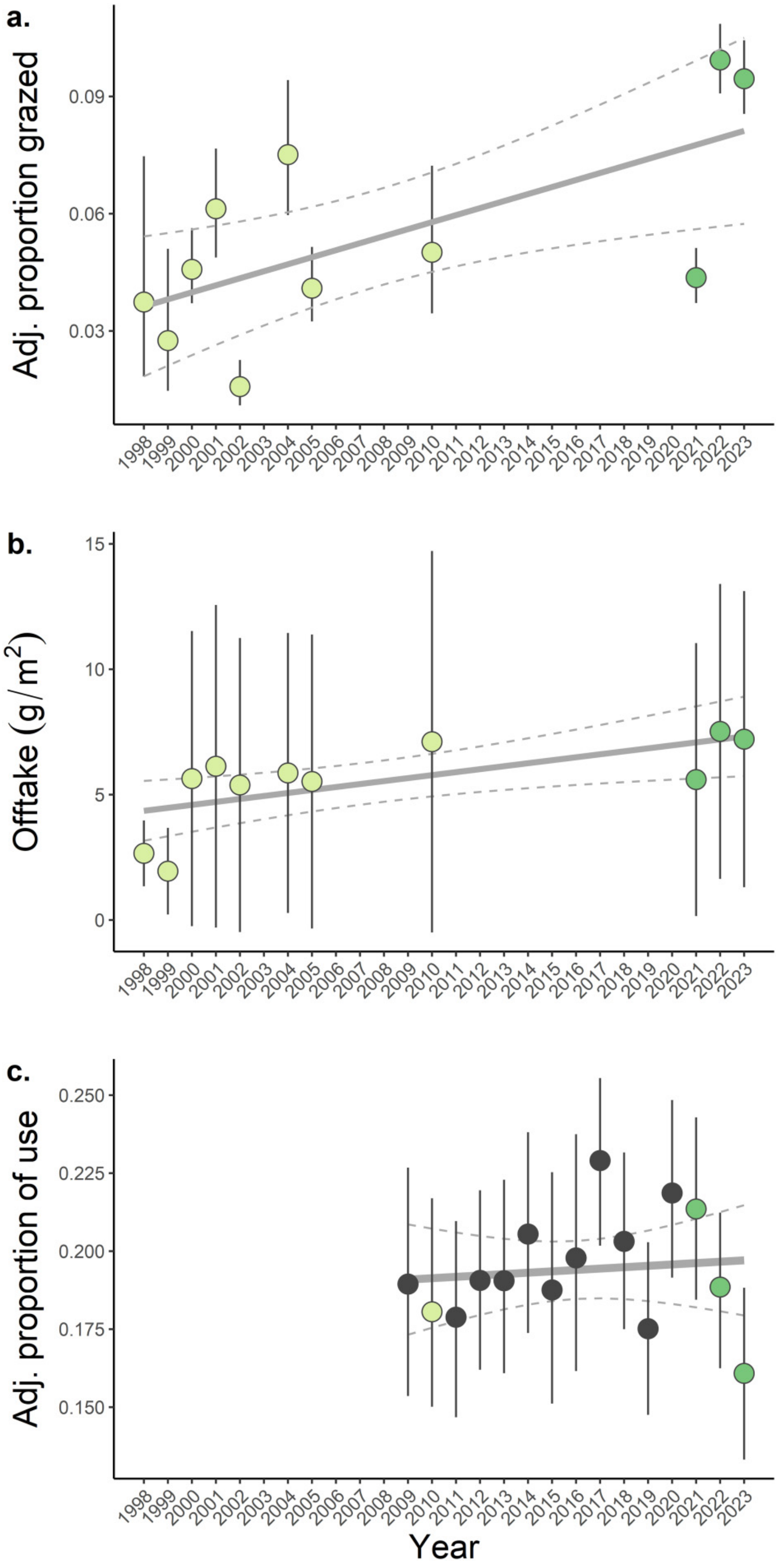


Table 1. Estimated effect sizes and 95% confidence intervals (CI) of fixed effects from the generalized linear mixed models predicting proportion of grass shoots grazed and the index of grass biomass offtake (g/m^2) by Svalbard reindeer in Semmeldalen, Svalbard, 1998–2023.

Model	Variable	Effect size	Lower CI	Upper CI
Proportion of shoots grazed	(intercept)	− 3.52	− 3.65	− 3.39
	Biomass	0.53	0.39	0.66
	Julian day	0.26	0.13	0.40
Biomass offtake (index)	(intercept)	0.80	0.61	0.98
	Biomass^2	0.82	0.67	0.97
	Julian day	0.18	0.05	0.31

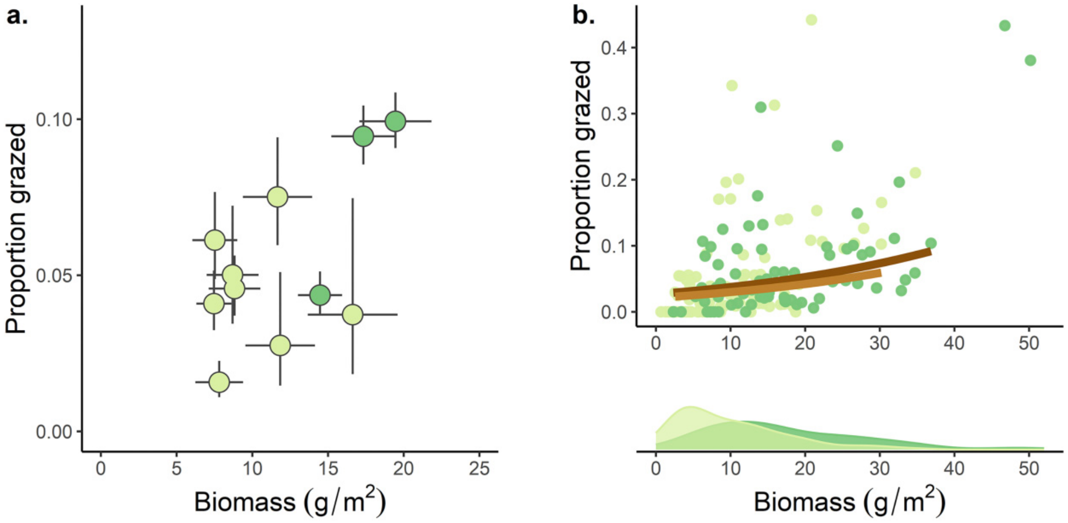
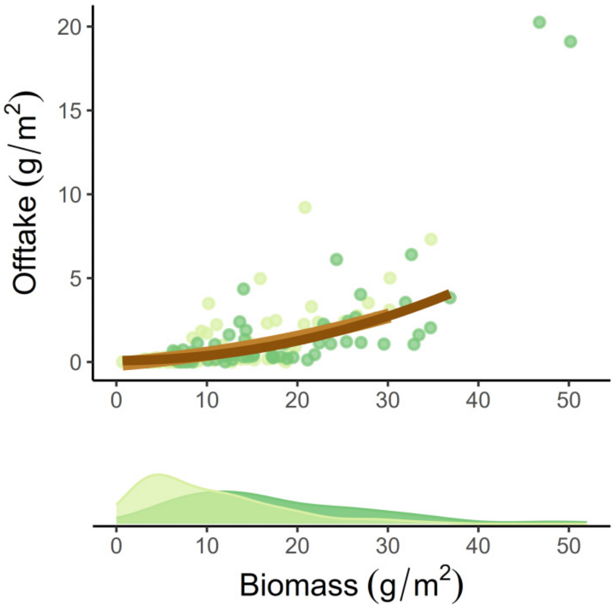


Fig. 4. (*a*) Annual means of proportion of grass shoots grazed and biomass with standard errors with historic years (1998–2010) in light green and current years (2021–2023) in dark green. (*b*) The effect of biomass (g/m^2) on proportion of grass shoots grazed at the plot scale observed historically (1998–2010; orange line) and currently (2021–2023; brown line). Points are the raw data, including four outliers excluded from the model, from historic (light green points) and current (dark green points) of proportion of grass shoots grazed relative to biomass. Density distributions of historic (light green polygon) and current (dark green polygon) observations of available biomass (g/m^2) in the lower panel.

fects of this process can be an underlying mechanism of food consumption observed of a population across a landscape (Rowcliffe et al. 1999). Although we did not evaluate intake rates at the individual level needed for explicit tests of functional responses, we did find evidence of an acceleration in food consumption among patches at low-biomass levels, suggesting the early phase of a sigmoidal, Type III functional response as a potential underlying mechanism. Type III functional responses are well supported conceptually but rarely captured in natural systems, because many studies fail to quantify food densities (or biomass) at the far ends of its gradients (i.e., low and high food densities or biomass; Kalinkat et al. 2023). Biomass did, indeed, increase with summer warming (ca. 86% increase) but was still low relative to other grassland systems (by an order of magnitude compared to temperate and arid grasslands; Hudson and Nietfeld 1985; Short 1985; Wilmshurst et al. 1995). The typical biomass values observed likely remains well below levels of food saturation needed to prompt the asymptote at the high end of the biomass gradient of a functional response. However, the exceptionally low offtake in patches at the low-end of the biomass gradient are consistent with the beginning of a Type III functional response.

Reindeer could have been switching food preferences at lower densities, which is a typical cause for the initial acceleration of a Type III functional response (Oaten and Murdoch 1975; Kondoh 2003). Even so, it may also just be that the energetic worth of foraging in low-density patches is not enough to entice foraging (aligned with optimal foraging theory; Charnov 1976), and reindeer are able to focus on newly available higher-biomass patches that meet energetic needs. Despite low biomass throughout the High Arctic (Arndal et al. 2009; Van der Wal and Stien 2014), the nutritional quality of food for herbivores is higher relative to lower-latitude regions (Van der Wal and Hessen 2009). It is unclear how grazing and fertilization from increased reindeer interact to influence nutritional quality of grasses (e.g., Van der Wal et al. 2004 found positive effects of fertilization, but negligible effects of reindeer herbivory were found by Petit Bon et al. 2023). Thus, evaluation of shifts in nutritional quality of

Fig. 5. The historic (1998–2010; orange line) and current (2021–2023; brown line) relationship between an index of biomass offtake (g/m^2) and available biomass (g/m^2) with 95% confidence bands between 1998 and 2023 in Semmeldalen, Svalbard. Points are the raw data, including four outliers excluded from the model, from historic (light green points) and current (dark green points) of offtake relative to biomass. Density distributions of historic (light green polygon) and current (dark green polygon) observations of available biomass (g/m^2) in the lower panel.



plants in response to Arctic greening and increased herbivory is still needed, including where shrub encroachment is occurring, as observed across large parts of the Arctic biome (Vowles and Bjork 2019). Nevertheless, the relatively high nutritional quality of Arctic plants in combination with newly available biomass—albeit still relatively low—may currently be sufficient to absorb heightened grazing pressure from increasing reindeer densities with Arctic greening.

Grazing pressure globally is typically low (Chapin et al. 2002), with even less consumption of vegetation in many tundra systems (McNaughton et al. 1989). Accordingly, we found low consumption of food by Svalbard reindeer (<10%). Other High Arctic large herbivores, such as muskoxen (*Ovibos moschatus*) in Greenland were observed to have low grazing pressure (<5%) and with little overall removal of vegetation, even at high-animal densities (Mosbacher et al. 2016). Indeed, our measure of removal of vegetation—offtake of grass biomass—was an index that assumed each grass shoot to be consumed entirely. We did not obtain measures of bite depth, which can vary by shoot mass and density to influence biomass offtake (Thompson Hobbs et al. 2003). Despite low values of estimated offtake of grass biomass (maximum 5 g/m^2 in a plot), our estimates were still likely to be exaggerations because we assumed complete bite depth in our estimation of biomass. Nevertheless, these low grazing pressure values in the High Arctic are substantially lower than those estimated for other northern-latitude systems. For example, Bråthen and Oksanen (2001) found semi-domesticated reindeer grazing to reduce grass abundance by 47% in northern Norway. The low proportions of grazing and estimated offtake of biomass we observed are unlikely to prompt ecosystem-wide overexploitation from herbivores in our system (Côté et al. 2004; Mysterud 2006; Van der Wal 2006; Vuorinen et al. 2021).

Impacts on foraging opportunity from large herbivores can be two sided: biomass removal typically influences foraging opportunity in a negative way (Bråthen and Oksanen 2001; Côté et al. 2004; Hansen et al. 2007), whereas grazing impacts that alter plant composition, growth, or quality are regularly positive by improving nutritional benefits for herbivores (McNaughton 1979; Van der Wal 2006; Olofsson et al. 2009; Bråthen et al. 2017). Our findings of Arctic greening absorbing the grazing impacts of more reindeer could explain why other studies have found Svalbard reindeer to have limited direct impact on vascular plant communities (Van der Wal and Brooker 2004; Petit Bon et al. 2023; but for indirect effects on vascular plants through lichen suppression see Van der Wal et al. 2001), despite the ability of reindeer to strongly shift vascular plant communities in other Arctic regions (Olofsson et al. 2004; Bråthen et al. 2007). Instead, it may be that available grass forage for reindeer is just enough to promote foraging optimization that enhances foraging opportunities (McNaughton 1979; Van der Wal 2006) through compensatory growth, moss removal and fertilization (Van der Wal and Brooker 2004; Van der Wal et al. 2004), and thus, with low-intensity grazing, reindeer may be cultivating food in a way that benefits them.

For capital breeders that rely on endogenous energy stores for reproduction, typical for Arctic vertebrates, forage availability during seasonal times of abundance (e.g., summer forage) are key for reproduction and survival during times of food scarcity (Barboza et al. 2008; Albon et al. 2017). Across latitudes, large herbivores living in environments with seasonal extremes in winter conditions are often limited by extreme climate events (Hansen et al. 2013; LaSharr et al. 2023), but improved per capita availability of summer forage can buffer large herbivores from extreme winter conditions and promote population growth (Monteith et al. 2014; Hansen et al. 2019*b*). We found that the newly widened gradient of available biomass in the High Arctic appeared to absorb the impacts of more large herbivores on the landscape, which supports notions of the positive contributions of improved summer foraging conditions enabling population growth. Increased plant biomass with little increase in grazing pressure and an extended snow-free season from warming may continue to buffer Svalbard reindeer and potentially other large herbivore populations from extreme winter events that can have detrimental impacts on survival and limits population growth (Albon et al. 2017; Loe et al. 2021).

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No author of this study has a conflict of interest in the work described in this manuscript.

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Supplementary material

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